

A Review of the Fossil Record of North American Turtles of the Clade *Pan-Testudinoidea*

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ABSTRACT

Turtles of the clade *Pan-Testudinoidea* have a rich fossil record in North America, including the Caribbean, ranging from the late Paleocene to the Holocene. All earlier reports cannot be substantiated herein. The earliest members of this clade probably immigrated in multiple waves from Asia. Current phylogenies of crown *Testudinoidea* recognize four primary clades: *Pan-Emyridae*, *Pan-Geoemydidae*, *Pan-Testudinidae*, and the lineage leading to *Platysternon megacephalum*. An updated global phylogeny allows attribution of fossils to these lineages with confidence that allows the discernment of new diversity trends and biogeographic patterns. The diversity of North American *Pan-Testudinidae* increased consistently throughout the Cenozoic and reached its peak in the early Miocene. The extinction of many testudinids at the end of the Pleistocene, however, decreased tortoise diversity toward its extant levels. The diversity of North American *Pan-Emyridae* and *Pan-Geoemydidae* shows opposite patterns. *Pan-Emyridae* are remarkably diverse today, but their diversity was low in the Eocene and only increased dramatically from the Oligocene and onwards. *Pan-Geoemydidae*, on the other side, were diverse in the late Paleocene to Eocene, but their diversity decreases to their extremely low present levels starting with the Oligocene. A taxonomic review of 191 named North and Central American pan-testudinoid taxa finds 57 nomina valida, 69 nomina invalida, 64 nomina dubia, and 1 nomen nudum.

KEYWORDS

Phylogeny, biogeography, paleoecology, *Testudinoidea*, *Testudinidae*, *Geoemydidae*, *Emyridae*

Introduction

The clade *Pan-Testudinoidea* is defined as referring to the total clade of crown *Testudinoidea* or the most inclusive clade containing the extant *Testudo graeca* Linnaeus, 1758, *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), and *Batagur* (orig. *Emys*) *baska* (Gray, 1831) (Joyce et al. 2004). It represents one of the most diverse and widespread clades of living turtles and includes the so-called pond turtles and land tortoises (TTWG 2017).

All known extant pan-testudinoids are characterized by the presence of a contact between the quadratojugal and the articular facet of the quadrate (Joyce and Bell 2004), the absence of inframarginal scutes, a biconvex eighth cervical vertebra, and a laterally curved iliac blade with a double origin for the iliotibialis muscle (Gaffney and Meylan 1988). Representatives of the clade

can furthermore be diagnosed by characters that show some reversal within the clade, in particular the absence of an epipterygoid participation to the trigeminal foramen, short squamosals that do not extend beyond the condylus occipitalis, fusion of the foramen alveolare inferius and foramen intermandibularis medius, presence of twelve pairs of marginal scutes, and well-developed axillary and inguinal butresses.

The pan-testudinoid fossil record is distributed on all continents except Antarctica. Extant pan-testudinoids show a less extensive range that includes much of the tropical to cold-temperate portions of the Americas, Africa, Asia, Europe, and Madagascar, as well as various islands throughout the Caribbean, Indonesian, and Japanese Archipelagos, the Galápagos, Aldabra, and the Seychelles (Ernst and Barbour 1989; TTWG 2017). In North and Central America, the

extant representatives of *Testudinoidea* include a single clade of *Testudinidae* with at least four species included in the genus *Gopherus*, almost the entire diversity of *Emydidae* (at least 45 species), and a single clade of *Geoemydidae* with at least nine species included in the genus *Rhinoclemmys* (TTWG 2017).

The fossil record of North American pan-testudinoids is quite rich due to the rigid nature of their shells and the extensive exploration of terrestrial localities on this continent. As a consequence, pan-testudinoid fossils are prevalent in North American institutions (Appendix 1). In general, the history of the study of the fossil record of North American pan-testudinoids parallels that of pan-trionychids (Vitek and Joyce 2015), not only in the authors involved and their contributions, but also the sheer number of taxa named based on undiagnostic material, the resulting inflated diversity, and the problem of wastebasket genera (e.g., “*Trionyx*” and “*Testudo*”). The early works of Leidy (e.g., Leidy 1851a, 1851b, 1851c, 1852a, 1852b, 1853, 1869; 1873), Cope (e.g., Cope 1871a, 1871b, 1871c, 1873a, 1873b, 1878, 1892a, 1892b), Hay (e.g., Hay 1899a, 1899b, 1902, 1904, 1906a, 1906b, 1908) and Gilmore (e.g., Gilmore 1915, 1920) are particularly notable, as these authors described the vast majority of named taxa. These authors, however, often named new species based on highly fragmentary material that must be considered to be undiagnostic beyond the level of the main pan-testudinoid clades (“families”) or even *Pan-Testudinoidea* in general. These early authors also named new genera that subsequently dominated the chelonian literature (Appendix 2), often by serving as wastebasket taxa themselves (e.g., *Stylemys* Leidy, 1851a; *Hadrianus* Cope, 1871b; *Echmatemys* Hay, 1906a). Regardless of the nomenclatural instability created by these early works, the extensive descriptions accompanied by drawings and photographs of specimens are unparalleled in the global pan-testudinoid literature, creating a solid base for work through the second half of the 20th century and the early 21st century.

More recent work on the fossil record of North American pan-testudinoids further increased our understanding of pond turtle and tortoise evolution and diversity on this continent. Among a multitude of scientists that worked with this group, the works of Auffenberg (e.g., Auffen-

berg 1958, 1962a, 1962b, 1963, 1964a, 1967, 1971, 1974), Bramble (1971, 1982), Crumly (1982, 1984a, 1984b, 1994), Franz (e.g., Franz 2014; Franz et al. 2001; Franz and Franz 2009; Franz and Woods 1983), Holman (1963, 1964, 1971a, 1972a, 1973a, 1976b, 1978, 1987a, 1995, 2002b), Holroyd (e.g., Holroyd et al. 2001; Holroyd and Rankin 2014), Hutchison (1980, 1992, 1996, 2013), Jackson (1975, 1976, 1978, 1988), Lichtig and Lucas (2015a, 2015b, 2015c, 2015d), and Williams (1950a, 1950b, 1952, 1953) are of particular note. In addition to descriptive and taxonomic work, the fossil record of North American pan-testudinoids has also provided the basis for taphonomic (e.g., Brand et al. 2000; Corsini et al. 2006; Corsini and Chamberlain 2009) and skeletochronological studies (Ehret 2007).

Any attempt to revise the fossil record of pan-testudinoids is hampered by the presence of “wastebasket taxa.” For example, the nomenclatural history of pan-testudinids is dominated by the improper use of *Testudo* Linnaeus, 1758 and *Geochelone* Fitzinger, 1835. *Testudo* was originally defined by Linnaeus as containing all turtles known to him but was later constricted as containing only a few species around the Mediterranean (e.g., Williams 1952). Later, nearly all derived tortoises without a cervical scute and most New World testudinids with a cervical scute were included under *Geochelone* (Auffenberg 1974, but see Crumly 1982, 1984a, 1984b). Convincing evidence for the proper application of these two names was only recently provided by molecular studies (e.g., Le et al. 2006; Fritz and Bininda-Emonds 2007).

The present paper provides a taxonomic review of the fossil record of all named pan-testudinoid taxa from North America, including Central America and the Caribbean. Most of the conclusions presented herein are based on published information supplemented by personal observations of select specimens. All conclusions regarding the availability, validity, and/or (either or both) synonymy of various taxa are therefore tentative. In contrast to previous reviews (e.g., Hay 1908; Kuhn 1964) that concluded, or presumed, nearly all named taxa to be valid, this chapter aims to provide a conservative list of valid taxa that serves as a starting point for future work. I am aware that many proposed subjective synonymies and dubious taxa will attract criticism, as I often

break with tradition, and I therefore feel obligated to explain the conceptual framework used herein. To establish the validity of a taxon, this work primarily uses characters that are clearly defined and useful in phylogenetic analysis (see Phylogenetic Relationships below). Previous work often used geographical and temporal arguments as a basis for taxonomic decisions, but these factors are here only used to corroborate synonymy suggested on morphological grounds. Especially for large-sized tortoises, I find it difficult to reject close relationships inferred from anatomical information based on geographic criteria alone, as large continental species (e.g., *Centrochelys sulcata* and *Stigmochelys pardalis*) today display large ranges (TTWG 2017).

A goal of this contribution is to detect and mend the preexisting inflated view of the taxic diversity for North American pan-testudinoids. Although only a fraction of the true fossil diversity is known for this clade worldwide, notable examples exist with implausibly high levels of named diversity. For example, at least 24 different pan-testudinoids have been named from the Eocene of the Fort Bridger area alone. The total named turtle diversity from that area exceeds 60 species. If extant levels of regional diversity are taken as a benchmark (e.g., a maximum of 19 species; Buhlmann et al. 2009), such high levels of taxic diversity seem improbable, especially for *Pan-Testudinoidea*. The number of valid taxa recognized herein (see Systematic Paleontology below) is similar to that of other sympatric and contemporary clades that were recently reviewed (see Vitek and Joyce 2015). Therefore, I firmly believe that the conservative approach used herein is an important first step towards a more realistic estimation of past pan-testudinoid diversity.

I am certain that the list of literature cited herein is far from exhaustive. In particular, I skipped some contributions that report material already known for a certain locality, especially from the Pleistocene. However, I am confident that all named taxa have been reviewed and that the temporal and geographical distribution of the clade as a whole approximates true patterns. Taxonomic information on extant pan-testudinoids is not included herein for brevity. However, several fossil occurrences of extant taxa are included to provide a better overview of their temporal and geographic distribution. The

anatomy of *Pan-Testudinoidea* will be treated elsewhere. For the purposes of this chapter, the approximate term “small-sized” refers to turtles with a midline shell length less than 30 cm, “middle-sized” to turtles between 30 and 60 cm, “large-sized” to turtles between 60 and 100 cm, and “giant” to those with a shell longer than 100 cm. Neural formulae are phrased using numbers for the number of sides of each neural (e.g., 4 for four-sided, 6 for six-sided) and letters referring to the position of the short lateral sides (e.g., A for anteriorly and P for posteriorly).

Two taxa are available that were originally thought to belong to *Pan-Testudinoidea* but are now considered to be members of other clades. These are *Gyremys spectabilis* Hay, 1908 from the Late Cretaceous (Campanian) of Montana, which was initially considered to be a putative member of Emydidae but more recently suggested to be a junior synonym of the baenid *Neurankylus* (Hutchison and Archibald 1986; Claude and Tong 2004), and *Clemmys backmani* Russell, 1934 from the early Paleocene of Saskatchewan (Canada), which was initially believed to be an emydid but now is agreed to by a macrobaenid (Brinkman et al. 2010). Several other Late Cretaceous taxa were referred to the testudinoid genus *Emys* during the mid 19th century (e.g., *Emys beatus*, *Emys firmus*, *Emys obscurus*, *Emys pravus*), but these have since been referred to the extinct clades *Adocidae* or *Paracryptodira* (Hay 1908). Estes et al. (1969), Ostrom (1970), and Parrish et al. (1987) reported potential testudinoid remains from the Cretaceous of North America, but I show below that this material likely lacks pan-testudinoid affiliations (see Paleobiogeography below).

This review of the fossil record of the North American *Pan-Testudinoidea* resulted in the recognition of 57 nomina valida, 69 nomina invalida, 64 nomina dubia, and 1 nomen nudum. Following the rules of the ICZN (1999), all valid binomials used herein conform to the gender agreement rule and do not use ligatures or diacritics. For institutional abbreviations see Appendix 1. Named North American pan-testudinoid genera are listed in Appendix 2.

Phylogenetic Relationships

The phylogenetic relationships of North American pond turtles and tortoises have never been

analyzed in detail or at a global scale, even though the group has been extensively studied at the alpha taxonomic level. A select number of taxa, however, have been analyzed with cladistic methodology. Hirayama (1984) used "*Echmatemys*" as an outgroup taxon for his analysis of extant *Geoemydidae* based on the scorings of an otherwise unpublished skull. His assumption that *Echmatemys* is the sister of all extant geoemydids remained unchallenged until now (e.g., Claude and Tong 2004). Crumly (1982, 1984a, 1984b) similarly presented a global phylogeny of *Testudinidae*, which remains one of the most comprehensive analyses of extinct tortoise taxa up to now. The resulting hypothesis of generic relationships of extant and extinct tortoises formulated some key concepts regarding the phylogenetic relationships of North American testudinids. In particular, *Hadrianus* and *Cymatholcus* were considered "primitive" and placed at the base within crown *Testudinidae*. *Styemys*, *Hesperotestudo*, and *Caudochelys*, on the other hand, were considered to be closely related with the extinct and extant members of *Gopherus*. The monophyly of this exclusively North American clade has been strongly supported throughout the vast majority of published works since the times of Hay (1908), based on geographic proximity and, partially, by the presence of a median premaxillary ridge (shared by *Gopherus* and *Styemys*). Bramble (1971) also suggested that New World testudinids form a monophyletic group, distinguished from the Old World tortoises by the presence of a separate foramen for the mandibular artery and the insertion of the deep biceps muscle in the ulna. More recently, however, those views were challenged by Crumly (1994) (*Styemys* and *Hesperotestudo* along the stem of *Testudininae*) and Meylan and Sterrer (2000) (*Styemys* is shown in a basal position in *Testudinidae*, between *Manouria* and the remaining tortoise taxa, but *Hesperotestudo* remains as sister to *Gopherus*). Interestingly, *Floridemys* is shown by Crumly (1984a, 1984b) to be placed within the "Geochelone complex." Some more inclusive pan-testudinoid clades have been the focus of detailed cladistic analyses, such as the emydid *Terrapene* (Joyce et al. 2012) and the testudinid *Gopherus* (Crumly 1994; Reynoso and Montellano-Balasteros 2004).

For the purposes of this contribution, I included all herein-recognized valid North

American pan-testudinoids into a recently published global matrix of *Pan-Testudinoidea* (Vlachos and Rabi 2017). The matrix, the resulting trees, and additional information pertaining to the analysis were deposited at MorphoBank Project 2794 (<http://morphobank.org/permalink/?P2794>). To utilize as much data as possible, information was included from synonymized taxa. The results are far from conclusive, likely because of missing data associated with use of mostly fragmentary specimens and published information. Trees were obtained by combining the expanded morphological matrix with the published molecular matrix of Guillon et al. (2012). A total evidence analyses was performed using TNT (Goloboff et al. 2008) under equal and implied weights (Goloboff 2014). The matrix was first analyzed in its entirety to clarify the placement of fossil taxa within the primary pan-testudinoid clades ("families"). Then, parts of the matrix were reanalyzed separately for each such clade, to achieve greater resolution at the generic and specific level. The same process was followed under implied weights. The trees presented herein (Figures 1 and 2) are a synthetic summary of results and should be viewed only as a working hypotheses for future analyses. Groupings that appear with solid lines were supported in all analyses, whereas those with dashed lines received only poor support. In the following section I will only discuss the topology in general, whereas detailed info on the monophyly and/or placement of certain clades is given below in the comment section of various taxa. These new results highlight that some valid species within North American *Pan-Testudinoidea* should perhaps receive new generic names to properly reflect their position. Given the preliminary nature of the analysis, combined with my reluctance for naming monotypic genera, I highlight phylogenetic ambiguity through the use of quotation marks.

The analysis in general supports previously published ideas regarding the placement of fossils in the primary clades of *Testudinoidea* (Figures 1 and 2). All analyzed fossil taxa were placed within crown *Testudinoidea* (Figures 1 and 2). The enigmatic *Cardichelyon rogerwoodi* is tentatively confirmed as the sister to *Platysternon megacephalum* (Figure 1). With exception of *Terrapene*, the interrelationships of *Pan-Emyridae* are generally poorly resolved (Figure 1). The group is therefore depicted tentatively herein in a "traditional" or

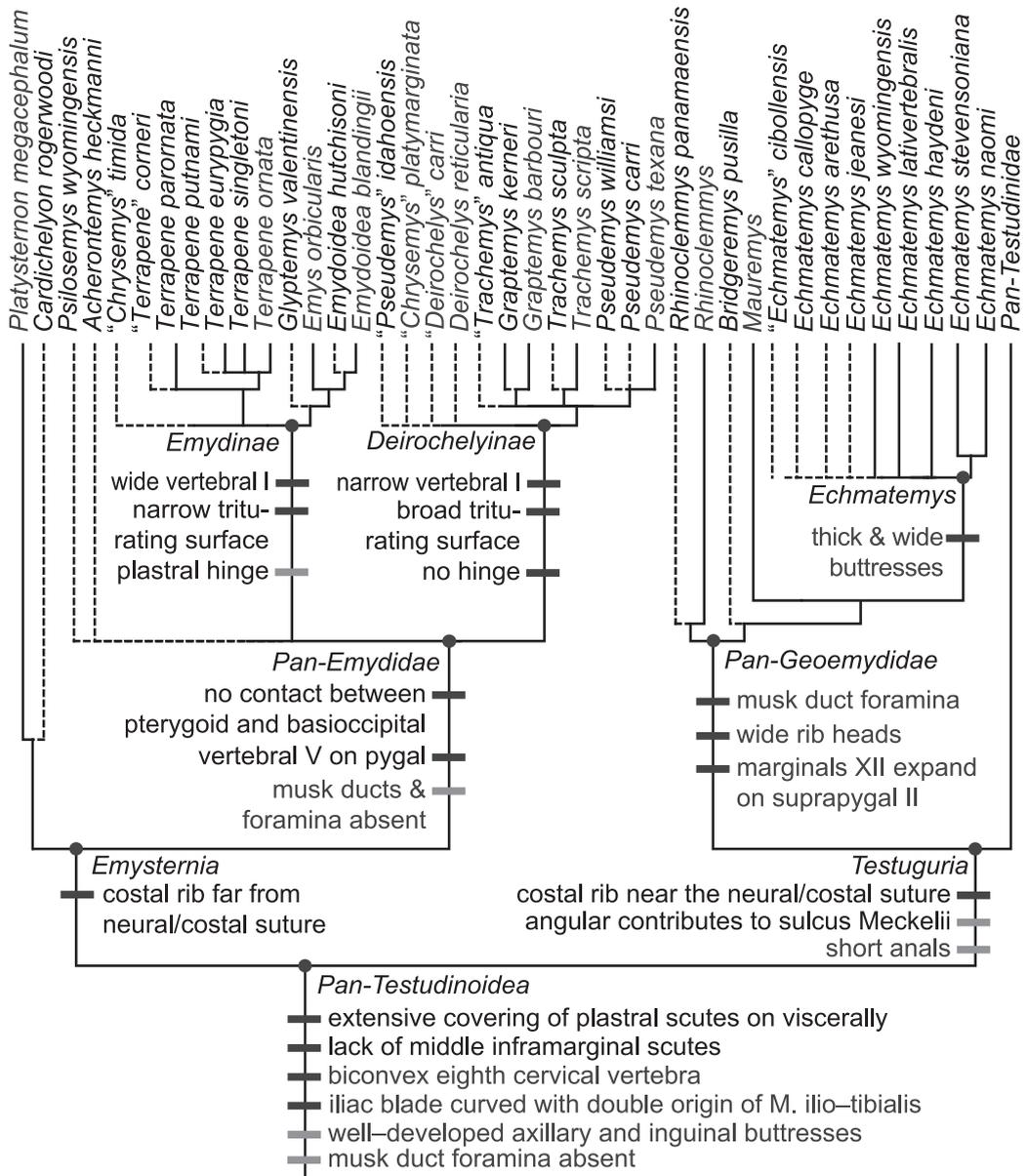


FIGURE 1. A phylogenetic hypothesis of valid pan-testudinoid taxa from North America to the exception of pan-testudinids. Solid lines indicate well-supported placements and dashed lines indicate hypothesized placements (see text for more details). The most important synapomorphies are indicated with thick black lines. Those indicated with grey are further differentiated within the clade. See Figure 2 for *Pan-Testudinidae*.

“prevailing” arrangement, and no new generic combinations are proposed. *Psilosemys wyomingensis* and *Acherontemys heckmanni* are tentatively placed in a basal polytomy with other clades of *Pan-Emydidae* (Figure 1).

The relationships retrieved for *Pan-Geoemydidae* are less conflicting (Figure 1). The sister-

group relationship of *Rhinoclemmys panamaensis* with crown *Rhinoclemmys* is moderately supported. The monophyly of most *Echmatemys* can be supported with confidence and, interestingly, all *Echmatemys* spp. are recovered in derived position within *Geoemydidae* as sister to *Mauremys*. This result is further discussed below.

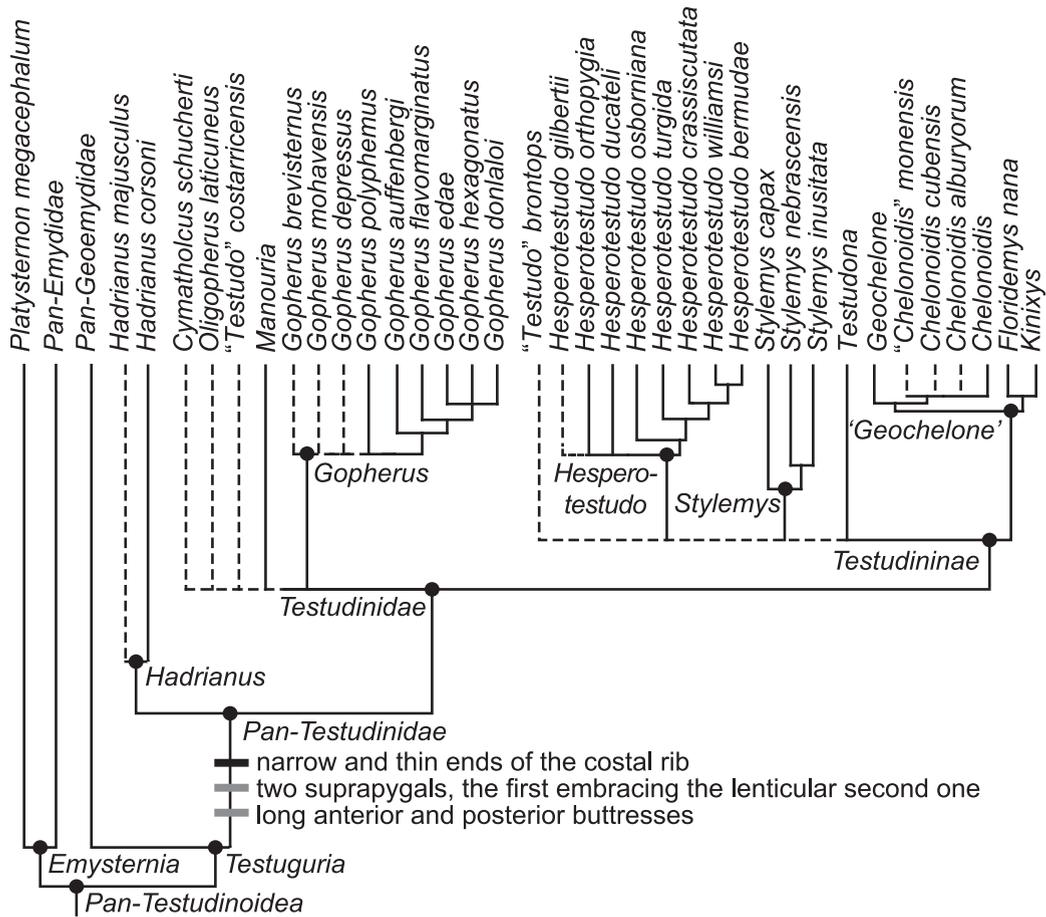


FIGURE 2. A phylogenetic hypothesis of valid pan-testudinid taxa from North America. Solid lines indicate well-supported placements and dashed lines indicate hypothesized placements (see text for more details). The most important synapomorphies are indicated with thick black lines. Those indicated with grey are further differentiated within the clade. See Figure 1 for *Pan-Geoemydidae* and *Emysternia*.

The relationships of *Pan-Testudinidae* are also well resolved (Figure 2). *Hadrianus* is placed with significant confidence along the stem of *Testudinidae*. Some other North American taxa (e.g., *Cymatholcus schucherti*, *Oligopherus laticuneus*, "*Testudo*" *costarricensis*) are retrieved as basal pan-testudinids as well, but whether they are placed along the stem or within crown *Testudinidae* is not clear. These taxa are therefore here shown in an unresolved polytomy with *Testudinidae*. The monophyly of three traditionally recognized clades (genera) is well supported (*Gopherus*, *Stylemys*, *Hesperotestudo*), but the relationships of some species within those clades are conflicting. I therefore here place these taxa in a

basal polytomy within each clade. Contrary to traditional views, these three clades are not retrieved as each other's closest relatives, supporting ideas already expressed by Crumly (1994) and Meylan and Sterrer (2000). *Stylemys* and *Hesperotestudo* hold a more derived position relative to *Gopherus*, as had been proposed already by Crumly (1994). It is not conclusive, however, whether they are placed within or outside *Testudininae* and they are therefore herein shown in a polytomy at the base of *Testudininae*. This result renders the presence of the premaxillary ridge homoplastic. The position of *Floridemys nana* within the "*Geochelone* complex" already suggested by Crumly (1984a, 1984b) is confirmed herein. Tortoises from the Caribbean

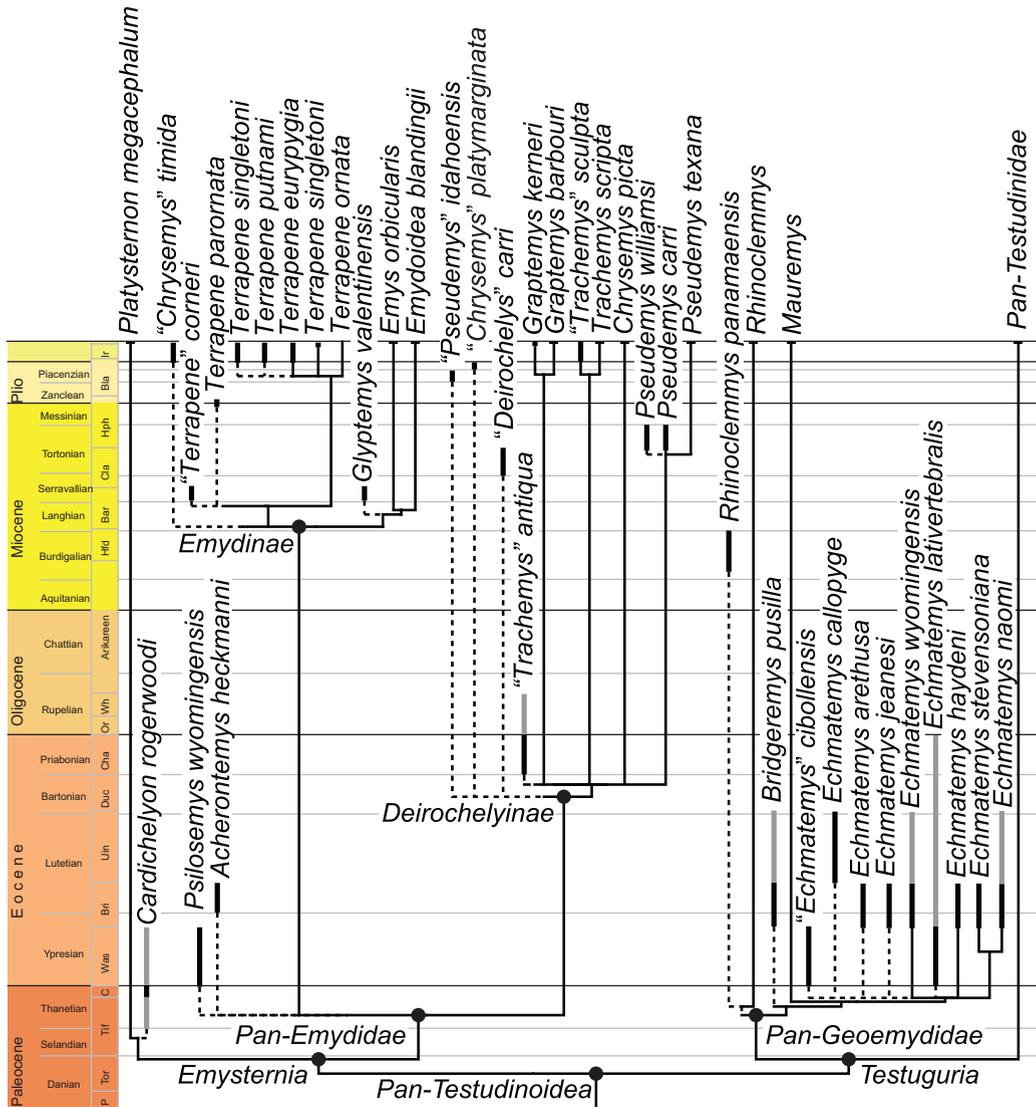


FIGURE 3. The stratigraphic distribution of valid pan-testudinoid taxa from North America to the exception of pan-testudinids. Black lines indicate temporal distribution based on type material. Gray lines indicate temporal distribution based on referred material. See Figure 4 for *Pan-Testudinidae*.

are certainly distinct from North American genera and closely related with the South American *Chelonoidis*. As these specimens are highly incomplete, however, it was not possible to further assess their placement herein.

As noted before, this analysis is far from conclusive and much work is still needed, but even these preliminary results highlight that the evolutionary and biogeographical history of North American pan-testudinoids was even more complex than previously thought (Figures 3 and 4).

Paleoecology

Extant testudinoids are adapted to a broad variety of nonmarine environments (Ernst and Barbour 1989). Several North American lineages document the independent secondary return to terrestrial environments. Among the mostly freshwater *Emydidae*, *Terrapene* spp. are adapted to terrestrial environments through the development a hyo-hyoplastral hinge, a highly domed shell that fuses with age, and robust limbs, but

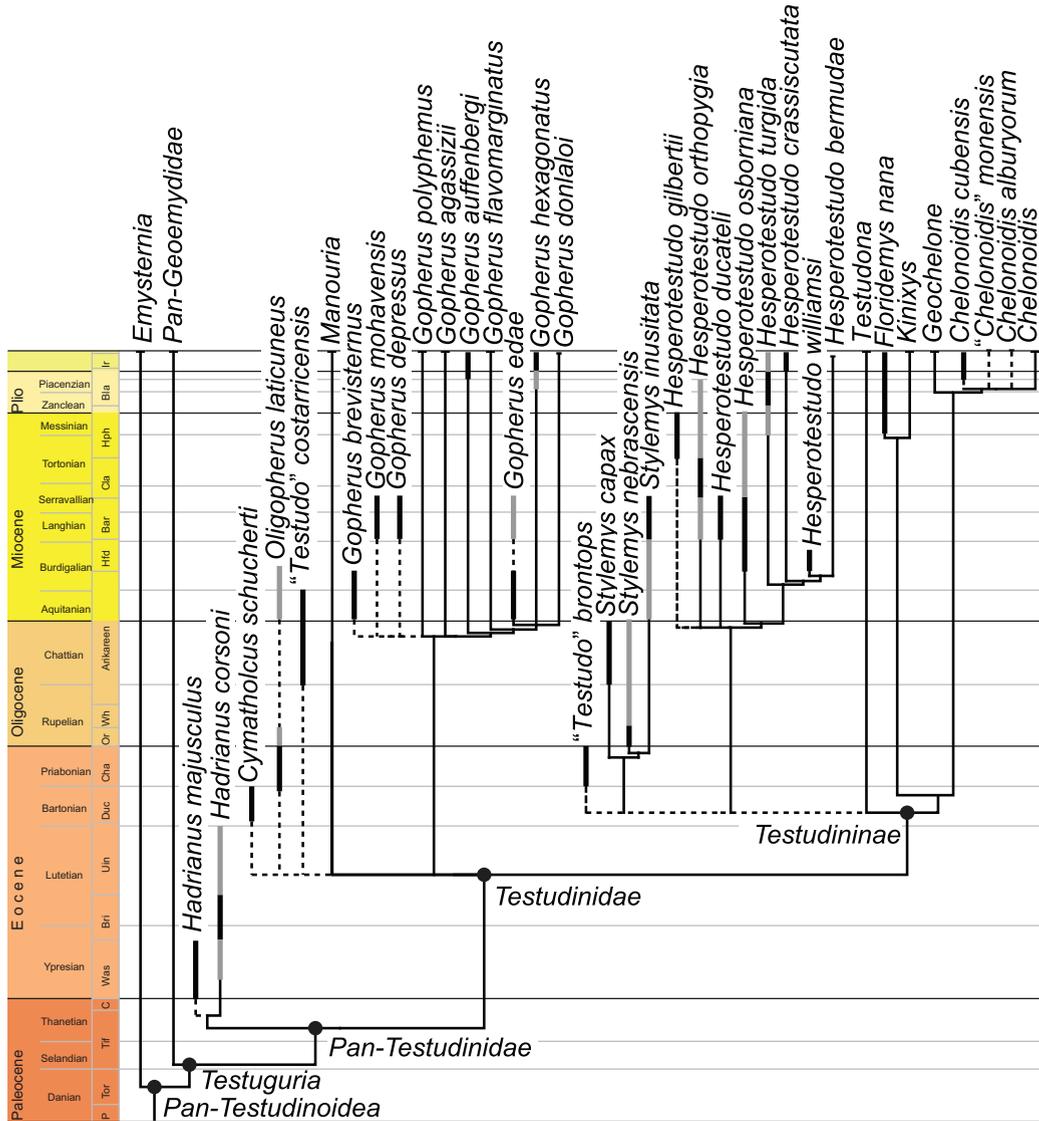


FIGURE 4. The stratigraphic distribution of valid pan-testudinid taxa from North America. Black lines indicate temporal distribution based on type material. Gray lines indicate temporal distribution based on referred material. See Figure 3 for *Pan-Geoemydidae* and *Emysternia*.

representatives of this clade typically stay close to freshwater resources (Ernst and Barbour 1989). Within the mostly aquatic *Geoemydidae*, members of *Rhinoclemmys* range from semiaquatic to terrestrial, but the terrestrial ones show a body plan that differs from that of box turtles by being more flattened and by lacking a hinge (Ernst and Barbour 1989). Finally, true tortoises are fully adapted to the terrestrial environments through a series of modifications to the skull, shell, and

appendicular skeleton. Some additional specializations are apparent within this group. *Gopherus* spp. are able to survive in arid and xeric environments by digging burrows (Bramble 1982). *Hesperotestudo* spp., on the other hand, developed extensive associations of bony osteoderms that cover the limbs, cloaca, and tail (Auffenberg 1963). Giant tortoises have long been used as indicators for mild and warm climate (Holman 1971a, 1976b, 1987a), but this view was recently

challenged, as mounting evidence is available that these animals could tolerate cooler temperatures in North America (Moll and Brown 2017). The diet of extant testudinoids ranges from herbivorous, to molluscivorous, to omnivorous (Ernst and Barbour 1989), but a general lack of skull material makes it difficult to assess the dietary preferences of most fossil representatives.

Paleobiogeography

The earliest pan-testudinoids are known from Asia (e.g., Sukhanov 2000) and it is generally presumed that the clade entered North America via the Bering Land Bridge during warm periods of the late Paleogene (Hutchison 1998, Joyce et al. 2016 and references therein). This conclusion is in broad accordance with the North American fossil record, which traces the group to the base of the Cenozoic. However, I here take the opportunity to briefly discuss a few earlier putative North American pan-testudinoid records, as an earlier dispersal to North America is sometimes discussed as well (Hutchison 2000a).

Ostrom (1970) described fragmentary turtles fossils from the Early Cretaceous (Albian) of Montana, of which most were referable to the helochelydrid *Naomichelys speciosa* and the paracryptodire "*Glyptops* sp.," which is likely an early baenid (Joyce and Lyson 2015). Ostrom (1970) also reported the proximal of a humerus that he felt to have similarities with that of the extant *Terrapene*, thereby hinting at the possible presence of a testudinoid in this assemblage. Considering that testudinoid fossils have otherwise not been found from similarly dated sediments throughout North America and that the partial humerus is consistent in its morphology with that of a paracryptodire, I here disregard this record as credible evidence for testudinoids in the Early Cretaceous of North America.

Parrish et al. (1987) described a steinkern from the Late Cretaceous (Cenomanian) of Alaska, which preserves the anterior part of a shell. In the absence of a costiform process and overall morphology of the sutures, they found similarities with early pan-testudinoids from Asia. As the steinkern does not preserve parts of the actual shell, I here note that the specimen is also consistent in its morphology with an adocusian or macrobaenid. Indeed, considering that

the common ancestor of all americhelydians likely migrated from Asia to North America during the mid-Cretaceous (Joyce et al. 2016), it is also possible that this fossil represents the pan-americhelydian stem lineage, which is expected to resemble early pan-testudinoids. Under the absence of further anatomical information, I disregard this fossil as a credible pan-testudinoid as well.

Estes (1964) and Estes et al. (1969) attributed with doubt fragmentary specimens from the Late Cretaceous (Maastrichtian) of Wyoming and Montana, respectively, to Emydinae (= *Pan-Emydidae* herein). In addition to shell fragments, Estes et al. (1969) highlighted the presence a cervical centrum with double concave articulations surfaces (Williams 1950a). However, more recent finds of the neck of Late Cretaceous adocusians (e.g., Meylan and Gaffney 1989; Brinkman and Peng 1996) reveals that this morphology is not unique to testudinoid turtles. Considering that extensive field work in Late Cretaceous (Maastrichtian) deposits of North America has not yet yielded any other testudinoid remains (e.g., Holroyd et al. 2014) and that the material reported by Estes (1964) and Estes et al. (1969) is not figured, I here disregard these reports.

In an early summary of the faunas from the early Paleocene of the San Juan Basin, New Mexico, Cope (1888) reported the presence of *Emys* sp., but it is unclear if he intended to report the presence of a testudinoid per se. Given that Cope (1888) did not figure or refer any material and that extensive field work in this region has not yielded any testudinoid remains since, I here disregard this record as well. Finally, McKenna et al. (1987) reported indeterminate pan-testudinoid remains from the early Paleocene of California, but the fossiliferous sediments have since been redated to be late Paleocene in age (Woodburne 2004). As such, there is no positive evidence for the presence of *Pan-Testudinoidea* in North America prior to the Late Paleocene.

The late Paleocene record of pan-testudinoids commences with the sudden appearance of the enigmatic *Cardichelyon rogerwoodi* in numerous localities in the latest Paleocene of Wyoming and Colorado, USA (Hutchison 2013; Figure 5 and Appendix 3). The diversity of turtles increased in North America at the Paleocene/Eocene boundary (Hutchison 1998). Holroyd and Hutchison

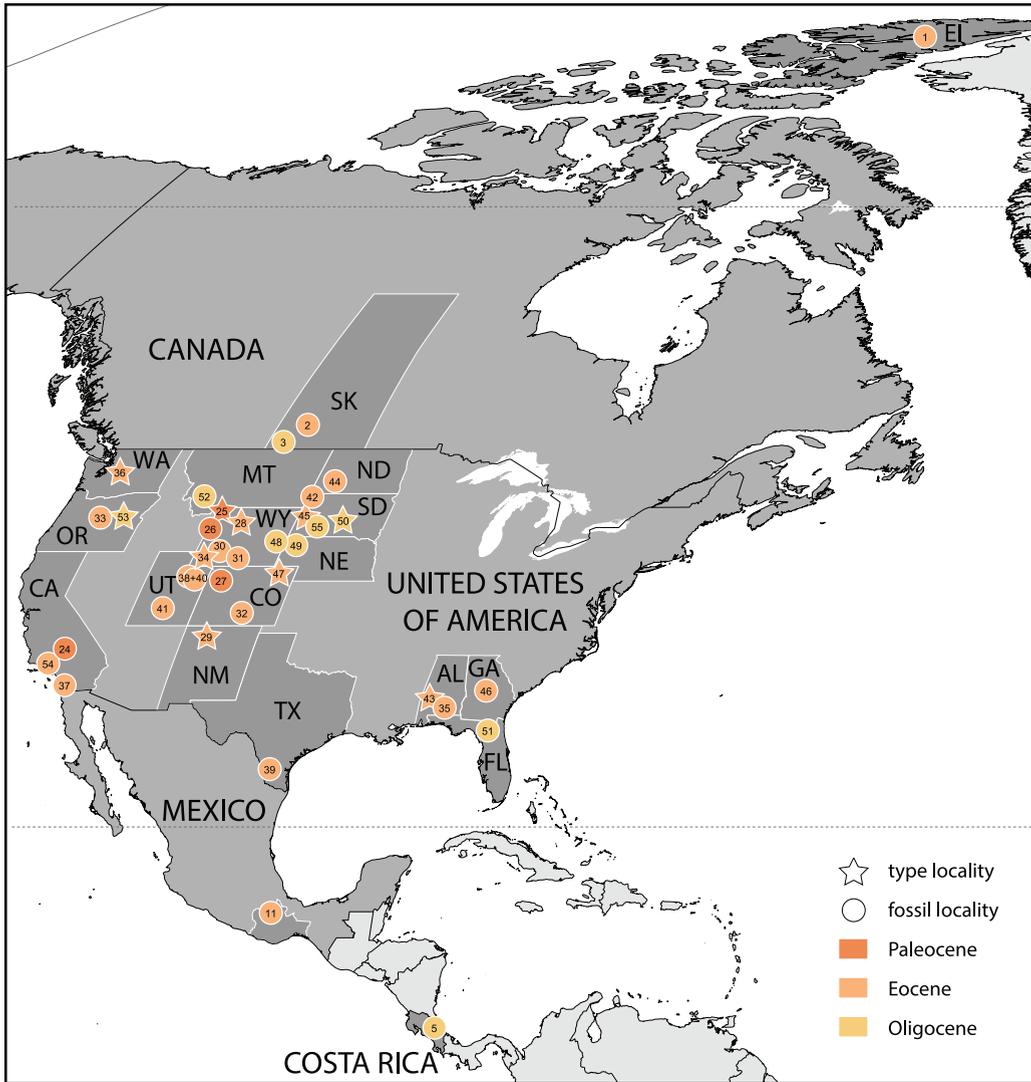


FIGURE 5. The geographic distribution of fossil pan-testudinoid turtles from the Paleogene of North America. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations:* AL, Alabama; CA, California; CO, Colorado; EI, Ellesmere Island; FL, Florida; GA, Georgia; MT, Montana; ND, North Dakota; NE, Nebraska; NM, New Mexico; OR, Oregon; SD, South Dakota; SK, Saskatchewan; TX, Texas; UT, Utah; WA, Washington; WY, Wyoming.

(2000) argued that global climate change was not correlated with diversification during the early Eocene but, rather, that warming allowed for increased migration of Asiatic lineages across high latitudes. Throughout the Eocene and Oligocene, pan-testudinoids were spread across much of continental North America (Figures 3 and 5). Panemydid and pan-testudinid records from the early Eocene of Ellesmere Island in the Canadian

Arctic (Estes and Hutchison 1980; Eberle and Greenwood 2012; Figure 5 and Appendix 3) are particularly notable as they represent the northernmost occurrences in the history of the clade. During the Neogene, the distribution of *Pan-Testudinoidea* is even more extensive by including records from Central America and the West Indies (Figure 6 and Appendix 3). The northernmost records are found in southern Saskatchewan,

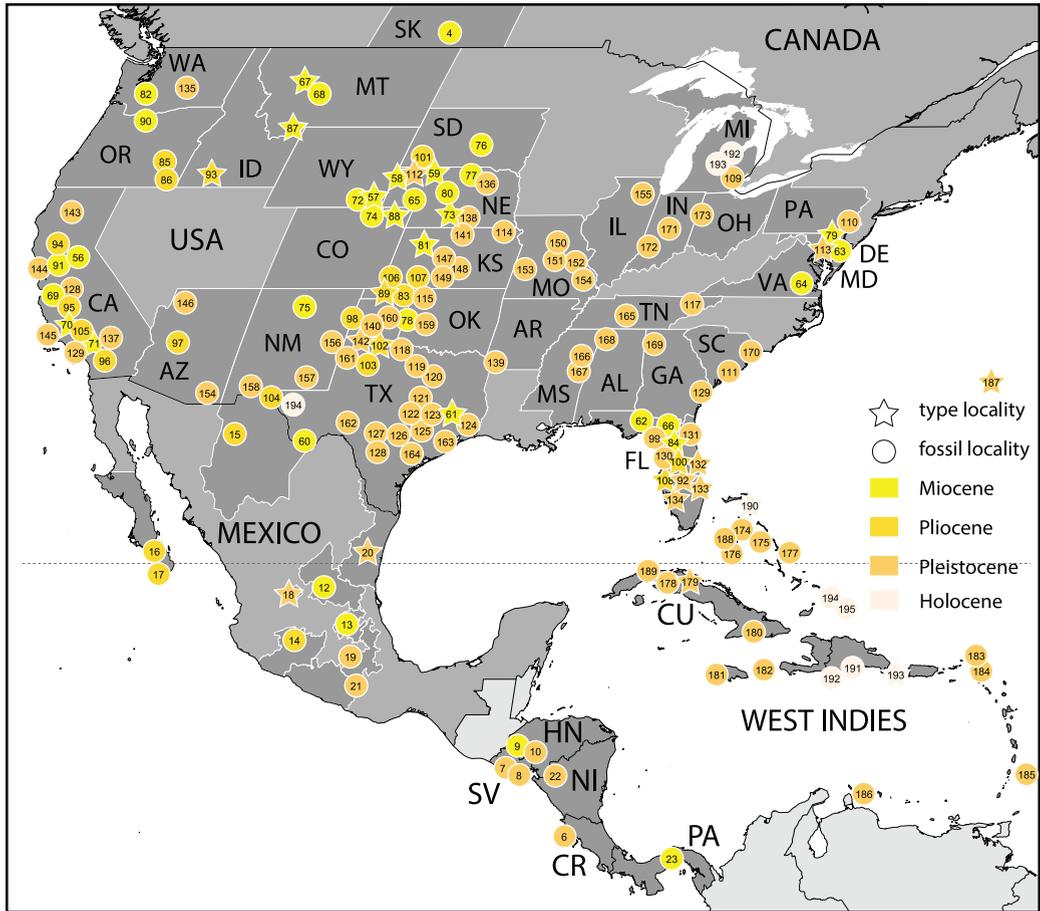


FIGURE 6. The geographic distribution of fossil pan-testudinoid turtles from the Neogene to Quaternary of North America, including the Caribbean. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. Numerous countries or states are not labeled for clarity. *Abbreviations:* AL, Alabama; AR, Arkansas; AZ, Arizona; CA, California; CO, Colorado; CR, Costa Rica; CU, Cuba; DE, Delaware; FL, Florida; GA, Georgia; HN, Honduras; ID, Idaho; IL, Illinois; IN, Indiana; KS, Kansas; MD, Maryland; MI, Michigan; MO, Missouri; MS, Mississippi; MT, Montana; NE, Nebraska; NI, Nicaragua; NI, Nicaragua; NM, New Mexico; OH, Ohio; OK, Oklahoma; OR, Oregon; PA, Pennsylvania; SC, South Carolina; SD, South Dakota; SK, Saskatchewan; SV, El Salvador; TN, Tennessee; TX, Texas; VA, Virginia; WA, Washington; WY, Wyoming.

Canada, with the peculiar exception of a putative testudinid record in the Pleistocene of Yukon Territory, Canada (King and Saunders 1986; Figure 5 and Appendix 3).

In the early Eocene, *Pan-Emydidae* is only represented by two species (*Psilosemys wyomingensis* and *Acherontemys heckmanni*) (Figure 3). From the late Eocene to early Oligocene, “*Trachemys*” *antiqua* is a common presence in South Dakota (Figure 3). This taxon is the only certain member of crown *Emydidae* known prior to the

Neogene and its position within *Deirochelyinae* infers the presence of crown *Deirochelyinae* since the Late Eocene. On the other hand, emydines are not represented in the North American fossil record until the middle Miocene (Figure 3). Most fossil emydids from North America have been recovered from Neogene sediments. These finds document the presence of most lineages that survive until the present.

In the early Eocene, *Pan-Geoemydidae* was already quite diverse, with at least eight clades

present, even with the conservative approach used herein (Figure 3). This diversity remains practically the same for the entire Eocene, until *Echmatemys* goes extinct. This loss of diversity of aquatic testudinoids in the Eocene/Oligocene boundary is compensated with the rise of emydidids from that time onwards (see above). After the end of the Eocene, only a single fossil geoemydid occurrence is available from the Miocene of Panama (a possible *Rhinoclemmys*).

The taxic diversity of pan-testudinids (Figure 4) is low in the early to middle Eocene, consisting only of *Hadrianus majusculus* in the earliest Eocene and followed by *Hadrianus corsoni* throughout much of the remaining Eocene. Tortoise diversity increased steadily from the late Eocene onwards (Figure 4). Possible stem testudinids appear in the end of the Eocene, with *Oligopherus laticuneus* in several localities in central United States and *Cymatholcus schucherti* in Alabama. The latter stands out among a handful of occurrences in southeastern United States in the Paleogene. During the late Eocene, I estimate the early diversification of crown *Testudininae* in North America, marked by the presence of “*Testudo*” *brontops* from South Dakota. In the late Eocene, pan-testudinids also reached their southernmost Paleogene extent in Oaxaca, Mexico (Jiménez-Hidalgo et al. 2015). Few tortoise taxa are known from the Oligocene, in particular the iconic *Stylemys nebrascensis*, a taxon known from possibly hundreds of specimens from different occurrences in northern-central United States and arguably the tortoise taxon with the richest fossil record. The northernmost records in the Oligocene in Saskatchewan, Canada (Figure 5 and Appendix 3). With the exception of referred material to *Oligopherus laticuneus* (type material of *Testudo undabuna* Loomis, 1909) and the uncertainty of the age of “*Testudo*” *costarricensis* (see relevant section), all Neogene records are referable to crown *Testudinidae*. Most Paleogene taxa are extinct at this point in time, with exception of some members of *Stylemys* persisting in the Neogene of Oregon and Montana. The Neogene record is marked by the presence of *Gopherus* and *Hesperotestudo*, a clade showing its distribution in the entire central-south United States from east to west (Figure 6). This clade is characterized by the development of large carapace sizes and the presence of heavy dermal armor. The presence of

several species of *Hesperotestudo* increases the taxic diversity of testudinids in the Neogene. The extinction of this clade at the end of the Pleistocene reduced the tortoise diversity towards the extant five species of *Gopherus*.

Systematic Paleontology

Valid Taxa

The following section includes a full list of all herein recognized named species of *Pan-Testudinoidea*. Extant taxa reported from the fossil record are not listed herein, but are included in the biogeographic summary (Appendix 3). See Appendix 4 for the hierarchical taxonomy of *Pan-Testudinoidea* as described in this work.

Pan-Testudinoidea Joyce et al., 2004

Phylogenetic definition. Following Joyce et al. (2004), the name *Pan-Testudinoidea* refers to the total clade of crown *Testudinoidea* (see below).

Diagnosis. Pan-testudinoids are herein diagnosed relative to other turtles by the extensive covering of the plastral scutes on the visceral side of the plastron, presence of axillary and inguinal scutes, well-developed axillary and inguinal buttresses, presence of musk duct foramina, a biconvex eighth cervical vertebra, and a curved iliac blade with a double origin for the M. iliobtibialis.

Comments. An important controversy in cryptodiran systematics has been the position of *Platysternon megacephalum*, which was either recovered within *Chelydridae* or *Testudinoidea*. I here follow the emerging molecular consensus that this taxon is nested within *Testudinoidea* as sister to Emydidae (e.g., Parham et al. 2006; Crawford et al. 2015; Pereira et al. 2017). The only relevance herein concerns the relationships of *Cardichelyon rogerwoodi* Hutchison, 2013 (see below) and its plausible platysternid relationships.

Cardichelyon rogerwoodi Hutchison, 2013

Taxonomic history. *Cardichelyon rogerwoodi* Hutchison, 2013 (new species).

Type material. YPM VP 014671 (holotype), an almost complete shell with associated appendicular skeleton (Hutchison 2013, figs. 26.8, 26.12a, b, 26.13).

Type locality. J.P. Reis Quarry, UMMP locality FG-10, Park County, Wyoming, USA (Figure 5); Fort Union Formation, Clarkforkian NALMA, Thanetian, late Paleocene (Hutchison 2013).

Referred material and range. Late Paleocene (Selandian–Thanetian), Tiffanian NALMA, Park County, Wyoming, USA (referred

material of Hutchison 2013); late Paleocene (Thanetian), Clarkforkian NALMA, Willwood Formation, Park County, Wyoming, USA (referred material of Hutchison 2013); late Paleocene (Thanetian), Clarkforkian NALMA, Chappo Member, Wasatch Formation, Lincoln County, Wyoming, USA (referred material of Holroyd and Rankin 2014); early Eocene (Ypresian), Wasatchian NALMA, Big Horn County, Wyoming, USA (referred material of Hutchison 2013).

Diagnosis. *Cardichelyon rogerwoodi* can be diagnosed as a representative of *Pan-Testudinoidea* based on the wide covering of the plastral scutes on the visceral side of the plastron and the presence of musk duct foramina. *Cardichelyon rogerwoodi* resembles *Platysternon megacephalum* by having extensive temporal roofing, a wide nuchal notch, short bridges, ventrally exiting musk ducts, the proportions of the plastral scutes, and a kinetic contact of the carapace with the hypoplastron. *Cardichelyon rogerwoodi* differs from *Platysternon megacephalum* based on the presence of an extensive axillary buttress, absence of a inguinal buttress, partial overlap of the pectoral–abdominal sulcus with the hyoplastral–hypoplastral suture, presence of well-developed gular horns that frame a median plastral depression, a reduced cervical scale, and the frequent absence of subdivided marginals XII.

Comments. *Cardichelyon rogerwoodi* is based on relatively rich material from the late Paleocene to early Eocene of Wyoming, USA (Hutchison 2013). The material associated with this taxon was originally referred to *Ptychogaster* sp. by Estes (1975) and by a series of informal names (see synonymy list in Hutchison 2013). Hutchison (2013) mentions the presence of this taxon as far north as Ellesmere Island (Arctic Canada) but this material is not yet published and this claim can therefore not be evaluated. *Cardichelyon rogerwoodi* has also been reported from the Clarkforkian–Wasatchian of Colorado (Lichtig and Lucas 2015b), but the figured material is too fragmentary and too poorly documented to allow confirmation of this identification. Hutchison (2013) noted that the broad plastron and extensive visceral overlap of the plastral scales favor emydid relationships, but I find these characters to be diagnostic for *Pan-Testudinoidea* in general. Hutchison (2013) furthermore argued for close relationships with the extant *Platysternon megacephalum*, especially using cranial characters, but the presence of a hinge between hyo-hypoplastra and the overlap of vertebral V and marginal XII onto the pygal are frequently encountered within *Pan-Emydidae*. Considering the sister group relationship of *Platysternon megacephalum* with *Emydidae*, I here retain the originally hypothesized position of *Cardichelyon rogerwoodi* as sister to *Platysternon megacephalum* while awaiting more formal assessment in a global context.

