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A NEW BOX TURTLE FROM THE MIOCENE/PLIOCENE BOUNDARY (LATEST HEMPHILLIAN) OF OKLAHOMA AND A REFINED CHRONOLOGY OF BOX TURTLE DIVERSIFICATION

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ABSTRACT—A near complete shell from the Hemphillian 4 (Miocene/Pliocene boundary) Buis Ranch local fauna of Beaver County, Oklahoma, represents a fossil box turtle. An anterior contact of neural III and neural V with costal III and costal V only, respectively, presence of a small contact between the suprapygal and eleventh peripherals, development of a thin peripheral lip for articulation with the posterior plastral lobe, placement of the vertebral III/IV sulcus on neural VII, presence of two anterior musk duct glands, a rounded posterior plastral lobe, an elongate shell outline, and a complete neural series diagnose the fossil as a new species, *Terrapene parornata* n. sp. A phylogenetic analysis of fossil box turtles places *T. parornata* along the phylogenetic stem of the extant taxon *T. ornata*. The holotype of '*Terrapene longinsulae*' cannot be distinguished from *Terrapene ornata* and is therefore synonymized. Finally, '*Terrapene*' *corneri* lacks characters of crown group *Terrapene* and may therefore represent a stem box turtle. The provenance of the holotype of '*Terrapene longinsulae*' is more poorly known than previously recognized and this specimen may originate from Kansas or Nebraska and be early Miocene to late Pleistocene in age. *Terrapene parornata* is therefore the oldest demonstrable representative of crown group *Terrapene* (ca. 5.3–4.6 Ma). '*Terrapene*' *corneri* from the late Barstovian of Nebraska and fragmentary material from the middle Barstovian of Nebraska by contrast are the oldest representative of the *Terrapene* lineage (ca. 14.5–11.5 Ma). A review of morphological characters related to shell kinesis reveals that most are highly correlated. The results of the phylogenetic analysis converge upon those of molecular data when these correlated characters are omitted from the analysis.

INTRODUCTION

NORTH AMERICAN box turtles of the clade *Terrapene* are among the most charismatic extant turtles. Four extant species of box turtles are currently recognized across North America. The eastern box turtle *Terrapene carolina* (Linnaeus, 1758) has the greatest distribution and is broadly found in all wooded regions in the eastern half of the United States and as two isolated populations along the east coast of Mexico. The ornate box turtle *Terrapene ornata* Agassiz, 1857 has a similarly wide distribution but prefers the notably drier habitat of the northern Mexican deserts and the Great Plains. The remaining two species have a more limited distribution: *Terrapene coahuila* Schmidt and Owens, 1944 is restricted to a single basin in Coahuila, Mexico and *Terrapene nelsoni* Stejneger, 1925 is restricted to a narrow coastal zone along the western coast of Mexico (Iverson, 1992; Ernst et al., 1994; Minx, 1996). Using morphological and molecular data (e.g., Milstead, 1969; Minx, 1996; Feldman and Parham, 2002), two primary subclades are typically recognized, the *ornata* group (*T. ornata* and *T. nelsoni*) and the *carolina* group (*T. carolina* and *T. coahuila*).

The vernacular name "box turtle" is fitting as all representatives of this clade are not only able to withdraw their head, tail, and limbs into their shell like most cryptodires, but to fully protect all soft parts by dislocating both girdles and closing the shell by pulling up the anterior and posterior ends of the plastron against the carapace (Bramble, 1974). The resulting morphological adaptations allow fragmentary elements to be diagnosed with ease. A number of partial skeletons and complete shells have been described from the Pleistocene of the southeastern United States and served as the basis for the initial recognition of numerous species (e.g., Cope, 1870, 1878; Hay, 1906, 1907, 1916, 1917, 1921; Gilmore, 1927; Oelrich, 1953). However, much of this material is now recognized as a gigantic Pleistocene taxon that is either conspecific with or the direct sister to *T. carolina* (e.g., Barbour and Stetson, 1931; Auffenberg, 1958; Milstead, 1969).

Although representatives of *Terrapene* are often the dominant reptilian faunal component by sheer numbers and biomass in many terrestrial habitats today (Ernst et al., 1994), Pliocene (e.g., Milstead, 1956; Auffenberg, 1967; Moodie and Devender, 1978) and Miocene (e.g., Holman, 1975; Holman and Corner, 1985; Holman, 1987) fossils are rare and consist mostly of fragments. The only exception of an otherwise poor pre-Pleistocene record is the holotype of '*Terrapene longinsulae*' Hay, 1908, a near-complete skeleton that has been described from "Upper Miocene to Lower Pliocene" sediments "at Long Island, Phillips County, Kansas" (Hay, 1908, p. 166). This taxon has been argued to be most closely related to *T. ornata* and used to postulate a Miocene divergence date of the *ornata* group from the *carolina* group (Milstead, 1956, 1967; Holman and Corner, 1985; Holman and Fritz, 2005). This claim is somewhat dubious, however, as no character evidence has ever been provided to support the phylogenetic placement of '*T. longinsulae*' and because the stratigraphic provenience of this taxon is unclear. A second taxon, '*Terrapene*' *corneri* Holman and Fritz, 2005, is based on the second-best preserved pre-Pleistocene fossil, a complete anterior plastral lobe from the middle Miocene (late Barstovian) Myers Farm Local Fauna of Webster County, Nebraska (Holman and Fritz, 2005). Although the provenience of this specimen is well documented, the fragmentary nature of the specimen makes it difficult to rigorously assess its phylogenetic position (Holman and Fritz, 2005).

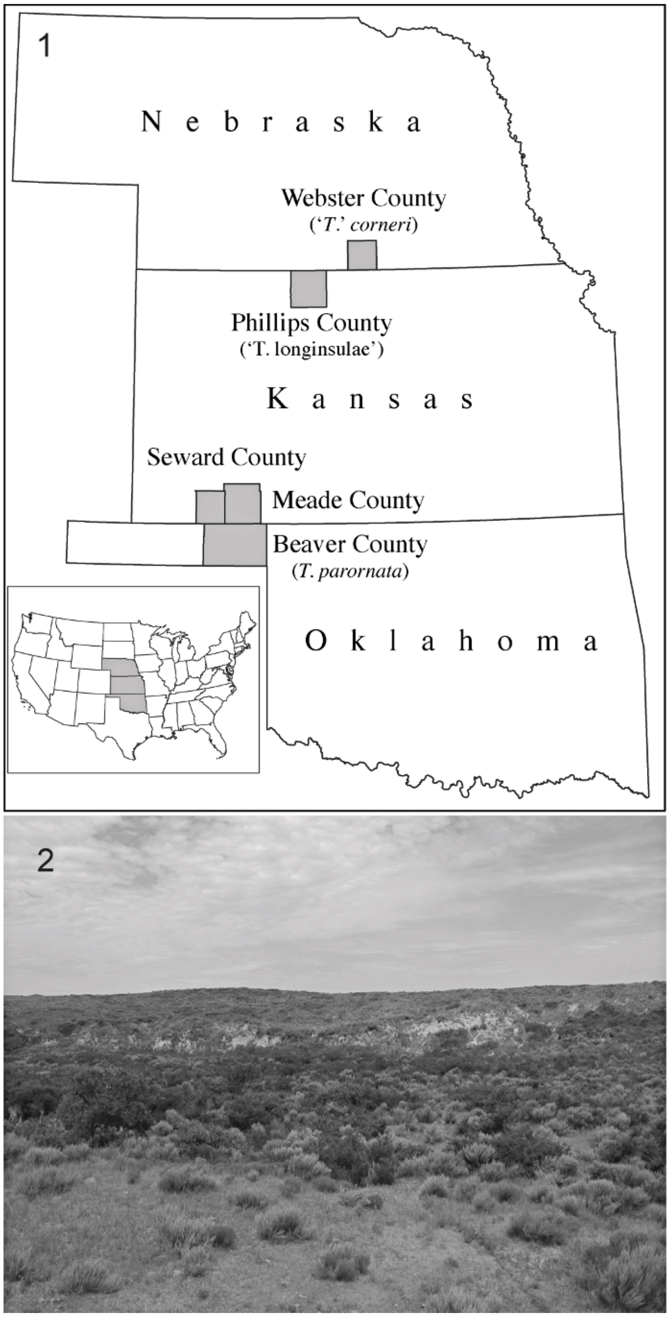

FIGURE 1—*1*, Map of the contiguous portion of the United States of America and the location of the five counties discussed in the text within the states of Kansas, Nebraska, and Oklahoma; *2*, photograph of OMNH VP locality no. V671 in Beaver County, Oklahoma from which OMNH 58158, holotype of *Terrapene parornata* n. sp., was recovered.

A near-complete box turtle shell from the early Pliocene (latest Hemphillian) Buis Ranch local fauna of Beaver County, Oklahoma represents the first well-dated and complete pre-Pleistocene box turtle fossil. The purpose of this contribution is to describe this fossil as a new species, *Terrapene parornata* n. sp., and to establish its phylogenetic relationships. Secondary aspects that arise from this study include a reassessment of the morphology, provenience, and taxonomy of *T. longinsulae*, the phylogenetic placement of '*T.*' *corneri*, the impact of correlated characters related to shell kinesis on the phylogenetic reconstruction of emydine turtles, and a refined chronology of box turtle evolution.

