

# THE BOX TURTLE GENUS *TERRAPENE* (TESTUDINES: EMYDIDAE) IN THE MIOCENE OF THE USA

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Middle and Late Miocene fossils of the box turtle genus *Terrapene* are reviewed. The oldest known *Terrapene* specimens originate from the Medial and Late Barstovian North American Land Mammal Ages of Nebraska. Two nuchal bones from the Egelhoff Local Fauna, Keya Paha County, Nebraska (Medial Barstovian Land Mammal Age, ca 14.5-13.0 million BP) and a left hyoplastron from the Stewart Quarry, Cherry County, Nebraska (Late Barstovian, ca 13.0-11.5 million BP) closely resemble recent *Terrapene ornata*. The presence of *T. ornata*-like box turtles in the Barstovian suggests that the extant species groups were already established by that time and that the genus *Terrapene* evolved distinctly before the Middle Miocene. An extinct subspecies of *T. ornata*, *T. o. longinsulae* Hay, 1908, is known from the Late Miocene (Clarendonian, ca 11.5-9.0 million BP) as well as from several Pliocene sites. It is unknown whether a Clarendonian *Terrapene* hyoplastron from the Ash Hollow Formation of Cherry County, Nebraska belongs to *T. o. longinsulae* or to another taxon. A nearly complete anterior plastral lobe from the Myers Farm Local Fauna, near Red Cloud, Webster County, Nebraska, from the Late Barstovian (ca 13.0-11.5 million BP) differs significantly from all other recent and fossil *Terrapene* taxa. This specimen serves as the holotype of a new extinct *Terrapene* species described herein. It is of unclear relationships and shares some characters with *T. coahuila* and others with *T. nelsoni* and *T. ornata*. A left humerus from the WaKeeney Local Fauna, Trego County, Kansas (Middle to Late Clarendonian Land Mammal Age, ca 10.0-9.0 million BP) compares well with humeri of recent *Terrapene carolina* and is the oldest *Terrapene* that resembles extant *T. carolina*. The second oldest one is from the latest Miocene McGeehee Site, Alachua County, Florida (Early Hemphillian, ca 8.5 million BP) and perhaps represents a fossil taxon known as *T. carolina putnami* Hay, 1908.

*Key words:* Chelonia, fossil, Neogene, North America, palaeontology

## INTRODUCTION

The North American box turtles, genus *Terrapene*, are small (maximum carapacial length of recent taxa 200 mm), mostly terrestrial emydine turtles with a plastral hinge between the hyoplastron and the hypoplastron, allowing complete shell closure. The ability to close the shell entirely (like a box) is facilitated by a morphologically specialized tripartite scapula. The same structure is found in the closely related, hinged North American *Emydoidea blandingii* (Bramble, 1974), suggesting that the hinge and the segmented scapula are shared derived characters of *Emydoidea* and *Terrapene* (Gaffney & Meylan, 1988; Fritz, 2003). No other North American emydines have a plastral hinge and a segmented scapula, but in the Palaearctic *Emys orbicularis*, a plastral hinge and a bipartite scapula occur (Bramble, 1974).

Box turtles form an essentially homogeneous group that has generally been taxonomically stable since the comprehensive studies of Milstead (1967, 1969) and Milstead & Tinkle (1967). *Terrapene* occurs only in the United States and Mexico. Four recent species are rec-

ognized, which are, with the exception of the aquatic *T. coahuila*, all mainly adapted to terrestrial habitats (Milstead, 1969; Ernst *et al.*, 1994; Minx, 1996; Dodd, 2001): (1) *Terrapene carolina* (Linnaeus, 1758) has four living subspecies restricted to the United States (*T. c. bauri*, *T. c. carolina*, *T. c. major*, and *T. c. triunguis*) and two restricted to Mexico (*T. c. mexicana* and *T. c. yucatanana*); (2) *Terrapene coahuila* Schmidt & Owens, 1944 is monotypic and exists only as an isolated population in Coahuila, Mexico; (3) *Terrapene nelsoni* Stejneger, 1925 has two living subspecies, both restricted to Mexico (*T. n. klauberi* and *T. n. nelsoni*); (4) *Terrapene ornata* (Agassiz, 1857) has two living subspecies, one (*T. o. luteola*) occurring both in the United States and Mexico, and one (*T. o. ornata*) only in the United States. However, recently it was suggested that the allopatric Mexican subspecies of *Terrapene carolina* might represent distinct species (Stephens & Wiens, 2003), *Terrapene mexicana* and *T. yucatanana*.

Two species groups, the “*carolina* group” and the “*ornata* group”, are recognized (e. g. Milstead, 1967, 1969; Milstead & Tinkle, 1967; Minx, 1996; Dodd, 2001). Characters used to define the two groups are summarized in Milstead & Tinkle (1967), Milstead (1969), and Dodd (2001). The *carolina* group consists of *T. carolina* and *T. coahuila* and the *ornata* group of

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*T. ornata* and *T. nelsoni*. In each group, one extinct taxon is known which is treated traditionally as a subspecies. *Terrapene carolina putnami* Hay, 1908 ranged from a very large to a huge size (more than 300 mm shell length, Holman, 1965; Milstead, 1969; Dodd, 2001). It is otherwise quite similar to the extant *T. c. major*. Therefore, Auffenberg (1958) and Milstead (1969) speculated that *T. c. putnami* was the direct predecessor of *T. c. major*, which was influenced and modified by intergradation with other subspecies. *T. c. putnami* occurred from the Miocene-Pliocene boundary (Late Hemphillian, ca 5.5-4.5 million years BP) to the end of the Pleistocene (latest Rancholabrean, ca 10,000 years BP, Auffenberg, 1958; Milstead, 1969; Holman & Clausen, 1984). Also an Early Hemphillian find (ca 8.5 million years BP) has been tentatively identified as *T. c. putnami* (Milstead, 1969). *Terrapene ornata longinsulae* Hay, 1908 is known from the Late Miocene (Clarendonian, ca 11.5-9.0 million years BP) as well as from several Pliocene sites (Milstead, 1969). It differs from the extant *Terrapene ornata* subspecies by the low angle of elevation of the first central scute and the low elevation of the third central scute, the lack of rugosity of the carapacial scutes and non-flaring and non-emarginated marginal scutes (Milstead, 1969). It is beyond the scope of the present paper to discuss the advantages and problems of assigning subspecific rank to fossil taxa.

Other *Terrapene* fossils have been described as extinct species (e. g. Hay, 1908*a,b*, 1916; see the review in Dodd, 2001); but these, often fragmentary remains were later assigned to modern species (Auffenberg, 1958; Milstead, 1969). A recent morphometric study of the Pleistocene taxon *Terrapene innoxia* Hay, 1916 (relegated to the synonymy of *Terrapene carolina bauri* by Auffenberg, 1958) was done by Ernst *et al.* (1998). These authors suggested that the referral of *T. innoxia* to *T. c. bauri* is in doubt, and that further analysis of variation within *T. c. bauri* and *T. c. major* will be necessary to find out whether *T. innoxia* warrants taxonomic recognition. We feel, that it is highly probable that *T. innoxia* represents an intergrade population between modern subspecies of *T. carolina*.

