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A new emydine species from the Medial Miocene (Barstovian) of Nebraska, USA with a new generic arrangement for the species of **Clemmys** sensu McDowell (1964) (Reptilia: Testudines: Emydidae)

With 11 figures

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Kurzfassung. Eine neue Emydinen-Art aus dem Mittel-Miozän (Barstovian) von Nebraska, USA, mit einer neuen Gattungseinteilung für die Arten von Clemmys sensu McDowell (1964) (Reptilia: Testudines: Emydidae). - Aufgrund der eindeutigen Paraphylie der Gattung *Clemmys* sensu McDowell (1964) wird vorgeschlagen, das Genus *Clemmys* RITGEN, 1828 auf die Typusart *Clemmys* guttata (SCHNEIDER, 1792) zu beschrän-ken. *Clemmys marmorata* (BAIRD & GIRARD, 1852), die Emydinen mit Plastralscharnier nähersteht als den bisher mit marmorata in der Gattung *Clemmys* zusammengefassten Arten mit starrem Plastron, wird als Vertreter der monotypischen Gattung Actinemys AGASSIZ, 1857 betrachtet. Clemmys insculpta (LE CONTE, 1830 [1829]) und Clemmys muhlenbergii (SCHOEPFF, 1801) werden als Angehörige einer weiteren distinkten Gattung eingestuft, für die der Name Glyptemys AGASSIZ, 1857 (Species typica: Testudo insculpta LE CONTE, 1830 [1829] = Glyptemys insculpta) gewählt wird. Dadurch erhält dieser Name Vorrang vor dem für Testudo muhlenbergii SCHOEPFF, 1801 errichteten Gattungsnamen Caleny's AGASSIZ, 1857. – Glyptemys valentinensis n. sp. wird anhand von umfangreichem Fundmaterial aus Nebraska (USA) beschrieben. Mit dieser neuen Art ist die Gattung Glyptemys seit dem Mittel-Miozän bekannt (mittleres bis oberes Barstovian: ca. 14,5-11,5 Mio. Jahre vor heute). Morphologisch ähnelt Glyptemys valentinensis der rezenten Glyptemys insculpta mehr als G. muhlenbergii. Es wird vermutet, dass sich G. insculpta aus G. valentinensis zwischen dem oberen Barstovian und dem oberen Hemphillian (11,5-5,5 Mio. Jahre vor heute) entwickelt hat. G. valentinensis könnte der letzte gemeinsame Vorfahre von G. insculpta und G. muhlenbergii sein, da Sequenzdaten des mitochondrialen Cytochrom b-Gens für eine Differenzierung beider Taxa genau im mittleren Barstovian (vor ca. 14,5 Millionen Jahren) sprechen.

Abstract. As there is convincing evidence for a paraphyly of the genus *Clemmys* sensu MCDOWELL (1964), it is suggested that *Clemmys* RITGEN, 1828 be restricted to its type species, Clemmys guttata (SCHNEIDER, 1792). Clemmys marmorata (BAIRD & GIRARD, 1852), a species more closely related to emydine taxa with a hinged plastron than to other species with nonhinged plastra previously referred to Clemmys, is treated as a member of the monotypic genus Actinemys AGASSIZ, 1857. Clemmys insculpta (LE CONTE, 1830 [1829]) and Clemmys muhlenbergii (SCHOEPFF, 1801) are regarded as representing another distinct ge-nus for which the name Glyptemys AGASSIZ, 1857 (species typica: Testudo insculpta LE CONTE, 1830 [1829] = Glyptemys insculpta) is given precedence over Calemys AGASSIZ, 1857, erected for Testudo muhlenbergii SCHOEPFF, 1801. – Based on a large amount of fos-sil material from Nebraska (USA), Glyptemys valentinensis n. sp. is described. With this new species, the genus Glyptemys is now known from the Middle Miocene (Medial to Late

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Barstovian: ca 14.5-11.5 Ma BP) to modern times. Glyptemys valentinensis is morphologically more similar to Glyptemys insculpta than to G. muhlenbergii. It is suggested that G. valentinensis gave rise to G. insculpta between Late Barstovian and Late Hemphillian times (11.5-5.5 Ma BP). As sequence data of the mitochondrial cytochrome b gene argue for a differentiation of G. insculpta and G. muhlenbergii exactly in Medial Barstovian times (ca 14.5 Ma BP), G. valentinensis could be the last common ancestor of G. insculpta and G. muhlenbergii.

Key words. Reptilia, Testudines, Emydidae, Clemmys, Actinemys marmorata, Clemmys guttata, Glyptemys insculpta, Glyptemys muhlenbergii n. comb., Glyptemys valentinensis n. sp., Medial Miocene, Barstovian, North America, USA, Nebraska.

Introduction

The fossil record of emydine turtles from the Medial Miocene has previously yielded substantial information only on the genera *Emydoidea* and *Terrapene* (HUTCHISON, 1981; HOL-MAN & CORNER, 1985; HOLMAN, 1987, 1995). In this study, we have been fortunate to have been able to study excellent fossil material of a new emydid species from the Barstovian Land Mammal Age (Middle Miocene) of Nebraska.

We refer the fossil species to the subfamily Emydinae and the genus *Clemmys* sensu MC-DOWELL (1964) for the following reasons:

- Palatine excluded from triturating surface (diagnostic for subfamily Emydinae; GAFFNEY & MEYLAN, 1988).
- (2) Humeropectoral sulcus crossing entoplastron (in the second subfamily Deirochelyinae, excluded from entoplastron; GAFFNEY & MEYLAN, 1988).
- (3) Rigid plastron with well developed bony bridge and plastral buttresses (in all other genera of the subfamily except *Clemmys* a plastral hinge is present and the bony bridge and plastral buttresses are strongly reduced or lacking; McDowell, 1964; BRAMBLE, 1974; GAFFNEY & MEYLAN, 1988; FRITZ, 2001).

In North America a few pre-Pleistocene fossils have been doubtfully referred to *Clemmys* (e. g. "*Clemmys*" morrisiae HAY, 1908 or "*C*." backmani RUSSEL, 1934) and do not compare well with modern species of the genus (sensu McDowell, 1964; cf. ESTES & HUTCHISON, 1980). The Upper Miocene *Clemmys saxea* HAY, 1903 is based on extremely fragmentary material, a pygal and a posterior peripheral (see figure 366 and plate 45 in HAY, 1908), and its allocation to *Clemmys* sensu McDowell, 1964 is doubtful.