Testudinoidea Fitzinger, 1826

Phylogenetic definition. Following Joyce et al. (2004), the name *Testudinoidea* refers to the crown clade arising from the last common ancestor of the testudinid *Testudo graeca* Linnaeus, 1758, the emydid *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), and the geoemydid *Batagur* (orig. *Emys*) *baska* (Gray, 1831).

Diagnosis. As for *Pan-Testudinoidea*.

Comments. As global phylogenies are still lacking for pan-testudinoids, it is currently not possible to rigorously diagnose the crown clade relative to its stem lineage.

Pan-Emydidae Joyce et al., 2004

Phylogenetic definition. Following Joyce et al. (2004), the name *Pan-Emydidae* refers to the total clade of crown clade *Emydidae* (see below).

Diagnosis. Pan-emydids can be diagnosed as pan-testudinoids based on full list of characters provided for that clade above. Members of *Pan-Emydidae* are differentiated relative to other pan-testudinoids by the absence of musk ducts and associated musk duct foramina, wide rib head, a broad costo-vertebral tunnel, presence of paired marginals XII, and the expansion of vertebral V onto the pygal.

Acherontemys heckmani Hay, 1899b

Taxonomic history. *Acherontemys heckmani* Hay, 1899b (new species).

Type material. USNM 4213 (holotype), an almost complete carapace (Hay 1899b, pl. 6; Hay 1908, fig. 281).

Type locality. Roslyn, Kittitas County, Washington, USA (Hay 1899b; Figure 5); Roslyn Sandstone, Chumstick Formation, late Bridgerian NALMA, Lutetian, middle Eocene (Hutchison 1992).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Acherontemys heckmani* is herein diagnosed as a member of *Pan-Emydidae* based on the full list of characters listed for that clade above. *Acherontemys heckmani* differs from all other North American emydidids in the presence of wide vertebral scutes that cover more than half of the carapacial width and the crossing of the anterior sulcus of vertebral IV onto neural VI.

Comments. *Acherontemys heckmani* is based on a single, almost complete, but crushed carapace from the middle Eocene of Washington, USA (Hay 1899b). *Acherontemys heckmani* was initially considered to be a member of *Chelydridae* (Hay 1899b, 1908). Hutchison (1992, 2008) more recently suggested, however, that this species is a member of *Emydidae*, based on the presumed presence of plastral buttresses, an assessment shared by Joyce (2016) and myself (see Diagnosis). The great width of the vertebral scutes distinguishes *Acherontemys heckmani* from other North American testudinoids. Vertebrals of similar width are known from some European geoemydidids (e.g., *Sakya*, *Sarmatemys*; see Danilov 2005 and references therein). In the original descriptions, Hay (1899b, 1908) mentions the presence of eight neurals and a single suprapygal, but personal observations confirm the presence of only seven neurals, of which the first is quadrangular and the rest hexagonal with short antero-lateral sides, and two suprapygals. Whereas suprapygal 1 is quadrangular and trapezoidal with a narrower anterior side, longer than

wide with a rounded posterior border, suprapyg II is much wider than long and hexagonal with anterolateral and posterolateral sides of equal width. This is the arrangement typical of *Pan-Emydidae*. Preliminary phylogenetic analysis cannot resolve the position of *Acherontemys heckmani* within *Pan-Emydidae* and it is therefore here placed in an unresolved basal polytomy at the base of that clade.

Psilosemys wyomingensis Hutchison, 2013

Taxonomic history. *Psilosemys wyomingensis* Hutchison, 2013 (new species).

Type material. UCMP 179440 (holotype), carapacial fragments (Hutchison 2013, fig. 26.14).

Type locality. Fifteen Mile Creek, Washakie County, Wyoming, USA (Hutchison 2013; Figure 5); Willwood Formation, Wasatchian NALMA, Graybullian subage, Ypresian, early Eocene (Hutchison 2013).

Referred material and range. Early Eocene (Ypresian), Wasatchian NALMA, Willwood Formation, Big Horn and Washakie County, Wyoming, USA (referred material of Hutchison 2013).

Diagnosis. *Psilosemys wyomingensis* can be diagnosed as a member of *Pan-Testudinoidea* based on an extensive visceral covering of the plastral scales, the presence of inguinal and axillary scutes, and well-developed axillary and inguinal buttresses and as a member of *Pan-Emydidae* based on the absence of musk duct foramina, expansion of vertebral V onto the pygal, and presence of paired marginals XII. *Psilosemys wyomingensis* differs from other members of *Pan-Emydidae* by the following combination of characters: pleural I that cover the lateral parts of the nuchal, pectorals located posterior to entoplastron, plastral buttress only reaching the costals, carapace only weakly sculpted at most, costal V shorter distally than costal VI, and presence of a small and narrow inguinal.

Comments. *Psilosemys wyomingensis* was described by Hutchison (2013) based on several specimens from Wyoming, USA. Hutchison (2013) suggested that this species lacks derived characters of crown *Emydidae* and should therefore be considered as its sister taxon. In my assessment, the wide cervical, narrow vertebrals, moderate flaring of the posterior carapace, osseous bridge, moderate development of buttresses, humero-pectoral sulcus posterior to the entoplastron, and absence of hyoploastral hinge suggest that *Psilosemys wyomingensis* may hold a more derived position within crown *Emydinae*. I nevertheless here tentatively place *Psilosemys wyomingensis* in an unresolved polytomy at the base of *Pan-Emydidae*.

Emydidae Bell, 1825

Phylogenetic definition. Following Joyce et al. (2004), the name *Emydidae* refers to the crown clade arising from the last common ancestor of the emydine *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758) and the deirochelyine *Chrysemys* (orig. *Testudo*) *picta* (Schneider, 1783).

Diagnosis. As for *Pan-Emydidae*.

Comments. In addition to the character listed herein (see above), members of this clade are diagnosed by characters from the skull and skeleton (see McDowell 1964), most of which cannot be observed in the fossil record, which consists mostly of shells. As such, the diagnoses provided focus on characters from the shell that are relevant to the fossil taxa recognized herein.

“Chrysemys” platymarginata Weaver and Robertson, 1967

Taxonomic history. *Chrysemys platymarginata* Weaver and Robertson, 1967 (new species); *Trachemys idahoensis* = *Trachemys platymarginata* Jackson 1988 (junior synonymy).

Type material. UF 11046 (holotype), a partial shell (Weaver and Robertson 1967, fig. 10).

Type locality. Haile 15A, Alachua County, Florida, USA (Weaver and Robertson 1967; Figure 6); late Blancan NALMA, Piacenzian, late Pliocene (Hulbert 2001).

Referred material and range. Late Pliocene (Piacenzian), late Blancan NALMA, Alachua County, Florida, USA (referred material of Auffenberg 2001).

Diagnosis. *“Chrysemys” platymarginata* can be diagnosed as a member of *Emydidae* based on the full listed of characters listed for that clade above. *“Chrysemys” platymarginata* differs from other emydids by the presence of protrusions on the posterior peripherals, a highly sculptured, deep, and wide nuchal notch, extensive gular overlap onto the epiplastra, and a long cervical.

Comments. *“Chrysemys” platymarginata* is based on a partial shell from the late Pliocene of Florida that was originally differentiated from other deirochelyines based on the depth of the nuchal notch and the smooth surface of the nuchal areas covered by the marginals (Weaver and Robertson 1967). Auffenberg (2001) more recently referred a complete shell to this species from similarly dated sediments, but did not provide a thorough description. Numerous additional specimens are apparently catalogued at UF, but these too are awaiting description. Although the validity of this taxon therefore appears to be well supported, it is difficult to assess its relationships. The overall morphology of *“Chrysemys” platymarginata* is consistent with a deirochelyine, but the strongly serrated posterior peripherals are more consistent with *Pseudemys* or *Graptemys* than with *Chrysemys* or *Trachemys*. I herein recognize the validity of this taxon, but highlight phylogenetic ambiguity through the use of quotes.

“Chrysemys” timida Hay, 1908

Taxonomic history. *Chrysemys timida* Hay, 1908 (new species); *Chrysemys picta* = *Chrysemys timida* Preston 1979 (junior synonymy); *Chrysemys picta bellii* = *Chrysemys timida* TTWG 2014 (junior synonymy).

Type material. YPM VPPU 010853 (holotype), a partial carapace (Hay 1908, fig. 449, pl. 46.2).

Type locality. Niobrara River, Sheridan County, Nebraska, USA (Hay 1908; Figure 6); Irvingtonian NALMA, Calabrian–Ionian, Pleistocene (Hay 1908; Woodburne 2004).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. “*Chrysemys*” *timida* can be diagnosed as a member of *Emydidae* based on the expansion of vertebral V onto the anterior part of the pygal and the presence of paired marginals XII. “*Chrysemys*” *timida* differs from other emydids by the presence of a vertebral I that is wider than the nuchal that contacts marginal II, presence of a boomerang-shaped suprapygal I that embraces the small and lenticular suprapygal II.

Comments. The type material of “*Chrysemys*” *timida* is composed of a partial carapace from the Pleistocene of Nebraska with clear emydid affinities. Hay (1908) originally attributed this species to *Chrysemys*, a deirochelyine, but without explicit justification. Although the available information is limited, the presence of a wide vertebral I recalls the condition seen in various emydines, but the absence of a bridge and plastron makes it difficult to further resolve relationships. This taxon is therefore herein placed in a basal polytomy within *Emydinae*. The unusual suprapygal/pygal configuration (see Diagnosis above) nevertheless allows for the establishment of a valid species. Preston (1979) stated that “*Chrysemys*” *timida* is synonymous with the extant *Chrysemys picta*, a view tentatively shared by TTWG (2014) and TEWG (2015), but the presence of a wide vertebral I that contacts marginal II clearly contradicts that assessment.

“*Deirochelys*” *carri* Jackson, 1978

Taxonomic history. *Deirochelys carri* Jackson, 1978 (new species).

Type material. UF 20908 (holotype), a partial shell (Jackson 1978, fig. 11).

Type locality. Love Site, near Archer, Alachua County, Florida, USA (Jackson 1978; Figure 6); Love Bone Bed, Clarendonian 3 NALMA, Tortonian, late Miocene (Woodburne 2004).

Referred material and range. Late Miocene (Tortonian), Clarendonian 3 NALMA, Alachua County, Florida, USA (referred material of Jackson 1978 and Auffenberg 2001).

Diagnosis. “*Deirochelys*” *carri* can be diagnosed as a member of *Emydidae* based on the presence of paired marginals XII and the expansion of vertebral V onto the pygal and as a member of *Deirochelys* based on the decoration of the shell, wider than long nuchal plate, overlap of the pleural I onto the lateral parts of the nuchal, unnotched peripherals, partial covering of the entoplastron by the gular scutes, and placement of the humero-pectoral sulcus posterior to the entoplastron. “*Deirochelys*” *carri* can be differentiated from other *Deirochelys* in the presence of a narrower neural, narrower costovertebral tunnel, wider covering of the pleural I onto the nuchal, and wider vertebrals.

Comments. “*Deirochelys*” *carri* is based on a partial shell from the late Miocene of Florida (Jackson 1978), but the morphology

of this specimen is poorly documented by only a line drawing. Auffenberg (2001) more recently depicted and referred a relatively complete shell from the type locality, but an extensive description is lacking once again. Additional material is held in the collections of UF, but still awaits description. Although I agree that the available material clearly shows the presence of a valid deirochelyine taxon, the sparse available character evidence makes it difficult for me to establish phylogenetic relationships rigorously. I particularly am not certain about the generic attribution of this taxon, as the great width of vertebral I is unusual for *Deirochelys*, an opinion shared by Jackson (1978). I therefore highlight taxonomic uncertainty through the use of quotes. This taxon should not be confused with the similarly dated *Pseudemys carri* (Rose and Weaver, 1966) (see below).

Glyptemys valentinensis Holman and Fritz, 2001

Taxonomic history. *Glyptemys valentinensis* Holman and Fritz, 2001 (new species).

Type material. USNM 76564 (holotype), a partial carapace (Holman and Fritz 2001, figs. 1, 2).

Type locality. Valentine Railway Quarry A, Cherry County, Nebraska, USA (Holman and Fritz 2001; Figure 6); Crookston Bridge Member, Valentine Formation, late Barstovian NALMA, Serravallian, middle Miocene (Holman and Fritz 2001).

Referred material and range. Middle Miocene (Serravallian), late Barstovian NALMA, Cherry and Brown Counties, Nebraska, USA (referred material of Holman and Fritz 2001).

Diagnosis. *Glyptemys valentinensis* can be diagnosed as a member of *Pan-Emydidae* based on the full list of characters listed for that clade above and as a member of *Glyptemys* based on the presence of a bell-shaped entoplastron. *Glyptemys valentinensis* can be differentiated from *Glyptemys insculpta* by smaller size, a more flattened shell, anteriorly-directed carapace striations, lack of pyramidal carapace sculpturing, a less flared and unsertated posterior carapacial margin, a flat cervical scute, a V-shaped groove on the visceral side of the nuchal, and a wide vertebral I that contacts marginal II.

Comments. This taxon was recently described in detail by Holman and Fritz (2001) based on multiple specimens and their results are followed herein. Holman and Fritz (2001) argued that *Glyptemys valentinensis* is the last common ancestor of the extant *Glyptemys insculpta* and *Glyptemys muhlenbergii*, but a phylogenetic analysis is still outstanding that would corroborate that claim.

Graptemys kernerii Ehret and Bourque, 2011

Taxonomic history. *Graptemys kernerii* Ehret and Bourque, 2011 (new species).

Type material. UF 239000 (holotype), a nearly complete skull (Ehret and Bourque 2011, figs. 2, 3).

Type locality. Suwannee River, boundary between Gilchrist and Dixie Counties, Florida, USA (Ehret and Bourque 2011; Figure

6); Rancholabrean NALMA, Ionian–Tarantian, late Pleistocene (Ehret and Bourque 2011).

Referred material and range. Late Pleistocene (Ionian–Tarantian), Rancholabrean NALMA, Gilchrist and Columbia Counties, Florida, USA (referred material of Ehret and Bourque 2011).

Diagnosis. *Graptemys kernerii* can be diagnosed as a member of *Pan-Emydidae* based on the full list of characters listed for that clade above and as a member of *Graptemys* based on the presence of broad and flat tritulating surfaces with contributions from the palatine and pterygoid, an interorbital region that is broader than the nasal chamber, and contact of the parietal with the palatine and of the pterygoid with the exoccipital. *Graptemys kernerii* differs from other *Graptemys* by the development of shorter and wider skull and mandibles, rounded and deeply notched border of maxilla, enlarged processus trochlearis oticum, a deep and trench-like canal for the stapedia artery on the parietal bone, a reduced inferior process of the parietal associated with an expanded passage between the orbital and inferior temporal fossae, a wider, U-shaped mandible, a shallow symphyseal sulcus for tritulating pads, a broad, thickened bulge at the symphysis that runs the entire length of the symphysis, and a low and round coronoid processes (based on Ehret and Bourque 2011).

Comments. *Graptemys kernerii* was recently described in detail by Ehret and Bourque (2011) based on beautifully preserved material from the Pleistocene of Florida. The validity and placement of this species are not controversial.

Pseudemys Gray, 1856

Type species. *Testudo concinna* LeConte, 1830.

Diagnosis. *Pseudemys* can be diagnosed as a member of *Emydidae* based on the full list of characters listed for that clade above. *Pseudemys* can be differentiated from other emydids by the presence of a short and deep skull, broad contact of the maxilla and quadratojugal, flattened ventrally mandible, a well-defined cusp at the anterior margin of the middle ridge of the upper tritulating surface, a long cervical scute, and lateral covering of the nuchal by pleural I.

Pseudemys carri (Rose and Weaver, 1966), comb. nov.

Taxonomic history. *Chrysemys carri* Rose and Weaver, 1966 (new species); *Chrysemys caelata* = *Chrysemys carri* Jackson 1976 (junior synonymy).

Type material. UF 9427 (holotype), an almost complete shell (Rose and Weaver 1966, fig. 41).

Type locality. McGehee Site, Alachua County, Florida, USA (Rose and Weaver 1966; Figure 6); early Hemphillian NALMA, Tortonian, late Miocene (Hulbert 2001).

Referred material and range. No material has been referred to date.

Diagnosis. *Pseudemys carri* can be diagnosed as a member of *Emydidae* and *Pseudemys* by the full list of shell characters listed for those clades above. *Pseudemys carri* differs from extant *Pseudemys* and *Pseudemys williamsi* in the long visceral and the longer ventral overlap of the gular onto the entoplastron. *Pseudemys carri* further differs from *Pseudemys concinna* and is more similar to *Pseudemys williamsi* in the unnotched pygal and the smooth border of the posterior peripherals and from *Pseudemys williamsi* in the rugose dorsal carapace surface.

Comments. *Pseudemys carri* and *Pseudemys williamsi* are based on relatively complete shell material from the same late Miocene locality in Florida (Rose and Weaver 1966; Auffenberg 2001). Only two differences are available to distinguish these two species: the length of visceral cervical scute overlap and the rugosity of the carapace, characters that are known to be diagnostic between closely related extant emydids. The presence of two species in the same locality is supported by the sympatry of extant *Pseudemys* species across much of the current range (TTWG 2017). *Pseudemys williamsi* and *Pseudemys carri* are therefore herein both considered to be valid. Jackson (1976) suggested that the late Miocene *Chrysemys carri* is a junior synonym of the Pleistocene *Pseudemys caelata*, but the latter is considered to be a nomen dubium herein. Rose and Weaver (1966) noted similarities of *carri* and *williamsi* with the extant *Pseudemys concinna* but referred both to *Chrysemys*, as this genus was then thought to be synonymous with *Pseudemys*. I here follow Auffenberg (2001) by referring both to *Pseudemys*. This taxon should not be confused with *Deirochelys carri* Jackson, 1978 (see above).

Pseudemys williamsi (Rose and Weaver, 1966)

Taxonomic history. *Chrysemys williamsi* Rose and Weaver, 1966 (new species); *Pseudemys williamsi* Auffenberg 2001 (new combination).

Type material. UF 11561 (holotype), an almost complete shell (Rose and Weaver 1966, fig. 1).

Type locality. McGehee Site, Alachua County, Florida, USA (Rose and Weaver 1966; Figure 6); early Hemphillian NALMA, Tortonian, late Miocene (Hulbert 2001).

Referred material and range. Late Miocene (Tortonian), early Hemphillian NALMA, type locality (referred material of Rose and Weaver 1966).

Diagnosis. *Pseudemys williamsi* can be diagnosed as a member of *Emydidae* and *Pseudemys* by the full list of shell characters listed for those clades above. *Pseudemys williamsi* resembles *Pseudemys concinna* in the presence of a short, viscerally-overlapped cervical onto the nuchal and short gular overlap on the entoplastron, but differs in the presence of an unnotched pygal and unserrated peripherals.

Comments. See *Pseudemys carri*.

“*Pseudemys*” *idahoensis* Gilmore, 1933

Taxonomic history. *Pseudemys idahoensis* Gilmore, 1933 (new species); *Trachemys idahoensis* = *Chrysemys platymarginata* Jackson 1988 (new combination, senior synonym).

Type material. USNM 12059 (holotype), an almost complete skeleton (Gilmore 1933, figs. 1–5, pls. 1–3).

Type locality. *Plessipus* Quarry, near Hagerman, Twin Falls County, Idaho, USA (Gilmore 1933; Figure 6); Hagerman lake beds, Blancan NALMA, Pliocene (Hart and Brueske 1999).

Referred material and range. No specimens have been referred to date.

Diagnosis. “*Pseudemys*” *idahoensis* can be diagnosed as a member of *Pan-Emydidae* based on the full list of characters provided for that clade above. “*Pseudemys*” *idahoensis* differs from *Pseudemys* in the absence of a contact between the maxilla and quadratojugal, smaller foramen palatinum posterius, the absence of cusps at the end of the median maxillary ridge, the presence of a longer pterygoid that touches the exoccipital and from *Graptemys* based on the contact between the maxilla and quadratojugal and contact of the pterygoid with the basioccipital. “*Pseudemys*” *idahoensis* furthermore differs from all other pan-testudinoidea in the presence of an anterolateral projection of vertebral I onto peripheral I in combination with an overlap of pleural 1 onto the lateral parts of the nuchal.

Comments. “*Pseudemys*” *idahoensis* is based on an almost complete skeleton from the Pliocene of Idaho (Gilmore 1933). The species was originally referred to *Pseudemys*, but Jackson (1988) felt attribution to *Trachemys* to be more appropriate, and the phylogenetic analysis of Joyce et al. (2013) suggested affinities with *Graptemys*. In my own assessment, the type material preserves characters that refute attributions both to *Pseudemys* and to *Graptemys*. I therefore here use the original generic attribution, highlighting phylogenetic uncertainty with quotation marks, and place “*Pseudemys*” *idahoensis* in a basal polytomy within *Deirochelyinae*.

Terrapene Merrem, 1820

Type species. *Testudo carolina* Linnaeus, 1758.

Diagnosis. *Terrapene* can be diagnosed as a member of *Emydidae* based on the full list of characters provided for that clade above. *Terrapene* can be differentiated from other emydidae by the development of a hinge between the hyoplastron and hypoplastron, ligamentous bridge, absence of buttresses, covering of the entoplastron by the gulars and humerals, medial contact of the posterior costals, and a single suprapygial.

Comments. Barbour and Stetson (1931) revised the Pleistocene species of *Terrapene* from Florida and concluded that the most important diagnostic characters for the various *Terrapene* spp. are the shape and proportions of the carapace, presence or absence of keels, shape of vertebral I, and amount of flaring of the posterior peripherals. In his revision of the Pleistocene species from Florida, Auffenberg (1958) later showed that these characters are quite variable within the genus. His revision of the taxonomy of Pleistocene *Terrapene* from Florida furthermore concluded that *Terrapene putnami* Hay, 1906a and, possibly, *Terrapene singletoni* Gilmore, 1927 are subspecies of the extant *Terrapene carolina* Linnaeus, 1758. The work of Auffenberg (1958) is largely followed here, but these taxa are elevated to the species level.

“*Terrapene*” *corneri* Holman and Fritz, 2005

Taxonomic history. *Terrapene corneri* Holman and Fritz, 2005 (new species).

Type material. USNM 21618 (holotype), a near complete anterior plastral lobe (Holman and Fritz 2005, fig. 4).

Type locality. USNM locality Wt-15A, Webster County, Nebraska, USA (Holman and Fritz 2005; Figure 6); Myers Farm local fauna, late Barstovian NALMA, Serravallian, middle Miocene (Holman and Fritz 2005).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Terrapene corneri* can be diagnosed as a member of *Pan-Emydidae* and *Terrapene* based on all characters listed above for these clades. *Terrapene corneri* resembles *Terrapene coahuila*, but differs from all other *Terrapene* species in the presence of wide visceral covering of the plastron by the gulars and humerals. *Terrapene corneri* differs from *Terrapene coahuila* by having a narrower anterior plastral lobe that is notched at the margins of the humerals and pectorals.

Comments. “*Terrapene*” *corneri* is based on a single plastral lobe from the Miocene of Nebraska that provides only limited anatomical information. With the exception of *Terrapene coahuila*, Holman and Fritz (2005) noted that this taxon is different from most extant and extinct *Terrapene* in the nature of the visceral covering of the plastron. The differences with the extant *Terrapene coahuila* mentioned by Holman and Fritz (2005) are few and possibly subject to variation (the shape of the anterior lobe), but are sufficient, for the moment, to tentatively propose the distinction between these two taxa with significant temporal and geographical distance. Joyce et al. (2012) included this taxon in their phylogenetic analysis and concluded that the taxon is highly unstable as a result of the large amount of missing data. They also found no support of the placement of this taxon within the crown *Terrapene* and therefore used quotation marks to highlight generic uncertainty. A reanalysis of the matrix of Joyce et al. (2012) using implicit enumeration in TNT (Goloboff et al. 2008) reveals that “*Terrapene*” *corneri* indeed is a wildcard taxon and may even be placed outside the *Emys* + *Terrapene*. In several trees, however, it is placed within crown *Terrapene*. “*Terrapene*” *corneri* is therefore herein placed in a basal polytomy along the stem of *Terrapene*.

Terrapene eurypygia (Cope, 1869–70) (= *Toxaspis anguillulatus* Cope, 1899)

Taxonomic history. *Cistudo eurypygia* Cope, 1869–70 (new species); *Terrapene eurypygia* Hay 1902 (new combination); *Terrapene eurypygia* = *Toxaspis anguillulata* Hay 1908 (senior synonym, mandatory change); *Terrapene carolina* = *Terrapene eurypygia* Milstead 1965 (junior synonymy); *Terrapene carolina carolina* = *Cistudo eurypygia* = *Testudo munda* = *Toxaspis anguillulatus* TEWG 2015 (junior synonymy).

Type material. AMNH 1484 (holotype), carapacial fragments (Hay 1908, figs. 466, 470).

Type locality. Oxford Neck, Talbot County, Maryland, USA (Cope 1869–70; Figure 6); Irvingtonian NALMA, Pleistocene (Hay 1908).

Referred material and range. Pleistocene, Irvingtonian NALMA, Montgomery County, Pennsylvania, USA (type material of *Toxaspis anguillulatus* and referred material of Hay 1902).

Diagnosis. *Terrapene eurypygia* can be diagnosed as a member of *Pan-Emydidae* based on the full list of characters mentioned above and of *Terrapene* based on the medial contact of costals VIII and the single suprapygal. *Terrapene eurypygia* differs from other *Terrapene* in the presence of a contact between the vertebral V and marginal X.

Comments. *Terrapene eurypygia* is based on material recovered from poorly dated cave sediments exposed in Maryland, USA (Hay 1908). I am unaware of any literature discussing the age of these cave deposits, but I tentatively conclude that the presence of *Mammuthus* renders an Irvingtonian age plausible. The type material consists of isolated carapace fragments from at least two individuals, in particular the anterior and posterior portions of a carapace and a peripheral series (Hay 1908). The material lacks a contact between vertebral I and marginal II, a medial contact of costals VIII is present, a single, pentagonal, suprapygal is present, vertebral V expands onto the pygal and contacts marginal X, and marginals XII are present. These characters allow attribution of *Terrapene eurypygia* to *Terrapene*. Milstead (1965) suggested that this taxon is synonymous with the extant *Terrapene carolina*, but I find that the contact between vertebral V and marginal X allows distinction from the extant *Terrapene carolina*. *Terrapene eurypygia* generally resembles *Terrapene coahuila*, but differs in the presence of a pentagonal suprapygal that contacts peripheral X along a short posterolateral suture. Given the geographic distance between extant *Terrapene coahuila* and *Terrapene eurypygia*, the latter is tentatively considered to be a valid species. The phylogenetic analyses presented herein universally recover *Terrapene eurypygia* within crown *Terrapene*.

The type material of *Toxaspis anguillulatus* consists of a partial carapace from the Pleistocene of Pennsylvania that was figured by Cope (1889) and Hay (1908). As correctly noted by Hay (1908), the unusual contact between the vertebral V and marginal X does not allow distinction from *Terrapene eurypygia*. As such, *Toxaspis anguillulatus* is herein considered to be its junior synonym.

Terrapene parornata Joyce et al., 2012

Taxonomic history. *Terrapene parornata* Joyce et al., 2012 (new species).

Type material. OMNH 58158 (holotype), an almost complete shell (Joyce et al. 2012, fig. 2).

Type locality. OMNH locality V671, Buckshot Arroyo, Beaver County, Oklahoma, USA (Figure 6); Buis Ranch local fauna, Hemphillian 4 NALMA, Messinian/Zanclean boundary, Miocene/Pliocene boundary (Joyce et al. 2012).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Terrapene parornata* can be diagnosed as a member of *Terrapene* based on the full list of characters provided above and of the *Terrapene ornata* group by the anterior contact of neurals III and IV with costals III and IV, respectively, presence of a small contact between the suprapygal and eleventh peripherals, and development of a thin peripheral lip for articulation with the posterior plastral lobe during shell closure. *Terrapene parornata* can be differentiated from other member of this group by presence of a complete neural series that fully separates the costals and placement of the vertebral III/IV sulcus on neural VII.

Comments. This species is based on a near complete shell from the Miocene/Pliocene boundary of Oklahoma and its validity is therefore not controversial. The phylogenetic analyses in Joyce et al. (2012) overall resulted in collapsed relationships within *Terrapene*, but *Terrapene parornata* was nevertheless proposed to be a sister of *Terrapene ornata* following the majority-rule topology. This study confirms these results and *Terrapene parornata* is therefore shown in a basal polytomy with other *Terrapene*.

Terrapene putnami Hay, 1906a

(= *Terrapene canaliculata* Hay, 1907 = *Terrapene antipex* Hay, 1916a = *Terrapene llanensis* Oelrich, 1953)

Taxonomic history. *Terrapene putnami* Hay, 1906a (new species); *Terrapene carolina putnami* = *Terrapene antipex* = *Terrapene canaliculata* Auffenberg 1958 (referral to subspecies level, junior synonymy); *Terrapene carolina major* = *Cistudo marnochii* = *Terrapene antipex* = *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene putnami* TTWG 2017 (junior synonymy).

Type material. UF 3066 (neotype), complete shell and associated skeletal elements (Ehret et al. 2013, fig. 1) that formally replaces AMNH 6097, the original type material of Hay (1906a) (see ICZN 2016).

Type locality. Haile 8A, Alachua County, Florida, USA (Ehret et al. 2013; Figure 6); red zone of Haile 8A deposits, late Rancholabrean, Ionian–Tarantian, late Pleistocene (Hulbert 2001; Ehret et al. 2013).

Referred material and range. Pleistocene, Hillsborough County, Florida, USA (type material of *Terrapene putnami*); Pleistocene, Whitemarsh or Skedaway Island, Georgia, USA (type material of *Terrapene canaliculata*; material referred to *Terrapene putnami* by Auffenberg 1958); Pleistocene, Rancholabrean NALMA, Vero Beach, St. Lucie County, Florida, USA (material referred to *Terrapene canaliculata* by Gilmore 1927); Pleistocene, Rancholabrean NALMA, Friesenhahn Cave, Bexar County, Texas, USA (material referred to *Terrapene canaliculata* by Milstead 1956); late Pleistocene, Brevard County, Florida, USA (material referred to *Terrapene putnami* by Hay 1916a); Pleistocene, Vero, St. Lucie County, Florida, USA (type material of *Terrapene antipex*; material referred to *Ter. putnami* by Auffenberg 1958); Pleistocene, St. Johns County, Florida, USA (material referred to *Terrapene antipex* by Hay 1916a); Pleistocene,

Alachua, Brevard, Citrus, Columbia, Hardy, Levy County, Manatee, Marlon, Orange, Pinellas, Sarasota, and St. Johns County, Florida, USA (referred material to *Terrapene putnami* by Auffenberg 1958); Pleistocene, Meade County, Kansas, USA (type material of *Terrapene llanensis*); Pleistocene, Miller County, Arkansas, USA (material referred to *Terrapene carolina putnami* by Davis et al. 2000); late Pleistocene, near Columbus, Mississippi (referred material to *Terrapene putnami* by Jackson and Kaye 1974a); late Pleistocene, Hickory County, Missouri (referred material to *Terrapene putnami* by Moodie and van Devender 1977).

Diagnosis. *Terrapene putnami* can be diagnosed as a member of *Terrapene* based on the full list of characters mentioned above. *Terrapene putnami* differs from other *Terrapene* by its large size, dorsoventrally depressed shell, widely flared peripherals, and the presence of a well developed axillary scute.

Comments. *Terrapene putnami* was originally based on a single hypoplastral bone from the Pleistocene of Florida that can be referred to *Terrapene* based on the presence of the hyo-hyoplastral hinge. Hay (1906a, 1908) diagnosed this taxon based on its larger size, but the reported maximum carapace length of 265 mm is actually within range of extant taxa (Burroughs et al. 2013 and references therein). Hay (1908) attributed additional specimens from Hillsborough County to this taxon some (Hay 1908), but as these specimens do not present overlapping parts with the type specimen, some uncertainty remains. The referred posterior carapace (Hay 1908, fig. 462) is certainly distinct from *Terrapene eurypygia* in the absence of contact between the vertebral V and marginal X. In his review of the Pleistocene turtles from Florida, Auffenberg (1958) redefined *Terrapene putnami* as a subspecies of *Terrapene carolina* and broadly referred all specimens of large size and a well-developed axillary scale.

Ehret et al. (2013) recently presented a formal request to replace the undiagnostic type specimen, AMNH 6097, with the neotype, UF 3066, which includes a complete shell and various appendicular elements, a case broadly supported (e.g., Thomson and Baggi 2014) and then approved (ICZN 2016). The designation of a neotype allows solidification of the validity of this taxon and refutation of proposed synonymies with extant *Terrapene* spp. All phylogenetic analyses herein recovered *Terrapene putnami* within crown *Terrapene*.

Terrapene singletoni Gilmore, 1927

Taxonomic history. *Terrapene singletoni* Gilmore, 1927 (new species); *Terrapene carolina singletoni* Auffenberg 1958 (new combination); *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene impressa* = *Terrapene innoxia* = *Terrapene llanensis* = *Terrapene singletoni* Kuhn 1964 (junior synonymy); *Terrapene carolina bauri* = *Terrapene innoxia* = *Trachemys nuchoecarinata* = *Terrapene singletoni* TEWG 2015 (junior synonymy).

Type material. USNM 11181 (holotype), a partial carapace (Gilmore 1927, pl. 1).

Type locality. 3 km west of Melbourne, Brevard County, Florida, USA (Gilmore 1927; Figure 6); late Pleistocene, Ranchoabrean NALMA (Gilmore 1927; Morgan and Seymour 1997).

Referred material and range. No referred material known to date.

Diagnosis. *Terrapene singletoni* can be diagnosed as a member of *Terrapene* based on the characters listed above. *Terrapene singletoni* differs from other *Terrapene* by its large-sized, thin shell, absence of a lateral keel above the bridge, less flared peripherals, and absence of an axillary scale.

Comments. *Terrapene singletoni* is based on a partial carapace from the Pleistocene of Florida (Gilmore 1927). In his revision of Pleistocene *Terrapene* from Florida, Auffenberg (1958) noted that *Terrapene singletoni* may be intermediate between *Terrapene putnami* and *Terrapene carolina* but, nevertheless, recognized it as a valid species based on the character listed in the diagnosis above. These views are followed herein. All phylogenetic analyses undertaken herein recover *Terrapene singletoni* within crown *Terrapene*.

“*Trachemys*” *antiqua* Clark, 1937

Taxonomic history. *Trachemys antiqua* Clark, 1937 (new species); *Pseudemys antiqua* Kuhn 1964 (new combination); *Chrysemys antiqua* Hutchison 1996 (new combination).

Type material. YPM VPPU 013839 (holotype), almost complete plastron with portions of the right bridge and carapace posterior border (Clark 1937, fig. 10).

Type locality. 3 km southeast of Cedar Butte, Pennington County, South Dakota, USA (Clark 1937; Figure 5); Chadron Formation, Chadronian NALMA, Priabonian, late Eocene (Clark 1937; Woodburne 2004).

Referred material and range. Late Eocene (Priabonian), Chadronian NALMA, White River Formation, Weld County, Colorado, USA; late Eocene (Priabonian), Chadronian NALMA, Chadron Formation, Stark County, North Dakota, and Indian Creek, Pennington County, South Dakota, USA; early Oligocene (early Rupelian), Brule Formation, Orellan NALMA, Dawes County, Nebraska, USA; early Oligocene, (mid Rupelian), Brule Formation, Whitneyan NALMA, Oglala Lakota (formerly Shannon) County, South Dakota, USA (referred material to *Chrysemys antiqua* of Hutchison 1996).

Diagnosis. “*Trachemys*” *antiqua* can be diagnosed as a member of *Emydidae* based on the characters mentioned above. “*Trachemys*” *antiqua* can be distinguished from other emydids based on the lateral covering of the nuchal by pleural I, no contact between vertebral I and marginal II, an elongated cervical scute, a wide and trapezoidal suprapygal I, small entoplastron, placement of humero-pectoral sulcus well posterior to the entoplastron, absence of plastral hinge, and contact between the inguinal and femoral scutes in ventral view.

Comments. “*Trachemys*” *antiqua* was first described based on a complete plastron and a partial carapacial from the late Eocene of South Dakota (Clark 1937). The preserved morphological information in the type specimen is not enough to diagnose a valid taxon. Hutchison (1996) more recently referred several specimens to this taxon that significantly expand the temporal range of this taxon to the early Oligocene and provide information regarding its entire shell morphology. Hutchison (1996) noted similarities of *antiqua* with the extant *picta* and therefore

united both within *Chrysemys*. In my opinion, it is difficult to find clear diagnostic characters for “*Trachemys antiqua*” due to its overall plesiomorphic pan-emydid morphology. My phylogenetic analysis variously places “*Trachemys antiqua*” either as sister to *Trachemys* + *Pseudemys* clade or as sister to all extant deirochelyines, thereby questioning an affiliation with *Chrysemys*, as already noted by Joyce et al. (2013). However, all analyses herein confirm the views of Near et al. (2005), Lourenço et al. (2012), and Joyce et al. (2013) that this is the oldest member of crown *Emydidae*. As more work is needed to characterize the morphology and phylogenetic relationships of this taxon, I here highlight taxonomic ambivalence through the use of quotation marks.

Trachemys sculpata Hay, 1908

Taxonomic history. *Trachemys sculpata* Hay, 1908 (new species); *Pseudemys sculpata* Kuhn 1964 (new combination); *Chrysemys scripta petrolei* = *Trachemys bisornata* = *Trachemys delicata* = *Trachemys euglypha* = *Trachemys sculpata* = *Trachemys trulla* Weaver and Robertson 1967 (junior synonymy); *Trachemys scripta scripta* = *Emys euglypha* = *Trachemys delicata* = *Trachemys sculpata* TEWG 2015 (junior synonymy).

Type material. USNM 16681 (holotype), a nuchal plate (Hay 1908, pl. 45.4).

Type locality. Peace River, Hillsborough County, Florida, USA (Hay 1908; Figure 6); Pleistocene (Hay 1908).

Referred material and range. Pleistocene, Hillsborough and Brevard County, Florida, USA (referred material of Hay 1916a and Gilmore 1930, respectively).

Diagnosis. *Trachemys sculpata* can be diagnosed as a member of *Pan-Emydidae* based on the characters listed for the clade above. *Trachemys sculpata* can be distinguished from other emydid based on the presence of wedge-shaped costals III–V in combination of hexagonal neural plates. *Trachemys sculpata* is associated with *Trachemys* based on the presence of an elongated cervical and covering of the lateral parts of the nuchal by pleural I.

Comments. The type material of *Trachemys sculpata* consists of a nuchal plate from the Pleistocene of Florida that has a long and narrow cervical scute and covering of the lateral parts of the nuchal by pleural I. Hay (1908) furthermore referred two hexagonal neurals with short antero-lateral sides and two partial costal plates from the type locality to this taxon. Like so many other taxa from the Pleistocene of Florida, the type material lacks diagnostic characters and under normal circumstances I would conclude this to be yet another nomen dubium. However, Hay (1916a) and Gilmore (1930) referred more complete material that reveals the unusual presence of wedge-shaped costals III–V that differ from those of pan-testudinids in not being associated with alternating quadrangular and octagonal neurals. All previously proposed synonymy with extant taxa (e.g., Weaver and Robertson 1967; TEWG 2015) can therefore be rejected with confidence. Assuming that the referred shells indeed represent the same taxon as the type specimen, I confirm the validity of *Trachemys sculpata*. The phylogenetic analysis performed herein

provides moderate support for a sister group relationship with extant *Trachemys*.

Pan-Geoemydidae Joyce, 2007

Phylogenetic definition. The name *Pan-Geoemydidae* is herein referred to the total clade of crown clade *Geoemydidae* (see below).

Diagnosis. Pan-geoemydids can be diagnosed as members of *Pan-Testudinoidea* based on the full list of characters presented for that clade above. Members of *Pan-Geoemydidae* are differentiated from other pan-testudinoids by the presence of musk ducts and associated musk duct foramina, wide rib heads, a narrow costo-vertebral tunnel, and paired marginals XII that expand on the suprapygal II.

Geoemydidae Theobald, 1868

Phylogenetic definition. The name *Geoemydidae* is here referred to the most inclusive crown clade that includes *Geoemyda* (orig. *Testudo*) *spengleri* (Gmelin, 1789), but not *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758) or *Testudo graeca* Linnaeus, 1758.

Diagnosis. As for *Pan-Geoemydidae*.

Comments. As global phylogenies are still lacking for pan-geoemydids, it is currently not possible to rigorously diagnose the crown clade relative to its stem lineage.

Bridgeremys pusilla (Hay, 1908) (= *Clemmys morrisiae* Hay, 1908)

Taxonomic history. *Echmatemys pusilla* Hay, 1908 (new species); *Rhinoclemmys pusilla* McDowell 1964 (new combination); *Bridgeremys pusilla* = *Clemmys morrisiae* Hutchison 2006 (new combination and senior synonym).

Type material. AMNH 5992 (holotype), a partial shell (Hay 1908, figs. 445, 446).

Type locality. Grizzly Buttes, Uinta County, Wyoming, USA (Hay 1908; Figure 5); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Referred material and range. Early–middle Eocene (Ypresian–Lutetian), Bridgerian NALMA, Sweetwater and Uinta Counties, Wyoming, USA (type material of *Clemmys morrisiae*; referred material of Hutchison 2006); middle Eocene (Lutetian), Uintan NALMA, Uintah County, Utah, USA (referred material of Gilmore 1915).

Diagnosis. *Bridgeremys pusilla* can be diagnosed as a member of *Geoemydidae* based on the presence of axillary and inguinal musk duct foramina and paired marginals XII that expand onto suprapygal II. *Bridgeremys pusilla* differs from all other North American *Geoemydidae* based on small size, presence of octagonal neurals (II or III) and hexagonal neurals with posterolateral short sides, a possible hinge between the hyo- and hypoplastra,

and poorly developed anal notch and axillary and inguinal buttresses.

Comments. *Echmatemys pusilla* is based on a partial shell from the Bridger Eocene of Wyoming (Hay 1908). Hutchison (2006) recently reviewed all material relevant to *Bridgeremys pusilla*, provided a complete account of its anatomy, and presented convincing evidence for its validity and placement within Geoemydidae. There is little doubt about the distinction of this turtle relative to coeval and sympatric *Echmatemys* spp. To highlight its distinct nature, Hutchison (2006) proposed the new genus *Bridgeremys* to include *Echmatemys pusilla* and its synonym *Clemmys morrisiae*. As both taxa were named in the same publication (Hay 1908), Hutchison (2006), as the first reviser, gave priority to *pusilla* over *morrisiae*, because it is based on more complete remains. McDowell (1964) concluded that *Echmatemys pusilla* can be placed within *Rhinoclemmys*, but Hutchison (2006) suggested instead that it is sister to this taxon. All equal-weighted phylogenetic analyses herein show that *Bridgeremys* is distinct, more basal than *Echmatemys*, and placed within the *Sacalia* + *Melanochelys* clade. Under implied weights, however (i.e., following weighting over homoplasy), *Bridgeremys* is placed in a more derived position, just basal to *Echmatemys*. The former hypothesis implies at least two dispersals of geoemydids from Asia to North America prior to the early Eocene, whereas the latter suggests only a single such event. If indeed closely related, the large apparent differences between the two taxa in the neural series may be the result of adaptation to different environments (i.e., a more terrestrial habitat for *Bridgeremys* and a more aquatic one for *Echmatemys* spp.) as suggested by Hutchison (1996). Based on these preliminary results, I will be retaining *Bridgeremys* as a distinct genus, as it highlights its differences with *Echmatemys* spp., even if they are closely related. See *Clemmys morrisiae* for further information on synonymy.

Echmatemys Hay, 1906a

Type species. *Emys septarius* Cope, 1873b, herein considered junior synonym of *Echmatemys stevensoniana* (Leidy, 1870a).

Diagnosis. *Echmatemys* can be diagnosed as a member of *Geoemydidae* based on the characters mentioned above. *Echmatemys* differs from other *Geoemydidae* based on the presence of narrow triturating surfaces, a short cervical scute, mostly hexagonal neurals II–VIII with short antero-lateral sides, a posteriorly flared carapace margin, anals that are shorter medially than the femorals, and well-developed axillary and inguinal buttresses.

Comments. Fossil turtles referable to *Echmatemys* are a common occurrence in Eocene deposits in Wyoming, Utah, and New Mexico. Many *Echmatemys* spp. were originally described as members of *Emys*, until Hay (1906a) created the new genus *Echmatemys* for Eocene turtles characterized by the presence of well-developed axillary and inguinal buttresses and a narrow triturating surface on the dentary. Within the context of North American pan-testudinoids, this group is easily identified based on its morphology. In recent years, *Echmatemys* has been interpreted as a member of *Geoemydidae* (Hirayama 1984; Claude

and Tong 2004), but its supposed basal position within this clade is questioned herein (see Phylogenetic Relationships above). The position within *Geoemydidae* is confirmed in particular by the presence of musk duct foramina (Claude and Tong 2004; Hutchison 2006). It is not always possible to observe this character in all *Echmatemys* spp. due to preservation, but I was able to clearly see them at least in *Echmatemys naomi* (anteriorly and posteriorly), *Echmatemys wyomingensis* (posteriorly), *Echmatemys jeanesi* type (posteriorly), *Echmatemys arethusia* type (anteriorly and posteriorly), and *Echmatemys cyane* (posteriorly). As a result, it is relatively easy to distinguish the members of *Echmatemys* from other North American pan-testudinoids. The diagnostic characters of this genus (narrow triturating surface, well-developed buttresses), together with the short cervical scute, support a derived position within *Geoemydidae*. All analyses herein, however, reveal a close relationship between *Echmatemys* and *Mauremys* based on the neural II–III pattern and the presence of a contact between vertebral I and marginal II, at least in some species of *Echmatemys*. It should be noted here, however, that this relationship is shown only on the basis of shell morphology as only limited information is available from skulls.

Because of the lack of apparent synapomorphies, Hirayama (1984) raised questions about the monophyly of *Echmatemys*. Although within the context of North American pan-testudinoids there is no issue with the monophyly of *Echmatemys*, the global total evidence analyses herein failed to show the monophyly of all valid *Echmatemys* spp., although both the equal- and implied-weight analyses supported the monophyly of a derived *Echmatemys* clade comprising the Bridgerian *Echmatemys haydeni*, *Echmatemys stevensoniana*, *Echmatemys naomi*, the Bridgerian–Uintan *Echmatemys wyomingensis*, and the Wasatchian–Uintan *Echmatemys lativertebralis* complex. In either case, *Echmatemys jeanesi* and *Echmatemys callopyge* are placed just outside of the core *Echmatemys* clade interspersed with various *Mauremys*. As such, these two species are only tentatively grouped with *Echmatemys* herein.

Hay (1906a) designated *Emys septarius* Cope, 1873b as the type species of *Echmatemys*, probably due to the clear presence of the enlarged inguinal buttresses that characterize the members of this genus. *Emys cibollensis* and *Emys lativertebralis* were the other two species originally included in this genus. Herein *Emys septarius* is considered to be a junior synonym of *Echmatemys stevensoniana*. Following Article 67.1.2 of the ICZN (1999), the name of the type species remains unchanged, but a reference to the synonymy is added above.

Soon after the establishment of *Echmatemys*, Hay (1908) referred many other previously named taxa to this genus and named several new species. Hay (1908) argued in favor of maintaining species that are typologically distinct and suggested that future authors with more information at hand should determine the validity of these species (Hay 1908). Since then, all named *Echmatemys* spp. were typically considered to be distinct, valid species, but some synonymies are proposed herein. The first named taxon within *Echmatemys* is *Emys wyomingensis* Leidy, 1869 from the Bridger Eocene of Wyoming. Leidy (1870a, b) later named three additional species, namely *stevensoniana*, *jeanesi*, and *haydeni*, from the same deposits, to which he later referred additional material (Leidy 1871c). Leidy (1873:140) later speculated that the four species he named may represent a single species but noted that “I admit that I may be wrong in this determination [i.e., referring all to a single species], but if such

is the case, it would appear that almost every specimen presents characters to distinguish a species.” In order to rigorously delimit *Echmatemys* species, a solid understanding is necessary of intraspecific variation. Crucial for this task is a slab with 18 specimens of *Echmatemys* from Wyoming, published by Gilmore (1945). Those specimens were not described in detail, but personal observations allow me to preliminarily assess intraspecific variation and to evaluate the diagnostic value of various characters used in the literature to distinguish species of *Echmatemys*. Hay (1908) proposed the synonymy of *wyomingensis* and *jeanesi*, but he considered *haydeni* and *stevensoniana* to be distinct species. In the view of Hay (1908), *haydeni* can be distinguished from the others by the greater visceral extent of the axillary and inguinal buttresses, but he did not clearly state differences between *stevensoniana* and *wyomingensis*. Two of the species named by Hay (1908) in particular, *callopyge* and *naomi*, as well as *lativertebralis* Cope, 1877a and possibly *cibollensis* Cope, 1877a, preserve characters that distinguish them from the Fort Bridger morphotypes and are treated as distinct species herein. All the above-mentioned taxa are used herein to characterize the basic morphotypes within *Echmatemys*: presence of octagonal neurals (in *wyomingensis* neural V/VI can be octagonal; in *haydeni* neural IV and/or neural II are octagonal; the rest are hexagonal with short anterolateral sides), covering of the lateral parts of the nuchal by pleural I (present in *jeanesi*, *lativertebralis*, *callopyge*), contact between vertebral I and marginal II (clear contact in *stevensoniana*, *lativertebralis*, *naomi*), shape of suprapygal I (rectangular as long as wide in *jeanesi*, *haydeni*, *callopyge*; longer than wide in *wyomingensis*, *lativertebralis*, *naomi*; much longer than wide in *stevensoniana*), crossing of suprapygal I by the vertebral IV/V sulcus (present in *stevensoniana*); position of humero-pectoral sulcus relative to the posterior side of the entoplastron (coinciding in *jeanesi*; crossing the posterior part in *wyomingensis*, *haydeni*, *stevensoniana*, *cibollensis*, *arethusia*, *callopyge*, *naomi*; just posterior to the entoplastron in *lativertebralis*), and development of axillary and inguinal buttresses (well-developed in *haydeni*, *lativertebralis*, *stevensoniana*, *naomi*, reaching or exceeding the middle of the costal; less-developed in *wyomingensis* and *jeanesi*, reaching less than a third of the costal). The diagnoses of these taxa are mostly formed based on the combination of characters mentioned above and all other taxa of *Echmatemys* are placed in their synonymy or are considered as *nomina dubia* herein. Previously, more than twenty different species of *Echmatemys* were considered to be valid, with some localities (e.g., Fort Bridger) containing up to ten sympatric species. This review is more conservative in recognizing only nine different species with at most four sympatric species at any given locality. Roberts (1962) performed a similar analysis on morphological variability of *Echmatemys* based on other material from Utah and also concluded that no more than four species of *Echmatemys* are present in any particular formation. These new estimates are in accordance with modern biodiversity “hotspots” in North America (see Buhlmann et al. 2009).

Lichtig and Lucas (2015a) recently discussed changes that occur in the ontogeny of *Echmatemys* and highlighted several characters that are subject to ontogenetic variation (e.g., presence of keels on the neurals, length of the plastron relative to its width, width and depression of scute sulci, size of gular projections). These insights were used herein to disregard previously used diagnostic characters.

Echmatemys arethusia Hay, 1908

Taxonomic history. *Echmatemys arethusia* Hay, 1908 (new species).

Type material. AMNH 5920 (holotype), a partial shell (Hay 1908, figs. 421, 422, pl. 49).

Type locality. Grizzly Buttes, Uinta County, Wyoming, USA (Hay 1908; Figure 5); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Echmatemys arethusia* can be diagnosed as a member of *Echmatemys* based on the characters mentioned above. *Echmatemys arethusia* differs from other *Echmatemys* based on the following combination of characters: hexagonal neurals with short antero-lateral sides, lack of contact between vertebral I and marginal II, lack of overlap of pleural I onto the nuchal, and entoplastron covered both by the gulars and pectorals.

Comments. *Echmatemys arethusia* is based on a partial from the Uintan NALMA of Utah (Hay 1908). The mosaic of characters found in this species (see Diagnosis above) distinguish it from other *Echmatemys* spp. However, the lack of the posterior portions of the carapace prevents documenting the morphology of posterior neurals and of the suprapygal/pygal area, which would allow further corroborating or overturning of the synonymies proposed herein. The validity of *Echmatemys arethusia* is therefore only tentative.

Echmatemys callopyge Hay, 1908

Taxonomic history. *Echmatemys callopyge* Hay, 1908 (new species); *Echmatemys septaria callopyge* = *Echmatemys hollandi* = *Echmatemys obscura* Roberts 1962 (referral to subspecies level, senior synonymy).

Type material. AMNH 2087 (holotype), a complete shell (Hay 1908, figs. 447, 448, pl. 52).

Type locality. White River, Uintah County, Utah, USA (Hay 1908; Figure 5); Uinta Formation, Uintan-2 NALMA, Lutetian, middle Eocene (Hay 1908; Woodburne 2004).

Referred material and range. Middle Eocene (Lutetian), Uintan NALMA, Uintah County, Utah, USA (referred material of Gilmore 1915).

Diagnosis. *Echmatemys callopyge* can be diagnosed as a member of *Echmatemys* based on the characters mentioned for that clade above. *Echmatemys callopyge* differs from other *Echmatemys* by the following combination of characters: no contact between vertebral I and marginal II, pleural I laterally covering the nuchal, entoplastron covered by both gulars and pectorals, femorals medially much shorter than anal scutes, anterior and posterior lobes well-rounded, and a narrow and rounded anal notch.