Institutional Abbreviations.—MCZ, Herpetology Department, Harvard Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, U.S.A.; USNM P, Department of Paleobiology, National Museum of Natural History, Washington D.C., U.S.A.; USNM R, Division of Amphibians and Reptiles, National Museum of Natural History, Washington D.C., U.S.A.; UNSM, University of Nebraska State Museum; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

GEOLOGICAL SETTINGS

The new fossil box turtle was collected from OMNH VP locality no. V671 in Beaver County, Oklahoma, a dry sandy arroyo locally known as Buckshot Arroyo that is part of the Buis Ranch locality (Fig. 1). Detailed locality data are available on file at the OMNH section of Vertebrate Paleontology. The Buis Ranch locality and local fauna were first described by Hibbard (1954). Hibbard (1954) gave a narrative description of the stratigraphy at the Buis Ranch locality and Buckshot Arroyo but did not provide measured stratigraphic sections. His Buis Ranch microvertebrate fauna came from what he called the Rexroad Formation, a unit he named in the Meade Basin in adjacent Meade County, Kansas. At Buis Ranch the Rexroad Formation as recognized by Hibbard (1954) comprises 8.4 m of fine sand and sandy silt overlying a caliche bed at the top of the Ogallala Formation, and with a caliche bed at its top. At Buis Ranch the Rexroad Formation is topographically lower than the top of Permian red beds that are exposed just upstream and downstream from the fossil locality. Vertebrate fossils that were collected later by Hibbard (1963) and others from the Buis Ranch local fauna originate from sites within 2 or 3 km along Buckshot Arroyo and another parallel arroyo.

Today sedimentary layers are poorly exposed at Buis Ranch because sand sagebrush, grasses, wild grape vines, and other vegetation largely obscure them. The Ogallala Formation (late Miocene and possibly early Pliocene) and the overlying Rexroad Formation (Pliocene) and Meade Formation (as called by Hibbard, 1954; Pleistocene) are relatively thin in the area, about 2.6 m, 8.4 m, and 7.0 m, respectively. The Ogallala Formation in particular often occurs in western Oklahoma and northwestern Texas as discontinuous fillings dipping at various angles into surface sinks of highly variable sizes. The sinks developed through subsurface salt dissolution and collapsed gypsum structures in the unconformably underlying Permian bedrock (Dolliver, 1984). Several factors, including the localized nature of the collapsed sinks, the isolated and vegetation-covered nature of the late Cenozoic rock units in the area, and the discontinuous nature of the outcrops due to historic agriculture, make recognition and correlation of the Ogallala Formation very difficult.

Honey et al. (2005), Izett and Honey (1995), and Martin et al. (2000, 2002, 2003) faced similar stratigraphic problems correlating the limited exposures of some of the same rock units across the Meade Basin in Meade County, Kansas, immediately north of Buis Ranch and Beaver County, Oklahoma. Their work called into question the usefulness of some previously named formations and members in the Meade Basin and they introduced informal names for units in order to place their local faunas stratigraphically (Honey et al., 2005). Their revisions included tentatively referring faunas from the Rexroad Formation of Meade Basin to the earliest Blancan (Martin et al., 2003). Buis Ranch and the surrounding areas south of the Cimarron River would benefit from a similar, intensive study.

Several subsequent studies (Tihen, 1955; Hazard, 1961; Hibbard, 1963; Stevens, 1966; Brattstrom, 1967; Holman, 1973; Werdelin, 1985; Wright, 1989; Parmley and Holman, 1995; Hulbert et al., 2005) made additions and taxonomic updates to Hibbard's (1954) initial Buis Ranch faunal list. Based on these literature sources, the Buis Ranch fauna includes at least: a salamander (*Ambystoma* sp.), "frogs or toads," a tortoise (*Hesperotestudo riggsi*), numerous snakes (*Elaphe* cf. *obsoleta*, *Elaphe buisi*, *Thamnophis* sp., *Heterodon plionasicus*, *Coluber constrictor*, *Lampropeltis triangulum*, *Crotalus* cf. *viridis*), a mole (*Scalopus* [*Hesperoscalops*] sp.), a skunk (*Buisnictis schoffi*), a fox (*Vulpes* sp.), a cat (*Felis rexroadensis*), numerous rodents (*Spermophilus* [*Buiscitellus*] *dotti*, *Spermophilus rexroadensis*, *Perognathus* cf. *mclaughlini*, *Prodipodomys* sp., *Pliogeomys buisi*, Cricetidae indet.), a rabbit (Leporidae indet.), a peccary (*Catagonus brachydontus*), a camel (*Pleiolama vera*), a rhinoceros (Rhinocerotidae indet.), and a horse (*Pseudhipparion simpsoni*).

Biochronologically the Buis Ranch fauna is considered to represent the Hemphillian 4 subdivision of the Hemphillian North American Land Mammal Age (Tedford et al., 2004), which in turn is correlated with the latest Miocene and earliest Pliocene. As noted by Tedford et al. (2004, p. 218), "[c]hronologically the latest (or late late) Hemphillian (Hh4) just extends across the Miocene–Pliocene boundary (5.3 Ma) to 4.6–4.9 Ma […]. This final phase of the Hemphillian begins at the [paleomagnetostratigraphic] chron C3r-C3An boundary at about 5.9 Ma (Berggren et al., 1995)". The Buis Ranch local fauna includes a rhinoceros tusk (see footnote in Hibbard, 1954, p. 358), which is consistent with a Hemphillian age, as rhinoceroses became extinct in North America at the close of the Hemphillian and are absent from Blancan faunas. The Buis Ranch local fauna includes none of the Hh4 "defining" taxa of Tedford et al. (2004) but does include the "characterizing" skunk *Buisnictis* sp. Additionally, the pocket gopher *Pliogeomys*, represented at Buis Ranch by *Pliogeomys buisi*, is characteristic of the late Hemphillian (Hh3 and Hh4; Tedford et al., 2004). *Pliogeomys buisi* or a similar species with rooted teeth also occurs in the Saw Rock Canyon fauna of Seward County, Kansas (adjacent to Meade County, Kansas, and Beaver County, Oklahoma; Fig. 1) but is absent from the earliest Blancan faunas of Meade County that have instead *Geomys* spp. with unrooted cheek teeth (Martin et al., 2000). Thus, the Buis Ranch local fauna can be restricted to the latest Hemphillian and is slightly younger than the Miocene–Pliocene epochal boundary in the early Pliocene. Its nearest correlative local fauna in the Meade Basin is Saw Rock Canyon, in contrast to most other local faunas in the Rexroad Formation that reflect an early Blancan age.

The box turtle described herein was collected from a poorly consolidated sand above a caliche layer, with a root cast horizon 1 m above it. The sand is probably the same unit that Hibbard (1954) called the Rexroad Formation and the caliche bed below it is likely the one capping the Ogallala Formation. The box turtle shell was found in 2000 by N. J. C. and K. L. Davies (OMNH) in the same sand unit as a dentary of the small horse *Pseudhipparion simpsoni* (Hulbert et al., 2005), as well as a partial dentary of another larger horse, a tortoise peripheral, the posterior portion of another turtle shell, and a ground squirrel dentary.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788
CRYPTODIRA Cope, 1868
TESTUDINOIDEA Fitzinger, 1826
EMYDIDAE Bell, 1825
TERRAPENE Merrem, 1820
'TERRAPENE' CORNERI Holman and Fritz, 2005

Type specimen.—UNSM 21618, a near complete anterior plastral lobe.

Type locality.—UNSM locality Wt-15A, Webster County, Nebraska (Holman and Fritz, 2005).

Type horizon.—Myers Farm Local Fauna, late Barstovian (middle Miocene, ca. 13.0–11.5 million BP, Holman and Fritz, 2005).

Diagnosis.—See Holman and Fritz (2005).

Comments.—Our phylogenetic analysis confirms that '*T.*' *corneri* is referable to the box turtle lineage but it cannot be attributed with any confidence to crown group *Terrapene*. We highlight this ambiguity by placing the genus name in quotes (for details, see Discussion below).

TERRAPENE PARORNATA new species
Figure 2

Type specimen.—OMNH 58158, a near complete shell.

Type locality.—OMNH VP locality no. V671, Buckshot Arroyo, Beaver County, Oklahoma, U.S.A. (Fig. 1).

Type horizon.—Buis Ranch local fauna, Hemphillian 4 (Miocene/Pliocene boundary).

Etymology.—A contraction between *para* (Greek: next, similar) and *ornata*, species epithet of the closest hypothesized extant relative of the new taxon.

Diagnosis.—*Terrapene parornata* is diagnosed as a representative of the *ornata* group by the following list of synapomorphies: neural III anteriorly contacts costal III only; neural V anteriorly contacts costal V only; presence of a small contact between the suprapygal and eleventh peripherals; and the development of a thin peripheral lip for articulation with the posterior plastral lobe during shell closure. *Terrapene parornata* is placed within the stem group of *T. ornata* by the presence of two anterior musk duct glands, but outside the clade formed by *T. ornata* and *T. longinsulae* through the presence of a rounded posterior plastral lobe and an elongate shell outline. The presence of a complete neural series that fully separates the costals and the placement of the vertebral III/IV sulcus on neural VII are unique autapomorphic characters within crown *Terrapene*.

TERRAPENE ORNATA Agassiz, 1857
Figures 3, 4

Lectotype.—MCZ 1536, an extant specimen collected in Iowa, designated as the lectotype by Smith and Smith (1979).

Referred fossil material.—USNM P 5983, holotype of '*Terrapene longinsulae*' Hay, 1908, a near complete skeleton collected near Long Island, Phillips County, Kansas; Miocene–Pleistocene.

Comments.—Please refer to the Discussion for an explicit rationale that outlines why the holotype of '*Terrapene longinsulae*' cannot be dated with any greater confidence than Miocene–Pleistocene and for a list of characters that supports its attribution to *T. ornata*.