Several Pliocene *Clemmys marmorata* finds have been recorded and a closely related or identical fossil species (*Clemmys hesperia* HAY, 1903) is known from the Pliocene of the Rattlesnake Beds of Rattlesnake Creek (BRATTSTROM & STURN, 1959; BURY, 1970; BURY & ERNST, 1977; GUSTAFSON, 1978; SMITH & SMITH, 1980). Another species closely resembling *Clemmys marmorata, Clemmys owyheensis* BRATTSTROM & STURN, 1959, was described from Hemphillian deposits of Dry Creek, a tributary of Crooked Creek near Rome, Malheur County, Oregon. It is also known from the Upper Pliocene near Hagerman, Twin Falls County, Idaho (ZUG, 1969). Recently a perfectly preserved shell of *Clemmys insculpta* was discovered in beds of the latest Miocene. This specimen is from east-central Nebraska and represents Late Hemphillian times (S. TUCKER personal communication).

The content of *Clemmys*

Regarding Recent species, the genus *Clemmys* has been taxonomically stable since McDo-WELL (1964), containing four species, namely (in alphabetical order): *Clemmys guttata* (SCHNEIDER, 1792), *Clemmys insculpta* (LE CONTE, 1830 [1829]), *Clemmys marmorata* (BAIRD & GIRARD, 1852), and *Clemmys muhlenbergii* (SCHOEPFF, 1801). However, new molecular data (BICKHAM et. al., 1996; BURKE et al., 1996; LENK et al., 1999), based on sequence data of a mitochondrial marker genes (16S ribosomal RNA gene, cytochrome b gene) provide convincing evidence that *Clemmys* is a paraphyletic assemblage of species, *C. gut-tata* probably being an early side branch and the sister group of all or at least nearly all other Emydinae. On the other hand, *C. marmorata* seems to be more closely related to emydines with a hinged plastron, particularly *Emys orbicularis* and *Emydoidea blandingii*, than to its "congeners" with a rigid plastron. It is noteworthy that the genus *Clemmys* sensu MCDOWELL (1964) was thought to have a basal position within the Emydinae (BRAMBLE, 1974) and was characterized by plesiomorphic rather than synapomorphic traits (cf. BRAMBLE, 1974; BURY & ERNST, 1977; GAFFNEY & MEYLAN, 1988; BURKE et al., 1996), especially the rigid plastron, the solid bony bridge, and the lack of a scapular suspensorium in the sense of BRAMBLE (1974).

BURKE et al. (1996) have speculated on taxonomic and nomenclatural changes that must result from the well substantiated paraphyly of *Clemmys*. They considered combining nearly all taxa (except *Clemmys insculpta* and *C. muhlenbergii*) of the subfamily Emydinae into *Emys* A. DUMÉRIL, 1806, the genus with the oldest available name. However, such a model would mask clear-cut monophyla within the Emydinae (especially the long recognized genus *Terrapene* with four species) and would combine morphologically and ecologically extremely distinct taxa. We present a more conservative generic arrangement as follows.

In all cladograms derived from molecular data, *Clemmys marmorata* is closer to the genera *Emys* and *Emydoidea* (taxa that have a plastral hinge) than to the hingeless *Clemmys guttata*, *C. insculpta*, and *C. muhlenbergii* (see the review in FRITZ, 2001). A justifiable hypothesis then is that the hingeless plastron of *C. marmorata* is in reality a secondary character and that the forerunners of this species once had hinged plastra (BURKE et al., 1996; FRITZ, 2001). This is attested to by the fact that the bony/horny seams on the bridge are still aligned in *C. marmorata* in a similar way to the hinged species, but unlike all other nonhinged species where the horny seams between pectorals and abdominals and submarginals are located on the hyo- and hypoplastra (see below). The most parsimonious nomenclatorial way to resolve this situation is to put *C. marmorata* in a monotypic genus to avoid combining hinged and nonhinged species in a single clade. For this genus the name *Actinemys* AGASSIZ, 1857 is available (species typica: *Actinemys marmorata* = *Emys marmorata* BAIRD & GIRARD, 1852).

According to molecular data (BICKHAM et. al., 1996; LENK et al., 1999) *C. guttata* represents an early side branch and the sister group of all or at least nearly all other Emydinae. To avoid too much nomenclatural instability, *C. guttata* should be put in a second monotypic genus, which must bear the name *Clemmys* as *Emys punctata* SCHOEPFF, 1792 = *Testudo guttata* SCHNEIDER, 1792 was designated as type species of *Clemmys* by BAUR (1892).

In all current investigations (BICKHAM et al., 1996; BURKE et al., 1996; LENK et al., 1999) there is consensus that the Recent species *C. insculpta* and *C. muhlenbergii* are closely related and form a monophyletic taxonomic unit. According to the cytochrome *b* data of LENK et al. (1999), the *insculpta-muhlenbergii*-clade is supported by a high bootstrap value of 98 (derived from 500 replicates). Similar high bootstrap values for this group were obtained by BICKHAM et al. (1996) based on sequence data of the mitochondrial 16S ribosomal RNA gene. The fossil to be described here also belongs to this clade and is most similar to the extant *Clemmys insculpta* and to a lesser extent to *C. muhlenbergii*. We refer it together with these two Recent species to the genus *Glyptemys* AGASSIZ, 1857 (species typica: *Glyptemys insculpta* = *Testudo insculpta* LE CONTE, 1830 [1829]). According to the First Reviser Principle (ICZN, 1999: 24.2), we give this name precedence over *Calemys* AGASSIZ, 1857 which was erected simultaneously for *Testudo muhlenbergii* SCHOEPFF, 1801, a species considered here as congeneric.

In the following we give diagnoses for the mentioned genera with unhinged plastron (color and pattern characters excluded):

Clemmys RITGEN, 1828 sensu stricto: Small turtles (shell length up to 12.5 cm) with a more or less smooth, broad, keelless and unserrated carapace. Premaxillary notch lacks adjacent tomiodonts. Foramen carotico-pharyngeale on the level of articular condyles. Alveolar shelf with lateral ridge. Carapacial front with unique opening: gulars forming a distinct, capsule-like groove in which the head fits exactly. Horny seams between submarginals and pectoral and abdominal scutes located on the hyo- and hypoplastra. Entoplastron diamond-shaped to roundish. Xiphiplastral notch moderate (combined from ERNST, 1972a; WARD, 1980; ERNST et al., 1994 and own unpublished data).

Content: Clemmys guttata (SCHNEIDER, 1792).

Actinemys AGASSIZ, 1857: Medium-sized turtles (shell length up to 19.0 cm) with a smooth and low, broad carapace which is widest behind the middle of the shell and usually lacks a keel. Premaxillary notch with adjacent tomiodonts. Foramen carotico-pharyngeale on the level of articular condyles. Alveolar shelf flat. Horny seams between submarginals and pectorals and abdominals on the bridge congruent with the suture between peripheral and hyo- and hypoplastral bones. Entoplastron diamond-shaped to roundish, in *A. owyheensis* and sometimes in *A. marmorata* with a prominent anterior knob. Xiphiplastral notch weak or absent. Free plastral rim, especially on the plastral forelobe, distinctly narrower than in *Clemmys* and *Glyptemys* (combined from BRATTSTROM & STURN, 1959; ZUG, 1969; BURY, 1970; WARD, 1980; ERNST et al., 1994 and own unpublished data).