Comments. *Echmatemys callopyge* is based on a complete shell from the Uinta Formation of Utah (Hay 1908). In a detailed analysis, Roberts (1962) concluded that *Echmatemys callopyge* cannot be distinguished from *Echmatemys septaria*, as he dismisses the width of the vertebral I as variable within a species. I here suggest, however, that this character is of diagnostic value within *Echmatemys* (see Comments for *Echmatemys* above). Not only the width of the vertebral I (e.g., if it is narrower than the nuchal or not) is diagnostic, but also the absence of contact of the vertebral I with the marginal II is diagnostic for this taxon. In addition to these characters, *Echmatemys callopyge* can be distinguished from *Echmatemys septaria* (= *Echmatemys stevensoniana* herein) based on the posterior extent of the vertebral IV, which crosses the neural VIII in *callopyge* and the suprapygal I in *stevensoniana* (see sections of *Echmatemys* and *Echmatemys stevensoniana*).

“Echmatemys” cibollensis (Cope, 1877a)

Taxonomic history. *Emys cibollensis* Cope, 1877a (new species); *Emys cibollensis* = *Emys euthmeta* Cope 1884 (junior synonymy); *Echmatemys cibollensis* Hay 1906a (new combination); *Echmatemys lativertebalis* = *Emys cibollensis* Lichtig and Lucas 2015d (junior synonymy).

Type material. USNM 2578 (lectotype), complete entoplastron (Cope 1877a, pls. 27.4, 28.3–6; Lichtig and Lucas 2015d).

Type locality. Gallina, Rio Arriba County, New Mexico, USA (Hay 1908; Figure 5); San Jose Formation, Wasatchian NALMA, Ypresian, early Eocene (Woodburne 2004).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. “*Echmatemys” cibollensis* can be diagnosed as a member of *Pan-Testudinoidea* based on the extensive covering of the plastral scutes viscerally and is tentatively associated with *Echmatemys* based on the morphology of the epiplastra. “*Echmatemys” cibollensis* differs from other *Echmatemys* by the restriction of the short and wide gulars to the epiplastra and medial covering of the epiplastra by the humeral scutes.

Comments. “*Echmatemys” cibollensis* is based on shell fragments, including a partial anterior plastral lobe, a part of the left hypo/xiphiplastron, and a peripheral (Hay 1908). Although such fragmented material is normally inadequate to clearly diagnose a taxon, the type material clearly documents that the gulars do not cover the entoplastron. This morphology has not been noted so far for any other extinct North American emydid or geoemydid. Cope (1884) suggested that *cibollensis* is a junior synonym of *Emys euthmeta*. The type material of *Emys euthmeta* includes a partial epiplastron that documents gulars that are much narrower than those of “*Echmatemys” cibollensis*, but it is not possible to observe if they cover the entoplastron. I therefore find *Emys euthmeta* to be a nomen dubium (see below). Lichtig and Lucas (2015d) suggested that the type material of “*Echmatemys” cibollensis* consists of more than one individual and designated the entoplastron USNM 2578 as the lectotype. They further suggested the synonymy between “*Echmatemys” cibollensis* and *Echmatemys lativertebalis*. In my

opinion, however, these two taxa can be distinguished by the absence of gular expansion onto the entoplastron seen in “*Echmatemys” cibollensis*. Although the absence of gulars that cover the entoplastron could be the result of intraspecific variation, I here tentatively recognize “*Echmatemys” cibollensis* as a distinct species to avoid masking this morphological difference. Based on the morphology of the epiplastral lip, *cibollensis* is probably a member of *Echmatemys*, but because information is missing for the carapace, I highlight phylogenetic uncertainty through the use of quotation marks.

Echmatemys haydeni (Leidy, 1870b)

Taxonomic history. *Emys haydeni* Leidy, 1870b (new species); *Echmatemys haydeni* Hay 1908 (new combination).

Type material. USNM 109 (holotype), a partial carapace (Leidy 1873, pl. 9.6; Hay 1908, figs. 404, 405, pl. 47.2).

Type locality. Near Fort Bridger, Uinta County, Wyoming, USA (Hay 1908; Figure 5); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Referred material and range. Early–middle Eocene (Ypresian–Lutetian), Bridgerian NALMA, Uinta County, Wyoming, USA (referred material of Hay 1908).

Diagnosis. *Echmatemys haydeni* can be diagnosed as a member of *Echmatemys* based on the characters mentioned above. *Echmatemys haydeni* differs from other *Echmatemys* based on the following combination of characters: highly differentiated neural series, with an octagonal neural IV and sometimes an octagonal neural II, and long contact between marginal I and pleural I.

Comments. See *Echmatemys*.

Echmatemys jeanesi (Leidy, 1870b) comb. nov.

Taxonomic history. *Emys jeanesi* Leidy, 1870b (new species); *Emys jeanesianus* Leidy 1871c (unjustified emendation); *Echmatemys wyomingensis* = *Emys jeanesi* Hay 1908 (junior synonymy).

Type material. USNM 962 (holotype), a partial shell (Leidy 1873, pl. 10; Hay 1908, figs. 392, 393).

Type locality. Near Fort Bridger, Uinta County, Wyoming, USA (Hay 1908; Figure 5); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Echmatemys jeanesi* can be diagnosed as a member of *Echmatemys* based on the characters mentioned above. *Echmatemys jeanesi* differs from other *Echmatemys* based on the following combination of characters: humero-pectoral sulcus crosses the entoplastron, neurals II–VIII hexagonal, pleural I

overlaps lateral parts of the nuchal, short suprapygal I, long covering of the hyoplastron by the abdominals.

Comments. See *Echmatemys*.

Echmatemys lativertebralis (Cope, 1877a)
 (= *Emys shaughnessiana* Cope, 1882 = *Chrysemys inornata* Loomis, 1904 = *Echmatemys rivalis* Hay, 1909 = *Echmatemys douglassi* Gilmore, 1915 = *Echmatemys hollandi* Gilmore, 1915 = *Graptemys cordifera* Clark, 1937)

Taxonomic history. *Emys lativertebralis* Cope, 1877a (new species); *Echmatemys lativertebralis* Hay 1906a (new combination); *Echmatemys lativertebralis* = *Emys megaulax* = *Emys pachylomus* = *Notomorpha testudinea* Lichtig and Lucas 2015a (senior synonymy); *Echmatemys lativertebralis* = *Emys cibollensis* Lichtig and Lucas 2015d (senior synonymy).

Type material. USNM 2576 (holotype), shell fragments constituting an almost complete shell (Cope 1877a, pl. 27; Hay 1908, figs. 375–378).

Type locality. Gallina, Rio Arriba County, New Mexico, USA (Hay 1908; Figure 5); San Jose Formation, Wasatchian NALMA, Ypresian, Eocene (Woodburne 2004).

Referred material and range. Early Eocene (Ypresian), Wasatchian NALMA, Sweetwater County, Wyoming, USA (type material of *Emys rivalis*) and Uintah County, Utah, USA (type material of *Echmatemys douglassi* and *Echmatemys hollandi*); early–middle Eocene (Ypresian–Lutetian), Bridgerian NALMA, Uinta County, Wyoming, USA (*Echmatemys jeanesianus* of Leidy 1871c, type material of *Emys shaughnessiana*); late Eocene (Priabonian), Chadronian NALMA, Oglala Lakota (formerly Shannon) and Washington Counties, South Dakota, USA (type material of *Chrysemys inornata* and *Graptemys cordifera*).

Diagnosis. *Echmatemys lativertebralis* can be diagnosed as a member of *Echmatemys* based on the full list of characters provided above for that clade. *Echmatemys lativertebralis* differs from other *Echmatemys* based on the following combination of characters: covering of the lateral parts of the nuchal by pleural I, contact between vertebral I and marginal II, longer than wide suprapygal I, humero-pectoral sulcus located posterior to the entoplastron, and well-developed axillary and inguinal buttresses.

Comments. The type specimen of *Emys lativertebralis* consists of numerous isolated plates of the same individual that were carefully combined to form an almost complete shell (Cope 1877a). The plates of Cope (1877a) were subsequently used by Hay (1908) to make reconstructions that remain to this day the primary reference for the morphology of this species. In the original figures, it is not possible to see the morphology of pleural I, but personal observations on the type material show that pleural I covers the lateral parts of the nuchal. The specimen shows differences with other *Echmatemys* spp., such as wide neurals (II–VIII typically hexagonal with short antero-lateral sides), position of vertebral III/IV sulcus on the posteriormost

part of neural V, a sinuous vertebral IV/V sulcus, a much longer than wide suprapygal I, long pectoral sulcus, and a deep and rounded anal notch. The placement of the humero-pectoral sulcus posterior to the entoplastron is a character that distinguishes all of the taxa mentioned above in the synonymy of *Echmatemys lativertebralis* from the remaining *Echmatemys*. Based on my own observations, I cannot reproduce a clear trend in the degree of pectoral covering on the entoplastron and I therefore tentatively propose a separation between *Echmatemys* with an entoplastron covered by gulars, humerals, and pectorals (most *Echmatemys*) and those covered only by gulars and humerals (i.e., the “*Echmatemys lativertebralis* complex”). *Echmatemys jeanesi* and “*Echmatemys*” *cibollensis* are two exceptions to the above-mentioned scheme (see relevant sections).

Some variation is apparent within the *Echmatemys lativertebralis* complex that may be used in the future as evidence for additional species. *Emys shaughnessiana* is almost identical to *Echmatemys lativertebralis*, showing all of the diagnostic characters mentioned above. *Chrysemys inornata* and *Echmatemys hollandi*, however, have pleural I covering the lateral parts of the nuchal, but do not show a contact between marginal II and vertebral I. Also, in *Chrysemys inornata* the vertebral IV/V sulcus is located on suprapygal I (as in *Echmatemys stevensoniana*). *Echmatemys douglassi* is the opposite, with a clear contact between vertebral I and marginal II, but it has a wide vertebral I that does not allow pleural I to expand onto the nuchal. *Echmatemys rivalis* and *Graptemys cordifera* share with *Echmatemys lativertebralis* only the long suprapygal I and the position of the humero-pectoral sulcus posterior to the entoplastron, but they have no contact between vertebral I and marginal II and no expansion of the pleural I onto the nuchal. There furthermore is a morphocline in the distance of the humero-pectoral sulcus compared with the posterior end of the entoplastron. The sulcus is placed just posteriorly to the entoplastron in *Echmatemys shaughnessiana*, clearly posteriorly to the entoplastron but in a short distance in *Echmatemys lativertebralis* and *Echmatemys rivalis*, and well-behind the entoplastron in *Echmatemys douglassi*, *Echmatemys hollandi*, *Chrysemys inornata* and *Graptemys cordifera*. At this point I am not confident to further divide this group based on these characters alone, but it should be noted that perhaps a distinction of the post-late Eocene taxa with the humero-pectoral sulcus situated clearly posterior to the entoplastron might be reasonable. Future work will hopefully clarify this issue. Lichtig and Lucas (2015a, 2015d) suggested a synonymy of *Echmatemys lativertebralis* with several taxa (see above). All suggested junior synonyms in Lichtig and Lucas (2015a) are herein found to be nomina dubia (see below), whereas “*Echmatemys*” *cibollensis* can be diagnosed as a distinct species (see above).

Echmatemys naomi Hay, 1908
 (= *Echmatemys obscura* Gilmore, 1915)

Taxonomic history. *Echmatemys naomi* Hay, 1908 (new species).

Type material. AMNH 5975 (holotype), a partial carapace (Hay 1908, figs. 442–444, pl. 51).

Type locality. Little Dry Creek, Grizzly Buttes, Uinta County, Wyoming, USA (Hay 1908; Figure 5); Bridger Formation,

Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Referred material and range. Early Eocene (Lutetian), Uintan NALMA, Uintah County, Utah, USA (type material of *Echmatemys obscura*); early–middle Eocene (Ypresian–Lutetian), Bridgerian NALMA, Twin Buttes, Uinta County, Wyoming, USA (material referred to *Echmatemys septaria septaria* by Roberts 1962).

Diagnosis. *Echmatemys naomi* can be diagnosed as a member of *Echmatemys* based on the characters listed for that clade above. *Echmatemys naomi* differs from other *Echmatemys* based on the following combination of characters: contact between marginal II and vertebral I, neural I much longer than wide, vertebral IV/V sulcus placed on the last neural, clear contact of large axillary scute with marginal IV and V, wide suprapygals V, and large inguinal scute that does not contact the femoral scute in ventral view.

Comments. *Echmatemys naomi* is based on a partial carapace from the Uinta Formation of Utah (Hay 1908). Among the various *Echmatemys* spp., the contact between the vertebral I and marginal II is present in *aegle*, *cyane*, *naomi*, *ocyrrhoe*, and *stevensoniana*, therefore providing some evidence for their synonymy. However, *Echmatemys naomi* Hay, 1908, shows differences (see Diagnosis above) that allow tentative distinction from the others. The limited preserved information of *Echmatemys obscura* does not allow resolution of its position within the *Echmatemys stevensoniana* + *Echmatemys naomi* clade, but the weakly developed axillary buttresses hint at a closer relationship with the latter. As such, *Echmatemys obscura* is herein considered to be a junior synonym of *Echmatemys naomi*.

Echmatemys stevensoniana (Leidy, 1870a)
(= *Emys septarius* Cope, 1873b = *Echmatemys aegle* Hay, 1908 = *Echmatemys cyane* Hay, 1908
= *Echmatemys ocyrrhoe* Hay, 1908)

Taxonomic history. *Emys stevensonianus* Leidy, 1870a (new species); *Emys stevensoni* Leidy 1871c (incorrectly spelled species epithet); *Echmatemys stevensoniana* Hay 1908 (new combination, justified emendation).

Type material. USNM 963 (anterior lobe), 965 (partial carapace), 967 (anterior lobe) (syntype series) (Leidy 1873, pl. 9.2–4).

Type locality. Near Fort Bridger, Uinta County, Wyoming, USA (Hay 1908; Figure 5); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay, 1908; Woodburne 2004).

Referred material and range. Early–middle Eocene (Ypresian–Lutetian), Bridger Formation, Bridgerian NALMA, Uinta and Sweetwater County, Wyoming, USA (type material of *Echmatemys aegle*, *Echmatemys cyane*, *Echmatemys ocyrrhoe*, *Emys septarius*; material referred to *Echmatemys aegle*, *Echmatemys septaria*, and *Echmatemys stevensoniana* by Hay 1908; material referred to *Echmatemys septaria* by Hutchison 2006).

Diagnosis. *Echmatemys stevensoniana* can be diagnosed as a member of *Echmatemys* based on the characters listed for that

clade above. *Echmatemys stevensoniana* differs from other *Echmatemys* based on the following combination of characters: neurals II–VIII hexagonal, suprapygals longer than wide and with narrow anterior border, contact of marginal II with vertebral I, and vertebral IV/V sulcus crossing suprapygals I.

Comments. The type material of *Echmatemys stevensoniana* consists of a partial carapace and two partial plastra that possess a rectangular neural I that is longer than wide, hexagonal neurals II–VIII with short antero-lateral borders, and a rhomboid entoplastron covered by gulars anteriorly and by pectorals posteriorly. Hay (1908) referred other specimens to this taxon, thereby adding to the above-mentioned combination of characters a clear contact between vertebral I and marginal II and a suprapygals I that is much longer than wide and crossed by the vertebral sulcus. Among the herein synonymized taxa, the posterior carapace is only available for *Echmatemys ocyrrhoe* and clearly similar to the condition seen in *Echmatemys stevensoniana*. The remaining taxa (*septaria*, *aegle*, *cyane*, *obscura*) show the characters of *Echmatemys stevensoniana*, but the lack of the posterior carapace does not allow a clear distinction from its sister taxon *Echmatemys naomi* (see above). As such, synonymy of the above mentioned taxa depends on secondary characters and especially the development of axillary and inguinal buttresses. Both have inguinal buttresses of similar length, but the axillary buttresses of *Echmatemys naomi* are thinner and shorter than those of *Echmatemys stevensoniana*. As such, *Emys septarius*, *Echmatemys aegle*, and *Echmatemys cyane* are tentatively considered as junior synonyms of *Echmatemys stevensoniana*, whereas *Echmatemys obscura* is considered as a junior synonym of *Echmatemys naomi* (see sections of those taxa for more information).

Echmatemys wyomingensis (Leidy, 1869)
(= *Echmatemys uintensis* Hay, 1908)

Taxonomic history. *Emys wyomingensis* Leidy, 1869 (new species); *Adocus wyomingensis* = *Emys wyomingensis* = *Baptemys wyomingensis* Cope 1869–70 (synonymy, new combination and incorrectly spelled species epithet); *Emys wyomingensis* Cope 1877a (incorrectly spelled species epithet); *Chrysemys wyomingensis* Hay 1904 (new combination); *Echmatemys wyomingensis* = *Emys jeanesi* Hay 1908 (new combination, senior synonymy).

Type material. ANSP 9777 (holotype), a left epiplastron (Leidy 1873, pl. 9.5).

Type locality. Near Fort Bridger, Uinta County, Wyoming, USA (Hay 1908; Figure 5); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Referred material and range. Early Eocene (Ypresian–Lutetian), Bridgerian NALMA, Bridger Formation, Uinta County, Wyoming, USA (material referred to *Emys wyomingensis* by Osborn et al. 1878 and Hay 1908); middle Eocene (Lutetian), Uintan NALMA, Uinta Formation, Uinta County, Wyoming, USA (type material of *Echmatemys uintensis*; material referred to *Echmatemys uintensis* by Gilmore 1915) and Uintah County, Utah, USA (material referred to *Echmatemys pusilla* by Gilmore 1915).

Diagnosis. *Echmatemys wyomingensis* can be diagnosed as a member of *Echmatemys* based on the characters mentioned above. *Echmatemys wyomingensis* differs from other *Echmatemys* based on the following combination of characters: presence of an octagonal neural (V or VI), presence of nine neurals, short contact between marginal I and pleural I, no contact between vertebral I and marginal II, and pectorals covering only the posterior part of the entoplastron.

Comments. *Emys wyomingensis* (= *Echmatemys wyomingensis*) has been named in Leidy (1869) based on a left epiplastron (see above). One year later, Leidy (1870a) named *Baptemys wyomingensis* from the same locality, based on an almost complete shell (Leidy 1873, pl. 11). Leidy (1870a) raised some doubts on the validity of *Emys wyomingensis* by saying that the epiplastron could belong the same animal as *Baptemys wyomingensis*. I am not sure if by that he meant the same individual or the same species, but the epiplastron of *Emys wyomingensis* is certainly a pan-testudinoid and clearly distinct from *Baptemys*. In the same year, Cope (1869–70) already suggested the synonymy between the two species, and placed them under *Adocus*. But shortly after, Leidy (1873) and Hay (1908) provided further evidence on the distinction of these two species. However, in the literature these taxa often get confused. See *Echmatemys*.

Rhinoclemmys panamaensis Cadena et al., 2012

Taxonomic history. *Rhinoclemmys panamaensis* Cadena et al., 2012 (new species).

Type material. UF 237887 (holotype), an almost complete shell (Cadena et al. 2012, figs. 3.1–4).

Type locality. West side of the Centenario Bridge, Panamá Oeste, Panama (Figure 6); Cucaracha Formation, Burdigalian, early–middle Miocene (Cadena et al. 2012).

Referred material and range. Early to middle Miocene of type locality, Panama (hypodigm of Cadena et al. 2012).

Diagnosis. *Rhinoclemmys panamaensis* can be diagnosed as a member of *Geoemydidae* based on the full list of characters provided above and as a member of *Rhinoclemmys* based on a smooth transition from the dorsal margin of the gular scale to the visceral surface of the epiplastron, presence of a small axillary scale, nuchal with a strong posteromedial concavity on the ventral surface, visceral gular margin very narrow at the midline, gradually widening or flaring posteriorly and overlapping, or nearly overlapping, the humeral along the margin of the epiplastron, moderately keeled nuchal with narrow and elongate semi-triangular cervical scale, and nuchal with broad sutural contact with neural I. *Rhinoclemmys panamaensis* differs from other *Rhinoclemmys* based on the presence of a quadrangular neural I, octagonal neural II, and wide gulars that form an angle greater than 90 degrees.

Comments. *Rhinoclemmys panamaensis* is based on a shell from the Miocene of Panama (Cadena et al. 2012) and represents the oldest record of this genus. The morphology of the gular scutes clearly distinguishes this taxon from other known testudinoids. In general, *Rhinoclemmys* is diagnosed by the presence of hexagonal neurals with short posterolateral sides (see McDowell

1964), but these are quadrangular in *Rhinoclemmys panamaensis*, as in *Pan-Emydidae*. Poor preservation of the rest of the neural series hinders clear interpretations of their shape. The presence of axillary musk duct foramina confirms the placement of this taxon within *Pan-Geoemydidae*. Cadena et al. (2012) attribute *panamaensis* to *Rhinoclemmys* based on several characters (see diagnosis), but some of these characters are also present on *Echmatemys*. The preservation and the lack of the posterior carapace does not allow the observation of some characters that could further help the affinities of this species. Based on the absence of the typical neural pattern of *Rhinoclemmys*, I am not so confident about the attribution of *panamaensis* to *Rhinoclemmys*. An attribution to *Echmatemys* is also possible but would imply a later survival of this clade in the Neogene. For the purposes of this chapter, however, I keep the original identification. *Rhinoclemmys* is the only extant geoemydid in the New World, distributed in Central and South America (Le and McCord 2008 and references therein). Members of *Rhinoclemmys* show some clear terrestrial adaptations and some works presented evidence of closer relationships with *Testudinidae* (morphology in Hirayama 1984; molecules in Spinks et al. 2004). Le and McCord (2008) recovered *Rhinoclemmys* as the basalmost clade within *Geoemydidae*, a position usually confirmed in subsequent analyses. Although this position would imply the presence of this clade for almost the entire Cenozoic, its fossil record is rather poor. In North and Central America only one clear occurrence is known from the Miocene of Panama (Cadena et al. 2012). All analyses herein have failed to associate any Eocene New World testudinoid (e.g., *Echmatemys*) with *Rhinoclemmys*, thereby suggesting an extended ghost lineage for the entire Paleogene.

Pan-Testudinidae Joyce et al., 2004

Phylogenetic definition. Following Joyce et al. (2004), the name *Pan-Testudinidae* refers to the total clade of *Testudinidae* (see below).

Diagnosis. Pan-testudinids can be differentiated from other pan-testudinoids by the presence of narrow and thin medial rib heads, two suprapyrgals, of which the first embraces the lenticular second, presence of long buttresses that barely touch the costal bones, and fused trochanters of the femur.

Cymatholcus schucherti (Hay, 1899b) (= *Cymatholcus longus* Clark, 1932)

Taxonomic history. *Hadrianus schucherti* Hay, 1899b (new species); *Cymatholcus schucherti* Williams 1950b (new combination); *Testudo schucherti* Kuhn 1964 (new combination); *Geochelone (Cymatholcus) schucherti* Coto Rojas and Acuña Mesén 1986 (new combination).

Type material. USNM 4046 (holotype), shell fragments (Hay 1899b, fig. 4; Hay 1908, fig. 481).

Type locality. Near former Cocoa post office, SW1/4 Section 13, T 11 N, R 5 W, Choctaw County, Alabama, USA (Hay 1899b; Cooke 1933; Figure 5); Jackson Formation, Duchesnean NALMA, Bartonian, late Eocene (Woodburne 2004).

Referred material and range. Late Eocene (Bartonian), Duchesnean NALMA, Duchesne River Formation, Uintah County, Utah, USA (type material of *Cymatholcus longus*).

Diagnosis. *Cymatholcus schucherti* can be diagnosed as a member of *Pan-Testudinidae* based on the characters listed for that clade above. *Cymatholcus schucherti* differs from other North American pan-testudinids in the restriction of the gulars to the epiplastra, shorter pectorals that medially have an almost parallel humero-pectoral and pectoro-abdominal sulci, and the presence of a deep, angular anal notch.

Comments. *Cymatholcus schucherti* is based on shell fragments from the Late Eocene of Utah (Hay 1899b). Hay (1899b) originally described this species as a member of *Hadrianus*, but he later questioned this assignment (Hay 1908) and suggested an affiliation with *Testudo* instead, possibly due to similarities in the morphology of the pectoral scutes. Clark (1932) named a large tortoise, *Cymatholcus longus*, from coeval deposits in Utah. The main character that Clark (1932) used to distinguish *longus* from *schucherti* is the strongly looped sulcus between the marginal and plastral scutes, whereas he considered other characters, such as costal differentiation, to be intermediate between the condition seen in *Hadrianus*, *Stylenys*, and *Testudo*. Williams (1950b) referred *schucherti* to *Cymatholcus* and suggested that it may even be conspecific with *longus*, a conclusion followed by Auffenberg (1974) as well. Indeed, based on the mutually preserved plastron, it is difficult to spot any significant differences between these two coeval taxa based on the published documentation and personal observations. Also, whereas the character listed by Clark (1932) is far from satisfying to support the distinction of *Cymatholcus*, the morphology of the pectoral scutes seems adequate enough to tentatively distinguish this large testudinid from the coeval *Hadrianus* and to support a more derived position within *Pan-Testudinidae*. However, the holotype of *Cymatholcus schucherti* is highly disarticulated and a careful revision is needed to check if the information provided by Hay (1899b, 1908) is accurate. In the phylogeny of Coto Rojas and Acuña Mesén (1986), *Cymatholcus schucherti* is recovered in a derived position within *Testudinidae* as a member of “*Geochelone*,” but as *Hadrianus* serves as the outgroup in this analysis, placement of all ingroup taxa within *Testudinidae* is actually an assumption. In the analysis presented herein, *Cymatholcus schucherti* is recovered in an unstable position along the stem of *Testudinidae*, but always in a more derived position than *Hadrianus*.

Hadrianus Cope, 1871b

Type species. *Testudo corsoni* Leidy, 1871b.

Diagnosis. *Hadrianus* can be diagnosed as a member of *Pan-Testudinidae* based on the characters listed for that clade above. *Hadrianus* can be differentiated from other pan-testudinids by the presence of 9 neurals, a neural formula of $6P < 6P < 4 < 6A < 6A < 6A < 6A < 6A$, a cervical scute, narrow vertebrals that are much longer than wide, overlap of pleural I onto the lateral parts of the nuchal, absence of well-developed epiplastral lip, and overlap of the gulars onto the anterior part of the entoplastron.

Comments. *Hadrianus* was erected by Cope (1871b) for *Hadrianus corsoni* (Leidy, 1871b), *Hadrianus octonaria* Cope (1871b), and *Hadrianus quadratus* (Cope, 1871b). Hay (1908) later designated *Testudo corsoni* as the type. Auffenberg (1971, 1974) suggested that *Hadrianus* is synonymous with *Manouria* on the basis of shell characters such as the presence of the cervical scute, divided supracaudal, wide shell, and absence of an epiplastral lip. Consequently, he included all *Hadrianus* species in the subgenus *Manouria*, under the genus *Geochelone*. However, these characters are symplesiomorphies and therefore cannot be used to diagnose a monophyletic group (see also Hutchison 1980 and Lichtig and Lucas 2015d). This review of the nine named species of *Hadrianus* from North America revealed that only two (*Hadrianus corsoni* and *Hadrianus majusculus*) can be confidently diagnosed as valid. All remaining names taxa are either junior synonyms of these or nomina dubia (see below). The phylogenetic analyses performed herein recovered *Hadrianus corsoni* and *Hadrianus majusculus* along the stem of *Testudinidae* with reasonable support. Due to incomplete scoring in the latter species, especially in the lack of information pertaining to the neural column, the sister-group relationship of the two species cannot be shown. However, there is no reason to suspect that they are not closely related and, as a result, they are here tentatively considered to be each others' immediate sisters. Based on all of the above, *Hadrianus* is included herein as a member of *Pan-Testudinidae*, placed in the stem of *Testudinidae*.

Hadrianus corsoni (Leidy, 1871b)

(= *Emys carteri* Leidy, 1871c = *Testudo hadriana* Cope, 1871a = *Hadrianus quadratus* Cope, 1871b = *Hadrianus octonaria* Cope, 1871b = *Hadrianus tumidus* Hay, 1908 = *Hadrianus robustus* Gilmore, 1915 = *Hadrianus utahensis* Gilmore, 1915 = *Geochelone gilmorei* Auffenberg, 1974)

Taxonomic history. *Testudo corsoni* Leidy, 1871b (new species); *Hadrianus corsoni* = *Emys carteri* Leidy 1873 (new combination and senior synonym); *Hadrianus corsonii* Cope 1875a (incorrect subsequent spelling); *Testudo* (*Hadrianus*) *corsini* Reinach 1900 (incorrect subsequent spelling); *Hadrianus corsoni* = *Testudo hadriana* = *Hadrianus quadratus* = *Hadrianus octonaria* Hay 1908 (senior synonym); *Geochelone* (*Manouria*) *corsoni* Auffenberg 1974 (new combination).

Type material. ANSP 10050 (holotype), an anterior plastral lobe (Leidy 1873, fig. 15.7).

Type locality. Grizzly Buttes, Uinta County, Wyoming, USA (Leidy 1871b; Figure 5); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Referred material and range. Early Eocene (Ypresian), late Wasatchian–early Bridgerian NALMA, Huerfano Formation, Huerfano County, Colorado, USA (referred material of Lichtig and Lucas 2015c); Middle Eocene (Ypresian–Lutetian), Bridgerian NALMA, Bridger Formation, Uinta County, Wyoming, USA (type material of *Emys carteri*, *Hadrianus octonaria*, *Hadrianus*

quadratus, and *Testudo hadriana*; material referred to *Hadrianus corsoni* by Leidy 1873, Cope 1875a, and Hay 1908; material referred to *Hadrianus octonaria* by Osborn et al. 1878); middle Eocene (Lutetian), Uintan NALMA, Uinta Formation, Uintah County, Utah, USA (type material of *Hadrianus tumidus*, *Hadrianus utahensis*, and *Hadrianus robustus*; referred material of Gilmore 1915).

Diagnosis. *Hadrianus corsoni* can be diagnosed as a pan-testudinid and as belonging to *Hadrianus* based on the characters listed for those clades above. *Hadrianus corsoni* differs from other *Hadrianus* based on the presence of a large entoplastron that is wider than long and a nearly straight femoro-anal sulcus.

Comments. Numerous species of *Hadrianus* have been named from the Eocene of Wyoming and Utah. Whereas *Hadrianus corsoni* (Leidy, 1871b), *Hadrianus quadratus* Cope, 1871a, and *Hadrianus octonarius* Cope, 1871b were named from the Bridger Basin of Wyoming, *Hadrianus tumidus* Hay, 1908, *Hadrianus robustus*, and *Hadrianus utahensis* Gilmore, 1915 are based on material from the Uinta Basin of Utah. I here synonymize all with *Hadrianus corsoni* for the following reasons. The taxa named by Cope (1871a, b) (i.e. *quadratus* and *octonarius*) were not figured nor described in detail, besides figures provided by Hay (1908). The description of *quadratus* offers no distinctive characters, whereas that of *octonarius* (Cope 1871b) matches that of Leidy (1871c) for *Emys carteri*. Moreover, Cope (1871b) distinguished *octonarius* from *quadratus* based on the slightly larger size of the former. Personal observations on the type specimen of *octonarius* reveal a peculiar morphology in the posterior portions of the carapace: the posterior sulcus of vertebral V sulcus coincides with the anterior border of suprapyg II, which, in return, is rounded and crossed entirely by the marginal XII sulcus, although it is important to note that the state of preservation is poor and some sutures may represent cracks. The shell is furthermore distorted significantly and some shapes therefore are not to be trusted. If true, this morphology would diagnose *octonarius* as a valid species, but I am not confident on that. The anterior region of the carapace is similar to *corsoni*, with a wide nuchal that is covered laterally by pleural I and a hexagonal neural I with short posterolateral sides. Given that *octonarius* originates from the same locality as *corsoni*, I tentatively considered it to be a junior synonym of *corsoni*. The same is proposed for *quadratus*. These synonymies had already been proposed by Hay (1908).

It is similarly difficult to find convincing evidence to support the presence of multiple species in the Uintan of Utah. *Hadrianus tumidus* Hay, 1908, was originally distinguished from *corsoni* by the relative height of bridge peripherals, the presence of a concavity in the posterior part of the plastron, the thicker xiphiplastral extremities, and the presence of a "ridge" on the lateral side of the carapace (sensu Hay 1908) that is difficult to observe. All of these differences are consistent with sexual dimorphism (plastral concavity, thickness of xiphiplastral extremities, size differences) or ontogeny (relative sizes of bridge peripherals). The species erected by Gilmore (1915) are better described, but it is again not possible to confidently distinguish them from *corsoni*. First of all, Gilmore (1915) was able to identify the presence of *corsoni* in Horizon C of the Uinta Formation based on a plastron that is indeed similar in most aspects to the Fort Bridger material of Leidy (1871b). From the same hori-

zon, however, he named *robustus* based on an anterior plastral lobe that he distinguished based on the size and shape of the pectorals. This difference, however, lies within the range of observed variability for *corsoni*, as documented by Bridger material reported by Leidy (1871b, 1873) and Hay (1908). From horizons B and C, Gilmore (1915) further named *utahensis* based on an almost complete plastron distinguished this time by the relative size of the bridge, the shape of the anal notch, and the size of the margins of the xiphiplastra. As explained above, these differences are consistent with ontogenetic and sexual variability. An interesting feature of this specimen, however, is that the entoplastron is not covered by the gular scutes in the illustration provided by Gilmore (1915), but this might be a misinterpretation as the left gular appears to cover the entoplastron in the photograph of the specimen. Given the geographic proximity of the discovered fossils and the similar age and stratigraphic position, it seems reasonable to refute the validity of these species and include them in the synonymy of *Hadrianus corsoni*.

Hadrianus majusculus Hay, 1904

Taxonomic history. *Hadrianus majusculus* Hay, 1904 (new species); *Testudo majusculus* Kuhn 1964 (new combination); *Geochelone majusculus* Auffenberg 1971 (new combination); *Geochelone (Manouria) majuscula* Auffenberg 1974 (new combination; mandatory change).

Type material. YPM VPPU 002793 (holotype), a nearly complete plastron with associated carapace (Hay 1904, fig. 5; Hay 1908, fig. 472).

Type locality. Murderer's Gap, Gallina, Rio Arriba County, New Mexico, USA (Hay 1904; Figure 5); San Jose Formation, Wasatchian NALMA, Ypresian, early Eocene (Hay 1908; Woodburne 2004).

Referred material and range. Early Eocene (Ypresian), Wasatchian NALMA, San Jose Formation, San Juan Basin, New Mexico (referred material of Lichtig and Lucas 2015d; material referred to *Hadrianus corsoni* by Cope 1875a, 1877a) and Willwood Formation, Big Horn Basin, Wyoming, USA (referred material of Hutchison 1980).

Diagnosis. *Hadrianus majusculus* can be diagnosed as a member of *Hadrianus* based on the absence of an epiplastral lip and the gulars overlapping the anterior part of the entoplastron. *Hadrianus majusculus* differs from other *Hadrianus* in the presence of higher peripherals, a small entoplastron that is longer than wide, a posteriorly concave humero-pectoral sulcus on both sides, and a laterally concave and widely omega-shaped femoro-anal sulcus.

Comments. *Hadrianus majusculus* is based on shell material from the early Eocene of New Mexico (Cope 1875a). The lack of information from the carapace prohibits a detailed diagnosis or rigorous assessment of phylogenetic relationships. The assignment of this species to *Hadrianus* is based on characters (see Diagnosis above) that are insufficient to group *majusculus* and *corsoni* in a global phylogenetic context. In a recent analysis, Pérez-García et al. (2016) recover the two in a clade supported by a single synapomorphy, the presence of nine neurals, but it is

not clear if *majusculus* was scored correctly given the poor preservation of this region. Therefore, I here use the geological age and geographical location to refer *majusculus* tentatively to *Hadrianus*. As specimens from New Mexico originally referred to *corsoni* by Cope (1875a, 1877a) are now considered to belong to *majusculus* (Hay 1908), the two species of *Hadrianus* are temporally and geographically distinct. Joyce et al. (2013) summarized concerns regarding the stratigraphic provenance of the type specimen and use the end of the Wasatchian (approximately 50.3 Ma) as a calibration point of this taxon. *Hadrianus majusculus* is the oldest pan-testudinid taxon known to date.

Oligopherus laticuneus (Cope, 1873a)
(= *Testudo thomsoni* Hay, 1908 = *Testudo undabuna* Loomis, 1909 = *Testudo praeextans* Lambe, 1913)

Taxonomic history. *Testudo laticuneus* Cope, 1873a (new species); *Testudo laticuneata* Loomis 1909 (unjustified emendation); *Gopherus laticuneus* Williams 1950b (new combination; incorrectly spelled species epithet); *Scaptochelys laticuneus* = *Testudo praeextans* Bramble 1982 (new combination, senior synonym); *Oligopherus laticuneus* Hutchison 1996 (new combination); *Oligopherus laticuneus* = *Oligopherus thomsoni* Hutchison 1996 (senior synonym).

Type material. AMNH 1160 (holotype), a shell and appendicular elements (Cope 1884, pl. 61.1; Hay 1908, figs. 509–515, pl. 67.1–2).

Type locality. Head of Horsetail Creek, Weld County, Colorado, USA (Hay 1908; Figure 5); Horsetail Creek Member, White River Formation, Chadronian NALMA, Priabonian, late Eocene (Woodburne 2004).

Referred material and range. Early Oligocene (early Rupelian), Orellan NALMA, Ziebach County, South Dakota, USA (type material of *Testudo thomsoni*) and Niobrara County, Wyoming, USA (referred material of Gilmore 1946; type material of *Testudo praeextans*; material referred to *Testudo praeextans* by Gilmore 1946); early Miocene, late Arikareean NALMA, Upper Harrison beds, Laramie County, Wyoming, USA (type material of *Testudo undabuna* Loomis, 1909).

Diagnosis. *Oligopherus laticuneus* can be diagnosed as a member of *Pan-Testudinidae* based on the presence of a rectangular neural III. *Oligopherus laticuneus* differs from other members of *Pan-Testudinidae* by the following combination of characters: low-domed shell, shell bones moderately thin, epiplastron flattened with a very shallow excavation, gular protrusion present, cervical scute wide as long and often wedge-shaped, pleural I not covering the nuchal, and presence of a pygal scute.

Comments. *Oligopherus laticuneus* is based on a partial skeleton from the late Eocene of Colorado (Cope 1873a; Hay 1908). The original figures of Cope (1884) and Hay (1908) are somewhat contradictory regarding the morphology of the posterior neurals and the medial contact of the costals, but these ambiguities were clarified by subsequent work by Gilmore (1946) and Hutchison (1996). Based on this updated information, it is not possible to

distinguish the shell of “*Testudo thomsoni* Hay, 1908, “*Testudo undabuna* Loomis, 1909, and “*Testudo praeextans* Lambe, 1913 from that of *Oligopherus laticuneus*. All of these taxa share, in addition to temporal and geographical proximity, the presence of a cervical scute that is as wide as long, a neural pattern of $6P < 6P < 4 < 6A < 6A < 6A < 6A < 6A$, fused marginals XII, and overall size. In addition, the skulls of “*Testudo thomsoni* and “*Testudo praeextans* are remarkably similar as well. Gilmore (1946) suggested the possible synonymy between “*Testudo thomsoni* and “*Testudo praeextans*. Hutchison (1996) on the other side included *thomsoni* and *praeextans* in the synonymy of *laticuneus*, under the new genus *Oligopherus*. Based on all available evidence, I cannot sufficiently support the distinction of any of the above-mentioned taxa and, as such, all are here included in the synonymy of *Oligopherus laticuneus*. The synonymized taxa morphologically compliment each other to render *Oligopherus laticuneus* one of the most completely known pan-testudinids. In the present phylogenetic analysis, this taxon is recovered in two different positions, either in the stem of *Testudinidae* (some equally weighted and all weighted analyses) or in a basal position between *Manouria* and *Gopherus* (some equally weighted analyses), showing a similar placement as “*Testudo costarricensis* (see above). As such, *Oligopherus laticuneus* is shown herein in an unresolved polytomy with basal Testudinidae, but in a more derived position than *Hadrianus*. The generic distinction proposed by Hutchison (1996) is therefore supported. A revision of this taxon should be an important task for the immediate future, as this would be the only stem testudinid from which the skull is known. This is particularly important for the North American testudinids, as the presence of a median premaxillary ridge is considered to be a key character that supports their monophyly, although this ridge is also perhaps homoplastically present in *Oligopherus laticuneus* (i.e., in the type material of “*Testudo praeextans*).

“*Testudo costarricensis* Segura Paguaga, 1944

Taxonomic history. *Testudo costarricensis* Segura Paguaga, 1944 (new species); *Geochelone costarricensis* Loveridge and Williams 1957 (new combination; incorrectly spelled species epithet).

Type material. MNCR, number unknown (holotype), a partial shell (Auffenberg 1971, fig. 8d–f).

Type locality. Milla 52, Peralta District, Cartago Province, Costa Rica (Segura Paguaga 1944; Figure 5); late Oligocene–early Miocene (Segura Paguaga 1944).

Referred material and range. No referred material known up to date.

Diagnosis. “*Testudo costarricensis* can be diagnosed as a member of *Pan-Testudinidae* based on the presence of a rectangular neural III. “*Testudo costarricensis* differs from most stem testudinids in the presence of neural differentiation with quadrangular and octagonal neurals, coincidence between the pleuro-marginal sulci and the costo-peripheral suture, and fusion of marginals XII and differs from crown *Testudinidae*, but resembles *Oligopherus laticuneus*, in the presence of a weakly-developed epiplastral lip and an anterior neural formula

of $6P < 6P < 4 < 8$. “*Testudo*” *costarricensis* differs from *Oligopherus laticuneus* in the absence of a contact between marginal VI and pleural III, the rounded anterior plastral lobe, and the overlap of the pectoral scutes on the posterior part of the entoplastron.

Comments. “*Testudo*” *costarricensis* is based on a shell from the late Oligocene or early Miocene of Costa Rica (Segura Paguaga 1944) with unclear affinities. Several characters (see Diagnosis above) support a basal placement of this taxon within crown *Testudinidae* between *Manouria* and *Gopherus*, but the neural formula is more consistent with a position along the tortoise stem. Among basal pan-testudinids, “*Testudo*” *costarricensis* most strongly resembles *Oligopherus laticuneus*, but several characters support a clear distinction (see Diagnosis above). The presence of an extensive overlap of the pectoral scutes onto the posterior parts of the entoplastron clearly distinguishes “*Testudo*” *costarricensis* from all other named North American *Pan-Testudinidae* and led Auffenberg (1971) to compare it with the Asian *Indotestudo*. He further suggested that this taxon is perhaps ancestral to the South American tortoises, an opinion later reiterated by Bramble (1971). Crumly (1984b) disagreed with both suggested affinities (i.e., with *Indotestudo* and *Chelonoidis*) but did not provide an alternative hypothesis. Although the validity of this taxon is clear to me, it cannot be referred to any named genus with confidence. I therefore here retain the original combination, but highlight ambiguity through the use of quotes.

Testudinidae Batsch, 1788

Phylogenetic definition. Following Joyce et al. (2004), the name *Testudinidae* refers to the most inclusive crown clade that includes *Testudo graeca* Linnaeus, 1758 and *Manouria* (orig. *Testudo*) *emys* (Schlegel and Müller, 1844), but not any emydid, geoemydid, or platysternid.

Diagnosis. Representatives of *Testudinidae* can be differentiated from other *Pan-Testudinoidea* by a skull with extensive temporal emargination, the presence of a median maxillary ridge, the presence of a well-developed ridge throughout the length of the vomer, the presence of neural differentiation consisting of octagonal and quadrangular neurals, good coincidence between the costo-peripheral suture and pleuro-marginal sulcus, fusion of the marginals XII into a supracaudal, narrow and thin rib heads, narrow costo-vertebral tunnel, presence of a well-developed epi-plastral lip, short pectorals, lack of an overlap of the entoplastron by the humero-pectoral sulcus, and fused femoral trochanters.

Chelonoidis Fitzinger, 1835

Type species. *Testudo boiei* Wagler, 1833 = *Testudo carbonaria* Spix, 1824.

Diagnosis. *Chelonoidis* can be diagnosed as a member of *Testudinidae* based on the full list of characters provided for that clade above. *Chelonoidis* can be differentiated from other testudinids based on the absence of a cervical scute, presence of a large entoplastron, pectoral scales that are narrower along the midline and antero-posteriorly expanded toward the marginal scutes, and presence of a triangular ventral ischial tubercle.

Comments. A detailed analysis of the fossil record of the Neotropical clade *Chelonoidis* will be given elsewhere (de la Fuente et al. in press), as the main distribution of the extant and extinct members of this genus is located in South America. Some Pleistocene and Holocene specimens, however, are found in the West Indies and therefore fall within the geographical focus of the present contribution. A total of four named taxa referable to this clade are known from the West Indies, of which three are considered valid herein (see below) and the remainder a nomen dubium (see *Emys sombreroensis* below). The origin of this South American clade of tortoises has been a matter of debate, but the prevailing hypothesis is that they originated from a dispersal event from Africa to South America that occurred at some point in the late Eocene to early Oligocene (see de la Fuente et al. 2014 for review and references therein). Members of this clade can be easily distinguished from North American taxa based on several characters from skull and shell (see Diagnosis above). As such, the identification of fossil material from the West Indies as *Chelonoidis* is done with confidence. Franz and Franz (2009) suggest that the wide distribution of these tortoises in the Bahamian archipelago and the Caribbean hints at multiple colonizations from South America in the mid- and late Tertiary. In the phylogenetic analyses performed herein, both *Chelonoidis alburyorum* and *Chelonoidis cubensis* are clearly associated with *Chelonoidis*, but “*Chelonoidis*” *monensis* is only recovered within the “*Geochelone* complex” due to the absence of shell information. The interrelationships of *Chelonoidis alburyorum* and *Chelonoidis cubensis* are poorly resolved within *Chelonoidis*. As such, “*Chelonoidis*” *monensis* is tentatively grouped with *Chelonoidis* and all valid taxa recognized herein are shown in an unresolved polytomy with crown *Chelonoidis*.

Chelonoidis alburyorum Franz and Franz, 2009

Taxonomic history. *Chelonoidis alburyorum* Franz and Franz, 2009 (new species).

Type material. UF 225400 (holotype), a skull, shell, and associated appendicular elements of an adult male (Franz and Franz 2009, figs. 2–15).

Type locality. Sawmill Sink (BNM Site No. AB-50), north of Cornwall Point, 37 km south of Marsh Harbour, Great Abaco Island, Little Bahamas Bank, Bahamas (Figure 6); unstratified peat deposits, Holocene, 2580 ± 50 to 2720 ± 40 yr BP (Franz and Franz 2009).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Chelonoidis alburyorum* can be diagnosed as a member of *Chelonoidis* based on the characters listed above. *Chelonoidis alburyorum* is differentiated from other *Chelonoidis* by the development of an elongate, high-domed, thin-walled shell, brachycephalic skull with a strap-like vomer, vaulted palate, undeveloped pedestal for origin of septum and weak septum-like ridge, and the absence of vertebral gibosities.

Comments. *Chelonoidis alburyorum* is based on a partial skeleton from the Holocene of the Bahamas (Franz and Franz 2009). Franz and Franz (2009) note the presence of a pair of holes on

the posterior end of the quadrate, where the squamosals would be present. They discussed whether the squamosals were truly absent or if these holes are the result of secondary removal and/or decomposition, but speculated that the squamosals were likely absent and that these holes were covered with membranous tissue (Franz and Franz 2009). Personal observations on skulls of the extant *Chelonoidis chilensis* revealed a similar morphology, as the squamosals appear not to be fully ossified and tightly attached to the quadrate, thereby often leaving two holes at the back of the quadrates. The material of *Chelonoidis alburyorum* is the most complete known from the West Indies, with several complete shells, a skull, and various appendicular elements, described and figured in detail by Franz and Franz (2009). Franz and Franz (2009) mention additional undescribed tortoise material in the Bahamian archipelago (Abaco, Moore's Island, Eleuthera, Mayaguana, Middle Caicos, Grand Turk). All phylogenetic analyses herein placed this taxon within *Chelonoidis*, but in an uncertain position. The recent molecular analyses of Kehlmaier et al. (2017) placed this taxon basal to the clade of *chilensis* + *nigra*.

Chelonoidis cubensis (Leidy, 1868b)

Taxonomic history. *Testudo cubensis* Leidy, 1868b (new species); *Testudo (Chelonoidis) cubensis* Williams 1950b (new combination); *Geochelone cubensis* Auffenberg 1971 (new combination); *Geochelone (Chelonoidis) cubensis* Auffenberg 1974 (new combination); *Chelonoidis cubensis* TEWG 2015 (referral to genus level).

Type material. ANSP 8923 (holotype), a partial costal (Williams 1950b, pl. 1).

Type locality. Chapapote (= Chapepote) spring, Baños de Ciego Montero, Cienfuegos (formerly Santa Clara) Province, Cuba (Figure 6); Pleistocene (Williams 1950b).

Referred material and range. Pleistocene, Santa Clara, Matanzas Province (referred material of Williams 1950b), and Havana Province, Cuba (referred material of Karl 1995).

Diagnosis. *Chelonoidis cubensis* can be diagnosed as a member of *Testudinidae* based on the presence of neural differentiation, a well-developed epiplastral lip, short pectorals, and a femur with fused trochanters and as a member of *Chelonoidis* based on the absence of cervical scute and the triangular ventral ischial tubercle. *Chelonoidis cubensis* can be differentiated from other *Chelonoidis* by the presence of a shallow nuchal notch, nuchal plate much wider than long, a well-developed gular protrusion, short gulars that never reach the entoplastron, expansion of the humerals onto the medial portions of the epiplastra, small entoplastron, humero-pectoral sulcus situated posterior to the entoplastron, contact between inguinal and femoral scutes in ventral view, and the development of a pronounced epiplastral lip.

Comments. *Chelonoidis cubensis* is based on a partial costal from the Pleistocene of Cuba (Leidy 1868b). Although the type material is not diagnostic, the referred material presented by Williams (1950b) allows a clear attribution to *Chelonoidis* due to the absence of a cervical scute and the triangular ventral ischial tubercle of the pelvis. Some of the specimens attributed to this

taxon (AMNH 6206) could be skull fragments of a nonturtle vertebrate. Within *Chelonoidis*, the Cuban taxon differs from the large-sized extinct forms from Argentina (e.g., *Chelonoidis australis* [Moreno, 1889], *Chelonoidis gallardoii* [Rovereto, 1914], and *Chelonoidis lutzae* Zacarias et al., 2013) in the morphology of the anterior plastral lobe, which shows short gulars that terminate anterior to the entoplastron. The same morphology can be noted in the tortoises of the Galápagos complex, but the Cuban taxon differs in having a thicker shell and a deep pit for the *M. latissimus dorsi* on the lateral side of the humerus (Williams 1950b). The distinct nature of this taxon is further corroborated by geographic concerns. *Chelonoidis cubensis* shares with the extinct Argentinian tortoises the presence of gibbosities in the vertebral area, although they are not as pronounced, possibly due to smaller size and a thinner shell. This character is also known in other extinct taxa, such as the African *Impregnochelys pachytestis* Meylan and Auffenberg, 1986. Williams (1950b) discussed the presence of the raised furrows in some costal and neural plates, which he considered to be a diagnostic feature for this taxon. I can confirm Williams's observations of the distribution of this character and corroborate the conclusion that the diagnosis of this taxon cannot be made on this character alone. Within *Chelonoidis*, however, this character is only known in some Galápagos tortoises. Williams (1950b) suggested that *Chelonoidis cubensis* is the result of a Miocene split of a species without a cervical in Central America to a lineage towards the West Indies and another lineage to South America. This "Central American" hypothesis is also expressed by Bramble (1971), together with southern North America as the place of origin of the ancestor of the Neotropical tortoises. Franz and Franz (2009) also suggested that the presence of a more-developed epiplastral lip in *Chelonoidis cubensis* distinguishes this taxon from *Chelonoidis alburyorum* and other Bahamian taxa, suggesting that it represents an independent invasion from South America and probably via a nuclear Central America. As all these taxa are nested within the "*Geochelone* complex," a South American origin appears more likely.

"*Chelonoidis*" *monensis* (Williams, 1952)

Taxonomic history. *Testudo (Monachelys) monensis* Williams, 1952 (new species); *Geochelone (Monachelys) monensis* Auffenberg 1974 (new combination); *Chelonoidis monensis* TEWG 2015 (new combination).

Type material. AMNH 1969 (holotype), a first dorsal vertebra (Williams 1952, fig. 1.e, pl. 44.4).

Type locality. Lirio Cave, Mona Island, Puerto Rico, USA (Figure 6); possibly sub-Holocene (Williams 1952).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. "*Chelonoidis*" *monensis* can be diagnosed as a member of *Testudinidae* based on the presence of a skull with extensive temporal emargination, the presence of a median maxillary ridge, and the presence of a well-developed ridge throughout the length of the vomer, as a member of *Chelonoidis* by the absence of a median ridge developed anteroposteriorly on the ventral side of the premaxillae, and as a member of the Galápa-

gos tortoise complex by the presence of an elongated first thoracic centrum. "*Chelonoidis monensis* is distinguished from the Galápagos tortoises by a narrower and more elongated first thoracic centrum.

Comments. In the original description of *Testudo monensis*, Williams (1952) suggested placing this taxon in a new monotypic genus, *Monachelys*. The main character to diagnose the genus was the elongated and narrow centrum of the first dorsal vertebra. However, personal observations reveal that the tortoises of the Galápagos complex also show elongated centra on the first dorsal vertebra, but differ from the Mona tortoise in being shorter and wider. The Mona tortoise also preserves a partial skull that shows no evidence of the median premaxillary ridge, thus allowing distinction from North American taxa (e.g., *Gopherus*, *Styemys*, *Hesperotestudo*). Based on all available information, as well as in the absence of conflicting evidence, the Mona tortoise can be considered to be a valid species and is tentatively included in the genus *Chelonoidis*.

Floridemys nana (Hay, 1916a)

Taxonomic history. *Bystra nanus* Hay, 1916a (new species); *Floridemys nanus* Williams 1950b (new combination).

Type material. USNM 10247 (holotype), an almost complete shell (Hay 1916a, pl. 1; Auffenberg 1963, fig. 25).

Type locality. Phosphate mine in Holder, Citrus County, Florida, USA (Hay 1916a; Figure 6); former "Alachua Formation," probably reworked material of the Hawthorn phosphorite deposit, NALMA unknown, late Miocene–Pleistocene (Scott 1988).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Floridemys nana* can be diagnosed as a member of *Testudinidae* by the presence of good coincidence of the costo-peripheral suture and pleuro-marginal sulci, the presence of a well-developed epiplastral lip, and the short pectorals. *Floridemys nana* differs from other *Testudinidae* in the presence of short and wide gular scutes with an almost transverse gularo-humeral sulcus that does not cover the entoplastron, with an almost straight gularo-humeral sulcus perpendicular to the midline.