DESCRIPTION OF OMNH 58158, HOLOTYPE OF TERRAPENE PARORNATA

Preservation.—OMNH 58158 is a generally well-preserved shell lacking any significant cranial, vertebral, or long bone

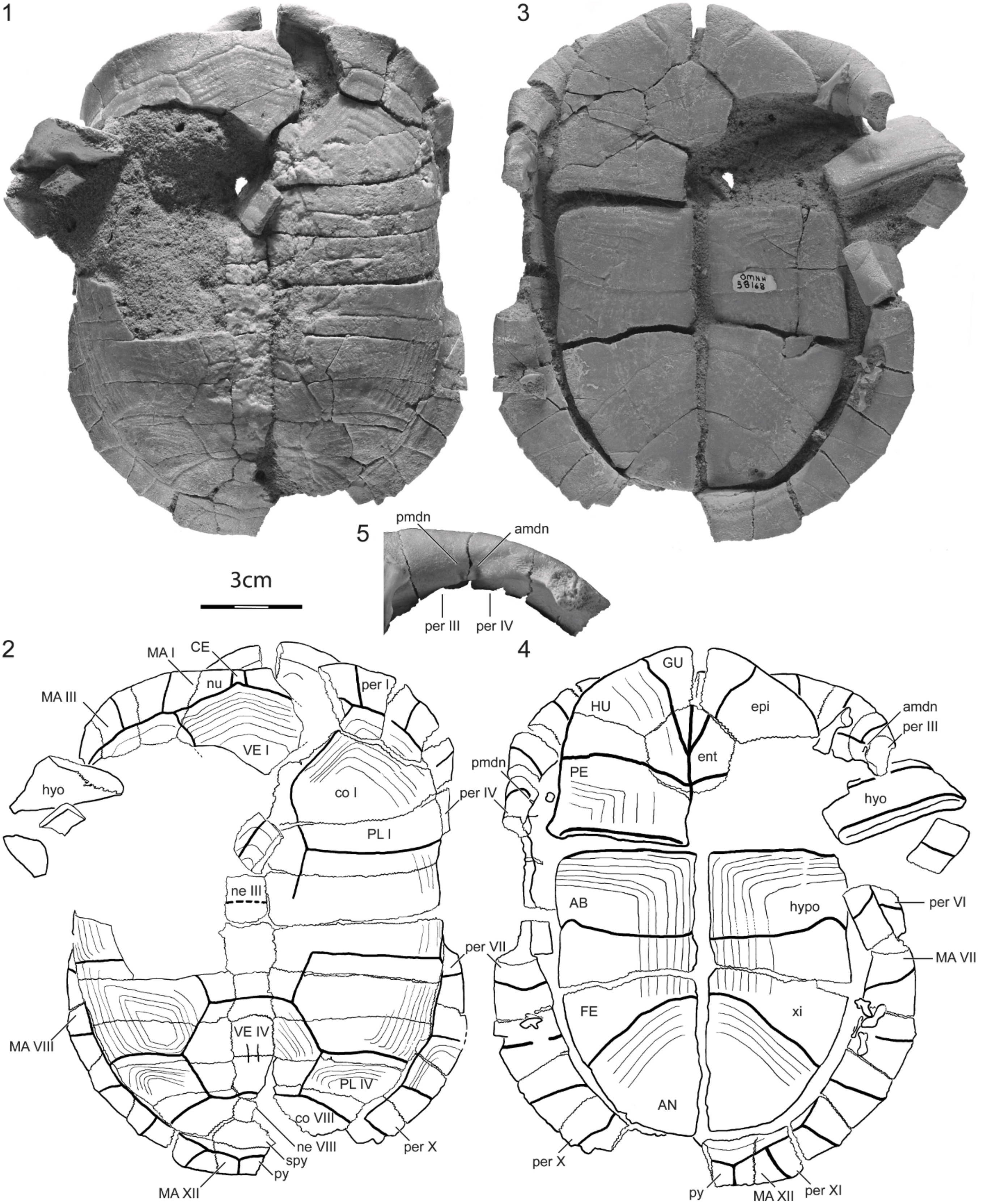

FIGURE 2—OMNH 58158, holotype of *Terrapene parornata* n. sp., latest Hemphillian (Miocene/Pliocene boundary) of Beaver County, Oklahoma. *1*, *2*, photograph and illustration, respectively, of shell in dorsal view; *3*, *4*, photograph and illustration, respectively, of shell in ventral view; *5*, medioventral view of left peripherals II–V. Abbreviations: AB=abdominal scute; amdn=anterior musk duct notch; AN=anal scute; CE=cervical scute; co=costal; ent=entoplastron; epi=epiplastron; FE=femoral scute; GU=gular scute; HU=humeral scute; hyo=hyoplastron; hypo=hypoplastron; MA=marginal scute; ne=neural; nu=nuchal; PE=pectoral scute; per=peripheral; PL=pleural scute; pmdn=posterior musk duct notch; py=pygal; spy=suprapygal; VE=vertebral scute; xi=xiphiplastron.

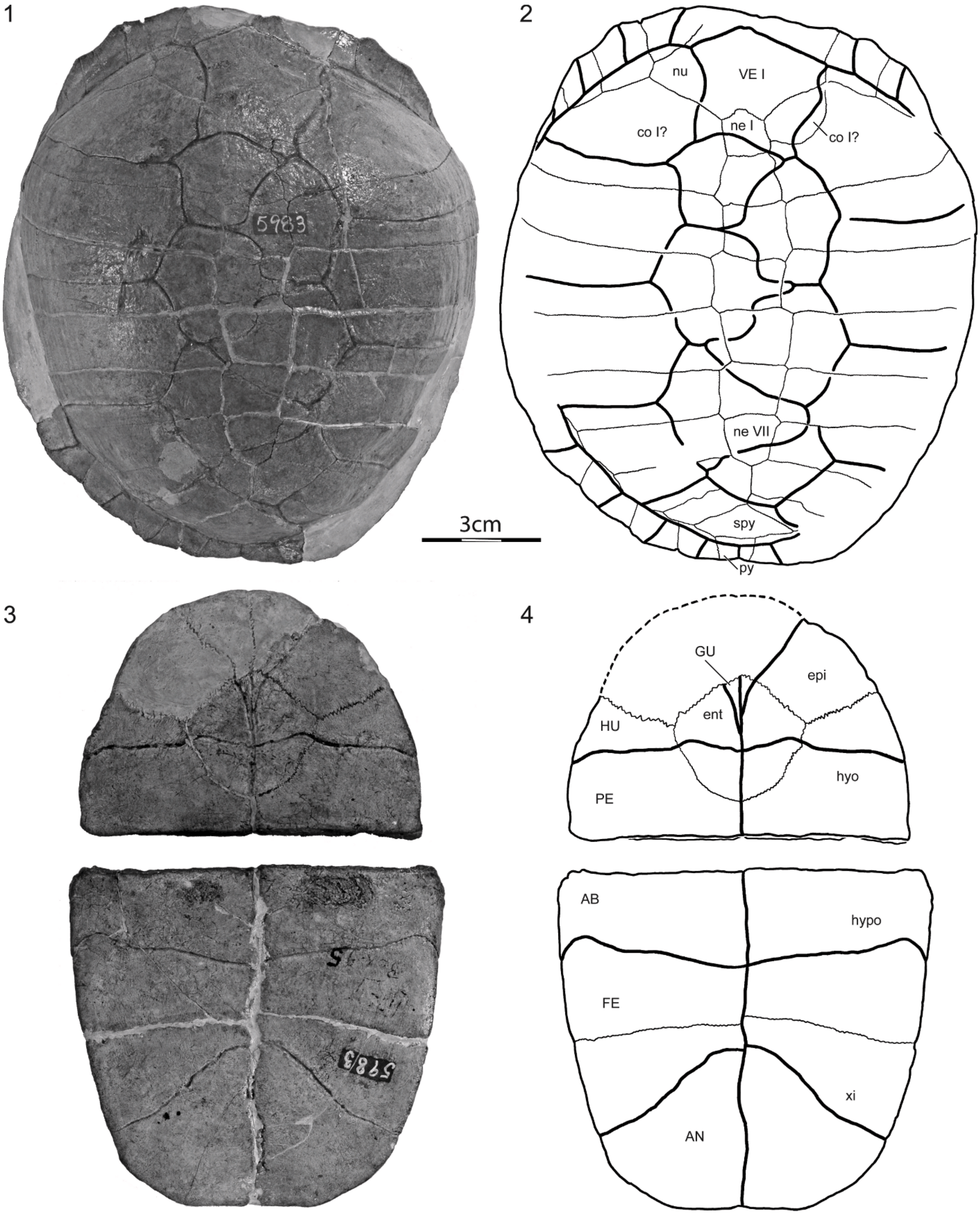

FIGURE 3—USNM P 5983, holotype of '*Terrapene longinsulae*', Miocene to Pleistocene of Kansas or Nebraska. *1*, *2*, photograph and illustration, respectively, of carapace in dorsal view; *3*, *4*, photograph and illustration, respectively, of plastron in ventral view. Abbreviations: AB=abdominal scute; AN=anal scute; co=costal; ent=entoplastron; epi=epiplastron; FE=femoral scute; GU=gular scute; HU=humeral scute; hyo=hyoplastron; hypo=hypoplastron; ne=neural; nu=nuchal; PE=pectoral scute; py=pygal; spy=suprapygal; VE=vertebral scute; xi=xiphiplastron.

FIGURE 4—USNM P 5983, holotype of '*Terrapene longinsulae*', Miocene to Pleistocene of Kansas or Nebraska. *1*, dorsal; *2*, ventral, and; *3*, right lateral view of cranium.

remains (Fig. 2). All sutures are open and all sulci are distinct. However, the surface of the bone near the top of the carapace is eroded and many sulci and sutures are therefore obscured in this area. The carapace is partially damaged and somewhat incomplete. The left peripheral series is complete, but right peripherals V–VI and X–XI are missing. The right costal series is complete, but left costals I–III and the proximal half of left costal IV are missing. A number of costal fragments are visible in dorsal view, others were collected disassociated from the specimen and are too fragmentary to warrant illustration. Most of the nuchal is preserved, but the posterior margins are damaged. Neurals I–II are missing, but the remaining portion of the neural and pygal series is complete. The plastron is completely preserved but the left hyoplastron is displaced dorsally. A few small limb bones, particularly phalanges, are associated with the specimen.