Content: Actinemys marmorata (BAIRD & GIRARD, 1852): Pliocene to Recent [the Pliocene species Clemmys hesperia HAY, 1903 from Oregon is included into the synonymy of the Recent species by BRATTSTROM & STURN, 1959 and BURY, 1970], Actinemys owyheensis (BRATTSTROM & STURN, 1959): Hemphillian to Upper Pliocene.

Glyptemys AGASSIZ, 1857: Small to medium-sized turtles (shell length 8.0-22.5 cm), with an elongated, keeled carapace which may be serrated posteriorly. Premaxillary notch with adjacent tomiodonts. Foramen carotico-pharyngeale located anteriorly of articular condyles. Alveolar shelf with lateral ridge. Horny seams between submarginals and pectoral and abdominal scutes located on the hyo- and hypoplastra. Entoplastron elongated to bell-shaped. Xiphiplastral notch moderate to well-developed (combined from ERNST, 1972b; ERNST & BURY, 1977; WARD, 1980; ERNST et al., 1994 and own unpublished data).

Content: *Glyptemys insculpta* (LE CONTE, 1830 [1829]): Late Hemphillian to Recent, *G. muhlenbergii* (SCHOEPFF, 1801): Middle to Late Pleistocene (Irvingtonian II, HOLMAN, 1977) to Recent, and the fossil to be described in the following from the Medial to Late Barstovian (Middle Miocene).

Systematic Paleontology

Modern comparative alcoholic and skeletal material for this study has been kindly provided by the Michigan State University Museum (MSU), East Lansing, Michigan, USA, the Natural History Museum (Naturhistorisches Museum) Vienna (NMW), Austria, and the State Museum for Zoology Dresden (Staatliches Museum für Tierkunde Dresden, MTKD), Germany. Most of the fossil specimens described below are in the University of Nebraska State Museum (UNSM), Lincoln, Nebraska, USA. All measurements are in millimeters. Pertinent matters bearing on the recognition and interpretation of the new species of *Glyptemys* follow below.

The Barstovian (Middle Miocene) sites of Nebraska. Most of the Barstovian Sites in Nebraska, including all of the ones yielding the new *Glyptemys* species of our report, come from the northern one-fourth of this elongate state in an area extending almost completely across the state from east to west from about L 98 in the east part of the state to L 102 in the west, a distance of about 350 kilometers. These sites are all associated with the Nio-

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brara River and its tributaries (see fig. on p. 87 in VOORHIES, 1990). The Niobrara River itself is today, as it also was in the Miocene, a braided stream which occupies a very broad channel that shifts back and forth in a very wide river bed. Such braided streams provide excellent places for the accumulation of vertebrate fossils, not only in the isolated oxbow ponds that form from time to time during storms, but in river channel situations that change rapidly from high energy to low energy depositional environments.

Turning to the time lines in this paper, the concept in North America is that the Miocene extends from about 24 million to about 5 million years before the present (BP). The Miocene begins in the later part of the Arikareean Land Mammal Age and lasts until the end of the Hemphillian. These Land Mammal Ages are as follow (HULBERT, 2001) [older to younger from bottom to top].

Hemphillian	9-5.5 million BP
Clarendonian	11.5-9 million BP
Barstovian	16.0-11.5 million BP
Hemingfordian	20-16 million BP
Late Arikareean	24-20 million BP

The Barstovian Land Mammal Age itself has been subdivided into early, medial, and late portions as follows (VOORHIES, 1990) [older to younger from bottom to top].

Late Barstovian	13-11.5 million BP
Medial Barstovian	14.5-13 million BP
Early Barstovian	16-14.5 million BP

The *Glyptemys* fossils described below have been collected only from the Medial and Late Barstovian.

Glyptemys valentinensis n. sp.

Holotype. – A carapace, complete except for part of the right posterior portion and a small part of the posteromedial portion: University of Nebraska State Museum (UNSM) No. 76564 (figs. 1 A, B and 2 A, B). This specimen was incorrectly identified as "*Chrysemys picta*" by HOLMAN & SULLIVAN (1981).

Locality and Horizon. – Valentine Railway Quarry A (University of Nebraska State Museum Locality Cr 12), Cherry County, Nebraska. Crookston Bridge Member, Valentine Formation. Miocene (Late Barstovian).

Paratypes. – I. The articulated carapace and plastron (fig. 3 A,B) of a male (UNSM 76233) from the West Valentine Quarry (UNSM Cr 114), Cherry County, Nebraska. Crookston Bridge Member, Valentine Formation. Miocene (Late Barstovian). II. The carapace, plastron (fig. 4 A, B), and fragmentary skull (fig. 4 C), and limb bones of a female (UNSM 46077) from the Crookston Bridge Quarry (UNSM Cr 15), Cherry County, Nebraska. Crookston Bridge Member, Valentine Formation. Miocene (Late Barstovian). III. The carapace (fig. 5 A) and plastron (fig. 5 B) of a male (UNSM 117972) from the Stewart Quarry (UNSM Cr 150), Cherry County, Nebraska. Crookston Bridge Member, Valentine Formation. Bridge Member, Valentine Formation. Miocene (Late Barstovian).

Referred material. – The numerous referred elements are from less complete specimens than the holotype and paratypes and many of them consist of individual bones. Among these individual bones, the nuchal, entoplastron, hypoplastron, and xiphiplastron were the most diagnostic. All of the referred elements are from Nebraska and all are from the Late Barstovian with the exception of specimens from the Norden Bridge Quarry (UNSM Bw 106) which is from the Medial Barstovian (see VOORHIES, 1990).

Fragment of the anterior part of a carapace. Including the nearly complete nuchal and parts of the neighboring bones: UNSM 76327 from the West Valentine Quarry (UNSM Cr 114), Cherry County.

Ten nuchals. One nuchal: Michigan State University Vertebrate Paleontology Collection MSU 947 (fig. 6 A) from the Norden Bridge Quarry (UNSM Bw 106), Brown County. One



Fig. 1: Photographs of holotype carapace (UNSM 76564) of Glyptemys valentinensis n. sp. A, dorsal view; B, ventral view. Each scale bar = 25 mm.



