Published in "Bulletin of the Peabody Museum of Natural History 60(2): 129–155, 2019" which should be cited to refer to this work.

A Review of the Fossil Record of Nonbaenid Turtles of the Clade *Paracryptodira*

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ABSTRACT

The fossil record of nonbaenid paracryptodires ranges from the Late Jurassic (Kimmeridgian) to the Paleocene of North America and Europe only. Earlier remains may be present as early as the Middle Jurassic (Bathonian). Only a single dispersal event is documented between the two continents after their breakup during the Cretaceous in the form of the appearance of the *Compsemys* lineage in the Paleocene of France. Nonbaenid paracryptodires were restricted to freshwater aquatic environments but display adaptations to diverse feeding strategies consistent with generalist, gape-and-suction, and hypercarnivorous feeding. Current phylogenies recognize two species-rich subclades within *Paracryptodira*, *Baenidae* and *Pleurosternidae*, which jointly form the clade *Baenoidea*. A taxonomic review of nonbaenid paracryptodires concludes that of 34 named taxa, 11 are nomina valida, 15 are nomina invalida, and 8 are nomina dubia.

KEYWORDS

Phylogeny, Biogeography, Paleoecology, *Paracryptodira*, *Baenoidea*, *Pleurosternidae*

Introduction

The term *Paracryptodira* is herein used to refer to the most inclusive clade of turtles that includes the Eocene baenid *Baena arenosa* Leidy, 1870 and the Late Jurassic pleurosternid *Pleurosternon bullockii* Owen, 1842, but no extant turtle (Lyson and Joyce 2011). The name was originally introduced by Gaffney (1975) to unite all turtles that possess a foramen posterius canalis carotici interni located midway along the contact of the basisphenoid with the pterygoid. Although Evans and Kemp (1976) soon after questioned the utility of this character, as it reasonably may be interpreted as a symplesiomorphy, more recent analyses of turtle relationships that densely sample at the species level typically retrieve the group of turtles with the paracryptodiran condition as monophyletic (e.g., Joyce 2007; Lyson and Joyce 2011; Joyce et al. 2016). As it is somewhat difficult to rigorously differentiate paracryptodires from sympatric helochelydrids (see Joyce et al. [2011] compared with Joyce [2017]), future work will need to clarify if all or parts of the latter, at least as currently understood, are nested within the other. The fossil record of *Baenidae*, one of the primary clades of *Paracryptodira*, was previously summarized by Joyce and Lyson (2015). We therefore here summarize the fossil record of the remainder of the group.

The idea that European pleurosternids and North American baenids form a group had already been proposed by Dollo (1886), who united these turtles in his classification. This arrangement was soon after supported by Lydekker (1889a), who proposed the redundant names Amphichelydia and Pleurosternidae based on a series of characters that now must be viewed as plesiomorphic (Gaffney 1975). The grouping of Lydekker (1889a) does not fully correspond to the current understanding of *Paracryptodira*, however, as it included the stem pleurodire *Platychelys oberndorferi* Wagner, 1853 and the helochelydrid

Helochelys danubina Meyer, 1854. Over the course of the succeeding decades, the meanings of the names *Amphichelydia* and *Pleurosternidae* were further removed from the currently hypothesized content of *Paracryptodira*, as increasing numbers of stem turtles were united with the former (e.g., Williston 1925; Nopcsa 1928), while the latter was increasingly circumscribed to the exclusion of baenids (e.g., Baur 1891; Hay 1908b; Gilmore 1919; Williams 1950). Although Gaffney (1975) could have used either name for the clade of turtles he recognized, we here conform to his choice of the new name *Paracryptodira*, as this has been firmly entrenched in the literature in the last decades.

For institutional abbreviations, see Appendix 1. Named nonbaenid paracryptodiran genera are listed in Appendix 2.

Skeletal Morphology

Cranium

At present, the skull is only known for five nonbaenid paracryptodires: *Compsemys victa* from the Paleocene of Colorado, USA (see Lyson and Joyce 2011); *Dorsetochelys typocardium* from the Early Cretaceous of the United Kingdom (see *Dorsetochelys delairi* of Evans and Kemp 1976); *Pleurosternon bullockii* from the Early Cretaceous of the United Kingdom (see *Mesochelys durlstonensis* of Evans and Kemp 1975 and *Pleurosternon bullockii* of Sterli et al. 2010); *Glyptops ornatus* from the Late Jurassic of Wyoming, USA (see *Glyptops plicatulus* of Gaffney 1979); and *Uluops uluops* from the Late Jurassic of Wyoming, USA (Carpenter and Bakker 1990). A well-preserved skull represents the holotype of *Dorsetochelys buzzops* (Bakker 1998), but as this specimen was never figured (only idealized sketches are available) and is now lost, it is disregarded herein. Although the available nonbaenid paracryptodire skulls are relatively complete, most are either heavily crushed (e.g., *Dorsetochelys typocardium*, *Glyptops ornatus*, and *Mesochelys durlstonensis*) or poorly documented (e.g., *Dorsetochelys typocardium* and *Uluops uluops*). The only remaining skull, that of *Compsemys victa*, is highly apomorphic and not representative for the group. We therefore do not figure any material herein and keep our summary to a minimum based on the sources cited previously.

The skulls of nonbaenid paracryptodires generally show poorly developed lower and upper temporal fenestrae (fully absent in *Compsemys victa*), but they range from flat and elongate with dorsally oriented orbits (e.g., *Glyptops ornatus*), to short and high with dorsolaterally oriented orbits (e.g., *Uluops uluops*), to triangular and massive with laterally oriented orbits (e.g., *Compsemys victa*). All forms possess relatively large nasals with a midline contact, relatively small prefrontals that lack a midline contact, frontals that contribute to the orbits (absent in *Compsemys victa*), parietals that contact the squamosals (unclear in *Compsemys victa*), jugals that contribute to the orbits (absent in *Glyptops ornatus*), and open incisurae columella auris (superficially enclosed in *Compsemys victa*). The pterygoids have been reported as lacking a midline contact in *Glyptops ornatus* and *Pleurosternon bullockii*, but this is probably a preservational artifact, especially as a midline contact is clearly present in all taxa where this region is sufficiently preserved. The foramen posterius canalis carotici interni enters the skull midway along the contact of the pterygoid with the basisphenoid, but it is unclear if the palatal branch of the internal carotid is present, considering that it has recently been shown to be absent in some baenids (Lipka et al. 2006; Rollot et al. 2018) and that the internal anatomy of no skull has of yet been studied. The basicranial region resembles that of most turtles by having an elongate basisphenoid and broad pterygoids, with the exception of *Compsemys victa*, which displays an extremely shortened basisphenoid and narrow pterygoids.

Much variation is apparent in the palate of nonbaenid paracryptodires, which highlights likely differences in feeding ecology. In *Glyptops ornatus* and *Pleurosternon bullockii*, the labial ridges are low, and the triturating surfaces narrow. The labial ridges are higher and the triturating surfaces are expanded in *Dorsetochelys typocardium* and *Uluops uluops*, particularly through contributions from the palatines. In contrast, the labial ridges of *Compsemys victa* are marked by a tooth-like median projection, and the broad secondary palate elaborated by low accessory ridges is formed by the maxillae, palatines, and vomer. These morphologies are broadly consistent with gape-and-suction feeding, generalist feeding, and macrocarnivory, respectively (see "Paleoecology").

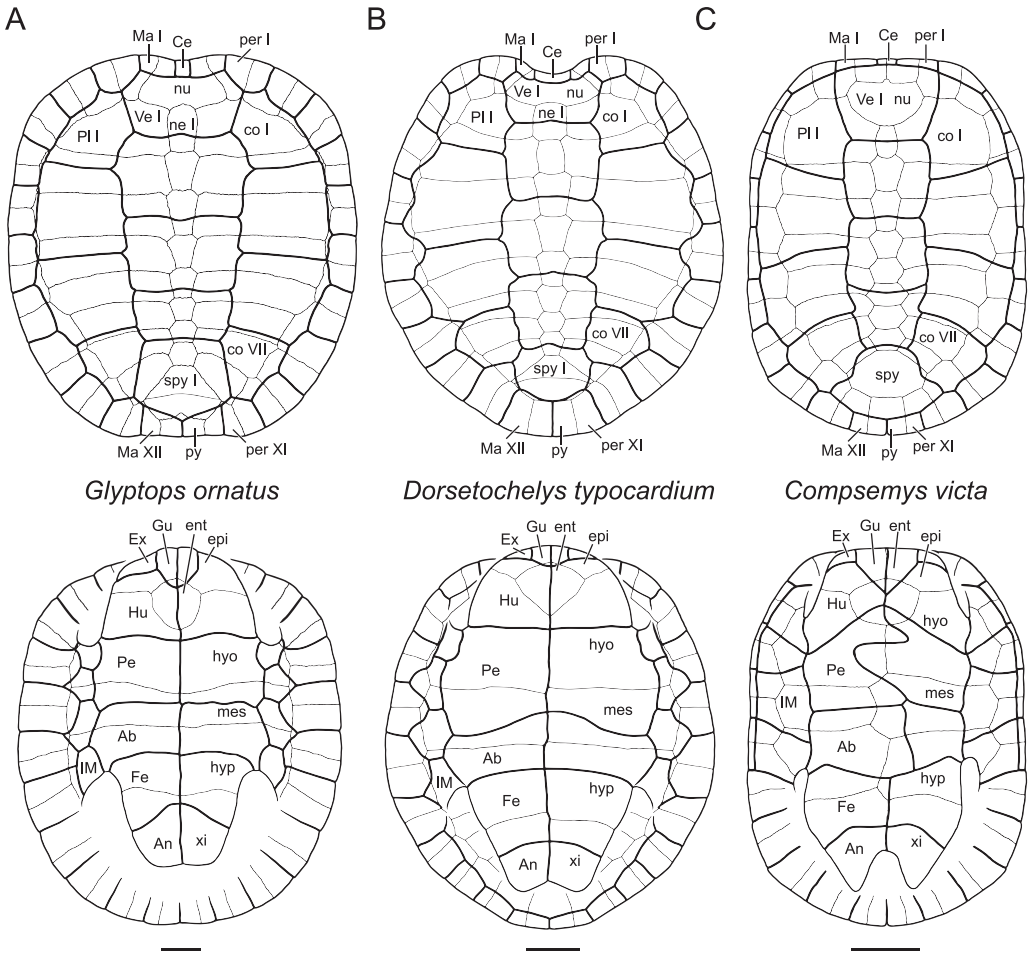

FIGURE 1. Shell morphology of basal *Paracryptodira* as exemplified by three species. **A,** *Glyptops ornatus* (redrawn from Gaffney 1979). **B,** *Dorsetochelys typocardium* (redrawn from Pérez-García 2014). **C,** *Compsemys victa* (redrawn from Gilmore 1919). *Abbreviations*: Ab, abdominal scute; An, anal scute; Ce, cervical scute; co, costal; ent, entoplastron; epi, epiplastron; Ex, extragular scute; Fe, femoral scute; Gu, gular scute; Hu, humeral scute; hyo, hyoplastron; hyp, hypoplastron; IM, inframarginal scute; Ma, marginal scute; mes, mesoplastron; ne, neural; nu, nuchal; Pe, pectoral scute; per, peripheral; Pl, pleural scute; py, pygal; spy, suprapygal; Ve, vertebral scute; xi, xiphiplastron. Scale bar approximates 5 cm.

Shell

Most of the herein recognized species are known from well-preserved shell material, but not all are sufficiently described. Informative descriptions are nevertheless available for *Compsemys victa* (Gilmore 1919; Figure 1C), *Dinochelys whitei* (Gaffney 1979), *Dorsetochelys typocardium* (Pérez-García 2014; Figure 1B), *Glyptops ornatus* (*Glyptops plicatulus* of Gaffney 1979; Figure 1A), *Pleurosternon bullockii* (Milner 2004), *Riodevemys inumbragigas* (Pérez-García, Royo-Torres, et al. 2015), *Selenemys lusitanica* (Pérez-García and Ortega 2011), and *Toremys cassiopeia* (Pérez-García, Espílez, et al. 2015).

The carapace of most nonbaenid paracryptodires resembles that of other basal turtles by consisting of a nuchal, 8 neurals that fully separate the costals along the midline, 8 pairs of costals, 11 pairs of peripherals, 2 suprapygals, and 1 pygal that are covered by 5 vertebrals, 4 pairs of pleurals, and 12 pairs of marginals (Figure 1). *Pleurosternon bullockii*, *Selenemys lusitanica*, and *Toremys cassiopeia* deviate from this pattern by lacking a cervical scute. *Compsemys victa* deviates

by consistently possessing only a single suprapygal. *Compsemys* spp. (Figure 1C) and *Selenemys lusitanica* deviate by showing a midline contact of peripheral I anterior to the nuchal. *Dorsetochelys typocardium* deviates by showing a distinct nuchal notch. The eighth neural regularly fuses with the first suprapygal, such as in *Compsemys russelli* and *Pleurosternon bullockii*.

The plastron of most nonbaenid paracryptodires consists of an entoplastron and pairs of epi-, hyo-, meso-, hypo-, and xiphiplastra covered by paired gulars, extragulars, humeral, pectorals, abdominals, femorals, and anals and four pairs of inframarginals. All bones and scutes have a straight midline contact with the exception of the extragulars and inframarginals (Figure 1). *Compsemys victa* (Figure 1C) and *Selenemys lusitanica* deviate from this pattern by having highly sinuous midline scute contacts; *Pleurosternon bullockii*, by possessing a single, median gular; and *Riodevemys inumbragigas*, by lacking a midline contact of the mesoplastra. The development of the plastral buttresses is only poorly documented.

Postcranium

Only small numbers of nonshell postcranials have been described for *Glyptops ornatus* (*Glyptops plicatulus* of Hay 1908b), *Riodevemys inumbragigas* (Pérez-García, Royo-Torres, et al. 2015), and *Toremys cassiopeia* (Pérez-García, Espílez, et al. 2015), but these remains are too fragmentary to allow drawing rigorous conclusions about the postcranial anatomy of these turtles.

Phylogenetic Relationships

The phylogenetic relationships of nonbaenid paracryptodires have only been explored in the more recent past. The global analysis of Joyce (2007) includes 11 paracryptodires, of which 6 are baenids and 5 are nonbaenids. The more narrowly focused analysis of paracryptodire relationships of Lyson and Joyce (2011), on the other hand, densely samples baenids but still only includes six nonbaenid species. The sample of nonbaenid species of the latter analysis was increased stepwise by Pérez-García and Ortega (2011), Pérez-García (2012), Pérez-García, Espílez, et al. (2015), and Pérez-García, Royo-Torres, et al. (2015) through the addition of European forms. The trees presented herein (Figures 2 and 3) adhere to the topology of Pérez-García, Royo-Torres, et al. (2015). All trees agree with each other by not supporting the historical dichotomy of paracryptodires into baenids and pleurosternids, but results are still too preliminary to allow drawing affirmative conclusions.

Paleoecology

Most nonbaenid paracryptodires have been collected from riverine and lacustrine sediments, and the group can therefore be reconstructed to have been freshwater aquatic. This conclusion is broadly consistent with the overall hydrodynamic shape of their shells, splayed femoral trochanters, at least as documented for *Glyptops ornatus* (*Glyptops plicatulus* of Hay 1908b) and *Toremys cassiopeia* (Pérez-García, Espílez, et al. 2015), and the aquatic feeding specializations apparent in the jaws (see following paragraph).

The significant amount of morphological variation apparent in the small set of available skulls (see "Skeletal Morphology") attests to much ecological plasticity within the group. The elongate skull with low labial margins of *Glyptops ornatus* and *Pleurosternon bullockii* is broadly consistent with gape-and-suction feeding (Pritchard 1984; Foth et al. 2017). The higher labial ridges and expanded triturating surfaces of *Dorsetochelys typocardium* and *Uluops uluops*, on the other hand, are consistent with dietary generalists (Foth et al. 2017). The massive skull of *Compsemys victa*, by contrast, is unique among turtles by being extremely thick boned, but its overall shape, in particular the toothlike median projection and reduced pterygoids, is highly reminiscent of the extant bigheaded turtle *Platysternon megacephalum* (Hutchison and Holroyd 2003) and suggests the lifestyle of a macrocarnivorous snapping turtle (Lyson and Joyce 2011; Foth et al. 2017).