Comments. *Floridemys nana* is based on a near-complete shell from the Neogene of Florida (Hay 1916). Although originally described as belonging to the new genus *Bystra*, Williams (1950b) noted homonymy with a named genus of Hymenoptera and proposed the new substitute name *Floridemys* (Williams 1950b). Both Hay and Williams highlighted the small size of this individual, with a carapace not exceeding 105 mm, although the individual appears to be an adult based on the complete closure of sutures. A detailed revision and updated figuration was provided by Auffenberg (1963), who reaffirmed the validity of this taxon. Several characters, in particular the shape of the nuchal plate, the hexagonal second neural, the shape of the epiplastral lip, and the shape of the femoro-anal sulcus, support a sister-group relationship with *Kinixys*. As *Kinixys* has a strongly mod-

ified carapace morphology due to the presence of a carapacial hinge, this sister-group relationship should be viewed with caution. However, all analyses, both under equal as well as implied weights, clearly place *Floridemys* as the only North American testudinid taxon within the clade of derived tortoises (*Testudininae*), in particular within the so-called "*Geochelone* complex." Placement of this taxon outside *Testudininae* would imply several additional steps. This derived position has been suggested by Crumly (1984a, 1984b) as well. The confirmation of this derived position of *Floridemys nana* raises questions regarding the paleobiogeographic history of this taxon, as it implies dispersal from Africa to southeastern North America in the Neogene or earlier. Auffenberg (1964b) suggested alternatively that *Floridemys nana* may be a late descendant of the *Styemys* lineage, but the shell morphology of both taxa is strikingly different. The specimen was originally described as originating from the Alachua Formation but, as this formation is currently not recognized and reported ages of fossils from these deposits range from the late Miocene to the Pleistocene (Scott 1988), the age of the specimen is uncertain.

Gopherus Rafinesque, 1832

Type species. *Testudo polyphemus* Daudin, 1802.

Diagnosis. *Gopherus* can be diagnosed as a member of *Testudinidae* based on the full list of characters listed above. *Gopherus* can be differentiated from other testudinids by the presence of a rectangular cervical scute that is wider than long, fused marginals XII, an epiplastral lip without prominent gular protrusion, a rounded humero-pectoral sulcus placed posterior to the entoplastron, and contacts of the radius with the distal carpals.

Comments. Several authorities support further generic distinctions within the extant gopher tortoises. The most common is the distinction of *Gopherus* Rafinesque, 1832 (including the extant *Gopherus polyphemus* and *Gopherus flavomarginatus*) from *Xerobates* Agassiz, 1857 (including the extant *Gopherus agassizii*, *Gopherus berlandieri*, and *Gopherus morafkai*). The characters supporting this distinction come mainly from the shell, with the low-domed forms grouped in *Gopherus* and the high-domed ones in *Xerobates* (see Bramble and Hutchinson 2014 for further characters). Following this scheme, extinct gopher tortoises can also be attributed to these two genera (Franz 2014), except for "*Testudo*" *laticunea*, which is typically placed in its own genus (*Oligopherus* Hutchison, 1996). Alternatively, several characters from the skull, shell, and appendicular skeleton related to burrowing led Bramble (1982) to divide the gopher tortoises into *Gopherus* and his new genus *Scaptochelys* Bramble, 1982, with "*Testudo*" *laticunea* included in *Gopherus*. Bramble (1982) showed that these two different groups have a different burrowing behavior and that *Gopherus agassizii* has an hypertrophied inner ear structure. Bramble and Hutchison (2014) included *Scaptochelys* in the synonymy of *Xerobates*. In any case, the proposed groupings of extant taxa are supported by molecular evidence, but always within a monophyletic *Gopherus* (e.g., Lamb and Lydeard 1994; Guillon et al. 2012; Pereira et al. 2017). As this generic distinction is not necessary, the simpler attribution of all gopher tortoises to *Gopherus* is followed herein.

Gopherus auffenbergi Mooser, 1972
(= *Gopherus pargensis* Mooser, 1980)

Taxonomic history. *Gopherus auffenbergi* Mooser, 1972 (new species); *Scaptochelys berlandieri* = *Gopherus auffenbergi* Bramble 1982 (junior synonymy); *Xerobates auffenbergi* Franz 2014 (new combination).

Type material. Unknown institution (holotype), a shell and associated appendicular elements with the temporary number FC 500 (Mooser 1972, figs. 1–3).

Type locality. Cedazo Ravine, 3.5 km northeast of Aguascalientes, Aguascalientes State, Mexico (Figure 6); Cedazo local fauna, late Blancan–Irvingtonian NALMA, Pleistocene (Mooser 1972; Woodburne 2004).

Referred material and range. Pleistocene of type locality, Aguascalientes State, Mexico (hypodigm of Mooser 1980).

Diagnosis. *Gopherus auffenbergi* can be diagnosed as a member of *Gopherus* based on the characters mentioned above. *Gopherus auffenbergi* differs from other *Gopherus* in the short costals III, V, and VII that allow a medial contact of the costals II, IV, and VI and the absence of gular covering of the entoplastron.

Comments. *Gopherus auffenbergi* is a small-sized *Gopherus* from the Pleistocene of Mexico that presents a peculiar morphology in that costals III, V, and VII are shortened and do not make contact with the peripherals, thus allowing the remaining costals to contact distally. It is not clear whether this morphology represents a teratomorphy or is indeed a diagnostic autapomorphy (as is the opinion of Mooser 1972). Furthermore, this taxon shows short gulars that are just touching the anterior part of the entoplastron. Bramble (1982) considered this taxon to be a synonym of the extant *Gopherus berlandieri*, a conclusion followed by Reynoso and Montellano-Ballesteros (2004), but in both cases no explicit evidence was presented to support this synonymy. A few years later, Mooser (1980) named *Gopherus pargensis* that he distinguished from *Gopherus auffenbergi* by the absence of a coincidence between the costo-peripheral suture and pleuro-marginal sulci. Although this character is not sufficient to diagnose this taxon, the figured specimen shows the above-mentioned costal morphology of *Gopherus auffenbergi*. This suggests that this peculiar morphology is not a teratomorphy and supports its distinction. As such, *Gopherus pargensis* is considered as a junior synonym of *Gopherus auffenbergi*. Based on all the above, *Gopherus auffenbergi* is considered to be a distinct species of *Gopherus*, highlighting the need for revision of the peculiar morphology of the costal plates of this taxon. The phylogenetic analyses presented herein universally recovered this taxon within crown *Gopherus*.

Gopherus brevisternus (Loomis, 1909)

Taxonomic history. *Testudo brevisterna* Loomis, 1909 (new species); *Gopherus brevisterna* Williams 1950b (new combination); *Gopherus brevisternus* Auffenberg 1974 (mandatory change).

Type material. ACM 2006 (holotype), a skull, shell, and associated appendicular elements (Loomis 1909, figs. 5–8).

Type locality. Muddy Creek, Laramie County, Wyoming, USA (Loomis 1909; Figure 6); Upper Harrison Formation, late Arikarean NALMA, Aquitanian, early Miocene (Woodburne 2004).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Gopherus brevisternus* can be diagnosed as a member of *Gopherus* based on the characters mentioned above. *Gopherus brevisternus* differs from other, early to middle Miocene *Gopherus* in the less differentiated neural series with an hexagonal neural IV and vertebrals that are much narrower than the pleurals. *Gopherus brevisternus* further differs from *Gopherus mohavensis* in the narrower cervical scute.

Comments. *Gopherus brevisternus* is known from a skull, mandible, shell, and appendicular elements described and figured by Loomis (1909) from the early Miocene of Wyoming. The presence of a less-differentiated neural series and the narrower vertebrals clearly distinguish this taxon from coeval *Gopherus* spp. (see Diagnosis above). The diagnostic characters of this taxon are also responsible for placing it in a basal position within *Gopherus*, but it is not certain whether it is part of the stem or the crown of *Gopherus*. As such, it is shown herein in an unresolved basal polytomy. In the work of Reynoso and Montellano-Ballesteros (2004) *Gopherus brevisternus* is recovered within the crown *Gopherus*, but neural characters were not included in their analysis.

Gopherus depressus Brattstrom, 1961
(= *Gopherus dehiscus* Des Lauriers, 1965)

Taxonomic history. *Gopherus depressus* Brattstrom, 1961 (new species); *Gopherus brattstromi* Auffenberg 1974 (new replacement name); *Scaptochelys mohavense* = *Gopherus depressus* = *Testudo milleri* Bramble 1982 (junior synonymy); *Gopherus mohavetus* = *Gopherus brattstromi* Reynoso and Montellano-Ballesteros 2004 (junior synonym).

Type material. LACM CIT498/5133 (holotype), a partial shell (Brattstrom 1961, figs. 7, 8).

Type locality. CIT locality 498, W1/2 NE1/4 Section 36, T 31 S, R 34 E, Tehachapi Mountains, Kern County, California, USA (Brattstrom 1961; Figure 6); Bopesta Formation, Barstovian NALMA, Langhian–Serravallian, middle Miocene (Franz 2014).

Referred material and range. Middle Miocene (Langhian–Serravallian), Barstovian NALMA, San Bernardino County, California, USA (type and referred material of *Gopherus dehiscus* of Des Lauriers 1965).

Diagnosis. *Gopherus depressus* can be diagnosed as a member of *Gopherus* based on the full list of characters provided above. *Gopherus depressus* differs from *Gopherus hexagonatus* in its smaller size and fully differentiated neural series, from *Gopherus mohavensis* in the narrower cervical, neural VI with short anterolateral sides, shorter pectorals medially, contact between the inguinals and femorals, and *Gopherus edae* in the narrower

vertebrals and the contact between the inguinal and femoral scute.

Comments. *Gopherus depressus* is based on a partial shell from the middle Miocene of California (Brattstrom 1961). Auffenberg (1974) created the new substitute name *Gopherus brattstromi* for *Gopherus depressus* to avoid confusion with *Testudo depressa* Cuvier, 1829 (not Guérin-Méneville, as Auffenberg writes), but that is rejected herein as both taxa are not currently placed in the same genus. *Gopherus depressus* is a middle-sized member of *Gopherus* that is similar in shell morphology with *Gopherus edae* in the presence of a fully differentiated neural series. Few characters are available to differentiate these two species (see Diagnosis above). Another taxon from the middle Miocene of California, *Gopherus dehisicus* Des Lauriers, 1965, shows a similar morphology to *Gopherus depressus*, but is a little smaller. As such, *Gopherus dehisicus* is herein considered to be a junior synonym of *Gopherus depressus*. *Gopherus mohavensis* appears to be distinct from *Gopherus depressus* (see below), and the two species were therefore sympatric during the middle Miocene. The phylogenetic analyses herein failed to recover the position of *Gopherus depressus* within *Gopherus* and it is therefore shown in a basal polytomy with other poorly resolved taxa.

Gopherus donlaloii Reynoso and Montellano-Ballesteros, 2004

Taxonomic history. *Gopherus donlaloii* Reynoso and Montellano-Ballesteros, 2004 (new species).

Type material. IGM 6076 (holotype), a skull, shell, and appendicular elements (Reynoso and Montellano-Ballesteros 2004, figs. 2–7).

Type locality. Lands of Ejido San Lázaro, Villagrán Municipality, Tamaulipas State, Mexico (Figure 6); Rancho Labrean NALMA, Ionian–Tarantian, late Pleistocene (Reynoso and Montellano-Ballesteros 2004; Woodburne 2004).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Gopherus donlaloii* can be diagnosed as a member of *Gopherus* based on the characters mentioned above. *Gopherus donlaloii* differs from other *Gopherus* by the following combination of characters: larger size, more oval shape of the external nares, with a broad ventral process of the prefrontal and a wide dorsal process of the premaxilla extending between the nares, premaxillary ridge ending in a T-shaped structure (not with a forked Y-shaped end), nasopalatine foramen considerably small and rounded, basioccipital and basipterygoid shortened antero-posteriorly, single inguinal scute separated from the femoral scute, and pisiform probably present and from *Gopherus hexagonatus* in the additional differentiation of the neural series.

Comments. *Gopherus donlaloii* is based on a partial skeleton from the late Pleistocene of Tamaulipas, Mexico (Reynoso and Montellano-Ballesteros 2004). In all phylogenetic analysis herein, *Gopherus donlaloii* is recovered in an unresolved polytomy with *Gopherus hexagonatus* and *Gopherus hollandi* and in

a derived position within crown *Gopherus*, forming a clade that is sister to *Gopherus flavomarginatus*. Given the list of valid species herein, these results are largely similar with those of Reynoso and Montellano-Ballesteros (2004).

Gopherus edae (Hay, 1906b) (= *Testudo hollandi* Hay, 1906b = *Testudo pansa* Hay, 1908 = *Testudo vaga* Hay, 1908)

Taxonomic history. *Testudo edae* Hay, 1906b (new species); *Gopherus edae* Williams 1950b (new combination); *Gopherus edae* = *Testudo hollandi* Bramble 1982 (senior synonym); [*Gopherus edae*] Reynoso and Montellano-Ballesteros 2004 (nomen dubium).

Type material. CM 1535 (holotype), a shell (Hay 1908, pl. 83.1–2).

Type locality. Near Running Water Creek, Sioux County, Nebraska, USA (Hay 1906b; Figure 6); Harrison Formation, late Arikareean NALMA, Aquitanian, early Miocene (Auffenberg 1974).

Referred material and range. Early Miocene (Aquitanian), late Arikareean NALMA, Harrison Formation, Sioux County, Nebraska, USA (type material of *Testudo hollandi*); middle Miocene (Langhian–Serravallian), Barstovian NALMA, Albany County, Wyoming, USA (type material of *Testudo vaga*) and Weld County, Colorado, USA (type material of *Testudo pansa*).

Diagnosis. *Gopherus edae* can be diagnosed as a member of *Gopherus* based on the characters mentioned above. *Gopherus edae* differs from *Gopherus brevisternus* in the presence of an octagonal neural IV and wider vertebrals, from *Gopherus mohavensis* in the narrower cervical, neural VI with short anterolateral sides, shorter pectorals medially, and contact between the inguinals and femorals, and from *Gopherus hexagonatus* in the fully differentiated neural series.

Comments. *Gopherus edae* Hay, 1906b is a medium-sized testudinid from the early Miocene of Nebraska. The type locality also yielded the type specimen of “*Testudo*” *hollandi* Hay, 1906b, which is identical to the morphology of *Gopherus edae*. From the middle Miocene of neighboring Wyoming and Colorado, two more taxa show a similar morphology. “*Testudo*” *vaga* Hay, 1908 is of similar size and shows a similar plastral morphology. “*Testudo*” *pansa* Hay, 1908 is also similar in morphology but is much larger in size, almost double, as well. Similarities between the above-mentioned taxa have been mentioned in several works, whereas the synonymy of “*Testudo*” *edae* and “*Testudo*” *hollandi* was proposed by Bramble (1982). Overall, the above mentioned taxa share a well-differentiated neural series (4<8<4<8<4<6A<6A<6A), a suprapyg 1 that surrounds the anterior part of the lenticular suprapyg 2, a wide cervical scute, wide vertebrals, long gulars that cover the entoplastron, a humero-pectoral sulcus that is situated posterior to the entoplastron, and a well-developed anal notch. Further work should investigate whether early Miocene taxa (“*Testudo*” *edae* and “*Testudo*” *hollandi*) show significant differences from middle Miocene ones (“*Testudo*” *pansa* and “*Testudo*” *vaga*). “*Testudo*”

edae and “*Testudo*” *hollandi* were simultaneously named (in Hay 1906b), but Bramble (1982), acting as the first reviser, gave priority to *edae*. Based on all of the above, all these taxa are placed in the synonymy of “*Testudo*” *edae*. All phylogenetic analyses herein place *Gopherus edae* in a derived position within crown *Gopherus*, in a polytomy with the Pleistocene *Gopherus hexagonatus* and *Gopherus donlaloii*. This position of *Gopherus edae* pushed the divergence of extant *Gopherus* prior to the early Miocene, concurring with molecular calibrations of this split that indicated a minimum age of 17 to 18 Ma (Lamb and Lydeard 1994).

Gopherus hexagonatus (Cope, 1893)
(= *Testudo campester* Hay, 1908 = *Bysmachelys canyonensis* Johnston, 1937 = *Gopherus huecoensis* Strain, 1966)

Taxonomic history. *Testudo hexagonata* Cope, 1893 (new species); *Gopherus hexagonata* Williams 1950b (new combination); *Gopherus hexagonatus* Auffenberg 1974 (mandatory change); *Gopherus hexagonatus* = *Gopherus laticaudatus* Preston 1979 (senior synonymy); [*Gopherus hexagonatus*] Reynoso and Montellano-Ballesteros 2004 (nomen nudum).

Type material. TMM 30967-1817 (holotype), shell fragments (Hay 1908, figs. 625, 626; Auffenberg 1962a, figs. 1, 2).

Type locality. Rock Creek, Tule Canyon, Briscoe County, Texas, USA (Cope 1893; Figure 6); Tule Formation, Irvingtonian NALMA, Calabrian, middle Pleistocene (Woodburne 2004).

Referred material and range. Late Pliocene, Blancan NALMA, Randall County (type material of *Bysmachelys canyonensis*), Crosby County (type material of *Testudo campester*), and Hudspeth County, Texas, USA (type material of *Gopherus huecoensis*); Late Pleistocene, San Patricio County and Wheeler County (referred material of Auffenberg 1962a); Pleistocene, Brown County, Kansas, USA (referred material of Hibbard 1960).

Diagnosis. *Gopherus hexagonatus* can be diagnosed as a member of *Gopherus* based on the characters mentioned above. *Gopherus hexagonatus* differs from other *Gopherus* to the exclusion of *Gopherus donlaloii* in its larger size and from *Gopherus donlaloii* in the presence of hexagonal neurals III–VIII.

Comments. *Gopherus hexagonatus* is based on shell fragments from the Pleistocene of Texas (Cope 1893). Although Reynoso and Montellano-Ballesteros (2004) concluded *Gopherus hexagonatus* to be a nomen dubium based on a lack of diagnostic features, I am compelled by the work of Auffenberg (1962a) that highlights systematic differences with all other species of *Gopherus* (see Diagnosis above). Other medium- to large-sized gopher tortoises have been named from the Plio–Pleistocene of Texas. *Testudo campester* Hay, 1908 is represented by a partial carapace and plastron and has a similar size to *Gopherus hexagonatus*. The preserved comparable elements do not show any differences. The shape of the pectoral scutes of “*Testudo*” *campester* is similar to *Gopherus* and this taxon, as such, is not similar to *Hesperotestudo*, as suggested by Auffenberg (1974). *Bysmachelys canyonensis* Johnston, 1937 from the early Pleis-

tocene of Texas is slightly larger than *Gopherus hexagonatus*, but the overall morphology of the plastron is nevertheless similar. This taxon also includes the skull and the appendicular elements that had been figured by Johnston (1937). As these figures are not so detailed, only a general similarity with *Gopherus* can be noted (i.e., in the brachycephalic shape of the skull). *Gopherus huecoensis* Strain, 1966 from the early Pleistocene of Texas is slightly smaller than the rest, but its morphology is once again comparable with that of *Gopherus hexagonatus*. Although Auffenberg (1974), Crumly (1994), and Franz (2014) suggested that *Gopherus huecoensis* may be synonymous with the extant *Gopherus flavomarginatus*, TEWG (2015) suggested that it is distinct. Indeed, based on the drawings of Strain (1966), *Gopherus huecoensis* appears to have a clear separation between the distal radius and the distal carpals and thus has a more elongated medial centrale compared with that of *Gopherus flavomarginatus*. Based on all of the above, “*Testudo*” *campester*, *Bysmachelys canyonensis*, and *Gopherus huecoensis* are herein considered to be junior synonyms of *Gopherus hexagonatus*. Preston (1979) suggested the synonymy of *Gopherus hexagonatus* with “*Testudo*” *laticaudata* Cope, 1893 and, as first reviser, chose the latter based on page priority, an opinion followed by TEWG (2015). However, “*Testudo*” *laticaudata* is shown herein to be a nomen dubium (see below). All phylogenetic analyses herein recovered *Gopherus hexagonatus* in a derived position within crown *Gopherus*, in an unresolved polytomy with the coeval large-sized *Gopherus donlaloii* from Mexico and the Miocene *Gopherus hollandi*.

Gopherus mohavensis (Merriam, 1919)

Taxonomic history. *Testudo mohavense* Merriam, 1919 (new species); *Gopherus mohavense* Williams 1950b (new combination); *Gopherus mohavetus* Des Lauriers 1965 (unjustified emendation); *Testudo mohavensis* Auffenberg 1974 (justified emendation); *Scaptochelys mohavense* = *Gopherus depressus* = *Testudo milleri* Bramble 1982 (new combination and senior synonymy); *Gopherus mohavetus* = *Gopherus brattstromi* Reynoso and Montellano-Ballesteros 2004 (senior synonymy); *Xerobates mohavetus* Franz 2014 (new combination).

Type material. UCMP 21575 (holotype), a shell (Merriam 1919, fig. 4).

Type locality. Barstow syncline, San Bernardino County, California, USA (Merriam 1919; Figure 6); Barstow beds, Barstovian NALMA, Langhian–Seravallian, middle Miocene (Auffenberg 1974; Woodburne 2004).

Referred material and range. Middle Miocene (Langhian–Seravallian), Barstovian NALMA, Kern County, California, USA (referred material of Brattstrom 1961).

Diagnosis. *Gopherus mohavensis* can be diagnosed as a member of *Gopherus* based on the characters mentioned above. *Gopherus mohavensis* differs from all other *Gopherus* in the cervical that is much wider than long and the much wider neural IV. *Gopherus mohavensis* further differs from *Gopherus hexagonatus* and *Gopherus brevisternus* in the well-differentiated neural series.

Comments. *Gopherus mohavensis* is based on a shell from the middle Miocene of California (Merriam 1919). Auffenberg (1974) attributed the emendation “*Gopherus mohavensis*” to Bataller (1926), but I am unable to confirm this. Instead, I note that Des Lauriers (1965) changed the specific name from *mohavense* to *mohavetus*, thus changing the entire suffix and not just the ending (footnote in Table 4 of Des Lauriers 1965). This is considered an unjustified emendation (ICZN 1999, Art. 33.2.3). Although not intentional, the spelling of Auffenberg (1974) is followed here for gender agreement. *Gopherus mohavensis* differs from other *Gopherus* in the presence of a cervical that is short and much wider than long, a character that is responsible for placing this taxon in a basal position. However, the phylogeny position of this taxon is not fully resolved herein and, as such, it is shown in a basal polytomy with *Gopherus*.

Hesperotestudo Williams, 1950b

Type species. *Testudo osborniana* Hay, 1908.

Diagnosis. *Hesperotestudo* can be diagnosed as a member of *Testudinidae* based on the characters mentioned above. *Hesperotestudo* differs from *Gopherus* and *Stylemys* in the presence of a deep pit in the premaxillae in ventral view, the extension of the lingual ridge to the maxilla, the long and narrow cervical scute, narrower pectorals, and the presence of dermal armor that covers the tail and/or limbs. *Hesperotestudo* further differs from *Gopherus* on the humero-pectoral sulcus that is perpendicular to the axial plane and from *Stylemys* in the presence of well-differentiated neurals, concave lateral parts of the humero-pectoral sulcus, and broad contact between the inguinal and femoral scutes.

Comments. *Hesperotestudo* Williams, 1950b was created as a subgeneric group within Nearctic “*Testudo*” to include mainly taxa with a heavy armor of dermal ossicles on the limbs and tail. A few years later, Auffenberg (1963) further divided the *Hesperotestudo* group (sensu Williams 1950b) by creating another subgenus, namely *Caudochelys* Auffenberg, 1963. He described the dermal armor in further detail, distinguishing the morphology of *Hesperotestudo* as having a caudal buckler and associated morphology of caudal vertebrae (see diagnosis above), whereas *Caudochelys* lacks the buckler and shows posterior limb armor. Clearly, both *Hesperotestudo* and *Caudochelys* are distinguished from the remaining North American tortoises based on the presence of dermal armor. However, Meylan and Sterrer (2000) consider *Caudochelys* to be a synonym of *Hesperotestudo*. Auffenberg (1963) proposed that *Hesperotestudo* contains *angusticeps*, *equicomis*, *incisa*, *impensa*, *orthopygia*, *osborniana* (type species), *pertenuis*, *riggsi*, *turgida*, and *wilsoni* and that *Caudochelys* included *arenivaga*, *crassiscutata* (type species), *laticaudata*, *rexroadensis*, *tedwhitei*, and, possibly, *Testudo hayi*. He furthermore concluded that the former lineage could be traced back to “*Testudo*” brontops and the latter to *Testudo ligonia* (Auffenberg 1963). Most of these taxa are herein found to be either nomina dubia or junior synonyms of other species of *Hesperotestudo*. All phylogenetic analyses herein recovered *crassiscutata* nested within *Hesperotestudo* and I therefore see no reason to maintain two genera. The phylogenetic analyses herein consistently recovered most of the *Hesperotestudo* spp. in a monophyletic group. The placement of the entire clade within

Testudinidae was not fully resolved, as under equal weights it is consistently recovered within *Testudininae*, but under implied weights *gilbertii* is placed in more basal positions in *Testudinidae*. As such, the clade is tentatively shown in a basal polytomy with *Testudininae*.

I here note the presence of imprints of the cranial scales onto the dorsal skull roof in representatives of this clade, in particular, in *angusticeps*, *osborniana*, and *impensa* (herein considered a junior synonym of *osborniana*). In all these cases, there is a single rounded and elongated scale that covers most of the frontals and part of the parietal, meeting anteriorly the paired elongated scutes that cover the prefrontals and the anterior parts of the frontals. This configuration resembles the type C in Crumly (1984b), which he reported for “*Geochelone*,” *Indotestudo*, *Manouria*, *Homopus*, and *Hesperotestudo*. Although it is difficult to observe this character in most fossil tortoises, its certain presence in some *Hesperotestudo* further indicates the distinction from *Gopherus*, which only shows several small scales on the skull (Crumly 1984b).

Hesperotestudo bermudae Meylan and Sterrer, 2000

Taxonomic history. *Hesperotestudo bermudae* Meylan and Sterrer, 2000 (new species).

Type material. BAMZ 1991-086 (holotype), a skull, partial shell, and appendicular elements (Meylan and Sterrer 2000, figs 1–7).

Type locality. No. 3 Vermont Valley Close, Smith’s Parrish, Bermuda (Figure 6); Upper Townhill Formation, 300,000 ± 10,000 BP, late Irvingtonian, Ionian, middle–late Pleistocene (Meylan and Sterrer 2000).

Referred material and range. Pleistocene, Bermuda (referred material of Olson and Meylan 2009).

Diagnosis. *Hesperotestudo bermudae* can be diagnosed as a member of *Hesperotestudo* based on the characters listed above. *Hesperotestudo bermudae* differs from other *Hesperotestudo* based on the presence of a thin, wide shell in which the ilium contacts costals VII and VIII, a significantly narrowed prootic in dorsal view, a cavum tympani that is divided into a more dorsal and a more ventral part by a sharp ridge that crosses the anterior surface of the cavum from just anterior to the incisura columellae auris to the suture with the quadratojugal, and an acromion process that forms a very high angle to the body of the scapula.

Comments. *Hesperotestudo bermudae* is based on a relatively complete skeleton from the late Pleistocene of Bermuda (Meylan and Sterrer 2000). This taxon is important for our understanding of the paleobiogeographic history of North America and of dispersal events between North and South America that occurred in the past (see Paleobiogeography section above). As Meylan and Sterrer (2000) correctly noted, it is easy to distinguish this taxon both from *Gopherus* and *Chelonoidis* and to attribute it to *Hesperotestudo* instead, thereby documenting yet another dispersal event from southeastern North America to the “West Indies.” The timing of this dispersal, however, is still an open question, although geological evidence suggests that it

must have happened in the last 600,000 years (Meylan and Sterrer 2000 and references therein). Meylan and Sterrer (2000) speculated that the ancestral stock may be from *Hesperotestudo crassiscutata*, but the analyses herein recovers the early Miocene *Hesperotestudo williamsi* from Texas as its sister, which would imply an earlier dispersal; however, this is contradicted by the geological age of Bermuda (Meylan and Sterrer 2000). Any alternative grouping with Pleistocene *Hesperotestudo* spp., interestingly, requires at least two additional steps.

Hesperotestudo crassiscutata (Leidy, 1889b)
(= *Testudo sellardsi* Hay, 1916a)

Taxonomic history. *Testudo crassiscutata* Leidy, 1889b (new species); *Geochelone* (*Caudochelys*) *crassiscutata* = *Eupachemys obtusa* = *Eupachemys rugosus* = *Testudo distans* = *Testudo luciae* = *Testudo obtusa* = *Testudo ocalana* = *Testudo sellardsi* Auffenberg 1963 (senior synonymy); *Geochelone crassiculata* Slaughter 1966 (incorrectly spelled species epithet); *Hesperotestudo crassiscutata* Preston 1979 (new combination).

Type material. USNM 983 (holotype), a partial plastron (Leidy 1889b, pl. 6.4–7; Hay 1908, figs. 616, 617; Auffenberg 1963, fig. 10).

Type locality. Peace River, near Arcadia, Hardee County, Florida, USA (Figure 6); Pleistocene (Auffenberg 1963).

Referred material and range. Pleistocene, near Tampa, Florida, USA (material referred to *Testudo crassiscutata* by Hay 1908); Pleistocene, Eichelberger Cave, Hillsborough River State Park, Hillsborough County, Reddick I and II, Mefford Cave II, Marion County, Melbourne, Brevard County, Ichetucknee River, Kanapaha, Prairie Creek, Rock Springs, Florida, USA (material referred to *Geochelone crassiscutata* by Auffenberg 1963); Pleistocene, Vero, St. Lucie County and Orange County, Florida, USA (type and referred material of *Testudo sellardsi* Hay, 1916a); Pleistocene, Lesley Shell Pit, Hillsborough County, Florida, USA (material referred to *Hesperotestudo crassiscutata* by Meylan 1995); Pleistocene, Brazos river, near Pittbridge, Burleson County, Texas, USA (material referred to *Testudo crassiscutata* by Hay 1916b); late Pleistocene, Haile cave, Alachua County, Florida, USA (material referred to *Geochelone crassiscutata* by Martin 1978); late Pleistocene, Ediston beach, Colleton County, South Carolina, USA (material referred to *Geochelone crassiscutata* by Dobie and Jackson 1979); late Pleistocene, Hopwood Farm locality, near Fillmore, Montgomery County, Illinois, USA (material referred to *Geochelone crassiscutata* by King and Saunders 1986); late Pleistocene, Devil's Den Sinkhole, Levy County, Florida, USA (material referred to *Geochelone crassiscutata* by Holman 1978).

Diagnosis. *Hesperotestudo crassiscutata* can be diagnosed as a member of *Hesperotestudo* based on the characters listed above. *Hesperotestudo crassiscutata* differs from other *Hesperotestudo* on the presence of dermal armor on the posterior limbs, instead of a caudal buckler, and larger size.

Comments. *Hesperotestudo crassiscutata* is based on a partial plastron from the Pleistocene of Florida (Leidy 1889b). This

species is certainly a derived testudinid and arguably the largest member of *Hesperotestudo*. Apart from the presence of posterior limb armor, instead of a caudal buckler, the skeletal morphology of this taxon is quite similar with other *Hesperotestudo*. The unique posterior limb armor of *Hesperotestudo crassiscutata* could represent an autapomorphic feature. An alternative explanation could be that this difference is due to sexual dimorphism within *Hesperotestudo*, in that males have a caudal buckler and females having posterior limb armor (or vice versa). Extant *Testudo hermanni* shows presence/absence of a tail spur in males/females, although this feature is not ossified. The posterior thigh region appears to be important for sexual courtship in tortoises, so dimorphism should not be unexpected in this area. The presence of this taxon in El Salvador and the West Indies (Cisneros 2005 and references therein) is only inferred by the large size of these fragments of testudinids and it is not confirmed herein.

Hesperotestudo ducatei (Collins and Lynn, 1936)

Taxonomic history. *Testudo ducatei* Collins and Lynn, 1936 (new species); *Geochelone ducatei* Auffenberg 1963 (new combination; incorrectly spelled species epithet); *Hesperotestudo ducatei* Weems and George 2013 (new combination).

Type material. USNM 13783 (holotype), carapacial fragments and associated plastron (Collins and Lynn 1936, pls. 3, 4).

Type locality. West side of the Chesapeake Beach-Plum Point road, 5.5 km south of the old Chesapeake Beach Railroad Station, Calvert County, Maryland, USA (Collins and Lynn 1936; Figure 6); Zone 10, Calvert Formation, Barstovian NALMA, Langhian–Serravallian, middle Miocene (Auffenberg 1974; Woodburne 2004).

Referred material and range. Middle Miocene of type locality, Maryland, USA (hypodigm of Weems and George 2013).

Diagnosis. *Hesperotestudo ducatei* can be diagnosed as a member of *Hesperotestudo* based on the characters listed above. *Hesperotestudo ducatei* differs from other *Hesperotestudo* in the presence of a pentagonal entoplastron.

Comments. *Hesperotestudo ducatei* is based on shell fragments from the middle Miocene of Maryland (Collins and Lynn 1936). The available material can clearly be referred to *Hesperotestudo* based on the morphology of the pectorals. This taxon is similar to *Hesperotestudo orthopygia* in the covering of the entoplastron by the gulars, placement of the humero-pectoral sulcus just behind the entoplastron, long pectorals, contact between inguinals and femorals, and short anals. It differs from this group, however, based on the presence of a pentagonal entoplastron. Taking geographic separation into account as well, *Hesperotestudo ducatei* is considered tentatively to be a valid species herein. Due to the lack of carapacial information, its position within *Hesperotestudo* is unclear, and it is therefore here shown in a basal polytomy within that clade.

Hesperotestudo gilbertii (Hay, 1899a)

Taxonomic history. *Testudo gilbertii* Hay, 1899a (new species); *Testudo gilberti* Hay 1908 (incorrectly spelled species epithet);

Geochelone (*Hesperotestudo*) *gilberti* Auffenberg 1974 (new combination, incorrectly spelled species epithet).

Type material. KU 1245 (holotype), a skull and mandible (Gilbert 1898, figs. 1–4; Hay 1908, pl. 80.2–5; Schultze et al. 1985).

Type locality. Phillips County, Kansas, USA (Gilbert 1898; Figure 6); Ogallala Formation, Hemphillian NALMA, Tortonian–Zanclean, late Miocene–early Pliocene (Schultze et al. 1985; Woodburne 2004).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Hesperotestudo gilbertii* can be diagnosed as a member of *Hesperotestudo* based on the characters listed for that clade above. *Hesperotestudo gilbertii* differs from *Hesperotestudo osborniana* and *Hesperotestudo orthopygia* in the ventral expansion of the postorbital that divides the jugal and quadratojugal, the longer vomer that divides most of the pterygoids, and in the visibility of the foramen praepalatinum on the ventral part of the premaxillae. *Hesperotestudo gilbertii* further differs from *Hesperotestudo orthopygia* in the longer frontals medially and the absence of contact between the parietal and the squamosal.

Comments. *Hesperotestudo gilbertii* is based on a cranium from the Mio/Pliocene of Kansas (Gilbert 1898). This taxon has been suggested to be a possible synonym of *Hesperotestudo osborniana* Auffenberg (1974), in which case it would have priority. However, based on the figures of Gilbert (1898) and the revised ones by Hay (1908), some important differences are apparent in the skull (see Diagnosis above) that tentatively support the distinction of both. In the preliminary analysis presented herein, *Hesperotestudo gilbertii* is not confidently recovered within *Hesperotestudo* due to the absence of shell information.

Hesperotestudo orthopygia (Cope, 1878)
(= *Xerobates cyclopygius* Cope, 1878 =
Caryoderma snovianum Cope, 1886 = *Testudo*
rexroadensis Oelrich, 1952 = *Geochelone*
nordensis Holman, 1973b)

Taxonomic history. *Xerobates orthopygius* Cope, 1878 (new species); *Testudo orthopygia* Hay 1899a (new combination; mandatory change); *Testudo orthopygia* = *Caryoderma snovianum* = *Xerobates cyclopygius* Hay 1908 (senior synonym); *Geochelone* (*Hesperotestudo*) *orthopygia* Williams 1950b (new combination).

Type material. AMNH 3929 (holotype), skull, shell, and appendicular elements (Hay 1908, figs. 579–590, pls. 80.1, 82).

Type locality. Decatur County, Kansas, USA (Cope 1878; Figure 6); Republican River Formation, Clarendonian NALMA, Tortonian; late Miocene (Schultze et al. 1985; Woodburne 2004).

Referred material and range. Middle Miocene (Serravallian), Barstovian NALMA, Brown County (referred material of Holman 1973b; type material of *Geochelone nordensis*), Cherry

County (referred material of Holman and Sullivan 1981) Keya Paha County, Nebraska, USA (referred material of Holman 1973a); late Miocene–early Pliocene (Tortonian–Zanclean), Clarendonian/Hemphillian NALMA, Decatur County (referred material of Hay 1908; type material of *Testudo cyclopygius* and *Caryoderma snovianum*) and Trego County, Kansas, USA (referred material of Holman 1975); late Miocene–early Pliocene, Stanislaus County, California, USA (referred material of Biewer et al. 2016); late Miocene or early Pliocene, Phillips County, Kansas, USA (referred material of Hay 1909); Pliocene, Blangan NALMA, Meade County, Kansas, USA (type material of *Testudo rexroadensis*).

Diagnosis. *Hesperotestudo orthopygia* can be diagnosed as a member of *Hesperotestudo* based on the characters listed above. *Hesperotestudo orthopygia* differs from *Hesperotestudo osborniana* by its taller and shorter skull, frontals medially shorter than prefrontals, longer crista supraoccipitalis, larger dentary angle, usually seven neurals, longer pectorals medially, and deeper anal notch and from *Hesperotestudo gilbertii* by the frontals medially shorter than prefrontals, the contact between the parietal and the squamosal, the clear contact between the jugal and quadratojugal, and the short vomer that only contacts the anterior part of pterygoids.

Comments. *Hesperotestudo orthopygia* is based on a partial skeleton from the late Miocene of Kansas (Cope 1878). Hay (1908) concluded that Cope (1878) has confused the anterior lobe of *Xerobates orthopygius* as the posterior lobe of *Xerobates cyclopygius*, a taxon that he had named in the same contribution. Hay (1908) noted that the name *cyclopygius* is a more fitting name but nevertheless, as first reviser, gave priority to *orthopygia* based on page priority. As such, *Xerobates cyclopygius* is herein considered to be a junior synonym of *Hesperotestudo orthopygia*. Williston (1898) noted that specimens that Cope (1886, 1889) had described as a new species of glyptodont, *Caryoderma snovianum*, are actually parts of the dermal armor referable to *Hesperotestudo*. Williston (1898) suggests that they could belong to *Testudo undata* (a nomen dubium herein), but no such dermal armor has been reported for this taxon. Later, Hay (1908) suggested that *Caryoderma snovianum* is a synonym of *Hesperotestudo orthopygia*, a conclusion followed herein, in part because both taxa originate from the same formation. The type material of *Testudo rexroadensis* Oelrich, 1952 originates from younger deposits, also from Kansas, but is nevertheless similar in morphology to *Hesperotestudo orthopygia*. However, the differences that Oelrich (1952) noted are consistent with sexual dimorphism and/or intraspecific variation and *Testudo rexroadensis* is therefore here considered to be a junior synonym of *Hesperotestudo orthopygia*. Another taxon that is similar to *Hesperotestudo orthopygia* is *Geochelone nordensis* Holman, 1973b. Holman (1973b) differentiated *Geochelone nordensis* from the coeval *Hesperotestudo orthopygia* based on size difference alone and suggested that *Geochelone nordensis* is closer to *Hesperotestudo williamsi* from Texas but, again, based on size only. In fact, *Geochelone nordensis* is similar to those taxa in plastral morphology, having gulars that cover the entoplastron, humero-pectoral sulcus just behind the entoplastron, rhomboidal entoplastron, contact between inguinals and femorals, and short anals. Personal observations of additional material attributed to *Geochelone nordensis* (USNM), from the type

locality that preserves the entire shell, confirm the similarity between *Geochelone nordensis* and *Hesperotestudo orthopygia*. Given that the intraspecific size difference in other *Hesperotestudo* taxa is great (Auffenberg 1963), *Geochelone nordensis* is tentatively listed here as a junior synonym of the larger, but coeval *Hesperotestudo orthopygia*. All implied-weights analyses herein consistently retrieved *Hesperotestudo orthopygia* as the basalmost member of *Hesperotestudo*.

Hesperotestudo osborniana (Hay, 1905)
(= *Testudo arenivaga* Hay, 1906b = *Testudo farri*
Hay, 1908 = *Testudo impensa* Hay, 1908 =
Testudo orthopygia angusticeps Matthew, 1924)

Taxonomic history. *Testudo osborniana* Hay, 1905 (new species); *Geochelone osborniana* Williams 1950b (new combination); *Geochelone* (*Hesperotestudo*) *osborniana* Auffenberg 1963 (new combination); *Hesperotestudo osborniana* Meylan and Sterrer 2000 (new combination).

Type material. AMNH 5868 (holotype), skull, shell, and appendicular elements (Hay 1908, figs. 552–562, pls. 72–75).

Type locality. Pawnee Creek, north of Sterling, Logan County, Colorado, USA (Hay 1908; Figure 6); Pawnee Creek Formation, Hemingfordian–Barstovian NALMA, Burdigalian–Serravallian, early–middle Miocene (Williams 1950b; Galbreath 1953; Woodburne 2004).

Referred material and range. Early Miocene (Aquitainian–Burdigalian), Hemingfordian NALMA, Sioux County, Nebraska, USA (type material of *Testudo angusticeps* Matthew, 1924; type and referred material of *Testudo arenivaga* of Loomis 1909); middle Miocene (Burdigalian–Serravallian), Hemingfordian–Barstovian NALMA, Logan County, Colorado, USA (referred material of Hay 1908); middle Miocene (Langhian–Serravallian), Barstovian NALMA, Montana, USA (type material of *Testudo farri*); late Miocene–early Pliocene, Loup Fork Formation (Tortonian–Zanclean), Hemphillian NALMA, Gallatin County, Montana, USA (type material of *Testudo impensa*).

Diagnosis. *Hesperotestudo osborniana* can be diagnosed as a member of *Hesperotestudo* based on the characters listed for that clade above. *Hesperotestudo osborniana* differs from *Hesperotestudo orthopygia* in having a skull low and elongate, frontals that are medially longer or equal to the prefrontals, a short crista supraoccipitalis, a narrower dentary angle, hexagonal neural VIII, extremely short pectorals medially, and a shallow anal notch and from *Hesperotestudo gilbertii* based on the clear contact between the jugal and quadratojugal and the short vomer that only contacts the anterior part of pterygoids.

Comments. *Hesperotestudo osborniana* Hay, 1905 is a large-sized testudinid with carapace length of up to 77.5 cm known from skull, shell, and appendicular remains (Hay 1908; Auffenberg 1963). This tortoise is characterized by the presence of heavy dermal armor in the tail in the form of dermal ossicles that fuse to form a caudal buckler. Two taxa from Montana are similar to *Hesperotestudo osborniana*: the middle-sized (33 cm) “*Testudo farri*” Hay, 1908 from the middle Miocene and the large-sized

(92 cm) “*Testudo impensa*” Hay, 1908 from the late Miocene. The former preserves only the shell, whereas the latter preserves the skull as well. Based on the shell, “*Testudo farri*” is similar to “*Testudo impensa*”. They are also similar to *osborniana* in shell and skull morphology, showing only small differences on the skull, in particular, the shape and size of the basisphenoid, which is longer and triangular in *osborniana* whereas it is V-shaped and shorter in *impensa*, and the posterior maxillary process, which is slightly larger in *osborniana*. These differences, as opposed to the general similarity of the remaining skeletal elements, do not seem sufficient at the moment to support the distinction of these coeval tortoise taxa. Auffenberg (1974) already suggested the synonymy between *Hesperotestudo osborniana* and “*Testudo impensa*”. Another middle Miocene taxon that is similar to *Hesperotestudo osborniana* is “*Testudo angusticeps*” Matthew, 1924 from the middle Miocene of Nebraska. Matthew (1924) originally described this large-sized (75 cm) tortoise as a “new mutant name” or as a subspecies of *orthopygius*, but the name first appears in a caption. The morphology of the skull is closer to *osborniana* than to *orthopygia* in the longer than wide skull and the longer frontals compared with the prefrontals. From the early Miocene of Nebraska, the type material of the middle-sized (larger than 50 cm) “*Testudo arenivaga*” Hay, 1906b is extremely limited and cannot allow the distinction of this taxon. However, Loomis (1909) referred new material to this species from the type locality (a cranium, a partial plastron, limb bones) that provides some additional anatomical information on *arenivaga*. Based on the combined information, it is not possible to distinguish *arenivaga* from *osborniana* as it shares all the characters mentioned in the diagnosis herein. In conclusion, “*Testudo arenivaga*”, “*Testudo farri*”, “*Testudo impensa*”, and “*Testudo angusticeps*” are tentatively considered herein as junior synonyms of *Hesperotestudo osborniana*. The phylogenetic analyses herein consistently recovered this taxon in a basal position within *Hesperotestudo*.

Hesperotestudo turgida (Cope, 1892a)
(= *Testudo incisa* Hay, 1916a = *Testudo riggsi*
Hibbard, 1944 = *Testudo wilsoni* Milstead,
1956 = *Geochelone johnstoni* Auffenberg
1962b = *Geochelone alleni* Auffenberg, 1966 =
Geochelone oelrichi Holman, 1972a = *Geochelone*
mlynarskii Auffenberg, 1988)

Taxonomic history. *Testudo turgida* Cope, 1892a (new species); *Gopherus turgida* Williams 1950b (new combination); *Geochelone* (*Hesperotestudo*) *turgida* Auffenberg 1962b (new combination).

Type material. ANSP 14689 (holotype), fragments of a carapace, plastron, and mandible (Oelrich 1957, fig. 1).

Type locality. Near the former town of Espuella, about 10 km southwest of Dickens, Dickens County, Texas, USA (Cope 1892a; Oelrich 1957; Figure 6); Blanco beds, Blancan NALMA, Piacenzian, late Pliocene (Oelrich 1957; Woodburne 2004).

Referred material and range. Late Miocene, “Alachua Formation,” Hemphillian NALMA, McGehee Site, 3 miles north of

Newberry, Alachua County, Florida, USA (type material of *Geochelone alleni* Auffenberg, 1966); late middle Pliocene, Ogallala Formation, late Hemphillian NALMA, Buis Ranch Fauna, Beaver County, Oklahoma, USA (referred material to *Testudo turgida* of Oelrich 1957); late Pliocene, Rexroad Formation, Saw Rock Canyon and Rexroad faunas, early Blancan NALMA, Cimarron Valley, Seward County, Kansas, USA (type material of *Testudo riggsi* Hibbard, 1944 and referred material to *Testudo turgida* of Oelrich 1957); late Pliocene, early Blancan NALMA, Near Mount Blanco, Blanco beds, Crosby County, Texas, USA (referred material to *Testudo turgida* of Cope 1893); Pliocene, Hemphillian NALMA, Manatee County, Florida, USA (referred material to *Geochelone turgida* of Webb and Tessman 1968); late Pliocene, Blancan III NALMA, Cita Canyon beds, North Cita Canyon, Randall County, Texas, USA (type material of *Geochelone johnstoni* Auffenberg, 1962b); early Pleistocene, Long Pine and Keim Formations, Blancan NALMA, Brown County, Nebraska, USA (type and referred material of *Geochelone oelrichi* Holman, 1972a); middle Pleistocene, Irvingtonian NALMA, near Coleman, Sumter County, Florida, USA (type and referred material of *Geochelone mlynarskii* Auffenberg, 1988); Pleistocene, Arredondo II, Haile, Ichetucknee River, Reddick I, Zuber, Florida, USA (referred material to *Geochelone turgida* of Auffenberg 1963); Pleistocene, Sangamon Interglacial, Ocala Lime Company Quarry, near Ocala, Marion County, Florida, USA (type material of *Testudo incisa* Hay, 1916a); Pleistocene, Rancho Labrean NALMA, Friesenhahn Cave, Bexar County, Texas, USA (type material of *Testudo wilsoni* Milstead 1956); early Pleistocene, late Blancan, Knox County, Nebraska, USA (referred material to *Geochelone oelrichi* of Rogers 1984); Pleistocene, Leisley Shell Pit, Hillsborough County, Florida, USA (referred material to *Hesperotestudo mlynarskii* of Meylan 1995); late Pleistocene, Brown Sands Wedge fauna and Eddy Cave, New Mexico, USA (referred material to *Geochelone wilsoni* of Moodie and van Devender 1979); late Pleistocene, Domebo site, Caddo County, Oklahoma, USA (referred material to *Geochelone wilsoni* of Moodie and van Devender 1979); late Pleistocene, Slaton quarry, Lubbock County, Texas, USA (referred material to *Geochelone wilsoni* of Moodie and van Devender 1979); late Pleistocene, Buckner Ranch site, Bee County, Texas, USA (referred material to *Geochelone wilsoni* of Moodie and van Devender 1979).

Diagnosis. *Hesperotestudo turgida* can be diagnosed as a member of *Hesperotestudo* based on the characters listed above. *Hesperotestudo turgida* differs from other *Hesperotestudo* in its smaller size, vaulted and thickened shell, epiplastra that expand beyond the anterior part of the carapace, significant gular protrusion, ventral keels on the epiplastra, and presence of a disproportionately large caudal buckler.

Comments. *Hesperotestudo turgida* is based on shell fragments and a partial mandible from the Pliocene of Texas (Cope 1892a) that remained unfigured for several decades (Oelrich 1957). In his review of the fossil tortoises from Florida, Auffenberg (1963) recognized a lineage from the Pliocene to Pleistocene that consists of *Hesperotestudo turgida*, *Testudo riggsi* Hibbard, 1944, *Geochelone johnstoni* Auffenberg 1962b, and *Testudo incisa* Hay, 1916a. For reasons that will be further discussed below, these taxa are considered here as synonymous, with *Hesperotestudo turgida* Cope, 1892a having priority. Although Hibbard (1944)

listed several characters that exclude *riggsi* from *Gopherus*, Williams (1950b) suggests that both *turgida* and *riggsi* should be included in the gopher tortoise lineage. Shortly after, Oelrich (1957) presents the first figuration of *turgida*, updated descriptions of *riggsi*, which he considered to be a synonym of *turgida*, and referred new material to *turgida*. Oelrich (1957) further reinstates the distinction of these taxa from *Gopherus*, as is confirmed by the presence of a caudal buckler on the new referred specimens. Kuhn (1964) suggested, also, the synonymy between *riggsi* and *turgida*, but without further justification. The final inclusion of these taxa in *Hesperotestudo* was made by Auffenberg (1962b, 1963) and followed henceforth. The type of *incisa* is only a left xiphiplastron, which is insufficient to diagnose a taxon by itself. Auffenberg (1963) referred additional specimens to this taxon and attempted to diagnose it only from Pleistocene representatives of *Hesperotestudo* (e.g., *crassiscutata*). Another Pleistocene form from Texas is "*Testudo wilsoni* Milstead, 1956. The overall morphology of this taxon is again similar to that of the *turgida* group, with the only possible difference being the slightly less protruding epiplastral lip. As this character is not sufficient to diagnose this taxon, *wilsoni* is here also included in the synonymy of *turgida*. Auffenberg (1962b) further named "*Geochelone johnstoni* from the Pleistocene of Texas based on material that was considered to be a new species in the unpublished and unfinished thesis of C.S. Johnston (see relevant section below). All the differences listed in Auffenberg (1962b) are within the observed variation of taxa here referred to *turgida*, and this taxon is therefore here synonymized with it, as has already been suggested by Oelrich (1957) in advance based on the unpublished thesis of C.S. Johnston. Auffenberg (1966) described "*Geochelone alleni* from the Pliocene of Florida, stating its similarity with *incisa* from the Pleistocene of Florida and differentiated it based on smaller adult size, thicker shell, and the absence of well-defined ventral keels on the epiplastra. These characters, however, are once again consistent with ontogenetic and/or sexual variation within *turgida*. Holman (1972a) described a new species, *Geochelone (Hesperotestudo) oelrichi*, from the Pleistocene of Nebraska as a member of the *turgida* line. Although he clearly placed this taxon close to *turgida* and *riggsi*, he nevertheless diagnosed it based on characters that are subject to variation, such as a less vaulted and thicker shell with pronounced knobs on the third marginal scutes. Overall, *oelrichi* cannot be differentiated with confidence from *turgida* and its synonymous taxa and as such it is included herein in the synonymy of *turgida*. Similarly, "*Geochelone mlynarskii* Auffenberg, 1988 from the middle Pleistocene of Florida presents little anatomic information and was diagnosed only by its smaller size. It is indistinguishable from *turgida* and its synonymous taxa and as such it is included herein in the synonymy of *turgida* as well.

The specimens attributed to *Hesperotestudo turgida* are smaller in size compared with *Hesperotestudo orthopygia* and *Hesperotestudo osborniana* (approximately 22–25 cm long) and all show the same shell morphology, characterized mainly by the presence of the caudal buckler and the presence of ventral keels on the gular part of the epiplastra. All synonymized taxa have been considered always close to each other and part of the same lineage (e.g., in Auffenberg 1963). At this point it seems unnecessary to provide further distinctions within this group, which is mainly distributed in south-central USA (Texas–Oklahoma–Kansas–Nebraska) and possibly in Florida as well; but,

as the temporal and geographical distribution of this taxon is relatively extensive, it is possible that a more detailed revision of the material will provide support for the validity of some of the synonymized taxa. Future work should focus on the alpha taxonomy of the taxa included. All phylogenetic analyses herein recovered *Hesperotestudo turgida* within *Hesperotestudo*.

Hesperotestudo williamsi (Auffenberg, 1964b),
comb. nov.

Taxonomic history. *Geochelone williamsi* Auffenberg, 1964b (new species); *Geochelone (Caudochelys) williamsi* Auffenberg 1974 (new combination).

Type material. TMM 31084-11 (holotype), a shell (Auffenberg 1964b, figs. 1, 2).