Fig. 2: Drawings showing relationships of epidermal scutes to bony plates of holotype carapace (UNSM 76564) of *Glyptemys valentinensis*. Bony seams in part reconstructed. – A, dorsal view; B, ventral view. Not to scale.

nuchal: UNSM 3008-96 from the Nenzel Quarry (UNSM Cr 143), Cherry County. Three nuchals: UNSM 1035-77, 2165-95, and 2270-95 from the Sand Lizard Quarry (UNSM Kx123), Knox County. Five nuchals: UNSM 117973, 117974, 117975, 117980, and 1192-96 from the Stewart Quarry (UNSM Cr 150), Cherry County.

Three epiplastra. Three right epiplastra UNSM 1639-95 and 1608-95 (2 epiplastra) are from the Stuart Quarry (NSM Cr 150), Cherry County.

Eight entoplastra. These entoplastra are parts of partial anterior plastral lobes. Six, UNSM 117976, 117977, 117978, 117979, 1232-96 (and one uncatalogued specimen) are from the Stewart Quarry (UNSM Cr 150), Cherry County. Two, UNSM 76234 and 76235 are from the West Valentine Quarry (UNSM Cr 114), Cherry County.

One left and three right hyoplastra. One right hyoplastron MSUVP 949 is from the Norden Bridge Quarry (UNSM Bw 106), Brown County. One right hyoplastron UNSM 1477-96 is from the Stewart Quarry (UNSM Cr 150), Cherry County. One right UNSM 76211 and one left UNSM 76210 hyoplastra are from the West Valentine Quarry (Cr 114), Cherry County. Six left and six right xiphiplastra. One left and one right xiphiplastron are each part of one half of a posterior plastral lobe: UNSM 2236-94 (left) is from the Railway Quarry B (UNSM Cr 13), Cherry County; and UNSM 1206-96 (right) is from the Stewart Quarry (UNSM Cr 150), Cherry County. One left and one right xiphiplastron are from a complete posterior plastral lobe: UNSM 76214 (Fig. 6 B, C) from the West Valentine Quarry (UNSM Cr 114), Cherry County (this specimen was formerly assigned to the extinct species Emydoidea hutchisoni HOLMAN, 1995, Fig. 4e, p. 552). Four left and four right xiphiplastra are individual specimens. One right xiphiplastron UNSM 2228-84 is from the Forked Hills Site (UNSM Bd 101), Boyd County. One left xiphiplastron UNSM 3302-93 is from the Railway Quarry B (UNSM Cr 13), Cherry County. Three left UNSM 117981, 117982, and 1338-95 and three right UNSM 117983, 117984, and 3302-93 xiphiplastra are from the Stewart Quarry (UNSM Cr 150), Cherry County.

Diagnosis. - This diagnosis is based is based on the entire known material of the species (hypodigm concept, vide LINCOLN et al., 1982). A Glyptemys similar to Glyptemys insculpta and differing from other Emydinae in having (1) a bell-shaped entoplastron, (2) a deep xiphiplastral notch, and (3) a very deep, elongate excavation (groove) along the midline of the plastron in males. Differing from Glyptemys insculpta in: (1) being smaller than most modern populations of G. insculpta, (2) having a more flattened shell than most modern populations of G. insculpta, (3) having the carapacial striations generally anteriorly directed rater than converging to a central apex, (4) lacking the upraised, pyramidal sculpturing on the carapace present in most modern populations of G. insculpta, (5) having the peripheral border of the carapace, especially the posterior portion less flared and not or at best very weakly serrated, (6) having the cervical scute not raised, and (7) having a distinct V-shaped groove on the ventral surface of the nuchal at the contact between the two adjacent areas of marginal overlap (a similar groove but with a wider angle occurs in *Clemmys* guttata). Other characters that, in combination, are useful in the definition of this species are: (1) carapace ovoid in dorsal view, (2) pattern of melanistic streaks visible in many areas on the holotype carapace, probably indicating a color pattern, at least in part, of dark streaks in life, (3) nuchal wider than long, (4) plastron ovoid in dorsal view, (5) plastron akinetic, (6) entoplastron encroached by both the gular-humeral and humeral pectoral sulci, (7) pectoral scute overlaps hyoplastron, (8) femoral scute broadly overlaps both hypoplastron and xiphiplastron.

Etymology. – The specific name *valentinensis* refers to the Valentine Formation where the type material was collected, in Nebraska, USA.

Description of the holotype (UNSM 76564). – In dorsal view, the carapace is ovoid in shape (see fig. 1 A), being wider posteriorly than anteriorly. The peripheral border of the carapace is not distinctly flared, on the other hand, the posterior half is more flared than the

anterior half. The borders of the epidermal scutes are moderately well-defined, but many of the borders of the bony plates are poorly defined or not defined at all. Elongate striations occur on the marginal and pleural areas and the first vertebral area, but are weak or absent on the more posterior vertebral areas. The striations on the posterior marginal and pleural areas are directed mainly anteriorly, but those on the pleural 1 and vertebral 1 are directed in a somewhat circular pattern. A pattern of weak, melanistic streaks may be discerned in many parts of the holotype carapace, probably indicating a color pattern, at least in part, of dark streaks in life.

Turning to the bony elements of the carapace in dorsal view, only the posterior border of the nuchal bone is well defined, but considering its relationships of this border to the first epidermal scutes on either side, the nuchal must have been distinctly broader than long as in the other 14 nuchals of this species available for study. The first neural bone is roughly oval in shape. The second neural is squarish and concave on its anterior end and slightly convex posteriorly. The third and fourth neurals are not well marked. The fifth neural is squarish but all four sides are concave. The sixth neural is broken off posteriorly and the other neurals are missing. The pygal is somewhat longer than wide, flattened dorsally, and moderately notched posteriorly. The costals, except for the somewhat irregularly shaped first costal are poorly defined. The peripherals are better defined posteriorly than anteriorly, but those that are well defined do not appear to differ from those of other *Glyptemys* species.

As for the epidermal scutes in dorsal view, the cervical scute is longer than wide as in other emydids, but it is not raised as in *Glyptemys insculpta*. The first four vertebral scutes are enlarged and are somewhat wider than long. The fifth vertebral scute cannot be discerned. Nothing appears to be noteworthy about the first three pleural scutes which are all about as wide as long, the first pleural being irregular in shape as usual in emydid turtles. The fourth pleural is missing because of breakage in the carapace. The posterior marginals are moderately well defined but appear similar to those in modern Emydinae with rigid plastron. However, in contrast to *Glyptemys insculpta*, the posterior margin of the carapace is unserrated.

Now turning to the holotype carapace in ventral view (see fig. 1 B), there is a distinct V-shaped groove in the ventral surface of the nuchal at the contact between the two adjacent areas of marginal scute underlap. Other than the high degree of scute underlap area that we shall address later, we can find no remarkable characters in this part of the carapace.