Carapace.—As preserved, the carapace is somewhat elongated, but clearly distorted through disarticulation. However, given that the posterior plastral lobe is about as wide at the hinge as long along the midline, proportions typical of elongate box turtles, we infer that the original shell shape was elongate and not round. The anterior and posterior carapace margins are smooth and an extremely shallow nuchal embayment is present that spans the width of the cervical scute and marginals I. A shallow peripheral gutter is present that originates at the anterior margin of peripheral III and terminates at the posterior margin of peripheral VI. Although much of the surface of the central portion of the carapace is eroded, it nevertheless is apparent that a weak keel existed at least along the central portion of the fourth vertebral scute along the contact of neurals VI and VII. Those portions of the vertebral and pleural scutes that have not been eroded clearly show impressions of growth annuli.

Nuchal.—Much of the nuchal is preserved, but most of its posterior contacts with the costals and neural I are damaged. The anterolateral contact with peripheral I is particularly well preserved on the left side.

Neurals.—Neural I is missing and it is difficult to discern its shape from the outline of the surrounding elements because the posteromedian portion of the nuchal is damaged, the anteromedial portion of costal II is covered by a bone fragment, and neural II is missing. A bone fragment identified as a costal fragment covers the area of neural II in dorsal view. Although neural II is missing, it is apparent that this bone laterally contacted costals II and III and therefore either had an octagonal or hexagonal outline with short posterior sides. Neural III is preserved in situ, contacts costals III laterally, and therefore has a square shape. Neural IV is the largest of the preserved neurals and contacts costals III anterolaterally, costals IV laterally, and costals V posterolaterally, and therefore has an octagonal outline. The right contacts of neural V are damaged due to a break in this region of the shell, but neural V nevertheless appears to have been a hexagonal element with short posterior sides and concave lateral margins. The anterior and posterior contact with neurals IV and VI are both rounded convexly to the anterior. Neural VI is almost square and has an anteriorly convex contact with neural V. It contacts neural V anteriorly, neural VII posteriorly, and costal VI laterally. Neural VII is the most elongate element of the neural series. It contacts neural VI anteriorly, neural VIII posteriorly, costals VI–VIII laterally, and has an irregular, stretched octagonal outline. Posterior to neural VII a small bone is visible with clear, interdigitated anterior, lateral, and posterior contacts with neural VII, costal VIII, and the suprapygal, respectively. The right lateral portion of this bone is damaged, as is the left lateral region of the right costal VIII. It is possible to interpret this bone as either neural VIII or as a dislodged portion of costal VIII. The presence of neural VIII is highly unusual for a representative of *Terrapene.* In all representatives of *Terrapene* that lack neural VIII, we observed that the costals meet one another along the midline. We therefore interpret this bone as neural VIII. This bone is the smallest bone of the neural series, has an elongate rectangular outline, and only contacts costals VIII laterally. The neural formula is ?-6/8-4-8-6-4-8-4. The intervertebral sulci cross the middle of neurals III and V, the posterior tip of neural VII, and likely crossed the middle of neural I as well.

Costals.—Eight pairs of costals are present. The medial contacts of the costals with the neurals are described above. The costals are greatly dorsoventrally curved and thereby produce the majority of the carapacial doming. Costals I–V are approximately equal in mediolateral width whereas costals

VI–VIII rapidly decrease in mediolateral width towards the posterior. All costals are approximately equal in anteroposterior length, with exception of costals I, which expand distally to about twice the anteroposterior length as the other elements. Similar to many representatives of Testudinidae, costals II–VI are slightly wedge-shaped, with costals II, IV, and VI expanding distally and costals III and V expanding medially. Costal I contacts the nuchal anteromedially, peripherals I–III anterolaterally, and nearly contacts peripheral IV posterolaterally. Costal II contacts the posterior tip of peripheral III anterolaterally (not fully apparent in dorsal view), all of peripheral IV laterally, and the anterior half of peripheral V posterolaterally. Costal III contacts the posterior half of peripheral V anterolaterally and the anterior half of peripheral VI posterolaterally. Costal IV contacts the posterior half of peripheral VI anterolaterally and the anterior two-thirds of peripheral VII posterolaterally. Costal V contacts the posterior third of peripheral VII anterolaterally and the anterior half of peripheral VIII posterolaterally. Costal VI contacts the posterior half of peripheral VIII anterolaterally and the anterior third of peripheral IX posterolaterally. Costal VII contacts the posterior two-thirds of peripheral IX anterolaterally and the anterior third of peripheral X posterolaterally. Costal VIII, finally, contacts the posterior two-thirds of peripheral X laterally, the anterior three quarters of peripheral XI posteriorly, and the suprapygal posteromedially. As in most turtles, the interpleural sulci cross costals II, IV, and VI and much of the surface of the costals is ornamented by the growth annuli of the pleural and vertebral scutes.

Peripherals.—Although portions of the peripheral series are missing or dislodged, it is apparent that OMNH 58168 had eleven pairs of peripherals. Peripherals I and XI contact the nuchal and the suprapygal and pygal medially, respectively. All remaining contacts of the peripherals with the costals are described above. A low peripheral gutter is developed parallel to the margin of the shell that originates at the anterior margin of peripheral III and terminates at the posterior margin of peripheral VI. The presence of two pairs of bony notches indicates the former presence of two pair of anterior musk ducts along the skin-scute sulcus: one at the posterior margin of peripheral III and the other at the anterior quarter of peripheral IV (Fig. 2.5). The ligamentous attachment sites of the plastron to the peripherals can be discerned by a roughened surface along the visceral side of the peripherals that stretches from the posterior quarter of peripheral IV to the anterior two thirds of peripheral VII. A distinct process protrudes from the visceral surface of peripheral V that acts as the fulcrum during closure of the shell. The peripherals posterior to the ligamentous bridge are thickened parallel to the edge of the plastron. An inset step against which the plastron abuts during closure of the shell is formed by the posterior two-thirds of peripheral X, all of peripheral XI, and the pygal. In dorsal view, the posterior peripherals slope straight downwards instead of being upturned. As such, there is no hint of a posterior gutter. The external surfaces of most peripherals are decorated by growth annuli of the marginal scutes, though less distinctly than those observable on the costals.

Pygal and suprapygal.—Only a single suprapygal is present. This element is slightly wider than the pygal and about as long as most neurals. It contacts neural VIII anteriorly, costals VIII anterolaterally, has a small posterolateral contact with peripheral XI, and a broad posterior contact with the pygal. The pygal is about the same size as most peripherals. It contacts the suprapygal anteriorly and peripherals XI laterally. The lateral margins of this element converge slightly towards the posterior. In ventral view, the pygal together with the posterior peripherals forms a step that receives the plastron during shell closure.

Cervical.—A single cervical scute is located at the anterior margin of the shell. It is about one and a half times longer than wide in dorsal view, slightly notched posteriorly, and contacts marginal I laterally and vertebral I posteriorly.

Vertebrals.—The full outline of the five vertebral scutes is unclear because much of the dorsal carapacial surface is eroded. Only the anterior half of vertebral I is clear. This element is slightly wider than the nuchal and the anterolateral corners therefore lap onto peripherals I. This element is likely pentagonal in shape and contacts the cervical anteriorly, marginals I anterolaterally, pleurals I posterolaterally, and, presumably, vertebral II posteriorly. Although neural I is missing, the medial apex of pleural I allows us to conclude that the sulcus between vertebrals I and II crossed this element, as in most other turtles. Vertebrals II and III are poorly preserved, but it is nevertheless possible to ascertain that they were both hexagonal in shape and have relatively straight margins. The medial apex of pleural II allows us to conclude again that the vertebral II/III sulcus crossed neural III, as in most other turtles. Vertebral IV is hexagonal with straight margins and slightly wider than long. Its anterior sulcus with vertebral III is clearly positioned over neural V, whereas the posterior sulcus with vertebral V is located over the protruding posterior tip of neural VII. Vertebral V is the widest of all vertebrals, though roughly as long as the other elements. It posteriorly contacts the posterior three quarters of marginal XI and all of marginal XII and clearly laps onto the anterior quarter of the pygal. Growth annuli of the vertebrals are preserved where the surface of the underlying bones is undamaged.

Pleurals.—Four pair of pleural scutes are present that are wider than the vertebral scutes and display the usual, alternating medial contacts with the vertebrals. Pleural I contacts the posterior fifth of marginal I, all of margins II–IV, and the anterior half of marginal V. Pleural II contacts the posterior half of marginal V, all of marginal VI, and the anterior four-fifths of marginal VII. Pleural III contacts the posterior fifth of marginal VII, all of marginal VIII, and the anterior two-thirds of marginal IX. Finally, pleural IV contacts the posterior third of marginal IX, all of marginal X, and the anterior quarter of marginal XI. Although the pleuromarginal sulcus often approaches the costoperipheral suture, it always remains situated on the peripherals. Clear growth annuli of the pleurals are preserved on the underlying costal bones.

Marginals.—Twelve pairs of marginals cover most of the rim of the carapace. Marginals I contact the cervical laterally, vertebral I posteromedially, and pleural I posterior. The intermediate contacts of marginals II–IX with the pleurals are described above. Marginals XI contact pleural IV anteriorly and vertebral V anteromedially. Marginals XII contacts vertebral V anteriorly and one another medially. The anterior portion of marginal XI nearly laps onto costal VIII but all other marginals are clearly restricted to the nuchal, peripherals, and pygal.