Paleobiogeography

All know paracryptodires have been collected from continental sediments across North America and western Europe, supporting the notion that these landmasses once formed a faunal province to the exclusion with the rest of the world (Hay 1908b; Hirayama et al. 2000; Pérez-García, Royo-Torres, et al. 2015; Joyce et al. 2016; Figures 4 and 5). The oldest remains were historically known from the

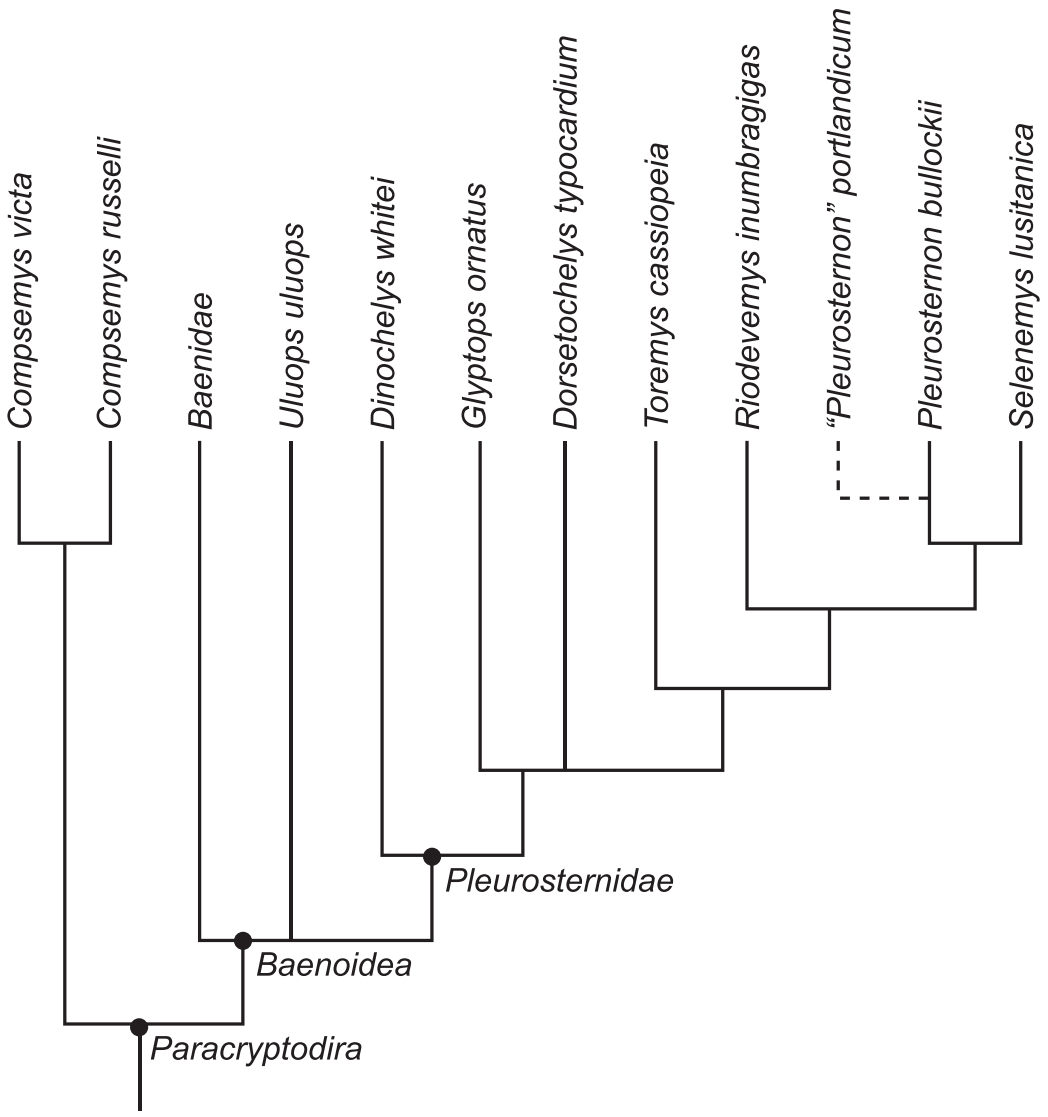

FIGURE 2. A phylogenetic hypothesis of valid nonbaenid paracryptodires (Pérez-García, Royo-Torres, et al. 2015). The dashed line highlights the manual insertion of "*Pleurosternon*" *portlandicum*.

Late Jurassic of North America and Europe (e.g., Lydekker 1889a; Marsh 1890), but histological analysis of fragments from the United Kingdom suggests that the group may reach back to the Middle Jurassic (Scheyer and Anquetin, 2008).

A series of valid species are herein recognized at the Jurassic-Cretaceous transition: *Dinochelys whitei* from the Late Jurassic (Tithonian) of Utah, USA (Gaffney 1979); *Dorsetochelys typocardium* from the Early Cretaceous (Berriasian) of the United Kingdom (Lydekker 1889a; Watson 1910b; Milner 2004; Pérez-García 2014); *Glyptops ornatus* from the Late Jurassic (Tithonian) of Utah and Wyoming, USA (Marsh 1890; Hay 1908b; Gilmore 1916b); *Pleurosternon bullockii* from the Early Cretaceous (Berriasian) of the United Kingdom (Owen 1842, 1853; Seeley 1869; Delair 1958; Milner 2004); "*Pleurosternon*" *portlandicum* from the Late Jurassic (Tithonian) of the United Kingdom (Lydekker 1889a); *Riodevemys inumbragigas* from the Late Jurassic (Tithonian) of Spain (Pérez-García, Royo-Torres, et al. 2015); *Selenemys lusitanica* from the Late Jurassic (Tithonian) of Portugal (Pérez-García and Ortega 2011); and

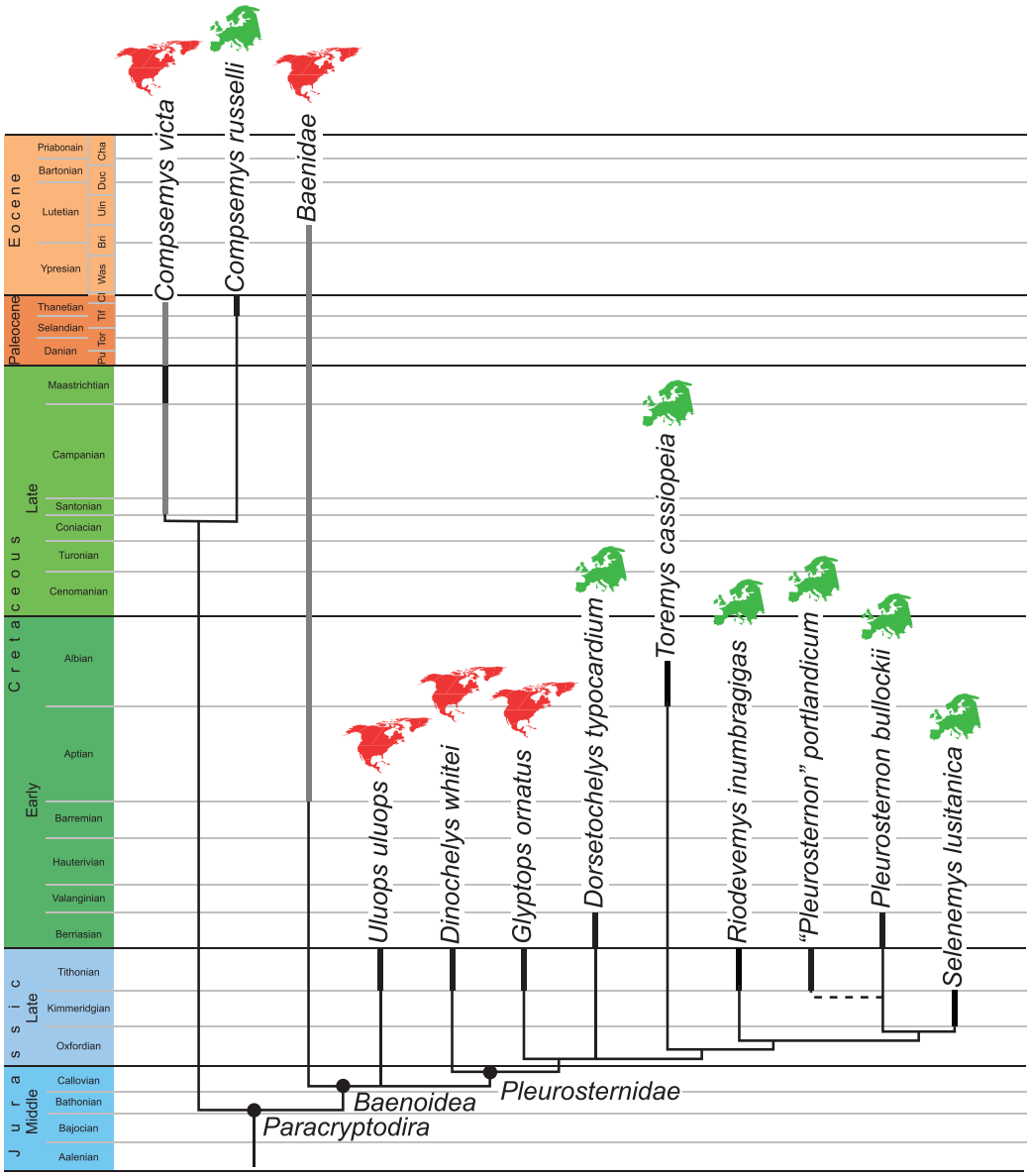

FIGURE 3. The stratigraphic and biogeographic distribution of valid nonbaenid paracryptodires. Black lines indicate temporal distribution based on type material. Gray lines indicate temporal distribution based on referred material.

Uluops uluops from the Late Jurassic (Tithonian) of Wyoming, USA (Carpenter and Bakker 1990).

A significant gap in the fossil record on both continents obscures the history of the group during the post-Berriasian Early Cretaceous after the separation of Europe and North America through the formation of the North Atlantic. Only fragments document the persistent presence of the group in the Early Cretaceous (Hauterivian–Barremian) of France and Spain, and later by remains of the pleurosternid *Toremys cassiopeia* from the late Early Cretaceous (Albian) of Spain (Pérez-García, Espílez, et al. 2015). In North America, the record continues in the late Early Cretaceous (Aptian/Albian [slashes used herein connote "or"]) in the form of the diverse clade *Baenidae*, which persists until the Eocene (see Joyce and Lyson [2015] for summary).

The *Compsemys* lineage is documented in the form of *Compsemys victa* from the Santonian to

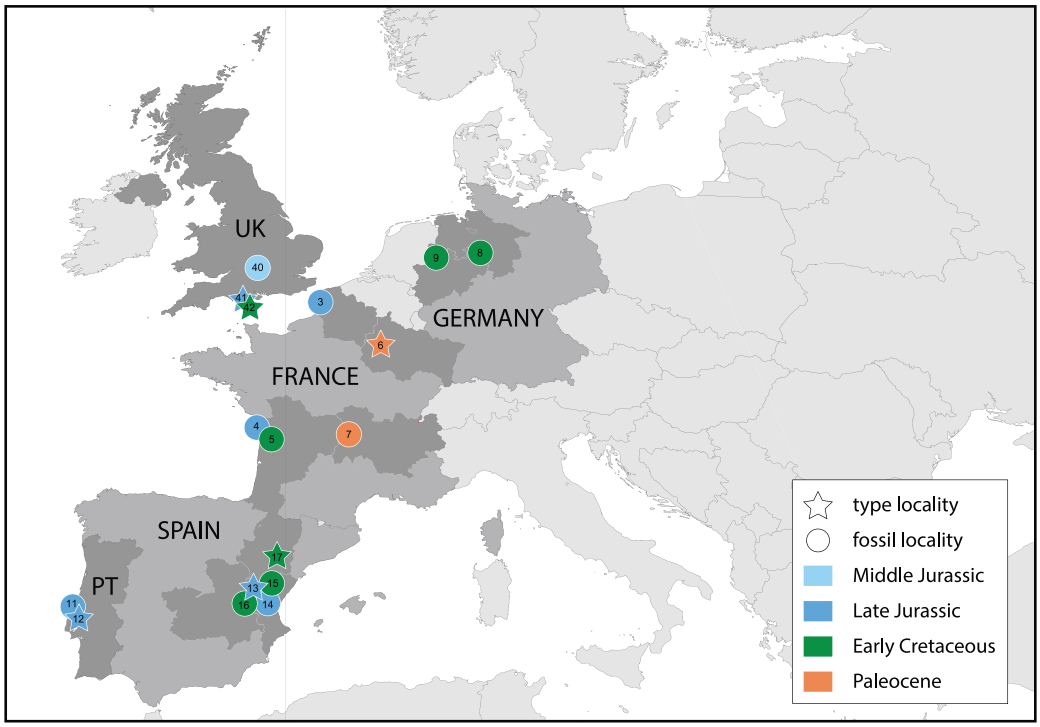

FIGURE 4. The geographic distribution of figured nonbaenid paracryptodires in Europe. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations:* PT, Portugal; UK, United Kingdom.

late Paleocene of Laramidia (see Lyson and Joyce [2011] for recent summary) and *Compsemys russelli* from the late Paleocene of France (Pérez-García 2012). As the lineage is more extensive in North America and otherwise absent from Europe, it seems that the *Compsemys russelli* lineage dispersed from North America to Europe during the early Paleocene via Greenland (Pérez-García 2012; Joyce et al. 2016). Current phylogenies place the *Compsemys* lineage outside of the clade formed by *Baenidae* and *Pleurosternidae* (Lyson and Joyce 2011; Pérez-García, Royo-Torres, et al. 2015). The group is therefore predicted to possess a ghost lineage that reaches back to the Late Jurassic.

Systematic Paleontology

Valid Taxa

See Appendix 4 for the hierarchical taxonomy of nonbaenid paracryptodires as described in this work.

Paracryptodira Gaffney, 1975

Phylogenetic definition. In accordance with Lyson and Joyce (2011), the name *Paracryptodira* is herein referred to the most inclusive clade containing *Pleurosternon bullockii* Owen, 1842 and *Baena arenosa* Leidy, 1870, but no species of extant turtle.

Diagnosis. Paracryptodires can be differentiated from all other turtles by symplesiomorphically showing a midline contact of the nasals and modest lower and upper temporal emarginations, lacking a midline contact of the prefrontals, and possessing large mesoplastra with a midline contact, and by apomorphically showing a dense surface texture that covers the skull and shell, a foramen posterius canalis carotici interni located halfway along contact between pterygoid and basisphenoid, and thickenings of the plastron medial to the bridges.

Compsemys Leidy, 1856

Type species. *Compsemys victa* Leidy, 1856.

Diagnosis. *Compsemys* can be diagnosed as a paracryptodire by the full list of characters provided for that clade above. *Compsemys* can be differentiated from all other paracryptodires by possessing greatly thickened skull bones; reduced temporal emarginations; expanded, rectangular quadratojugals; a postorbital contribution to the small, fully enclosed cavum

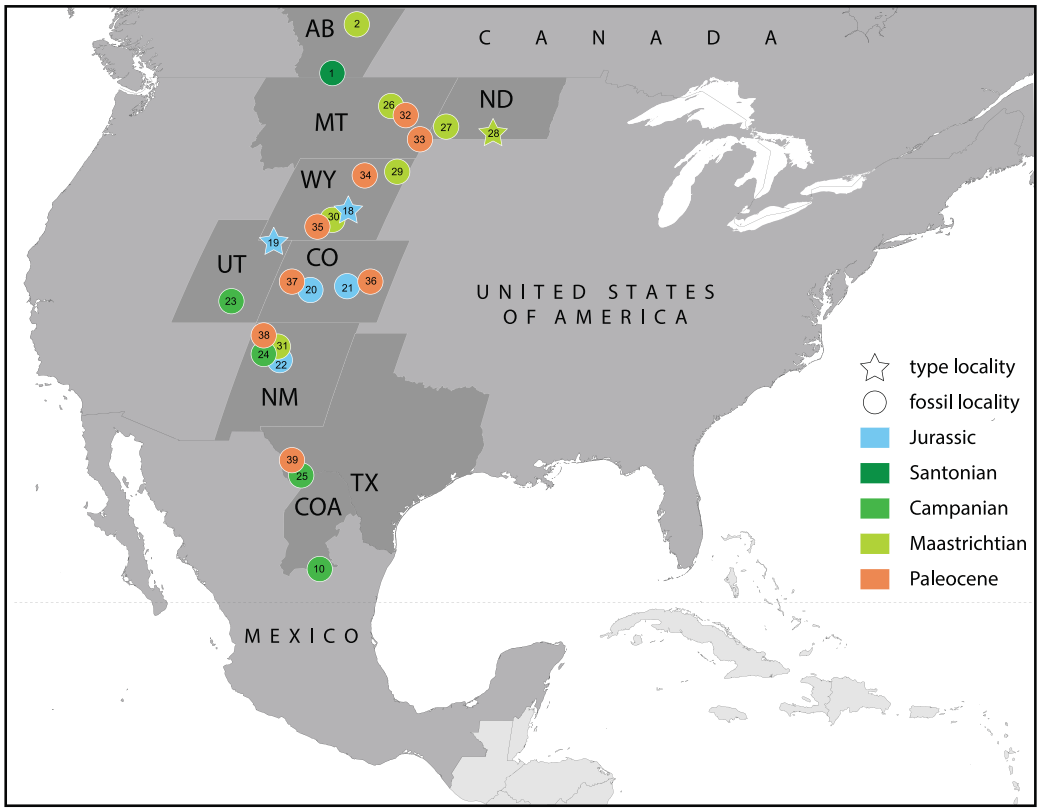

FIGURE 5. The geographic distribution of figured nonbaenid paracryptodires in North America. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations:* AB, Alberta; CO, Colorado; COA, Coahuila; ND, North Dakota; NM, New Mexico; MT, Montana; TX, Texas; UT, Utah; WY, Wyoming.

tympani; a median, hooklike tomial process; an expanded secondary palate with a broad contribution from the vomer and palatines; a midline contact of peripheral I anterior to the nuchal combined with a loss of contact between costal I and peripheral I (also present in *Selenemys lusitanica*); large mesoplastra with an offset midline contact; a deeply sinuous midline sulcus; and a deep anal notch.

Compsemys victa Leidy, 1856 (= *Compsemys parva* Hay, 1910 = *Compsemys puercensis* Gilmore, 1919 = *Compsemys torrejonensis* Gilmore, 1919 = *Compsemys vafer* Hay, 1910)

Taxonomic history. *Compsemys victus* Leidy, 1856 (new species); *Compsemys victa* Hay 1908b (variant spelling of species epithet); *Compsemys victas* Kuhn 1964 (misspelled species epithet); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* Gaffney 1972 (senior synonym); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* = *Emys obscurus* = *Glyptops depressus* Lyson and Joyce 2011 (senior synonym).

Type material. USNM 960 (holotype), shell fragments, including a neural and a costal (Leidy 1860, pl. 11.5–7; Hay 1908b).

Type locality. Long Lake (Leidy 1856), 30 miles (ca. 50 km) southeast of Bismarck, North Dakota (Gaffney 1972; Figure 5); Hell Creek Formation, Maastrichtian, Late Cretaceous (Lyson and Joyce 2011).

Referred material and range. Late Cretaceous (Santonian) Milk River Formation of Alberta (Brinkman 2003); Late Cretaceous (Campanian) Cerro del Pueblo Formation of Coahuila, Mexico (Rodriguez de la Rosa and Cevallos-Ferriz 1998; Brinkman and Rodriguez de la Rosa 2006), Aguja Formation of Texas (Tomlinson 1997), Kaiparowits Formation of Utah (Lyson and Joyce 2011; Hutchison et al. 2013), Kirtland and Fruitland Formations of New Mexico (Armstrong-Ziegler 1980; McCord 1996; Lyson and Joyce 2011; Sullivan et al. 2013); Late Cretaceous (Maastrichtian) Scollard Formation of Alberta, Canada (Brinkman 2003; Lyson and Joyce 2011), Hell Creek Formation of Montana (Hay 1908b; Estes et al. 1969; Gaffney 1972; Hutchison and Archibald 1986; Holroyd et al. 2014) and North Dakota (Leidy 1856; Holroyd and Hutchison 2002; Lyson and Joyce 2011), Lance Formation (Hay 1908b; Whitmore and Martin 1986; Holroyd and Hutchison 2002) and Ferris Formation (Lillegraven

and Eberle 1999) of Wyoming, Ojo Alamo Formation of New Mexico (Gilmore 1916a; McCord 1996; Jasinski et al. 2011); early Paleocene Fort Union Formation (Puercan North American Land Mammal Age [NALMA]) of Montana (Hutchison and Archibald 1986; Lyson and Joyce 2011; Holroyd et al. 2014) and Wyoming (Bartels 1980), Ferris Formation (Puercan NALMA) of Wyoming (Lyson and Joyce 2011), Denver Formation (Puercan NALMA) of Colorado (Hutchison and Holroyd 2003), Nacimiento Formation (Puercan–Torrejonian NALMAs) of New Mexico (including type material of *Compsemys parva*, *Compsemys puercensis*, *Compsemys torrejonensis*, and *Compsemys vafer*; Hay 1910; Gilmore 1919; McCord 1996; Lyson and Joyce 2011), Tongue River Formation (Torrejonian NALMA) of Montana (Estes 1976; Lyson and Joyce 2011); late Paleocene deBeque Formation (Tiffanian–Clarkforkian NALMAs) of Colorado (Burger 2007; Lichtig and Lucas 2015); Paleocene Black Peaks Formation (Tiffanian NALMA) of Texas (Tomlinson 1997).