Measurements. – Greatest length of carapace 159.2, greatest width of carapace 112.9, greatest height of carapace through the area of greatest width of carapace 32.9, nuchal scute length 9.5, anterior nuchal width 1.5, posterior nuchal width 3.5, nuchal scute underlap length 12.5, first submarginal underlap length at middle of scute 17.9.

Description of paratype I (UNSM 76233). – This paratype (see fig. 3 A, B), consisting of a fused carapace and plastron, is identifiable as a male based on the deep longitudinal cavity along the midline of the plastron. The length of the carapace of this specimen is actually 141.0, but a small portion of the posterior edge of the carapace is broken off so that we estimate a greatest carapace length of about 150.0. The greatest height through the plastron and the carapace of this specimen is 43.8. The greatest plastral length is 138.4. The lengths of seams between the various plastral scutes are as follow: intergular, 22.7; interhumeral, 11.2; interpectoral, 20.2; interabdominal, 27.4; interfemoral, 24.2. Because of breakage, the length of the interanal seam could not be taken. The length of the nuchal scute is 7.8, its anterior width 3.2, and its posterior width 0.9.

The shape of the carapace in dorsal view is not as flared posteriorly as in the holotype. It is not known whether this is because of sexual dimorphism since the type could be a female and this specimen is a male or because of post mortem distortion during the fossilization process. We are prone to think that it is because of the latter. The very deep plastral conca-



Fig. 3: Photographs of paratype I articulated shell (UNSM 76233) of *Glyptemys valenti*nensis. A, dorsal view; B, ventral view. Not to scale.

vity in this specimen is most similar to that that occurs in *Glyptemys insculpta* within emydine turtles. The dorsoventral flattening of the shell in this specimen (fig. 6 D) is similar to that in the holotype.

Description of paratype **II** (UNSM 46077). – This female specimen consists of both a carapace and a plastron (see fig. 4 A, B) as well as a fragmentary skull (see fig. 4 C) and a few postcranial elements. The general shape of both the carapace and plastron is oval, with the widest portion of each unit being about at the middle of the longitudinal axis. General measurements are as follow. Greatest length of carapace 149.0, greatest width of carapace 109.7, greatest length of plastron 150.0, greatest width of plastron 83.7. The carapace is somewhat eroded as are all of the paratypes and it is difficult to accurately identify scute seams and bone sutures as in these other specimens. Moreover, middle of the right side of the carapace has a rugose, somewhat bubbly texture which one of us (JAH) has frequently seen in the prepared shells of Florida box turtles (*Terrapene carolina bauri*) that were burned in wild fires.

On the other hand, the nuchal bone is well defined. It is wider (33.4) than long (28.7) with a ratio of the length divided by width of 85.9 %. The nuchal scute has a greatest length of 7.3 and a greatest width of 4.6. The nuchal scute underlap length is 11.7, its greatest underlap width being 4.0. A very weak pygal notch is present with a greatest length of 1.8. The other bones and scutes that can be recognized in 46077 do not appear to differ from those of the holotype.

The plastron (see fig. 4 A, B, fig. 9 D) lacks a longitudinally concavity so that 46077 has been designated a female. In the anterior lobe of the plastron the entoplastron is well-defined and it is bell-shaped and somewhat constricted anteriorly as in *Glyptemys insculpta*.



Fig. 4: Photographs of paratype II plastron and fragmentary skull (UNSM 46077) of *Glyptemys valentinensis*. – A, plastron in ventral view; B, plastron in dorsal (visceral) view (scale bar = 15 mm); C, fragmentary skull in dorsal view (scale bar = 5 mm).



Fig. 5: Photographs of paratype III articulated shell (UNSM 117972) of male *Glyptemys valentinensis.* – Å, dorsal view; B, ventral view.

About the anterior one-third of the entoplastron is crossed by the V-shaped gular-humeral seam and about the posterior one-third is crossed by the humeral-pectoral seam, each half of which being slightly convex on either side of the midline. The xiphiplastral notch is well-developed as in *Glyptemys insculpta* and is estimated as being about 7.4.

The skull of 46077 (see fig. 4 C) is fragmentary and eroded. It is short and broad and the orbits are proportionally large as is usual in modern testudinoids (e. g. see KUHN, 1966: Fig. 4, p. 23) and they are relatively anteriorly placed. The foramen magnum is rounded. The palatine is excluded from the triturating surface. Measurements are: greatest length of skull from tip of right maxilla to end of occipital condyle 25.7, greatest width of skull 23.6, greatest width of occipital condyle 3.0, greatest width of foramen magnum 4.0, distance between inner edge of right exoccipital and most posterior edge of ventral side of skull 7.8, greatest length of right orbit 8.4.

A complete right femur is 34.4 in its greatest length. It has almost the exact small degree of curvature that is observable in the right femur of a modern female *Actinemys marmorata* (MSU 4050) with a greatest plastral length of 150.0 and a greatest femoral length of 38.0. This small degree of curvature, however, is also observable in a femur of a female *Glyptemys insculpta* (MSU 4381) with a plastral length of 176.0 and a greatest femoral length of 44.6. The proximal end of the right femur of 46077 is more similar to *A. marmorata* than to *G. insculpta* in that the head is longer and narrower in the former two species, but 46077 is similar to *G. insculpta* and differs from *A. marmorata* in that the ulnar (greater) tuberosity is less flaring.

The head of the right humerus of 46077 is compressed and elongate as in modern species of *Glyptemys* and therefore is more adapted to swimming than strict terrestrial locomotion as in the round humeral head of the Testudinidae (e. g. see "*Testudo*" humeral figs. and comments in HAY, 1908).



Fig. 6: Drawings of referred specimens of *Glyptemys valentinensis*. A, nuchal (MSU 947) in dorsal view from the Medial Barstovian Norden Bridge Quarry of Nebraska; B, dorsal (visceral) and C, ventral view of posterior lobe of plastron (UNSM 76214) from the Late Barstovian West Valentine Quarry of Nebraska. [This specimen was previously assigned to the extinct species *Emydoidea hutchisoni* HOLMAN, 1995]; D, articulated shell in lateral view of paratype I (UNSM 76233) to show shape of *C. valentinensis* in this aspect. The scale line = 25 mm and applies to all drawings.

Description of paratype III (UNSM 117972). – This specimen consists of both a carapace (see fig. 5 A) and a plastron (see fig. 5 B). The elongated concavity along the midline of the plastron of this specimen indicates that it is a male. The general shape of both the carapace and the plastron is oval, with the widest portion of each unit being about at the middle of the longitudinal axis. General measurements are as follow. Greatest length of carapace 171.3, greatest width of carapace, 124.8; greatest length of plastron 148.4, greatest width of plastron 85.0; greatest depth of xiphiplastral notch 10.2, greatest depth of pygal notch 5.4.

