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, Baenidae, 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
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 basioccipital 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 macro-carnivory, respectively (see “Paleoecology”).

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**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 plicatus* 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.
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* (redrawn from Pérez-García 2014), *Glyptops ornatus* (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 suprapygal, 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-, hypo-, meso-, and xiphiplastrs 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 known 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
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; Perez-Garcia 2014); *Glytops 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 (Perez-Garcia, Royo-Torres, et al. 2015); *Selenemys lusitanica* from the Late Jurassic (Tithonian) of Portugal (Perez-Garcia and Ortega 2011); and

![Figure 2. A phylogenetic hypothesis of valid nonbaenid paracryptodires (Perez-Garcia, Royo-Torres, et al. 2015). The dashed line highlights the manual insertion of "Pleurosternon" portlandicum.](http://doc.rero.ch)
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...
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 Pleurosternum 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...
Compsemys victa Leidy, 1856 (= Compsemys parva Hay, 1910 = Compsemys puercensis Gilmore, 1919 = Compsemys torrejonensis Gilmore, 1919 = Compsemys vafer Hay, 1910)

**Taxonomic history.** Compsemys victa Leidy, 1856 (new species); Compsemys victa Hay 1908b (variant spelling of species epithet); Compsemys victis Kuhn 1964 (missspelled 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 obscura = 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); Hutchinson 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; Hutchinson and Archibald 1986; Holroyd et al. 2014) and North Dakota (Leidy 1836; Holroyd and Hutchinson 2002; Lyson and Joyce 2011), Lance Formation (Hay 1908b; Whitmore and Martin 1986; Holroyd and Hutchinson 2002) and Ferris Formation (Lillegraven 2002).

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**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.
early Paleocene Fort Union Formation (Puercan North American Land Mammal Age [NALMA]) of Montana (Hutchinson 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 (Hutchinson and Holroyd 2003), Nacimiento Formation (Puercan–Torrejonian NALMAs) of New Mexico (including type material of Compsemys parva, Compsemys puercaensis, 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–Clarkforian 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 puercaensis 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 obsoletus and Glyptops depressus should be added to the list of synonyms as well (see Emys obsoletus 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 Hutchinson 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 (Hutchinson 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 (Hutchinson 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 solemyd Naumichelys. 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 Dermatemysidae, 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 Neurvankylus spp. and therefore suggested affinities with Pleurostenidae. Gaffney (1972) once again favored affiliations with Baenidae, whereas Hutchinson and Holroyd (2003) favored those with Pleurostenidae. The phylogenetic analysis of Lyson and Joyce (2011) concluded that Compsemys victa is a paracryptodire closely affiliated with neither pleurosternals nor baenids. However, given that relationships among nonbaenid paracryptodires are far from resolved, this conclusion must be viewed with caution.

**Compsemys russelli** (Pérez-Garcia, 2012), comb. nov.

**Taxonomic history.** Bernuchelus russelli Pérez-Garcia, 2012 (new species).

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

**Type locality.** Mournas quarry, Berru, Marne, France (Figure 4); Sables de Bracheux Formation, MP 6, upper Thanetian, late Paleocene (Pérez-Garcia 2012).
Referred material and range. Late Paleocene (Thanetian) of Marine 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 Marine, 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 Pey-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 European form as a paracryptodire.

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 the exception of a lack of surficial shell sculpturing. Dinochelys whitei can be differentiated from all other paracryptodires by sympleiomorphically lacking a midline contact of peripheral I (in contrast to Seleneymys lusitanica and Compsemys spp.) and a nuchal notch (in contrast to Dorsetochelys typocardium), by possessing a cervical (in contrast to Pleurosternum bulbocic, Seleneymys lusitanica, and Toremys cassiopea) and a midline contact of the mesoplastra (in contrast to Rhodevemys inombragious 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 platicephalus 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 Utiasp uhaps) 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) Thalassemy ruetimeyeri Lydekker, 1899a)

Taxonomic history. Pleurosternum typocardium Seeley, 1869 (new species); Glyptops ruetimeyeri = Pleurosternon typocardium Watson 1910a (junior synonym); Pleurosternum bulbocic = Pleurosternum concinnum = Pleurosternum emarginatum (pro parte) = Pleurosternum ovatum = Pleurosternum oweni = Pleurosternum sedgwicki = Pleurosternum typocardium = Pleurosternum varistarti [sic] Delair 1958 (junior synonym and incorrect spelling of genus name); “Glyptops” typocardium = Thalassemy ruetimeyeri Milner 2004 (new combination, senior synonym); Ballerstedtia typocardia = Thalassemy ruetimeyeri Karl, Gröning, et al. 2012 (new combination, senior synonym, variant spelling); Dorsetochelys typocardium = Ballerstedtia bueckebergensis = Dorsetochelys delairi = Thalassemy 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 Bückeburg Formation, Bückeburg, Lower Saxony, Germany (hypodigm of Pérez-García 2014, including type material of Ballerstedtia bueckebergensis, Dorsetochelys delairi, and Thalassemy 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 sympleiomorphically...
lacking a midline contact of peripheral I (in contrast to Selene-
mys 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 Dorsochelys 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 Bouleenger (1887) and Lydekker (1889a) were unable to
assess its taxonomic standing. Watson (1910a) noted that See-
ley’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 rue-
timeyeri, 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 buckebergensis, based on several speci-
cimens from the late Berriasian of western Germany (Karl,
Gröning, et al. 2012). Pérez-García (2014) soon after highlighted
that the characters used by Karl, Gröning, et al. (2012) to distin-
guish their new species of Ballerstedtia are present in both
species and that Ballerstedtia buckebergensis therefore does not
represent a distinct species.