Plastron.—The plastron is complete and, with exception of the left hyoplastron, fully articulated. As is typical for box turtles, the plastron bones are organized into separate anterior and posterior plastral lobes and only connected to the carapace through ligaments. The actual hinge between the two lobes is formed by a deep groove that runs along the posterior margin of the hyoplastra within which the narrow, anterior edge of the hypoplastra can rotate.

Anterior plastral lobe.—The anterior plastral lobe consists of the epiplastra, entoplastron, and hyoplastra. Its midline length is 61 mm and its posterior width at the hinge is 78 mm. The lip formed by the plastral scutes can be partially observed in dorsal view on the epiplastra and the disarticulated hyoplastron. The anterior lip formed by the gulars is approximately 5 mm wide and, for the small area where it is visible, runs parallel to the anterior plastral margin. The visceral view of the hyoplastron reveals that the lip formed by the pectoral is only 2 mm wide and that the lip formed by the humeral expands towards the anterior. The epiplastra are trapezoidal in shape, form the anterior half of the anterior plastral margin, and contact one another broadly along the midline. The entoplastron is pentagonal in shape and is situated between the epiplastra and hyoplastra. The posterior margins of the hyoplastra form a deep groove for articulation with the posterior plastral lobe. The dislocated left hyoplastron reveals that the anterior plastral buttress is highly reduced and only consists of a small, blunt ridge at the posterolateral corner of the hyoplastron.

The anterior plastral lobe was covered during life by a pair of gulars, humerals, and pectorals. The gulars broadly contact one another along the midline and lap halfway onto the entoplastron. The lateral contacts of the gulars with the humerals exhibit two smooth undulations. The humerals broadly contribute to the anterior plastral margin but only have a short contact with one another over the entoplastron. The humeropectoral sulcus crosses the posterior edge of the entoplastron. The remaining portion of the anterior plastral lobe is covered by the pectoral. The pectoral/abdominal sulcus coincides fully with the hyo/hypoplastral suture, thus allowing fully closure of the shell.

Posterior plastral lobe.—The posterior plastral lobe is formed by the hypoplastra and xiphiplastra. The midline length of the lobe is 77 mm and its anterior width at the hinge is 78 mm. The elements of the posterior lobe are disarticulated, but all elements are flat, indicating that a deep depression is lacking. The specimen is therefore either female or originates from a taxon lacking this sexual characteristic of males (Minx, 1996). The xiphiplastra have a greater surface area than the hypoplastra. The posterior plastral lobe cannot be observed in visceral view and the lip formed by the scutes can therefore not be assessed. Enough can be seen from the side, however, to reveal that the posterior plastral buttress is fully reduced. The abdominal scutes cover the anterior three-quarters of the hypoplastra and the anal scutes the posterior three-quarters of the xiphiplastra. The abdominal/femoral sulcus is generally straight, but shows a small inflection near the bridge region. The femoral/anal sulcus gently curves from the midline to the posterior margin of the lobe.

REDESCRIPTION OF THE HOLOTYPE OF ‘*TERRAPENE LONGINSULAE*’

‘*Terrapene longinsulae*’ is based on a single specimen, USNM P 5983, which consists of a near complete skeleton that includes most of the shell, a well-preserved skull, and some limb bones (Figs. 3, 4). Our primary objective is to highlight the irregular morphology of the carapace. We therefore only provide a brief description of the shell and omit the skull and postcranial elements completely. All material was observed directly to score this taxon for the phylogenetic analysis.

Carapace.—The carapace is nearly complete and only lacks portions of the nuchal region, both bridge regions, and the right posterior margin. The outline is notably round. The midline series of elements is complete, consisting of the nuchal, seven neurals, a suprapygal, and a pygal. However, the nuchal is not symmetrical and neurals II–VII have differing contacts on the right and left side. The costal and peripherals elements are also highly irregular, although only the costal elements can be observed in detail. On the right side, nine costal elements can be counted, where the regular count of eight costal elements can be observed on the left side. The first left costal I medially contacts two neurals, not one, which is not usual for representatives of *Terrapene*. The overlying vertebral and pleural scutes are even more irregular. Instead of the usual series of five vertebrals, eight irregular vertebrals are present that are arranged in an alternating, step-like pattern. Both sides exhibit four pleurals, but these scutes are arranged in an offset pattern from one another. With exception of vertebral I, it is therefore not possible to correctly homologize these elements.

Plastron.—In contrast to the carapace, the plastron exhibits no irregularities. The gulars and pectorals clearly lap onto the entoplastron. The pectoral abdominal sulcus fully coincides with the hyo/hypoplastral suture, enabling full plastral kinesis. The posterior plastral lobe is widest at the hinge and is noticeably flattened along its posterior boarder.

PHYLOGENETIC ANALYSIS

We test the phylogenetic placement of *Terrapene parornata* n. sp., *T. longinsulae*, and ‘*T*’. *corneri* by integrating these three fossil taxa into an analysis of all currently accepted extant emydine turtles using morphological evidence. The analysis is primarily based on the testudinoid character list of Joyce and Bell (2004), but characters were added particularly from the detailed analysis of *Terrapene* populations of Minx (1996). *Chrysemys picta* and *Deirochelys reticularia* were designated as outgroup taxa. All taxa were scored based on either the literature (e.g., Minx, 1996; Joyce and Bell, 2004) and/or personal observations of osteological material. The scorings of Minx’s (1996) populations were combined into the species they represent.

A number of characters were omitted from the analysis after scoring. In particular, characters 1–3, 7, 8, 10–13, 15, 18–20, 22–36, 40–42, 44–46, 48, 55, 58, 59, 62, 63, and 66, 67 were omitted from the character list of Joyce and Bell (2004), because they are uninformative within the context of this analysis. A number of characters were omitted from Minx (1996) as well, in particular characters HC, BS, NG, IC, DS, and PB, all of which are autapomorphic and cannot be scored for either of the two fossil taxa. PR, PF2 of Minx (1996) are too variable and we cannot replicate MS, HP, AS, IS, IB, IL, AN, CS of Minx (1996). Missing data were scored as ‘?’. The complete list of 44 morphologically informative characters for 14 ingroup and 2 outgroup taxa is provided in Appendix 1. The list of extant specimens used in addition to those cited by Joyce and Bell (2004) is compiled in Appendix 2. The character taxon matrix is provided in Appendix 3.

Three separate maximum parsimony analyses were performed using PAUP 4.0b10 (Swofford, 2002). Eight characters (4, 5, 8, 10, 15, 22, 33, and 35) form morphoclines and were ordered in all analyses. The remaining characters were run unordered. All characters were left unweighted, a branch-and-bound search was used with minimum branch lengths set to collapse, and support was calculated for each node using bootstrap frequencies (Felsenstein, 1985) with 10,000

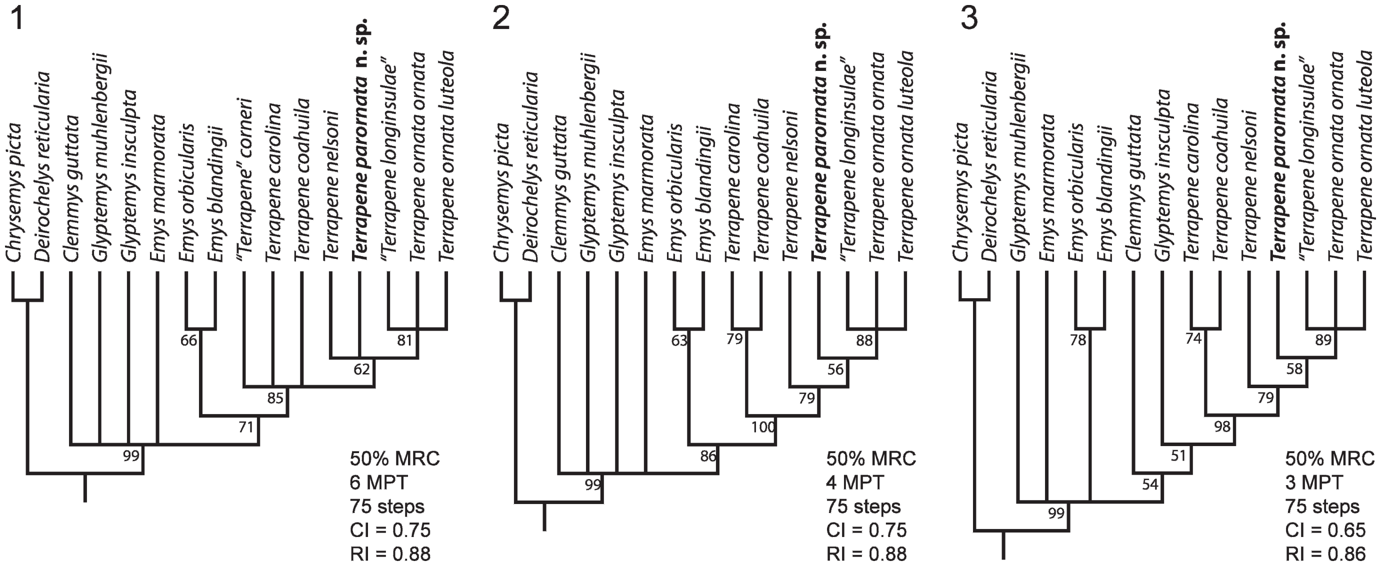

FIGURE 5—Fifty percent (50%) majority rule consensus (MRC) trees resulting from bootstrap analyses, including bootstrap values. *1*, analysis of the complete character taxon matrix; *2*, analysis using all characters after removal of the wildcard taxon '*Terrapene*' *corneri*; *3*, analysis omitting the wildcard taxon '*Terrapene*' *corneri* and all characters pertaining to shell kinesis.

bootstrap replicates and 100 random sequence addition replicates. Bootstrap frequencies >70% are considered strong support (Hillis and Bull, 1993).