The central part of this carapace has been crushed downward during the fossilization process and this has caused an irregular concavity in the middle of the upper shell. This same crushing process may also be responsible for the splaying out of the individual peripheral bones of about the posterior one-third of the shell. On the anterior part of the shell this crushing has caused an overriding of some of the costal bones. All of this displacement makes it very difficult to see the individual sutures and seams in dorsal view. As far as these structures can be made out, the carapace does not differ from either the holotype or paratype **I**. Unfortunately, the nuchal bone, although obviously wider than long, has been badly crushed.

Turning now to the plastron, the entoplastron is bell-shaped and constricted anteriorly as in *Glyptemys insculpta* thus differing from other Emydinae in this distinctive character.



Fig. 7: Top row: drawings of entoplastra in ventral view of fossil *Glyptemys valentinensis* from the Stewart Quarry (Cr 150), Cherry County, Nebraska, Late Barstovian. UNSM numbers in order from left to right: 76235, 111792, 1232-96, 117978, 117979, 1274-95, and 117977. Bottom row: drawings of entoplastra in ventral view of modern *Glyptemys insculpta* from Michigan, USA. MSU numbers in order from left to right: 4373 (female), 4380 (female), 4381 (female), 14435 (male), 4377 (male), 4375 (female). The scale bar = 25 mm and applies to all drawings.



Fig. 8: Drawings of forelobes of plastra of emydine turtles in ventral view. A, Clemmys guttata (MTKD 12365); B, Glyptemys muhlenbergii (MSU 3810); C, Glyptemys insculpta (MSU 4374); D, Glyptemys valentinensis (UNSM 76235); E, Actinemys marmorata (MSU 14447); F, Emys orbicularis (MTKD 12363); G, Emydoidea blandingii (MTKD 8480); H, Terrapene carolina (MTKD 8481). Not to scale.



Fig. 9: Visceral (dorsal) aspects of the plastra of emydine turtles. A, Clemmys guttata (MTKD 35625); B, Glyptemys muhlenbergii (MSU 3810); C, Glyptemys insculpta (MSU 4374); D, Glyptemys valentinensis (UNSM 46077); E, Actinemys marmorata (MSU 14447); F, Emys orbicularis (MTKD 12363); G, Emydoidea blandingii (MTKD 8480); H, Terrapene carolina (MTKD 8481). Not to scale.

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About the anterior one-third of the entoplastron is crossed by the V-shaped gular-humeral seam and about the posterior one-third of the entoplastron is crossed by the humeral-pectoral seam, which is slightly convex anteriorly on either side of the midline. Other sutures and seams are very difficult to discern. A well-developed xiphiplastral notch is present at the terminal end of the plastron, another character that is found in *Glyptemys insculpta*, but not in the other Emydinae.

Comments on characters of Glyptemys valentinensis

Carapacial striations. The longitudinal carapacial striae in *Glyptemys valentinensis* (see figs. 1 A and 5 A) and in *Glyptemys insculpta* are not present in *Emydoidea blandingii*. These striations are present in the other Emydinae, but are most pronounced in *G. insculpta*. These striations appear to be associated with areas of growth in all of the Emydinae that have them. More than just reflecting growth stages, it would seem probable that these raised areas would also increase the surface area for temperature regulation and metabolic transport as shown in the histological study of the shell surface of turtles (ANDREWS, 2000). Modern *Glyptemys insculpta* are consummate baskers, even in weather that is too cool for most chelonians (J. H. HARDING, personal communication to JAH, April, 2001).

Entoplastral shape and structure. The large sample of *Glyptemys valentinensis* entoplastra clearly indicates a shape and structure (fig. 7, top row) that is much more similar to that of *G. insculpta* (fig. 7, bottom row) than any other Emydinae (fig. 8). In both *G. valentinensis* and *G. insculpta* the entoplastron is bell-shaped and has the humeral-pectoral seam crossing the entoplastron well anterior to the posterior end of the bone (see figs. 7 and 8 C, D). All of the other Emydinae figured normally do not have a bell-shaped entoplastron (fig. 8 A-H). In *Actinemys marmorata* the entoplastron is roughly diamond-shaped rather than bell-shaped. However, some specimens may possess prominent anterior knobs on the entoplastra, like the fossil *A. owyheensis* (ZUG, 1969). In *Actinemys* the humeral-pectoral seam crosses well anterior to the end of the bone (fig. 8 E) as in *G. valentinensis* and *G. insculpta*. *Clemmys guttata* also has a somewhat diamond-shaped entoplastron, but the humeral-pectoral seam tends to cross the entoplastron more anteriorly (fig. 8 A) than in *Actinemys* and in *G. valentinensis* and *G. insculpta*.

The entoplastron of the small *Glyptemys muhlenbergii* is diamond-shaped (fig. 8 B), but the humeral-pectoral seam is congruent with the posterior border of the bone. *Emys orbicularis* has the entoplastron roughly diamond-shaped, but rather short and wide, with the humeral-pectoral seam close to or congruent with the posterior border of the bone (fig. 8 F). In *Emydoidea blandingii* the entoplastron (fig. 8 G) is octagonal to orbicular-rhomboidal (vide LAWRENCE, 1955: fig. 14, p. 43) in shape and the humeral-pectoral seam tends to be either congruent with the posterior border of the entiplastron or posterior to the entire bone.

Finally, the entoplastra of the species of *Terrapene* seem to be particularly unique among the Emydinae. Although the entoplastron is broadly diamond shaped and the humeral-pectoral seam almost always crosses the entoplastron, the bone is deeply embedded in the forelobe of the plastron. In fact the *Terrapene* entoplastron is embedded and fused with the plastral forelobe to such an extent that it is very difficult to make out the outline of this central bone on the external surface of the plastron in skeletal material (fig. 8 H). This situation may be functionally associated with the solidification of this unit of the highly kinetic shell of *Terrapene*, like the obvious elevation and thickening of the plastral bone in the center of the plastral hindlobe.

Shape of gular margin. In most emydines, including *Glyptemys valentinensis*, the gular margin on the epiplastra is more or less truncate or rounded. In *Actinemys marmorata* the gular margin is protruding, with more or less angular edges at the horny gular-humeral



Fig. 10: Variation of ratio total length (TL) / nuchal scute underlap (NSU) in emydine turtles.

tues. gut – Clemmys guttata (n = 23), muh – Glyptemys muhlenbergii (n = 6), ins – Glyptemys insculpta (n = 24), mar – Actinemys marmorata (n = 8), bla – Emydoidea blandingii (n = 19), coa – Terrapene coahuila (n = 15), orb – Emys orbicularis orbicularis (n = 6), fri – Emys orbicularis fritzjuergenobsti (n = 9), gal – Emys orbicularis galloitalica (n = 10), val – Glyptemys valentinensis (n = 4). In each sample the vertical line indicates the total variation, the black rectangle indicates 1 SE on each side of the mean, the hollow rectangle indicates 1 SD on each side of the mean, and the horizontal line indicates the mean. The arrows indicate a narrow vs. wide nuchal scute underlap.