In the present paper we deal with the scanty fossil material from the Middle and Late Miocene of Nebraska (Barstovian) and Kansas (Clarendonian) which was described in part earlier by Holman (1975, 1987) and Holman & Corner (1985). The material from the Barstovian of northwest Nebraska represents the earliest *Terrapene* known. Further, we review other Miocene *Terrapene*.

## LOCALITIES, MATERIALS AND METHODS

### THE FOSSIL LOCALITIES

We follow the concept that the Miocene extends from about 24 million to about 5 million years before the present (abbreviated here as BP). The Miocene in North

America begins in the later part of the Arikareean North American Land Mammal Age (NALMA) and continues to near the end of the Hemphillian NALMA. These Land Mammal Ages are as follow (Hulbert, 2001) [older to younger from bottom to top]:

Hemphillian	9.0-5.5 million BP
Clarendonian	11.5-9.0 million BP
Barstovian	16.0-11.5 million BP
Hemingfordian	20.0-16.0 million BP
Late Arikareean	24.0-20.0 million BP

The Barstovian NALMA that we will be mainly dealing with here has been subdivided into early, medial, and late portions (Voorhies, 1990):

Late Barstovian	13.0-11.5 million BP
Medial Barstovian	14.5-13.0 million BP
Early Barstovian	16.0-14.5 million BP

*The Medial Barstovian Site.* The Egelhoff Local Fauna (University of Nebraska State Museum, UNSM Collecting Locality Kp-101), also called the Egelhoff Quarry by Voorhies (1990), occurs in a road-cut north of the Niobrara River in Keya Paha County in northwest Nebraska. It is in the lower part of the Valentine Formation. Fossil material from this horizon was for years considered to overlap the Miocene-Pliocene boundary, but now is placed in the Middle Miocene in the Medial Barstovian NALMA (Voorhies, 1990). The upper fossiliferous unit of the Egelhoff Local Fauna is composed of unconsolidated, crossbedded sand with fine gravel near the base. Bulk screening (sieving) of the fine gravel lenses has yielded the great majority of the Egelhoff fossils and produced the *Terrapene* nuchal bones discussed below. Morris F. Skinner of Ainsworth, Nebraska discovered the site in 1964 and since then the site has been sampled by several institutions, including the Michigan State University Museum field parties which collected the *Terrapene* material in the interval between 1974 and 1978. Holman (1987) discussed previous herpetological studies at this site and Voorhies (1990) provided an expanded list of amphibians and reptiles.

*The Late Barstovian Sites.* The Myers Farm Local Fauna Quarry (UNSM Collecting Locality Wt-15A) lies in Webster County in southeastern Nebraska on the property of the Gary Myers family of Red Cloud. The site was discovered and studied by Corner (1976, 1977) who determined the Myers Local Fauna is stratigraphically equivalent to the type Valentine Quarry (Railroad Quarry) of north-central Nebraska. It is thus younger than the Egelhoff Local Fauna above and represents the Late Barstovian Land Mammal Age.

The Stewart Quarry (UNSM Coll. Loc. Cr 150) is a relatively new site in Cherry County, north-central Nebraska. Field crews from University of Nebraska State Museum have collected from this site since the early-

middle 1990s. This site also represents the Late Barstovian Land Mammal Age (M. J. Voorhies, pers. comm.).

*The Clarendonian Site.* The WaKeeney Local Fauna (University of Michigan Collecting Locality No. UMK6-59) occurs on the Lowell Hillman Ranch in Trego County, in northwestern Kansas. The site was discovered by Lester F. Phillis in the early 1940's. Wilson (1968) published a comprehensive work on the vertebrates of the site. Later, J. A. Holman and field crews from the Michigan State University Museum (1969-1973) collected more than 100 tons of fossiliferous matrix from the site, adding to the known vertebrate fauna. Holman (1975) published a comprehensive report on the WaKeeney herpetofauna where he mentioned the *Terrapene* finding. Based on his analysis of the mammalian remains, Wilson (1968) assigned the WaKeeney Local Fauna to the Middle to Late Clarendonian Land Mammal Age (10.0-9.0 million BP).

#### SPECIMENS STUDIED

The *Terrapene* fossils described below are in the Michigan State University Museum Vertebrate Paleontological Collection, East Lansing (MSUVP) and in the University of Nebraska State Museum, Lincoln (UNSM). We compared the fossil specimens with 82 skeletons of recent *Terrapene* species, representing both extant species groups and most of the recognized recent taxa. Skeletal material of *Terrapene carolina yucatanica*, *T. ornata luteola* and *T. nelsoni klauberi* is extremely rare in museum collections (if existent at all) and was not available for comparison. The comparative recent material is from the holdings of the Michigan State University Museum, East Lansing (MSU), the Museum of Zoology (= Museum für Tierkunde) Dresden (MTD), and the University of Michigan Museum of Zoology, Ann Arbor (UMMZ) and is listed as follows:

*Terrapene coahuila* (n=5): MSU 3509-3510, 4108-4110; *Terrapene carolina bauri* (n=9): MSU 479, 487, 489, 521, 599, 629, 1306, 3061, 3825; *Terrapene carolina carolina* (n=22): MSU 510, 1401, 1696, 3454, 3941, 4020, 4115-4117, 4120, 4311, 4395, 12954, 13006, 13019, 14371, 14439-14440, 14442, MTD 8481, 42836, 43908; *Terrapene carolina major* (n=3): MSU 490, 3220, 3957; *Terrapene carolina mexicana* (n=1): MSU 3025; *Terrapene carolina triunguis* (n=16): MSU 1056, 4044, 4118-4119, 4349, 12958, 12963, 12966-12967, 12977, 12979, 13020, 14348-14350, 14362; *Terrapene nelsoni nelsoni* (n=1): UMMZ 128400; *Terrapene ornata ornata* (n=25): MSU 1563, 2091, 2815, 3023, 3107, 3147, 3149-3150, 3175, 3217, 3364, 3467, 3774, 4384, 12955, 12962, 12969, 12973, 12976, 13016-13018, MTD 43905-43906, 43334.

#### SYSTEMATIC PALAEOZOOLOGY

*TERRAPENE* CF. *ORNATA* (AGASSIZ, 1857) (FIGS. 1 AND 2)

*Material.* Two nuchal bones, MSUVP 809A and 809B from the Egelhoff Local Fauna (UNSM Kp-101),

Keya Paha County, Nebraska; Middle Miocene (Medial Barstovian Land Mammal Age, ca 14.5-13.0 million BP). A left hyoplastron, UNSM 122393 from the Stewart Quarry (UNSM Cr-150), Cherry County, Nebraska; Middle Miocene (Late Barstovian Land Mammal Age, ca 13.0-11.5 million BP). A third nuchal bone (MSUVP 809C) from a juvenile specimen and a fragmentary right femur (MSUVP 809D) from the Egelhoff Local Fauna are much eroded and are only identifiable as *Terrapene*. All Egelhoff Local Fauna specimens were identified as *Terrapene* sp. indet. by Holman (1987).