Diagnosis. *Compsemys victa* can be diagnosed as a paracryptodire and a representative of *Compsemys* by the full list of characters provided for those clades above. *Compsemys victa* can most readily be differentiated from *Compsemys russelli* by possessing only a single, large suprapygal that has a lateral contact with peripheral X.

Comments. *Compsemys victa* is based on an assortment of shell fragments that were collected near Long Lake (Leidy 1856) in what is now the state of North Dakota (Gaffney 1972). The Late Cretaceous (Maastrichtian) Hell Creek Formation is exposed in this area, and it is therefore highly likely that this fossil was collected from that stratum (Lyson and Joyce 2011), not from the Jurassic, as stated by Cope (1870). Hay (1910) established two species from New Mexico based on fragmentary material: *Compsemys parva* and *Compsemys vafer*. Gilmore (1919) referred more complete shell material to the two species of Hay (1910) and furthermore established two additional species based on more complete material, *Compsemys puercensis* and *Compsemys torrejonensis*, which he diagnosed relative to one another by differences in the size of the eighth costal and in the shape of the anal notch. It is important to note that the shells reported by Gilmore (1919) are composed of eroded fragments that were assembled with plaster into three-dimensional models. Various purported differences therefore seem to be a result of imperfect reconstructions, such as the unnaturally broad and square anal notch of the shell Gilmore (1919) referred to *Compsemys vafer*. The apparent difference in the shape of the anal notch is otherwise consistent with sexual dimorphism as seen in various extant turtles as well. We therefore agree with the original assessment of Gaffney (1972) that all named taxa from New Mexico should be synonymized with *Compsemys victa* but disagree with Lyson and Joyce (2011) that *Emys obscurus* and *Glyptops depressus* should be added to the list of synonyms as well (see *Emys obscurus* and *Glyptops depressus* below). We furthermore agree with Gaffney (1972) and Lyson and Joyce (2011) that it is prudent for the moment to refer all fragmentary material from the Campanian to Paleocene to *Compsemys victa*.

Lyson and Joyce (2011) recently provided the description of a skull of *Compsemys victa* based on material first reported by Hutchison and Holroyd (2003). The skull of this turtle is unique by being triangular, lacking emarginations, and showing a strong median premaxillary hook, small, medially oriented eyes and ears, a small brain case, and unusually thick bones. An overall shape resemblance of the skull and shell with that of the extant bigheaded turtle *Platysternon megacephalum* suggests that *Compsemys victa* was a hypercarnivorous snapping turtle that likely could not retract its head within the shell (Hutchison and Holroyd 2003; Lyson and Joyce 2011). The preponderance of *Compsemys victa* material in muddy overbank deposits suggests that this aquatic turtle preferred ponded habitats (Hutchison and Holroyd 2003; Lyson and Joyce 2011).

Given the highly characteristic shell texture of *Compsemys victa*, we readily accept all reports of this taxon that are either associated with figures or specimen numbers. The earliest record is a fragment from the Santonian of Alberta (Brinkman 2003). Russell (1935) also reported a fragment from the same time and region, but this clearly represents the shell of the solemydid *Naomichelys*. *Compsemys victa* has been broadly reported from Late Cretaceous (Campanian) to Paleocene localities across the central portions of Laramidia (see "Referred material and range" above). We cannot confirm reports made by Winchester et al. (1916) and Robison (1986) for the Late Cretaceous (Maastrichtian) of South Dakota and early Paleocene of Utah, respectively, although we find it highly plausible that these regions yield this taxon as well. *Compsemys victa* occurs consistently in all major Late Cretaceous (Campanian) to Paleocene localities in the southern Rocky Mountains but is notably absent from the northern record during the Campanian and seems to be a rare occurrence in general in the southern provinces of Canada. The northern distribution of this species may therefore have been controlled by climate (Brinkman 2003).

The phylogenetic relationships of *Compsemys victa* were historically unclear, because informative shell and skull material was lacking. Hay (1908b) originally thought *Compsemys victa* to be referable to *Dermatemydidae*, as he presumed it to lack mesoplastra, but the discovery of more complete remains with well-developed mesoplastra allowed him to soon after change his mind in favor of *Baenidae* (Hay 1910). Gilmore (1919) noted similarities in the shell sculpturing of *Compsemys victa* with *Glyptops* spp. and *Neurankylus* spp. and therefore suggested affinities with *Pleurosternidae*. Gaffney (1972) once again favored affiliations with *Baenidae*, whereas Hutchison and Holroyd (2003) favored those with *Pleurosternidae*. The phylogenetic analysis of Lyson and Joyce (2011) concluded that *Compsemys victa* is a paracryptodire closely affiliated with neither pleurosternids nor baenids. However, given that relationships among nonbaenid paracryptodires are far from resolved, this conclusion must be viewed with caution.

Compsemys russelli (Pérez-García, 2012), comb. nov.

Taxonomic history. *Berruchelus russelli* Pérez-García, 2012 (new species).

Type material. MNHN BR9110 (holotype), a nuchal (Pérez-García 2012, fig. 2).

Type locality. Mouras quarry, Berru, Marne, France (Figure 4); Sables de Bracheux Formation, MP 6, upper Thanetian, late Paleocene (Pérez-García 2012).

Referred material and range. Late Paleocene (Thanetian) of Marne and Puy-de-Dôme, France (hypodigm of Pérez-García 2012).

Diagnosis. *Compsemys russelli* can be diagnosed as a paracryptodire and a representative of *Compsemys* by the full list of shell characters provided for those clades above. *Compsemys russelli* can most easily be differentiated from *Compsemys victa* by possessing two suprapygals that lack lateral contact with peripheral X.

Comments. Although *Compsemys russelli* is typified by a single nuchal from the late Paleocene (Thanetian) of Department of Marne, France, the type locality yielded a relatively rich fragment fauna that documents most parts of the shell (Pérez-García 2012). Additional fragments are available from similarly dated sediments from the Department of Puy-de-Dôme farther to the south. The possible presence of a derived paracryptodire reminiscent of *Compsemys victa* had already been hinted at by Broin (1977) and Lapparent de Broin (2001), but the formal description of *Compsemys russelli* only occurred recently (Pérez-García 2012). Although the French material is characterized by a texture that is different from that in *Compsemys victa* by being more variable and subdued, many morphological details, in particular the inset nuchal, well-developed mesoplastra, highly sinuous plastral sulcus, and deep nuchal notch, confirm close relationship. Indeed, the two forms are nearly identical in all important aspects. Given that it seems all but certain that the European form derives from its North American relatives (Pérez-García 2012), we find it prudent to unite the French and North American species into the genus *Compsemys* to avoid rendering the North American taxon paraphyletic. In addition to the trionychid *Axestemys vittata*, the presence of *Compsemys russelli* in the Paleocene of Europe is evidence for faunal exchange between North America and Europe during the early Paleogene (Georgalis and Joyce 2017).

Dinochelys whitei Gaffney, 1979

Taxonomic history. *Dinochelys whitei* Gaffney, 1979 (new species).

Type material. DNM 986–991 (holotype), a complete shell with associated postcranial elements (Gaffney 1979, figs. 3–5).

Type locality. Dinosaur Park Visitor Center, Uintah County, Utah (Figure 5); Brushy Basin Member, Morrison Formation (Gaffney 1979), Tithonian, Late Jurassic (Maidment et al. 2017).

Referred material and range. Late Jurassic (Kimmeridgian) of Como Bluff, Wyoming, USA (hypodigm of Gaffney 1979).

Diagnosis. *Dinochelys whitei* can be diagnosed as a paracryptodire by the full list of shell characters provided for that clade above with exception of a lack of surficial shell sculpturing. *Dinochelys whitei* can be differentiated from all other paracryptodires by symplesiomorphically lacking a midline contact of peripheral I (in contrast to *Selenemys lusitanica* and *Compsemys* spp.) and a nuchal notch (in contrast to *Dorsetochelys typocardium*), by possessing a cervical (in contrast to *Pleurosternon bullockii*, *Selenemys lusitanica*, and *Toremys cassiopeia*) and a midline contact of the mesoplastra (in contrast to *Riodevemys inumbragigas* and most baenids), and by apomorphically possessing wide vertebrals and lacking surficial shell sculpturing.

Comments. *Dinochelys whitei* is based on a nearly complete shell from the Late Jurassic (Tithonian) Dinosaur Park Visitor Center located near Jepsen, Utah (Gaffney 1979). The shell differs substantially from that of *Glyptops ornatus* (*Glyptops plicatulus* of Gaffney 1979), and we therefore agree that it represents a valid taxon. *Dinochelys whitei* is notably smooth shelled relative to *Glyptops ornatus*, and we therefore reluctantly maintain its placement as a separate genus. All three skull morphotypes currently documented from the Morrison Formation (e.g., "*Dorsetochelys buzzops*," *Glyptops ornatus*, and *Uluops uluops*) are associated with textured shells, which further supports the validity of this taxon. We herein disregard all juvenile specimens referred to this taxon (Gaffney 1979; Brinkman et al. 2000), as we do not believe that the broad vertebral scutes they show should be used to support taxonomic decisions.

Dorsetochelys typocardium (Seeley, 1869) (= *Ballerstedtia bueckebergensis* Karl, Gröning, et al., 2012 = *Dorsetochelys delairi* Evans and Kemp, 1976) *Thalassemys ruetimeyeri* Lydekker, 1889a)

Taxonomic history. *Pleurosternon typocardium* Seeley, 1869 (new species); *Glyptops ruetimeyeri* = *Pleurosternon typocardium* Watson 1910a (junior synonym); *Pleurosternum bullockii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* = *Pleurosternum oweni* = *Pleurosternum sedgwicki* = *Pleurosternum typocardium* = *Pleurosternum vansittardi* [*sic*] Delair 1958 (junior synonym and incorrect spelling of genus name); "*Glyptops*" *typocardium* = *Thalassemys ruetimeyeri* Milner 2004 (new combination, senior synonym); *Ballerstedtia typocardia* = *Thalassemys ruetimeyeri* Karl, Gröning, et al. 2012 (new combination, senior synonym, variant spelling); *Dorsetochelys typocardium* = *Ballerstedtia bueckebergensis* = *Dorsetochelys delairi* = *Thalassemys ruetimeyeri* Pérez-García 2014 (new combination, senior synonym).

Type material. CAMSM J5329 (holotype), a nearly complete carapace (Milner 2004, fig. 8; Pérez-García 2014, figs. 1a, 3a, 4a, and 5b).

Type locality. Swanage, Dorset, United Kingdom (Seeley 1869); Purbeck Limestone Group, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Referred material and range. Early Cretaceous (Berriasian) of the Purbeck Limestone Group, Swanage, Dorset, United Kingdom; Early Cretaceous (late Berriasian) of the Bückeberg Formation, Bückeburg, Lower Saxony, Germany (hypodigm of Pérez-García 2014, including type material of *Ballerstedtia bueckebergensis*, *Dorsetochelys delairi*, and *Thalassemys ruetimeyeri*).

Diagnosis. *Dorsetochelys typocardium* can be diagnosed as a paracryptodire by the full list of characters provided for that clade above. *Dorsetochelys typocardium* can be differentiated from all other paracryptodires by symplesiomorphically

lacking a midline contact of peripheral I (in contrast to *Selenemys lusitanica* and *Compsemys* spp.), by possessing a cervical (in contrast to *Pleurosternon bullockii*, *Selenemys lusitanica*, and *Toremys cassiopeia*) and a midline contact of the mesoplastra (in contrast to *Riodevemys inumbragigas* and most baenids), and by apomorphically possessing a deep nuchal notch and slightly expanded triturating surfaces with a elongate contribution from the palatines.

Comments. The taxonomic history of *Dorsetochelys typocardium* is somewhat tortuous. The holotype, a carapace from the Purbeck Limestone Group, was initially described by Seeley (1869). As Seeley (1869) did not provide any figures, Lydekker and Boulenger (1887) and Lydekker (1889a) were unable to assess its taxonomic standing. Watson (1910a) noted that Seeley's (1869) *Pleurosternon typocardium* seemed to be the same as *Glyptops ruetimeyeri*, a species described by Lydekker (1889a), but he nevertheless continued usage of the name *Glyptops ruetimeyeri*, even though *Pleurosternon typocardium* has priority. Nearly a century later, Milner (2004) described the specimen that Seeley (1869) had originally named *Pleurosternon typocardium*, confirmed the synonym of Watson (1910a), and concluded that the name "*Glyptops*" *typocardium* should be given priority. Milner (2004) furthermore tentatively referred the species to "*Glyptops*," as he saw similarities with this North American turtle. Karl, Gröning, et al. (2012) instead highlighted differences and proposed the new genus name *Ballerstedtia*. Karl, Gröning, et al. (2012) furthermore recognized a new species, *Ballerstedtia bueckebergensis*, based on several specimens from the late Berriasian of northwestern Germany (Karl, Gröning, et al. 2012). Pérez-García (2014) soon after highlighted that the characters used by Karl, Gröning, et al. (2012) to distinguish their new species of *Ballerstedtia* are present in both species and that *Ballerstedtia bueckebergensis* therefore does not represent a distinct species.

Evans and Kemp (1976) described an isolated cranium from the Purbeck Limestone Group as the new taxon *Dorsetochelys delairi*. Milner (2004) suggested that this cranium probably belonged to the shell-based species *Pleurosternon typocardium*, but this proposal lacked morphological support. Pérez-García (2014) reached the same conclusion by noting that the ornamentation on the dorsal surface of the skull roof of the holotype of *Dorsetochelys delairi* matches that of the shell of *Pleurosternon typocardium*. This conclusion seems reasonable because other nonbaenid paracryptodires are also characterized by the presence of a similar ornamentation on the external surface of the bones of the shell and the skull roof (e.g., *Pleurosternon bullockii* and *Glyptops ornatus*). Pérez-García (2014) therefore proposed the new combination *Dorsetochelys typocardium*. We concur with this conclusion herein as well.

The shell anatomy of *Dorsetochelys typocardium* long remained poorly understood because of an unfortunate combination of factors, including the absence of illustration of Seeley's (1869) *Pleurosternon typocardium* and the apparent loss of the holotype of *Thalassemys ruetimeyeri*. Milner (2004) was able to clarify the distinctive carapace anatomy of *Dorsetochelys typocardium*. He furthermore speculated that other specimens of this species likely existed in historical collections, but that they were probably misidentified as representatives of *Pleurosternon bullockii*. This was recently confirmed by the referral of several historical specimens housed in different British museums (Pérez-García 2014). The shell of *Dorsetochelys typocardium* is notably characterized by a deep nuchal emargination, an inverted pentagonal shape, relatively narrow vertebral scutes, a moderately developed anal notch, and a shell bone surface ornamentation consisting of a low vermiculate pattern forming a poorly defined or coarse pitting with striations perpendicular to the plate margins. The skull of *Dorsetochelys typocardium* is relatively long and broad posteriorly. A second, undescribed cranium (DORCM G.10715) from the Purbeck Limestone Group was tentatively referred to *Dorsetochelys delairi* by Milner (2004), but our preliminary study of this specimen indicates that it is not a paracryptodire.

The phylogenetic analysis of Joyce (2007) concluded based on the skull of *Dorsetochelys typocardium* only (his *Dorsetochelys delairi*) that this taxon is a paracryptodire placed just outside the clade formed by *Baenidae* and *Pleurosternidae*. The more recent analysis of Pérez-García, Royo-Torres, et al. (2015), however, concluded based on the combined skull and shell anatomy of this taxon that *Dorsetochelys typocardium* forms a polytomy with *Glyptops ornatus* (their *Glyptops plicatulus*) at the base of *Pleurosternidae*. This conclusion further supports the notion that all known Mesozoic European paracryptodires are pleurosternids.

Glyptops ornatus Marsh, 1890 (= *Glyptops utahensis* Gilmore, 1916b)

Taxonomic history. *Glyptops ornatus* Marsh, 1890 (new species); *Glyptops plicatulus* = *Glyptops ornatus* Baur 1891 (junior synonym); *Glyptops plicatulus* = *Glyptops ornatus* = *Glyptops utahensis* Gaffney 1979 (junior synonym).

Type material. YPM VP 001784 (holotype), a partial, crushed skull (Marsh 1890, pl. 7.1; Hay 1908b, pl. 5.2).

Type locality. Quarry 9, Como Bluff, Albany County, Wyoming, USA (Gaffney 1979; Figure 5); Brushy Basin Member, Morrison Formation, Kimmeridgian, Late Jurassic (Turner and Peterson 1999).

Referred material and range. Late Cretaceous (Kimmeridgian–Tithonian) Morrison Formation of Utah (type material of *Glyptops utahensis* Gilmore 1916b) and Wyoming, USA (*Glyptops plicatulus* of Hay 1908b).

Diagnosis. *Glyptops ornatus* can be diagnosed as a paracryptodire by the full list of characters provided for that clade above. *Glyptops ornatus* can be differentiated from all other paracryptodires by symplesiomorphically lacking a midline contact of peripheral I (in contrast to *Selenemys lusitanica* and *Compsemys* spp.); by possessing a cervical (in contrast to *Pleurosternon bullockii*, *Selenemys lusitanica*, and *Toremys cassiopeia*), paired gulars (in contrast to *Pleurosternon bullockii*), and a midline contact of the mesoplastra (in contrast to *Riodevemys inumbragigas* and most baenids); and by apomorphically possessing an elongate skull with low labial ridges and narrow triturating surfaces.