The first analysis assesses the phylogenetic position of all fossils using the complete character matrix (Fig. 5a; CI=0.7467; RI=0.8750; RC=0.6533). An Adam's consensus of the resulting topologies of the first analysis (not shown) indicates that the phylogenetic position of '*T.*' *corneri* is highly unstable and that it behaves like a rogue taxon. This is likely caused by missing data, as '*T.*' *corneri* is known from an anterior plastron only and could only be scored for seven of 48 characters.

The second analysis replicates the first analysis but '*T.*' *corneri* is omitted (Fig. 5b; CI=0.7467; RI=0.8827; RC=0.6591). The result is a significantly better-resolved tree that replicates the previous analysis by uniting all emydine turtles with shell kinesis into a monophyletic clade. To test the impact of characters pertaining to shell kinesis, a third analysis was run that omits eight characters that pertain to the emydine shell closure system (i.e., characters 36–44; Fig. 5c; CI=0.7407; RI=0.8641; RC=0.6555).

DISCUSSION

The geological provenience of 'Terrapene longinsulae'.—'*Terrapene longinsulae*' was described by Hay (1908) based on a nearly complete skeleton that includes a well-preserved shell and skull (Figs. 3, 4). The specimen was collected with funding from the U. S. Federal government by John Bell Hatcher for Othniel Charles Marsh of Yale College in 1884 and sent to YPM in New Haven and later to the USNM in Washington DC where it is now permanently housed. The specimen was part of a large shipment from Orleans, Nebraska that mostly consisted of fossils from the well-dated "Long Island Quarry E" located near Long Island, Kansas that produced large quantities of the rhinoceros *Teleoceras fossiger*. However, a note in YPM's accession ledgers specifically indicates that USNM P 5983 did not originate from Quarry E, but rather was included in a box of fossils from "Long Island and Sand Hill, Kansas." This specimen may therefore have been collected anywhere within the broader vicinity of Long Island, perhaps even in nearby Nebraska. Miocene to Pleistocene sediments are broadly exposed in the area surrounding Quarry E. It is therefore currently impossible to date this specimen with any precision. A few previous authors have dated this specimen, but a sufficient rationale was never provided (e.g., upper Miocene to lower Pliocene, Hay, 1908; lower Pliocene, Auffenberg, 1958; mid-Pliocene to mid-Pleistocene, Milstead, 1967; late Miocene, Holman and Fritz, 2005). We speculate that these authors were not aware of the poor provenience of this specimen and therefore presumed this fossil to originate from the well-dated *Teleoceras* quarries of Long Island, Kansas. It therefore appears clear to us that the divergence between the *ornata* group and *carolina* group should not be dated using this specimen as has repeatedly been done in the past (e.g., Milstead, 1956, 1967; Holman and Corner, 1985; Holman and Fritz, 2005).

The taxonomic affinities of 'Terrapene longinsulae'.—Although the shells of most turtle species are morphologically homogeneous, a significant amount of variation is known to occur. A number of studies have demonstrated that the most common type of variation consists of split elements or supernumerary elements that produce small, localized irregularities (e.g., Coker, 1910; Zangerl and Johnson, 1957). In addition to these minor types of variation, wild populations of turtles, including *Terrapene* (Lynn, 1937), occasionally yield specimens with highly irregular, asymmetric shells, similar to that of the holotype *T. longinsulae* (e.g., Parker, 1901; Coker, 1910; Zangerl and Johnson, 1957). The causes of these abnormalities remain uncertain, although recent studies found correlations with latitude (Davy and Murphy, 2009) and with inbreeding (Velo-Antón et al., 2011). It is clear, however, that taxa should not be diagnosed using characters derived from such irregular material. In the case of the holotype of *T. longinsulae,* which exhibits several abnormalities (see above), the carapace morphology should mostly be ignored when assessing its phylogenetic affinities.

Hay (1908) already noted that USNM P 5983 is most similar to the extant taxon *T. ornata* but listed a small number of differences, in particular, a constriction of the carapace at the eighth peripheral relative to the hinge line, near parallel posterior portions of the mandibular rami, and the absence of a mid-dorsal keel. The carapace of this specimen is slightly crushed, only the left eighth peripheral is preserved, and much of the remaining shell margin is reconstructed. The mandibles are slightly crushed and damaged as well. We therefore feel that the first two distinctions are dubious and likely the effect of taphonomic processes. The development of the mid-dorsal keel is highly variable among various species of *Terrapene* (Minx, 1996) and this proposed diagnostic character is therefore not a convincing autapomorphy either.

Although Hay (1908) and many other authors have noted a great resemblance between *T. longinsulae* and *T. ornata* (e.g., Oelrich, 1953; Milstead, 1956, 1967; Legler, 1960; Holman and Fritz, 2005), no characters were provided to support this assertion. In our character matrix of 45 characters, *T. longinsulae* can be scored for 28 characters and, in every instance, scores identical to both subspecies of *T. ornata*. Among these characters, two are unique to *T. longinsulae* and *T. ornata*: the development of a noticeably rounded carapace in dorsal view and the development of a flat, transverse edge along the posterior rim of the posterior plastral lobe. The near-complete absence of a mid-dorsal keel is a third character that may potentially be unique to these two taxa, but this character could not be scored for *T. parornata* and may therefore be diagnostic of a more inclusive clade. Given that *T. longinsulae* shares a number of similarities with *T. ornata*, but lacks differences, we conclude that these taxa are indeed fully synonymous. We are not able, however, to determine whether *T. longinsulae* is placed within the crown of *T. ornata*, or along its phylogenetic stem.

Taxonomic and phylogenetic affinities of OMNH 58158.—Our phylogenetic analyses all agree in regards to the hypothesized relationships within the clade *Terrapene*. OMNH 58158 is firmly placed within the *ornata* group (i.e., the clade formed by *T. ornata* and *T. nelsoni*) by the following list of synapomorphies: neural III anteriorly contacts costal III only; neural V anteriorly contacts costal V only; presence of a large contact between the suprapygal and eleventh peripherals; and the development of a thin peripheral lip for articulation with the posterior plastral lobe during shell closure. The presence of two anterior musk duct glands, a character unique to *T. ornata* among all turtles (Waagen, 1972) allows placing OMNH 58158 within the stem group of *T. ornata*. In contrast to the holotype of *T. longinsulae*, OMNH 58158 scores similar, but not identical, to *T. ornata*. The lack of a rounded carapacial outline in dorsal view and the lack of a flattened posterior plastral rim therefore allow placing OMNH 58158 outside the clade formed by *T. longinsulae* and *T. ornata*. Under the absence of other characters we would have considered *T. parornata* as a metataxon that forms part of the direct, ancestral lineage of *T. ornata*, but the lack of a medial contact among the posterior costals and the placement of the posterior sulcus of vertebral III on the neural VII allow diagnosing OMNH 58158 as a separate evolutionary lineage.

Taxonomic affinities of 'Terrapene' corneri.—'*Terrapene*' *corneri* is a fossil turtle taxon based on an isolated anterior plastral lobe from the middle Miocene (late Barstovian) Myers Farm Local Fauna of Webster County, Nebraska (Holman and Corner, 1985; Holman and Fritz, 2005). Holman and Fritz (2005) noted that '*T.*' *corneri* exhibits an eclectic mix of characters found among extant species of *Terrapene* and abstained from diagnosing this taxon any further than *Terrapene*. To allow clear communication with molecular biologists, we herein restrict the meaning of *Terrapene* to the crown clade formed by the four currently recognized extant taxa, *T. carolina*, *T. ornata*, *T. nelsoni*, *and T. coahuila*. Holman and Fritz (2005) list a number of characters that this taxon shares with extant *Terrapene*, but given that these are all herein interpreted as *Terrapene* synapomorphies that evolved along the stem lineage leading to crown *Terrapene*, the possibility remains that '*T.*' *corneri* is situated outside the crown. The only convincing similarity that Holman and Fritz (2005) noted with an extant representative of *Terrapene* is the broad exposure of the gular scutes on the visceral side of the plastron, which also occurs in *T. coahuila*. However, given that this character broadly occurs outside of *Terrapene*, our analysis interprets this character as a symplesiomorphy. With a lack of evidence to support the placement of '*T.*' *corneri* within crown *Terrapene*, we feel it more prudent to refer this taxon to the stem-clade of *Terrapene*. Given the fragmentary nature of this specimen, however, we refrain from naming a new genus and highlight our reservations through the use of quotation marks.

Timing of the divergence of crown Terrapene.—As complex as the morphological adaptations are that allow representatives of *Terrapene* to withdraw inside their shells (Bramble, 1974), this clade only has a limited fossil record. When assessing the temporal evolution of *Terrapene* it is important to conceptualize the difference between the origin of the *Terrapene* stem lineage and the origin of the *Terrapene* crown group. Some previous authors have acknowledged this difference and specifically date the origin of the *carolina* and *ornata* subgroups, which are equivalent to the origin of the crown group (e.g., Milstead, 1956, 1967; Holman and Corner, 1985; Holman and Fritz, 2005). Yet, fragmentary material is regularly referred to '*Terrapene*' as long as it exhibits diagnostic traits seen in extant representatives of this clade.

The holotype of *T. longinsulae* was often listed as the oldest known box turtle (e.g., Auffenberg, 1958; Milstead, 1969), but we demonstrate above that the stratigraphic provenience of this specimen is unclear. Considering that it scores identical in our analysis to extant *T. ornata*, it is plausible that this specimen originates from Pleistocene sediments, but this assertion remains highly speculative. Given that *T. parornata* n. sp. is unambiguously placed by our analysis along the phylogenetic stem lineage of *T. ornata*, however, we now have evidence that the *T. ornata* stem lineage, the *ornata* group, and crown *Terrapene* are at least latest late Hemphillian in age (ca. 5.3–4.6 Ma). All post-Hemphillian material previously reported in the literature is younger than this specimen and is therefore uninformative when assessing the age of all clades that pertain directly to *T. ornata*. We therefore focus on reviewing previously reported material from the Miocene.