*Identification.* The nuchal bones MSUVP 809A and 809B (Fig. 1) resemble *Terrapene ornata* and the single *T. n. nelsoni* (UMMZ 128400) studied in that they are markedly shorter and wider than in *T. carolina* and *T. coahuila*. They do not resemble nuchal bones of any other Nearctic turtle. The cervical scute impressions on the nuchal bones are similar to *T. ornata* and differ from *T. carolina*, *T. coahuila* and *T. n. nelsoni* in being clearly shorter and wider. The encroachment of the pleural sulci on the nuchal bone is more extensive in the fossil and in *T. ornata* than in *T. carolina*, *T. coahuila*, and *T. n. nelsoni*. These characters could not be observed in the Late Barstovian material described as a

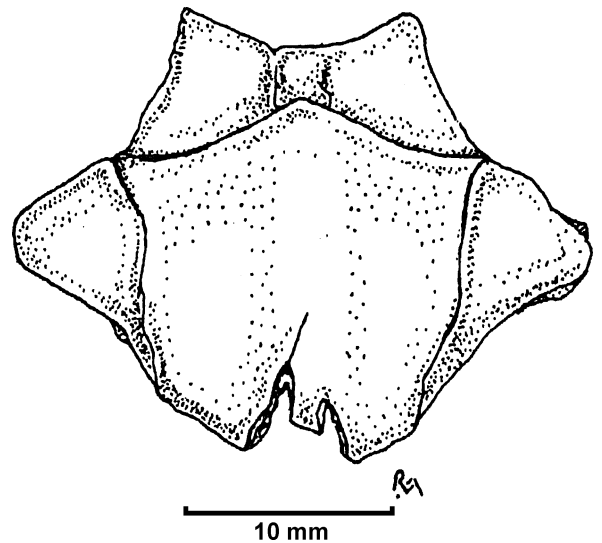


FIG. 1. *Terrapene* cf. *ornata* from the Egelhoff Local Fauna, Keya Paha County, Nebraska; Middle Miocene (Medial Barstovian Land Mammal Age, ca 14.5-13.0 million BP). Nuchal bone (MSUVP 809A). Drawing reproduced from Holman (1987).

new species below. The left hyoplastron UNSM 122393 (Fig. 2) resembles recent *T. ornata* and differs from all other species of *Terrapene* in its narrow humeral scute overlap and reduced articular surface for the bridge (Fig. 3). It resembles all other *Terrapene* species but differs from the Late Barstovian species in having the anterodorsal hinge line area extruded over the ventral hinge line area (Fig. 2).

*TERRAPENE* *CORNERI* N. SP. (FIG. 4)

*Holotype.* An anterior plastral lobe, complete except for a small piece of the right hyoplastron posterior to the

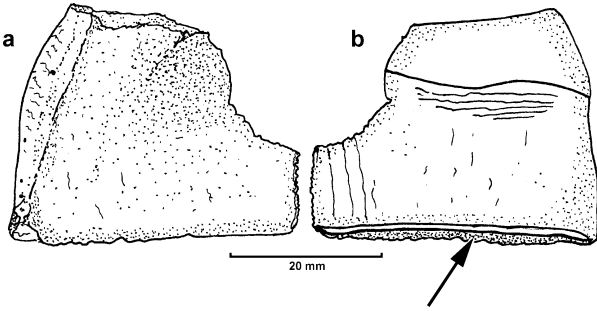


FIG. 2. *Terrapene* cf. *ornata* from the Stewart Quarry, Cherry County, Nebraska; Middle Miocene (Late Barstovian Land Mammal Age, ca 13.0-11.5 million BP). Left hyoplastron (UNSM 122393): (a) dorsal aspect, (b) ventral aspect. Arrow: anterodorsal hinge line area extruded over ventral hinge line area.

entoplastron, UNSM 21618. This specimen was identified as *Terrapene* sp. by Holman & Corner (1985).

**Locality and Horizon.** Myers Farm Local Fauna, near Red Cloud, Webster County, Nebraska (UNSM Wt-15A); Middle Miocene (Late Barstovian Land Mammal Age, ca 13.0-11.5 million BP).

**Etymology.** Named in recognition of vertebrate palaeontologist R. George Corner who collected the holotype.

**Diagnosis.** *Terrapene corneri* resembles recent *Terrapene* and differs from all other emydine genera in having, in combination: (1) a kinetic plastron composed of a single grooved hinge with the pectoral-abdominal sulcus congruent with the hinge line, (2) plastral buttresses absent, and (3) the entoplastron encroached by both the gular-humeral and humeral-pectoral sulci. *Terrapene corneri* differs from all other living and fossil *Terrapene* taxa in having the following unique character combination: (a) presence of an epiplastral beak produced by two symmetrical gular notches, (b) very wide gular and humeral overlap, (c) notches in humeral and pectoral margin, and (d) anterodorsal border of hinge line area not extruded over anteroventral border of this area.

*T. corneri* differs from all *Terrapene* species except *T. coahuila* by the very wide gular and humeral overlap. An epiplastral beak resembling the condition in *T.*