Comments. Turtles are reported to be regular occurrences in the Morrison Formation (Foster and McMullen 2017), but surprisingly little material of better quality has been described, and the taxonomy of the group is therefore wanting. *Glyptops* (orig. *Compsemys*) *plicatulus* is the first turtle named from the Morrison Formation. It is based on a small assortment of shell

fragments collected from outcrops near Garden Park, Colorado (Cope 1877). The holotype does not bear any characters of particular significance beyond its unusual surface texture consisting of densely packed crenulations and tubercles. Marsh (1890) soon after described *Glyptops ornatus* based on a partial skull from Como Bluff, Wyoming. Marsh (1890) also reported a partial carapace from the type locality with a similar surface to that of *Compsemys plicatulus*, but he was hesitant to refer the shell to the skull, as they were not found in direct association. Baur (1891) felt less hesitant and referred all turtle material from Como Bluff to *Glyptops plicatulus* as he believed it to be plausible that the locality only yielded a single species. Hay (1908a, 1908b) conformed to the synonymy of Baur (1891) and referred additional material to *Glyptops plicatulus*, including a carapace from an undisclosed quarry at Como (Hay 1908a) and a nearly complete skeleton from the Bone Cabin Quarry at Como (Hay 1908b), which is located in the Late Jurassic (Kimmeridgian) Salt Wash Member of the Morrison Formation (Turner and Peterson 1999). Gilmore (1916b), on the other hand, broke with the taxonomic tradition set by Baur (1891) by naming a new species, *Compsemys utahensis*, this time from the Carnegie Quarry in Utah, which is located in the Kimmeridgian Brushy Basin Member of the Morrison Formation (Turner and Peterson 1999). As the Morrison Formation seemed to have yielded only a single skull morphotype associated with shell material reminiscent of *Glyptops plicatulus*, Gaffney (1979) much later united all textured shells and their associated skulls into *Glyptops plicatulus*, including the types of *Glyptops ornatus* and *Glyptops utahensis*, as opposed to *Dinochelys whitei* (see above), which is characterized by the absence of surface sculpturing.

A series of more recent finds has revealed that two additional skull morphotypes are associated with crenulated shell material: *Uluops uluops* (Carpenter and Bakker 1990; see below) and the enigmatic "*Dorsetochelys buzzops*" (Bakker 1998; see below). Unfortunately, even though these new skull morphotypes are associated with postcranial material, their shells remain undescribed. Although additional study will need to clarify if both new taxa are valid, we agree that they are systematically different from the skull morphotype preserved in the type of *Glyptops ornatus* and the referred specimen from the Bone Cabin Quarry (Hay 1908b).

We here consider the type of *Glyptops plicatulus* to be a nomen dubium, because the texture of its shell is not unique among basal paracryptodires. As a result, *Glyptops ornatus* is reinstated as valid. Although the type skull of *Glyptops ornatus* and the skull from the Bone Cabin Quarry are of poor quality, we agree that they are referable to the same taxon, as both are notably narrow and have narrow triturating surfaces and low maxillae. The Bone Cabin Quarry specimen therefore documents the shell morphology of *Glyptops ornatus*. We agree with Gaffney (1979) that the shell morphology of the type of *Glyptops utahensis* fully corresponds to that of the Bone Cabin Quarry specimen, and we here therefore synonymize *Glyptops utahensis* with *Glyptops ornatus*. As the morphology of all other specimens from the Late Jurassic of North America remains undescribed, we finally refer all other crenulated shell material to *Glyptops* sp. Our taxonomic concept of *Glyptops ornatus* greatly resembles that of the taxonomic concept of Gaffney (1979) for *Glyptops plicatulus* by including the types of *Glyptops ornatus*, *Glyptops utahensis*, and the Bone Cabin Quarry specimen, but it differs by excluding all other referred specimens with crenulated shell material. All herein referred specimens of *Glyptops ornatus* were extensively described by Gaffney (1979) under the name *Glyptops plicatulus*.

Glyptops ornatus has been included under the name *Glyptops plicatulus* in all phylogenetic analyses that are based on the character-taxon matrix of Joyce (2007). Most analysis concludes that this turtle is a basal pleurosternid (e.g., Joyce 2007; Lyson and Joyce 2011; Pérez-García, Royo-Torres, et al. 2015). The narrow skull and jaws suggest that this aquatic turtle was a generalist.

The name *Glyptops* has been used in the last 100 years as a wastebasket taxon for all Late Jurassic to Early Cretaceous turtles with a fine sculpted ("pleurosternid") shell surface texture. As this texture persists among basal baenids, such as *Arundelemys dardeni*, *Trinitichelys hiatti*, and *Neurankylus* spp. (Joyce and Lyson 2015), it is clear that surface texture is not sufficient to diagnose a turtle as belonging to *Glyptops*. We here refer all isolated shell material with textured surface from the Late Jurassic Morrison Formation to *Paracryptodira* indet., in particular from Colorado (Cope 1877; Brinkman et al. 2000), New Mexico (Lucas et al. 2006), Utah (Gaffney 1979), and Wyoming (Marsh 1890; Hay 1908a, 1908b; Gaffney 1972). Additional remains have been reported from the Morrison Formation of Montana, South Dakota, and Oklahoma (e.g., Foster and McMullen 2017), but we cannot reproduce these reasonable claims, as specimen numbers or figures are lacking. We herein do not summarize the fossil record of textured shell fragments from the Early Cretaceous of North America, as these likely represent baenids (see Joyce and Lyson [2015] for a summary of more complete material).

Pleurosternon bullockii (Owen, 1842) (= *Megasternon koenigii* Gray, 1870 = *Mesochelys durlstonensis* Evans and Kemp, 1975 = *Pleurosternon concinnum* Owen, 1853 = *Pleurosternon ovatum* Owen, 1853 = *Pleurosternon oweni* Seeley, 1869 = *Pleurosternon sedgwicki* Seeley, 1869 = *Pleurosternon vansittarti* Seeley, 1869)

Taxonomic history. *Platemys bullockii* Owen, 1842 (new species); *Platemys bullochii* Giebel 1847 (incorrect spelling of species name); *Emys bullochii* Gervais 1859 (new combination and incorrect spelling of species name); *Digerrhum bullockii* Cope 1870 (new combination); *Megasternon koenigii* = *Platemys bullockii* Gray 1870 (objective synonym); *Pleurosternon bullockii* Rütimeyer 1873 (new combination); *Pleurosternum bullockii* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* Lydekker and Boulenger 1887 (senior synonym and incorrect spelling of genus name); *Pleurosternum bullockii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* Lydekker 1889b (senior synonym and incorrect spelling of genus name); *Pleurosternum bullockii* = *Megasternum koenigii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* Lydekker 1889a (senior synonym and incorrect spelling of genus name); *Pleurosternum bullockii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* = *Pleurosternum oweni* = *Pleurosternum*

sedgwicki = *Pleurosternum typocardium* = *Pleurosternum vansittardi* [*sic*] Delair 1958 (senior synonym and incorrect spelling of genus name); *Pleurosternon bullockii* = *Mesochelys durlstonensis* = *Pleurosternon concinnum* = *Pleurosternon emarginatum* (pro parte) = *Pleurosternon ovatum* = *Pleurosternon oweni* = *Pleurosternon sedgwicki* = *Pleurosternon vansittarti* Milner 2004 (senior synonym).

Type material. NHMUK R911 (holotype), a large, complete plastron (Owen and Bell 1849, pl. 21; Milner 2004, fig. 3).

Type locality. Purbeck, probably near Swanage, Dorset, United Kingdom (Lyddeker and Boulenger 1887; Figure 4); Purbeck Limestone Group, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Referred material and range. Early Cretaceous (Berriasian) of the Purbeck Limestone Group, Isle of Purbeck, Dorset, United Kingdom (including type material of *Megasternon koenigii*, *Mesochelys durlstonensis*, *Pleurosternon concinnum*, and *Pleurosternon ovatum*; Owen 1853; Gray 1870; Evans and Kemp 1975; Milner 2004).

Diagnosis. *Pleurosternon bullockii* can be diagnosed as a paracryptodire by the full list of characters provided for that clade above. *Pleurosternon bullockii* can be differentiated from all other paracryptodires by symplesiomorphically lacking a midline contact of peripheral I (in contrast to *Selenemys lusitanica* and *Compsemys* spp.), by having a midline contact of the mesoplastra (in contrast to *Riodevemys inumbragigas* and most baenids), by apomorphically lacking a cervical (as in *Selenemys lusitanica* and *Toremys cassiopeia*), and by having only a single gular and an elongate skull with low labial ridges and narrow triturating surfaces.

Comments. *Pleurosternon bullockii* is based on a large, complete plastron from the Purbeck Limestone Group of Dorset, United Kingdom, but this specimen was originally reported erroneously as originating from the Eocene London Clay of Sheppey, United Kingdom, and referred to the recent pleurodiran genus *Platemys* (Owen 1842; Owen and Bell 1849). In subsequent years, several other specimens from the Purbeck Limestone Group were identified as distinct species and placed in the new genus *Pleurosternon* (Owen 1853, Seeley 1869), a genus that is typified by *Pleurosternon concinnum* Owen, 1853. The real provenance and age of the holotype specimen of *Pleurosternon bullockii* were only established at the end of the 19th century (Lydekker and Boulenger 1887), although Rütimeyer (1873) had already noted that this specimen was undoubtedly a representative of the genus *Pleurosternon*.

Owen (1853) described four new species for his new genus *Pleurosternon*: *Pleurosternon concinnum*, *Pleurosternon ovatum*, *Pleurosternon emarginatum*, and *Pleurosternon latiscutatum*. The syntype series of the latter two species are now synonymized with *Hylaeochelys belli* (in part for *Pleurosternon emarginatum*; see Lydekker and Boulenger 1887), a pancryptodiran turtle (see Pérez-García 2012) that will be treated elsewhere. *Pleurosternon concinnum* and *Pleurosternon ovatum* were initially distinguished based on minor differences (outline of the carapace and width of the first vertebral scute) but are unanimously regarded as junior synonyms of *Pleurosternon bullockii* since Lydekker and Boulenger (1887) and Lydekker (1889a, 1889b).

Seeley (1869) proposed four new names of *Pleurosternon* based on material from the Purbeck Limestone Group in Swanage: *Pleurosternon oweni*, *Pleurosternon sedgwicki*, *Pleurosternon typocardium*, and *Pleurosternon vansittarti*. Lydekker (1889a) noted that he was unable to assess these species and their possible affinities with *Pleurosternon bullockii* without seeing the material. Watson (1910a) apparently saw Seeley's (1869) material because he concluded in a note that *Pleurosternon typocardium* was identical to *Thalassemys ruetimeyeri* (see above), and that *Pleurosternon oweni*, *Pleurosternon sedgwicki*, and *Pleurosternon vansittarti* seemed to be typical examples of *Pleurosternon bullockii*. Delair (1958), on the other hand, synonymized all of Seeley's (1869) material with *Pleurosternon bullockii*. More recently, Milner (2004) confirmed Watson's (1910a) observations by setting *Pleurosternon typocardium* apart from the rest (see *Dorsetochelys typocardium* above). Although the holotypes of *Pleurosternon oweni*, *Pleurosternon sedgwicki*, and *Pleurosternon vansittarti* still remain to be described, we here conform to the synonymy of Milner (2004) as the morphology of *Pleurosternon bullockii* is strikingly different from that of *Pleurosternon* (now *Dorsetochelys*) *typocardium*.

Megasternon koenigii has repeatedly been cited by previous authors as a synonym of *Pleurosternon bullockii*, but variably attributed to different publications by Gray (see Lydekker 1889a; Woodward and Sherborn 1890; Kuhn 1964). The genus name *Megasternon* first appeared in isolation in Gray (1842). Without species name and proper description, *Megasternon* must be considered unavailable at that time. The species name *Megasternon koenigii* first appeared in Gray (1844), again without description or indication, so this name must be considered a nomen nudum. *Megasternon koenigii* finally became available when Gray (1870) mentioned it again with a clear indication to both Gray (1844) and Owen and Bell's (1849) illustration of the holotype of *Platemys bullockii*. *Megasternon koenigii* Gray, 1870 is therefore a junior objective synonym of *Pleurosternon bullockii* (Owen, 1842).

Pleurosternon bullockii is a large species with a carapace length reaching up to 560 mm in the largest individuals (Milner 2004). The carapace is relatively flat, oval in shape, and almost without nuchal emargination. A small posterior notch is present on the pygal bone. The plastron is characterized by a broad, rounded anterior plastral lobe; broad mesoplastra meeting in the midline; and a deep, V-shaped xiphiplastral notch. The shell bone surface ornamentation consists of small, regular, and clearly defined pits with fine striations perpendicular to the plate margins.

A well-preserved skull from the Purbeck Limestone Group in Durlston Bay was described by Evans and Kemp (1975) as a distinct species, *Mesochelys durlstonensis*. A fragmentary postcranium was found associated with this skull. Since Gaffney and Meylan (1988), *Mesochelys durlstonensis* is treated as a junior synonym of *Pleurosternum bullockii*, and this unique specimen is used in all subsequent phylogenetic studies to score the cranial anatomy of the latter species. However, Milner (2004) was the first to properly assess this synonymy by comparing the shell remains associated with the skull with the turtle material known from the Purbeck Limestone Group. Based on several morphological arguments (similar surface ornamentation, posterior marginal scutes covering the distal part of costals, and presence of a deep, V-shaped xiphiplastral notch), he concluded that

Mesochelys durlstonensis was indeed a junior synonym of *Pleurosternon bullockii* (Milner 2004).

Pleurosternon bullockii was reported from the Tithonian of northern France (Sauvage 1894, 1900, 1912, 1921), but this material must be regarded as indeterminate (Lapparent de Broin et al. 1996; Lapparent de Broin 2001). The species was also reported from the Early Cretaceous (Berriasian) of Germany (Karl et al. 2007), but we identify this material as *Pleurosternidae* indet. as it consists of steinkerns only.

"*Pleurosternon*" *portlandicum* Lydekker, 1889a

Taxonomic history. *Pleurosternum portlandicum* Lydekker, 1889a (new species and incorrect spelling of genus name).

Type material. NHMUK OR44807 (holotype), an incomplete plastron with articulated left peripherals (Lydekker 1889a, fig. 47).

Type locality. Isle of Portland, Dorset, United Kingdom (Figure 4); Portland Oolite, Tithonian, Late Jurassic (Lydekker 1889a).

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

Diagnosis. "*Pleurosternon*" *portlandicum* can be diagnosed as a paracryptodire by the presence of expanded mesoplastra with a midline contact, a textured shell surface, and overall similarity with *Pleurosternon bullockii*. "*Pleurosternon*" *portlandicum* can be differentiated from *Pleurosternon bullockii* in its finer surface texture and inframarginals that do not broadly overlap the peripherals.

Comments. "*Pleurosternon*" *portlandicum* is based on an imperfect plastron from the Tithonian of the Isle of Portland, Dorset, United Kingdom (Lydekker 1889a). It is therefore only slightly older than the earliest Cretaceous (Berriasian) *Pleurosternon bullockii* from the same region. The surface ornamentation on the plastral bones consists of small, regular, and clearly defined pits with striations perpendicular to plate margins. This is very similar to *Pleurosternon bullockii*, but pits are sparser. The entoplastron is about as wide as long in "*Pleurosternon*" *portlandicum*, but usually wider than long in *Pleurosternon bullockii*. The intergular scute is described as pyriform and narrow posteriorly (Lydekker 1889a), but personal observation of the holotype reveals this area to be abnormal in the development of three asymmetric gulars. Finally, the inframarginals do not extend laterally onto the ventral part of the peripherals. Although more specimens are needed to improve our understanding of this taxon, we here provisionally accept the validity of "*Pleurosternon*" *portlandicum* based on these differences combined with its stratigraphic age. However, as all characters that would unambiguously link this taxon with *Pleurosternon bullockii* are not preserved in the holotype, in particular the single median gular, deep anal notch, and lacking cervical scute, we here highlight phylogenetic uncertainty by placing *Pleurosternon* in quotes.

Riodevemys inumbragigas Pérez-García, Royo-Torres, et al., 2015

Taxonomic history. *Riodevemys inumbragigas* Pérez-García, Royo-Torres, et al., 2015 (new species).

Type material. MAP CPT-1423 (holotype), a nearly complete but disarticulated shell with some elements of the pectoral and pelvic girdles (Pérez-García, Royo-Torres, et al. 2015, figs. 2 and 3).

Type locality. Riodeva, Teruel, Spain (Figure 4); Villar del Arzobispo Formation, middle to late Tithonian, Late Jurassic (Pérez-García, Royo-Torres, et al. 2015).

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

Diagnosis. *Riodevemys inumbragigas* can be diagnosed as a paracryptodire by the full list of shell characters provided for that clade above. *Riodevemys inumbragigas* can most readily be differentiated from all other basal paracryptodires by apomorphically lacking a midline contact of the mesoplastra and from most baenids by lacking well-developed inguinal and axillary buttresses.

Comments. *Riodevemys inumbragigas* is based on a single, disarticulated shell from the Tithonian of Riodeva, Teruel Province, Spain (Pérez-García, Royo-Torres, et al. 2015). This species differs from other basal paracryptodires in having an intermediate size (carapace length about 35 cm), a relatively wide shell, and an absent (or very reduced) medial contact of the mesoplastra, as well as the presence of a modest pygal notch. Similar to many basal paracryptodires, the external surface of the shell bones is decorated with low tubercles joining to form vermiculate ridges and striations perpendicular to the plate margins.

Selenemys lusitanica Pérez-García and Ortega, 2011

Taxonomic history. *Selenemys lusitanica* Pérez-García and Ortega, 2011 (new species).

Type material. ALTSHN 066 (holotype), a complete plastron with associated partial carapace (Pérez-García and Ortega 2011, fig. 2).

Type locality. Santa Rita, Torres Vedras, Lisbon District, Portugal (Figure 4); Alcobaça Formation, Lourinhã Group, upper Kimmeridgian, Late Jurassic (Pérez-García and Ortega 2011).

Referred material and range. Late Jurassic (upper Kimmeridgian) of Torres Vedras, Lisbon District, Portugal (hypodigm of Pérez-García and Ortega 2011).