Type locality. Garvin Gully, 3 km north of Navasota, Grimes County, Texas, USA (Auffenberg 1964b; Figure 6); lower Oakville Member, Oakville Formation, early Hemingfordian NALMA, Burdigalian, early Miocene (Albright 1994; Woodburne 2004).

Referred material and range. No specimens have been referred to this taxon to date.

Diagnosis. *Hesperotestudo williamsi* can be diagnosed as a member of *Hesperotestudo* based on the characters mentioned above. *Hesperotestudo williamsi* differs from other members of *Hesperotestudo* in the presence of an octagonal neural VI.

Comments. *Hesperotestudo williamsi* is based on a shell from the early Miocene of Texas (Auffenberg 1964b). Auffenberg (1964b) suggested that this small- to middle-sized tortoise (shell length 33.4 cm) is close to *Testudo ducateli* Collins and Lynn, 1936. The presence of an octagonal sixth neural seems to distinguish this taxon from the remaining *Hesperotestudo*, but only with the information of the skull will it be possible to more rigorously assert the validity of this taxon. The phylogenetic analyses herein recovered *Hesperotestudo williamsi* in a derived position within *Hesperotestudo*, as sister to *Hesperotestudo bermudae* because of the shared coincidence of the position of the humero-pectoral sulcus with the posterior end of the entoplastron. This sister-group relationship is interesting as it provides credit to the hypothesis of Meylan and Sterrer (2000) that *Hesperotestudo* dispersed from the southeastern U.S. to Bermuda.

Stylemys Leidy, 1851a

Type species. *Stylemys nebrascensis* Leidy, 1851a.

Diagnosis. *Stylemys* can be diagnosed as a member of *Testudinidae* based on the full list of characters listed for that clade above. *Stylemys* can be differentiated from other testudinids by the presence of a premaxillae ridge with a corresponding dentary symphyseal groove, a neural pattern of 4>6A/8>6A/4>6A>6A>6A>6A>6A, the absence of epiplastral excavation, and placement of the medially straight and anterolaterally convex humero-pectoral sulcus posterior to the entoplastron.

Comments. Auffenberg (1964a) provided the most recent revision of this taxon and a new diagnosis that is followed herein. The less differentiated neural series, the absence of an epiplastral excavation, and the less specialized shape of the anterior lobe distinguish *Stylemys* from *Gopherus*. Several characters from the shell are used to distinguish the various taxa (e.g., the neural pattern; see Auffenberg 1964a). However, a palstral character that appears appears to be diagnostic for all *Stylemys* is the shape of the humero-pectoral sulcus (see Diagnosis above). Given that *Stylemys* of the best-known fossil testudinids worldwide, possibly with hundreds of shells having been found (Hay 1908), a meticulous revision of this material could provide even more characters from the shell to distinguish the members of this clade and to understand the morphological variability within *Stylemys*. All phylogenetic analyses herein recovered *Stylemys* as a monophyletic group, but its placement within *Testudinidae* is not clearly resolved. Maximum parsimony analyses under equal and implied weights recovered *Stylemys* in various positions within *Testudinidae* and, in particular, in the stem of *Testudininae* or within the “*Geochelone* complex.” On the other hand, a sister-group relationship with *Gopherus* was not supported in any case. As such, *Stylemys* is shown herein in a basal polytomy with *Testudininae*.

The presence of *Stylemys* outside the United States is difficult to establish. Fragmentary remains from Saskatchewan, Canada (Cope 1891) can only be identified as members of *Testudinidae*. I am also unable to confirm the identification of *Stylemys* from the late Eocene of Mexico based on the shell fragment figured by Jiménez-Hidalgo et al. (2015). Auffenberg (1964a) tentatively assigned to *Stylemys* non-North American taxa such as “*Stylemys*” *bottii* de Stefano, 1902, “*Testudo*” *canetotiana* Lartet, 1851, “*Testudo*” *frizaciana* Lartet, 1851, and “*Testudo*” *pygmaea* Lartet, 1851 from the Miocene of France and “*Stylemys*” *karakolensis* Riabinin, 1927 from the Oligocene–early Miocene of Turkestan, but I cannot here confirm any of these based on the available published information.

Stylemys capax Hay, 1908
(= *Stylemys conspecta* Hay, 1908)

Taxonomic history. *Stylemys capax* Hay, 1908 (new species); *Stylemis capax* Szalai 1930 (incorrectly spelled genus name).

Type material. AMNH 1357 (holotype), a complete shell (Hay 1908, figs. 498, 499).

Type locality. Near junction of North and South Forks of John Day River, Grant County, Oregon, USA (Hay 1908; Figure 5); Turtle Cove Member, Middle John Day Formation, Arikareean-2 NALMA, Chattian, late Oligocene (Hay 1908; Retallack et al. 1999; Woodburne 2004).

Referred material and range. Late Oligocene (Chattian), Arikareean 2 NALMA, Grant County, Oregon, USA (type and material referred to *Stylemys conspecta* by Brattstrom 1961).

Diagnosis. *Stylemys capax* can be diagnosed as a member of *Stylemys* based on the characters mentioned above. *Stylemys capax* differs from other *Stylemys* in having an octagonal neural II, vertebral I and pleural I expanding on the peripherals, and anal scutes medially shorter than the femorals.

Comments. *Stylemys capax* and its synonym *Stylemys conspecta* were named as new species by Hay (1908) based on material from the same locality initially attributed to *Stylemys nebrascensis* by Cope (1884). Although Hay (1908) noted several times the similarities between the two new taxa, he justified the specific distinction on characters that are consistent with intraspecific variation, in particular, differences to the width of the neurals, proportions of the shell, and thickness of the peripherals. The only difference that may be of taxonomic value is the position of the humeropectoral sulcus, which is located posterior to the entoplastron in *capax* but coincides medially with the posterior margin of the entoplastron in *conspecta*, but the limited number of specimens does not allow further evaluation of the utility of this character. The fact that the specimens come from the same locality corroborates the conclusion that these two taxa could be considered synonymous. As the two names are simultaneously published, I, as first reviser, select *Stylemys capax* as the valid name for this taxon. Several characters seem to support the distinction of *capax* from *nebrascensis*, a conclusion that is corroborated by the significant temporal and geographical separation between the two taxa. Among the material assigned to *nebrascensis* (see below), the type of *Emys culbertsonii* shows a significant similarity with *capax* in the presence of an octagonal neural II, but *culbertsonii* is distinguished from *capax* on the coincidence between the costo-peripheral suture and pleuro-marginal sulci on the anterior peripherals and on the longer medially anals compared with the median length of the femorals. The phylogenetic analyses herein recover *capax* in a basal position within *Stylemys*.

Stylemys inusitata (Hay, 1906b), comb. nov.
(= *Testudo copei* Koerner, 1940 = *Testudo primaeva* Oelrich, 1950)

Taxonomic history. *Testudo inusitata* Hay, 1906b (new species); *Testudo innistata*, *Testudo innuistata* Szalai 1930 (incorrect spelled species epithet); *Gopherus inusitata* Williams 1950b (new combination); *Geochelone (Hesperotestudo) inusitata* Auffenberg 1974 (new combination).

Type material. CM 311 (holotype), a partial shell (Hay 1906b, pls. 3–4; Hay 1908, pl. 68).

Type locality. Near Canyon Ferry, Broadwater County, Montana, USA (Hay 1906b; Figure 6); Deep River Formation, Barstovian NALMA, Langhian–Serravallian, middle Miocene (Auffenberg 1974; Woodburne 2004).

Referred material and range. ?Early Miocene, Madison County, Montana, USA (type material of *Testudo primaeva*); Late Miocene (Langhian–Serravallian), Barstovian NALMA, Meagher County, Montana, USA (type material of *Testudo copei*).

Diagnosis. *Stylemys inusitata* can be diagnosed as a member of *Stylemys* based on the hexagonal neurals II–VII and the shape of the humero-pectoral sulcus. *Stylemys inusitata* differs from *Stylemys nebrascensis* in the more prominent epiplastral lip and the short gulars that do not cover the entoplastron and from *Stylemys capax* in the absence of octagonal neural II and absence of gulars covering of the anterior part of the entoplastron.

Comments. *Stylemys inusitata* is based on a partial shell from the middle Miocene of Montana (Hay 1906b). Although the presence of hexagonal neurals II–VII suggests close relationships with *Stylemys nebrascensis*, the presence of a prominent epiplastral lip led Hay to include this taxon under *Testudo* (e.g., Hay 1908). However, later forms of *Stylemys* (e.g., *Stylemys capax*) show a more prominent epiplastral lip compared with Oligocene *Stylemys nebrascensis*. As such, it is proposed here tentatively that “*Testudo*” *inusitata* is a member of *Stylemys*. “*Testudo*” *copei* Koerner, 1940 was later considered as a member of *Gopherus* (Williams 1950b; Auffenberg 1974). However, the morphology of the lateral parts of the humero-pectoral sulcus (being anteriorly convex) allows the identification of this taxon as a member of *Stylemys* as defined herein. The same generic combination is given by Crumly (1994), but without justification. Even Koerner (1940) stated that “*Testudo*” *copei* closely resembles “*Testudo*” *inusitata* and “*Testudo*” *emiliae*, herein considered as member of *Stylemys*, as well. Although Auffenberg (1974) suggests that it might be conspecific with “*Testudo*” *emiliae*, herein it is considered as a synonym of *St. nebrascensis*. The differences suggested by Koerner (1940) are either misinterpreted (e.g., width of nuchal as compared with first vertebral) or within the observed variability (e.g., relative proportions of neurals and vertebrae). Another taxon from Montana that shows a similar morphology is “*Testudo*” *primaeva* Oelrich, 1950. As the type material of this taxon is highly fragmented, most of the following conclusions are based on the reconstructions of Oelrich (1950). Some of the characters seen in those reconstructions (e.g., the covering of the pleurals I on the lateral parts of the nuchal) are not possible to confirm from observations on the published photographs of Oelrich (1950). The remaining morphological characters that can be confirmed (hexagonal neurals II–VII, gulars not covering the entoplastron, lateral parts of the humero-pectoral sulcus being convex) and the overall shape of the plastron (gular protrusion, anal notch) are similar to *Stylemys inusitata*. The temporal (Miocene) and geographical (Montana) of the taxa mentioned above could provide some additional support to their synonymy. As such, both “*Testudo*” *copei* and “*Testudo*” *primaeva* are considered herein as junior synonyms of *Stylemys inusitata*. In all phylogenetic analysis herein, *St. inusitata* is recovered as the sister taxon of *St. nebrascensis* because of their similarities on the neural series.

Stylemys nebrascensis Leidy, 1851a
(= *Emys hemispherica* Leidy, 1851b = *Testudo lata* Leidy, 1851b = *Emys oweni* Leidy, 1851c =
Emys culbertsonii Leidy, 1852a = *Testudo amphithorax* Cope, 1873a = *Testudo ligonius* Cope, 1873a = *Testudo emiliae* Hay, 1908 =
Gopherus neglectus Brattstrom, 1961)

Taxonomic history. *Stylemys nebrascensis* Leidy, 1851a (new species); *Testudo nebrascensis* Leidy 1852b (new combination); *Stylemys nebrascensis* Cope 1869–70 (incorrectly spelled species epithet); *Stylemys nebrascensis* = *Emys hemispherica* = *Emys oweni* = *Emys culbertsonii* = *Testudo lata* Hay 1908 (senior synonymy); *Stylemys nebrascensis* Prothero 2012 (incorrectly spelled species epithet).

Type material. USNM 97 (holotype), a partial shell (Leidy 1853, pl. 19).

Type locality. White River badlands, South Dakota, USA (Leidy 1873; Figure 5); Orellan Formation, White River Group, Orellan NALMA, early Rupelian, early Oligocene (Woodburne 2004).

Referred material and range. Priabonian, Chadronian NALMA, White River Formation, Weld County (referred material of Hutchison 1996; type material of *Testudo amphithorax* and *Testudo ligonius*) and Logan County, Colorado, USA (referred material of Hay 1908 and Galbreath 1953); Dawes and Sioux County, Nebraska, USA (referred material of Hay 1908 and Hutchison 1996); “White River Badlands,” Pennington County, and Jackson County, South Dakota, USA (referred material of *St. nebrascensis* by Case 1919, 1936 and Sinclair 1924; type material of *Emys culbertsonii*, *Emys hemispherica*, *Emys oweni*, and *Testudo lata*), and Niobrara County, Wyoming, USA (referred material of Lambe 1913 and Case 1925); late Oligocene (early Chattian), Arikareean 2 NALMA, Oglala Lakota (formerly Shannon) County, South Dakota (type material of *Testudo emiliae*) and Ventura County, California, USA (type and referred material of *Gopherus neglectus* of Brattstrom, 1961).

Diagnosis. *Stylemys nebrascensis* can be diagnosed as a member of *Stylemys* based on the characters listed above. *Stylemys nebrascensis* can be differentiated from other *Stylemys* based on the presence of a premaxillae ridge with a corresponding dentary symphyseal groove, a neural pattern of 4>6A>6A>6A>6A>6A>6A, weakly-developed epiplastral lip with absent or shallow epiplastral excavation, and a humero-pectoral sulcus that is situated posterior to the entoplastron and that is medially straight and anterolaterally convex.

Comments. *Stylemys nebrascensis* Leidy, 1851a is one of the many tortoise taxa named in the early works of Leidy, including *Testudo lata* Leidy, 1851b, *Emys hemispherica* Leidy, 1851b, *Emys oweni* Leidy, 1851c, and *Emys culbertsonii* Leidy 1852a based on material from what is now South Dakota (formerly the Nebraska Territory). Ever since Hay (1908), these taxa are considered as synonyms of *Stylemys nebrascensis*. The specimen used to designate these new taxa were figured by Leidy (1873) and show some difference in size and anatomy of the shell. In particular, the second neural is octagonal in *culbertsonii* but hexagonal in the rest. The gulars do not cover the anterior entoplastron and are in contact with its anterior margin in *oweni*, but they expand in the rest to cover the anterior entoplastron. The humero-pectoral sulcus coincides medially with the posterior border of the entoplastron in *hemispherica* and *oweni*, but it is situated posteriorly in *nebrascensis*, *culbertsonii*, and *lata*. Therefore one might group the tortoises from South Dakota into three groups based on their morphology: the *nebrascensis-lata* group, the *hemispherica-oweni* group, and the *culbertsonii* group. However, all of these are united by the shape of the humero-pectoral sulcus and are roughly similar in their remaining shell morphology. The above-mentioned differences, however, are consistent with intraspecific variation observed among extant testudinids and I therefore here follow the synonymy of these species as first proposed by Hay (1908). The morphology of “*Testudo amphithorax*” and “*Testudo ligonius*” Cope, 1873a is similar to the morphology of coeval, *nebrascensis*, in the coincidence of

pleuro-marginal sulci and costo-peripheral suture on the anterior peripherals, the similar suprapygial/pygal configuration, the similar humero-pectoral sulcus, and the general morphology of the plastron. Therefore, both taxa are here considered to be a synonym of *nebrascensis* as well. “*Testudo emiliae*” Hay, 1908 is also based on material from the Oligocene of South Dakota. Although some authors (e.g., Williams 1950b) suggested that *emiliae* is a member of *Gopherus*, I agree with the view of Bramble (1971) and Crumly (1994) that it is member of *Stylemys* instead. This is particularly evident in the less-developed epiplastral lip and in the shape of the humero-pectoral sulcus that is medially perpendicular to the axial plane and laterally convex anteriorly. In contrast, the humero-pectoral sulcus in *Gopherus* is rounded, being concave posteriorly in the medial part. The overall morphology of the preserved shell is once again similar to *nebrascensis* and, particularly, to the material attributed to *oweni*, and *emiliae* is therefore herein considered to be a junior synonym of *nebrascensis* as well. *Gopherus neglectus* Brattstrom, 1961 was finally described as a gopher tortoise as well, but was soon after placed in *Stylemys* by Bramble (1971) and Crumly (1994). I once again cannot find significant differences with *nebrascensis* and therefore synonymize these taxa as well.

“*Testudo*” *brontops* Marsh, 1890

Taxonomic history. *Testudo brontops* Marsh, 1890 (new species); *Geochelone brontops* Auffenberg 1963 (new combination); *Hesperotestudo brontops* Hutchison 1996 (new combination).

Type material. YPM VP 000608 (holotype), complete shell (Hay 1908, figs. 504, 505, pl. 65).

Type locality. SE corner of Pennington County, South Dakota, USA (Marsh 1890; Figure 5); Chadron Formation, Chadronian NALMA, Priabonian, late Eocene (Auffenberg 1974; Woodburne 2004; Benton et al. 2015).

Referred material and range. Late Eocene (Priabonian), Chadronian NALMA, Pennington County, South Dakota, USA (referred material of Hay 1908 and Clark 1937).

Diagnosis. “*Testudo*” *brontops* can be diagnosed as a member of *Testudinidae* based on the coincidence between the pleuro-marginal sulci and the costo-peripheral suture, the fused marginals XII, the well-differentiated neural series, and the presence of a well-developed epiplastral lip. “*Testudo*” *brontops* can be differentiated from stem and basal testudinids (e.g., *Hadrianus*, *Oligopherus*) based on the 4<8<4<8 anterior neural formula. “*Testudo*” *brontops* can be differentiated from other testudinids with a cervical scute (e.g., *Gopherus*, *Stylemys*, *Hesperotestudo*) based on the medially convex humero-pectoral sulcus that overlaps the posterior part of the entoplastron.

Comments. “*Testudo*” *brontops* is based on a complete shell from South Dakota originally considered to be Miocene (Marsh 1890), then Oligocene (e.g., Auffenberg 1974), but is now dated late Eocene (Benton et al. 2015). “*Testudo*” *brontops* is clearly a large-sized (carapace length is 71.1 cm) member of *Testudinidae* and possibly more derived than other Eocene North American pan-testudinids (e.g., *Hadrianus*, *Cymatholcus*, *Oligopherus*) by

being referable to crown *Testudinidae* (see Diagnosis above). However, the morphology of the pectoral scutes in the medial parts resembles that of *Hadrianus* in being convex medially. The nonparallel sides of the pectoral scutes medially distinguish “*Testudo*” *brontops* from several derived testudinids (*Hesperotestudo*, *Stylemys*), but the well-differentiated neural pattern could argue for a derived position within *Testudinidae*. The phylogenetic analyses herein always recover “*Testudo*” *brontops* in a more derived position compared with *Gopherus*, but never with *Hesperotestudo* nor with *Stylemys*. Its position within crown *Testudininae* is not clear. As such, it is placed herein in an unsolved polytomy with *Testudininae*. Further work should aim to clarify its position within *Testudinidae*, as it may well be a North American representative of the early crown testudinid diversification documented in Europe (*Cheirogaster maurini*) and Africa (*Gigantochersina ammon*), inferred also in the molecular clock analysis of Lourenço et al. (2012). Taking into account other North American pan-testudinids that could be placed within the crown (see above), it appears that by the late Eocene crown testudinids were already present and well diversified in North America.

Invalid and Problematic Taxa

Bismachelys canyonensis Johnston, 1937
nomen invalidum
(junior synonym of *Gopherus hexagonatus*
[Cope, 1893])

Taxonomic history. *Bismachelys canyonensis* Johnston, 1937 (new species); *Gopherus canyonensis* Williams 1950b (new combination); *Gopherus pertenuis* = *Gopherus canyonensis* Preston 1979 (junior synonymy).

Type material. PPHM 1534 (holotype), a skull, plastron, and associated limb elements (Johnston 1937, figs. 1–10).

Type locality. North Cita Canyon, center of W1/2 Section 164, block 6, Randall County, Texas, USA (Johnston 1937); Cita Canyon beds, Blanco III NALMA, Piacenzian, late Pliocene (Woodburne 2004).

Comments. Contrary to Preston (1979) and TEWG (2015), *Bismachelys canyonensis* is not considered to be a synonym of *Testudo pertenuis*, as the latter is herein considered to be a nomen dubium. See *Gopherus hexagonatus* (above) for more information.

Chelonoidis marcanoi Turvey et al., 2017
nomen dubium

Taxonomic history. *Chelonoidis marcanoi* Turvey et al., 2017 (new species).

Type material. NHMUK 36954 (holotype), a right humerus (Turvey et al. 2017, fig. 2a, b); NHMUK 36955 (paratype), a shell fragment (Turvey et al. 2017, fig. 2c, h); MNHNSD 23.1054–23.1064 (paratypes), humeri, femora, and shell fragments (Turvey et al. 2017, figs. 3, 4); UF 26095–26100 (paratypes), a humerus and shell fragments (Franz and Woods 1983, figs. 1, 2).

Type locality. Cueva del Papayo, Pedernales Province, Dominican Republic; undifferentiated cave deposits, late Pleistocene–Holocene, late Quaternary (Turvey et al. 2017).

Comments. The type material of *Chelonoidis marcanoi* consists only of a right humerus from the Dominican Republic, but the paratypes from four nearby caves add to the morphology of this taxon in the form of additional humeri, a partial femur, and some shell fragments, in particular, peripheral plates, costal fragments, and a possible partial anterior plastral lobe (Turvey et al. 2017). The paratype material includes fragmentary remains previously reported by Franz and Woods (1983). The fossils are poorly time-calibrated, as they contain to little collagen to allow absolute dating, but they are probably late Quaternary in age (Turvey et al. 2017). I agree with Turvey et al. (2017) that this material is more similar to Neotropical *Chelonoidis* than to Nearctic tortoises. However, in my opinion, the preserved anatomical information is not sufficient to properly diagnose this taxon as an unambiguous member of *Chelonoidis*. This is, in part, because I find it difficult to confirm some of the anatomical identifications, as many surface are eroded. For example, the two specimens identified as epiplastra (Turvey et al. 2017, fig. 4a, b, d, e) could easily represent other parts of the shell, like the ventral parts of bridge peripherals (Turvey et al. 2017: fig. 4a, e) or hyo- or hypoplastral fragments (Turvey et al. 2017: fig. 4b, e). These minor adjustments, however, would affect some characters of the diagnosis. Although it is plausible that many islands in the Caribbean Basin were inhabited by distinct species of tortoise in the past, the anatomical information preserved at hand does not allow for a clear diagnosis that does not take geography into consideration. I therefore here consider *Chelonoidis marcanoi* to be a nomen dubium and attribute the material to aff. *Chelonoidis* indet.

Caryoderma snovianum Cope, 1886
nomen invalidum

(junior synonym of *Hesperotestudo orthopygia*
[Cope, 1878])

Taxonomic history. *Caryoderma snovianum* Cope, 1886 (new species); *Testudo snoviana* Hay 1902 (new combination, mandatory change); *Testudo orthopygia* = *Caryoderma snovianum* = *Xerobates cyclopygius* Hay 1908 (junior synonymy).

Type material. KU 1262 (holotype), osteoderms and an ungual (Cope 1889, pl. 32; Schultze et al. 1985).

Type locality. Decatur County, Kansas, USA (Cope 1878); Ogallala Formation, Hemphillian NALMA, Tortonian–Zanclean, late Miocene–early Pliocene (Schultze et al. 1985).

Comments. See *Hesperotestudo orthopygia* above.

Chrysemys (?*Pseudemys*) *hibbardi* Preston, 1979
nomen dubium

Taxonomic history. *Chrysemys* (?*Pseudemys*) *hibbardi* Preston, 1979 (new species).

Type material. UMMP 333333 (holotype), an anterior plastral lobe with associated peripherals IX and XI (Preston 1979, fig.

8a–c); UMMP 61846 (paratype), a left epiplastron fragmentary peripheral X (Preston 1979, fig. 8d).

Type locality. Dees' Ranch, N1/2 SW1/4 Section 10, T 27 N, R 24 W, Harper County, Oklahoma, USA (Preston 1979); Dobby Springs and Mt. Scott local faunas, Rancholabrean NALMA, Ionian–Tarantian, Pleistocene (Preston 1979; Woodburne 2004). The paratype is from Scott local fauna of nearby Meade County, Kansas, USA (Preston 1979).

Comments. The type material of *Chrysemys hibbardi* consists of an anterior plastral lobe and associated peripherals from the Pleistocene of Oklahoma (Preston 1979). The type material documents some anatomical information such as the extension of the pleural scutes onto the peripherals, a wide visceral covering of the anterior plastral lobe by the scutes, a rounded anterior lobe, absence of an epiplastral lip, covering of the anterior part of the entoplastron by the gulars, placement of the humero-pectoral sulcus posterior to the entoplastron, and presence of long pectorals. These characters, however, do not allow for the rigorous diagnosis of a valid species, and *Chrysemys hibbardi* is therefore herein considered to be a nomen dubium.

Chrysemys inflata Weaver and Robertson, 1967 nomen dubium

Taxonomic history. *Chrysemys inflata* Weaver and Robertson, 1967 (new species); *Trachemys inflata* Auffenberg 2001 (new combination).

Type material. UF 12469 (holotype), a nuchal (Weaver and Robertson 1967, fig. 3).

Type locality. Palmetto Washer, east of Mulberry, Polk County, Florida, USA; Bone Valley Formation, Hemphillian 4, Zanclean, early Pliocene (Weaver and Robertson 1967; Woodburne 2004).

Comments. *Chrysemys inflata* is known from a nuchal plate only and was differentiated based on the presence of a deep nuchal notch associated with a significant cervical scute protrusion (Weaver and Robertson 1967). As this morphology is common within emydids, this specimen can only be diagnosed as a member of *Emydidae*. As such, *Chrysemys inflata* is herein considered to be a nomen dubium.

Chrysemys inornata Loomis, 1904 nomen invalidum (junior synonym of *Echmatemys lativertebralis* [Cope, 1877a])

Taxonomic history. *Chrysemys inornata* Loomis, 1904 (new species); *Graptemys inornata* Hay 1908 (new combination); *Pseudograptemys inornata* Hutchison 1996 (new combination).

Type material. ACM 3607 (holotype), an almost complete shell (Loomis 1904, figs. 10, 11; Hay 1908, figs. 455, 456).

Type locality. 16 km east of Creston, Pennington County, South Dakota, USA; Chadron Formation, Chadronian NALMA, late Eocene (Loomis 1904; Woodburne 2004).

Comments. *Chrysemys inornata* is known from an almost complete shell from the Eocene of South Dakota whose generic attribution has historically been problematic. The locality description is consistent with a location in Pennington County, not Meade County, South Dakota as stated by Hay (1908). Loomis (1904) suggested that this taxon shows several similarities with *Echmatemys lativertebralis* in the morphology of the shell but also noted differences in the presence of a dorsal keel in the posterior part of the carapace and differences in the size of the posterior neurals and suprapygal. Loomis (1904) further suggested that the two species differ in the absence of pleural I covering the lateral parts of the nuchal in *Echmatemys lativertebralis*, but this character cannot be observed clearly in this taxon. The uncertainty in the generic attribution of this taxon was affirmed by Hay (1908), who questioned its attribution to *Chrysemys* and suggested, with doubt, its inclusion in *Graptemys*. The phylogenetic analysis of Joyce et al. (2013), finally, resulted in a position outside crown *Emydidae*. In the holotype of *Chrysemys inornata*, pleural I covers the lateral parts of the nuchal, neurals II–VIII are hexagonal with short antero-lateral sides, the gulars cover the entoplastron, and the humero-pectoral sulcus is situated posterior to the entoplastron. This taxon therefore clearly resembles the morphology of *Echmatemys lativertebralis* and its synonymous taxa. As such, *Chrysemys inornata* is herein considered as a junior synonym of *Echmatemys lativertebralis*.

Chrysemys isoni Weems and George, 2013 nomen dubium

Taxonomic history. *Chrysemys isoni* Weems and George, 2013 (new species).

Type material. CMM 4664 (holotype), a partial nuchal (Weems and George 2013, fig. 6).

Type locality. Pamunkey River, boundary of King William and New Kent Counties, Virginia, USA; Calvert Formation, Burdigalian–Serravallian, early to middle Miocene (Weems and George 2013).

Comments. *Chrysemys isoni* is based on a partial nuchal and was diagnosed relative to the extant *Chrysemys picta* based on differences to the length of the cervical scute, thickness of the nuchal, and crenulation of the anterior nuchal border (i.e., the presence of a nuchal notch and a protrusion). In my experience, however, these characters are quite variable within *Chrysemys picta*, in particular, and *Pan-Emydidae*, in general. As I further find a partial nuchal to be insufficient to diagnose a valid species within *Pan-Emydidae*, I here conclude *Chrysemys isoni* to be a nomen dubium.

Chrysemys limnodytes Galbreath, 1948a nomen dubium

Taxonomic history. *Chrysemys limnodytes* Galbreath, 1948a (new species).

Type material. KU 7676 (holotype), a partial shell (Galbreath 1948a, pl. 1).

Type locality. Section 15, Beaver County, Oklahoma, USA; marl beds below the leaf zone, Laverne Formation, Clarendonian

NALMA, Serravallian–Tortonian, middle Miocene (Galbreath 1948a; Woodburne 2004).

Comments. *Chrysemys limnodytes* is based on a partial shell from the middle Miocene of Oklahoma. In the original description, Galbreath (1948a) suggested that this taxon is morphologically intermediate between extant *Chrysemys* and *Pseudemys*, but he attributed it to the former. Although I find the identification of this taxon as an emydid to be unproblematic, the overall lack of morphological characters does not allow me to diagnose this as a valid taxon. I therefore here consider *Chrysemys limnodytes* to be a nomen dubium.

Cistudo marnochii Cope, 1877b
nomen dubium

Taxonomic history. *Cistudo marnochii* Cope, 1877b (new species); *Terrapene marnochii* Hay 1902 (new combination); *Terrapene marnochi* Hay 1902 (unjustified emendation); *Terrapene carolina* = *Terrapene marnochi* Milstead 1965 (junior synonymy); *Terrapene carolina major* = *Cistudo marnochii* = *Terrapene antipex* = *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene putnami* TEWG 2015 (junior synonymy).

Type material. A posterior plastral lobe (holotype), not figured, and now considered lost (Hay 1908).

Type locality. Precise locality unknown, Atascosa County, Texas, USA; Pleistocene (Hay 1908).

Comments. *Cistudo marnochii* is based on the posterior lobe of a plastron from the Pleistocene of Texas (Cope 1877b). The specimen was never figured and had apparently been lost by the beginning of the 20th century (Hay 1908). The description of Cope (1877b) indicates the presence of a hyo-hypoplastral hinge and a femoro-anal configuration consistent with a referral to *Terrapene*. According to Cope (1877b), the character that distinguishes this taxon from other *Terrapene* is its large size, but this by itself is not sufficient to properly diagnose the taxon. As the type specimen is missing, I herein consider this taxon to be a nomen dubium. Hay (1908) referred a complete carapace from the *Equus* beds of San Diego Creek, Texas to this taxon, but this referral cannot be confirmed due to the difficulties listed above.

Clemmys hesperia Hay, 1903
nomen dubium

Taxonomic history. *Clemmys hesperia* Hay, 1903 (new species); *Clemmys marmorata* = *Clemmys hesperia* Brattstrom and Sturn 1959 (junior synonymy).

Type material. UCMP 2219 (holotype), a left hypoplastron (Hay 1903, figs. 1–3; Hay 1908, figs. 361–365, pl. 45.4–7).

Type locality. Rattlesnake Creek, Oregon, USA (Hay 1903); Rattlesnake Formation, late early Hemphillian NALMA, late Tortonian–early Messinian, late Miocene (Prothero et al. 2006).

Comments. The type and referred material of *Clemmys hesperia* consists of isolated shell fragments that preserved only limited anatomical information (Hay 1903). Among others, the ento-

plastron can be reconstructed to have been covered posteriorly by the pectoral scutes, the pleural lapped onto the peripherals, and the plastral scutes show an extended coverage on the visceral surface. These characters are common within *Testudinoidea*, and further identification is not possible. I therefore regard this taxon to be a nomen dubium. Brattstrom and Sturn (1959) synonymized *Clemmys hesperia* with *Clemmys marmorata* by stating that the morphology of *Clemmys hesperia* falls within the range of *Clemmys marmorata*, but this referral was likely dominated by geographic concerns.

Clemmys hutchensorum Bourque, 2016
nomen dubium

Taxonomic history. *Clemmys hutchensorum* Bourque, 2016 (new species).

Type material. UF 315019 (holotype), a left epiplastron (Bourque 2016, fig. 2a, b); UF 315018 (paratype), a left xiphiplastron (Bourque 2016, fig. 2c, d).

Type locality. Inglis 1C, Citrus County, Florida, USA; latest Blanton NALMA, Tarantian, early Pleistocene (Bourque 2016).

Comments. The type and referred material of *Clemmys hutchensorum* from the Pleistocene of Florida consist of isolated shell fragments including an epiplastron, xiphiplastron, and anal remains. The species was diagnosed as a member of *Clemmys* due to the presence of an epiplastral protrusion along the gularohumeral sulcus (humeral cusp sensu Bourque 2016). Observation of extant *Clemmys guttata* (USNM collection) reveals that this character is quite variable, not only in the degree of the cusp development but also in the position of the sulcus relative to the cusp. The diagnostic characters of this taxon (epiplastron as long as wide, long gular that overlap on the epiplastron, straight gular margin, rounded xiphiplastral extremities, weak anal notch, slightly concave lateral margin of the xiphiplastra) are furthermore found to be within the morphological variation observed of *Clemmys guttata*, specifically, but also among emydids, in general. As the available anatomical information does not allow for an identification beyond the level of *Emydidae*, *Clemmys hutchensorum* is herein considered to be a nomen dubium.

Clemmys morrisiae Hay, 1908
nomen invalidum
(junior synonym of *Bridgeremys pusilla*
[Hay, 1908])

Taxonomic history. *Clemmys morrisiae* Hay, 1908 (new species); *Bridgeremys pusilla* = *Clemmys morrisiae* Hutchison 2006 (junior synonymy).

Type material. AMNH 6029 (holotype), a partial shell (Hay 1908, figs. 359, 360, pl. 45.1–3).

Type locality. Grizzly Buttes, Uinta County, Wyoming, USA (Hay 1908); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908).

Comments. See *Bridgeremys pusilla* for more information.

Clemmys owyheensis Brattstrom and Sturn, 1959
nomen invalidum
(junior synonym of *Emys marmorata*
[Baird and Girard 1852])

Taxonomic history. *Clemmys owyheensis* Brattstrom and Sturn, 1959 (new species).

Type material. LACM CIT.5123 (holotype), an entoplastron (Brattstrom and Sturn 1959, pl. 21c); LACM CIT.5127 (paratype), an entoplastron (not figured); LACM CIT. 5124–5126 (paratypes), three epiplastra (not figured).

Type locality. Locality 62, Dry Creek, Owyhee, Malheur County, Oregon, USA (Brattstrom and Sturn 1959); Hemphillian NALMA, late Miocene (Woodburne 2004).

Comments. *Clemmys owyheensis* is based on an entoplastron from the late Miocene of Oregon (Brattstrom and Sturn 1959). According to Brattstrom and Sturn (1959), this taxon is differentiated from the extant *Emys marmorata* by the presence of an anterior knob on the entoplastron and the angle of the gularo-humeral sulci, but I find these characters to be insufficient to diagnose a taxon. Instead, I find all available material to be highly consistent in its morphology with the extant *Emys marmorata*. I therefore here conclude *Clemmys owyheensis* to be its junior synonym.

Clemmys percrassus Cope, 1899
nomen dubium

Taxonomic history. *Clemmys percrassus* Cope, 1899 (new species); *Clemmys percrassa* Hay 1908 (justified emendation); *Geochelone (Hesperotestudo) percrassa* Parris and Daeschler 1995 (new combination).

Type material. ANSP 152 (holotype), isolated fragments of a plastron (Cope 1899, pl. 18.1a–g).

Type locality. Port Kennedy Cave, Montgomery County, Pennsylvania, USA (Cope 1899); Irvingtonian NALMA, Pleistocene (Woodburne 2004).

Comments. The type material of *Clemmys percrassus* consists of isolated fragments of a plastron from the Pleistocene of Pennsylvania with limited anatomical information. The nuanced differences noted by Cope (1899) in the size and shape of these fragments are not adequate to properly diagnose a species. Whereas Hay (1908) suggested that *Clemmys percrassus* could be a tortoise based on the thickness of the peripherals, Parris and Daeschler (1995) suggested a close relationship with *Hesperotestudo* based on the morphology of the xiphiplastra, but the observed characters also occur in coeval *Echmatemys* spp. As the material precludes rigorous identification, I consider *Clemmys percrassus* to be a nomen dubium.

Clemmys saxea Hay, 1903
nomen dubium

Taxonomic history. *Clemmys saxea* Hay, 1903 (new species).

Type material. UCMP 2191 (holotype), a pygal plate (Hay 1903, fig. 6; Hay 1908, fig. 366, pl. 45.8–10).

Type locality. Beaver Creek, near Crooked River, Oregon, USA (Hay 1903); Mascall Formation, Barstovian NALMA, Langhian–Serravallian, middle Miocene (Woodburne 2004).

Comments. The type material of *Clemmys saxea* consists of an isolated pygal plate, which shows the expansion of vertebral V onto the pygal and the presence of marginals XII. Holman and Fritz (2001) concluded that attribution of this taxon to *Clemmys* is doubtful, although one must keep in mind that *Clemmys* was circumscribed differently at the time of Hay (1903). I here conclude that the limited character evidence is only sufficient for diagnoses to the level of *Pan-Emydidae* and otherwise consider *Clemmys saxea* to be a nomen dubium.

Cymatholcus longus Clark, 1932
nomen invalidum
(junior synonym of *Cymatholcus schucherti*
[Hay, 1899b])

Taxonomic history. *Cymatholcus longus* Clark, 1932 (new species); *Cymatholcus (Geochelone) longus* Auffenberg 1974 (new combination).

Type material. CM 11891 (holotype), a partial shell and associated limb elements (Clark 1932, figs. 1–10).

Type locality. Hoot Owl Canyon, Vernal, Uintah County, Utah, USA (Clark 1932); Duchesne River Formation, Duchesnean NALMA, Bartonian, late Eocene (Clark 1932; Murphey et al. 2011).

Comments. See *Cymatholcus schucherti*.

Deirochelys floridana Hay, 1908
nomen dubium

Taxonomic history. *Deirochelys floridana* Hay, 1908 (new species); *Pseudemys floridana* Jackson 1964 (new combination); *Pseudemys nelsoni* = *Deirochelys floridana* TEWG 2015 (junior synonymy).

Type material. USNM 16679 (holotype), a nuchal bone (Hay 1908, fig. 450, pl. 54.1–2).

Type locality. Peace River, Hillsborough County, Florida, USA (Hay 1908); Peace Creek beds, Pleistocene (Hay 1908).

Comments. The type and only known specimen of this taxon is a complete nuchal plate from the Pleistocene of Florida figured and described by Hay (1908). This plate shows a greatly elongated cervical scute that is slightly narrower anteriorly and covers half of the nuchal length. Laterally, pleural I covers the lateral parts of the nuchal. Hay (1908) suggested that this nuchal is sufficient to diagnose an extinct species of *Deirochelys*. Based on metric similarities, Jackson (1964) suggested, instead, that this taxon is valid but closest to the extant *Pseudemys nelsoni*. I find

the length and shape of the cervical scute to be closer to *Deirochelys* than *Pseudemys*, but more material is necessary for a confident identification. I therefore refer the holotype to *Deirochelys* indet. and consider *Deirochelys floridana* to be a nomen dubium.

Echmatemys aegle Hay, 1908
nomen invalidum
(junior synonym of *Echmatemys stevensoniana*
[Leidy, 1870a])

Taxonomic history. *Echmatemys aegle* Hay, 1908 (new species).

Type material. AMNH 5909 (holotype), a complete plastron and some carapacial bones (Hay 1908, figs. 436–438).

Type locality. Grizzly Buttes, Uinta County, Wyoming, USA (Hay 1908); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908).

Comments. See *Echmatemys stevensoniana* above.

Echmatemys cyane Hay, 1908
nomen invalidum
(junior synonym of *Echmatemys stevensoniana*
[Leidy, 1870a])

Taxonomic history. *Echmatemys cyane* Hay, 1908 (new species).

Type material. AMNH 5924 (holotype), a partial shell (Hay 1908, figs. 423–427, pl. 49).

Type locality. Grizzly Buttes, Uinta County, Wyoming, USA (Hay 1908); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908).

Comments. See *Echmatemys stevensoniana* above.

Echmatemys depressa Gilmore, 1915
nomen dubium

Taxonomic history. *Echmatemys depressa* Gilmore, 1915 (new species).

Type material. CM 2936 (holotype), a partial carapace (Gilmore 1915, fig. 16, pl. 23).

Type locality. 10 km east of Myton, Uintah County, Utah, USA (Gilmore 1915); Uinta C, Uinta Formation, Uintan NALMA, Lutetian, middle Eocene (Gilmore 1915; Prothero 1996).

Comments. The type material of *Echmatemys depressa* is a partial carapace of a small turtle (CL = 135 mm) that lacks most of the anterior, posterior, and left lateral parts. The specimen preserves a dorsal keel, a series of hexagonal neurals with short antero-lateral sides, possibly a single suprapygal, and short and wide vertebrals that cover half of the costal plates. The available anatomical information neither justifies the validity of a separate species nor allows attribution to any other valid species of *Ech-*

matemys. Wide vertebrals are known from *Acherontemys heckmanni*, but the presence of the dorsal keel and the small size in *Echmatemys depressa* are more consistent with young age. *Echmatemys depressa* is therefore herein considered to be a nomen dubium and identified as a member of *Echmatemys*.

Echmatemys douglassi Gilmore, 1915
nomen invalidum
(junior synonym of *Echmatemys lativertebralis*
[Cope, 1877a])

Taxonomic history. *Echmatemys douglassi* Gilmore, 1915 (new species).

Type material. CM 3244 (holotype), an almost complete shell (Gilmore 1915, figs. 11, 12, pl. 22).

Type locality. South branch of Red Bluff Wash, above the well on the road between Bonanza and Kennedy's Hole, Uinta Basin, Uintah County, Utah, USA (Gilmore 1915); Uinta B, Uinta Formation, Uintan NALMA, Lutetian, middle Eocene (Gilmore 1915; Prothero 1996).

Comments. See *Echmatemys lativertebralis* above.

Echmatemys hollandi Gilmore, 1915
nomen invalidum
(junior synonym of *Echmatemys lativertebralis*
[Cope, 1877a])

Taxonomic history. *Echmatemys hollandi* Gilmore, 1915 (new species); *Echmatemys septaria callopyge* = *Echmatemys hollandi* = *Echmatemys obscura* Roberts 1962 (junior synonymy).

Type material. CM 3249 (holotype), a partial carapace (Gilmore 1915, fig. 13, pl. 23).

Type locality. Skull Butte, southwest of well no. 2, Uinta Basin, Uintah County, Utah, USA (Gilmore 1915); Uinta B, Uinta Formation, Uintan NALMA, Lutetian, middle Eocene (Gilmore 1915; Prothero 1996).

Comments. See *Echmatemys lativertebralis* (above).

Echmatemys obscura Gilmore, 1915
nomen invalidum
(junior synonym of *Echmatemys naomi* Hay,
1908)

Taxonomic history. *Echmatemys obscura* Gilmore, 1915 (new species); *Echmatemys septaria callopyge* = *Echmatemys hollandi* = *Echmatemys obscura* Roberts 1962 (junior synonymy).

Type material. CM 3252 (holotype), a partial shell (Gilmore 1915, figs. 14, 15, pl. 24).

Type locality. Devil's Playground, south of Kennedy's Hole, Uinta Basin, Uintah County, Utah, USA (Gilmore 1915); Uinta

C, Uinta Formation, Uintan NALMA, Lutetian, middle Eocene (Gilmore 1915; Prothero 1996).

Comments. See *Echmatemys naomi* above.

Echmatemys ocyrrhoe Hay, 1908
nomen invalidum
(junior synonym of *Echmatemys stevensoniana*
[Leidy, 1870a])

Taxonomic history. *Echmatemys ocyrrhoe* Hay, 1908 (new species).

Type material. AMNH 5933 (holotype), an almost complete shell (Hay 1908, figs. 432, 433).

Type locality. Church Buttes, Uinta County, Wyoming, USA (Hay 1908); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Comments. See *Echmatemys stevensoniana* above.

Echmatemys rivalis Hay, 1909
nomen invalidum
(junior synonym of *Echmatemys lativertebralis*
[Cope, 1877a])

Taxonomic history. *Echmatemys rivalis* Hay, 1909 (new species); *Echmatemys rivalensis* Hay 1930 (incorrectly spelled species epithet).

Type material. USNM 5781 (holotype), a partial shell (Hay 1909, figs. 2, 3).

Type locality. North part of the Rawlins coal field, Sweetwater County, Wyoming, USA (Hay 1909); Wasatch Formation, Wasatchian NALMA, Ypresian, early Eocene (Hay 1909; Woodburne 2004).

Comments. See *Echmatemys lativertebralis* above.

Echmatemys uintensis Hay, 1908
nomen invalidum
(junior synonym of *Echmatemys wyomingensis*
[Leidy, 1869])

Taxonomic history. *Echmatemys uintensis* Hay, 1908 (new species).

Type material. YPM VPPU 011198 (holotype), a complete shell (Hay 1908, pl. 53).

Type locality. White River, Utah, USA (Hay 1908); Uinta Formation, Uintan NALMA, Lutetian, middle Eocene (Hay 1908; Woodburne 2004).

Comments. See *Echmatemys wyomingensis* above.

Emydoidea hutchisoni Holman, 1995
nomen dubium

Taxonomic history. *Emydoidea hutchisoni* Holman, 1995 (new species); *Emydoidea hutchchisoni* Holman 2002b (incorrect spelling of species epithet).

Type material. UNSM 76200 (holotype), a nuchal bone (Holman 1995, fig. 1a); USNM 76201 and 76202 (paratypes), two nuchal bones (Holman 1995, fig. 1b).

Type locality. West Valentine Quarry, Cherry County, Nebraska, USA (Holman 1995); Valentine Formation, late Barstovian NALMA, Serravallian, middle Miocene (Holman 1995).

Comments. *Emydoidea hutchisoni* is based on an assortment of fragments from the middle Miocene of Nebraska, of which an isolated nuchal serves as the holotype (Holman 1995). This taxon has a somewhat confusing history, as Holman (2002a) referred several specimens to this taxon, including an almost complete plastron, but soon after rejected most referrals (Holman 2002b). At present, *Emydoidea hutchisoni* is therefore restricted to the nuchal plates (Holman 2002b). Although some of the material previously referred to *Emydoidea hutchisoni* is enticing in that it shows evidence for hinges or unusually formed anal notches, the material from Nebraska apparently does not allow for the rigorous association of material with taxa. I therefore consider *Emydoidea hutchisoni* to be a nomen dubium and refer the fragments to *Pan-Emydinæ* and *Pan-Deirochelyinæ* indet. Bever et al. (2003) reported the discovery of a near-complete hinged emyidine from the middle Miocene of Brown County. The description of this material will hopefully help in clarifying the validity and morphology of middle Miocene turtles from the central United States.

Emys carteri Leidy, 1871c
nomen invalidum
(junior synonym of *Hadrianus corsoni*
[Leidy, 1871b])

Taxonomic history. *Emys carteri* Leidy, 1871c (new species); *Hadrianus corsoni* = *Emys carteri* Leidy 1873 (junior synonym); *Hadrianus corsoni* = *Testudo hadriana* = *Hadrianus quadratus* = *Hadrianus octonaria* Hay 1908 (junior synonymy).

Type material. ANSP 10054 (holotype), part of the carapace and an almost complete plastron (Leidy 1873, pl. 11).

Type locality. Grizzly Buttes, Uinta County, Wyoming, USA (Leidy 1871c); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Comments. See *Hadrianus corsoni* above.

Emys culbertsonii Leidy, 1852a
nomen invalidum
(junior synonym of *Styemys nebrascensis*
[Leidy, 1851a])

Taxonomic history. *Emys culbertsonii* Leidy, 1852a (new species); *Testudo culbertsonii* Leidy 1852b (new combination); *Stylemys culbertsonii* Cope 1869–70 (new combination); *Stylemys nebrascensis* = *Emys hemispherica* = *Emys oweni* = *Emys culbertsonii* = *Testudo lata* Hay 1908 (junior synonymy).

Type material. USNM 2348 (holotype), a partial shell (USNM database; Leidy 1853, pls. 22, 24.2).

Type locality. White River badlands, South Dakota, USA (Leidy 1873); Brule series, Orellan member, White River Formation, Orellan NALMA, early Rupelian, early Oligocene (Auffenberg 1974; Woodburne 2004).

Comments. See *Stylemys nebrascensis*.

Emys euglypha Leidy, 1889a nomen dubium

Taxonomic history. *Emys euglypha* Leidy, 1889a (new species); *Trachemys euglypha* Hay 1908 (new combination); *Trachemys euglypha* Hay 1916a (incorrectly spelled species epithet); *Pseudemys euglypha* Kuhn 1964 (new combination); *Chrysemys scripta petrolei* = *Trachemys bisornata* = *Trachemys delicata* = *Trachemys euglypha* = *Trachemys sculpta* = *Trachemys trulla* Weaver and Robertson 1967 (junior synonymy); *Trachemys scripta scripta* = *Emys euglypha* = *Trachemys delicata* = *Trachemys sculpta* TEWG 2015 (junior synonymy).

Type material. The holotype, a nuchal plate (Leidy 1889a, pl. 4, fig. 1) has been reported lost (Hay 1908).

Type locality. Peace River, Florida, USA (Leidy 1889a); Peace Creek beds, Pleistocene (Hay 1908).

Comments. The type material of *Emys euglypha* consists of a nuchal plate that has a long and narrow cervical scute and covering of the lateral parts of the nuchal by pleural I. Given the lack of diagnostic characters, the uncertain provenience of the type material, and the loss of the type specimen, I herein consider *Emys euglypha* to be a nomen dubium.

Emys euthnetus Cope, 1873b nomen dubium

Taxonomic history. *Emys euthnetus* Cope, 1873b (new species); *Emys cibollensis* = *Emys euthneteta* Cope 1884 (junior synonymy); *Echmatemys euthneteta* Hay 1908 (new combination; mandatory change).

Type material. USNM 4125 (holotype), shell fragments (Cope 1884, pl. 18.34–42).

Type locality. Black Buttes, Sweetwater County, Wyoming, USA (Cope 1873b); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Cope 1873b; Woodburne 2004).

Comments. The type material of *Emys euthneteta* consists of a few shell fragments, including two neurals, peripherals, and a left epiplastron (Cope 1884). Their small size and lack of sutures suggests that they belong to a juvenile individual. As such, the few

characters that can be discerned (e.g., hexagonal neurals with short antero-lateral sides, narrow gular scutes) should be interpreted with caution. The preserved morphology does not allow diagnosis within *Pan-Testudinoidea*. *Emys euthneteta* is therefore here considered to be a nomen dubium. The material that Hay (1908) referred to this taxon consists of fragmented costal and plastral specimens that are herein referred to *Echmatemys* sp.

Emys hemispherica Leidy, 1851b nomen invalidum (junior synonym of *Stylemys nebrascensis* [Leidy, 1851a])

Taxonomic history. *Emys hemispherica* Leidy, 1851b (new species); *Testudo hemispherica* Leidy 1852b (new combination); *Stylemys nebrascensis* = *Emys hemispherica* = *Emys oweni* = *Emys culbertsonii* = *Testudo lata* Hay 1908 (junior synonymy).

Type material. USNM 98 (holotype), a partial shell (USNM database; Leidy 1853, pls. 20, 24.3).

Type locality. White River badlands, South Dakota, USA (Leidy 1873); Brule series, Orellan member, White River Formation, Orellan NALMA, early Rupelian, early Oligocene (Auffenberg 1974; Woodburne 2004).

Comments. See *Stylemys nebrascensis*.

Emys latilabiatatus Cope, 1871c nomen dubium

Taxonomic history. *Emys latilabiatatus* Cope, 1871c (new species); *Emys latilabiata* Hay 1902 (justified emendation); *Echmatemys latilabiata* Hay 1908 (new combination).

Type material. The holotype, a complete shell (Cope 1871c), has already historically been considered lost (Cope 1884; Hay 1908).

Type locality. Black's Fork, Wyoming, USA (Cope 1871c); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Comments. The type specimen of *Emys latilabiata* has been lost for more than 130 years (Cope 1884) and has never been figured. As no diagnostic features can be inferred for this species based on the rudimentary description provided by Cope (1871c, 1884), I here consider *Emys latilabiata* to be a nomen dubium.

Emys megaulax Cope, 1873b nomen dubium, designation of lectotype

Taxonomic history. *Emys megaulax* Cope, 1873b (new species); *Emys megaulax* = *Emys pachylomus* Cope 1884 (senior synonymy); *Echmatemys megaulax* Hay 1908 (new combination); *Echmatemys lativertebralis* = *Emys megaulax* = *Emys pachylomus* = *Notomorpha testudinea* Lichtig and Lucas 2015a (junior synonymy).

Type material. USNM 4061, in part (lectotype), a neural (Cope 1884, pl. 18.26); USNM 4061, in part (paralectotypes), disarticulated shell fragments (Cope 1884, pl. 18.27–33).

Type locality. Black Buttes, Sweetwater County, Wyoming, USA (Cope 1873b); Wasatch Formation, Wasatchian NALMA, Ypresian, early Eocene (Hay 1908; Woodburne 2004).

Comments. The type material of *Emys megalax* consists of fragments of a shell, including three neurals, some partial costals, and peripherals from the Eocene of Wyoming (Cope 1873b). Personal observation of this material revealed that it represents a chimera, as numerous trionychid fragments are intermixed with fragments referable to *Echmatemys*. Given the disarticulated nature of the syntypes and the possibility that they represent different individuals, I here designate the neural figured by Cope (1884, pl. 18.26) as the lectotype of *Emys megalax*. This action, however, renders this taxon an unambiguous nomen dubium, as this element alone does not diagnose a valid taxon.

Emys oweni Leidy, 1851c
nomen invalidum

(junior synonym of *Stylemys nebrascensis*
[Leidy, 1851a])

Taxonomic history. *Emys oweni* Leidy, 1851c (new species); *Testudo oweni* Leidy 1852b (new combination); *Stylemys nebrascensis* = *Emys hemispherica* = *Emys oweni* = *Emys culbertsonii* = *Testudo lata* Hay 1908 (junior synonymy).

Type material. USNM 95 (holotype), a partial shell (Leidy 1853, pls. 21, 24.4).