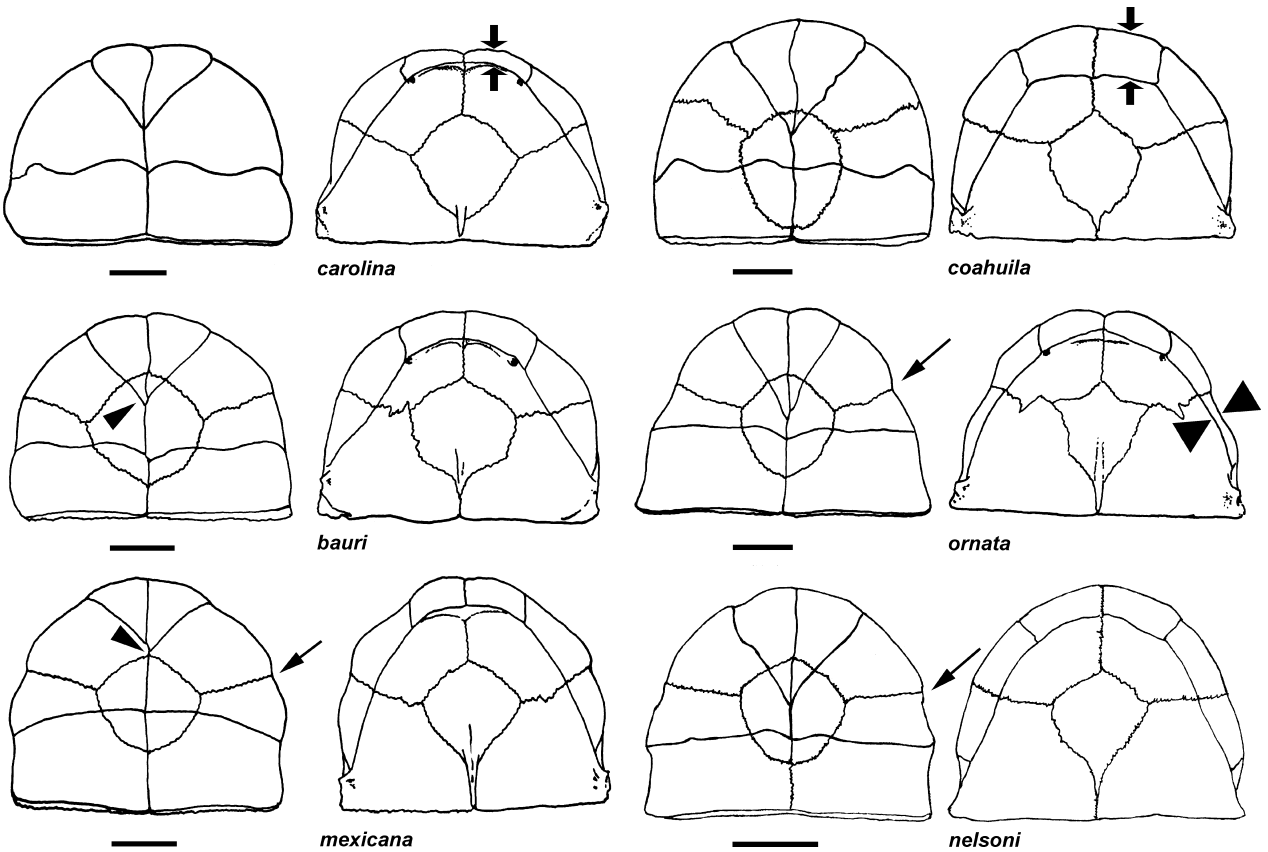


FIG. 3. Anterior plastral lobes of extant *Terrapene*. Ventral (left) and dorsal (right) aspects. Scale bars: 15 mm. *Terrapene carolina carolina*, specimen with externally entirely fused bony seams (MSU 1696, arrows: narrow gular overlap); *Terrapene carolina bauri* (MSU 3825, triangle: gular-humeral seams encroaching entoplastron); *Terrapene carolina mexicana* (MSU 3025, triangle: gular-humeral seams excluded from entoplastron, arrow: lateral notch at juncture of epiplastra and hyoplastra); *Terrapene coahuila* (MSU 4108, arrows: wide gular overlap); *Terrapene ornata ornata* (MSU 3217, arrow: lateral notch at juncture of epiplastra and hyoplastra, triangles: narrow humeral overlap); *Terrapene nelsoni nelsoni* (UMMZ 128400, arrow: lateral notch at juncture of epiplastra and hyoplastra).

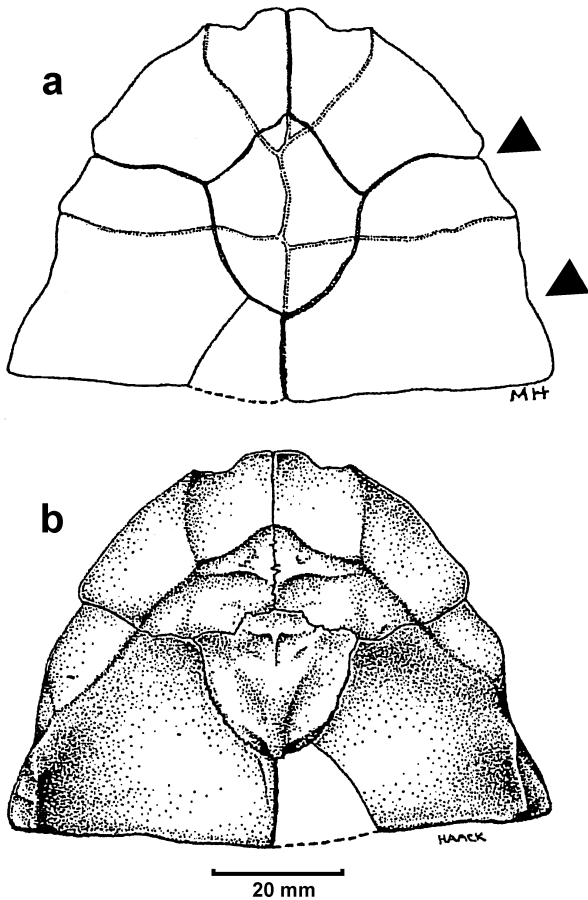


FIG. 4. *Terrapene corneri* n. sp., Myers Farm Local Fauna, near Red Cloud, Webster County, Nebraska; Middle Miocene (Late Barstovian Land Mammal Age, ca 13.0-11.5 million BP). Holotype, plastral forelobe (UNSM 21618): (a) ventral aspect, (b) dorsal aspect. Triangles: humeral and pectoral notches. The humeral notch is at the juncture of epiplastra and hyoplastra. Drawings reproduced from Holman & Corner (1985).

*corneri* may occur sporadically only in *T. coahuila*. *T. corneri* differs from *T. coahuila* significantly in the general shape of the plastral forelobe (*T. corneri*: narrow and anteriorly pointed, humeral and pectoral margin notched; *T. coahuila*: wide and rounded, humeral and pectoral margin not notched). *T. corneri* is similar to most *T. ornata* and the two sole *T. nelsoni* and *T. carolina mexicana* specimens studied and differs from all other *Terrapene* in having lateral notches in the anterior plastral lobe on the epiplastral and hyoplastral juncture, i. e., on the humeral margin. *T. ornata* and *T. nelsoni* differ from *T. corneri* by the ventrally more rounded entoplastron and their deep encroachment of the gular-humeral seams on the entoplastron. The single *T. carolina mexicana* studied differs from *T. corneri* in that the gular-humeral sulci are excluded from the entoplastron in *T. c. mexicana*.