Diagnosis. *Selenemys lusitanica* can be diagnosed as a paracryptodire by the full list of shell characters provided for that clade above. *Selenemys lusitanica* can be differentiated from all other paracryptodires by apomorphically possessing a midline contact of peripheral I anterior to the nuchal (as in *Compsemys* spp.) combined with the absence of a cervical (as in *Pleurosternon bullockii* and *Toremys cassiopeia*).

Comments. *Selenemys lusitanica* is based on a small series of specimens from the upper Kimmeridgian of Portugal (Pérez-García and Ortega 2011). This is a medium-sized basal

paracryptodire (carapace length about 25 to 30 cm) that is characterized by a relatively broad carapace and a medial contact of peripheral I anterior to the nuchal plate excluding the latter from the anterior carapace margin.

Toremys cassiopeia Pérez-García, Espílez, et al., 2015

Taxonomic history. *Toremys cassiopeia* Pérez-García, Espílez, et al., 2015 (new species).

Type material. MAP AR-1-4893 (holotype), a relatively complete shell with appendicular elements (Pérez-García, Espílez, et al. 2015, fig. 2); MAP AR-1-4863 (paratype), a fragmentary shell with appendicular elements (Pérez-García, Espílez, et al. 2015, fig. 3); MAP AR-1-3923 (paratype), a partial and disarticulated shell (Pérez-García, Espílez, et al. 2015, fig. 4).

Type locality. Ariño, Teruel Province, Spain (Figure 4); Lower Escucha Formation, lower Albian, Early Cretaceous (Pérez-García, Espílez, et al. 2015).

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

Diagnosis. *Toremys cassiopeia* can be diagnosed as a paracryptodire by the full list of shell characters provided for that clade above. *Toremys cassiopeia* can be differentiated from all other paracryptodires by symplesiomorphically lacking a midline contact of peripheral I (in contrast to *Selenemys lusitanica* and *Compsemys* spp.), by possessing paired gulars (in contrast to *Pleurosternon bullockii*), and by apomorphically lacking a cervical (as in *Pleurosternon bullockii* and *Selenemys lusitanica*).

Comments. *Toremys cassiopeia* is based on three partial shells from the lower Albian of Teruel Province, Spain (Pérez-García, Espílez, et al. 2015). As in most basal paracryptodires, the external surface of the shell bones of this turtle is ornamented with a pattern of low tubercles often joining to form vermiculate ridges. Well-developed striations are also present perpendicular to the sutural margins of the shell plates. *Toremys cassiopeia* notably differs from other basal paracryptodires by its young stratigraphic age, small size (carapace length about 15 cm), nuchal bone with reduced anterior margin, and anteriorly particularly wide vertebral (Pérez-García, Espílez, et al. 2015).

Uluops uluops Carpenter and Bakker, 1990

Taxonomic history. *Uluops uluops* Carpenter and Bakker, 1990 (new species).

Type material. UCM 53971 (holotype), a partial skull (Carpenter and Bakker 1990, fig. 4).

Type locality. Breakfast Bench locality, Como Bluff, Albany County, Wyoming, USA (Carpenter and Bakker 1990; Figure 5); Brushy Basin Member, Morrison Formation, Tithonian, Late Jurassic (Turner and Peterson 1999).

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

Diagnosis. *Uluops uluops* can be diagnosed as a paracryptodire by the full list of cranial characters provided for that clade above. *Uluops uluops* can readily be differentiated from *Dorsetochelys typocardium*, *Glyptops ornatus*, and *Pleurosternon bullockii* by having a notably short and high skull; from *Compsemys victa* by lacking an expanded secondary palate and a median tomial hook; and from baenids by lacking accessory triturating ridges and expanded prefrontal lappets.

Comments. *Uluops uluops* is based on a well-preserved partial skull from the Late Jurassic Morrison Formation of Colorado (Carpenter and Bakker 1990). The type skull has not yet been figured, but a reconstructive illustration highlights many differences with the skull of the coeval *Glyptops ornatus*, in particular by being significantly higher and broader. We can confirm these differences based on personal observations of the holotype. The validity of this taxon is therefore unproblematic. Preliminary analyses place *Uluops uluops* in a polytomy with pleurosternids and baenids (Lyson and Joyce 2011; Pérez-García, Royo-Torres, et al. 2015), but this is likely to change in the future through the additional study of the skull and the discovery of shell material. We specifically note that many fragments herein referred to "*Glyptops*" indet. based on their sculpturing may well represent *Uluops uluops*.

The name *Uluops uluops* is somewhat unusual for a recently proposed name by being an absolute tautonym (i.e., a binomen where the genus is spelled identically to the associated species epithet). However, this choice of name is explicitly endorsed by the International Code on Zoological Nomenclature (ICZN 1999).

Invalid and Problematic Taxa

Ballerstedtia bueckebergensis Karl, Gröning, et al., 2012 nomen invalidum (junior synonym of *Dorsetochelys typocardium* [Seeley, 1869])

Taxonomic history. *Ballerstedtia bueckebergensis* Karl, Gröning, et al., 2012 (new species); *Dorsetochelys typocardium* = *Ballerstedtia bueckebergensis* = *Dorsetochelys delairi* = *Thalassemys ruetimeyeri* Pérez-García 2014 (junior synonym).

Type material. GZG BA533a–c (holotype), internal and external imprint of a shell (Karl, Gröning, et al. 2012, pl. 1; Pérez-García 2014, fig. 2).

Type locality. Bückeburg, Lower Saxony, Germany; Bückeberg Formation, late Berriasian, Early Cretaceous (Karl, Gröning, et al. 2012).

Comments. See *Dorsetochelys typocardium* (above) for discussion.

Chelys blakii Mackie, 1863 nomen dubium

Taxonomic history. *Chelys*? *blakii* Mackie, 1863 (new species); *Protochelys stricklandi* = *Chelys*? *blakei* (?) Lydekker 1889a (junior synonym and incorrectly spelled species epithet);

[*Protochelys blakii*] = *Testudo stricklandi* Anquetin and Claude 2008 (new combination, senior synonym, nomen dubium).

Type material. NHMUK OR37979 (holotype), an isolated right coracoid (Mackie 1863, unnumbered figure; Anquetin and Claude 2008, fig. 2).

Type locality. Stonesfield, Oxfordshire, United Kingdom (Mackie 1863); Stonesfield Slate, Taynton Limestone Formation, middle Bathonian, Middle Jurassic (Torrens 1980; Boneham and Wyatt 1993).

Comments. *Chelys*? *blakii* is based on an isolated right coracoid from the Middle Jurassic of Stonesfield, United Kingdom (Mackie 1863). Lydekker (1889a) tentatively synonymized this taxon with *Protochelys stricklandi* (Phillips, 1871), which is based on a collection of isolated shell scutes from the same locality. Anquetin and Claude (2008) more recently concluded that all available turtle material from Stonesfield represents a single taxon, *Protochelys blakii*, which they considered to be a nomen dubium. There is no definitive evidence that the coracoid and the isolated scutes belong to a single taxon, apart from the fact that they were found at the same locality. Therefore, we consider them separately in the present work. Although chelonian in nature, the isolated coracoid from Stonesfield is undiagnostic at the species level, and *Chelys*? *blakii* must be regarded as a nomen dubium.

The turtle material from Stonesfield, notably the scutes referred to *Testudo stricklandi* (see below), has been considered by some authors to belong to pleurosternids (Bergounioux 1955; Romer 1956, 1966). However, there is little support for this conclusion, and the present material should be regarded as *Testudinata* indet. (Anquetin and Claude 2008).

Compsemys parva Hay, 1910 nomen invalidum (junior synonym of *Compsemys victa* Leidy, 1856)

Taxonomic history. *Compsemys parva* Hay, 1910 (new species); *Compsemys parvus* Kuhn 1964 (alternative spelling of species epithet); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* Gaffney 1972 (junior synonym); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* = *Emys obscurus* = *Glyptops depressus* Lyson and Joyce 2011 (junior synonym).

Type material. USNM 6548 (holotype), shell fragments (Hay 1910, fig. 1, pl. 10.1–3).

Type locality. Near Ojo Alamo (Hay 1910), San Juan County, New Mexico, USA; Nacimiento Formation, Puercan or Torrejonian NALMA, Danian, early Paleocene (Gaffney 1972; Sullivan and Lucas 1986).

Comments. See *Compsemys victa* (above) for discussion.

Compsemys plicatulus Cope, 1877 nomen dubium

Taxonomic history. *Compsemys plicatulus* Cope, 1877 (new species); *Glyptops plicatulus* Hay 1908a (new combination); *Glyptops plicatulus* = *Glyptops ornatus* Baur 1891 (senior synonym); *Glyptops plicatulus* = *Glyptops ornatus* = *Glyptops utahensis* Gaffney 1979 (senior synonym).

Type material. AMNH 6099 (holotype), a partial costal and associated plastral fragments (Hay 1908b, pl. 5.1; Gaffney 1979, fig. 1).

Type locality. Garden Park, Cañon City, Fremont County, Colorado, USA (Gaffney 1979); Brushy Basin Member, Morrison Formation, Tithonian, Late Jurassic (Turner and Peterson 1999).

Comments. See *Glyptops ornatus* (above) for discussion.

Compsemys puercensis Gilmore, 1919 nomen invalidum (junior synonym of *Compsemys victa* Leidy, 1856)

Taxonomic history. *Compsemys puercensis* Gilmore, 1919 (new species); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* Gaffney 1972 (junior synonym); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* = *Emys obscurus* = *Glyptops depressus* Lyson and Joyce 2011 (junior synonym).

Type material. USNM 8544 (holotype), shell fragments (Gilmore 1919, fig. 3, pl. 3).

Type locality. Northwest of Kimbetoh, north line of Section 27, T 23 N, R 9 W, San Juan County, New Mexico, USA (Gilmore 1919); Nacimiento Formation, Puercan NALMA, Danian, early Paleocene (Gilmore 1919; Gaffney 1972; Sullivan and Lucas 1986).

Comments. See *Compsemys victa* (above) for discussion.

Compsemys torrejonensis Gilmore, 1919 nomen invalidum (junior synonym of *Compsemys victa* Leidy, 1856)

Taxonomic history. *Compsemys torrejonensis* Gilmore, 1919 (new species); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* Gaffney 1972 (junior synonym); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* = *Emys obscurus* = *Glyptops depressus* Lyson and Joyce 2011 (junior synonym).

Type material. USNM 8549 (holotype), a nearly complete shell (Gilmore 1919, figs. 5 and 6, pl. 4).

Type locality. Northeast of Kimbetoh, Section 17, T 23 N, R 8 W, San Juan County, New Mexico, USA (Gilmore 1919); Nacimiento Formation, Torrejonian NALMA, Danian, early Paleocene (Gilmore 1919; Gaffney 1972; Sullivan and Lucas 1986).

Comments. See *Compsemys victa* (above) for discussion.

Compsemys vafer Hay, 1910 nomen invalidum (junior synonym of *Compsemys victa* Leidy, 1856)

Taxonomic history. *Compsemys vafer* Hay, 1910 (new species); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* Gaffney 1972 (junior synonym); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* = *Emys obscurus* = *Glyptops depressus* Lyson and Joyce 2011 (junior synonym).

Type material. USNM 6551 (holotype), shell fragments (Hay 1910, figs. 2–5, pl. 10.4–5).

Type locality. Near Ojo Alamo (Hay 1910), San Juan County, New Mexico, USA; Nacimiento Formation, Puercan or Torrejonian NALMA, Danian, early Paleocene (Gaffney 1972; Sullivan and Lucas 1986).

Comments. See *Compsemys victa* (above) for discussion.

Desmemys bertelsmanni Wegner, 1911 nomen dubium

Taxonomic history. *Desmemys bertelsmanni* Wegner, 1911 (new species), *Desmemys bertelsmanni* Karl, Nyhuis, et al. 2012 (unjustified neotype designation), *Desmemys berstelsmanni* Pérez-García, Royo-Torres, et al. 2015 (incorrectly spelled species epithet).

Type material. GUM uncat. (holotype), a nearly complete shell with associated limb and girdle remains (Wegner 1911, figs. 1 and 2, pls. 8 and 9), now considered lost (Karl, Nyhuis, et al. 2012).

Type locality. Gerdemann clay pit, Gronau, North Rhein-Westphalia, Germany; Bückeberg Formation, Berriasian, Early Cretaceous (Wegner 1911; Karl, Nyhuis, et al. 2012).

Comments. *Desmemys bertelsmanni* is based on a relatively complete shell and associated limb and girdle remains that were collected from a clay pit in Gronau, Germany, and described and figured in detail by Wegner (1911). The specimen can confidentially be interpreted as a paracryptodire, as it possesses well-developed mesoplastra, in contrast to coeval thalassochelydians (Anquetin et al. 2017), and a finely textured shell, in contrast to coeval helochelydrids (Joyce 2017). The specimen is otherwise characterized by being relatively small (carapace length approximately 18 cm), by having well-developed fontanelles in the carapace and plastron, and by having radiating scute patterns. It therefore seems all but certain that this is a juvenile individual. Gaffney (1979) noted that *Desmemys bertelsmanni* is similar to *Dinochelys whitei* by possessing these radiating scute patterns, but we do not believe this to be particularly meaningful, as *Dinochelys whitei* is mostly known from juvenile material as well. To our knowledge, *Desmemys bertelsmanni* has not been included in a phylogenetic analysis to date.

Karl, Nyhuis, et al. (2012) more recently designated a neotype for *Desmemys bertelsmanni* as they concluded that the holotype had been destroyed during World War II. We here reject this designation, as it disregards nearly all rules set forth by the ICZN (1999) in regard to the designation of a neotype. In particular, the authors do not sufficiently show loss of the holotype, they do not outline why the purported loss of the holotype creates taxonomic instability that needs to be addressed, and they do not discuss why they believe the neotype to be consistent with the morphology of *Desmemys bertelsmanni*. In addition, the proposed neotype, a fragmentary hyoplastron from the type locality, does not create stability, as it is undiagnostic beyond *Testudinata* indet. and therefore cannot serve as a meaningful name bearer. We therefore here maintain the status of the purportedly lost holotype. We agree with Jansen and Klein (2014) that the juvenile specimen from Oker, Germany, which had been referred to *Desmemys bertelsmanni* by Karl, Nyhuis, et al. (2012), is not diagnosable as a paracryptodire and rather represents a eucryptodire instead.

In contrast to all previous authors, we here conclude *Desmemys bertelsmanni* to be a nomen dubium, as the type specimen represents a juvenile individual. As a result, most bones are poorly ossified, and most scute sulci are not preserved, making it impossible to rigorously compare this taxon with roughly coeval paracryptodires such as *Dorsetochelys typocardium*, *Pleurosternon bullockii*, and *Riodevemys inumbragigas*.

Dorsetochelys delairi Evans and Kemp, 1976 nomen invalidum (junior synonym of *Dorsetochelys typocardium* [Seeley, 1869])

Taxonomic history. *Dorsetochelys delairi* Evans and Kemp, 1976 (new species); *Dorsetochelys typocardium* = *Ballerstedtia bueckebergensis* = *Dorsetochelys delairi* = *Thalassemys ruetimeyeri* Pérez-García 2014 (junior synonym and new combination).

Type material. DORCM G23 (holotype), a dorsoventrally crushed skull (Evans and Kemp 1976, figs. 1 and 2; Gaffney 1979, figs. 26–28; Pérez-García 2014, fig. 5).

Type locality. Swanage, Dorset, United Kingdom (Evans and Kemp 1976); Purbeck Limestone Group, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Comments. See *Dorsetochelys typocardium* (above) for discussion.

Dorsetochelys buzzops Bakker, 1998 nomen dubium

Taxonomic history. *Dorsetochelys buzzops* Bakker, 1998 (new species).

Type material. TGM 5001 (holotype), a skull (Bakker 1998, figs. 5 and 6) with associated postcranial skeleton, now considered lost.

Type locality. Breakfast Bench locality, Como Bluff, Albany County, Wyoming, USA (Bakker 1998); Brushy Basin Member, Morrison Formation, Tithonian, Late Jurassic (Turner and Peterson 1999).

Comments. *Dorsetochelys buzzops* is based on a fossil turtle from the Late Jurassic of Wyoming (Bakker 1998). Although the type specimen supposedly includes much of the skeleton, it was only documented in the form of a single figure, which consists of three reconstructive illustrations. As the type specimen is now considered lost (J.-P. Cavigelli, pers. comm., 2018), we conclude this taxon to be a nomen dubium, as its morphology cannot be replicated.

Emys obscurus Leidy, 1856 nomen dubium

Taxonomic history. *Emys obscurus* Leidy, 1856 (new species); *Compsemys obscurus* Cope 1870 (new combination); *Compsemys obscura* Hay 1908b (alternative spelling of species epithet); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* = *Emys obscurus* = *Glyptops depressus* Lyson and Joyce 2011 (junior synonym).

Type material. An isolated costal (holotype; Leidy 1860, pl. 11.4), now lost (Hay 1908b).

Type locality. Long Lake (Leidy 1856), 30 miles (ca. 50 km) southeast of Bismarck, North Dakota (Gaffney 1972); Hell Creek Formation, Maastrichtian, Late Cretaceous (Lyson and Joyce 2011).

Comments. *Emys obscurus* is based on an isolated costal that was likely collected from Late Cretaceous (Maastrichtian) sediments exposed in the vicinity of the type locality in North Dakota, USA (Leidy 1856; Lyson and Joyce 2011). Hay (1908b) referred fragmentary remains from the Late Cretaceous (Maastrichtian) of Montana to *Emys obscurus* but provided no explicit rationale for that decision, beyond similarities in sculpturing. Lyson and Joyce (2011), on the other hand, synonymized *Emys obscurus* with *Compsemys victa* but did not provide an explicit justification for that taxonomic decision. Other paleontologists have ignored this species.

The holotypes of *Emys obscurus* and *Compsemys victa* are figured on the same plate (Leidy 1860). Whereas the holotype of *Emys obscurus* is smooth, that of *Compsemys victa* is characterized by the finely crenulated surface texture noted as diagnostic for that species. We presume that Lyson and Joyce (2011) accidentally viewed the wrong specimen when proposing that *Emys obscurus* is a junior synonym of *Compsemys victa*, as the former taxon shows no apparent similarities with the latter. As the holotype is now lost and lacks apparent similarities with other taxa, we here declare *Emys obscurus* to be a nomen dubium instead.

Glyptops depressus Hay, 1908b nomen dubium

Taxonomic history. *Glyptops depressus* Hay, 1908b (new species); [*Glyptops depressus*] Gaffney 1979 (nomen dubium); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys torrejonensis* = *Compsemys vafer* = *Emys obscurus* = *Glyptops depressus* Lyson and Joyce 2011 (junior synonym).