Milstead (1969) mentioned a number of fragmentary remains from the early, mid, and late Hemphillian (late Miocene) of Florida, but none of these specimens were figured or described and, with exception of the early Hemphillian specimen FLMNH 9367, no specimen numbers were provided. We therefore disregard this material from further consideration.

Holman and Fritz (2005) more recently provided a comprehensive summary of all other known Miocene box turtle specimens: two nuchals and a left hyoplastron from the middle Barstovian (ca. 14.5–13.0 Ma) of Nebraska, the holotype of '*T.*' *corneri* from the late Barstovian of Nebraska (ca. 13.0–11.5 Ma), and an isolated humerus from the middle to late Clarendonian of Kansas (ca. 10.0–9.0 Ma). In all cases, Holman and Fritz (2005) undertook a careful analysis of similarities, but in the absence of a placement of this material in a global phylogenetic analysis, it remains unclear whether these characters represent synapomorphies or symplesiomorphies. In all cases, however, it is apparent that these fragments exhibit true synapomorphies with extant representatives of *Terrapene*. We therefore conclude that whereas *T. parornata*

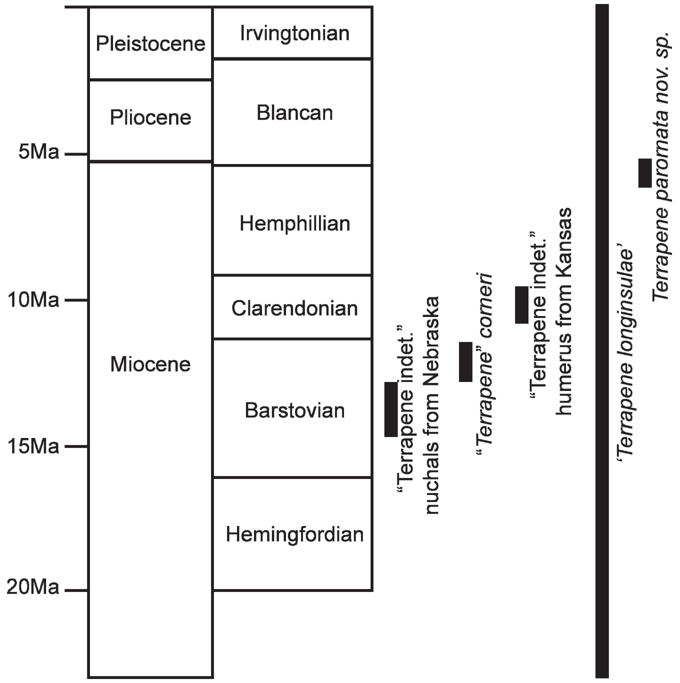

FIGURE 6—The stratigraphic distribution of fossil turtle material discussed in the text. The range of the North American Land Mammal Ages listed in this section follow Holman and Fritz (2005).

represents the oldest crown representative, the middle Barstovian remains from Nebraska represent the oldest stem-group representatives of *Terrapene* (Fig. 6).

Phylogenetic relationships among emydines and the evolution of plastral kinesis within the clade.—Ever since McDowell (1964) proposed splitting all "pond turtles" into two monophyletic clades, the phylogenetic relationships of Emydidae have been vigorously debated. McDowell (1964) suggested that Emydidae (his Emydinae) be split into the *Emys*, *Deirochelys*, and *Chrysemys* "complexes." Particularly the formation of the *Deirochelys* complex demanded ad hoc explanations regarding character evolution, as it requires that the plastral kinesis evident in *Emys blandingii* be derived independently from that of *Terrapene*. Noting these difficulties, Bramble (1974) proposed that all emydid turtles with plastral kinesis form a monophyletic group and that *Emys orbicularis*, *Emys blandingii*, and *Terrapene* form an evolutionary ladder reflecting the acquisition of an ever more complex shell closure system. Given the great number of highly unique characters that Bramble (1974) amassed to support this conclusion, in particular the acquisitions of supernumerary scapular bones, morphologists have generally accepted or replicated this phylogenetic arrangement (e.g., Gaffney and Meylan, 1988; Burke et al., 1996; Joyce and Bell, 2004). More recent molecular phylogenies have been rather consistent in supporting the monophyly of Bramble's (1974) *Clemmys* complex, but also demand a less parsimonious evolution of shell kinesis among emydines (e.g., Bickham et al., 1996; Feldman and Parham, 2002; Spinks and Shaffer, 2009). Depending on the molecular topology proposed and the character optimization chosen, shell kinesis either developed twice within Emydinae, or some taxa secondarily lost their kinetic abilities. The consequences for morphological evolution are drastic under both scenarios.

Given that the development of shell kinesis demands an extreme reconstruction of the shell in turtles (Bramble, 1974), it is possible that many morphological characters are correlated and that use of these characters unnecessarily weights the analysis in favor of a monophyletic clade of kinetic turtles. For instance, the development of a hinge between the hyo- and hypoplastra demands an overlap of the pectoral/abdominal sulcus with the hyo/hypoplastral suture, as the plastral scutes normally hinder movement between the suture (Hutchison and Bramble, 1981). Kinesis at this hinge furthermore demands losing the osseous connection between the plastron and the carapace, reduction of the anterior and plastral buttresses, development of an osseous pivot, and a reorganization of the scapula, for instance, through the acquisition of supernumerary bones (Bramble, 1974). This a priori assumption is supported by recent work (Angielczyk et al., 2011) that demonstrates a tight correlation between plastron shape and the presence of a hinge among emydine turtles.

To test a potential correlation between the characters, we developed a comprehensive emydine character matrix and reevaluated all previously proposed characters in the process. In total, we conclude that eight characters (characters 36–44) pertain directly to the development of plastral kinesis. Although a significant amount of correlation is apparent within the data (see Appendix 1), these eight characters are not completely correlated. Not all taxa with a ligamentous bridge (i.e., *Emys marmorata*) are kinetic, but all kinetic taxa have a ligamentous bridge. Not all kinetic taxa have fully reduced buttresses (i.e., *Emys orbicularis* and *Emys blandingii*), but all taxa with reduced buttresses are kinetic. Finally, not all taxa with kinesis have an osseous pivot (i.e., *Emys orbicularis*), but all taxa with a pivot are kinetic. To test the impact of these eight characters, we ran a reduced analysis that excluded them. The resulting topology (Fig. 5b) is striking in that it converges upon the results proposed by molecular studies, in particular by not uniting all turtles with shell closure into a clade and by placing *Clemmys guttata* as sister to a monophyletic *Terrapene*. Minor differences are nevertheless apparent in that the monophyly of *Emys* and *Glyptemys* is not supported and that *Glyptemys insculpta* is interpreted as the immediate sister of *Terrapene*. Although the detailed phylogenetic position of some taxa still need to be worked out, we feel that the general convergence upon the molecular results reveals that characters pertaining to shell closure unnecessarily skew the results towards a monophyletic clade of kinetic emydines. This 'morphological long branch attraction' will perhaps be resolved in the future through the addition of more fossils that will either document the character evolution proposed by the molecular studies or continue to support the monophyly of kinetic emydines.

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ACCEPTED 2 SEPTEMBER 2011

APPENDIX 1

List of morphological characters used in phylogenetic analysis. An asterisk denotes characters that form a morphocline and can be ordered.

Cranial Characters:

Character 1: Jugal-pterygoid contact (see Joyce and Bell, 2004, 4): 0=present, medial process of jugal well-developed and touching the pterygoid; 1=absent, medial process reduced.

Character 2: Jugal-palatine contact (see Joyce and Bell, 2004, 5): 0=absent; 1=present.

Character 3: Jugal-epipterygoid contact (Joyce and Bell, 2004, 6): 0=clearly absent; 1=present, or almost present, epipterygoid forms a long lateral process that approaches the jugal.

*Character 4: Antero-posterior "width" of postorbital bar (Minx, 1996, PO): 0=wide; 1=narrow; 2=extremely narrow.

*Character 5: Temporal arch (Minx, 1996, ZA): 0=temporal arch complete; 1=temporal arch not fully ossified, but jugal and quadratojugal processes remain; 2=temporal arch absent, processes absent.

Comments: Character 9 of Joyce and Bell (2004) was worded to encompass morphological variation to the temporal arch seen throughout all of Testudinoidea and to allow objectively scoring poorly known taxa. Within the ingroup of this study, the reduction of the temporal arch only occurs within *Terrapene* and the mode of reduction is well understood. We therefore follow the wording and scoring of Minx (1996).

Character 6: Size of the foramen orbito-nasale (Joyce and Bell, 2004, 14): 0=small, less than 1/6 of orbit length; 1=large, more than 1/6 of orbit length.

Character 7: Parietal-palatine contact (Burke et al., 1996, 19): 0=present; 1=absent.

Postcranial Characters:

*Character 8: Squared mid-dorsal keel of bony carapace (modified from Minx, 1996, MK): 0=absent; 1=moderately developed; 2=prominently developed.

Comments: The original character of Minx (1996) pertains to the mid-dorsal keel of emydines in general. We presume the keel was scored based on dry or wet specimens with attached scutes because Minx (1996) mentions that the keel may be worn, something that more plausibly happens to the external scutes. The external morphology of the scutes does not fully mirror the morphology of the underlying bone, similar to the ramphotheca of turtles (see Joyce and Bell, 2004). However, given that the focus of this study is to assess the phylogenetic affinities of fossil emydines, specimens that lack scutes, we rescored this character to apply to the bony shell only. Furthermore, given that much variation is apparent regarding the development of the mid-dorsal keel, we herein restrict our character to the development of a more or less prominent squared off bony mid-dorsal keel, which is only found in various species of *Terrapene* and *Glyptemys insculpta*.