Type locality. White River badlands, South Dakota, USA (Leidy 1873); Brule series, Orellan member, White River Formation, Orellan NALMA, early Rupelian, early Oligocene (Auffenberg 1974; Woodburne 2004).

Comments. See *Stylemys nebrascensis*.

Emys pachylomus Cope, 1873b
nomen dubium

Taxonomic history. *Emys pachylomus* Cope, 1873b (new species); *Echmatemys megalax* = *Emys pachylomus* Cope 1884 (junior synonymy); *Echmatemys lativertebralis* = *Emys megalax* = *Emys pachylomus* = *Notomorpha testudinea* Lichtig and Lucas 2015a (junior synonymy).

Type material. Type material unknown (see Comments below).

Type locality. Black Buttes, Sweetwater County, Wyoming, USA (Cope 1873b); Wasatch Formation, Wasatchian NALMA, Ypresian, early Eocene (Hay 1908; Woodburne 2004).

Comments. In the type description of *Emys pachylomus*, Cope (1873b) mentioned the presence of an entoplastron, but he did not list or figure any specimens. In a later contribution, Cope (1884) synonymized *Emys pachylomus* with *Emys megalax*, but did not highlight which specimens he originally thought to be *Emys pachylomus*. Hay (1908) later figured an entoplastron (AMNH 1180) that he believed to be the type of *Emys pachylomus*, but he did not explain how he arrived at that conclusion. Although it is possible that this bone indeed represents the entoplastron to which Cope (1873b) referred, I find no conclusive

evidence that this must be true. I therefore herein disregard *Emys pachylomus* as a nomen dubium.

Emys petrolei Leidy, 1868a
nomen dubium, subsequent lectotype
designation

Taxonomic history. *Emys petrolei* Leidy, 1868a (new species); *Trachemys petrolei* Hay 1908 (new combination, initial lectotype designation); *Pseudemys petrolei* Kuhn 1964 (new combination); *Chrysemys scripta petrolei* Rose and Weaver 1966 (new combination); *Chrysemys scripta petrolei* = *Trachemys bisornata* = *Trachemys delicata* = *Trachemys euglypha* = *Trachemys sculpta* = *Trachemys trulla* Weaver and Robertson 1967 (referral to subspecies level, senior synonymy); *Trachemys scripta elegans* = *Emys petrolei* = *Pseudemys bisornatus* = *Trachemys trulla* TEWG 2015 (junior synonymy).

Type material. AMNH 3933, in part (lectotype), left epiplastron; AMNH 3933, in part (paralectotypes), a nuchal, a right epiplastron, a left hypoplastron, and a right xiphiplastron (Leidy 1873, pl. 9.7; Hay 1908, pl. 46.3–4).

Type locality. Hardin County, Texas, USA (Leidy 1868a; Pleistocene (Hay 1908).

Comments. The type material of *Emys petrolei* consists of shell fragments from the Pleistocene of Texas (Leidy 1868a), of which Hay (1908) selected the two epiplastra from two individuals as the lectotypes of this species. As lectotypes should ideally represent a single individual only, I here secondarily designate the left epiplastron as the final lectotype for this taxon. According to Hay (1908), the remaining paralectotypes, namely a nuchal, a left hypoplastron, and a right xiphiplastron, probably do not belong to the same species (Hay 1908). I can neither refute nor confirm this claim, because these specimens do not preserve comparable information with the lectotype epiplastra. The combined anatomical information of the specimens referred to this taxon shows the presence of a long cervical scute, pleural I covering the lateral parts of the nuchal, and a deep angular anal notch. Hay (1908) suggested that the nuchal could belong to *Trachemys bisornata* (a nomen dubium herein). Rose and Weaver (1966), on the other hand, suggest that *Emys petrolei* is conspecific with *Trachemys scripta*. In my opinion, the preserved information does not allow proper diagnosis of this taxon within *Testudinoidea*. As such, *Emys petrolei* is herein considered to be a nomen dubium.

Emys septarius Cope, 1873b
nomen invalidum
(junior synonym of *Echmatemys stevensoniana*
[Leidy, 1870a])

Taxonomic history. *Emys septarius* Cope, 1873b (new species); *Echmatemys septaria* Hay 1906a (new combination, mandatory change).

Type material. USNM 4088, a partial plastron, and USNM 4114, several disarticulated shell fragments (syntype series) (Cope 1873b, pl. 17, figs. 9–13).

Type locality. South Bitter Creek, Sweetwater County, Wyoming, USA (Cope 1873b); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Comments. The type material of *Emys septarius* consists of a partial plastron and several disarticulated shell fragments from the Eocene of Wyoming that preserve little anatomical information. Hay (1908) referred additional specimens to *Emys septarius* and designated this species as the type species of *Echmatemys*. The type and the referred material of Hay (1908) shows a clear contact between vertebral I and marginal II, which allows the establishment of synonymy with *Echmatemys stevensoniana*. A close resemblance of this material with *Echmatemys stevensoniana* was already noted by Hay (1908) and the minute differences previously used to distinguish the two species are certainly within the range of the expected variation. Specimens originally referred to *Echmatemys septaria* are important because they are disarticulated and allow observation of two important characters: the presence of extremely wide and well-developed buttresses, a diagnostic characteristic of *Echmatemys*, and the development of wide, flattened rib heads placed near the neural/costal suture, a character that allows attribution to *Pan-Geoemydidae*. Roberts (1962) referred USNM 16687 to this species, but I here refer this specimen to *Echmatemys naomi* instead (see above).

Emys shaughnessiana Cope, 1882
nomen invalidum
(junior synonym of *Echmatemys lativertebralis*
[Cope, 1877a])

Taxonomic history. *Emys shaughnessiana* Cope, 1882 (new species, inadvertent error); *Emys shaughnessiana* Cope, 1884 (justified emendation); *Echmatemys shaughnessiana* Hay 1908 (new combination).

Type material. AMNH 1069 (holotype), an almost complete shell (Cope 1884, pl. 23.3–8; Hay 1908, figs. 428–431, pl. 50.1–2).

Type locality. Cottonwood Creek, Uinta County, Wyoming, USA (Cope 1882); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Comments. The original spelling of the specific epithet is *shaughnessiana* (Cope 1882). Cope (1884) later fully described this taxon and wrote the specific epithet as *shaughnessiana*, explicitly stating that is named after his friend Arthur O'Shaughnessy (Cope 1884). As such, the original spelling should be seen as an inadvertent error (sensu ICZN 1999, Art. 32.5 and relevant example) and the subsequent spelling of Cope (1884) is a justified emendation (ICZN 1999, art. 33.2.2). See *Echmatemys lativertebralis* for further information.

Emys sombreroensis Leidy, 1868b
nomen dubium

Taxonomic history. *Emys sombreroensis* Leidy, 1868b (new species); *Testudo sombreroensis* Williams 1950b (new combina-

tion); *Geochelone sombreroensis* Auffenberg 1967 (new combination); *Geochelone (Chelonoidis) sombreroensis* Auffenberg 1974 (new combination).

Type material. ANSP 10054 (holotype), posterior part of a plastron (Spamer and Daeschler 1995, fig. 23).

Type locality. Sombrero Island, Anguilla (Leidy 1869); Sombrero guano, Pleistocene (Leidy 1869; Spamer et al. 1995).

Comments. *Emys sombreroensis* is based on an initially unfigured partial plastron recovered from guano deposits on Sombrero Island in the Lesser Antilles (Leidy 1868b). The specimen was reported long ago by Williams (1950b) and Auffenberg (1974) but more recently recovered (Spamer et al. 1995) and, finally, figured (Spamer and Daeschler 1995). In the absence of figures, Williams (1950b) speculated that this taxon is a possible testudinid due to the presence of an anal notch. This view was followed in subsequent works (e.g., Auffenberg 1974). The shape of the posterior lobe indeed hints towards testudinid affinities but further identification is not possible. Auffenberg (1967, fig. 1) provides a relatively accurate reconstruction of this taxon based on measurements provided by Leidy (1868b) and referred additional material from the island, in particular a partial epiplastron and a partial humerus, but these add little additional information. TEWG (2015) recently considered *Emys sombreroensis* to be valid, but that is apparently based on the assumption that every island was formerly inhabited by a distinct taxon, not on character evidence. In the lack of diagnostic characters that would allow diagnosing this taxon within Pan-Testudinidae, *Emys sombreroensis* is herein considered to be a nomen dubium.

Emys twentei Taylor, 1943
nomen invalidum
(subjective junior synonym of *Emydoidea*
blandingii [Holbrook, 1838])

Taxonomic history. *Emys twentei* Taylor, 1943 (new species); *Emydoidea twentei* Hibbard and Taylor 1960 (new combination); *Emydoidea blandingii* = *Emys twentei* Preston and McCoy 1971 (junior synonymy).

Type material. KU 6478 (holotype), a partial carapace (Taylor 1943, pl. 20).

Type locality. KU Loc. 7, southwest of Meade, Meade County, Kansas, USA (Taylor 1943); high terrace sands, Pleistocene (Taylor 1943).

Comments. *Emys twentei* is based on a partial carapace from the Pleistocene of Kansas (Taylor 1943). This taxon was originally diagnosed from *Emys blandingii* by having wider vertebrals, a longer bridge of the plastron, and a broader carapace, but I agree with Preston and McCoy (1971) that these fall within the observed range of variation apparent among extant *Emys blandingii*. As such, I herein place *Emys twentei* in synonymy with *Emys blandingii*.

Eupachemys obtusus Leidy, 1877
nomen dubium

Taxonomic history. *Eupachemys obtusus* Leidy, 1877 (new species); *Eupachemys rugosus* Leidy, 1889b (ex errore for *Eupachemys robustus* or new combination of *Emys rugosa*); *Testudo obtusa* Hay 1908 (new combination, mandatory change); *Geochelone* (*Caudochelys*) *crassiscutata* = *Eupachemys obtusa* = *Eupachemys rugosus* = *Testudo distans* = *Testudo luciae* = *Testudo obtusa* = *Testudo ocalana* = *Testudo sellardsi* Auffenberg 1963 (senior synonymy); *Geochelone* (*Caudochelys*) *crassiscutata* = *Eupachemys obtusa* = *Eupachemys rugosus* Auffenberg 1974 (justified emendation, junior synonymy).

Type material. ANSP 10197 (holotype, Gillette 1977), a single peripheral (Leidy 1877, pl. 34.4–5; Hay 1908, figs. 614, 615).

Type locality. Ashley River, South Carolina, USA (Leidy 1877); phosphate beds, extract age unknown, Cenozoic (Hay 1908).

Comments. *Eupachemys obtusus* is based on a single peripheral from South Carolina (Leidy 1877) that, at best, can be concluded to be Pleistocene in age (Hay 1908). Hay (1908) used the large size of the specimen to infer a close relationship with *Hesperotestudo* (formerly *Testudo*) *crassiscutata*, but, in my opinion, large size is sufficient neither to diagnose a valid taxon nor to diagnose the type beyond the level of *Pan-Testudinoidea*. As such, *Eupachemys obtusus* is considered herein as a nomen dubium.

Hay (1908), Auffenberg (1963), and TEWG (2015) indicate that Leidy (1889b) used in error the combination *Eupachemys rugosus* for *Eupachemys obtusus*. A review of the work of Leidy (1889b) reveals, however, that *Eupachemys rugosus* may not be an error but, rather, a new combination for the extant turtle *Emys rugosa*. First, Leidy (1877) names *Eupachemys obtusus* based on a single peripheral plate (see above). Then, Leidy (1889b) assigns two peripheral plates of large size to the extant *Emys rugosa*. This is not an error, because he deliberately used the name “red-leg terrapin.” In the next paragraph, Leidy (1889b) further writes about another specimen that resembles the bone described in Leidy (1877). He then writes: “[i]t is uncertain whether it belongs to the same individual, or even species, with the former specimens [i.e., those referred to *Emys rugosa*]” Leidy (1889b:29). As such, it is possible that Leidy (1889b) simply meant that all these specimens are similar to *Emys rugosa*, whom he moved under *Eupachemys* as a new combination.

Floridemys hurdi Weems and George, 2013
nomen dubium

Taxonomic history. *Floridemys hurdi* Weems and George, 2013 (new species).

Type material. CMM 4666 (holotype), nuchal (Weems and George 2013, fig. 12).

Type locality. Beach beneath Randle Cliff, Calvert County, Maryland, USA; Shattuck zones 4–11, early Barstovian NALMA, late Burdigalian–Langhian, middle Miocene (Weems and George 2013).

Comments. *Floridemys hurdi* is based on an isolated nuchal that does not allow rigorously diagnosing a valid species. Considering also the unknown provenance of the specimen, *Floridemys hurdi* is herein considered to be a nomen dubium.

Geochelone alleni Auffenberg, 1966
nomen invalidum
(junior synonym of *Hesperotestudo turgida*
[Cope, 1892a])

Taxonomic history. *Geochelone alleni* Auffenberg, 1966 (new species).

Type material. UF 9370 (holotype), a partial carapace, complete plastron, and associated caudal buckler (Auffenberg 1966, figs. 1, 2, pl. 102).

Type locality. McGehee Site, 5 km north of Newberry, Alachua County, Florida, USA (Auffenberg 1966); early Hemphillian NALMA, Tortonian, late Miocene (Hulbert 2001).

Comments. See *Hesperotestudo turgida* above.

Geochelone johnstoni Auffenberg, 1962b
nomen invalidum
(junior synonym of *Hesperotestudo turgida*
[Cope, 1892a])

Taxonomic history. *Geochelone johnstoni* Auffenberg, 1962b (new species).

Type material. PPHM 1540 (holotype), a complete shell (Auffenberg 1962b, fig. 1).

Type locality. Cita Canyon, Harell Ranch, Randall County, Texas, USA (Parris and Daeschler 1995, contra Auffenberg 1962b); Cita Canyon beds, Blancan III NALMA, late Pliocene (Woodburne 2004).

Comments. *Geochelone johnstoni* was named by Auffenberg (1962b) in honor of C. Stuart Johnston, who died before completing his thesis, which contained the description of the new species, *Testudo rugosa* (Oelrich 1957; Auffenberg 1962b). The unfinished thesis of Johnston does not constitute published work (ICZN 1999, art. 8, 9), whereas the following citations of that name (in Oelrich 1957 and Auffenberg 1962b) did not treat it as a valid name (see ICZN 1999, Art. 11.5.2). As such, *Testudo rugosa* Johnston should be considered to be a nomen nudum. The synonymy of *Geochelone johnstoni* with *Hesperotestudo turgida* is discussed above.

Geochelone mlynarskii Auffenberg, 1988
nomen invalidum
(junior synonym of *Hesperotestudo turgida*
[Cope, 1892a])

Taxonomic history. *Geochelone mlynarskii* Auffenberg, 1988 (new species).

Type material. UF 18960 (holotype), a partial plastron (Auffenberg 1988, pls. 29–32).

Type locality. Near Coleman, Sumter County, Florida, USA (Auffenberg 1988); late Irvingtonian NALMA, middle Pleistocene (Woodburne 2004).

Comments. see *Hesperotestudo turgida* above.

Geochelone nordensis Holman, 1973b
nomen invalidum
(junior synonym of *Hesperotestudo orthopygia*
[Cope, 1878])

Taxonomic history. *Geochelone nordensis* Holman, 1973b (new species)

Type material. MSU 714 (holotype), a partial shell (Holman 1973b, fig. 2).

Type locality. South of the Norden Bridge, Brown County, Nebraska, USA (Holman 1973b); Norden Bridge local fauna, late Barstovian NALMA, Serravallian, middle Miocene (Holman 1973b; Woodburne 2004).

Comments. See *Hesperotestudo orthopygia* above.

Geochelone oelrichi Holman, 1972a
nomen invalidum
(junior synonym of *Hesperotestudo turgida*
[Cope, 1892a])

Taxonomic history. *Geochelone (Hesperotestudo) oelrichi* Holman, 1972a (new species).

Type material. UMMP 56298 (holotype), a partial shell with associated appendicular elements (Holman 1972a, figs. 20–24).

Type locality. Wilbur Magill pasture, Brown County, Nebraska, USA (Holman 1972a); Long Pine Formation, late Blancan NALMA, Piacenzian–Gelasian, late Pliocene–early Pleistocene (Auffenberg 1962b; Woodburne 2004).

Comments. see *Hesperotestudo turgida* above.

Gopherus dehiscus Des Lauriers, 1965
nomen invalidum
(junior synonym of *Gopherus depressus*
Brattstrom, 1961)

Taxonomic history. *Gopherus dehiscus* Des Lauriers, 1965 (new species); *Geochelone (Hesperotestudo) dehiscus* Crumly 1994 (new combination, incorrectly spelled genus name).

Type material. LACM 400(26)/5178 (holotype), the internal cast of a shell (Des Lauriers 1965, fig. 1).

Type locality. Cajon Pass, west end of Cajon valley, San Bernardino County, California, USA (Des Lauriers 1965);

Barstovian NALMA, Langhian–Serravallian, middle Miocene (Des Lauriers 1965; Woodburne 2004).

Comments. Although the holotype of *Gopherus dehiscus* is only a cast that partially preserves the internal imprints of a shell, Des Lauriers (1965) presented seven other specimens from the same locality that allow characterization of the morphology of this taxon in greater detail. See *Gopherus depressus* above for synonymy with that taxon.

Gopherus huecoensis Strain, 1966
nomen invalidum
(junior synonym of *Gopherus hexagonatus*
[Cope, 1893])

Taxonomic history. *Gopherus huecoensis* Strain, 1966 (new species); *Gopherus flavomarginatus* = *Gopherus huecoensis* Bramble 1982 (junior synonymy); *Gopherus heucoensis* Crumly 1994 (incorrectly spelled species epithet).

Type material. TMM 40240-27 (holotype), a plastron with associated appendicular elements (Strain 1966, pl. 2–6).

Type locality. Madden Arroyo, Hudspeth County, Texas, USA (Strain 1966); Fort Hancock Formation, late Blancan NALMA, Piacenzian–Gelasian, late Pliocene–early Pleistocene (Woodburne 2004; Franz 2014).

Comments. See *Gopherus hexagonatus* above.

Gopherus neglectus Brattstrom, 1961
nomen invalidum
(junior synonym of *Stylemys nebrascensis*
[Leidy, 1851a])

Taxonomic history. *Gopherus neglectus* Brattstrom, 1961 (new species); *Stylemys neglectus* Bramble 1971 (new combination).

Type material. LACM CIT.126/1672 (holotype), a partial shell (Brattstrom 1961, figs. 1–4).

Type locality. Key Quarry, Ventura County, California, USA (Brattstrom 1961); Upper Sespe Formation, early Arikareean, Chattian, late Oligocene (Woodburne 2004; Franz 2014).

Comments. See *Stylemys nebrascensis* above.

Gopherus pargensis Mooser, 1980
nomen invalidum
(junior synonym of *Gopherus auffenbergi*
Mooser, 1972)

Taxonomic history. *Gopherus pargensis* Mooser, 1980 (new species).

Type material. TMM 41536-29 (holotype), a partial carapace (Mooser 1980, fig. 5).

Type locality. Cedazo Ravine, 5.5 km northeast of Aguascalientes, Aguascalientes State, Mexico (Mooser 1980); Cedazo local fauna, late Blancan–Irvingtonian NALMA, Pleistocene (Woodburne 2004).

Comments. See *Gopherus auffenbergi* above.

Gopherus praecedens Hay, 1916a
nomen dubium

Taxonomic history. *Gopherus praecedens* Hay, 1916a (new species); *Gopherus polyphemus* = *Gopherus praecedens* = *Testudo atascosae* TEWG 2015 (junior synonymy).

Type material. USNM 8828 (holotype), a left xiphiplastron (Hay 1916a, pl. 4.1–2), formerly cataloged under FGS 5463.

Type locality. Vero, St. Lucie County, Florida, USA (Hay 1916a); Pleistocene (Hay 1916a).

Comments. The type material of *Gopherus praecedens* consists of a left xiphiplastron (Hay 1916a) that shows a constriction in the femoro-anal sulcus, a shallow, wide, and angular anal notch, thickened and rounded xiphiplastral extremities, and a straight femoro-anal sulcus. Overall, the preserved morphology of this specimen cannot allow a diagnosis beyond the level of *Testudinidae* and, as such, *Gopherus praecedens* is herein considered to be a nomen dubium.

Graptemys cordifera Clark, 1937
nomen invalidum
(junior synonym of *Echmatemys lativertebralis*
[Cope, 1877a])

Taxonomic history. *Graptemys cordifera* Clark, 1937 (new species).

Type material. YPM VPPU 013838 (holotype), an almost complete shell (Clark 1937, figs. 11, 12).

Type locality. West side of Quinn Draw, 8 km from the mouth of Quinn Draw, Washington County, South Dakota, USA (Clark 1937); middle Chadron Formation, Chadronian NALMA, Priabonian, late Eocene (Clark 1937; Woodburne 2004).

Comments. See *Echmatemys lativertebralis* above.

Hadrianus allabiatius Cope, 1871c
nomen dubium

Taxonomic history. *Hadrianus allabiatius* Cope, 1871c (new species); *Achilemys allabiata* Hay 1908 (new combination, justified emendation).

Type material. USNM 4054 (holotype), partial carapace and plastron (Hay 1908, figs. 482–485).

Type locality. Bad Lands of Cottonwood Creek, Uinta County, Wyoming, USA (Cope 1871c); Level B, Bridger Formation,

Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Comments. *Hadrianus allabiatius* is based on shell fragments from the Eocene of Wyoming (Cope 1871c). Cope (1871c) originally referred this taxon to *Hadrianus*, but Hay (1908) later defined a new genus for this taxon, *Achilemys*, based on the absence of a thickened epiplastral lip, the posteriorly flared carapacial margin, and a significant overlap of vertebral V onto the suprapygal I. These characters indeed differentiate *Achilemys* from *Hadrianus*, but they are frequently present in other pan-testudinoids (Claude and Tong 2004) and therefore have limited utility at a broader scale. Personal observations on the type material further reveal that the sulcus between marginals XII crosses the pygal and suprapygal II, a configuration reminiscent of *Echmatemys*. Given the lack of diagnostic characters, *Hadrianus allabiatius* is herein considered to be a nomen dubium. Use of *Achilemys* is thereby rendered problematic (see Claude and Tong 2004; Pérez-García and Vlachos 2014). Osborn et al. (1878) referred two ungual phalanges to *Hadrianus allabiatius*, but this attribution is doubtful, given the absence of comparable material in the type specimens. These phalanges are herein referred to *Pan-Testudinoidea* indet.

Hadrianus quadratus Cope, 1871b
nomen invalidum
(objective junior synonym of *Testudo hadriana*
Cope, 1871a; junior synonym of *Hadrianus*
corsoni [Leidy, 1871b])

Taxonomic history. *Testudo hadriana* = *Hadrianus quadratus* Cope, 1871b (new species and objective junior synonymy); *Hadrianus corsoni* = *Testudo hadriana* = *Hadrianus quadratus* = *Hadrianus octonaria* Hay 1908 (junior synonymy).

Type material. Collection unknown, two syntypes, a near complete shell and a plastron (Cope 1871b, not figured).

Type locality. Bad Lands of Cottonwood Creek, Uinta County, Wyoming, USA (Leidy 1871b); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Comments. Cope (1871a) named *Testudo hadriana* based on shell material from the Eocene of Wyoming but shortly afterwards provided a new name for the same specimens, *Hadrianus quadratus* Cope, 1871b. As such, *Hadrianus quadratus* Cope, 1871b is an objective junior synonym of *Testudo hadriana* Cope, 1871a. *Hadrianus quadratus* Cope, 1871b should not be confused as a new combination of *Testudo quadrata* Cope, 1884 (see *Testudo quadrata* Cope, 1884). See *Hadrianus corsoni* for subjective synonymy.

Hadrianus octonaria Cope, 1871b
nomen invalidum
(junior synonym of *Hadrianus corsoni*
[Leidy, 1871b])

Taxonomic history. *Hadrianus octonaria* Cope, 1871b (new species); *Hadrianus corsoni* = *Testudo hadriana* = *Hadrianus quadratus* = *Hadrianus octonaria* Hay 1908 (junior synonymy).

Type material. Collection unknown, a plastron (Cope 1871b, not figured).

Type locality. Cottonwood Creek, Uinta County, Wyoming, USA (Cope 1871b); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Comments. See *Hadrianus corsoni*.

Hadrianus robustus Gilmore, 1915
nomen invalidum
(objective senior synonym of *Geochelone*
(*Manouria*) *gilmorei* Auffenberg, 1974; junior
synonym of *Hadrianus corsoni* [Leidy, 1871b])

Taxonomic history. *Hadrianus robustus* Gilmore, 1915 (new species); *Geochelone* (*Manouria*) *gilmorei* Auffenberg, 1974 (new substitute name; new combination).

Type material. CM 3342 (holotype), the anterior portions of a plastron (Gilmore 1915, fig. 19, pl. 25.2).

Type locality. Near Kennedy Hole, Uintah County, Utah, USA (Gilmore 1915); Horizon C, Uinta Formation, Uintan NALMA, Lutetian, Eocene (Gilmore 1915; Woodburne 2004).

Comments. *Hadrianus robustus* is based on a partial plastron from the Eocene of Utah (Gilmore 1915). Auffenberg (1974) proposed a substitute name for *Hadrianus robustus*, *Geochelone* (*Manouria*) *gilmorei*, because the specific name *robusta* (or *robustus* depending on the sex) was preoccupied for *Testudo robusta* Leith-Adams, 1877. As such, the two specific names *robustus/robusta* are secondary homonyms as they have been established for different nominal taxa (ICZN 1999, Art. 57.3). As the two taxa are not considered congeneric herein, the junior name is to be rejected (ICZN 1999, art. 59.2). See *Hadrianus corsoni* (above) for the subjective synonymy.

Hadrianus tumidus Hay, 1908
nomen invalidum
(junior synonym of *Hadrianus corsoni*
[Leidy, 1871b])

Taxonomic history. *Hadrianus tumidus* Hay 1908 (new species); *Testudo tumidus* Kuhn 1964 (new combination); *Geochelone* (*Manouria*) *tumida* Auffenberg 1974 (new combination; subsequent spelling).

Type material. AMNH 6076 (holotype), a partial plastron (Hay 1908, fig. 480).

Type locality. White River, Uintah County, Utah, USA (Hay 1908); Bridger Formation, Uintan NALMA, Lutetian, Eocene (Hay 1908; Woodburne 2004).

Comments. See *Hadrianus corsoni* above.

Hadrianus utahensis Gilmore, 1915
nomen invalidum
(junior synonym of *Hadrianus corsoni*
[Leidy, 1871b])

Taxonomic history. *Hadrianus utahensis* Gilmore, 1915 (new species); *Geochelone* (*Manouria*) *utahensis* Auffenberg 1974 (new combination).

Type material. CM 2343 (holotype), a plastron and portions of the carapace (Gilmore 1915, fig. 20, pl. 26.1).

Type locality. Near Kennedy Hole, Uintah County, Utah, USA (Gilmore 1915); Horizon B, Uinta Formation, Uintan NALMA, Lutetian, Eocene (Gilmore 1915; Woodburne 2004).

Comments. See *Hadrianus corsoni* above.

Hybemys arenarius Leidy, 1871a
nomen dubium

Taxonomic history. *Hybemys arenarius* Leidy, 1871a (new species); *Hybemys arenaria* Hay 1908 (justified emendation).

Type material. ANSP indet. (holotype), a peripheral plate (Leidy 1873, pl. 15.9), now considered missing (Spamer et al. 1995).

Type locality. Little Sandy Creek, Sweetwater County, Wyoming, USA (Leidy 1871a); Bridger A, Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Leidy 1873; Hay 1908).

Comments. The type material of *Hybemys arenaria* consists of a single peripheral plate that is now considered missing from the collections of ANSP (Spamer et al. 1995). The specimen, as figured in Leidy (1873), reveals that the pleural scutes expand on the peripherals, which, at best, diagnosis this taxon as a nontestudinid. Leidy (1871a, 1873) and Hay (1908) remarked on the thickness of this plate, but that is not sufficient to diagnose a valid taxon either. *Hybemys arenaria* is therefore herein considered to be a nomen dubium diagnosable only to the level of *Testudinoidea* indet.

Notomorpha testudinea Cope, 1872
nomen dubium, designation of lectotype

Taxonomic history. *Notomorpha testudinea* Cope, 1872 (new species); *Emys testudineus* Cope 1873b (new combination; unjustified emendation); *Echmatemys testudinea* Hay 1908 (new combination); *Echmatemys lativertebalis* = *Emys megaulax* = *Emys pachylomus* = *Notomorpha testudinea* Lichtig and Lucas 2015a (junior synonymy); *Echmatemys tesudinea* Lichtig and Lucas 2015a (incorrectly spelled species epithet).

Type material. USNM 4103 (lectotype), posterior plastral lobe fragment (Cope 1884, pl. 23.13).

Type locality. Near Bear River, 10 km north of Evanston, Uinta County, Wyoming, USA (Cope 1872); Wasatch Formation (Hay

1908), Wasatchian NALMA, Ypresian, early Eocene (Woodburne 2004).

Comments. *Notomorpha testudinea* is based on shell fragments from the Eocene of Wyoming (Cope 1872). This taxon has long been thought to be a testudinoid and was therefore referred to *Echmatemys* (Hay 1908). However, Joyce and Bourque (2016) recently highlighted that it also serves as the type species of *Notomorpha*, not the kinosternoid *Baptemys garmanii* as previously thought, which raises questions regarding the validity of *Echmatemys*. A revision of the type material of *Notomorpha testudinea* reveals two important issues: a potential mixing of testudinoid and kinosternoid material in the type material of Cope (1872) and the absence of diagnostic information for the testudinoid material. The entoplastron (Cope 1884, pl. 23.12) is only crossed by a sulcus longitudinally. Because the entoplastron of all testudinoids from North America, including all known species of *Echmatemys*, is either covered anteriorly by the gulars or posteriorly by the pectorals, or both, the entoplastron of *Notomorpha testudinea* is notably different. Instead, attribution to a kinosternoid taxon is more probable, as their entoplastron is usually crossed only by the sulcus between the gulars (Joyce and Bourque 2016). On the other hand, a fragment of the border of a posterior plastral lobe (Cope 1884, pl. 23.13) is consistent with testudinoid affinities due to the wide covering of the scutes on the visceral side. Finally, there is no clear connection between the two specimens and difference in thickness also suggest that they are not part of the same individual. I here conclude the original type material to be a chimera and designate the testudinoid plastral fragment as the lectotype of *Notomorpha testudinea*, which, however, renders this taxon a nomen dubium, as it is not diagnostic at the species level. The validity of *Echmatemys* is thereby secured.

Palaeothecha polycypha Cope, 1871a
nomen dubium

Taxonomic history. *Palaeothecha polycypha* Cope, 1871a (new species); *Emys polycyphus* Cope 1873b (new combination; unjustified emendation).

Type material. USNM 4097 (holotype), two neurals and a peripheral (Cope 1884, pl. 18.20–22).

Type locality. Wyoming, USA (Cope 1871a); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Hay 1908; Woodburne 2004).

Comments. The type specimens of *Palaeothecha polycypha* is from an unknown Bridger Eocene locality in Wyoming and consist of some neural plates, which reveal the presence of a dorsal keel, and a peripheral. Cope (1871a) presumed that the holotype belongs to a skeletally mature individual and therefore named a new genus and species based on the presence of a keel and small size, but he soon after reassigned *polycypha* to *Emys* (Cope 1873b). Hutchison (2006) noted that the type material of *Palaeothecha polycypha* might represent a juvenile *Echmatemys* and that this taxon should be treated as a nomen vanum or nomen dubium (Hutchison 2006). This is broadly consistent with the conclusions of Lichtig and Lucas (2015a) in regards to

the juvenile morphology in *Echmatemys* spp. As it is suboptimal to base a fossil taxon on a juvenile, *Palaeothecha polycypha* is herein considered to be a nomen dubium.

Palaeothecha terrestris Cope, 1871a
nomen dubium

Taxonomic history. *Palaeothecha terrestris* Cope, 1871a (new species); *Emys terrestris* Cope 1873b (new combination); *Rhinoclemys terrestris* West and Hutchison 1981 (new combination, inadvertent error).

Type material. USNM 2107 (holotype), a neural, costal, and epiplastron (Cope 1884, pl. 18.23–25).

Type locality. Near Fort Bridger, Uinta County, Wyoming, USA (Cope 1872); Bridger Formation, Bridgerian NALMA, Ypresian–Lutetian, early–middle Eocene (Cope 1872).

Comments. *Palaeothecha terrestris* is similar to *Palaeothecha polycypha* (see above) in that the type material consists of a keeled neural and costal plates from the Bridger Eocene of Wyoming. Hutchison (2006) suggested that the type material of *Palaeothecha terrestris* may represent a juvenile *Echmatemys* and that this taxon should be treated as a nomen vanum or nomen dubium as diagnostic characters are lacking (Hutchison 2006). He furthermore noted that the type neural may be referable to *Bridgeremys*, highlighting that this taxon may be a chimera. I agree with this assessment and conclude that *Palaeothecha terrestris* is a nomen dubium.

Pseudemys bisornatus Cope, 1877b
nomen dubium

Taxonomic history. *Pseudemys bisornatus* Cope, 1877b (new species); *Trachemys bisornata* Hay 1902 (new combination; mandatory change); *Pseudemys bisornata* Kuhn 1964 (justified emendation); *Chrysemys scripta petrolei* = *Trachemys bisornata* = *Trachemys delicata* = *Trachemys euglypha* = *Trachemys sculpta* = *Trachemys trulla* Weaver and Robertson 1967 (junior synonymy); *Trachemys scripta elegans* = *Emys petrolei* = *Pseudemys bisornatus* = *Trachemys trulla* TEWG 2015 (junior synonymy).

Type material. ANSP 9843 (holotype), a partial carapace (Hay 1908, pl. 56.1).

Type locality. Precise locality unknown, Atascosa County, Texas, USA (Cope 1877b; Hay 1908); *Equus* beds, Pleistocene (Hay 1908).

Comments. The type material of *Pseudemys bisornata* consists of a partial carapace from the Pleistocene of Texas (Cope 1877b) that preserves the nuchal, neurals I–II and IV–V (4<6A<6A<6A<6A), and parts of right costals I–IV. The presence of an elongated nuchal and the covering of the lateral parts of the nuchal by pleural I only allow for diagnosis to the level of *Pan-Emydidae*. As the specimen otherwise lacks diagnostic characters, it is herein considered to be a nomen dubium.

Pseudemys caelata Hay, 1908
nomen dubium

Taxonomic history. *Pseudemys caelata* Hay, 1908 (new species); *Chrysemys carri* = *Chrysemys caelata* Jackson 1976 (new combination and senior synonymy).

Type material. USNM 2508 (holotype), nuchal (Hay 1908, pl. 57.1; Jackson 1976, fig. 1a, d).

Type locality. Mixson's Bone Bed, Levy County, Florida, USA (Hay 1908; Jackson 1976); Pleistocene (Hay 1908).

Comments. The type material of *Pseudemys caelata* was recovered from Pleistocene sediments exposed in Florida and consists of several costal, plastral, and peripheral fragments and an isolated nuchal that documents a long and wide cervical scute and covering of the lateral parts of the nuchal by pleural I. Hay (1908) stated that the nuchal should serve as the holotype if USNM 2508 is revealed to consist of numerous individuals. I therefore consider the nuchal to be the holotype of *Pseudemys caelata* fixed by the original designation of Hay (1908). Hay (1908) differentiated this taxon from extant *Trachemys* by the overlap of pleural I onto the nuchal, but a review of extant material reveals that this is a frequent character among *Trachemys* spp. Jackson (1976) referred *caelata* to *Chrysemys* and synonymized it with *Chrysemys carri* Rose and Weaver, 1966. In my opinion, however, the available material lacks sufficient characters evidence to diagnose a valid taxon. As such, *Pseudemys caelata* is herein considered to be a nomen dubium.

Pseudemys extincta Hay, 1908
nomen dubium

Taxonomic history. *Pseudemys extincta* Hay, 1908 (new species); *Pseudemys rubriventris* = *Pseudemys extincta* TEWG 2015 (junior synonymy).

Type material. USNM 16678 (holotype), a nuchal plate (Hay 1908, pl. 54.13).

Type locality. Peace River, Hillsborough County, Florida, USA (Hay 1908); Pliocene (Hay 1908).

Comments. The type material of *Pseudemys extincta* consists of a nuchal plate from the Pliocene of Florida that reveals that the nuchal was covered anteriorly by a long, anteriorly-narrowing cervical scute and laterally by pleural I. TEWG (2015) tentatively synonymized *Pseudemys extincta* with *Pseudemys rubriventris* following earlier suggestions by Hay (1908) and Preston (1979) on their similarity. Like so many other taxa based on an isolated nuchal, I find the character evidence insufficient to diagnose a valid taxon. As such, *Pseudemys extincta* is herein considered to be a nomen dubium.

Pseudemys floridana persimilis Hay, 1916a
nomen dubium

Taxonomic history. *Pseudemys floridana persimilis* Hay, 1916a (new subspecies); *Pseudemys peninsularis* = *Pseudemys floridana persimilis* TEWG 2015 (junior synonymy).

Type material. USNM 8829 (holotype), a pair of epiplastra (Hay 1916a, pl. 5.6–8).

Type locality. Vero, St. Lucie County, Florida, USA (Hay 1916a); Pleistocene (Hay 1916a).

Comments. *Pseudemys floridana persimilis* is based on two epiplastra from the Pleistocene of Florida (Hay 1916a). The type material was originally deposited in the collections of the FGS (FGS 7098), but it now is housed at USNM. As the type material only preserves enough anatomical information to allow diagnosing the remains as a member of Pan-Emyridae, I consider this taxon to be a nomen dubium.

Pseudemys hillii Cope, 1878
nomen dubium

Taxonomic history. *Pseudemys hillii* Cope, 1878 (new species); *Trachemys hillii* Hay 1902 (new combination; variant spelling).

Type material. AMNH 2425 (holotype), a partial shell (Hay 1908, figs. 451, 452, pl. 55).

Type locality. Decatur County, Kansas, USA (Cope 1878); Ogallala Formation, Barstovian–Hemphillian NALMA, middle–late Miocene (Ludvigson et al. 2009).

Comments. The type material of *Pseudemys hillii* consists of a partial shell that is sufficiently preserved to allow for the reconstruction presented by Hay (1908, figs. 451, 452). Many diagnostic parts, however, such as the anterior parts of the carapace and plastron, are missing. The preserved parts of the shell indicate a turtle with primarily hexagonal neurals with short anterolateral sides, a vertebral V that expands on the pygal, the presence of 12 pairs of marginals, long pectorals that are placed posterior to the entoplastron, anals that are medially longer than the femorals, and a weak anal notch. These characters only allow identifying *Pseudemys hillii* as a member of *Pan-Emyridae* and are not sufficient to properly diagnose this taxon. As such, *Pseudemys hillii* is herein considered to be a nomen dubium.

Rhinoclemmys nicoyana Acuña-Mesén
and Laurito-Mora, 1996
nomen dubium

Taxonomic history. *Rhinoclemmys nicoyana* Acuña-Mesén and Laurito-Mora, 1996 (new species).

Type material. MNCR G-24NC (holotype), shell fragments (Acuña-Mesén and Laurito-Mora 1996, figs. 2–6).

Type locality. Bottom of the Nacaome River, Guanacaste Province, Costa Rica; late Pleistocene (Acuña-Mesén and Laurito-Mora 1996).

Comments. The type material of *Rhinoclemmys nicoyana* from the Pleistocene of Costa Rica consists of a nuchal that was covered anteriorly by a cervical and laterally by pleural I, plastral fragments that indicate the absence of a plastral hinge, and an entoplastron crossed by the humero-pectoral sulcus. The

preserved anatomical characters do not allow identification beyond the level of *Pan-Testudinoidea*. As such, *Rhinoclemmys nicoyana* is herein considered to be a nomen dubium.

Stylemys calaverensis Sinclair, 1903
nomen dubium

Taxonomic history. *Stylemys calaverensis* Sinclair, 1903 (new species).

Type material. UCMP 8097 (holotype), the deformed anterior portions of a shell (Sinclair 1903, figs. 1, 2; Hay 1908, figs. 502, 503).

Type locality. 3 km south of Vallecito, Calaveras County, California, USA (Sinclair 1903); auriferous gravels, Miocene (Auffenberg 1974).

Comments. *Stylemys calaverensis* is based on a partial shell from the Miocene of California (Sinclair 1903). As the type specimen is crushed and deformed, few characters are apparent and Hay (1908) and Auffenberg (1974) therefore doubted referral to *Stylemys*. In my opinion, the available information is insufficient to either diagnose *Stylemys calaverensis* as a distinct species or to refer it to any other species. I therefore consider *Stylemys calaverensis* to be a nomen dubium.

Stylemys conspecta Hay, 1908
nomen invalidum

(junior synonym of *Stylemys capax* Hay, 1908)

Taxonomic history. *Stylemys conspecta* Hay, 1908 (new species).

Type material. AMNH 1358 (holotype), a complete shell (Hay 1908, figs. 500, 501).

Type locality. Near junction of North and South Forks of John Day River, Grant County, Oregon, USA (Hay 1908); middle John Day Formation, Arikareean-2 NALMA, Chattian, late Oligocene (Woodburne 2004).

Comments. See *Stylemys capax* above.

Stylemys oregonensis Leidy, 1871d
nomen dubium

Taxonomic history. *Stylemys oregonensis* Leidy, 1871d (new species); [*Stylemys oregonensis*] Auffenberg 1974 (nomen dubium).

Type material. Collection and number unknown (holotype), a neural plate (Leidy 1873, pl. xv, fig. 10).

Type locality. Crooked River, near John Day River, Grant County, Oregon, USA (Leidy 1871d); middle John Day Formation, Arikareean-2 NALMA, Chattian, late Oligocene (Woodburne 2004).

Comments. *Stylemys oregonensis* was described on the basis of a single octagonal neural from the late Oligocene of Oregon that

is crossed by an intervertebral sulcus. Leidy (1871d, 1873) interpreted this specimen as a neural III, but Hay (1908) suggested that it could be a neural V. As no member of *Stylemys* is known to have an octagonal neural that is crossed by intervertebral sulci, this specimen may alternatively belong to another tortoise clade from North America with octagonal neurals (e.g., *Hesperotestudo*, *Gopherus*). Auffenberg (1974) placed *Stylemys oregonensis* on a list of taxa based on material that is insufficient to be identified to the species level. I agree with this assessment and therefore regard *Stylemys oregonensis* as a nomen dubium.

Terrapene antipex Hay, 1916a
nomen invalidum
(junior synonym of *Terrapene putnami*
Hay, 1906a)

Taxonomic history. *Terrapene antipex* Hay, 1916a (new species); *Terrapene canaliculata* = *Terrapene antipex* Gilmore 1927 (junior synonymy); *Terrapene carolina putnami* = *Terrapene antipex* = *Terrapene canaliculata* Auffenberg 1958 (junior synonymy); *Terrapene antiquior* Kuhn 1964 (unjustified emendation); *Terrapene antiqua* Kuhn 1964 (unjustified emendation); *Terrapene carolina major* = *Cistudo marnochii* = *Terrapene antipex* = *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene putnami* TEWG 2015 (junior synonymy).

Type material. USNM 8820 (holotype), a posterior plastral lobe (Hay 1916a, pl. 5.1–5).

Type locality. Vero, St. Lucie County, Florida, USA (Hay 1916a); stratum 2, Vero beach, Pleistocene (Auffenberg 1958).

Comments. Hay (1916a) noted in the type description that the type material of *Terrapene antipex* is deposited in the collections of the FGS (FGS 5960), but it currently is part of the collections of USNM. The characters used by Hay (1916a) to diagnose this taxon, in particular its size, thickness of the shell, and presence of a keel, are insufficient to differentiate this taxon from valid extant and extinct members of *Terrapene*. Gilmore (1927) alternatively considered *Terrapene antipex* to be a synonym of *Terrapene canaliculata*, which, in return, is herein considered to be the junior synonym of *Terrapene putnami* based on similarities in proportions, an opinion shared by Auffenberg (1958). As I agree with this opinion as well, I here regard *Terrapene antipex* as a junior synonym of *Terrapene putnami*.

Terrapene bulverda Hay, 1921
nomen dubium

Taxonomic history. *Terrapene bulverda* Hay, 1921 (new species); *Terrapene carolina triunguis* = *Terrapene bulverda* = *Terrapene impressa* = *Terrapene llanensis* = *Terrapene whitneyi* TEWG 2015 (junior synonymy).

Type locality. Friesenhahn Cave, Bexar County, Texas, USA (Hay 1921; Milstead 1956); Rancholabrean NALMA, Ionian–Tarantian, Pleistocene (Hay 1921).

Type material. USNM 9221 (holotype), posterior portions of a carapace (Hay 1921, fig. 4).

Comments. *Terrapene bulverda* is based on a partial carapace originally thought to have been collected from a cave near Bulverde, Comal County, Texas (Hay 1921), but the specimen actually originated from Friesenhahn Cave in neighboring Bexar County, Texas (Milstead 1956). In the type description, Hay (1921) indicated that he had access to several specimens representing multiple individuals from this locality, but he was unsure whether all specimens belong to one species. As such, he named this species on the basis of a fragment of a posterior carapace and only provisionally referred the rest (Hay 1921). Hay (1921) differentiated this taxon based on small differences to the height of posterior marginals, but I am not able to see significant differences from most known *Terrapene*. Milstead (1956) synonymized *Terrapene bulverda* with *Terrapene canaliculata*, but I here instead interpret this taxon as a nomen dubium.

Terrapene canaliculata Hay, 1907
nomen invalidum
(junior synonym of *Terrapene putnami*
Hay, 1906a)

Taxonomic history. *Terrapene canaliculata* Hay, 1907 (new species); *Terrapene canaliculata* = *Terrapene antipex* Gilmore 1927 (senior synonymy); *Terrapene carolina putnami* = *Terrapene antipex* = *Terrapene canaliculata* Auffenberg 1958 (junior synonymy); *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene impressa* = *Terrapene innoxia* = *Terrapene llanensis* = *Terrapene singletoni* Kuhn 1964 (junior synonymy); *Terrapene carolina major* = *Cistudo marnochii* = *Terrapene antipex* = *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene putnami* TEWG 2015 (junior synonymy).

Type material. USNM 5500 (holotype), isolated shell fragments (Hay 1907, figs. 5–7; Hay 1908, figs. 463–465).

Type locality. Whitemarsh or Skedaway Island, below Savannah, Georgia, USA (Hay 1907); Pleistocene (Hay 1907).

Comments. The type material of *Terrapene canaliculata* consists of isolated shell fragments from the Pleistocene of Georgia. Based on the available information, is not possible to confirm the presence of the diagnostic hyo-hypoplastral hinge of *Terrapene*. If indeed these specimens belong to a box turtle, then the published entoplastron (Hay 1908) could be of some diagnostic value, as the humero-pectoral sulcus is situated in the posteriormost part of the entoplastron. In extant *Terrapene*, as well as in *Terrapene eurypygia*, this sulcus is placed more anteriorly. Auffenberg (1958) reviewed all material from Florida that had previously been referred to *Terrapene canaliculata* and concluded that this taxon should be considered to be a junior synonym of *Terrapene putnami*, a view tentatively followed herein.

Terrapene formosa Hay, 1916a
nomen invalidum
(junior synonym of *Terrapene carolina*
[Linnaeus, 1758])

Taxonomic history. *Terrapene formosa* Hay, 1916a (new species); *Terrapene carolina* = *Terrapene innoxia* = *Terrapene formosa*

Auffenberg 1958 (junior synonymy); *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene impressa* = *Terrapene innoxia* = *Terrapene llanensis* = *Terrapene singletoni* Kuhn 1964 (junior synonymy); *Terrapene carolina major* = *Cistudo marnochii* = *Terrapene antipex* = *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene putnami* TEWG 2015 (junior synonymy).

Type material. USNM 8825 (holotype), posterior portions of a carapace (Hay 1916a, pl. 4.3).

Type locality. Ocala, Marion County, Florida, USA (Hay 1916a); Ocala limestone, Pleistocene (Hay 1916a; Auffenberg 1958).

Comments. *Terrapene formosa* is based on a partial carapace from the Pleistocene of Florida (Hay 1916a). In the original publication, Hay (1916a) noted that the type material of *Terrapene formosa* is deposited in the collections of the FGS (FGS 2973), but currently is part of the collections of USNM. As Auffenberg (1958) noted, *Terrapene formosa* is poorly defined and broadly overlaps in its morphology with the fossil *Terrapene innoxia* Hay, 1916a and the extant *Terrapene carolina carolina*. The view of Auffenberg (1958) is followed herein and *Terrapene formosa* is therefore considered to be a junior synonym of *Terrapene carolina*.

Terrapene hibernaculum Auffenberg, 1959
(in Kuhn 1964)
nomen nudum

Type material. Not applicable (see comments).

Type locality. Not applicable (see comments).

Comments. Auffenberg (1959) published an article hypothesizing that the Pleistocene locality of Reddick 1b in Florida may represent a fossilized *Terrapene hibernaculum*, the formal term for a winter refuge for hibernating animals. Kuhn (1964) apparently misunderstood the title and believed that Auffenberg (1959) had proposed a new taxon, *Terrapene hibernaculum*. Obviously, this nomen does not satisfy the provisions of Article 13 (ICZN 1999) and should be considered to be a nomen nudum.

Terrapene impressa Hay, 1924
nomen dubium

Taxonomic history. *Terrapene impressa* Hay, 1924 (new species); *Terrapene canaliculata* = *Terrapene impressa* Milstead 1956 (junior synonymy); *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene impressa* = *Terrapene innoxia* = *Terrapene llanensis* = *Terrapene singletoni* Kuhn 1964 (junior synonymy); *Terrapene carolina triunguis* = *Terrapene bulverda* = *Terrapene impressa* = *Terrapene llanensis* = *Terrapene whitneyi* TEWG 2015 (junior synonymy).

Type material. Unknown collection (holotype), an anterior plastral lobe (Hay 1924, fig. 5).

Type locality. North to Pittbridge, Brazos river, Hidalgo falls, Washington County, Texas, USA (Hay 1924); Pleistocene (Hay 1924).

Comments. The type specimen of *Terrapene impressa* is clearly a member of *Terrapene* based on the presence of a hyohypoplastral hinge and scute morphology. Hay (1924) diagnosed this species based on the presence of deep sulci, but Milstead (1956) later suggested that this feature is not enough to diagnose it and he included it to the synonymy of *Terrapene canaliculata*. Based on all the available evidence, the type material of *Terrapene impressa* cannot be diagnosed within *Terrapene* and I therefore considered it to be a nomen dubium. I was not able to locate the holotype of this species.

Terrapene innoxia Hay, 1916a
nomen invalidum
(junior synonym of *Terrapene carolina*
[Linnaeus, 1758])

Taxonomic history. *Terrapene innoxia* Hay, 1916a (new species); *Terrapene carolina* = *Terrapene innoxia* = *Terrapene formosa* Auffenberg 1958 (junior synonymy); *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene impressa* = *Terrapene innoxia* = *Terrapene llanensis* = *Terrapene singletoni* Kuhn 1964 (junior synonymy); *Terrapene carolina bauri* = *Terrapene innoxia* = *Trachemys nuchoarinata* = *Terrapene singletoni* TEWG 2015 (junior synonymy).

Type material. USNM 8824 (holotype), a complete carapace (Hay 1916a, pl. 6.1–4).

Type locality. Vero, St. Lucie County, Florida, USA (Hay 1916a); Pleistocene (Hay 1916a).

Comments. Hay (1916a) noted in the type description that the type material of *Terrapene innoxia*, a complete carapace of small size from the Pleistocene of Florida, is deposited in the collections of the FGS (FGS 7080), but currently is part of the collections of USNM. The main characters used by Hay (1916a) and Auffenberg (1958) to distinguish this taxon are its small size, the degree of flaring of the posterior peripherals, the height of the shell, the less-developed nuchal notch, and the larger cervical scute. All of these characters are quite variable in extant members of *Terrapene* (see Auffenberg 1958 and Burroughs et al. 2013) and are insufficient to diagnose this taxon. Overall, this material shows no differences with the extant *Terrapene carolina carolina*. The view of Auffenberg (1958) is therefore followed herein and *Terrapene innoxia* is considered to be a junior synonym of *Terrapene carolina*.

Terrapene llanensis Oelrich, 1953
nomen invalidum
(junior synonym of *Terrapene putnami*
Hay, 1906a)

Taxonomic history. *Terrapene llanensis* Oelrich, 1953 (new species); *Terrapene canaliculata* = *Terrapene formosa* = *Terrapene impressa* = *Terrapene innoxia* = *Terrapene llanensis* = *Terrapene singletoni* Kuhn 1964 (junior synonymy); *Terrapene carolina triunguis* = *Terrapene bulverda* = *Terrapene impressa* = *Terrapene llanensis* = *Terrapene whitneyi* TEWG 2015 (junior synonymy).

Type material. UMMP 26957 (holotype), a partial carapace and posterior plastral lobe (Oelrich 1953, pl. 1.1).

Type locality. Shorts Creek, Lone Tree Arroyo, Meade County, Kansas, USA (Oelrich 1953); late Pleistocene (Oelrich 1953).

Comments. *Terrapene llanensis* is based on a partial shell from the late Pleistocene of Kansas (Oelrich 1953). Oelrich (1953) noted similarities between *Terrapene llanensis* and *Terrapene canaliculata*, but distinguished the two taxa based on small differences to the proportions of the scutes. As these characters are subject to a significant amount of variation within *Terrapene* (e.g., Auffenberg 1958; Burroughs et al. 2013), it is not possible to confidently distinguish the two taxa. As such, *Terrapene llanensis* is herein considered to be a junior synonym of *Terrapene putnami*.

Terrapene longinsulae Hay, 1909
nomen invalidum
(junior synonym of *Terrapene ornata*
[Agassiz 1857])

Taxonomic history. *Terrapene longinsulae* Hay, 1909 (new species); *Terrapene ornata longinsulae* Milstead 1956 (new combination); *Terrapene ornata* = *Terrapene longinsulae* Joyce et al. 2012 (junior synonymy).

Type material. USNM 5983 (holotype), a skull, almost complete shell, and associated appendicular elements (Hay 1909, pl. 26; Joyce et al. 2012, figs. 3, 4).

Type locality. Long Island, Philips County, Kansas, USA (Hay 1909); precise geological provenance unknown; Miocene–Pleistocene (Joyce et al. 2012).