Type material. USNM 5731 (holotype), a small, heavily weathered shell lacking all peripherals (Hay 1908b, figs. 33 and 34; Gaffney 1979, figs. 3–5).

Type locality. Colorado, USA; possibly Late Cretaceous of Denver Basin (Hay 1908b).

Comments. *Glyptops depressus* is based on a small shell that lacks all peripheral elements (Hay 1908b). Although it seems all but certain that the specimen originates from Colorado, only a note associated with the specimen hints at its possible origin from the Denver Basin (Hay 1908b), which would imply a Late Cretaceous (Maastrichtian) to Paleocene age. The surface of the type is completely worn, and it is therefore possible to establish neither the surface texture of the specimen nor even the placement of sulci. Gaffney (1979) treated *Glyptops depressus* as a nomen dubium but noted that the large mesoplastra are consistent with a referral to *Paracryptodira* (his *Baenidae*). Lyson and Joyce (2011), on the other hand, synonymized *Glyptops depressus* with *Compsemys victa* but did not provide an explicit rationale. Given that the morphology apparent in *Glyptops depressus* is fully consistent with *Compsemys victa* by having a large entoplastron that is broader than long, large mesoplastra that contact one another along the midline, broad, regular-shaped neurals with anterior short sides, and an anteriorly protruding costal I that forms a V-shaped space for the inset nuchal, we here agree with Lyson and Joyce (2011) that it seems highly plausible that *Glyptops depressus* is indeed synonymous with *Compsemys victa*. However, given that the locality data are indeed unclear, we here agree with Gaffney (1979) that it is more prudent to consider this taxon a nomen dubium.

Glyptops utahensis Gilmore, 1916b nomen invalidum (junior synonym of *Glyptops ornatus* Marsh, 1890)

Taxonomic history. *Glyptops utahensis* Gilmore, 1916b (new species); *Glyptops plicatulus* = *Glyptops ornatus* = *Glyptops utahensis* Gaffney 1979 (junior synonym).

Type material. CM 3412 (holotype), a complete shell (Gilmore 1916b, figs. 1 and 2, pl. 1); CM 3380 (paratype), a nearly complete shell (Gilmore 1916b, pl. 2).

Type locality. Carnegie Dinosaur Quarry, near Jensen, Uinta County, Utah (Gilmore 1916b); Brushy Basin Member, Morrison Formation, Kimmeridgian, Late Jurassic (Turner and Peterson 1999).

Comments. See *Glyptops ornatus* (above) for discussion.

Megasternon koenigii Gray, 1870 nomen invalidum (junior objective synonym of *Pleurosternon bullockii* [Owen, 1842])

Taxonomic history. [*Megasternon koenigii*] Gray, 1844 (nomen nudum); *Megasternon koenigii* = *Platemys bullockii* Gray 1870 (new species and objective synonym); *Pleurosternum bullockii* = *Megasternum koenigii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* Lydekker 1889a (junior synonym and incorrect spelling of genus name).

Type material. NHMUK R911 (holotype), a plastron (Owen and Bell 1849, pl. 21; Milner 2004, fig. 3).

Type locality. Purbeck, probably near Swanage, Dorset, United Kingdom (Lyddeker and Boulenger 1887; Lydekker 1889a); Purbeck Limestone Group, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Comments. See *Pleurosternon bullockii* (above) for discussion.

Mesochelys durlstonensis Evans and Kemp, 1975 nomen invalidum (junior synonym of *Pleurosternon bullockii* [Owen, 1842])

Taxonomic history. *Mesochelys durlstonensis* Evans and Kemp, 1975 (new species); *Pleurosternon bullockii* = *Mesochelys durlstonensis* = *Pleurosternon concinnum* = *Pleurosternon emarginatum* (pro parte) = *Pleurosternon ovatum* = *Pleurosternon oweni* = *Pleurosternon sedgwicki* = *Pleurosternon vansittarti* Milner 2004 (junior synonym).

Type material. UMCZ T1041 (holotype), a nearly complete cranium and partial postcranium (Evans and Kemp 1975, figs. 1–9, pls. 4 and 5; Gaffney 1979, figs. 23, 26–28).

Type locality. Durlston Bay, Dorset, United Kingdom (Evans and Kemp 1975); Purbeck Limestone Group, possibly Durlston Formation, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Comments. See *Pleurosternon bullockii* (above) for discussion.

Pleurosternon concinnum Owen, 1853 nomen invalidum (junior synonym of *Pleurosternon bullockii* [Owen, 1842])

Taxonomic history. *Pleurosternon concinnum* Owen, 1853 (new species); *Platemys concinna* Maack 1869 (new combination); *Pleurosternum bullockii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* Lydekker 1889b (junior synonym and incorrect spelling of genus name); *Pleurosternum bullockii* = *Megasternum koenigii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* Lydekker 1889a (junior synonym and incorrect spelling of genus names); *Pleurosternum bullockii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* = *Pleurosternum oweni* = *Pleurosternum sedgwicki* = *Pleurosternum typocardium* = *Pleurosternum vansittardi* [*sic*] Delair 1958 (junior synonym and incorrect spelling of genus name); *Pleurosternon bullockii* = *Mesochelys durlstonensis* = *Pleurosternon concinnum* = *Pleurosternon emarginatum* (pro parte) = *Pleurosternon ovatum* = *Pleurosternon oweni* = *Pleurosternon sedgwicki* = *Pleurosternon vansittarti* Milner 2004 (junior synonym).

Type material. DORCM G.17 (holotype), the nearly complete shell of a subadult individual (Owen 1853, pls. 2 and 3).

Type locality. Purbeck, Dorset, United Kingdom (Owen 1853); Purbeck Limestone Group, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Comments. See *Pleurosternon bullockii* (above) for discussion.

Pleurosternon ovatum Owen, 1853 nomen invalidum (junior synonym of *Pleurosternon bullockii* [Owen, 1842])

Taxonomic history. *Pleurosternon ovatum* Owen, 1853 (new species); *Platemys ovata* Maack 1869 (new combination); *Pleurosternum bullockii* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* Lydekker and Boulenger 1887 (junior synonym and incorrect spelling of genus name); *Pleurosternum bullockii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* Lydekker 1889b (junior synonym and incorrect spelling of genus name); *Pleurosternum bullockii* = *Megasternum koenigii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* Lydekker 1889a (junior synonym and incorrect spelling of genus names); *Pleurosternum bullockii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* = *Pleurosternum oweni* = *Pleurosternum sedgwicki* = *Pleurosternum typocardium* = *Pleurosternum vansittardi* [*sic*] Delair 1958 (junior synonym and incorrect spelling of genus name); *Pleurosternon bullockii* = *Mesochelys durlstonensis* = *Pleurosternon concinnum* = *Pleurosternon emarginatum* (pro parte) = *Pleurosternon ovatum* = *Pleurosternon oweni* = *Pleurosternon sedgwicki* = *Pleurosternon vansittarti* Milner 2004 (junior synonym).

Type material. NHMUK OR28618 (holotype), a complete carapace (Owen 1853, pl. 7; Milner 2004, fig. 5a).

Type locality. Swanage, Dorset, United Kingdom (Owen 1853; Lydekker 1889a); Purbeck Limestone Group, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Comments. See *Pleurosternon bullockii* (above) for discussion.

Pleurosternon oweni Seeley, 1869 nomen invalidum (junior synonym of *Pleurosternon bullockii* [Owen, 1842])

Taxonomic history. *Pleurosternon oweni* Seeley, 1869 (new species); *Pleurosternum bullockii* = *Pleurosternum*

concinnum = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* = *Pleurosternum oweni* = *Pleurosternum sedgwicki* = *Pleurosternum typocardium* = *Pleurosternum vansittardi* [*sic*] Delair 1958 (junior synonym and incorrect spelling of genus name); *Pleurosternon bullockii* = *Mesochelys durlstonensis* = *Pleurosternon concinnum* = *Pleurosternon emarginatum* (pro parte) = *Pleurosternon ovatum* = *Pleurosternon oweni* = *Pleurosternon sedgwicki* = *Pleurosternon vansittarti* Milner 2004 (junior synonym).

Type material. CAMSM J5328, a carapace lacking most of the carapacial rim (Seeley 1869; Milner 2004, not figured).

Type locality. Swanage, Dorset, United Kingdom (Seeley 1869); Purbeck Limestone Group, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Comments. Seeley (1869) coined dozens of names in his index on the fossils held in the collections of Cambridge University in Cambridge, United Kingdom, including *Pleurosternon oweni*, *Pleurosternon sedgwicki*, and *Pleurosternon vansittarti*. The name names are associated with descriptions but are not accompanied by figures. We were under the initial impression that none of these names are available in accordance with the rules of the ICZN (1999, art. 11.5, 15), as Seeley (1869, p. xv) specifically noted in the introduction that they were only intended "for convenience" and are "not necessarily to take rank as names of described species." However, the tentative nature of Seeley's (1869) statements does not allow considering his newly proposed names as unavailable on this ground alone (M. Kottelat, pers. comm., 2019). We therefore concur with previous authors in recognizing the availability of these three names but agree that they are junior synonyms of *Pleurosternon bullockii* (e.g., Watson, 1910a; Delair 1958; Milner 2004).

Pleurosternon sedgwicki Seeley, 1869 nomen invalidum (junior synonym of *Pleurosternon bullockii* [Owen, 1842])

Taxonomic history. *Pleurosternon sedgwicki* Seeley, 1869 (new species); *Pleurosternum bullockii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* = *Pleurosternum oweni* = *Pleurosternum sedgwicki* = *Pleurosternum typocardium* = *Pleurosternum vansittardi* [*sic*] Delair 1958 (junior synonym and incorrect spelling of genus name); *Pleurosternon bullockii* = *Mesochelys durlstonensis* = *Pleurosternon concinnum* = *Pleurosternon emarginatum* (pro parte) = *Pleurosternon ovatum* = *Pleurosternon oweni* = *Pleurosternon sedgwicki* = *Pleurosternon vansittarti* Milner 2004 (junior synonym).

Type material. CAMSM J5326 (holotype), a complete carapace (Seeley 1869; Milner 2004, not figured).

Type locality. Swanage, Dorset, United Kingdom (Seeley 1869); Purbeck Limestone Group, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Comments. See *Pleurosternon oweni* (above) for discussion.

Thalassemys ruetimeyeri Lydekker, 1889a nomen invalidum (junior synonym of *Dorsetochelys typocardium* [Seeley, 1869])

Taxonomic history. *Thalassemys ruetimeyeri* Lydekker, 1889a (new species); *Glyptops ruetimeyeri* = *Pleurosternon typocardium* Watson 1910a (new combination and senior synonym); "*Glyptops*" *typocardium* = *Thalassemys ruetimeyeri* Milner 2004 (junior synonym); *Ballerstedtia typocardia* = *Thalassemys ruetimeyeri* Karl, Gröning, et al. 2012 (junior synonym); *Dorsetochelys typocardium* = *Ballerstedtia bueckebergensis* = *Dorsetochelys delairi* = *Thalassemys ruetimeyeri* Pérez-García 2014 (junior synonym).

Type material. NHMUK OR40676 (holotype), the central portions of a carapace (Lydekker 1889a, fig. 36; Milner 2004, fig. 9; Pérez-García 2014, figs. 1 and 5).

Type locality. Swanage, Dorset, United Kingdom (Lydekker 1889a; Figure 4); Purbeck Limestone Group, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Comments. See *Dorsetochelys typocardium* (above) for discussion.

Pleurosternon vansittarti Seeley, 1869 nomen invalidum (junior synonym of *Pleurosternon bullockii* [Owen, 1842])

Taxonomic history. *Pleurosternon vansittarti* Seeley, 1869 (new species); *Pleurosternum bullockii* = *Pleurosternum concinnum* = *Pleurosternum emarginatum* (pro parte) = *Pleurosternum ovatum* = *Pleurosternum oweni* = *Pleurosternum sedgwicki* = *Pleurosternum typocardium* = *Pleurosternum vansittardi* [*sic*] Delair 1958 (junior synonym and incorrect spelling of genus name); *Pleurosternon bullockii* = *Mesochelys durlstonensis* = *Pleurosternon concinnum* = *Pleurosternon emarginatum* (pro parte) = *Pleurosternon ovatum* = *Pleurosternon oweni* = *Pleurosternon sedgwicki* = *Pleurosternon vansittarti* Milner 2004 (junior synonym).

Type material. CAMSM J5327 (holotype), a nearly complete carapace (Seeley 1869; Milner 2004, not figured).

Type locality. Swanage, Dorset, United Kingdom (Seeley 1869); Purbeck Limestone Group, Berriasian, Early Cretaceous (Allen and Wimbledon 1991; Feist et al. 1995; Milner 2004).

Comments. See *Pleurosternon oweni* (above) for discussion.

Probaena sculpta Hay, 1903 nomen dubium

Taxonomic history. *Probaena sculpta* Hay, 1903 (new species); [*Probaena sculpta*] Gaffney 1979 (nomen dubium).

Type material. CM 917 (holotype), a small, nearly complete shell (Hay 1903, pl. 3; Hay 1908b, pl. 7.5).

Type locality. Marsh-Felch Quarry, 8 miles (ca. 13 km) north of Cañon City (Hay 1903), Fremont County, Colorado, USA; Brushy Basin Member, Morrison Formation, Kimmeridgian, Late Jurassic (Turner and Peterson 1999).

Comments. *Probaena sculpta* is based on a near-complete shell from the Morrison Formation of Colorado (Hay 1903). The type locality is now known as the Marsh-Felch Quarry and to be of Late Jurassic (Tithonian) age (Turner and Peterson 1999). The holotype is only 105 mm long and therefore clearly represents a juvenile. We therefore agree with Gaffney (1979) that this taxon should be regarded as a nomen dubium, as juveniles rarely display enough characters to allow diagnosing a valid taxon. We instead refer this fragment to *Paracryptodira* indet.

Testudo stricklandi Phillips, 1871
nomen dubium

Taxonomic history. *Testudo stricklandi* Phillips, 1871 (new species); *Protochelys stricklandi* = *Chelys*? *blakei* (?) Lydekker 1889a (senior synonym); [*Protochelys blakii*] = *Testudo stricklandi* Anquetin and Claude 2008 (junior synonym).

Type material. OUMNH J77375 and J77376 (syntype), a complete first vertebral scute preserved on two slabs (Phillips 1871, fig. 41.10–11; Anquetin and Claude 2008, fig. 3C and D); other syntypes cannot be identified (see below).

Type locality. Stonesfield, Oxfordshire, United Kingdom (Phillips 1871); Stonesfield Slate, Taynton Limestone Formation, middle Bathonian, Middle Jurassic (Torrens 1980; Boneham and Wyatt 1993).

Comments. *Testudo stricklandi* is based on a series of isolated shell scutes from the Middle Jurassic of the Stonesfield Slate housed at the OUMNH (Phillips 1871). Only one of these syntypes can be identified with confidence based on illustrations that accompany the type description (see above). Four additional fossil scutes from Stonesfield are still present at the OUMNH, but it remains uncertain whether these are part of the syntype series (Anquetin and Claude 2008). Lydekker (1889a) proposed the new combination *Protochelys stricklandi* for this material and referred a collection of similar fossil scutes from Stonesfield housed at the NHMUK. He also tentatively proposed to include an isolated coracoid, the holotype of *Chelys*? *blakii* Mackie, 1863 (Lydekker 1889a). In accordance with this author, Anquetin and Claude (2008) reassessed all of the available turtle material from Stonesfield as a single taxon, *Protochelys blakii*, which they considered to be a nomen dubium. However, because there is no evidence that the coracoid and scutes belong to a single taxon (see *Chelys*? *blakii*, above), we treat *Chelys*? *blakii* and *Testudo stricklandi* as two separate taxa in the present review.

Testudo stricklandi is known only from isolated carapacial scutes, which represents a rare occurrence in the fossil record (Anquetin and Claude 2008). These vertebral scutes are wider than long, and the pleural scutes are slightly longer than wide. The configuration is relatively common in stem turtles and basal crown-group turtles and provides few characters of diagnostic value. Therefore, in accordance with Anquetin and Claude (2008), we consider *Testudo stricklandi* to be a nomen dubium herein.

The turtle material from Stonesfield has been considered by some authors to belong to pleurosternids (Bergounioux 1955; Romer 1956, 1966), but there is no support for this conclusion. This material should therefore be regarded as *Testudinata* indet. (Anquetin and Claude 2008).

Acknowledgments

We would like to thank Adán Pérez-Garcia, Serjoscha Evers, Larry Gall, and an anonymous reviewer for thoughtful comments that helped improve the quality of this manuscript. Tyler Lyson and Yann Rollot are thanked for discussion. Maurice Kottelat is thanked for helping resolve issues related to rules of the ICZN.

Received 6 February 2019; revised and accepted 29 May 2019.