Character 9: Co-ossification of the carapace (Minx, 1996, CO): 0=sutures remain open throughout life; 1=many carapacial sutures fuse in adult specimens.

*Character 10: Outline of carapace in dorsal view (Minx, 1996, EC): 0=shell noticeably elongate; 1=shell oval; 2=shell noticeably rounded.

Character 11: Anterior contacts of neural III (modified from Joyce and Bell, 2004, 37+38; Minx, 1996, NC): 0=in most specimens costal III only; 1=always costal II and III.

Character 12: Anterior contacts of neural IV (modified from Joyce and Bell, 2004, 37+38; Minx, 1996, NC): 0=in many specimens costal IV only; 1=always costal III and IV.

Character 13: Anterior contacts of neural V (modified from Joyce and Bell, 2004, 37+38; Minx, 1996, NC): 0=in most specimens costal V only; 1=always costal IV and V.

Character 14: Anterior contacts of neural VII (modified from Joyce and Bell, 2004, 37+38; Minx, 1996, NC): 0=costal VII only; 1=costal VI and VII.

*Character 15: Medial contact of posterior costal bones (expanded from Joyce and Bell, 2004, 39): 0=absent; 1=medial contact of 8th costals only; 2=medial contact of 7th and 8th costals.

Character 16: Position of the posterior sulcus of the fourth vertebral scute (modified from Joyce and Bell, 2004, 43): 0=sulcus lies on the seventh or eighth neural; 1=sulcus lies on the first pygal or on the suture between the eighth neural and first pygal; 2=eighth neural absent, sulcus overlies costals that meet at the midline.

Character 17: Contact of the second marginal scute with the first vertebral scute (Joyce and Bell, 2004, 47): 0=absent; 1=present.

Character 18: Overlap of first pleural scute onto nuchal (Zug, 1969): 0=absent or just barely lapping onto nuchal; 1=clearly present.

Character 19: Depression between the twelfth pair of marginals (Minx, 1996, IM): 0=absent; 1=present.

Character 20: Number of suprapygals: 0=two suprapygals present; 1=one suprapygal present.

Character 21: Suprapygal contact with eleventh peripheral (reworded from Minx, 1996, SP): 0=large contact between suprapygal and eleventh peripheral; 1=contact between suprapygal and eleventh peripheral small or absent.

*Character 22: Posterior peripheral shape (modified Minx, 1996, TP): 0=peripherals thin; 1=peripherals slightly thickened and with small lip for plastron; 2=peripherals greatly thickened and with large lip for plastron.

Character 23: Presence of musk glands (Joyce and Bell, 2004, 56): 0=axillary gland present only; 1=musk glands absent.

Comment: All taxa were scored based on the observations of Waagen (1972).

Character 24: Anterior musk glands: 0=one pair present; 1=two pairs present.

Character 25: Presence of anterior musk duct foramina (Joyce and Bell, 2004, 57): 0=musk glands and their foramina present; 1=musk glands present, but, at most, only bony notches developed.

Comment: Character state 2 of character 57 of Joyce and Bell (2004) is redundant with character state 2 of character 56. We therefore omit this character state herein and score all taxa that lack musk glands as inapplicable.

Character 26: Cornified apical scale (Minx, 1996, AP): 0=absent; 1=present.

Character 27: Intersection of the entoplastron by the humeropectoral sulcus (modified from Joyce and Bell, 2004, 60): 0=absent or just barely present; 1=clearly present.

Character 28: Posterior plastron width (Minx, 1996, WP): 0=greatest at hinge; 1=femoral scutes as wide as hinge or greatest width at femoral scutes.

Character 29: Posterior rim of posterior plastral lobe forms flat, transverse edge (Minx, 1996, LR): 0=absent; 1=present.

Character 30: Distinct depression in plastron of males (modified from Minx, 1996, CP): 0=absent; 1=present.

Character 31: Anal notch of the plastron (Joyce and Bell, 2004, 61): 0=present or reduced; 1=absent.

Character 32: Dorsal exposure of gular scutes along the midline: 0=gulars dorsally overlap approximately 50% of the epiplastra along the midline; 1=gulars dorsally overlap approximately 25% of the epiplastra along the midline.

*Character 33: Manual formula (Joyce and Bell, 2004, 68a, in part; Minx, 1996, PF1): 0=2-3-3-3-3; 1=2-3-3-3-2 or 2-3-3-2-2; 2=2-2-2-2-2.

Character 34: Male clasping claw (Minx, 1996, CC): 0=absent; 1=present.

*Character 35: Hind foot webbing (modified from Joyce and Bell, 2004, 69; Burke et al., 1996, 6): 0=webbing extends to the base of the claws; 1=webbing extends only to the penultimate joint; 2=webbing absent between the toes.

Detailed 'box turtle' characters

Character 36: Sutured contact between plastron and carapace (Joyce and Bell, 2004, 50): 0=present, plastron and carapace are tightly connected by an osseous bridge; 1=absent, plastron is attached to carapace by connective tissue.

Character 37: Anterior plastral kinesis (Burke et al., 1996, 16): 0=absent; 1=present.

Character 38: Posterior plastral kinesis (Burke et al., 1996, 15): 0=absent; 1=present.

*Character 39: Presence and development of anterior buttresses (Joyce and Bell, 2004, 51): 0=anterior buttresses absent; 1=anterior buttresses present but small, and not in contact with the first costal bones; 2=anterior buttresses well developed and in clear contact with the first costal bones.

*Character 40: Presence and development of posterior buttresses (modified from Joyce and Bell, 2004, 52): 0=posterior buttresses absent; 1=posterior buttresses present but small, and not in contact with the costal bones; 2=posterior buttresses well developed and in clear contact with costal bones.

Character 41: Medially-directed pivoting process for plastral hinge developed on fifth peripheral bone (modified from Joyce and Bell, 2004, 53): 0=absent; 1=present, narrow process that protrudes from fifth peripheral; 2=broad shelf that protrudes from fifth peripheral.

Character 42: Complete or almost complete overlap of hyoplastron/hypoplastron suture by the pectoral/abdominal sulcus (Joyce and Bell, 2004, 54): 0=absent; 1=present.

Character 43: Development of a suprascapula (Joyce and Bell, 2004, 64; Minx, 1996, SC, in part): 0=absent; 1=present.

Character 44: Development of an episcapula (Joyce and Bell, 2004, 65; Minx, 1996, SC, in part): 0=absent; 1=present.

Comment: In our opinion the length of the scapular processes is correlated in the ingroup with the presence of suprascapulae and episcapulae, the scapular process being shorter in animals with these supernumerary bones.

APPENDIX 2

List of specimens used in developing the character taxon matrix.

All scorings are based on the observations of Minx (1996), Joyce and Bell (2004), and were supplemented by the following specimens:

Deirochelys reticularia: USNM R 11610, USNM R 80965, USNM R 62219, USNM R 523807;

Clemmys guttata: USNM R 217286, USNM R 220860, USNM R 220861, USNM R 108921, USNM R 521165, USNM R80942;

Emys blandingii: USNM R 220869, USNM R 292994, USNM R 167554, USNM R 7551;

Emys marmorata: USNM R 73265, USNM R 220752, USNM R 22052;

Emys orbicularis: USNM R 499024, USNM R 154507;

Glyptemys muhlenbergii: USNM R 94454, USNM R 238368, USNM R 220866, USNM R 194857, USNM137377;

Glyptemys insculpta: USNM R 63089, USNM R 167535, USNM R 288352, USNM R 279316, USNM R 220865, USNM192780;

Terrapene ornata ornata: all material of Joyce and Bell (2004) is referable to this taxon, USNM R 7542;

Terrapene ornata luteola: USNM R 246659, USNM R 246660, USNM R 246666, USNM R 246664, USNM R 246669, USNM R 246643;

Terrapene nelsoni: USNM R 149710;

Terrapene carolina: USNM R 219064;

Terrapene coahuila USNM R 166370, USNM R 166369, USNM R 166368, USNM R 166366, USNM R 159575.

APPENDIX 3

Morphological character taxon matrix used in the phylogenetic analysis. a=0/1, b=0/1/2.

Chrysemys picta	0110010000	111100a?00	001--0a-00	0000000022	0000
Deirochelys reticularia	0010000000	1111001a00	001--00-00	0000000022	0000
Clemmys guttata	1000001000	1111010100	0000001-00	0010100022	0000
Glyptemys muhlenbergii	1000001000	1111000000	0000000-00	0010100022	0000
Glyptemys insculpta	1000001100	101100010a	0000001-00	0010100022	0000
Emys marmorata	1000001000	1111001000	1000001-00	0110010022	0000
Emys orbicularis	0000001000	1110011000	1000100000	0110111011	0110
Emys blandingii	0000001000	1110011000	0000100000	0010111111	2111
Terrapene carolina	100ab01211	1111120101	02a0101101	1110211100	1111
Terrapene coahuila	?000001110	1111220101	0200101101	1010211100	1111
Terrapene nelsoni	1??22??10a	0101?20?1?	110011?100	1121211100	1111
Terrapene ornata ornata	1002201002	0101120101	1101111010	1121211100	1111
Terrapene ornata luteola	1002201002	0101120101	1101111010	11?1?11100	1111
'*Terrapene longinsulae*'	1002201002	--------01	-10???101?	1???11100	1111
Terrapene parornata n. sp.	????????01	0101000101	11011?100?	11??11100	11??
'*Terrapene*' *corneri*	??????????	??????????	??????1???	?0???1110?	?1??