*Description of the Holotype (modified from Holman & Corner, 1985).* The elongated holotype anterior plastral lobe implies that the plastron is ovoid in shape. The length of the forelobe is approximately 60 mm, the width 85 mm. It has a small, but distinct epiplastral beak

produced by the encroachment of two notches on the anterior edge of the epiplastron (margin of gular scutes). The anterior borders of these notches are slightly sinuate. There is also a lateral notch on each side of the anterior part of the lobe at the juncture of the epiplastral and hyoplastral bones (margin of humeral scutes) and at the medial hyoplastral margin (margin of pectoral scutes); these notches are very broadly V-shaped. In ventral view, the gular scute impressions form a triangle with the apex of the triangle directed posteriorly. The apex of the triangle enters the anterior part of the entoplastral bone. Each of the humeral scute impressions is roughly triangular with the apices of the triangles directed posteromedially. The median contacts between the gular and humeral scutes are about equal in length. The median contact between the humeral scutes extends about two-thirds the length of the entoplastron. The pectoral scutes are rectangular in shape. The anterior part of their median contact extends to about the posterior one-third of the length of the entoplastron. The epiplastral bones are very roughly triangular in shape, with the apices of these triangles directed anteromedially. The entoplastron is very roughly ovoid, with the anterior one-third forming a triangular apex anteriorly and the posterior two-thirds forming a roughly triangular apex extending posteriorly. About the anterior one-sixth of the bone is encroached by the gular-humeral sulci which are directed anteromedially; and about the posterior one-third of the bone is encroached by the humeral-abdominal sulci which are at right angles to the median axis of the bone. The postero-medial corner of the right hyoplastron is broken just below the entoplastron. There is no dorsal projection of the hinge line over the ventral portion of the hinge line.

In dorsal (visceral) view, the shell bones have about the same general shape and relationships to one another, except that in this view the entoplastron is roughly triangular in shape with its apex directed posteriorly. This allows a median contact between the epiplastral bones for almost their entire lengths. The basal portion of a ventrally posteriorly projecting spike is present, the anterior portion of the spike obviously having been broken off during the breakage in the posterior part of the lobe. A shallow but well developed depression in the dorsal surface of each epiplastron corresponds to the area for the insertion of the cervico-plastral ligament (aponeural cavity). The raised areas covered by gular and humeral scute overlap in life are wide. The articulation of the bridge is very robust.

*Comparison with other taxa.* A comparison with plastral forelobes of recent *Terrapene* leads to an estimated carapacial length of approximately 150-160 mm for the *Terrapene corneri* holotype. This is a size typical for most recent *Terrapene* taxa. In old adults of recent *Terrapene* species the bony seams of the shell are barely discernible on the shell surface due to a synostotical fusion of the sutures. This is illustrated in Fig. 3 for a *Terrapene carolina carolina* specimen (MSU 1696). In the *T. corneri* holotype all sutures on the anterior

plastral lobe are well developed externally (Fig. 4), suggesting either a character state like most other emydines (that may be interpreted as plesiomorphic) or a subadult or young adult specimen.

The holotype of *T. corneri* does not resemble what might be called a "characteristic" *Terrapene* anterior plastral lobe. Corner (1977) succinctly stated this in reference to UNSM 21618, "Fossil turtles are common throughout the Tertiary of the Great Plains; most can readily be assigned to modern genera but such is not the case for an unusual form collected from Early Valentinian deposits near Red Cloud (UNSM Coll. Loc. Wt-15A), Webster County, Nebraska".

Holman & Corner (1985) compared UNSM 21618 in detail with other taxa and presented convincing arguments for assigning it to *Terrapene*. We will not repeat their comparison with Asian box turtles (*Cuora*, family Geoemydidae) here, but wish to emphasize that in the emydine genera *Emys* and *Emydoidea*, the humeral-pectoral sulcus is either entirely excluded from or barely entering the posterior part of the entoplastron, whereas in *Terrapene* the area is markedly encroached by this sulcus (Holman & Corner, 1985; Holman & Fritz, 2001). According to Holman & Corner (1985), UNSM 21618 resembles the extant *T. coahuila* in two characters which were not observed in other recent species: (1) The very wide areas where the gular and humeral scutes overlap the dorsal surface of the plastron, and (2) the large bridge articulations of the posterolateral portion of each side of the anterior plastral lobe.

A comparison of the plastral forelobe of *T. corneri* with recent *Terrapene* species follows (Fig. 3). The general shape of the *T. corneri* forelobe resembles a few *T. ornata* in that it is narrow and anteriorly somewhat pointed. In most *T. ornata* and all other taxa, the plastral forelobe has a more rounded appearance. In *T. corneri* the plastral margin is notched on the humeral margin at the borderline between the epiplastra and hyoplastra. A further notch occurs on each side on the pectoral margin. The same character state is found in most *T. ornata*. In a *T. n. nelsoni* (UMMZ 128400) the condition is similar to *T. ornata* and *T. corneri*. The forelobe is not emarginated there in *T. coahuila* and is not or is only feebly emarginated in most *T. carolina*. However, in our sole *T. carolina mexicana* (MSU 3925) there is a notch at the epiplastral-hyoplastral juncture, like in *T. ornata*, *T. nelsoni*, and *T. corneri*. If the margin of the anterior lobe is notched in the other comparative material of *T. carolina*, the emarginations are confined to the seam between humeral and pectoral scutes, not to the borderline between epiplastra and hyoplastra. The entoplastron of *T. corneri* is elongated, and on the dorsal (visceral) side escutcheon-shaped. Ventrally, its anterior portion is somewhat acutely triangular; the gular-humeral seams encroach the entoplastron only moderately. In *T. carolina* the entoplastron is wide and generally broadly diamond-shaped in dorsal aspect. Ventrally, it is broadly octagonal to round and its anterior portion is only infrequently triangular; and if so, it is

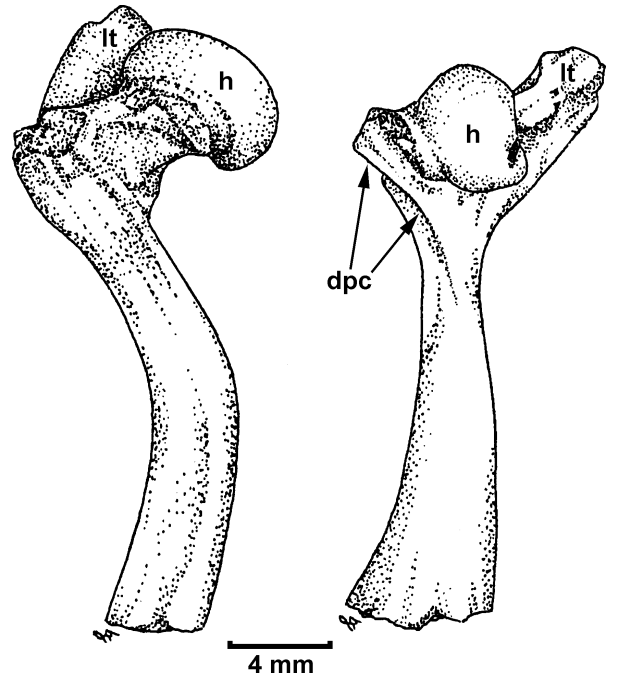


FIG. 5. *Terrapene* cf. *carolina* from the WaKeeney Local Fauna, Trego County, Kansas; Late Miocene (Middle to Late Clarendonian Land Mammal Age, ca 10.0-9.0 million BP). Left humerus (MSUVP 775), distal articulation destroyed. Abbreviations: h, head; lt, lateral tubercle (greater tuberosity); dpc, deltopectoral crest.

wide-angled. As in *T. corneri*, the gular-humeral seams only moderately encroach the entoplastron. In our *T. carolina mexicana* specimen, however, the gular-humeral sulci are excluded from the entoplastron. Compared with *T. carolina*, the entoplastron in *T. coahuila* may be somewhat more elongated. Otherwise the character states found *T. coahuila* are similar to *T. carolina*. In *T. ornata*, and the sole plastral forelobe of *T. n. nelsoni* studied by us, the entoplastron is rounded in ventral aspect and dorsally diamond-shaped. In contrast to *T. corneri*, *T. coahuila*, and *T. carolina*, the gular-humeral seams encroach deeply onto the entoplastron in *T. ornata* and *T. n. nelsoni*.