Appendix 1
Institutional Abbreviations

ALTSHN	Associação Leonel Trindade–Sociedade de História Natural, Torres Vedras, Portugal
AMNH	American Museum of Natural History, New York, New York, USA
CAMSM	Sedgwick Museum, University of Cambridge, Cambridge, United Kingdom
CM	Carnegie Museum of Natural History, Pittsburg, Pennsylvania, USA
DNM	Dinosaur National Monument, Jensen, Utah, USA
DORCM	Dorset County Museum, Dorchester, United Kingdom
GUM	Geomuseum der Universität Münster, Münster, Germany
GZG	Geowissenschaftliches Zentrum der Universität Göttingen, Göttingen, Germany
MAP	Museo Aragonés de Paleontología, Teruel, Spain
MNHN	Muse¥um national d'Histoire naturelle, Paris, France
NHMUK	Natural History Museum, London, United Kingdom
OUMNH	Oxford University Museum of Natural History, Oxford, United Kingdom
TGM	Tate Geological Museum, Casper, Wyoming, USA

UCM	University of Colorado Museum of Natural History, Boulder, Colorado, USA
UMCZ	Museum of Zoology, University of Cambridge, Cambridge, United Kingdom
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA
YPM VP	Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

Appendix 2
Named Nonbaenid Paracryptodiran Genera

Ballerstedtia Karl, Gröning, et al., 2012 (type species: *Pleurosternon typocardium* Seeley, 1869)

Berruchelus Pérez-García, 2012 (type species: *Berruchelus russelli* Pérez-García, 2012)

Compsemys Leidy, 1856 (type species: *Compsemys victa* Leidy, 1856)

Desmemys Wegner, 1911 (type species: *Desmemys bertelsmanni* Wegner, 1911)

Digerrhum Cope, 1870 (type species: *Platemys bullockii* Owen, 1842)

Dinochelys Gaffney, 1979 (type species: *Dinochelys whitei* Gaffney, 1979)

Dorsetochelys Evans and Kemp, 1976 (type species: *Dorsetochelys delairi* Evans and Kemp, 1976)

Glyptops Marsh, 1890 (type species: *Glyptops ornatus* Marsh, 1890)

Megasternon Gray, 1870 (type species: *Megasternon koenigii* Gray, 1870 [junior objective synonym of *Platemys bullockii* Owen, 1842])

Mesochelys Evans and Kemp, 1975 (type species: *Mesochelys durlstonensis* Evans and Kemp, 1975)

Pleurosternon Owen, 1853 (type species: *Pleurosternon concinnum* Owen, 1853)

Probaena Hay, 1903 (type species: *Probaena sculpta* Hay, 1903)

Protochelys Lydekker, 1889a (type species: *Testudo stricklandi* Phillips, 1871)

Riodevemys Pérez-García, Royo-Torres, et al., 2015 (type species: *Riodevemys inumbragigas* Pérez-García, Royo-Torres, et al., 2015)

Selenemys Pérez-García and Ortega, 2011 (type species: *Selenemys lusitanica* Pérez-García and Ortega, 2011)

Toremys Pérez-García, Espílez, et al., 2015 (type species: *Toremys cassiopeia* Pérez-García, Espílez, et al., 2015)

Uluops Carpenter and Bakker, 1990 (type species: *Uluops uluops* Carpenter and Bakker, 1990)

Appendix 3
Biogeographic Summary of Nonbaenid Paracryptodiran Turtles

Numbers in brackets reference Figures 3 and 4.

Abbreviation: TL, type locality.

Canada

[1] Late Cretaceous, Santonian; Alberta; *Compsemys* sp. (Brinkman 2003)

[2] Late Cretaceous, Maastrichtian; Alberta; *Compsemys victa* (Lyson and Joyce 2011; *Compsemys* sp. of Brinkman 2003)

France

[3] Late Jurassic, Tithonian; Department of Pas-de-Calais; *Pleurosternidae* indet. (Lapparent de Broin et al. 1996; Lapparent de Broin 2001; *Pleurosternon bullockii* of Sauvage 1894, 1900, 1912, 1921)

[4] Late Jurassic, Tithonian; Department of Charente-Maritime; *Pleurosternidae* indet. (*Pleurosternidae* indet. and *Pleurosternon* sp. of Vullo et al. 2014)

[5] Early Cretaceous, Hauterivian–Barremian; Departments of Charente and Charente-Maritime; *Pleurosternidae* indet. (*Pleurosternidae* indet. and *Pleurosternon* sp. of Néraudeau et al. 2012)

[6] Late Paleocene, Thanetian; Department of Marne; *Compsemys russelli* (TL) (Pérez-García 2012; *Compsemys* sp. of Broin 1977, Lapparent de Broin 2001)

[7] Late Paleocene, Thanetian; Department of Puy-de-Dôme; *Compsemys russelli* (Pérez-García 2012; *Compsemys* sp. of Broin 1977, Lapparent de Broin 2001)

Germany

[8] Early Cretaceous, late Berriasian; Lower Saxony; *Dorsetochelys typocardium* (*Ballerstedtia bueckebergensis* of Karl, Gröning, et al. 2012; *Dorsetochelys typocardium* of Pérez-García 2014), *Pleurosternidae* indet. (*Pleurosternon bullockii* of Karl et al. 2007)

[9] Early Cretaceous, late Berriasian; North Rhein-Westphalia; *Paracryptodira* indet. (*Desmemys bertelsmanni* of Wegner 1911; Karl, Nyhuis, et al. 2012)

Mexico

[10] Late Cretaceous, Campanian; Coahuila; *Compsemys victa* (Rodriguez-de la Rosa and Cevallos-Ferriz 1998; Brinkman and Rodriguez de la Rosa 2006)

Portugal

[11] Late Jurassic, late Kimmeridgian; Leiria District; *Paracryptodira* indet. (*Platychelys* indet. of Bräm 1973; *Pleurosternidae* indet. of Scheyer and Anquetin 2008)

[12] Late Jurassic, late Kimmeridgian; Lisbon District; *Selenemys lusitanica* (TL) (Pérez-García and Ortega 2011)

Spain

[13] Late Jurassic, Tithonian; Aragon; *Riodevemys inumbragigas* (TL) (Pérez-García, Royo-Torres, et al. 2015)

[14] Late Jurassic, Kimmeridgian–Tithonian; Valencia; *Pleurosternon* indet. (Pérez-García 2009; *Pleurosternon portlandicum*? of Royo Gómez 1926)

[15] Early Cretaceous, Barremian; Aragon; *Pleurosternidae* indet. (Pérez-García et al. 2013)

[16] Early Cretaceous, Barremian; Castilla–La Mancha; *Pleurosternidae* indet. (Lapparent de Broin 2001)

[17] Early Cretaceous, early Albian; Aragon; *Toremys cassiopeia* (TL) (Pérez-García, Espílez, et al. 2015)

United States of America

[18] Late Jurassic, Kimmeridgian–Tithonian; Wyoming; *Dinochelys whitei* (Gaffney 1979), *Glyptops ornatus* (TL) (Marsh 1890; *Glyptops plicatulus* of Hay 1908b), *Uluops uluops* (TL) (Carpenter and Bakker 1990), *Paracryptodira* indet. (*Glyptops ornatus* of Marsh 1890; *Glyptops plicatulus* of Hay 1908a, 1908b, Gaffney 1972)

[19] Late Jurassic, Kimmeridgian; Utah; *Dinochelys whitei* (TL) (Gaffney 1979), *Glyptops ornatus* (*Glyptops utahensis* of Gilmore 1916b), *Paracryptodira* indet. (*Glyptops plicatulus* of Gaffney 1979)

[20] Late Jurassic, Kimmeridgian; western Colorado; *Paracryptodira* indet. (*D. whitei* of Brinkman et al. 2000)

[21] Late Jurassic, Kimmeridgian–Tithonian; central Colorado; *Paracryptodira* indet. (*Glyptops plicatulus* of Cope 1877), *Paracryptodira* indet. (*Probaena sculpta* of Hay 1903)

[22] Late Jurassic, Kimmeridgian (Turner and Peterson 1999); New Mexico; *Paracryptodira* indet. (*Glyptops plicatulus* of Lucas et al. 2006)

[23] Late Cretaceous, Campanian; Utah; *Compsemys victa* (Lyson and Joyce 2011; Hutchison et al. 2013)

[24] Late Cretaceous, Campanian; New Mexico; *Compsemys victa* (Lyson and Joyce 2011; Sullivan et al. 2013; *Compsemys* sp. of Armstrong-Ziegler 1980 and McCord 1996)

[25] Late Cretaceous, Campanian; Texas; *Compsemys victa* (Tomlinson 1997)

[26] Late Cretaceous, Maastrichtian; Montana; *Compsemys victa* (Hay 1908b; Estes et al. 1969; Gaffney 1972; Hutchison and Archibald 1986; Holroyd et al. 2014)

[27] Late Cretaceous, Maastrichtian; western North Dakota; Maastrichtian, *Compsemys victa* (Holroyd and Hutchison 2002; Lyson and Joyce 2011)

[28] Late Cretaceous, Maastrichtian; central North Dakota; Maastrichtian, *Compsemys victa* (TL) (Leidy, 1856)

[29] Late Cretaceous, Maastrichtian; Lance Basin, Wyoming; *Compsemys victa* (Hay 1908b; Whitmore and Martin 1986; Holroyd and Hutchison 2002)

[30] Late Cretaceous, Maastrichtian; Hanna Basin, Wyoming; *Compsemys victa* (Lillegraven and Eberle 1999)

[31] Late Cretaceous, Maastrichtian; New Mexico; *Compsemys victa* (McCord 1996; Jasinski et al. 2011; = *Compsemys* sp. of Gilmore 1916a)

[32] Early Paleocene, Puercan NALMA; Montana; *Compsemys victa* (Hutchison and Archibald 1986; Lyson and Joyce 2011; Holroyd et al. 2014)

[33] Early Paleocene, Torrejonian NALMA; Montana; *Compsemys victa* (Estes 1976; Lyson and Joyce 2011)

[34] Early Paleocene, Puercan NALMA; Big Horn Basin, Wyoming; *Compsemys victa* (Bartels 1980)

[35] Early Paleocene, Puercan NALMA; Hanna Basin, Wyoming; *Compsemys victa* (Lyson and Joyce 2011)

[36] Early Paleocene, Puercan NALMA; Denver Basin, Colorado; *Compsemys victa* (Hutchison and Holroyd 2003)

[37] Late Paleocene, Tiffanian–Clarkforkian NALMAs; Piceance Creek Basin, Colorado; *Compsemys victa* (Burger 2007; Lichtig and Lucas 2015)

[38] Early Paleocene, Puercan–Torrejonian NALMAs; New Mexico; *Compsemys victa* (McCord 1996; Lyson and Joyce 2011; = *C. parva* and *C. vafer* of Hay 1910; = *C. parva*, *C. vafer*, *C. puercensis*, and *C. torrejonensis* of Gilmore 1919)

[39] Paleocene; Texas; *Compsemys victa* (Tomlinson 1997)

United Kingdom

[40] Middle Jurassic, Bathonian; Oxfordshire; *Pleurosternidae* indet. (Gillham 1994; Scheyer and Anquetin 2008)

[41] Late Jurassic, Tithonian; Dorset; "*Pleurosternon*" *portlandicum* (TL) (Lydekker 1889a)

[42] Early Cretaceous, Berriasian; Dorset; *Dorsetochelys typocardium* (TL) (Lydekker 1889a; Watson 1910b; "*Glyptops*" *typocardium* of Milner 2004; *Dorsetochelys typocardium* of Pérez-García 2014), *Pleurosternon bullockii* (TL) (Owen 1842, 1853; Seeley 1869; Delair 1958; Milner 2004)

Appendix 4
Hierarchical Taxonomy of *Paracryptodira*

Paracryptodira Gaffney, 1975
- *Compsemys* Leidy, 1856
  - *Compsemys victa* Leidy, 1856
  - *Compsemys russelli* (Pérez-García, 2012), comb. nov.
- *Uluops uluops* Carpenter and Bakker, 1990
- *Baenidae* Cope, 1873 (see Joyce and Lyson [2015] for review)
- *Pleurosternidae* Cope, 1868
  - *Dinochelys whitei* Gaffney, 1979
  - *Dorsetochelys typocardium* (Seeley, 1869)
  - *Glyptops ornatus* Marsh, 1890
  - *Pleurosternon* Owen, 1853
    - *Pleurosternon bullockii* (Owen, 1842)

"*Pleurosternon*" *portlandicum* Lydekker, 1889a
Riodevemys inumbragigas Pérez-García, Royo-Torres, et al., 2015
Selenemys lusitanica Pérez-García and Ortega, 2011
Toremys cassiopeia Pérez-García, Espílez, et al., 2015

Literature Cited

Allen, P. and W.A. Wimbledon. 1991. Correlation of NW European Purbeck-Wealden (nonmarine Lower Cretaceous) as seen from the English type-areas. Cretaceous Research 12(5):511–526.

Anquetin, J. and J. Claude. 2008. Reassessment of the oldest British turtle: *Protochelys* from the Middle Jurassic Stonesfield Slate of Stonesfield, Oxfordshire, UK. Geodiversitas 30(2):331–344.

Anquetin, J., C. Püntener and W.G. Joyce. 2017. A review of the fossil record of turtles of the clade *Thalassochelydia*. Bulletin of the Peabody Museum of Natural History 58(2): 317–369.

Armstrong-Ziegler, J.G. 1980. Amphibia and Reptilia from the Campanian of New Mexico. Fieldiana, Geology 4:1–39.

Bakker, R.T. 1998. Dinosaur mid-life crisis: the Jurassic-Cretaceous transition in Wyoming and Colorado. New Mexico Museum of Natural History and Sciences Bulletin 14:67–77.

Bartels, W.S. 1980. Early Cenozoic reptiles and birds from the Bighorn Basin, Wyoming. University of Michigan Papers on Paleontology 24:73–79.

Baur, G. 1891. Notes on some little known American fossil tortoises. Proceedings of the Academy of Natural Sciences of Philadelphia 43:411–430.

Bergounioux, F.-M. 1955. Testudinata. In: J. Piveteau, ed. Traité de Paléontologie, Volume 5. Paris: Masson et Cie. pp. 487–544.

Boneham, B.F.W. and R.J. Wyatt. 1993. The stratigraphical position of the Middle Jurassic (Bathonian) Stonesfield Slate of Stonesfield, Oxfordshire, UK. Proceedings of the Geologists' Association 104(2):123–136.

Bräm, H. 1973. Chelonia from the Upper Jurassic of Guimarota mine (Portugal). Contribuição para o conhecimento da Fauna do Kimeridgiano da Mina de Lignito Guimarota (Leiria, Portugal). Memórias dos Serviços geológicos de Portugal 22:135–141.

Brinkman, D.B. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. Canadian Journal of Earth Sciences 40(4):557–571.

Brinkman, D.B. and R. Rodriguez de la Rosa. 2006. Nonmarine turtles from the Cerro del Pueblo Formation (Campanian), Coahuila State, Mexico. New Mexico Museum of Natural History and Science Bulletin 35:229–234.

Brinkman, D.B., K. Stadtman and D. Smith. 2000. New material of *Dinochelys whitei* Gaffney, 1979, from the Dry Mesa Quarry (Morrison Formation, Jurassic) of Colorado. Journal of Vertebrate Paleontology 20(2):269–274.

Broin, F. de. 1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. Paris: Éditions du muséum. (Mémoires du Muséum National d'histoire naturelle, nouvelle série, Series C, Sciences de la terre 38.) 366 pp.

Burger, B.J. 2007. A new late Paleocene vertebrate fauna from the Ohio Creek Formation of western Colorado. Mountain Geologist 44(3):141–150.

Carpenter, K. and R.T. Bakker. 1990. A new latest Jurassic vertebrate fauna, from the highest levels of the Morrison Formation at Como Bluff, Wyoming, with comments on Morrison biochronology. Part II. A new baenid turtle. Hunteria 2:3–4.

Cope, E.D. 1868. On the origin of genera. Proceedings of the Academy of Natural Sciences of Philadelphia 20:242–300.

—1870. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Transactions of the American Philosophical Society 14(1):1–252.

—1873 [1872] Descriptions of some new Vertebrata from the Bridger Group of the Eocene. Proceedings of the American Philosophical Society 12(86):460–465.

—1877. On reptilian remains from the Dakota Beds of Colorado. Proceedings of the American Philosophical Society 17(100):193–196.

Delair, J.B. 1958. The Mesozoic reptiles of Dorset. Part one. Proceedings of the Dorset Natural History and Archaeological Society 79:47–72.

Dollo, L. 1886. Première note sur les chéloniens du Bruxelliens (Éocène moyen) de la Belgique. Bulletin du Musée Royal d'Histoire Naturelle Belgique 4:75–96.

Estes, R. 1976. Middle Paleocene Lower Vertebrates from the Tongue River Formation, southeastern Montana. Journal of Paleontology 50(3):500–520.

Estes, R., P. Berberian and C.A.M. Meszoely. 1969. Lower vertebrates from the Late Cretaceous Hell Creek Formation, McCone County, Montana. Breviora 337:1–33.

Evans, J. and T.S. Kemp. 1975. The cranial morphology of a new Lower Cretaceous turtle from southern England. Palaeontology 18(1):25–40.

—1976. A new turtle skull from the Purbeckian of England and a note on the early dichotomies of cryptodire turtles. Palaeontology 19(2):317–324.

Feist, M., R.D. Lake and C.J. Wood. 1995. Charophyte biostratigraphy of the Purbeck and Wealden of southern England. Palaeontology 38(2):407–442.

Foster, J.R. and S.K. McMullen. 2017. Paleobiogeographic distribution of Testudinata and neosuchian Crocodyliformes in the Morrison Formation (Upper Jurassic) of North America: Evidence of habitat zonation? Palaeogeography, Palaeoclimatology, Palaeoecology 468:208–215.

Foth, C., E. Ascarrunz and W.G. Joyce. 2017. Still slow, but even steadier: an update on the evolution of turtle cranial disparity interpolating shapes along branches. Royal Society Open Science 4:170899.

Gaffney, E.S. 1972. The systematics of the North American family Baenidae (Reptilia, Cryptodira). Bulletin of the American Museum of Natural History 147:241–320.

—1975. A phylogeny and classification of higher categories of turtles. Bulletin of the American Museum of Natural History 155:387–436.

—1979. The Jurassic turtles of North America. Bulletin of the American Museum of Natural History 162:91–136.

Gaffney, E.S. and P.A. Meylan. 1988. A phylogeny of turtles. In: M.J. Benton, ed. The Phylogeny and Classification

of the Tetrapods, Volume 1. Oxford: Clarendon Press. pp. 157–219.

Georgalis, G.L. and W.G. Joyce. 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History 58:115–208.

Gervais, P. 1859. Zoologie et paléontologie françaises: Nouvelles recherches sur les animaux vertébrés dont on trouve les ossements enfouis dans le sol de la France et sur leur comparaison avec les espèces propres aux autres régions du globe. Paris: Arthus Bertrand. 544 pp.

Giebel, C.G. 1847. Fauna der Vorwelt mit steter Berücksichtigung der lebenden Thiere. Erster Band: Wirbelthiere. Zweite Abtheilung: Vögel und Amphibien. Leipzig, Germany: F.A. Brockhaus. 217 pp.

Gillham, C. 1994. A fossil turtle (Reptilia: Chelonia) from the Middle Jurassic of Oxfordshire, England. Neues Jahrbuch der Geologie und Paläontologie. Monatshefte 10:581–596.

Gilmore, C.W. 1916a. Contributions to the geology and paleontology of San Juan County, New Mexico. 2. Vertebrate faunas of the Ojo Alamo, Kirtland and Fruitland formations. U.S. Geological Survey Professional Paper 98:279–308.

—1916b. Description of a new species of tortoise from the Jurassic of Utah. Annals of the Carnegie Museum 10:7–12.