Comments. *Terrapene longinsulae* is based on a partial skeleton from Kansas with poor provenance (Hay 1909). Joyce et al. (2012) recently revised this taxon and indicated a few problems. In particular, the unclear geographical provenance of the type precludes dating it precisely. Furthermore, the carapace of this taxon is highly irregular, both in the neural contacts and in the presence of extra vertebral scutes, arranged in an alternating, step-like pattern. Finally, the preserved information from the shell and skull does not allow distinction from the extant *Terrapene ornata*, leading to the proposed synonymy of the two taxa. The same reasoning is followed herein and *Terrapene longinsulae* is therefore considered to be a junior synonym of *Terrapene ornata*.

Terrapene whitneyi Hay, 1916b
nomen invalidum
(junior synonym of *Terrapene ornata*
[Agassiz, 1857])

Taxonomic history. *Terrapene whitneyi* Hay, 1916b (new species); *Terrapene carolina triunguis* = *Terrapene whitneyi* Milstead 1965 (junior synonymy); *Terrapene carolina triunguis* = *Terrapene bulverda* = *Terrapene impressa* = *Terrapene llanensis* = *Terrapene whitneyi* TEWG 2015 (junior synonymy).

Type material. USNM 8617 (holotype), a complete shell (Hay 1916b, pls. 1.4–5, 2.1).

Type locality. City of Austin, Travis County, Texas, USA (Hay 1916b); Pleistocene (Hay 1916b).

Comments. *Terrapene whitneyi* is based on a complete shell from the Pleistocene of Texas that was originally deposited in the collections of the University of Texas (Hay 1916b), but currently is part of the collections of USNM. The characters used to diagnose this species included the shape of the shell, the absence of a dorsal keel, and long anal scutes compared with femorals. Milstead (1956) considered *Terrapene whitneyi* to be a valid species, but attributed specimens that Hay (1916b) had referred to this taxon from Friesenhahn Cave to *Terrapene canaliculata*. He further suggested that *Terrapene whitneyi* and *Terrapene longinsulae* are morphologically close to *Terrapene ornata* and that *Terrapene whitneyi* is best considered to be a synonym of *Terrapene canaliculata*. Based on all the available information, it is not possible to distinguish the type material of *Terrapene whitneyi* from the extant *Terrapene ornata*. As such, *Terrapene whitneyi* is herein considered to be a junior synonym of *Terrapene ornata*.

Testudo amphithorax Cope, 1873a
nomen invalidum
(junior synonym of *Stylemys nebrascensis*
[Leidy, 1851a])

Taxonomic history. *Testudo amphithorax* Cope, 1873a (new species); *Geochelone amphithorax* Auffenberg 1963 (new combination); *Stylemys amphithorax* Auffenberg 1964a (new combination); *Stylemys amphithorax* Coto Rojas and Acuña Mesén 1986 (incorrectly spelled species epithet); *Testudo ligonia* = *Stylemys amphithorax* Hutchison 1996 (synonymy).

Type material. AMNH FR1139, FR1145, FR1147, FR1156, and FR1159 (syntypes), carapacial and plastral fragments (AMNH database; Hay 1908, figs. 526–530).

Type locality. Horsetail Creek, Weld County, Colorado, USA (Cope 1873a); Horsetail Creek Member, White River Formation, Chadronian NALMA, Priabonian, late Eocene (Woodburne 2004).

Comments. See *Stylemys nebrascensis* above.

Testudo orthopygia angusticeps Matthew, 1924
nomen invalidum
(junior synonym of *Hesperotestudo osborniana*
[Hay, 1905])

Taxonomic history. *Testudo orthopygia angusticeps* Matthew, 1924 (new subspecies); *Geochelone angusticeps* Auffenberg 1963 (elevation to species level, new combination); *Geochelone (Hesperotestudo) orthopygia angusticeps* Auffenberg 1974 (new combination).

Type material. AMNH 6295 (holotype), a skull (Matthew 1924, fig. 61).

Type locality. Sheep Creek Quarry, Stonehouse Draw, Sioux County, Nebraska, USA (Matthew 1924); lower Sheep Creek beds, late Hemingfordian NALMA, Burdigalian–Langhian, early Miocene (Auffenberg 1974; Woodburne 2004).

Comments. See *Hesperotestudo osborniana* above.

Testudo annae Hay, 1923b
nomen dubium

Taxonomic history. *Testudo annae* Hay, 1923b (new species); *Geochelone (Caudochelys) annae* Auffenberg 1974 (new combination); *Hesperotestudo annae* = *Testudo francisi* TEWG 2015 (senior synonymy).

Type material. TMM TAMU 3-2405 (holotype), a right epiplastron (Hay 1923b, pl. 8.3).

Type locality. Brazos River, near Pittbridge, Burleson County, Texas, USA (Hay 1923b); Pleistocene (Auffenberg 1974).

Comments. The type material of *Testudo annae* is from the Pleistocene of Texas and consists of a right epiplastron that possesses a well-developed epiplastral lip. Hay (1923b) suggested that this species is close to *Hesperotestudo crassiscutata* based on size and thickness, but Auffenberg (1974) later suggested a possible synonymy between the two species. The preserved information allows identification only as a member of *Testudinidae*, and *Testudo annae* is therefore considered to be a nomen dubium herein.

Testudo arenivaga Hay, 1906b
nomen invalidum
(junior synonym of *Hesperotestudo osborniana*
[Hay, 1905])

Taxonomic history. *Testudo arenivaga* Hay, 1906b (new species); *Geochelone (Caudochelys) arenivaga* Auffenberg 1963 (new combination); *Geochelone (Hesperotestudo) arenivaga* Auffenberg 1974 (new combination).

Type material. CM 1509 (holotype), carapacial fragments (Hay 1906b, pl. 16.6–8; Hay 1908, figs. 563–565).

Type locality. 2 miles north of Agate Springs, Sioux County, Nebraska, USA (Hay 1906b); early Miocene (Hay 1908).

Comments. See *Hesperotestudo osborniana* above.

Testudo atascosae Hay, 1902b
nomen dubium

Taxonomic history. *Testudo atascosae* Hay, 1902b (new species); *Gopherus atascosae* Hay 1924 (new combination); *Gopherus polyphemus* = *Gopherus atascosae* Crumly 1994 (junior synonymy); *Gopherus polyphemus* = *Gopherus praecedens* = *Testudo atascosae* TEWG 2015 (junior synonymy).

Type material. ANSP 9791–9794 (syntypes), plastral fragments (Hay 1902b, figs. 1–5).

Type locality. Atascosa County, Texas, USA (Hay 1902b); Pleistocene (Auffenberg 1974).

Comments. The type material of *Testudo atascosae* consists of a partial anterior and posterior plastral lobe from the Pleistocene of Texas (Hay 1902b). The precise setting of the type locality is unclear and the Pleistocene age is therefore only probable (Hay 1902b). The anterior lobe shows a well-developed epiplastral lip with a flat dorsal surface and narrow gulars that cover the anterior part of the entoplastron. The posterior lobe shows short anals, a femoro-anal sulcus that is developed almost perpendicular to the midline, and a deep and angular anal notch. Hay (1921) referred a femur from Friesenhahn Cave to this taxon, but only geographic concerns support this assignment. Crumly (1994) suggested that *Testudo atascosae* is a synonym of *Gopherus polyphemus* but provided no justification for that assessment. Overall, the anatomical information from both the type and referred material does not allow diagnosis beyond the level of *Testudinidae*. Based on all the above, *Testudo atascosae* is herein considered to be a nomen dubium.

Testudo campester Hay, 1908
nomen invalidum
(junior synonym of *Gopherus hexagonatus*
[Cope, 1893])

Taxonomic history. *Testudo campester* Gidley, 1903 (nomen nudum); *Testudo campester* Hay, 1908 (new species); *Gopherus campester* Williams 1950b (new combination); *Geochelone (Hesperotestudo) campester* = *Testudo rexroadensis* Auffenberg 1974 (new combination and synonymy); *Hesperotestudo campester* = *Testudo rexroadensis* TEWG 2015 (referral to genus level and synonymy).

Type material. AMNH 3930 (holotype), a partial shell (Hay 1908, figs. 610–613).

Type locality. Near Mt. Blanco, Crosby County, Texas, USA (Hay 1908); lower Blanco beds, early Blancan NALMA, Zanclean, early Pliocene (Auffenberg 1974; Woodburne 2004).

Comments. *Testudo campester* is based on a partial shell from the Pliocene of Texas (Hay 1908). Gidley (1903) included *Testudo campester* in his list of taxa from Blanco beds of Texas without any indication that it represents a new species nor followed by any authorship. In the footnote he indicates that the list comes from Cope (1893), but *Testudo campester* is not included in that list. *Testudo campester* Gidley, 1903 is not accompanied by description, definition, or indication and as such can be considered as a nomen nudum (ICZN 1999, Art. 12) and therefore is not an available name. The name was instead made available by Hay (1908). Auffenberg (1974) suggested that *Testudo campester* is a synonym of *Testudo rexroadensis*, thus a member of *Hesperotestudo*; this opinion is followed by TEWG (2015) as well. Herein I show that *Testudo campester* is actually a member of *Gopherus* (see *Gopherus hexagonatus*).

Testudo copei Koerner, 1940
nomen invalidum
(junior synonym of *Stylemys inusitata*
[Hay, 1906b])

Taxonomic history. *Testudo copei* Koerner, 1940 (new species); *Gopherus copei* Williams 1950b (new combination); *Stylemys copei* Crumly 1994 (new combination).

Type material. YPM VP 013953 (holotype), an almost complete shell (Koerner 1940, pl. 1.2).

Type locality. Section 14, Meagher County, Montana, USA (Koerner 1940); Deep River Formation, early Barstovian NALMA, Langhian, middle Miocene (Woodburne 2004).

Comments. See *Stylemys inusitata* above.

Testudo culbratus Cope, 1873a
nomen dubium

Taxonomic history. *Testudo culbratus* Cope, 1873a (new species); *Testudo cultratus* Cope 1884 (unjustified emendation of prevailing use); *Testudo cultrata* Hay 1908 (justified emendation); *Geochelone cultrata* Auffenberg 1963 (new combination); [*Testudo cultrata*] Hutchison 1996 (nomen dubium).

Type material. Collection unknown, isolated fragments of the shell (Cope 1884, pl. 63, figs. 1–3), now considered lost (see Comments below).

Type locality. Head of Horsetail Creek, Weld County, Colorado, USA (Cope 1873a; Auffenberg 1974); Horsetail Creek Member, White River Formation, Chadronian NALMA, Priabonian, late Eocene (Auffenberg 1974).

Comments. *Testudo cultratus* is based on isolated shell fragment from the late Eocene of Colorado. Although Hay (1908) was unable to locate the material at the AMNH and USNM, Auffenberg (1974) indicated the material to be stored at USNM. However, no such record exists in the USNM database. I therefore here consider the type material to be lost. The original spelling for this taxon is *Testudo culbratus* Cope, 1873a, but Cope (1884) later made an unjustified emendation to *Testudo cultratus*. As this unjustified emendation has been in prevailing use since then and always attributed to the original author (in fact there are no other records of the original spelling) it must be considered a justified emendation (ICZN 1999, Art. 33.2.3.1). However, the type material preserves little anatomical information and cannot be diagnosed within *Pan-Testudinoidea*. As such, *Testudo cultrata* is considered herein to be a nomen dubium.

Testudo distans Hay, 1916a
nomen dubium

Taxonomic history. *Testudo distans* Hay, 1916a (new species); *Geochelone (Caudochelys) crassiscutata* = *Eupachemys obtusa* = *Eupachemys rugosus* = *Testudo distans* = *Testudo luciae* = *Testudo obtusa* = *Testudo ocalana* = *Testudo sellardsi* Auffenberg 1963 (new combination and junior synonymy).

Type material. USNM 8819 (holotype), an entoplastron (Hay 1916a, pl. 3.9; Auffenberg 1963, fig. 19). Originally catalogued as FGS 4289.

Type locality. Pit 5 of the Florida Lime Company, Ocala, Marion County, Florida, USA (Hay 1916a; Auffenberg 1963); Pleistocene (Hay 1916a).

Comments. *Testudo distans* is based on an isolated entoplastron, approximately 10 cm long, from the Pleistocene of Ocala, Florida (Hay 1916a). The type is distinguished from the remaining elements from Ocala by a partial covering of the entoplastron by the pectoral scutes. Although this character clearly distinguished this element from other material from Ocala, the holotype is undiagnostic within *Pan-Testudinoidea* and too fragmentary to allow the recognition of a valid species. Therefore *Testudo distans* is herein considered to be a nomen dubium.

Testudo emiliae Hay, 1908
nomen invalidum
(junior synonym of *Stylemys nebrascensis*
Leidy, 1851a)

Taxonomic history. *Testudo emiliae* Hay, 1908 (new species); *Gopherus emiliae* Williams 1950b (new combination); *Stylemys emiliae* Bramble 1971 (new combination).

Type material. AMNH 6135 (holotype), a partial shell (Hay 1908, pl. 70).

Type locality. Porcupine Creek, Oglala Lakota (formerly Shannon) County, South Dakota, USA (Hay 1908); lower Rosebud Formation, Arikareean NALMA, late Oligocene–early Miocene (Auffenberg 1974; Woodburne 2004).

Comments. See *Stylemys nebrascensis* above.

Testudo equicomis Hay, 1917
nomen dubium

Taxonomic history. *Testudo equicomis* Hay, 1917 (new species); *Geochelone equicomis* Auffenberg 1962b (new combination); *Geochelone (Hesperotestudo) equicomis* Auffenberg 1974 (new combination).

Type material. USNM 10944 (holotype), a right epiplastron and right hypoplastron (Hay 1917, pls. 1.1–3, 3.1).

Type locality. Cragin Quarry, Meade County, Kansas, USA (Hay 1917); Kingsdown Formation, Ranchoabrean NALMA, Ionian–Tarrantian, Pleistocene (Auffenberg 1974).

Comments. The type material of *Testudo equicomis* from the Pleistocene of Kansas consists of a right hypoplastron and a right epiplastron that has a flat epiplastral lip with gulars covering the anterior part of the entoplastron (Hay 1917). Based on the preserved information, this material cannot be diagnosed beyond the level of *Testudinidae* and, as such, *Testudo equicomis* is herein considered to be a nomen dubium.

Testudo exornata Lambe, 1906
nomen dubium

Taxonomic history. *Testudo exornata* Lambe, 1906 (new species); *Geochelone exornata* Auffenberg 1963 (new combination).

Type material. CMN 6292 (holotype), costal fragment; CMN 6230–6231 (paratypes), costal fragments (Lambe 1906, pl. 3.1–3; Hay 1908, figs. 506–508).

Type locality. Bone Coulee, Cypress Hills, Assiniboia, Saskatchewan, Canada (Lambe 1906); Rupelian, early Oligocene (Lambe 1906).

Comments. *Testudo exornata* is based on costal fragments from the early Oligocene of Saskatchewan that do not present any diagnostic features that would allow distinction of this taxon within *Pan-Testudinidae*. *Testudo exornata* is therefore herein considered to be a nomen dubium.

Testudo farri Hay, 1908
nomen invalidum
(junior synonym of *Hesperotestudo osborniana*
[Hay, 1905])

Taxonomic history. *Testudo farri* Hay, 1908 (new species); *Geochelone farri* Auffenberg 1963 (new combination); *Geochelone (Hesperotestudo) farri* Auffenberg 1974 (new combination).

Type material. YPM VPPU 010486 (holotype), a shell (Hay 1908, figs. 548, 549, pl. 69.1–2).

Type locality. Smith River valley, Montana, USA (Hay 1908); Deep River Formation, Barstovian NALMA, Langhian–Serravallian, middle Miocene (Auffenberg 1974).

Comments. See *Hesperotestudo osborniana* above.

Testudo francisi Hay, 1923b
nomen dubium

Taxonomic history. *Testudo francisi* Hay, 1923b (new species); *Geochelone (Caudochelys) francisi* Auffenberg 1974 (new combination); *Hesperotestudo annae* = *Testudo francisi* TEWG 2015 (junior synonymy).

Type material. TMM TAMU 23-2242 (holotype), a right epiplastron (Hay 1923b, pl. 8.5).

Type locality. Temple, Bell County, Texas, USA (Hay 1923b); Pleistocene (Auffenberg 1974).

Comments. *Testudo francisi* is based on a partial epiplastron from the Pleistocene of Texas that shows a well-developed epiplastral lip that is nearly flat dorsally. Hay (1923b) suggested that *Testudo francisi* is different from *Hesperotestudo crassiscutata* and close to *Testudo sellardsi* and *Testudo luciae* (both nomina dubia herein), but later Auffenberg (1974) suggested that it is closer to *Hesperotestudo crassiscutata*. The preserved informa-

tion allows identification only as a member of *Testudinidae* and, as such, *Testudo francisi* is herein considered to be a nomen dubium.

Testudo hadriana Cope, 1871a
nomen invalidum
(objective senior synonym of *Hadrianus quadratus* Cope, 1871b; junior synonym of *Hadrianus corsoni* [Leidy, 1871b])

Taxonomic history. *Testudo hadriana* Cope, 1871a (new species); *Testudo hadriana* = *Hadrianus quadratus* Cope 1871b (senior synonym); *Hadrianus corsoni* = *Testudo hadriana* = *Hadrianus quadratus* = *Hadrianus octonaria* Hay 1908 (junior synonymy).

Type material. see *Hadrianus quadratus* above.

Type locality. see *Hadrianus quadratus* above.

Comments. see *Hadrianus quadratus* above.

Testudo hayi Sellards, 1916
nomen dubium

Taxonomic history. *Testudo hayi* Sellards, 1916 (new species); *Gopherus hayi* Williams 1950b (new combination); *Geochelone (Caudochelys) hayi* = *Geochelone lousekressmani* Auffenberg 1963 (new combination and senior synonymy).

Type material. USNM 8815 (holotype), carapacial and plastral fragments (Auffenberg 1963, fig. 20).

Type locality. Amalgamated Phosphate Company pit, Brewster County, Florida, USA (Sellards 1916); Bone Valley Gravel Formation, Blacan NALMA, Pliocene (Auffenberg 1963).

Comments. The type material of *Testudo hayi* is from the Pliocene of Florida (Sellards 1916), but it is highly fragmentary and does not allow a clear diagnosis relative to other taxa. *Testudo lousekressmani* has been named from the same locality (Wark 1929). Auffenberg (1963) noted a possible confusion of the type material of *lousekressmani* with that of *hayi*, and errors in the reconstructions made by Wark (1929). As Auffenberg (1963) states that both taxa had the same specimen number it is also possible that they are objective synonyms. However, personal observations on the USNM material of *Testudo hayi* does not confirm this hypothesis, at least compared with the descriptions provided by Wark (1929). Auffenberg (1963) also noted a considerable difference in size between the two type specimens. Although no differences are apparent between *hayi* and *lousekressmani* based on the information provided by Auffenberg (1963), both taxa are too fragmentary allow diagnosing a valid testudinid. I therefore consider both *Testudo hayi* and *Testudo lousekressmani* to be nomina dubia. The referred specimens to *Testudo hayi* of Auffenberg (1963) from other localities in Florida are also interpreted herein as specimens of an indeterminate *Testudinidae*.

Testudo hollandi Hay, 1906b
nomen invalidum
(junior synonym of *Gopherus edae* [Hay, 1906b])

Taxonomic history. *Testudo hollandi* Hay, 1906b (new species); *Gopherus hollandi* Williams 1950b (new combination); *Gopherus edae* = *Testudo hollandi* Bramble 1982 (junior synonymy).

Type material. CM 1561 (holotype), a shell (Hay 1908, pl. 81.1–2).

Type locality. Near Running Water Creek, Sioux County, Nebraska, USA (Hay 1906b); Harrison Formation, Arikareean NALMA, Rupelian–Burdigalian, late Oligocene–early Miocene (Auffenberg 1974; Woodburne 2004).

Comments. see *Gopherus edae* above.

Testudo impensa Hay, 1908
nomen invalidum
(junior synonym of *Hesperotestudo osborniana* [Hay, 1905])

Taxonomic history. *Testudo impensa* Hay, 1908 (new species); *Geochelone impensa* Auffenberg 1963 (new combination); *Geochelone (Hesperotestudo) impensa* Auffenberg 1974 (new combination).

Type material. AMNH 5867 (holotype), a skull, shell, and appendicular elements (Hay 1908, figs. 566–571, pls. 76, 77).

Type locality. Between Madison and Gallatin rivers, Gallatin County, Montana, USA (AMNH database); Loup Fork Formation, Hemphillian NALMA, Tortonian–Zanclean, late Miocene–early Pliocene (AMNH database; Hay 1908; Woodburne 2004).

Comments. See *Hesperotestudo osborniana* above.

Testudo incisa Hay, 1916a
nomen invalidum
(junior synonym of *Hesperotestudo turgida* [Cope, 1892a])

Taxonomic history. *Testudo incisa* Hay, 1916a (new species); *Gopherus incisa* Williams 1950b (new combination); *Geochelone incisa* Ray 1957 (new combination); *Geochelone (Hesperotestudo) incisa* Auffenberg 1962b (new combination).

Type material. USNM 8821 (holotype), a left xiphiplastron (Hay 1916a, pl. 3.5–8).

Type locality. Ocala Lime Company Quarry, near Ocala, Marion County, Florida, USA (Hay 1916a; Auffenberg 1974); Pleistocene (Auffenberg 1974).

Comments. See comments in *Hesperotestudo turgida* above.

Testudo klettiana Cope, 1875b
nomen dubium

Taxonomic history. *Testudo klettiana* Cope, 1875b (new species); *Geochelone klettiana* Auffenberg 1963 (new combination).

Type material. USNM 2127 (holotype), a pygal plate (Hay 1908, fig. 574).

Type locality. Near San Ildefonso Pueblo, Santa Fé County, New Mexico, USA (Cope 1875b); "Loop Fork" Santa Fe series, Barstovian NALMA, Langhian–Serravallian, middle Miocene (Auffenberg 1974).

Comments. The type material of *Testudo klettiana* Cope, 1875b is a single pygal that is not intersected by an intermarginal sulcus. This material is undiagnostic within *Testudinidae* and *Testudo klettiana* is therefore herein considered to be a nomen dubium.

Testudo lata Leidy, 1851b
nomen invalidum
(junior synonym of *Stylemys nebrascensis*
Leidy, 1851a)

Taxonomic history. *Testudo lata* Leidy, 1851b (new species); *Stylemys nebrascensis* = *Emys hemispherica* = *Emys oweni* = *Emys culbertsonii* = *Testudo lata* Hay 1908 (junior synonymy).

Type material. ANSP 10072 (holotype), a partial shell (Spamer et al. 1995; Leidy 1853, pls. 23, 24.1).

Type locality. White River badlands, South Dakota (Leidy 1873); Brule series, Orellan member, White River Formation, Orellan NALMA, early Rupelian, early Oligocene (Auffenberg 1974; Woodburne 2004).

Comments. See *Stylemys nebrascensis*.

Testudo laticaudata Cope, 1893
nomen dubium

Taxonomic history. *Testudo laticaudata* Cope, 1893 (new species); *Testudo laticaudata* Wilson 1950 (incorrectly spelled species epithet); *Geochelone (Caudochelys) laticaudata* Auffenberg 1963 (new combination); *Testudo laticaudata* Kuhn 1964 (incorrectly spelled species epithet); *Gopherus laticaudatus* Auffenberg 1974 (new combination); *Gopherus hexagonatus* = *Gopherus laticaudatus* Preston 1979 (junior synonymy).

Type material. TMM 41412-2 (holotype), a right epiplastron and xiphiplastron (Cope 1893, pl. 22; Hay 1908, figs. 623, 624).

Type locality. Rock Creek, Tule Canyon, Briscoe County, Texas, USA (Cope 1893); Rock Creek local fauna, Tule Formation, Irvingtonian NALMA, Calabrian, middle Pleistocene (Woodburne 2004).

Comments. *Testudo laticaudata* is based on two plastron fragments from the Pleistocene of Texas that are undiagnostic

beyond *Testudinidae*. Therefore *Testudo laticaudata* is herein considered to be a nomen dubium.

Testudo ligonius Cope, 1873a
nomen invalidum
(junior synonym of *Stylemys nebrascensis*
Leidy, 1851a)

Taxonomic history. *Testudo ligonius* Cope, 1873a (new species); *Testudo ligonia* Hay 1908 (justified emendation); *Geochelone ligonia* Auffenberg 1963 (new combination); *Stylemys ligonia* Auffenberg 1964a (new combination); *Testudo ligonia* = *Stylemys amphithorax* Hutchison 1996 (synonymy).

Type material. AMNH 1148 (holotype), carapacial and plastral fragments (Hay 1908, figs. 516–525).

Type locality. Horsetail Creek, Weld County, Colorado, USA (Cope 1873a); Horsetail Creek Member, White River Formation, Chadronian NALMA, Priabonian, late Eocene (Woodburne 2004).

Comments. See *Stylemys nebrascensis* above.

Testudo louisekressmani Wark, 1929
nomen dubium

Taxonomic history. *Testudo louisekressmani* Wark, 1929 (new species); *Geochelone (Caudochelys) hayi* = *Geochelone louisekressmani* Auffenberg 1963 (new combination; junior synonymy);

Type material. Possibly USNM 8815 (formerly FGS V 1803 and 5001) (holotype), part of the carapace (Wark 1929, fig. 1).

Type locality. Amalgamated Phosphate Company pit, Brewster County, Florida, USA (Wark 1929); Bone Valley Gravel Formation, Blacan NALMA, Pliocene (Auffenberg 1963).

Comments. See *Testudo hayi*.

Testudo luciae Hay, 1916a
nomen dubium

Taxonomic history. *Testudo luciae* Hay, 1916a (new species); *Geochelone luciae* Ray 1957 (new combination); *Geochelone (Caudochelys) crassiscutata* = *Eupachemys obtusa* = *Eupachemys rugosus* = *Testudo distans* = *Testudo luciae* = *Testudo obtusa* = *Testudo ocalana* = *Testudo sellardsi* Auffenberg 1963 (junior synonymy).

Type material. USNM 8818 (holotype), a partial right hypoplastron (Hay 1916a, pl. 9.5; Auffenberg 1963, fig. 17).

Type locality. Vero, St. Lucie County, Florida, USA (Hay 1916a); Pleistocene (Hay 1916a).

Comments. *Testudo luciae* is based on a partial right hypoplastron from the Pleistocene of Florida that does not preserve

enough anatomical information to diagnose it beyond the level of *Pan-Testudinidae*. Based on what is preserved, I can only estimate that it belonged to a tortoise of the size of *Hesperotestudo crassiscutata*. *Testudo luciae* is herein considered to be a nomen dubium.

Testudo milleri Brattstrom, 1961
nomen dubium

Taxonomic history. *Testudo milleri* Brattstrom, 1961 (new species); *Geochelone milleri* Auffenberg 1974 (new combination); *Scaptochelys mohavense* = *Gopherus depressus* = *Testudo milleri* Bramble 1982 (junior synonymy); *Tsetudo milleri* Reynoso and Montellano-Ballesteros 2004 (incorrectly spelled genus name).

Type material. LACM CIT494/5129 (holotype), a partial shell (Brattstrom 1961, figs. 5, 6).

Type locality. Barstow syncline, Mojave desert, San Bernardino County, California, USA (Brattstrom 1961); Barstow beds, Barstovian NALMA, Langhian–Serravallian, middle Miocene (Auffenberg 1974; Woodburne 2004).

Comments. *Testudo milleri* is based on a partial shell from the middle Miocene of California (Brattstrom 1961). Although originally placed in *Testudo* by Brattstrom (1961), *Testudo milleri* was tentatively placed in *Caudochelys* by Auffenberg (1974). I agree with Reynoso and Montellano-Ballesteros (2004) that this taxon is related with *Gopherus* instead, based on the presence of long pectorals and the sinuous pectoro-abdominal sulcus. *Testudo milleri* apparently had a narrow cervical scute and a possible synonymy with *Gopherus mohavensis*, the other named tortoise from this locality, as suggested by Reynoso and Montellano-Ballesteros (2004), therefore cannot be confirmed. Given a lack of otherwise diagnostic characters, I here regard this taxon to be a nomen dubium.

Testudo munda Hay, 1921
nomen dubium

Taxonomic history. *Testudo munda* Hay, 1921 (new species); *Terrapene carolina carolina* = *Cistudo eurypygia* = *Testudo munda* = *Toxaspis anguillulatus* TEWG 2015 (junior synonymy).

Type material. USNM 8944 (holotype), shell fragments (Hay 1921, pl. 3.1–3).

Type locality. Whitesburg, Hamblen County, Tennessee, USA; Pleistocene (Hay 1921).

Comments. The type material of *Testudo munda* consists of isolated fragments of a shell from the Pleistocene of Tennessee (Hay 1921). The peripheral plate shows an overlap of the pleural scutes onto the peripherals, whereas the partial plastron has medially elongated anal scutes and a femoro-anal sulcus that forms an acute angle with the midline. It is not clear why Hay (1921) suggested that this material belongs to a testudinid, but most probably he did so because of the thickness and ornamentation of the bones preserved. However, the plastral characters

preserved are more consistent with affinities with *Terrapene*. In any case, as this specimen lacks diagnostic characters beyond *Pan-Testudinoidea*, *Testudo munda* is herein considered to be a nomen dubium.

Testudo niobrarensis Leidy, 1858
nomen dubium

Taxonomic history. *Testudo niobrarensis* Leidy, 1858 (new species); *Stylemys niobrarensis* Leidy 1873 (new combination); *Geochelone (Hesperotestudo) niobrarensis* Auffenberg 1974 (new combination).

Type material. USNM 956 (holotype), an anterior plastral lobe (Leidy 1873, pl. 3.4; Hay 1908, figs. 575–578)

Type locality. Precise locality not known, deposits of Niobrara river, Nebraska, USA (Leidy 1858); Loup Fork Formation, late Arikarean, early Miocene (USNM database).

Comments. *Testudo niobrarensis* was described on the basis on fragmentary shell material and appendicular elements from the Miocene of Nebraska (Leidy 1858). Leidy (1873) attributed this taxon to *Stylemys* and noted a possible synonymy with *Stylemys nebrascensis*. Hay (1908), on the other hand, concluded this taxon to be a distinct species, but referred it again to *Testudo*. In my opinion, the type material is not diagnostic for a valid species, as the characters that can be discerned by the presented material (e.g., hexagonal neurals, suprapygal crossed by a transverse sulcus, presence of an epiplastral lip, gulars covering the anterior part of entoplastron) are shared with most the New World testudinids. As the precise locality of this taxon is furthermore not known, I conclude *Testudo niobrarensis* to be a nomen dubium.

Testudo ocalana Hay, 1916a
nomen dubium

Taxonomic history. *Testudo ocalana* Hay, 1916a (new species); *Geochelone ocalana* Ray 1957 (new combination); *Geochelone (Caudochelys) crassiscutata* = *Eupachemys obtusa* = *Eupachemys rugosus* = *Testudo distans* = *Testudo luciae* = *Testudo obtusa* = *Testudo ocalana* = *Testudo sellardsi* Auffenberg 1963 (junior synonymy).

Type material. USNM 8822 (holotype), a left epiplastron (Hay 1916a, pl. 3.1; Auffenberg 1963, fig. 18).

Type locality. Fissure in a quarry of the Florida Lime Company, Ocala, Marion County, Florida USA; Pleistocene (Hay 1916a; Auffenberg 1963).

Comments. The type material of *Testudo ocalana* consists of a left epiplastron from the Pleistocene of Florida that has a well-developed epiplastral lip with a flat to rounded dorsal surface. Ventrally, the gulars are narrow and cover the anterior part of the entoplastron. Overall, the preserved information is not sufficient to diagnose the specimen beyond the level of *Testudinidae*. As such, *Testudo ocalana* is herein considered to be a nomen dubium.

Testudo pansa Hay, 1908

nomen invalidum

(junior synonym of *Gopherus edae* [Hay, 1907])

Taxonomic history. *Testudo pansa* Hay, 1908 (new species); *Gopherus pansa* Williams 1950b (new combination); *Gopherus pansus* Auffenberg 1974 (justified emendation).

Type material. AMNH 5869 (holotype), a shell and pelvis (Hay 1908, figs. 550, 551, pl. 71.1–2).

Type locality. Near the state lines of Colorado and Nebraska, north of Sterling, Weld County, Colorado, USA (Hay 1908); Pawnee Creek Formation, Barstovian NALMA, Langhian–Seravallian, middle Miocene (Auffenberg 1974; Woodburne 2004).

Comments. See *Gopherus edae* above.

Testudo peragrans Hay, 1906b

nomen dubium

Taxonomic history. *Testudo peragrans* Hay, 1906b (new species); *Geochelone peragrans* Auffenberg 1963 (new combination).

Type material. CM 1101 (holotype), a skull and shell (Hay 1906b, figs. 1–5; Hay 1908, figs. 534–538).

Type locality. South of McCartney Mountain, north of Dillon, Beaverhead County, Montana, USA (Hay 1906b); Oligocene or early Miocene (Hay 1906b).

Comments. *Testudo peragrans* is based on a skull and shell from the mid-Cenozoic of Montana (Hay 1906b) that is too poorly preserved to allow discerning diagnostic characters. As such, *Testudo peragrans* Hay, 1906b is here considered to be a nomen dubium.

Testudo pertenuis Cope, 1892b

nomen dubium

Taxonomic history. *Testudo pertenuis* Cope, 1892b (new species); *Testudo pertenuis* Kuhn 1964 (incorrectly spelled species epithet); *Gopherus pertenuis* Auffenberg 1974 (new combination); *Gopherus pertenuis* = *Gopherus canyonensis* Preston 1979 (senior synonymy); *Gopherus pertenuis* Crumly 1994 (incorrectly spelled species epithet).

Type material. TMM 40287-32 (holotype), shell fragments (Cope 1892b, figs. 1, 2; Hay 1908, fig. 609).

Type locality. Near Mount Blanco, Crosby County, Texas, USA (Cope 1892b); Blanco beds, early Blancan NALMA, late Pliocene (Auffenberg 1974).

Comments. *Testudo pertenuis* is based on highly fragmentary shell remains from the late Pliocene of Texas (Cope 1892b). *Testudo pertenuis* is regularly considered to be a valid taxon synonymous with *Bysmachelys canyonensis* (Auffenberg 1974; Preston 1979; TEWG 2015), but I find the available material too

fragmentary to allow recognition of a valid taxon. I therefore regard this taxon to be a nomen dubium.

Testudo praeextans Lambe, 1913

nomen invalidum

(junior synonym of *Oligopherus laticuneus*

[Cope, 1873a])

Taxonomic history. *Testudo praeextans* Lambe, 1913 (new species); *Gopherus praeextans* Williams 1950b (new combination); *Scaptochelys laticunea* = *Testudo praeextans* Bramble 1982 (junior synonymy); *Oligopherus praeextans* Franz 2014 (new combination).

Type material. CMN 8401 (holotype), shell (Lambe 1913, pl. IV–V).

Type locality. Old Woman Creek, Niobrara County, Wyoming, USA (Lambe 1913); Orellan NALMA, early Rupelian, early Oligocene (Auffenberg 1974; Woodburne 2004).

Comments. See *Oligopherus laticuneus* above.

Testudo primaeva Oelrich, 1950

nomen invalidum

(junior synonym of *Stylemys inusitata*

[Hay, 1906b])

Taxonomic history. *Testudo primaeva* Oelrich, 1950 (new species); *Geochelone (Hesperotestudo) primaeva* Auffenberg 1974 (new combination).

Type material. UMMMP 25758 (holotype), a partial shell (Oelrich 1950, pl. 1.1–2).

Type locality. West side of Sweetwater Creek, Belmont Park Ranch, Madison County, Montana, USA (Oelrich 1950); ?early Miocene (Oelrich 1950).

Comments. See *Stylemys inusitata* above.

Testudo quadratus Cope, 1884

nomen dubium

Taxonomic history. *Testudo quadratus* Cope 1884 (new species); *Testudo quadrata* Hay 1908 (justified emendation); *Geochelone quadrata* Auffenberg 1963 (new combination); *Oligopherus quadratus* Franz 2014 (new combination).

Type material. AMNH 1149 (holotype), a fragmentary epiplastron and partial nuchal (Hay 1908, figs. 532, 533).

Type locality. Head of Horsetail Creek, Weld County, Colorado, USA (Cope 1884); White River Formation, Chadronian NALMA, Priabonian, late Eocene (Auffenberg 1974; Woodburne 2004).

Comments. The type material of *Testudo quadratus* from the late Eocene of Colorado consists of a partial epiplastron with an epiplastral lip and a partial nuchal plate with a shallow

emargination at the level of the wide and long cervical scute (Cope 1884). The referred material of Gilmore (1946) consists of an epiplastral fragment, which shows a covering of the anterior part of the entoplastron by the gulars. The characters preserved in either specimen do not allow a confident diagnosis of this taxon beyond the level of *Pan-Testudinidae*. As such, *Testudo quadrata* Cope, 1884 is herein considered to be a nomen dubium. This taxon is not to be confused with *Hadrianus quadratus* Cope, 1871b (see relevant section).

Testudo rexroadensis Oelrich, 1952
nomen invalidum
(junior synonym of *Hesperotestudo orthopygia*
[Cope, 1878])

Taxonomic history. *Testudo rexroadensis* Oelrich, 1952 (new species); *Geochelone* (*Caudochelys*) *rexroadensis* Auffenberg 1963 (new combination); *Geochelone* (*Hesperotestudo*) *campester* = *Testudo rexroadensis* Auffenberg 1974 (junior synonymy).

Type material. UMMP 28124 (holotype), parts of a shell and appendicular elements; UMMP 9399 (paratype), parts of a carapace and a complete plastron (Oelrich 1952, figs. 1–4).

Type locality. Wendell Fox pasture (holotype) and Rexroad pasture (paratype), Meade County, Kansas, USA (Oelrich 1952); Rexroad Formation, Blancan NALMA, late Pliocene (Oelrich 1952).

Comments. See *Hesperotestudo orthopygia* above.

Testudo riggsi Hibbard, 1944
nomen invalidum
(junior synonym of *Hesperotestudo turgida*
[Cope, 1892a])

Taxonomic history. *Testudo riggsi* Hibbard, 1944 (new species); *Gopherus riggsi* Williams 1950b (new combination); *Geochelone* (*Hesperotestudo*) *riggsi* Auffenberg 1962b (new combination).

Type material. KU 6789 (holotype), a complete shell (Hibbard 1944, figs. 1, 2; Oelrich 1957, figs. 2, 3).

Type locality. Seward County, Kansas, USA (Hibbard 1944); Saw Rock Canyon fauna, Rexroad Formation, early Blancan NALMA, Zanclean–Piacenzian, Pliocene (Auffenberg 1974).

Comments. See comments in *Hesperotestudo turgida* above.

Testudo sellardsi Hay, 1916a
nomen invalidum
(junior synonym of *Hesperotestudo crassiscutata*
[Leidy, 1889b])

Taxonomic history. *Testudo sellardsi* Hay, 1916a (new species); *Geochelone sellardsi* Ray 1957 (new combination); *Geochelone* (*Caudochelys*) *crassiscutata* = *Eupachemys obtusa* = *Eupachemys rugosus* = *Testudo distans* = *Testudo luciae* = *Testudo*

obtusa = *Testudo ocalana* = *Testudo sellardsi* Auffenberg 1963 (junior synonymy).

Type material. USNM 8817 (holotype), a left xiphiplastron (Hay 1916a, pl. 8.6–8; Auffenberg 1963, fig. 17).

Type locality. Vero, St. Lucie County, Florida, USA (Hay 1916a); Pleistocene (Hay 1916a).

Comments. The type specimen of *Testudo sellardsi* consists of a partial left xiphiplastron that has part of the femoro-anal sulcus and that allows reconstruction of a rounded and shallow anal notch. As this material is fully consistent with that of *Hesperotestudo crassiscutata* and originates from temporal and geographic proximity, I consider *Testudo sellardsi* to be a junior synonym of *Hesperotestudo crassiscutata*.

Testudo tedwhitei Williams, 1953
nomen dubium

Taxonomic history. *Testudo tedwhitei* Williams, 1953 (new species); *Geochelone tedwhitei* Ray 1957 (new combination).

Type material. MCZ 2020 (holotype), a complete plastron (Williams 1953, pl. 1).

Type locality. Thomas Farm, Gilchrist County, Florida, USA (Williams 1953); Hawthorne Formation, early Hemingfordian NALMA, Burdigalian, early Miocene (Auffenberg 1974).

Comments. *Testudo tedwhitei* is based on a complete plastron from the early Miocene of Florida (Williams 1953). On the basis of the well-differentiated neural series and the morphology of the humero-pectoral sulcus, *Testudo tedwhitei* is clearly a member of the *Hesperotestudo* clade. However, in the absence of skull remains, the plastron and carapace morphology of *Testudo tedwhitei* is not sufficient to differentiate it from known valid *Hesperotestudo* species from the Miocene (see above). As such, *Testudo tedwhitei* is herein considered to be a nomen dubium.

Testudo thomsoni Hay, 1908
nomen invalidum
(junior synonym of *Oligopherus laticuneus*
[Cope, 1873a])

Taxonomic history. *Testudo thomsoni* Hay, 1908 (new species); *Geochelone thompsoni* Auffenberg 1963 (new combination; incorrectly spelled species epithet); *Oligopherus laticuneus* = *Oligopherus thomsoni* Hutchison 1996 (new combination and junior synonymy).

Type material. AMNH 3940 (holotype), a skull, shell fragments, and associated appendicular elements (Hay 1908, pl. 66.1–5).

Type locality. Corral Draw, Ziebach County, South Dakota, USA (Hay 1908); lower Oreadon beds, Orellan NALMA, early Rupelian, early middle Oligocene (Auffenberg 1974).

Comments. See *Oligopherus laticuneus* above.

Testudo uintensis Gilmore, 1915
nomen dubium

Taxonomic history. *Testudo uintensis* Gilmore, 1915 (new species); *Stylemys uintensis* Auffenberg 1974 (new combination).

Type material. CM 2331 (holotype), almost complete shell (Gilmore 1915, figs. 21, 22, pl. 27).

Type locality. Near Kennedy Hole, Uintah County, Utah, USA (Gilmore 1915); "Horizon B," Uinta Formation, Uintan NALMA, Lutetian, early Eocene (Woodburne 2004).

Comments. *Testudo uintensis* is based on an almost complete shell from the early Eocene of Utah (Gilmore 1915). Gilmore (1915) found similarities between this tortoise and the much larger *Gigantochersina ammon* from the Eocene of Egypt (Andrews 1906) in the presence of an octagonal neural VI. An octagonal neural VI, however, is only shown in the restored figure in Andrews (1906, fig. 88), whereas the accompanying plate clearly shows a hexagonal neural VI with short antero-lateral sides (Andrews 1906, pl. 24). This neural pattern and the presence of only seven neurals in the Uintan specimen were the main characters that led Gilmore (1915) to distinguish this taxon from *Hadrianus*, although the two taxa share the presence of paired marginal XII. However, the preservation of the specimen (as figured by Gilmore 1915) does not allow a clear assessment of the shape of the first neural, and it is also difficult to discern whether the neural VI is indeed hexagonal. Besides the similarity of the divided supracaudal, the plastron of *Testudo uintensis* is roughly similar to that of the *Hadrianus* specimens described by Gilmore (1915) (considered herein as synonyms of *Hadrianus corsoni*). It is difficult for me to assess if the characters observed by Gilmore are sufficient to allow specific distinction. It is likely that the morphology of this specimen highlights a close relationship with *Hadrianus* and that *Testudo uintensis* might be a synonym of *Hadrianus corsoni* (see relevant section). Also, the attribution of the material to *Stylemys* by Auffenberg (1974) cannot be justified as the presence of marginal XII and the neural pattern clearly distinguish *uintensis* from *Stylemys*. Pending a revision of this specimen, *Testudo uintensis* is here considered to be a nomen dubium and its type material is re-identified as *Hadrianus* sp.

Testudo undabuna Loomis, 1909
nomen invalidum
(junior synonym of *Oligopherus laticuneus*
[Cope, 1873a])

Taxonomic history. *Testudo undabuna* Loomis, 1909 (new species); *Gopherus undabuna* Williams 1950b (new combination); *Geochelone undabuna* Auffenberg 1964b (new combination); *Stylemys undabunus* Crumly 1994 (new combination; unjustified emendation).

Type material. ACM 2007 (holotype), a carapace (Loomis 1909, fig. 9).

Type locality. Muddy Creek, Laramie County, Wyoming, USA (Loomis 1909); Upper Harrison beds, Arikarean NALMA, late

Rupelian–Burdigalian, early Miocene (Auffenberg 1974; Woodburne 2004).

Comments. *Testudo undabuna* is based on a carapace from the early Miocene of Wyoming (Loomis 1909). The same locality also yielded the type of *Gopherus brevisternus*, which is distinct from *Testudo undabuna* in the presence of an octagonal neural II (Loomis 1909), instead of hexagonal neurals I and II, and a quadrangular neural III. This neural pattern is also found in *Oligopherus laticuneus* from the early and middle Oligocene of Colorado and Wyoming. Franz (2014) listed *Testudo undabuna* as an unresolved *Gopherus* taxon, but I here synonymize it with *Oligopherus laticuneus*. This implies an extensive ghost lineage that crossed the late Oligocene. See also *Oligopherus laticuneus* for further information.

Testudo undata Cope, 1875b
nomen dubium

Taxonomic history. *Lestudo undata* Cope, 1875b (new species; incorrectly spelled genus name); *Xerobates undata* Gilbert 1898 (new combination); *Geochelone undata* Auffenberg 1963 (new combination).

Type material. USNM 2126 (holotype), posterior peripherals and pygal (Cope 1875b, pl. 67; Hay 1908, fig. 573).

Type locality. Near San Ildefonso Pueblo, Santa Fé County, New Mexico, USA (Cope 1875b); Santa Fe marl series, Barstovian NALMA, middle Miocene (Auffenberg 1974; USNM database).

Comments. *Testudo undata* is based on fragmentary carapacial remains from the Miocene of New Mexico (Cope 1875b), in particular several medium-sized posterior peripherals and an associated pygal. These remains are insufficient to diagnose a valid taxon. As such, *Testudo undata* is herein considered to be a nomen dubium. Gilbert (1898) provisionally referred skull material to this taxon but, given the lack of comparable elements with the type material of *Testudo undata*, it is not possible to confirm this identification. Hay (1899a) referred the skull to a new species, *Testudo gilbertii* (see *Hesperotestudo gilbertii* above).

Testudo vaga Hay, 1908
nomen invalidum
(junior synonym of *Gopherus edae* [Hay, 1907])

Taxonomic history. *Testudo vaga* Hay, 1908 (new species); *Gopherus vaga* Williams 1950b (new combination); *Gopherus vagus* Auffenberg 1974 (justified emendation).

Type material. AMNH 1327 (holotype), a shell (Hay 1908; figs. 539–547, pl. 19.5).

Type locality. Near Laramie Peak, Albany County, Wyoming, USA (Hay 1908); Deep River beds, Barstovian NALMA, Langhian–Serravallian, middle Miocene (Auffenberg 1974).

Comments. see *Gopherus edae* above.

Testudo wilsoni Milstead, 1956
nomen invalidum
(junior synonym of *Hesperotestudo turgida*
[Cope, 1892a])

Taxonomic history. *Testudo wilsoni* Milstead, 1956 (new species); *Geochelone (Hesperotestudo) wilsoni* Auffenberg 1962b (new combination).

Type material. TMM 933–3585 (holotype), a shell (Auffenberg 1963, fig. 30).

Type locality. Friesenhahn Cave, Bexar County, Texas, USA (Milstead 1956); Rancholabrean NALMA, Ionian–Tarantian, Pleistocene (Auffenberg 1974; Woodburne 2004).

Comments. See comments in *Hesperotestudo turgida* above.

Toxaspis anguillulatus Cope, 1899
nomen invalidum
(junior synonym of *Terrapene eurypygia*
[Cope, 1869–70])

Taxonomic history. *Toxaspis anguillulatus* Cope, 1899 (new species); *Terrapene eurypygia* = *Toxaspis anguillulata* Hay 1908 (junior synonym, mandatory change); *Terrapene carolina carolina* = *Cistudo eurypygia* = *Testudo munda* = *Toxaspis anguillulatus* TEWG 2015 (junior synonymy).

Type material. ANSP 155 (holotype), a partial carapace (Cope 1899, pl. 14.1; Hay 1908, fig. 469).

Type locality. Port Kennedy Cave, Montgomery County, Pennsylvania, USA (Cope 1899); Irvingtonian NALMA, Calabrian–Ionian, Pleistocene (Woodburne 2004).

Comments. See *Terrapene eurypygia*.

Trachemys delicata Hay, 1916a
nomen dubium

Taxonomic history. *Trachemys delicata* Hay, 1916a (new species); *Pseudemys delicata* Kuhn 1964 (new combination); *Chrysemys scripta petrolei* = *Trachemys bisornata* = *Trachemys delicata* = *Trachemys euglypha* = *Trachemys sculpta* = *Trachemys trulla* Weaver and Robertson 1967 (junior synonymy); *Trachemys scripta scripta* = *Emys euglypha* = *Trachemys delicata* = *Trachemys sculpta* TEWG 2015 (junior synonymy).

Type material. USNM 8823 (formerly FGS 3738; holotype), a costal plate (Hay 1916a, pl. 7.1).

Type locality. Near Labelle, Lee County, Florida, USA (Hay 1916a); possibly Pliocene (Hay 1916a).

Comments. The type material of *Trachemys delicata* consists of a costal plate that was collected in Neogene deposits of uncertain age in Florida (Hay 1916a). Hay (1916a) used a more delicate

sculpturing as compared with *Trachemys scripta* to diagnose this taxon, but I find this characteristic to be insufficient to diagnose a valid taxon. I therefore here consider *Trachemys delicata* to be a nomen dubium.

Trachemys jarmani Hay, 1908
nomen dubium

Taxonomic history. *Trachemys jarmani* Hay, 1908 (new species); *Pseudemys jarmani* Kuhn 1964 (new combination); *Pseudemys nelsoni* = *Trachemys jarmani* TEWG 2015 (junior synonymy)

Type material. USNM 16671 (holotype), a nuchal plate (Hay 1908, pl. 45.10).

Type locality. Peace River, Florida, USA; Pliocene (Hay 1908).

Comments. *Trachemys jarmani* is based on a nuchal from the Pliocene of Florida (Hay 1908) that has a long and narrow cervical scute and that was laterally covered by pleural I. Hay (1908) noted that the nuchal is peculiar in having an anteriorly convex posterior border and in being shortened. The posterior extension of the nuchal therefore appears to be missing. Hay (1908) suspected that this morphology hints at the presence of broad neurals, which would define this taxon. Personal observations of this specimen confirm that the posterior margin is an intact sutural surface, rather than a broken area. However, the possibility of a plate anomaly cannot be excluded. In addition to the nuchal, Hay (1908) reported two partial costal plates. Rose and Weaver (1966) referred the nuchal of this taxon to the extant *Deirochelys reticularia*, but I find the available evidence insufficient and therefore consider *Trachemys jarmani* to be a nomen dubium.

Trachemys nuchocharinata Hay, 1916a
nomen dubium

Taxonomic history. *Trachemys nuchocharinata* Hay, 1916a (new species); *Pseudemys nuchocharinata* Kuhn 1964 (new combination); *Terrapene carolina bauri* = *Terrapene innoxia* = *Trachemys nuchocharinata* = *Terrapene singletoni* TEWG 2015 (junior synonymy).

Type material. USNM 8830 (formerly FGS 4437; holotype), a partial nuchal (Hay 1916a, pl. 6, fig. 5).

Type locality. Intercostal Waterway, 32 km miles north of St. Augustine, St. John's County, Florida, USA; Pleistocene (Hay 1916a).

Comments. *Trachemys nuchocharinata* is based on a partial nuchal from the Pleistocene of Florida that was diagnosed by the presence of a narrow cervical and a lateral covering by pleural I, combined with the presence of a median keel (Hay 1916a). Auffenberg (1958) noted that this nuchal is similar to that of *Terrapene carolina*, an opinion followed by Rose and Weaver (1966). Although this view is likely correct, the preserved information does not allow supporting the validity of a distinct species. As such, *Trachemys nuchocharinata* is herein considered to be a nomen dubium.

Trachemys trulla Hay, 1908
nomen dubium

Taxonomic history. *Trachemys trulla* Hay, 1908 (new species); *Pseudemys trulla* Kuhn 1964 (new combination); *Chrysemys scripta petrolei* = *Trachemys bisornata* = *Trachemys delicata* = *Trachemys euglypha* = *Trachemys sculpta* = *Trachemys trulla* Weaver and Robertson 1967 (junior synonymy); *Trachemys scripta elegans* = *Emys petrolei* = *Pseudemys bisornatus* = *Trachemys trulla* TEWG 2015 (junior synonymy).

Type material. AMNH 3934 (holotype), isolated plastral fragments (Hay 1908, fig. 453, pl. 56.2–6).

Type locality. Hardin County, Texas, USA (Hay 1908); Pleistocene (Hay 1908).

Comments. The type material of *Trachemys trulla* consists of isolated fragments from the Pleistocene of Texas that allow for the reconstruction of the plastron (Hay 1908). Among other characters, the plastron shows a well-rounded anterior lobe, an entoplastron covered by the gulars but not by the pectorals, placement of the pectoro-abdominal sulcus anterior to the hyohyoplastral suture, and a small anal notch. Hay (1908) already noted that the plastral morphology is similar to extant members of *Trachemys* but established a new taxon on minute differences to the shape of gularo-humeral sulcus and the outline of the anterior lobe. In my opinion, however, these characters are subject to variation and not sufficient to establish a separate taxon. As such, *Trachemys trulla* is herein considered herein to be a nomen dubium.

Xerobates cyclopygius Cope, 1878
nomen invalidum
(junior synonym of *Hesperotestudo orthopygia*
[Cope, 1878])

Taxonomic history. *Xerobates cyclopygius* Cope, 1878 (new species); *Testudo cyclopygia* Hay 1899a (new combination; mandatory change); *Testudo orthopygia* = *Caryoderma snovianum* = *Xerobates cyclopygius* Hay 1908 (junior synonymy).

Type material. AMNH 1322–1324 (holotype), shell fragments (Hay 1908, pl. 19.6–7).

Type locality. Decatur County, Kansas, USA (Cope 1878); Ogallala Formation, Barstovian–Hemphillian NALMA, middle–late Miocene (Ludvigson et al. 2009).