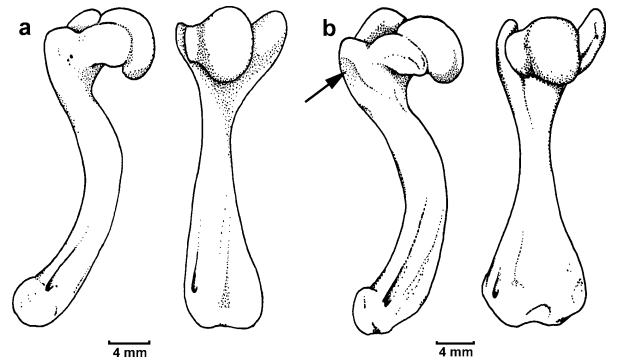


FIG. 6. Left humeri of (a) extant *Terrapene carolina carolina* (MSU 14439) and (b) extant *Terrapene ornata ornata* (MSU 3217). Arrow indicating the concavity formed by the deltopectoral crest in *T. ornata*.

Among the recent *Terrapene* taxa, *T. coahuila* resembles *T. corneri* in that one of five *T. coahuila* specimens studied has an epiplastral beak similar to *T. corneri*. Also, only *T. coahuila* has a wide gular and humeral overlap as observed in *T. corneri*. However, the general shape of the plastral forelobe differs significantly in both species: In *T. coahuila*, the forelobe is wide and rounded; in *T. corneri* it is narrow and anteriorly pointed (cf. Figs. 3 and 4). A further similarity between *T. corneri* and *T. coahuila* is the strong articulation of the bridge. On the other hand, the elongated shape of the *T. corneri* anterior plastral lobe is similar to some *T. ornata*, and the plastral notches at the borderline between epiplastra and hyoplastra in *T. corneri* resemble the condition found in *T. ornata*, *T. nelsoni*, and the sole *T. carolina mexicana* specimen studied. Thus, characters of several distinct recent taxa seem to be combined in *T. corneri*.

*TERRAPENE* CF. *CAROLINA* (LINNAEUS, 1758) (FIG. 5)

**Material.** A nearly complete left humerus, MSUVP 775 from the WaKeeney Local Fauna (UM-K6-59), Trego County, Kansas; Late Miocene (Middle to Late Clarendonian Land Mammal Age, ca 10.0-9.0 million BP).

**Identification.** This left humerus has been assigned to *Terrapene* cf. *carolina* by Holman (1975). Here we compare it with additional material of recent box turtles. The humerus is readily identifiable as *Terrapene* in having a compressed rather than a rounded head, a lateral tubercle that is directed more upward than outward, a deltopectoral crest that is directed more upward than inward, a moderately narrow excavation between the lateral tubercle and the deltopectoral crest, and a dorsoventrally bowed shaft. The humerus resembles the living species *T. carolina* and *T. coahuila* rather than *T. ornata* and *T. nelsoni* on the basis of what we believe is a strong character. In medial view in *T. carolina* and *T. coahuila*, the dorsolateral border of the deltopectoral crest is flat and the posterior portion of this crest is produced as a knob (also known as the minor tuberosity), whereas in *T. ornata* and *T. nelsoni* the dorsolateral border of the deltopectoral crest is concave and the posterior portion of the crest is produced upward as a knob (Fig. 6). The fossil is similar to *T. carolina* and *T. coahuila* in this character, but the crest is more expanded laterally than in either of the living species.

Parenthetically, we note that humeri of recent *T. carolina* and *T. coahuila* appear more slender than in *T. ornata* and *T. nelsoni* because in the latter the proximal and distal articulations are relatively broader. In *T. ornata* in particular, the lateral tubercle is stronger than in *T. carolina* and reflected somewhat inward. The fossil humerus resembles *T. carolina* in that its shaft appears more slender than in *T. ornata* and in that its greater tuberosity is not inwardly reflected.

The Clarendonian *Terrapene* hyoplastron from the Ash Hollow Formation of Cherry County, Nebraska

mentioned by Hutchison (1981) was unfortunately not available to us.

## DISCUSSION

We record the earliest known *Terrapene* as *T. cf. ornata* from the Middle Miocene (Medial Barstovian NALMA, ca 14.5-13.0 million BP) Egelhoff Site, in northwest Nebraska. The oldest record of *T. ornata* is of the extinct subspecies *T. ornata longinsulae* Hay, 1908 from the Late Miocene (Clarendonian, ca 11.5-9.0 million BP). Fossils from several Pliocene sites have been attributed to the same taxon (Milstead, 1969). The Egelhoff *T. cf. ornata* nuchals resemble *T. o. longinsulae* in representing small box turtles (maximum carapace length of *T. o. longinsulae* 125 mm in known specimens; Milstead, 1969). Based on a comparison with modern adult *T. o. ornata* from Trego County, Kansas, the fossil nuchal MSUVP 809A represents a box turtle with a straight line carapace length of approx. 95 mm and the fossil nuchal MSUVP 809B represents a specimen with a carapace length of approx. 75 mm. The left hyoplastron UNSM 122393 corresponds in size to extant *T. o. ornata* with a ca 100 mm straight line carapacial length. Obviously the two nuchal bones and the left hyoplastron do not represent an adequate sample, but the possibility remains that the Middle Miocene *T. cf. ornata* might have been even smaller than the Late Miocene *T. o. longinsulae*.

Milstead (1969) reports that *T. o. longinsulae* have smooth shells that differ from the rugose shells of modern *T. ornata*. The two Middle Miocene nuchals are both dorsally smooth and lack the distinct narrow keels that occur in modern *T. ornata* nuchals. This may indicate close relationships between the two forms. Nevertheless, we hesitate to assign the two nuchal bones to the extinct subspecies because of the lack of other shell elements.