—1919. Reptilian faunas of the Torrejon, Puerco, and underlying Upper Cretaceous formations of San Juan County, New Mexico. U.S. Geological Survey Professional Paper 119:1–68.

Gray, J.E. 1842. Synopsis of the Contents of the British Museum. London: G. Woodfall and Son. 308 pp.

—1844. Catalogue of the Tortoises, Crocodiles, and Amphisbaenians, in the Collection of the British Museum. London: Edward Newman. 80 pp.

—1870. Supplement to the Catalogue of Shield Reptiles in the Collection of the British Museum. Part I. Testudinata (Tortoises). London: Taylor and Francis. 79 pp.

Hay, O.P. 1903. Description of a new genus and species of tortoise from the Jurassic of Colorado. Annals of the Carnegie Museum 2:201–204.

—1908a. Descriptions of five species of North American fossil turtles, four of which are new. Proceedings of the United States National Museum 35:161–169.

—1908b. The fossil turtles of North America. Carnegie Institution of Washington Publication 75:1–568.

—1910. Descriptions of eight new species of fossil turtles from west of the one hundredth meridian. Proceedings of the United States National Museum 38:307–326.

Hirayama, R., D.B. Brinkman and I.G. Danilov. 2000. Distribution and biogeography of non-marine Cretaceous turtles. Russian Journal of Herpetology 7(3):181–198.

Holroyd, P.A. and J.H. Hutchison. 2002. Patterns of geographic variation in latest Cretaceous vertebrates: evidence from the turtle component. Geological Society of America Special Papers 361:177–190.

Holroyd, P.A., G.P. Wilson and J.H. Hutchison. 2014. Temporal changes within the latest Cretaceous and early Paleogene turtle faunas of northeastern Montana. Geological Society of America Special Papers 503:299–312.

Hutchison, J.H. and J.D. Archibald. 1986. Diversity of turtles across the Cretaceous/Tertiary boundary in northeastern Montana. Palaeogeography, Palaeoclimatology, Palaeoecology 55(1):1–22.

Hutchison, J.H. and P.A. Holroyd. 2003. Late Cretaceous and early Paleocene turtles of the Denver Basin, Colorado. Rocky Mountain Geology 38(1):121–142.

Hutchison, J.H., M.J. Knell and D.B. Brinkman. 2013. Turtles from the Kaiparowits Formation, Utah. In: A.L. Titus and M.A. Loewen, eds. At the Top of the Grand Staircase: The Late Cretaceous of Southern Utah. Bloomington, IN: Indiana University Press. pp. 295–318.

[ICZN] International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. 4th ed. London: International Trust for Zoological Nomenclature. 306 pp.

Jansen, M. and N. Klein. 2014. A juvenile turtle (Testudines, Eucryptodira) from the Upper Jurassic of Langenberg Quarry, Oker, northern Germany. Palaeontology 57(4):743–756.

Jasinski, S.E., R.M. Sullivan and S.G. Lucas. 2011. Taxonomic composition of the Alamo Wash local fauna from the Upper Cretaceous Ojo Alamo Formation (Naashoibito Member), San Juan Basin, New Mexico. Bulletin of the New Mexico Museum of Natural History and Science 53:216–271.

Joyce, W.G. 2007. Phylogenetic relationships of Mesozoic turtles. Bulletin of the Peabody Museum of Natural History 48(1):3–102.

—2017. A review of the fossil record of basal Mesozoic turtles. Bulletin of the Peabody Museum of Natural History 58(1):65–113.

Joyce, W.G., S.D. Chapman, R.T.J. Moody and C.A. Walker. 2011. The skull of the solemydid turtle *Helochelydra nopcsai* from the Early Cretaceous (Barremian) of the Isle of Wight (UK) and a review of Solemydidae. Special Papers in Paleontology 86:75–97.

Joyce, W.G. and T.R. Lyson. 2015. A review of the fossil record of turtles of the clade *Baenidae.* Bulletin of the Peabody Museum of Natural History 56(2):147–183.

Joyce, W.G., M. Rabi, J.M. Clark and X. Xu. 2016. A toothed turtle from the Late Jurassic of China and the global biogeographic history of turtles. BMC Evolutionary Biology 16:236.

Karl, H.-V., E. Gröning, C. Brauckmann and M. Reich. 2012. *Ballerstedtia bueckebergensis*, a new turtle from the Early Cretaceous Wealden facies of Germany (Testudines: Pleurosternidae). Studia Palaeocheloniologica 4:47–60.

Karl, H.-V., C.J. Nyhuis and L. Schleicher. 2012. Redescription of *Desmemys bertelsmanni* (Wegner, 1911) from the Upper Jurassic and Lower Cretaceous of Germany (Testudines: Pleurosternidae). Studia Palaeocheloniologica 4:31–46.

Karl, H.-V., U. Staesche, G. Tichy, J. Lehmann and S. Peitz. 2007. Systematik der Schildkröten (Anapsida: Chelonii) aus Oberjura und Unterkreide von Nordwestdeutschland. Geologisches Jahrbuch, Reihe B 98:5–89.

Kuhn, O. 1964. Fossilium Catalogus, Volume 1: Animalia, Part 107, Testudines. 's-Gravenhage, the Netherlands: Ysel Press. 299 pp.

Lapparent de Broin, F. de. 2001. The European turtle fauna from the Triassic to the Present. Dumerilia 4(3):155–217.

Lapparent de Broin, F. de, B. Lange-Badré and M. Dutrieux. 1996. Nouvelles découvertes de tortues dans le Jurassique supérieur du Lot (France) et examen du taxon Plesiochelyidae. Revue de Paléobiologie 15:533–570.

Leidy, J. 1856. Notices of extinct Vertebrata discovered by Dr. F. V. Hayden, during the expedition to the Sioux country

under the command of Lieut. G. K. Warren. Proceedings of the Academy of Natural Sciences of Philadelphia 8:311–312.
—1860. Extinct Vertebrata from the Judith River and Great Lignite formations of Nebraska. Transactions of the American Philosophical Society, New Series 11:139–154.
—1870. [Descriptions of *Emys jeanesi*, *Emys haydeni*, *Baena arenosa*, and *Saniwa ensidens*.] Proceedings of the Academy of Natural Sciences of Philadelphia 22:123–124.
Lichtig, A.J. and S.G. Lucas. 2015. Paleocene-Eocene turtles of the Piceance Creek Basin, Colorado. New Mexico Museum of Natural History and Science Bulletin 67:145–152.
Lillegraven, J.A. and J.J. Eberle. 1999. Vertebrate faunal changes through Lancian and Puercan time in southern Wyoming. Journal of Paleontology 73(4):691–710.
Lipka, T.R., F. Therrien, D.B. Weishampel, H.A. Jamniczky, W.G. Joyce, M.W. Colbert and D.B. Brinkman. 2006. A new turtle from the Arundel Clays (Potomac Formation, Early Cretaceous) of Maryland, U.S.A. Journal of Vertebrate Paleontology 26(2):300–307.
Lucas, S.G., L.F. Rinehart and A.B. Heckert. 2006. *Glyptops* (Testudines, Pleurosternidae) from the Upper Jurassic Morrison Formation, New Mexico. In: J.R. Foster and S.G. Lucas, eds. Paleontology and Geology of the Upper Jurassic Morrison Formation. Albuquerque, NM: New Mexico Museum of Natural History and Science. (Bulletin 36.) pp. 97–99.
Lydekker, R. 1889a. Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History). Part III. The Order Chelonia. London: Trustees of the British Museum. 309 pp.
—1889b. On certain chelonian remains from the Wealden and Purbeck. Quarterly Journal of the Geological Society 45:511–518.
Lydekker, R. and G.A. Boulenger. 1887. Notes on Chelonia from the Purbeck, Wealden and London-clay. Geological Magazine 4:270–275.
Lyson, T.R. and W.G. Joyce. 2011. Cranial anatomy and phylogenetic placement of the enigmatic turtle *Compsemys victa* Leidy, 1856. Journal of Paleontology 85(4):789–801.
Maack, G.A. 1869. Die bis jetzt bekannten fossilen Schildkröten und die im oberen Jura bei Kelheim (Bayern) und Hannover neu aufgefundenen ältesten Arten derselben. Palaeontographica 18:193–336.
Mackie, S.J. 1863. Turtles in the Stonesfield Slate. Geologist 6(2):41–43.
Maidment, S.C.R., D. Balikova and A.R. Muxworthy. 2017. Magnetostratigraphy of the Upper Jurassic Morrison Formation at Dinosaur National Monument, Utah, and prospects for using magnetostratigraphy as a correlative tool in the Morrison Formation. In: K.E. Zeigler and W.G. Parker, eds. Terrestrial Depositional Systems. Amsterdam: Elsevier. pp. 279–302.
Marsh, O.C. 1890. Notice of some extinct Testudinata. American Journal of Science 40:177–179.
McCord, R.D. 1996. Turtle biostratigraphy of Late Cretaceous and Early Tertiary continental deposits San Juan Basin, New Mexico. Fossils of Arizona 4:135–153.
Meyer, H. von. 1854. Mittheilung, an Professor Bronn gerichtet. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde 1854:575–581.
Milner, A.R. 2004. The turtles of the Purbeck Limestone Group of Dorset, southern England. Palaeontology 47(6): 1441–1467.
Néraudeau, D., R. Allain, M. Ballèvre, D.J. Batten, E. Buffetaut, J.P. Colin, M.P. Dabard, et al. 2012. The Hauterivian–Barremian lignitic bone bed of Angeac (Charente, south-west France): stratigraphical, palaeobiological and palaeogeographical implications. Cretaceous Research 37:1–14.
Nopcsa, F. 1928. The genera of reptiles. Palaeobiologica 1:163–188.
Owen, R. 1842. Report on British fossil reptiles. Part II. In: Report of the Eleventh Meeting of the British Association for the Advancement of Science; Held at Plymouth in July 1841. London: Murray. pp. 60–204.
—1853. Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Part I. Chelonia. Palaeontographical Society Monograph 7:1–12.
Owen, R. and T. Bell. 1849. Monograph of the fossil Reptilia of the London Clay, and of the Bracklesham and other Tertiary beds. Part I. Chelonia. London: Palaeontographical Society. (Monograph 2.) 76 pp.
Pérez-García, A. 2009. Revisión histórica y sistemática de las primeras citas de quelonios del Cretácico español. Revista Española de Paleontología 24(1):93–104.
—2012. *Berruchelus russelli*, gen. et sp. nov., a paracryptodiran turtle from the Cenozoic of Europe. Journal of Vertebrate Paleontology 32(3):545–556.
—2014. Revision of the poorly known *Dorsetochelys typocardium*, a relatively abundant pleurosternid turtle (Paracryptodira) in the Early Cretaceous of Europe. Cretaceous Research 49:152–162.
Pérez-García, A., E. Espílez, L. Mampel and L. Alcalá. 2015. A new European Albian turtle that extends the known stratigraphic range of the Pleurosternidae (Paracryptodira). Cretaceous Research 55:74–83.
Pérez-García, A. and F. Ortega. 2011. *Selenemys lusitanica*, gen. et sp. nov., a new pleurosternid turtle (Testudines: Paracryptodira) from the Upper Jurassic of Portugal. Journal of Vertebrate Paleontology 31(1):60–69.
Pérez-García, A., R. Royo-Torres and A. Cobos. 2015. A new European Late Jurassic pleurosternid (Testudines, Paracryptodira) and a new hypothesis of paracryptodiran phylogeny. Journal of Systematic Palaeontology 13(4):351–369.
Pérez-García, A., T.M. Scheyer and X. Murelaga. 2013. The turtles from the uppermost Jurassic and Early Cretaceous of Galve (Iberian Range, Spain): anatomical, systematic, biostratigraphic and palaeobiogeographical implications. Cretaceous Research 44:64–82.
Phillips, J. 1871. Geology of Oxford and the Valley of the Thames. Oxford: Clarendon Press. 523 pp.
Pritchard, P.C.H. 1984. Piscivory in turtles, and evolution of the long-necked Chelidae. Zoological Society of London, Symposium 52:87–110.
Robison, S.F. 1986. Paleocene (Puercan-Torrejonian) mammalian faunas of the North Horn Formation, central Utah. Brigham Young University Geology Studies 33:87–133.
Rodriguez de la Rosa, R.A. and S.R.S. Cevallos-Ferriz. 1998. Vertebrates of the El Pelillal locality (Campanian, Cerro del Pueblo Formation), southeastern Coahuila, Mexico. Journal of Vertebrate Paleontology 18(4):751–764.
Rollot, Y., T.R. Lyson and W.G. Joyce. 2018. A description of the skull of *Eubaena cephalica* (Hay, 1904) and new insights

into the cranial circulation and innervation of baenid turtles. Journal of Vertebrate Paleontology 38(3):e1474886.
ROMER, A.S. 1956. Osteology of the Reptiles. Chicago: University of Chicago Press. 772 pp.
—1966. Vertebrate Paleontology. 3rd ed. Chicago: University of Chicago Press. 468 pp.
ROYO GÓMEZ, J. 1926. Los vertebrados del Cretácico español de facies weáldica. Boletín del Instituto Geológico de España 47:171–176.
RUSSELL, L.S. 1935. Fauna of the Upper Milk River beds, southern Alberta. Transactions of the Royal Society of Canada 29:115–128.
RÜTIMEYER, L. 1873. Die fossilen Schildkröten von Solothurn und der übrigen Juraformation. Neue Denkschriften der allgemeinen schweizerischen naturforschenden Gesellschaft 25:1–185.
SAUVAGE, H.É. 1894. Les reptiles du terrain jurassique du Boulonnais. Comptes Rendus de l'Académie des Sciences, Paris 119:926–927.
—1900. Catalogue des reptiles trouvés dans le terrain jurassique supérieur du Boulonnais. Comptes Rendus de l'Association française pour l'avancement des sciences 1899:416–419.
—1912. Les tortues du terrain jurassique supérieur du Boulonnais. Bulletin de la Société académique de l'arrondissement de Boulogne-sur-Mer 9(1910–1912):103–107.
—1921. Catalogue des reptiles jurassiques du Boulonnais. Bulletin de la Société académique de l'arrondissement de Boulogne-sur-Mer 10(1913–1921):253–264.
SCHEYER, T.M. AND J. ANQUETIN. 2008. Bone histology of the Middle Jurassic turtle shell remains from Kirtlington, Oxfordshire, England. Lethaia 41(1):85–96.
SEELEY, H.G. 1869. Index to the Fossil Remains of Aves, Ornithosauria, and Reptilia, from the Secondary System of Strata Arranged in the Woodwardian Museum of the University of Cambridge. Cambridge: Deighton, Bell. 143 pp.
STERLI, J., J. MÜLLER, J. ANQUETIN AND A. HILGER. 2010. The parabasisphenoid complex in Mesozoic turtles and the evolution of the testudinate basicranium. Canadian Journal of Earth Sciences 47(10):1337–1346.
SULLIVAN, R.M., S.E. JASINSKI AND S.G. LUCAS. 2013. Re-assessment of late Campanian (Kirtlandian) turtles from the Upper Cretaceous Fruitland and Kirtland Formations, San Juan Basin, New Mexico, USA. In: D.B. Brinkman, P.A. Holroyd and J.D. Gardner, eds. Morphology and Evolution of Turtles. Dordrecht, the Netherlands: Springer. pp. 337–387.
SULLIVAN, R.M. AND S.G. LUCAS. 1986. Annotated list of lower vertebrates from the Paleocene Nacimiento Formation (Puercan-Torrejonian), San Juan Basin, New Mexico. Journal of Herpetology 20(2):202–209.
TOMLINSON, S.L. 1997. Late Cretaceous and Early Tertiary turtles from the Big Bend region, Brewster County, Texas [dissertation]. Lubbock, TX: Texas Tech University. 194 pp.
TORRENS, H.S. 1980. Bathonian correlation chart. In: J.C.W. Cope, K.L. Duff, C.F. Parsons, H.S. Torrens, W.A. Wimbledon, and J.K. Wright, eds. A Correlation of Jurassic Rocks in the British Isles. Part 2, Middle and Upper Jurassic. Oxford: Blackwell Scientific. (Geological Society of London, Special Reports 15.) pp. 21–45.
TURNER, C.E. AND F. PETERSON. 1999. Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the Western Interior, U.S.A. In: D.D. Gillette, ed. Vertebrate Paleontology in Utah. Salt Lake City, UT: Utah Geological Survey. pp. 77–114.
VULLO, R., D. ABIT, M. BALLÈVRE, J.-P. BILLON-BRUYAT, R. BOURGEAIS, E. BUFFETAUT, V. DAVIERO-GOMEZ, ET AL. 2014. Palaeontology of the Purbeck-type (Tithonian, Late Jurassic) bonebeds of Chassiron (Oléron Island, western France). Comptes Rendus Palevol 13(5):421–441.
WAGNER, A. 1853. Beschreibung einer fossilen Schildkröten und etlicher anderer Reptilien-Überreste aus den lithographischen Schiefern und dem Grünsandsteine von Kelheim. Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-physikalische Klasse 7:241–264.
WATSON, D.M.S. 1910a. A chelonian from the Purbeck of Swanage, Dorset. Geological Magazine 7(8):381.
—1910b. *Glyptops ruetimeyeri* (Lyd.), a chelonian from the Purbeck of Swanage. Geological Magazine 7(7):311–314.
WEGNER, T. 1911. *Desmemys Bertelsmanni* n. g. n. sp. Ein Beitrag zur Kenntnis der Thalassemydidae Rütimeyer. Palaeontographica 58:105–132.
WHITMORE, J.L. AND J.E. MARTIN. 1986. Vertebrate fossils from the Greasewood Creek locality in the Late Cretaceous Lance Formation of Niobrara County, Wyoming. Proceedings of the South Dakota Academy of Sciences 65:33–50.
WILLIAMS, E.E. 1950. Variation and selection in the cervical central articulations of living turtles. Bulletin of the American Museum of Natural History 94:511–561.
WILLISTON, S.W. 1925. The Osteology of the Reptiles. Cambridge,: Harvard University Press. 300 pp.
WINCHESTER, D.E., C.J. HARES, E.R. LLOYD AND E.M. PARKS. 1916. The lignite field of northwestern South Dakota. Bulletin of the U.S. Geological Survey 627:1–169.
WOODWARD, A.S. AND C.D. SHERBORN. 1890. A Catalogue of British Fossil Vertebrata. London: Dulau. 396 pp.

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.