Fig. 11: Variation of ratio forelobe length (FL) / gular scute overlap (GSO) in emydine turtles.

gut – Clemmys guttata (n = 24), muh – Glyptemys muhlenbergii (n = 6), ins – Glyptemys insculpta (n = 25), mar – Actinemys marmorata (n = 8), bla – Emydoidea blandingii (n = 20), coa – Terrapene coahuila (n = 15), orb – Emys orbicularis orbicularis (n = 5), fri – Emys orbicularis fritzjuergenobsti (n = 9), gal – Emys orbicularis galloitalica (n = 10), val – Glyptemys valentinensis (n = 2). The arrows indicate a narrow vs. wide gular scute overlap. For further explanations see fig. 10.

seam. In *C. guttata* the gulars are forming a distinct, capsule-like groove, the skull fitting exactly into it. On both sides of this groove, along the gular-humeral seams of the visceral side of the plastron, the epiplastra are extremely swollen, reaching more than double the normal thickness of the plastral forelobe. Only in *G. insculpta*, the Recent species with the greatest overall similarity to *G. valentinensis*, the gular margin bears near the gular-humeral seam small cusps which are lacking in some specimens of *G. valentinensis* but present in others (fig. 8 and 9).

Deeply notched xiphiplastron (see figs. 4 A, B, 5 B, 6 B, C, and 9). This deep xiphiplastral notch can be found among Emydinae species only in *Glyptemys valentinensis* and *G. insculpta*. This notch also makes it possible for one to identify individual xiphiplastra as *G. valentinensis*. We have not yet determined a functional advantage in this notching. An obvious difference between the xiphiplastral of *G. valentinensis* and *G. insculpta* exists however in shape: The lateral xiphiplastral margin is moderately rounded in the Miocene species whereas in *G. insculpta*, with the exception of some aged specimens, an conspicuous "step" is located at the areas corresponding to the femorals and anals (compare fig. 9 C and D).

Deep longitudinal excavation (groove) in males. Among emydid specimens we have observed, only male *Glyptemys insculpta* have longitudinal grooves like male *G. valentinensis* (see fig. 5 B). This groove probably is associated with the length and tenacity of copulatory capture by male *G. insculpta* (J. H. HARDING, personal communication to JAH).

Width of carapacial and plastral lips. In *Glyptemys valentinensis* the free shell rims, both on the carapace and on the plastron, are very wide. Despite the fact that we were able to study rich fossil material, a problem was to eliminate size related variation due to the fragmentary condition of many fossil specimens. To quantify and compare the width of the shell rims with Recent emydines, we used the following characters:

As an indicator for the width of the carapacial lips, we measured the distance from the carapacial fore edge to the sulcus where the ventrally underlapping horny carapacial scute and the skin meet along the midline of the nuchal scute (see fig. 10: nuchal scute underlap = NSU). To represent the width of the plastral lips we measured the distance from the plastral fore edge to the sulcus where the dorsally overlapping horny plastral scute and the skin meet along the midseam of the gulars (see fig. 11: gular scute overlap = GSO). To eliminate the effect of size related variation and allowing direct comparisons, we divided the straight line carapace length (total length, TL) by the nuchal scute underlap and the straight line plastral forelobe length (FL) by the gular scute overlap.

The Miocene species has very wide free carapacial and plastral rims, as evident from figs. 9-11. Most New World emydines are similar in this character, whereas the free shell rims are distinctly narrower in the Old World *Emys orbicularis*. However, it is remarkable that *Actinemys marmorata* is similar to the Old World *Emys*, especially regarding the quotient FL/GSO. On the other hand, wide shell rims seem to be an ancestral character in the *Emys* lineage, too, as the earliest Palaearctic fossils of *Emys* from the Middle or Upper Miocene are known to have wide shell rims like the Nearctic species (CHKHIKVADZE, 1983, 1989; FRITZ, 1995). In the Old World lineage, the shell rims became successively narrower from the Upper Miocene onwards, first on the forelobe and then on the hindlobe, and it seems that the condition of the Recent *Emys orbicularis* with narrow shell rims on both plastral lobes was not achieved before the Plio- Pleistocene boundary (Upper Akchagyl to Lower Apsheron and Villafranca; CHKHIKVADZE, 1983; FRITZ, 1995).

Discussion

 $Glyptemys \ valentinensis$ is a Middle Miocene (Medial to Late Barstovian: ca 14.5-11.5 Ma BP) species that is most closely related to the Late Miocene (Late Hemphillian) and modern

G. insculpta and to a somewhat lesser extent, *G. muhlenbergii*. Regarding the relationships of *G. valentinensis* to other emydine species with rigid plastron, *Actinemys marmorata* has not only narrower shell rims than other Nearctic taxa, but its horny seams are congruent with the synostosial seam between the peripheral bones and the hyo- and hypoplastra; a character state that is similar to the condition found in all species with hinged plastra where the bony bridge is replaced by a syndesmotic fusion of carapace and plastron. In the other Recent emydine species with a rigid plastron and in *G. valentinensis*, however, the horny seams between the submarginals and the pectoral and abdominal scutes extend onto the bony plastron (in other words the hyo- and hypoplastra, compare fig. 8 for plastral forelobes). Parenthetically we point out, that on the basis of skeletal material studied by us, we were unable to confirm the contention of BRAMBLE (1974) that the plastral buttresses are reduced in *A. marmorata*.

In the emydine genera with a plastral hinge, we find that *Emys* and *Emydoidea* differ from all species with a rigid plastron in having an extremely elongated spiny process of the distal entoplastron. The dissection of six fresh *Emys orbicularis* by UF did not show any functional significance of this character, at least any that could be attested to by attached muscles or ligaments. In *Terrapene*, the genus with the most effective plastral hinge (BRAMBLE, 1974), this spine is present but much weaker.

Regarding the phyletic relationships between *Glyptemys valentinensis*, *G. insculpta*, and *G. muhlenbergii*, we bring attention to the fact that the perfectly preserved complete shell of a large adult male *G. insculpta* has recently been unearthed from the latest Miocene (Late Hemphillian) of eastern-central Nebraska (S. TUCKER and J. H. HARDING, personal communication to JAH, June 1, 2001). Moreover, one of us (JAH) has twice examined this specimen recently and emphatically concurs with J. H. HARDING. On the other hand, as far as is known, the only fossil record of *G. muhlenbergii* is from the Middle to Late Pleistocene (Irvingtonian II) Cumberland Cave Site, Maryland, USA (HOLMAN, 1977, for dating see BELL, 2000).