Beside the left hyoplastron from the Stewart Quarry described herein, two other emydine turtles have been identified from this site, a *Chrysemys* species (Holman, 2002) and an extinct *Glyptemys* (Holman & Fritz, 2001), *G. valentinensis*. Other herpetofaunal remains have not been published from this site. It is assumed that the climate was similar during the deposition of the fauna at the Stewart Quarry as at other nearby Middle and Late Barstovian riparian faunas in north-central Nebraska which probably existed in a subtropical or at least equable, dry grassland habitat (Voorhies, 1990; J. A. Holman, unpubl.). Such conditions probably existed also at the Egelhoff Site in the Medial Barstovian.

The relationships of *Terrapene corneri* from the Middle Miocene (Late Barstovian) Myers Farm Local Fauna in southeastern Nebraska are uncertain. Some characters of *T. corneri* clearly resemble the recent *T. coahuila*, namely the very wide gular and humeral overlap and the strong hyoplastral bridge articulations. But it is also noteworthy that the entoplastron of *T. corneri* is elongated, and that among the recent species, only *T.*

*coahuila* has a somewhat elongate entoplastron. In addition, an epiplastral beak similar to that of *T. corneri* is presently known to occur sporadically only in *T. coahuila*. It has been often hypothesized that *T. coahuila* is the most ancestral form among the recent *Terrapene* species (Auffenberg, 1958; Legler, 1960; Burke *et al.*, 1996). Williams *et al.* (1960) and Bramble (1974) even suggested it was ancestral to the entire genus. However, new analyses of morphological (Minx, 1996) and molecular data sets (Feldman & Parham, 2002) have provided convincing evidence that *T. coahuila* is more closely related to *T. carolina* than to *T. nelsoni* or *T. ornata*, as earlier suggested by Milstead (1967, 1969) and Milstead & Tinkle (1967).

According to the morphological similarities mentioned above, one could speculate that *T. coahuila* is a descendent of *T. corneri*. If this is the case, *T. corneri* would represent the oldest record for the *carolina* group of *Terrapene*. On the other hand, notches at the sutures between the epiplastra and hyoplastra, as in *T. corneri*, do not occur in *T. coahuila* (and *T. carolina*, with the exception of *T. c. mexicana*) but they do in both species of the *ornata* group (*T. nelsoni*, *T. ornata*). Also the elongated shape of the *T. corneri* plastral forelobe is similar to some *T. ornata*. Thus, the Late Barstovian *T. corneri* appears to have morphological characters of both recent species groups. However, *T. corneri* is too young for being the last common ancestor of both groups as the Medial Barstovian Egelhoff Fauna fossils resemble the extant *T. ornata*. Therefore, we cannot exclude that *T. corneri* is a dead end lineage within *Terrapene*, perhaps representing the sister taxon of a clade containing the recent *carolina* and *ornata* groups.

Parenthetically, the considerable number of distinctive characters of our sole *T. carolina mexicana* anterior plastral lobe (MSU 3025) could support the recent suggestion of Stephens & Wiens (2003) that *mexicana* represents a distinct species rather than a subspecies of *T. carolina*. There is no obvious subspecies-specific variation among the specimens of other *T. carolina* subspecies studied by us. However, as we cannot exclude the possibility that the observed differences in our *mexicana* specimen are only individual aberrations, an investigation involving more osteological *mexicana* material is highly warranted.

In contrast to *T. cf. ornata* from the Middle Miocene (Medial and Late Barstovian) of northern Nebraska that existed in a semitropical or equable but dry grassland situation, *T. corneri* from the Late Barstovian Myers Farm Local Fauna of southeastern Nebraska lived in a moister, tropical to subtropical situation. The Myers Farm mammalian fauna differs from those of similar age in north-central Nebraska in consisting of fewer open-plains species and also has more southern species such as the artiodactyls *Prosynthetoceras* sp., *Longirostromeryx blicki* and *Pseudoparablastomeryx francesita*. Moreover, the perissodactyls also differ in that there is a decidedly higher frequency of low-crowned anchitherine horses (Corner, 1976) and tapirs (Schultz *et al.*,

1975) at Myers Farm than in the north-central Nebraska sites. The absence of the zapodid genus *Megasmithus*, the almost total lack of heteromyids, and an abundance of cricetid rodents are also distinct from north-central Nebraska where *Megasmithus* and various heteromyid species dominate the rodent fauna (Korth, 1979, 1980). Turning to the reptile fauna, one finds an undetermined trionychid, an undetermined emydid, *Terrapene corneri*, a giant and a smaller species of the tortoise, *Hesperotestudo*, as well as the alligator snapping turtle, *Macrochelys* sp. and two extinct boid snakes, seven colubrid snakes, an elapid and a viperid snake (Holman, 1977; Holman & Corner, 1985). It has long been suggested that the presence in fossil fauna of large land tortoises of the genus *Hesperotestudo* (long referred to as "*Geochelone*") suggests a climate with very mild winters where temperatures seldom if ever dropped to freezing (e. g. Hibbard, 1960). Considering the mammalian and herpetofauna of the Myers Farm locality, together, it seems likely that the climate in which all of these animals lived must have been at least as mild as that of the Gulf Coastal Plain of the United States today, and that winters were perhaps even milder.

The Clarendonian humerus from the WaKeeney Local Fauna (Trego County, Kansas), which is already discussed by Holman (1975), is the oldest *Terrapene* that we are aware of that resembles extant *T. carolina*. The second oldest one is from the latest Miocene McGeehee Site, Alachua County, Florida (Early Hemphillian, ca 8.5 million BP). It was tentatively assigned to *T. carolina putnami* (Milstead, 1969). Unfortunately, the taxonomic allocations of the Clarendonian *Terrapene* hyoplastron from the Ash Hollow Formation of Cherry County, Nebraska mentioned by Hutchison (1981) and of two Late Hemphillian nuchals from Knox County, Nebraska (Parmley, 1992) are unknown.

The *Terrapene* fossils discussed here emphasize that extant emydid turtle genera already existed in the Barstovian. Beside the *Terrapene* findings, the emydid genera *Emydoidea* (Hutchison, 1981; Holman, 1995, 2002) and *Glyptemys* (Holman & Fritz, 2001) are known from this Land Mammal Age. This suggests that the modern emydid turtle genera evolved distinctly earlier. Some of the Barstovian *Terrapene* fossils resemble *T. ornata*. Therefore, it is likely that the extant species groups of *Terrapene* were already established in that time and that the genus is distinctly older than the Middle Miocene.

#### ACKNOWLEDGEMENTS

Thanks go to the University of Michigan Museum of Zoology and the University of Nebraska State Museum for loaning specimens. Laura Abraczinskas (Michigan State University Museum) made MSU *Terrapene* available to U. Fritz. M. Delfino, C. H. Ernst and an anonymous reviewer provided helpful comments on the manuscript.