Comments. See *Hesperotestudo orthopygia*.

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Appendix 1 Institutional Abbreviations

ACM	Beneski Museum of Natural History, Amherst College, Amherst, Massachusetts, USA
AMNH	American Museum of Natural History, New York, New York, USA
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
BAMZ	Bermuda Aquarium, Natural History Museum and Zoo, Bermuda
BNM	Bahamas National Museum, The Bahamas
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
CMM	Calvert Marine Museum, Solomons, Maryland, USA
CMN	Canadian Museum of Nature, Ottawa, Canada
FGS	Florida State Geological Survey, Tallahassee, Florida, USA
IGM	Museo de Paleontología, Universidad Nacional Autónoma de México, Mexico City, Mexico
KU	University of Kansas Museum of Natural History, Lawrence, Kansas, USA
LACM	Los Angeles County Museum, Los Angeles, California, USA
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, USA

MNCR	National Museum of Costa Rica, San José, Costa Rica	<i>Eupachemys</i> Leidy, 1877 (type species: <i>Eupachemys obtusa</i> Leidy, 1877)
MNHNSD	Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic	<i>Floridemys</i> Williams, 1950b (type species: <i>Bystra nanus</i> Hay, 1916a)
MSU	Michigan State University, East Lansing, Michigan, USA	<i>Hadrianus</i> Cope, 1871b (type species: <i>Testudo corsoni</i> Leidy, 1871b)
NHMUK	The Natural History Museum, London, UK	<i>Hesperotestudo</i> Williams, 1950b (type species: <i>Testudo osborniana</i> Hay, 1908)
OMNH	Oklahoma Museum of Natural History, Norman, Oklahoma, USA	<i>Hybemys</i> Leidy, 1871a (type species: <i>Hybemys arenarius</i> Leidy, 1871a)
PPHM	Panhandle Plains Historical Museum, Canyon, Texas, USA	<i>Monachelys</i> Williams, 1952 (type species: <i>Testudo monensis</i> Williams, 1952)
TMM	Texas Memorial Museum, Austin, Texas, USA	<i>Notomorpha</i> Cope, 1872 (type species: <i>Notomorpha testudinea</i> Cope, 1872)
UCMP	University of California Museum of Paleontology, Berkeley, California, USA	<i>Oligopherus</i> Hutchison 1996 (type species: <i>Testudo latiduncus</i> Cope, 1873a)
UF	University of Florida, Gainesville, Florida, USA	<i>Palaeotheca</i> Cope, 1871a (type species: <i>Palaeotheca polycypha</i> Cope, 1871a)
UMMP	University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA	<i>Pseudograptemys</i> Hutchison 1996 (type species: <i>Chrysemys inornata</i> Loomis, 1904)
UNSM	University of Nebraska State Museum, Lincoln, Nebraska, USA	<i>Stylemys</i> Leidy, 1851a (type species: <i>Stylemys nebrascensis</i> Leidy, 1851a)
USNM	United States National Museum of Natural History, Washington DC, USA	<i>Toxaspis</i> Cope, 1899 (type species: <i>Toxaspis anguillulata</i> Cope, 1899)
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA	<i>Psilosemys</i> Hutchison, 2013 (type species: <i>Psilosemys wyomingensis</i> Hutchison, 2013)

Appendix 2 Named North American Fossil Pan-Testudinoid Genera

- Achilemys* Hay, 1908 (type species: “*Hadrianus*” *allabiatatus* Cope, 1871c)
- Acherontemys* Hay, 1899b (type species: *Acherontemys heckmani* Hay, 1899b)
- Bridgeremys* Hutchison, 2006 (type species: *Echmatemys pusilla* Hay, 1908)
- Bysmachelys* Johnston, 1937 (type species: *Bysmachelys canyonensis* Johnston, 1937)
- Bystra* Hay, 1916a (type species: *Bystra nanus* Hay, 1916a)
- Cardichelyon* Hutchison, 2013 (type species: *Cardichelyon rogerwoodi* Hutchison, 2013)
- Caryoderma* Cope, 1886 (type species: *Caryoderma snovianum* Cope, 1886)
- Caudochelys* Auffenberg, 1963 (type species: *Testudo crassiscutata* Leidy, 1889b)
- Cymatholcus* Clark, 1932 (type species: *Cymatholcus longus* Clark, 1932, herein considered as a junior synonym of “*Hadrianus*” *schucherti* Hay, 1899b)
- Echmatemys* Hay, 1906a (type species: *Emys septaria* Cope, 1873b)

Appendix 3 Biogeographical Summary of North American Fossil *Pan-Testudinoidea*

Numbers in brackets reference Figures 5 and 6. *Abbreviation*: TL, Type locality.

Canada

- [1] Early Eocene, Wasatchian–Bridgerian NALMA, Ypresian–Lutetian; Ellesmere Island; *Pan-Emydidae* indet.; *Pan-Geoemydidae* indet.; *Pan-Testudinidae* indet. (Emydidae and Testudinidae indet. of Estes and Hutchison 1980; Bataguridae, Emydidae, Platysternidae, and Testudinidae indet. of Eberle and Greenwood 2012)
- [2] Middle Eocene, Uintan NALMA, Lutetian; Saskatchewan; *Pan-Emydidae* indet., *Pan-Testudinidae* indet. (Emydidae and Testudinidae indet. of Hutchison and Storer 1998)
- [3] Late Eocene–Oligocene, Chadronian–early Arikarean NALMA, Priabonian–Chattian; Saskatchewan; *Pan-Testudinidae* indet. (*Testudo exornata* of Lambe 1906) (Cope 1891; Lambe 1906; Storer 2002; Holman 1972b)
- [4] Middle Miocene, Barstovian NALMA, Langhian–Serravallian; Saskatchewan; *Testudinidae* indet. (Holman 1971a; Holman and Tokaryk 1987).

Costa Rica

- [5] Late Oligocene–early Miocene; Cartago Province; “*Testudo*” *costarricensis* (TL) (Segura Paguaga 1944)
- [6] Late Pleistocene; Guanacaste Province; *Pan-Testudinoidea* indet. (including *Rhinoclemmys nicoyana* of Acuña-Mesén and Laurito-Mora 1996)

El Salvador

- [7] Early–middle Pleistocene; San Salvador Department; *Emydidae* indet., *Testudinidae* indet. (*Hesperotestudo crassiscutata* of Cisneros 2005)
- [8] Late Pleistocene; San Miguel Department; *Testudinidae* indet. (*Geochelone* sp. of Webb and Perrigo 1984)

Honduras

- [9] Late Miocene; Gracias fauna (various localities), Gracias Formation, Lempira Department; *Emydidae* indet., *Testudinidae* indet. (*Rhinoclemmys* sp. and *Geochelone* sp. of Webb and Perrigo 1984)
- [10] Late Pleistocene; Orillas del Humuya; *Emydidae* indet. (*Rhinoclemmys* sp. of Webb and Perrigo 1984)

Mexico

- [11] Late Eocene; Oaxaca; *Pan-Testudinidae* indet. (aff. *Hadrianus* sp. and *Stylomys* sp. of Jiménez-Hidalgo et al. 2015)
- [12] Late Miocene; San Luis Potosí; *Pan-Testudinoidea* indet. (cf. *Trachemys* sp. of Ferrusquía-Villafranca et al. 2014)
- [13] Late Miocene, Hemphillian NALMA; Hidalgo; *Testudinoidea* indet. (*Pseudemys* sp. of Castillo-Cerón et al. 1996)
- [14] Pliocene; Goleta Formation, Michoacán de Ocampo; *Testudinidae* indet. (*Testudo* sp. of Brattstrom 1955)
- [15] Early Pliocene, late Hemphillian NALMA; Chihuahua; *Gopherus* sp. (Brattstrom 1961)
- [16] Pliocene–Pleistocene; Baja California Sur; *Testudinidae* indet. (*Geochelone* sp. of Flores-Villela 1993)
- [17] Pliocene–Pleistocene; Baja California Sur; *Testudinidae* indet. (*Geochelone* sp. of Flores-Villela 1993)
- [18] Pliocene–Pleistocene, late Blancan–Irvingtonian NALMA; Aguascalientes; *Gopherus auffenbergi* Mooser 1972 (TL) (including *Gopherus pargensis* of Mooser 1980), *Gopherus flavomarginatus* (Mooser 1972, 1980)
- [19] Pleistocene; Puebla; *Trachemys* sp. (Herrera-Flores 2009)
- [20] Late Pleistocene, Rancholabrean NALMA; Tamaulipas; *Gopherus donlatoi* (TL) (Reynoso and Montellano-Ballesteros 2004)
- [21] Late Pleistocene; Oaxaca; *Gopherus* sp. (Cruz et al. 2009)

Nicaragua

- [22] Late Pleistocene; Estelí Department; *Testudinoidea* indet. (Page 1978; Lucas et al. 2008).

Panama

- [23] Early to middle Miocene, Burdigalian; west side of the Centenario Bridge, in the Panama Canal Basin; *Rhinoclemmys panamaensis* (TL), *Rhinoclemmys* sp., *Testudinidae* indet. (Cadena et al. 2012)

United States of America

- [24] Late Paleocene, early Tiffanian NALMA, Selandian; California; *Pan-Testudinoidea* indet. (*Emydidae* indet. of McKenna et al. 1987; Woodburne 2004)
- [25] Late Paleocene, Tiffanian–Clarkforkian NALMA, Selandian–Thanetian; Big Horn Basin, Wyoming; *Cardichelyon rogerwoodi* (TL); *Pan-Emydidae* indet. (Estes 1975; Hutchison 2013)
- [26] Late Paleocene, Clarkforkian NALMA, Thanetian; Green River Basin, Wyoming; *Cardichelyon rogerwoodi* (Holroyd and Rankin 2014)
- [27] Late Paleocene–early Eocene, Clarkforkian–Wasatchian NALMA, Thanetian–Ypresian; Piceance Basin, Colorado; *Echmatemys* sp.; *Pan-Testudinoidea* indet. (*Cardichelyon* cf. *Cardichelyon rogerwoodi* and *Echmatemys* cf. *Echmatemys lativertebrales* of Lichtig and Lucas 2015b)
- [28] Early Eocene, Wasatchian NALMA, Ypresian; Big Horn Basin, Wyoming; *Cardichelyon rogerwoodi*, *Echmatemys* sp., *Hadrianus majusculus*, *Psilosemys wyomingensis* (TL), *Pan-Emydidae* indet. (Cope 1881; Gilmore 1920; Hutchison 1980, 2013; Holroyd et al. 2001)
- [29] Early Eocene, Wasatchian NALMA, Ypresian; San Juan Basin, New Mexico; *Hadrianus majusculus* (TL), “*Echmatemys*” *cibollensis* (TL), *Echmatemys lativertebrales* (TL) (Cope 1875a, 1877a; Hay 1904; Lichtig and Lucas 2015d)
- [30] Early Eocene, Wasatchian NALMA, Ypresian; Green River Basin, Wyoming; *Pan-Testudinoidea* indet. (*Notomorpha testudinea* of Cope 1872 in part)
- [31] Early Eocene, Wasatchian NALMA, Ypresian; Washakie Basin, Wyoming; *Pan-Testudinoidea* indet. (*Emys pachylomus* Hay 1908), *Echmatemys lativertebrales* (*Emys rivalis* of Hay 1909)
- [32] Early Eocene, late Wasatchian–early Bridgerian NALMA, Ypresian; Raton Basin, Colorado; *Echmatemys* sp., *Hadrianus corsoni* (Lichtig and Lucas 2015c)
- [33] Early–middle Eocene, Bridgerian NALMA, Ypresian–Lutetian; Oregon; *Pan-Testudinidae* indet. (= *Hadrianus* sp. of Hanson 1996)
- [34] Early–middle Eocene, Bridgerian NALMA, Ypresian–Lutetian; Green River Basin, Wyoming; *Bridgeremys pusilla* (TL) (including *Clemmys morrisiae* of Hay 1908), *Echmatemys arethusa* (TL), *Echmatemys haydeni* (TL), *Echmatemys jeansi* (TL), *Echmatemys lativertebrales* (*Emys shaughnessiana* of Cope 1882), *Echmatemys naomi* (TL), *Echmatemys*

- stevensoniana* (TL) (including *Emys septaria* of Cope 1873b, *Echmatemys aegle* of Hay 1908, *Echmatemys cyane* of Hay 1908, and *Echmatemys ocyrrhoe* of Hay 1908), *Echmatemys wyomingensis* (TL) (including *Echmatemys uintensis* of Hay 1908, *Echmatemys pusilla* of Gilmore 1915), *Echmatemys* sp. (*Palaeotheca polycypha* Cope 1872), *Hadrianus corsoni* (TL) (including *Emys carteri* Leidy 1871c, *Testudo hadriana* Cope 1871a, *Hadrianus quadratus* Cope 1871b, and *Hadrianus octonaria* Cope 1871b), *Hadrianus* sp. (*Testudo uintensis* of Gilmore 1915), *Pan-Testudinoidea* indet. (*Emys latilabiata* Cope 1871c, *Emys euthmeta* of Hay 1908, *Hadrianus allabiatius* of Cope 1871c, *Hybemys arenarius* of Leidy 1871a, and *Palaeotheca terrestris* of Cope 1872) (Cope 1871a, 1871b, 1871c, 1872, 1873b, 1875a, 1882; Hay 1908, 1909; Gilmore 1915, 1945; Hutchison 2006, 2013; Leidy 1869, 1870a, 1870b, 1871c, 1873; Lichtig and Lucas 2015a; Osborn et al. 1878; West and Hutchison 1981)
- [35] Early–middle Eocene, Bridgerian NALMA, Ypresian–Priabonian; Alabama; *Pan-Emydidae* indet. (Holman and Case 1988)
- [36] Middle Eocene, late Bridgerian NALMA, Lutetian; Washington; *Acherontemys heckmani* (TL) (Hay 1899b)
- [37] Middle Eocene, Uintan NALMA, Lutetian; California; *Pan-Testudinidae* indet. (Golz and Lillegraven 1977)
- [38] Middle Eocene, Uintan NALMA, Lutetian; Uinta Basin, Utah; *Bridgeremys pusilla*, *Echmatemys callopyge* (TL), *Echmatemys lativertebralis* (including *Echmatemys douglassi* and *Echmatemys hollandi* of Gilmore 1915), *Echmatemys naomi* (including *Echmatemys obscura* of Gilmore 1915), *Echmatemys* sp. (*Echmatemys depressa* of Gilmore 1915), *Hadrianus corsoni* (including *Hadrianus tumidus* of Hay 1908 and *Hadrianus robustus* and *Hadrianus utahensis* of Gilmore 1915), *Hadrianus* sp. (Hay 1908; Gilmore 1915; Gunnell and Bartels 1999)
- [39] Middle Eocene, late Uintan NALMA, late Lutetian; Texas; *Pan-Testudinidae* indet. (= *Hadrianus* sp. of Westgate 1989)
- [40] Late Eocene, Duchesnean NALMA, Bartonian; Uinta Basin, Utah; *Cymatholcus schucherti* (*Cymatholcus longus* of Clark 1932)
- [41] Late Eocene, Duchesnean NALMA, Bartonian; Sevier Plateau, Utah; *Echmatemys* sp., *Pan-Geoemydidae* indet. (= *Rhinoclemmys* sp. of Eaton et al. 1999)
- [42] Late Eocene, Duchesnean NALMA, Bartonian; South Dakota; *Pan-Testudinoidea* indet. (= *Graptemys*? sp. of Bjork 1967)
- [43] Late Eocene, Duchesnean NALMA, Bartonian; Alabama; *Cymatholcus schucherti* (TL) (Hay 1899b)
- [44] Late Eocene, Chadronian NALMA, Priabonian; North Dakota; “*Trachemys*” *antiqua* (Hutchison 1996); *Pan-Testudinidae* indet. (= *Stylemys* sp. of Cope 1883)
- [45] Late Eocene, Chadronian NALMA, Priabonian; South Dakota; *Echmatemys lativertebralis* (including *Chrysemys inornata* of Loomis 1904 and *Graptemys cordifera* of Clark 1937), “*Trachemys*” *antiqua* (TL), “*Testudo*” *brontops* (TL) (Marsh 1890; Hay 1908; Clark 1937; Hutchison 1996)
- [46] Late Eocene, Chadronian NALMA, Priabonian; Georgia; *Pan-Testudinoidea* indet. (Parmley et al. 2006)
- [47] Late Eocene–early Oligocene, Chadronian–Orellan NALMA, Priabonian–early Rupelian; Colorado; *Oligopherus laticuneus* (TL); *Stylemys nebrascensis* (including *Testudo amphithorax* and *Testudo ligonius* Cope 1873a), “*Trachemys*” *antiqua*, *Pan-Testudinidae* indet. (*Testudo quadrata* of Cope 1884), *Pan-Testudinoidea* indet. (*Testudo culbratus* of Cope 1873a) (Cope 1873a, 1884; Hay 1908; Galbreath 1953; Hutchison 1996)
- [48] Early Oligocene, Orellan NALMA, early Rupelian; Wyoming; *Oligopherus laticuneus* (*Testudo praeextans* of Lambe 1913), *Stylemys nebrascensis*, *Pan-Testudinidae* indet. (Lambe 1913; Case 1925; Gilmore 1945, 1946)
- [49] Early Oligocene, Orellan NALMA, early Rupelian; Nebraska; *Oligopherus laticuneus*, *Stylemys nebrascensis*, “*Trachemys*” *antiqua* (Hay 1908; Hutchison 1996, Ehret 2007)
- [50] Early Oligocene, Orellan–Whitneyan NALMA, early Rupelian; South Dakota; *Oligopherus laticuneus* (*Testudo thomsoni* of Hay 1908), *Stylemys nebrascensis* (TL) (including *Emys culbertsonii* of Leidy 1852a, *Emys hemispherica* and *Testudo lata* of Leidy 1851b, *Emys oweni* of Leidy 1851c), “*Trachemys*” *antiqua* (Leidy 1851a, 1851b, 1851c, 1852a; Marsh 1890; Case 1919, 1936; Hutchison 1996; Boyd and Welsh 2014)
- [51] Early Oligocene, Whitneyan NALMA, mid Rupelian; Florida; *Pan-Testudinidae* indet., *Pan-Emydidae* indet. (= *Floridemys* sp. and *Pseudemys* sp. of Patton 1969)
- [52] Late Oligocene–early Miocene, Arikarean NALMA; Montana; *Stylemys inusitata* (*Testudo primaeva* of Oelrich 1950), *Pan-Testudinidae* indet. (*Testudo peragrans* of Hay 1907)
- [53] Late Oligocene, Arikarean-2 NALMA, Chattian; Oregon; *Stylemys capax* (TL) (including *Stylemys conspecta* of Hay 1908), *Stylemys nebrascensis*, *Stylemys* sp. (*Stylemys oregonensis* of Leidy 1871d), *Pan-Emydidae* indet. (*Clemmys saxea* of Hay 1903) (Cope 1884; Hay 1908; Brattstrom 1961)
- [54] Late Oligocene, early Arikarean NALMA; California; *Stylemys nebrascensis* (including *Gopherus neglectus* of Brattstrom 1961), *Pan-Testudinidae* indet. (Brattstrom 1961; Golz and Lillegraven 1977)
- [55] Late Oligocene, early Arikarean NALMA, Chattian; South Dakota; *Stylemys nebrascensis* (including *Testudo emiliae* Hay 1908)
- [56] Miocene; California; *Pan-Testudinidae* indet. (*Stylemys calaverensis* of Sinclair 1903)

- [57] Early Miocene, late Arikareean NALMA, Aquitanian–Burdigalian; Wyoming; *Gopherus brevisternus* (TL) (Loomis 1909), *Oligopherus laticuneus* (*Testudo undabuna* of Loomis 1909)
- [58] Early Miocene, late Arikareean–Hemingfordian NALMA, Burdigalian–Langhian; Nebraska; *Hesperotestudo osborniana* (*Testudo arenivaga* of Hay 1906b; *Testudo angusticeps* of Matthew 1924), *Gopherus edae* (TL) (*Testudo hollandi* of Hay 1906b), *Pan-Testudinidae* indet. (*Testudo niobrarensis* of Leidy 1858)
- [59] Early–middle Miocene, Arikareean–late Barstovian NALMAs, Aquitanian–Serravallian; Cherry County, Nebraska; *Chrysemys* cf. *picta*, *Glyptemys valentinensis* (TL), *Hesperotestudo orthopygia*, *Emydidae* indet., *Pan-Testudinoidea* indet. (including *Emydoidea hutchisoni* of Holman 1995) (Holman and Sullivan 1981; Holman 1981, 1995, 2002a, 2002b; Holman and Fritz 2001)
- [60] Early Miocene, late Arikareean NALMA, Aquitanian–Burdigalian; Brewster County, Texas; *Hesperotestudo* sp. (= ?*Geochelone* sp. of Stevens et al. 1969)
- [61] Early Miocene, late Arikareean NALMA, Aquitanian–Burdigalian; Newton County, Texas; *Emydidae* indet., *Hesperotestudo* sp. (Albright 1994), *Hesperotestudo williamsi* (Auffenberg 1964b) (TL)
- [62] Early Miocene, late Arikareean NALMA, Aquitanian–Burdigalian; Florida; *Hesperotestudo* sp., *Pseudemys* sp. (Olsen 1964)
- [63] Early Miocene, middle Burdigalian; Delaware; *Hesperotestudo* sp., *Chrysemys* sp. (Weems and George 2013)
- [64] Early–middle Miocene, Burdigalian–Serravallian; Virginia; *Trachemys* sp., *Pan-Emydidae* indet. (*Chrysemys isoni* Weems and George 2013)
- [65] Early Miocene, Hemingfordian NALMA, Burdigalian; Nebraska; *Testudinidae* indet. (Yatkola 1976)
- [66] Early Miocene, Hemingfordian NALMA, Burdigalian; Florida; *Hesperotestudo* sp. (*Testudo tedwhitei* of Williams 1953)
- [67] Middle Miocene, Barstovian NALMA, Langhian–Serravallian; Broadwater County, Montana; *Stylemys inusitata* (TL) (Hay 1906b)
- [68] Middle Miocene, Barstovian NALMA, Langhian–Serravallian; Meagher County, Montana; *Hesperotestudo osborniana* (*Testudo farrri* of Hay 1908), *Stylemys inusitata* (*Testudo copei* of Koerner 1940)
- [69] Middle Miocene, Barstovian NALMA, Langhian–Serravallian; Fresno County, California; *Hesperotestudo* sp. (Kelly and Stewart 2008)
- [70] Middle Miocene, Barstovian NALMA; Langhian–Serravallian; Kern County, California; *Gopherus depressus* (TL), *Gopherus mohavensis* (Brattstrom 1961)
- [71] Middle Miocene, Barstovian NALMA, Langhian–Serravallian; San Bernardino County, California; *Gopherus mohavensis* (Merriam 1919) (TL), *Gopherus depressus* (*Gopherus dehiscus* of Des Lauriers 1965), *Gopherus* sp. (*Testudo milleri* Brattstrom 1961)
- [72] Middle Miocene, Barstovian NALMA, Langhian–Serravallian; Wyoming; *Gopherus edae* (*Testudo vaga* of Hay 1908)
- [73] Middle Miocene, late Barstovian NALMA, Serravallian; Webster County, Nebraska; *Hesperotestudo* cf. *orthopygia*, *Hesperotestudo* sp. “*Terrapene*” *corneri* (TL), *Emydidae* indet. (Holman and Corner 1985; Holman and Fritz 2005)
- [74] Middle Miocene, Barstovian NALMA, Langhian–Serravallian; Colorado; *Gopherus edae* (*Testudo pansa* of Hay 1908)
- [75] Middle Miocene, Barstovian NALMA, Langhian–Serravallian; New Mexico; *Testudinidae* indet. (*Testudo klettiana* and *Testudo undata* of Cope 1875b)
- [76] Middle Miocene, Barstovian NALMA, Langhian–Serravallian; South Dakota; *Testudinidae* indet. (Green 1965)
- [77] Middle–late Miocene, Langhian–Serravallian, Barstovian NALMA; Boyd County, Nebraska; *Chrysemys* sp., *Clemmys* sp., *Hesperotestudo orthopygia*, *Terrapene* sp., *Terrapene* cf. *ornata*, *Emydidae* indet. (= ?*Chrysemys* cf. *picta* of Holman 1976a), *Pan-Testudinoidea* indet. (Holman 1973a, 1976a, 1987b, 2002a, 2002b; Holman and Fritz 2005)
- [78] Middle Miocene, Barstovian NALMA, Langhian–Serravallian; Oklahoma; *Hesperotestudo* sp., *Gopherus* sp., *Terrapene* sp., *Emydidae* indet., *Testudinidae* indet., (Czaplewski 2008)
- [79] Middle Miocene; Barstovian NALMA, Langhian–Serravallian; Maryland; *Hesperotestudo ducateli* (TL), *Pan-Testudinoidea* indet. (*Floridemys hurdi* of Weems and George 2013) (Collins and Lynn 1936; Weems and George 2013)
- [80] Middle Miocene, middle Barstovian–Clarendonian NALMA, Langhian–Serravallian; Nebraska; *Chrysemys* sp., cf. *Clemmys* sp., *Hesperotestudo orthopygia* (*Geochelone nordensis* of Holman 1973b), *Hesperotestudo* sp., *Trachemys* sp., *Pan-Emydidae* indet., *Pan-Testudinoidea* indet. (Holman 1973b, 1976a, 1977, 1996, 2002a, 2002b; Holman and Fritz 2001; Holman and Parmley 2005; Joeckel 1988; Voorhies et al. 1987)
- [81] Middle Miocene–early Pliocene, Barstovian–Blancan NALMA; Phillips County, Kansas; *Hesperotestudo gilbertii* (TL), *Hesperotestudo orthopygia* (TL) (including *Caryoderma snovianum* of Cope 1886 and *Xerobates cyclopygius* of Cope 1878), *Hesperotestudo* sp., *Terrapene ornata* (*Terrapene longinsulæ* of Hay 1909), *Terrapene* cf. *carolina*, *Pan-Emydidae* indet. (including *Pseudemys hillii* of Hay 1908) (Gilbert 1898; Hay 1899a, 1909; Holman 1975, Holman and Fritz 2005)
- [82] Late Miocene, Clarendonian NALMA, Serravallian–Tortonian; Washington; *Emydidae* indet. (Martin and Pagnac 2009)
- [83] Middle Miocene, Clarendonian NALMA, Serravallian–Tortonian; Oklahoma; *Emydidae* indet. (*Chrysemys limnodytes* of Galbreath 1948a)

- [84] Late Miocene, Clarendonian–Hemphillian NALMA, Serravallian–Messinian; Florida: “*Deirochelys*” *carri* (TL), *Floridemys nana* (TL), *Hesperotestudo turgida* (*Geochelone alleni* of Auffenberg 1966), *Pseudemys carri* (TL), *Pseudemys williamsi* (TL) (Auffenberg 1963; Hay 1916a; Jackson 1978; Rose and Weaver 1966)
- [85] Late Miocene, early Hemphillian NALMA, Tortonian–Messinian; Oregon; *Testudinoidea* indet. (*Clemmys hesperia* of Hay 1903)
- [86] Late Miocene, Hemphillian NALMA, Tortonian–Messinian; Malheur County, Oregon; *Emys marmorata* (including *Clemmys owyheensis* of Brattstrom and Sturn 1959)
- [87] Late Miocene, Hemphillian NALMA, Tortonian–Messinian; Montana; *Hesperotestudo osborniana* (*Testudo impensa* of Hay 1908)
- [88] Late Miocene, Hemphillian NALMA, Tortonian–Messinian; Colorado; *Hesperotestudo osborniana* (TL) (Hay 1905)
- [89] Late Miocene–early Pliocene, Hemphillian NALMA; Oklahoma; *Hesperotestudo turgida* (Oelrich 1957), *Hesperotestudo* sp., *Terrapene parornata* (TL), *Testudinidae* indet. (Hibbard 1954; Milstead 1967; Joyce et al. 2012)
- [90] Late Miocene–early Pliocene; Oregon; cf. *Hesperotestudo orthopygia* (Fry 1973)
- [91] Late Miocene–early Pliocene; California; *Hesperotestudo orthopygia* (Biewer et al. 2016)
- [92] late Miocene–Pleistocene, Hemphillian–Rancholabrean NALMA; Peace Creek Fauna, Florida; *Hesperotestudo crassiscutata* (TL), *Terrapene putnami*, *Emydidae* indet. (including *Chrysemys inflata* of Weaver and Robertson 1967), *Testudinidae* indet. (including *Testudo hayi* of Sellards 1916 and *Testudo louisekressmani* of Wark 1929) (Leidy 1889b; Sellards 1916; Wark 1929; Auffenberg 1958, 2001)
- [93] Pliocene, Blancan NALMA; Idaho; “*Pseudemys*” *idahoensis* (TL), *Clemmys owyheensis* (Gilmore 1933; Zug 1969)
- [94] Pliocene, Blancan NALMA; Tehama County, California; *Testudinidae* indet. (= *Testudo* sp. of van der Hoof 1933)
- [95] Pliocene, Blancan NALMA; Kings and Los Angeles County, California; *Hesperotestudo* sp., *Clemmys marmorata* (Miller and Downs 1974; Boessenecker and Poust 2015)
- [96] Pliocene; Riverside County, California; *Clemmys marmorata* (Brattstrom and Sturn 1959)
- [97] Pliocene, Blancan NALMA; Arizona; *Emydidae* indet., *Hesperotestudo* sp. (Czaplewski 1987)
- [98] Pliocene, Blancan NALMA; Deaf Smith County, Texas; *Testudinidae* indet. (Norton 1954)
- [99] Pliocene, Blancan NALMA; Florida; *Pan-Testudinoidea* indet. (*Trachemys delicata* of Hay 1916a)
- [100] Pliocene, Blancan NALMA; Florida: “*Chrysemys*” *platymarginata* (TL), *Hesperotestudo crassiscutata* (Auffenberg 1963; Gilmore 1933)
- [101] Early Pliocene, Blancan NALMA; South Dakota; *Pan-Testudinidae* indet. (Green 1956)
- [102] Late Pliocene, Blancan NALMA; Dickens County, Texas; *Hesperotestudo turgida* (TL) (Cope 1892a)
- [103] Late Pliocene, Blancan NALMA; Crosby County, Texas; *Gopherus hexagonatus* (*Testudo campester* of Hay 1908), *Hesperotestudo turgida*, *Testudinidae* indet. (*Testudo pertenuis* of Cope 1892b) (Cope 1892a, 1893; Hay 1908)
- [104] Late Pliocene, late Blancan NALMA; Hedspeth County, Texas; *Gopherus hexagonatus* (*Gopherus huecoensis* of Strain 1966)
- [105] Pliocene–Pleistocene; Kern County, California; *Clemmys marmorata*, *Gopherus agassizi* (Brattstrom 1953; Brattstrom and Sturn 1959)
- [106] Pliocene–Pleistocene, Blancan–Rancholabrean NALMA; Seward County, Kansas; *Chrysemys picta*, *Emydoidea blandingii*, *Gopherus* sp., *Hesperotestudo turgida* (*Testudo riggsi* of Hibbard 1944), *Terrapene ornata* (Hibbard 1944; Oelrich 1957; Milstead 1967; Preston 1971, 1979)
- [107] Pliocene–Pleistocene, Blancan–Rancholabrean NALMA; Meade County, Kansas; *Chrysemys picta*, *Emydoidea blandingii* (*Emys twentei* of Taylor 1943), *Hesperotestudo orthopygia* (including *Testudo rexroadensis* of Oelrich 1952), *Hesperotestudo* sp., *Testudinidae* indet. (*Testudo equicomis* of Hay 1917), *Terrapene ornata*, *Terrapene putnami* (*Terrapene llanensis* of Oelrich 1953), *Pseudemys scripta* (Taylor 1943; Oelrich 1952; Hibbard 1951; Hibbard and Taylor 1960; Milstead 1967; Preston 1979; Holman 1986b, 1987a)
- [108] Pliocene–Pleistocene; Peace Creek Fauna, Florida; *Deirochelys reticularia*, *Deirochelys* sp. (*Deirochelys floridana* of Hay 1908), *Gopherus polyphemus*, *Gopherus* sp., *Hesperotestudo crassiscutata*, *Hesperotestudo turgida*, *Hesperotestudo mlynarskii*, *Pseudemys* sp., *Terrapene putnami* (TL), *Terrapene carolina*, *Trachemys scripta*, *Trachemys sculpta* (TL), *Trachemys* sp., *Testudinoidea* indet. (including *Emys euglypha* of Leidy 1889a and *Pseudemys extincta* and *Trachemys jarmani* of Hay 1908) (Hay 1908, 1916a, 1923a; Gilmore 1930; Auffenberg 1958, 2001; Webb and Tessman 1968; Jackson 1978; Meylan 1995; Franz and Quitmyer 2005)
- [109] Pleistocene; Michigan; *Chrysemys* sp. (Wilson 1966, 1967)
- [110] Pleistocene, Irvingtonian NALMA, Calabrian–Ionian; Pennsylvania; *Clemmys insculpta*, *Emydoidea blandingii*, *Terrapene eurypygia* (type material of *Toxaspis anguillulata* of Cope 1899), *Pan-Testudinoidea* indet. (*Clemmys percrassa* of Cope 1899) (Cope 1899; Hay 1902; Parris and Daeschler 1995)
- [111] Pleistocene; Ashley River, South Carolina; *Gopherus polyphemus*, *Hesperotestudo crassiscutata*, *Terrapene carolina*, *Trachemys scripta*, *Malaclemmys terrapin*, *Pseudemys nelsoni*, *Pseudemys* cf. *floridana*, *Pan-Testudinoidea* indet. (*Eupachemys obtusus* of Leidy 1877) (Dobie and Jackson 1979; Franz and Quitmyer 2005)

- [112] Pleistocene, Irvingtonian NALMA, Calabrian-Ionian; Sheridan County, Nebraska; "*Chrysemys*" *timida* (TL) (Hay 1908)
- [113] Pleistocene, Irvingtonian NALMA; Oxford Neck MD, Talbot County, Maryland; *Terrapene eurypygia* (Cope 1869, 1870) (TL)
- [114] Pleistocene; Brown County, Kansas; *Chrysemys picta*, *Gopherus hexagonatus*, *Hesperotestudo turgida* (*Geochelone oelrichi* of Holman 1972a), *Hesperotestudo* sp., *Pseudemys* sp. (Hibbard 1960; Auffenberg 1962b; Holman 1972a)
- [115] Pleistocene, Rancholabrean NALMA; Harper County, Oklahoma; *Chrysemys picta*, *Hesperotestudo* sp., *Pseudemys* sp., *Terrapene ornata*, *Testudinoidea* indet. (*Chrysemys hibbardi* of Preston 1979) (Galbreath 1948b; Preston 1979; Akersten and McDonald 1991)
- [116] Pleistocene; Miller County, Arkansas; *Terrapene putnami* (Davis et al. 2000)
- [117] Pleistocene; Hamblen County, Tennessee; *Pan-Testudinoidea* indet. (*Testudo munda* of Hay 1921)
- [118] Pleistocene; Hardeman and Foard County, Texas; *Hesperotestudo* sp., *Pseudemys* sp., *Terrapene* sp. (Holman 1964; Preston 1979)
- [119] Pleistocene; Denton County, Texas; *Hesperotestudo* sp. *Terrapene carolina*, *Terrapene ornata*, *Pseudemys scripta* (Holman 1963)
- [120] Pleistocene; Dallas County, Texas; *Graptemys geographica*, *Hesperotestudo* cf. *crassiscutata*, *Terrapene carolina*, *Testudinidae* indet. (Hay 1924; Slaughter 1966)
- [121] Pleistocene; McLennan and Milam County, Texas; *Chrysemys picta*, *Graptemys pseudogeographica*, *Terrapene carolina*, *Testudinidae* indet. (Hay 1924; Preston 1979)
- [122] Pleistocene; Bell County, Texas; *Testudinidae* indet. (*Testudo francisi* of Hay 1923b) (Hay 1923b, 1924)
- [123] Pleistocene; Brazos and Washington County, Texas; *Hesperotestudo crassiscutata*, *Terrapene ornata*, *Testudinidae* indet. (*Testudo annae* of Hay 1923b), (Hay 1916b, 1923b, 1924)
- [124] Pleistocene; Hardin County, Texas; *Emydidae* indet. (*Trachemys trulla* of Hay, 1908), *Testudinidae* indet., *Pan-Testudinoidea* indet. (*Emys petrolei* of Leidy 1868a) (Leidy 1868a, Hay 1908, 1924)
- [125] Pleistocene; Washington County, Texas; *Chrysemys belli*, *Terrapene ornata*, *Terrapene* sp. (*Terrapene impressa* of Hay 1924), *Testudinidae* indet. (Hay 1924)
- [126] Pleistocene; Travis County, Texas; *Terrapene ornata* (*Terrapene whitneyi* of Hay 1916b)
- [127] Pleistocene, Rancholabrean NALMA; Bexar County, Texas; *Hesperotestudo turgida* (*Testudo wilsoni* of Milstead 1956), *Terrapene ornata*, *Terrapene putnami* (Milstead 1956), *Terrapene* sp. (*Terrapene bulverda* of Hay 1921) (Hay 1921; Milstead 1956)
- [128] Pleistocene; Atascosa County, Texas; *Terrapene* sp. (*Cistudo marnochii* of Cope 1877b), *Pan-Emydidae* indet. (*Pseudemys bisornata* of Cope 1877b), *Testudinidae* indet. (*Testudo atascosae* of Hay 1902)
- [129] Pleistocene; Chatham County, Georgia; *Terrapene putnami* (including *Terrapene canaliculata* of Hay 1907), *Hesperotestudo* sp. (Hay 1907; Auffenberg 1958; Hulbert and Pratt 1998)
- [130] Pleistocene, Rancholabrean NALMA; Florida: *Deirochelys* sp., *Gopherus polyphemus*, *Hesperotestudo crassiscutata*, *Hesperotestudo turgida* (including *Testudo incisa* of Hay 1916a and *Geochelone mlynarskii* of Auffenberg 1988), *Pseudemys* sp., *Terrapene carolina* (including *Terrapene formosa* of Hay 1916a), *Terrapene putnami*, *Emydidae* indet. (*Clemmys hutchensorum* of Bourque 2016), *Testudinidae* indet. (including *Testudo ocalana* of Hay 1916a), *Pan-Testudinoidea* indet. (including *Testudo distans* of Hay 1916a) (Auffenberg 1958, 1963, 2001; Bourque 2016; Hay 1916a; Holman 1958, 1959b; Jackson 1978; Franz and Quitmyer 2005; Martin 1978)
- [131] Pleistocene; St. Johns County, Florida; *Terrapene putnami* (Auffenberg 1958), *Pan-Testudinoidea* indet. (= type material of *Trachemys nuchocarinata* Hay 1916a)
- [132] Late Pleistocene, Rancholabrean NALMA; Orange County, Florida; *Clemmys* sp., *Gopherus* sp., *Terrapene carolina*, *Terrapene putnami*, *Terrapene singletoni* (TL), *Trachemys sculpta* (Hay 1916a; Gilmore 1927, 1930; Auffenberg 1958; Long 1993; Franz and Quitmyer 2005)
- [133] Pleistocene; St. Lucie and Indian River County, Florida; *Deirochelys* sp. (Hay 1916a; Gilmore 1927; Loomis 1927; Auffenberg 1958; Jackson 1978), *Hesperotestudo crassiscutata* (*Testudo sellardsi* Hay 1916a), *Terrapene carolina* (*Terrapene innoxia* of Hay 1916a), *Terrapene putnami* (including *Terrapene antipex* of Hay 1916a), *Pan-Emydidae* indet. (*Pseudemys floridana persimilis* of Hay 1916a), *Testudinidae* indet. (including *Gopherus praecedens* and *Testudo luciae* of Hay 1916a)
- [134] Pleistocene, Rancholabrean NALMA; Williston and Waccasassa River, Devil's Den Sinkhole, Mixson's Bone Bed, Levy County, Suwannee River, boundary between Gilchrist and Dixie Counties, Columbia, Florida; *Terrapene carolina*, *Terrapene putnami*, *Pseudemys scripta*, *Pseudemys floridana*, *Deirochelys reticularia*, *Graptemys kernerii* (TL), *Hesperotestudo turgida*, *Hesperotestudo crassiscutata*, *Gopherus polyphemus*, *Pan-Testudinoidea* indet. (= type material of *Pseudemys caelata* Hay 1908) (Hay 1908; Auffenberg 1958; Holman 1959a, 1978; Jackson 1975, 1978; Ehret and Bourque 2011)
- [135] Early Pleistocene; White Bluffs, Washington; *Clemmys marmorata* (Brattstrom and Sturn 1959)
- [136] Early Pleistocene; Knox County, Nebraska; *Chrysemys picta*, *Emydoidea blandingi*, *Gopherus polyphemus*, *Hesperotestudo turgida*, *Hesperotestudo* sp., *Pseudemys scripta bisornata*, *Terrapene* sp., *Emydidae* indet. (Parmley 1988, 1992; Rodgers 1984)

- [137] Middle-late Pleistocene; San Bernardino County, California; *Gopherus agassizii*, *Hesperotestudo* sp. (Brattstrom 1961; Wagner and Prothero 2001)
- [138] Late Pleistocene; Nuckolls County, Nebraska; *Chrysemys picta*, *Hesperotestudo* sp. (Preston 1979)
- [139] Early Pleistocene; Cochise County, Arizona; *Terrapene* cf. *ornata*, *Gopherus* sp. (Gazin 1942; Brattstrom 1955; Moodie and van Devender 1978)
- [140] Late Pliocene, Blancan III NALMA; Randall County, Texas; *Gopherus hexagonatus* (*Bysmachelys canyonensis* of Johnston 1937), *Hesperotestudo turgida* (*Geochelone johnstoni* of Auffenberg 1962b)
- [141] Middle Pleistocene, Irvingtonian NALMA; Jewell County, Kansas; *Chrysemys picta*, *Hesperotestudo* sp., *Trachemys scripta* (Rodgers 1982)
- [142] Middle Pleistocene, Calabrian, Irvingtonian NALMA; Briscoe County, Texas; *Testudinidae* indet. (*Testudo laticaudata* of Cope 1893), *Gopherus hexagonatus* (TL) (Cope 1884, 1893; Hay 1924)
- [143] Late Pleistocene; Shasta County, California; *Clemmys marmorata*, *Testudinidae* indet. (Sinclair 1904; Brattstrom 1955)
- [144] Late Pleistocene; Irvingtonian NALMA, San Francisco Bay, California; *Emydoidea* indet. (Savage 1951)
- [145] Late Pleistocene; Santa Barbara County, California; *Clemmys marmorata* (Brattstrom 1955)
- [146] Late Pleistocene; lower Grand Canyon, Arizona; *Gopherus agassizii* (van Devender et al. 1977; Mead 1981a, b)
- [147] Late Pleistocene; Ellsworth, Rezabek, and Lincoln County, Kansas; *Chrysemys picta*, *Gopherus* sp. (Preston 1979)
- [148] Late Pleistocene; McPherson County, Kansas; *Pseudemys* sp. (Holman 1971b)
- [149] Late Pleistocene; Rice County, Kansas; *Chrysemys picta* (Preston 1979)
- [150] Late Pleistocene; Boone County, Missouri; *Emydoidea* sp., *Terrapene* sp. (Preston 1979)
- [151] Late Pleistocene; Moniteau County, Missouri; *Emydoidea* sp., *Terrapene* sp. (Preston 1979)
- [152] Late Pleistocene; Franklin County, Missouri; *Terrapene* sp. (Preston 1979)
- [153] Late Pleistocene; Hickory County, Missouri; *Chrysemys* sp., *Terrapene putnami* (Moodie and van Devender 1977)
- [154] Late Pleistocene; Perry County, Missouri; *Terrapene* sp. (Preston 1979)
- [155] Late Pleistocene; Montgomery County, Illinois; *Hesperotestudo crassiscutata* (King and Saunders 1986)
- [156] Late Pleistocene; Roosevelt County, New Mexico; *Hesperotestudo turgida*, *Terrapene ornata ornata* (Milstead 1967; Moodie and van Devender 1979; Stock and Bode 1936)
- [157] Late Pleistocene; Eddy County, New Mexico; *Gopherus agassizii* (van Devender et al. 1976), *Hesperotestudo turgida* (= *Geochelone wilsoni* of Moodie and van Devender 1979)
- [158] Late Pleistocene; Doña Ana County, New Mexico; *Gopherus agassizii*, *Gopherus* sp. (Brattstrom 1961; van Devender et al. 1976)
- [159] Late Pleistocene; Caddo County, Oklahoma; *Hesperotestudo turgida* (= *Geochelone wilsoni* of Moodie and van Devender 1979)
- [160] Late Pleistocene; San Patricio and Wheeler County, Texas; *Gopherus hexagonatus* (Auffenberg 1962a)
- [161] Late Pleistocene; Lubbock County, Texas; *Hesperotestudo turgida* (= *Geochelone wilsoni* of Moodie and van Devender 1979), *Terrapene carolina* (Holman 1969)
- [162] Late Pleistocene, Rancholabrean NALMA; Schulze Cave, Edwards County, Texas; *Hesperotestudo turgida*, *Terrapene ornata* (Parmley 1986)
- [163] Late Pleistocene; Harris County, Texas; *Chrysemys scripta*, *Hesperotestudo* sp., *Terrapene carolina trianguis* (McClure and Milstead 1967; Preston 1979)
- [164] Late Pleistocene; Bee County, Texas; *Graptemys pseudogeographica*, *Hesperotestudo turgida* (= *Geochelone wilsoni* of Moodie and van Devender 1979), *Hesperotestudo* sp. *Terrapene carolina* (Preston 1979; Moodie and van Devender 1979)
- [165] Late Pleistocene; Maury County, Tennessee; *Clemmys insculpta* (Parmalee and Klippel 1981)
- [166] Late Pleistocene; Clay and Lowndes County, Mississippi; *Emydoidea blandingii*, *Gopherus* sp. *Hesperotestudo* cf. *crassiscutata* (Jackson and Kaye 1974a, b, 1975; Franz and Quitmyer 2005)
- [167] Late Pleistocene; near Columbus, Mississippi; *Terrapene putnami* (Jackson and Kaye 1974a)
- [168] Late Pleistocene; Colbert County, Alabama; *Chrysemys picta*, *Graptemys geographica*, *Pseudemys concinna*, *Pseudemys* sp. (Holman et al. 1990)
- [169] Late Pleistocene; Bartow County, Georgia; *Clemmys insculpta* (Holman 1976b)
- [170] Late Pleistocene; Horry County, South Carolina; *Gopherus polyphemus* (Franz and Quitmyer 2005)
- [171] Latest Pleistocene; Hancock County, Indiana; *Chrysemys picta* (Holman 1992)
- [172] Latest Pleistocene; Daviess County, Indiana; *Chrysemys picta*, *Emydoidea blandingii*, *Graptemys* sp., *Pseudemys* sp. (Holman 1992)
- [173] Latest Pleistocene-Holocene; Darke County, Ohio; *Chrysemys picta* (Holman 1986a, 1992)

West Indies

- [174] Pleistocene; New Provenance, Bahamas; *Testudinidae* indet. (*Geochelone* sp. of Auffenberg 1967)
- [175] Pleistocene; Moore's Island and Abaco, Bahamas; *Testudinidae* indet. (Franz and Franz 2009)
- [176] Pleistocene; Barbados; *Testudinidae* indet. (*Geochelone* sp. of Ray 1964)
- [177] Pleistocene; San Salvador (= Watling's Island), Bahamas; *Emydoidea* indet., *Testudinidae* indet. (Olson et al. 1990)

- [178] Pleistocene; Matanzas Province, Cuba; *Chelonoidis cubensis* (Williams 1950b)
- [179] Pleistocene; Cienfuegos Province, Cuba; *Chelonoidis cubensis* (TL); *Emydidae* indet. (Leidy 1868b; Williams 1950b)
- [180] Pleistocene; Oriente Province, Cuba; *Emydidae* indet. (Williams 1950b)
- [181] Pleistocene; Saint Elizabeth Parish, Jamaica; *Testudinoidea* indet. (Anthony 1920; Williams 1950b)
- [182] Pleistocene; Navassa Island; *Pan-Testudinidae* indet., *Pan-Emydidae* indet. (*Emydidae* indet. of Auffenberg 1967)
- [183] Pleistocene; Sombrero Island, Anguilla; *Pan-Testudinidae* indet. (including the type material of *Emys sombrerensis* of Leidy 1868b)
- [184] Pleistocene; Anguilla; *Chelonoidis* sp. (cf. *Geochelone carbonaria* of Lazell 1993)
- [185] Pleistocene; Bahamas; *Pan-Testudinidae* indet. (Auffenberg 1967)
- [186] Pleistocene; Curaçao; *Testudinidae* indet. (*Geochelone* sp. of Hooijer 1963)
- [187] Late Pleistocene; Smith's Parrish, Bermuda; *Hesperotestudo bermudae* (TL) (Meylan and Sterrer 2000; Olson and Meylan 2009)
- [188] Late Pleistocene; Andros, Bahamas; *Testudinidae* indet. (Auffenberg 1967)
- [189] Late Pleistocene–Holocene; Havana Province, Cuba; *Chelonoidis cubensis* (Karl 1995)
- [190] Holocene; Great Abaco Island, Bahamas; *Chelonoidis alburyorum* (TL) (Franz and Franz 2009)
- [191] Holocene; San Cristobal Province, Dominican Republic; *Chelonoidis* sp. (Franz and Woods 1983; Turvey et al. 2017)
- [192] Late Pleistocene–Holocene; Pedernales Province, Dominican Republic; *Chelonoidis* sp. (type material of *Chelonoidis marcanoi* Turvey et al. 2017)
- [193] Holocene; Mona Island, Puerto Rico; “*Chelonoidis*” *monensis* (TL) (Williams 1952)
- [194] Late Holocene; Middle Caicos Island, Turks and Caicos Islands; *Chelonoidis* sp. (Franz et al. 2001)
- [195] Late Holocene; Grand Turk Island, Turks and Caicos Islands; *Chelonoidis* sp. (Franz et al. 2001)
- “*Chrysemys*” *platymarginata* Weaver and Robertson, 1967
- “*Chrysemys*” *timida* Hay, 1908
- “*Deirochelys*” *carri* Jackson, 1978
- Glyptemys valentinensis* Holman and Fritz, 2001
- Graptemys kernerii* Ehret and Bourque, 2011
- Pseudemys* Gray, 1856
- Pseudemys carri* (Rose and Weaver, 1966)
- Pseudemys williamsi* (Rose and Weaver, 1966)
- “*Pseudemys*” *idahoensis* Gilmore, 1933
- Terrapene* Merrem, 1820
- “*Terrapene*” *corneri* Holman and Fritz, 2005
- Terrapene eurypygia* (Cope, 1869–70)
- Terrapene parornata* Joyce et al., 2012
- Terrapene putnami* Hay, 1906a
- Terrapene singletoni* Gilmore, 1927
- “*Trachemys*” *sculpta* Hay, 1908
- “*Trachemys*” *antiqua* Clark, 1937
- Pan-Geoemydidae* Joyce et al., 2004
- Geoemydidae* Theobald, 1868
- Bridgeremys pusilla* (Hay, 1908)
- Echmatemys* Hay, 1906a
- Echmatemys arethusa* Hay, 1908
- Echmatemys callopyge* Hay, 1908
- “*Echmatemys*” *cibollensis* (Cope, 1877a)
- Echmatemys haydeni* (Leidy, 1870b)
- Echmatemys jeansi* (Leidy, 1870b)
- Echmatemys lativertebralis* (Cope, 1877a)
- Echmatemys naomi* Hay, 1908
- Echmatemys stevensoniana* (Leidy, 1870a)
- Echmatemys wyomingensis* (Leidy, 1869)
- Rhinoclemmys panamaensis* Cadena et al., 2012
- Pan-Testudinidae* Joyce et al., 2004
- Cymatholcus schucherti* (Hay, 1899a)
- Hadrianus* Cope, 1871b
- Hadrianus corsoni* (Leidy, 1871b)
- Hadrianus majusculus* Hay, 1904
- Oligopherus laticuneus* (Cope, 1873a)
- “*Testudo*” *costarricensis* Segura Paguaga, 1944
- Testudinidae* Batch, 1788
- Chelonoidis* Fitzinger, 1835
- Chelonoidis alburyorum* Franz and Franz, 2009
- Chelonoidis cubensis* (Leidy, 1868b)
- “*Chelonoidis*” *monensis* (Williams, 1952)
- Floridemys nana* (Hay, 1916a)
- Gopherus* Rafinesque, 1832
- Gopherus auffenbergi* Mooser, 1972
- Gopherus brevisternus* (Loomis, 1909)
- Gopherus depressus* Brattstrom, 1961
- Gopherus donlaloii* Reynoso and Montellano-Ballesteros, 2004
- Gopherus edae* (Hay, 1907)
- Gopherus hexagonatus* (Cope, 1893)
- Gopherus mohavensis* (Merriam, 1919)
- Hesperotestudo* Williams, 1950b
- Hesperotestudo bermudae* Meylan and Sterrer, 2000
- Hesperotestudo crassiscutata* (Leidy, 1889b)
- Hesperotestudo ducatelii* (Collins and Lynn, 1936)
- Hesperotestudo gilbertii* (Hay, 1899a)

Appendix 4

Hierarchical Taxonomy of North American Fossil *Pan-Testudinoidea*

Pan-Testudinoidea Joyce et al., 2004

Cardichelyon rogerwoodi Hutchison, 2013

Testudinoidea Fitzinger, 1826

Pan-Emydidae Joyce et al., 2004

Acherontemys heckmani Hay, 1899b

Psilosemys wyomingensis Hutchison, 2013

Emydidae Bell, 1825

Hesperotestudo orthopygia (Cope, 1878)
Hesperotestudo osborniana (Hay, 1905)
Hesperotestudo turgida (Cope, 1892a)
Hesperotestudo williamsi (Auffenberg, 1964b)
Stylemys Leidy, 1851a
Stylemys capax Hay, 1908
Stylemys inusitata (Hay, 1906b)
Stylemys nebrascensis Leidy, 1851a
 "Testudo" *brontops* Marsh, 1890

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Editor's note: This article is intended to be included with others in a forthcoming book being coordinated by Walter G. Joyce to elucidate the fossil record of turtles. The individual articles that will form the components of this book are being published separately in the next several volumes of the *Bulletin of the Peabody Museum of Natural History*.