From the paleontological standpoint, it appears reasonable to suggest that *G. insculpta* evolved from *G. valentinensis* sometime between Late Barstovian and Late Hemphillian times (11.5-5.5 Ma BP). Because of the very poor fossil record of *G. muhlenbergii*, it is difficult to speculate on its relationships to *G. valentinensis*. However, a sequence analysis of the mitochondrial cytochrome b gene (LENK et al., 1999: tab. 1) showed a genetic distance estimate of 5.79 % between *G. insculpta* and *G. muhlenbergii*. If a molecular clock with a substitution rate of 0.4 % sequence divergence per 1 million years is applied, as accepted for many chelonians (AVISE et al., 1992; BOWEN et al., 1993; LAMB & LYDEARD, 1994; WALKER & AVISE, 1998; LENK et al., 1999), this argues for a separation between both taxa about 14.5 million years ago, what would be exactly in the Medial Barstovian. Hence, *G. valentinensis* could be indeed a candidate for being the last common ancestor of *G. insculpta* and *G. muhlenbergii*.

A key to the bony portions of the shell and femora of Emydinae

This key was set up with the identification of fossil specimens in mind. The fossil species *Actinemys owyheensis* is not sufficiently known for being included into the key and could be identical with *A. marmorata* (see ZuG, 1969). Also the fossil *Emydoidea hutchisoni* is not included here as new material of this form is now being studied:

- 1. Shell completely kinetic, entoplastron ventrally embedded in plastral forelobe of adults. *Terrapene*
- Shell partially kinetic, entoplastron ventrally sutured to other bones of the plastral forelobe of adults.

- 3A. Nuchal bone longer than wide or about as wide as long; deep acromial excavations on dorsal part of epiplastron; femoral scute overlap as wide as it is long; entoplastron often not encroached by humeral-pectoral seam; widened xiphiplastral shelf; xiphiplastral floor deeply excavated.
 Emydoidea blandingii
- 3B. Nuchal bone wider than long; acromion excavations on dorsal part of epiplastron shallow; femoral scute overlap somewhat longer than wide; humeral-pectoral seam close to or congruent with posterior edge of entoplastron; xiphiplastral shelf not widened; xiphiplastral floor shallowly excavated. *Emys*
- 4. Shell akinetic, entoplastron bell-shaped, deep xiphiplastral notch. 5
- 5A. Upraised, pyramidal sculpturing on carapace, nuchal scute area on nuchal bone strongly raised, posterior peripheral area of carapace relatively widely flared.

Glyptemys insculpta

5B. No upraised pyramidal sculpturing on carapace, nuchal scute area on nuchal bone flattened, posterior peripheral area of carapace not distinctly flared.

Glyptemys valentinensis

- Shell akinetic, entoplastron not bell-shaped, xiphiplastral notch very shallow or absent.
- Carapace length 80-125 mm in adults, femoral shaft distinctly bowed, sutures between submarginals and pectorals and abdominals located on the plastral part of the bridge.
 8
- 8A. Entoplastron not crossed by humeral-pectoral seam or with humeral-pectoral seam congruent with posterior edge of the bone. *Glyptemys muhlenbergii*
- 8B. Entoplastron with humeral-pectoral seam crossing middle of the bone. Clemmys guttata
- 9. Carapace length 90-190 mm in adults, femoral shaft not distinctly bowed, humeralpectoral seam located on posterior part of entoplastron, seams between submarginals and pectorals and abdominals on the bridge congruent with the suture between peripheral and hyo- and hypoplastral bones. Actinemys marmorata

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List of recent specimens studied

All are alcoholic specimens unless otherwise noted.

Actinemys marmorata: MSU 4050 (skeleton), MSU 14447 (skeleton), MTKD 8977, MTKD 9055, MTKD 11641, MTKD 14474, MTKD 24914-24915, MTKD 40105 (skeleton), MTKD 40208, NMW 1731 (skeleton), NMW 1733 (skeleton).

Clemmys guttata: MSU 2100-2101 (skeletons), MSU 2103 (skeleton), MSU 2105 (skeleton), MSU 2107-2109 (skeletons), MSU 4982 (skeleton), MSU 4984 (skeleton), MSU 6230 (skeleton), MSU 10063 (skeleton), MSU 11393 (skeleton), MSU 11395 (skeleton), MSU 14162 (skeleton), MTKD 12365 (skeleton), MTKD 32907, MTKD 35625 (skeleton), MTKD 35743, MTKD 35910-35911, MTKD 37022, MTKD 37619, MTKD 39485-39486, MTKD 39848, MTKD 40062, NMW 1723-1724 (skeletons).

Emydoidea blandingii: MSU 2231 (skeleton), MSU 2233 (skeleton), MSU 2450 (skeleton), MSU 3457 (skeleton), MSU 3522 (skeleton), MSU 3525 (skeleton), MSU 3527 (skeleton), MSU 3942 (skeleton), MSU 3995 (skeleton), MSU 13021 (skeleton), MSU 13065 (skeleton), MTKD 8480 (skeleton), MTKD 8998, MTKD 9533, MTKD 12445, MTKD 14538, MTKD 14599, MTKD 30059, MTKD 30358, MTKD 39718 (skeleton), MTKD 39843, MTKD 40870, NMW 1756-1757 (skeletons).

Emys orbicularis orbicularis: MTKD 12363 (skeleton), MTKD 29434-29437, MTKD 33708, MTKD 39070.

Emys orbicularis fritzjuergenobsti: MTKD 11120-11121, MTKD 14351, MTKD 32361, MTKD 32363-32364, MTKD 39817, MTKD 40375-40377.

Emys orbicularis galloitalica: MTKD 34287, MTKD 35567, MTKD 35867-35869, MTKD 39081-39083, MTKD 39099, MTKD 39127.

Glyptemys insculpta: MSU 3096 (skeleton), MSU 4371-4381 (skeletons), MSU 14390-14392 (skeletons), MSU 14435 (skeleton), MTKD 3589 (skeleton), MTKD 17090, MTKD 19214, MTKD 32536, MTKD 35635, MTKD 35853, MTKD 35914, MTKD 39491-39494, NMW 1725 (skeleton).

Glyptemys muhlenbergii: MSU 3810 (skeleton), MTKD 11952, MTKD 31716, MTKD 31784, MTKD 32519, MTKD 33747, MTKD 39484, MTKD 41373 (skeleton), NMW 1730 (skeleton)

Terrapene carolina: MTKD 8481 (skeleton), MTKD 42836 (skeleton).

Terrapene coahuila: MSU 3509-3510 (skeletons), MSU 4108-4110 (skeletons), MTKD 24273-24274, MTKD 28017-28020, MTKD 28461, MTKD 37177, MTKD 37192-37193.

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