## REFERENCES

- Auffenberg, W. (1958). Fossil turtles of the genus *Terrapene* in Florida. *Bulletin of the Florida State Museum* **3**, 53-92.
- Bramble, D. M. (1974). Emydid shell kinesis: biomechanics and evolution. *Copeia* **1974**, 707-727.
- Burke, R. L., Leuteritz, T. E. & Wolf, A. J. (1996). Phylogenetic relationships of emydine turtles. *Herpetologica* **52**, 572-584.
- Corner, R. G. (1976). *An early Valentinian vertebrate local fauna from southern Webster County, Nebraska*. Lincoln: M.S. Thesis, University of Nebraska.
- Corner, R. G. (1977). An unusual fossil turtle from the early Valentinian of Nebraska. *Proceedings of the Nebraska Academy of Sciences* **87**, 40.
- Dodd, C. K. (2001). *North American Box Turtles. A Natural History*. Norman: University of Oklahoma Press.
- Ernst, C. H., Lovich, J. E. & Barbour, R. W. (1994). *Turtles of the United States and Canada*. Washington, D. C. and London: Smithsonian Institution Press.
- Ernst, C. H., Wilgenbusch, J. C., Boucher, T. P. & Sekscienski, S. W. (1998). Morphometrics of the fossil box turtle, *Terrapene innoxia* Hay, 1916, from Florida. *Chelonian Conservation and Biology* **2**, 603-607.
- Feldman, C. R. & Parham, J. F. (2002). Molecular phylogenetics of emydine turtles: taxonomic revision and the evolution of shell kinesis. *Molecular Phylogenetics and Evolution* **22**, 388-398.
- Fritz, U. (2003). *Die Europäische Sumpfschildkröte*. Bielefeld: Laurenti Verlag.
- Gaffney, E. S. & Meylan, P. A. (1988). A phylogeny of turtles. In *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*, 157-219. Benton, M. J. (Ed). Oxford: Clarendon Press.
- Hay, O. P. (1908a). *The Fossil Turtles of North America*. Washington, D. C.: Carnegie Institute of Washington, Publication No. 75.
- Hay, O. P. (1908b). Descriptions of five species of North American fossil turtles, four of which are new. *Proceedings of the U.S. National Museum* **35**, 161-169.
- Hay, O. P. (1916). Descriptions of some Floridian fossil vertebrates, belonging mostly to the Pleistocene. *Florida State Geological Survey, Annual Report* **8**, 40-76.
- Hibbard, C. W. (1960). Pliocene and Pleistocene climates in North America. *Annual Report, Michigan Academy of Science, Arts and Letters* **62**, 5-30.
- Holman, J. A. (1965). A huge Pleistocene box turtle from Texas. *Quarterly Journal of the Florida Academy of Science* **28**, 345-238.
- Holman, J. A. (1975). Herpetofauna of the WaKeeney Local Fauna (Lower Pliocene: Clarendonian) of Trego County, Kansas. *University of Michigan Papers on Paleontology* **12**, 49-66.
- Holman, J. A. (1977). Upper Miocene snakes (Reptilia, Serpentes) from southeastern Nebraska. *Journal of Herpetology* **11**, 323-335.
- Holman, J. A. (1987). Herpetofauna of the Egelhoff Site (Miocene: Barstovian) of north-central Nebraska. *Journal of Vertebrate Paleontology* **7**, 109-120.
- Holman, J. A. (1995). A new species of *Emydoidea* (Reptilia: Testudines) from the Late Barstovian (Medial Miocene) of Cherry County, Nebraska. *Journal of Herpetology* **29**, 548-553.
- Holman, J. A. (2002). The status of *Emydoidea hutchisoni* Holman, 1995. *Michigan Academician* **34**, 393-394.
- Holman, J. A. & Clausen, C. (1984). Fossil vertebrates associated with Paleo-Indian artifact at Little Salt Spring, Florida. *Journal of Vertebrate Paleontology* **4**, 146-154.
- Holman, J. A. & Corner, R. G. (1985). A Miocene *Terrapene* (Testudines: Emydidae) and other Barstovian turtles from south-central Nebraska. *Herpetologica* **41**, 88-93.
- Holman, J. A. & Fritz, U. (2001). A new emydine species from the Middle Miocene (Barstovian) of Nebraska, USA with a new generic arrangement for the species of *Clemmys* sensu McDowell (1964). *Zoologische Abhandlungen, Museum für Tierkunde Dresden* **51**, 331-353.
- Hulbert, R. C. (2001). Florida fossil vertebrates. In *The Fossil Vertebrates of Florida*, 25-33. Hulbert, R. C. (Ed). Gainesville: University Press of Florida.
- Hutchison, J. H. (1981). *Emydoidea* (Emydidae, Testudines) from the Barstovian (Miocene) of Nebraska. *PaleoBios* **37**, 1-6.
- Korth, W. W. (1979). Geomyoid rodents from the Valentine Formation of Knox County, Nebraska. *Annals of Carnegie Museum* **48**, 287-310.
- Korth, W. W. (1980). Cricetid and zapodid rodents from the Valentine Formation of Knox County, Nebraska. *Annals of Carnegie Museum* **49**, 307-322.
- Legler, J. M. (1960). Natural history of the ornate box turtle, *Terrapene ornata ornata* Agassiz. *University of Kansas Publications, Museum of Natural History* **11**, 527-669.
- Milstead, W. W. (1967). Fossil box turtles (*Terrapene*) from central North America, and box turtles from eastern Mexico. *Copeia* **1967**, 168-179.
- Milstead, W. W. (1969). Studies on the evolution of box turtles (genus *Terrapene*). *Bulletin of the Florida State Museum* **14**, 1-113.
- Milstead, W. W. & Tinkle, D. W. (1967). *Terrapene* of western Mexico, with comments on the species groups in the genus. *Copeia* **1967**, 180-187.
- Minx, P. (1996). Phylogenetic relationships among the box turtles, genus *Terrapene*. *Herpetologica* **52**, 584-597.
- Parmley, D. (1992). Turtles of the Late Hemphillian (latest Miocene) of Knox County, Nebraska. *Texas Journal of Science* **44**, 339-348.
- Schultz, C. B., Martin, L. D. & Corner, R. G. (1975). Middle and late Cenozoic tapirs from Nebraska. *Bulletin of the University of Nebraska State Museum* **10**, 1-21.

- Stephens, P. R. & Wiens, J. J. (2003). Ecological diversification and phylogeny of emydid turtles. *Biological Journal of the Linnean Society* **79**, 577-610.
- Voorhies, M. R. (1990). *Vertebrate paleontology of the proposed Norden Reservoir area, Brown, Cherry, and Keya Paha Counties, Nebraska*. Lincoln: Division of Archaeological Research, Department of Anthropology, University of Nebraska.
- Williams, E. E., Smith, H. M. & Chrapliwy, P. S. (1960). Turtles and lizards from northern Mexico. *Transactions of the Illinois Academy of Sciences* **53**, 36-45.
- Wilson, R. L. (1968). Systematics and faunal analysis of a lower Pliocene assemblage from Trego County, Kansas. *Contributions from the Museum of Paleontology, University of Michigan* **22**, 75-126.

Accepted: 29.1.04