Evans and Kemp (1976) described an isolated cranium from
the Purbeck Limestone Group as the new taxon Dorse-
tochelys delairi. Milner (2004) suggested that this cranium prob-
able 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 Dorsochelys delairi matches that of the shell of Pleu-
rosternon typocardium. This conclusion seems reasonable
because other nonbaenid paracryptodires are also characterized
by the presence of a similar ornamentation on the external sur-
face of the bones of the shell and the skull roof (e.g., Pleuro-
ston bullockii and Glyptops ornatus). Pérez-García (2014)
therefore proposed the new combination Dorsochelys typocardium.
We concur with this conclusion herein as well.

The shell anatomy of Dorsochelys typocardium long
remained poorly understood because of an unfortunate combi-
nation of factors, including the absence of illustration of Seeley’s
(1869) Pleurosternon typocardium and the apparent loss of the
holotype of Thalassemy ruetimeyeri. Milner (2004) was able to
clarify the distinctive carapace anatomy of Dorsochelys 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 Dorsochelys 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 orna-
mentation consisting of a low vermiculate pattern forming a
poorly defined or coarse pitting with striations perpendicular
to the plate margins. The shell of Dorsochelys typocardium is
relatively long and broad posteriorly. A second, undescribed cra-
nium (DOMRC G.10715) from the Purbeck Limestone Group
was tentatively referred to Dorsochelys 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 Dorsochelys typocardium only (his Dorsochelys
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 Dorsochelys typocardium forms a polytomy with
Glyptops ornatus (their Glyptops plicatus) at the base of Pleu-
rosternidae. 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 plicatus = Glyptops ornatus Baur 1891 (junior syn-
onym); Glyptops plicatus = Glyptops ornatus = Glyptops uta-
henis 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, Morri-
son Formation, Kimmeridgian, Late Jurassic (Turner and Peter-
son 1999).

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

Diagnosis. Glyptops ornatus can be diagnosed as a paracryp-
todire by the full list of characters provided for that clade above.
Glyptops ornatus can be differentiated from all other paracryp-
todires by sympleiomorphically lacking a midline contact of
peripheral I (in contrast to Selenemys lusitanica and Compsemys
spp.); by possessing a cervical (in contrast to Pleurosternon bul-
lockii, Selenemys lusitanica, and Toremys cassiopeia), paired
gulars (in contrast to Pleurosternon bullockii), and a midline con-
tact of the mesoplastra (in contrast to Riodevemys inumbragigas
and most baenids); and by apomorphically possessing an elon-
gate 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 sur-
prisingly little material of better quality has been described,
and the taxonomy of the group is therefore wanting. Glyptops
(ory. Compsemys) plicatus 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 Comino 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 Comino 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 Comino (Hay 1908a) and a nearly complete skeleton from the Bone Cabin Quarry at Comino (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). If 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: Ulaops ulasops (Carpenter and Bakker 1990; see below) and the enigmatic ‘Dorsoechelys bruicops’ (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 types are associated with postcranial material, their shells remain undescibed. We finally refer all other crenulated shell material: Glyptops ornatus was extensively described by Gaffney (1979) under the name Glyptops ornatus. 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, Roys-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, Trinitschelys huatti, and Neurankylus sp. (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 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 [2013] for a summary of more complete material).

Pleurosternon bullockii (Owen, 1842) (= Megasternon koenigi Gray, 1870 = Mesochelys durstonensis Evans and Kemp, 1975 = Pleurosternon concinnum Owen, 1853 = Pleurosternon ovatum Owen, 1853 = Pleurosternon oweni Seeley, 1869 = Pleurosternon sedgwickii Seeley, 1869 = Pleurosternon vansittarti Seeley, 1869)

Taxonomic history: Platemyx bullockii Owen, 1842 (new species); Platemyx bullockii Giebel 1847 (incorrect spelling of species name); Emys bullockii Gervais 1859 (new combination and incorrect spelling of species name); Digerrham bullockii Cope 1870 (new combination); Megasternon koenigi = Platemys bullockii Gray 1870 (objective synonym); Pleurosternon bullockii Rümeymer 1873 (new combination); Pleurosternum bullockii = Pleurosternum emarginatum (pro parte) = Pleurosternum ovatum Lydekker and Boulenge 1887 (senior synonym and incorrect spelling of genus name); Pleurosternum bullockii = Pleurosternum concinnum = Pleurosternum emarginatum (pro parte) = Pleurosternum ovatum Lydekker and Boulenge 1887 (senior synonym and incorrect spelling of genus name); Pleurosternum bullockii = 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

men, 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, Roys-Torres, et al. 2015).
sedgwicki = Pleurosternum typocardium = Pleurosternum van-  
sittiarti [sic] Delair 1958 (senior synonym and incorrect spelling  
of genus name); Pleurosternon bullockii = Mesochelys durito-  
nensis = Pleurosternon concinnum = Pleurosternon emarginatum  
(pro parte) = Pleurosternon ovatum = Pleurosternon oweni =  
Pleurosternon sedgwicki = Pleurosternon vanzittarti 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 (Lydekker 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 koenigi,  
Mesochelys durithostensis, Pleurosternon concinnum, and Pleu-  
rosternon 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 a midline contact of peripheral  
I (in contrast to Selenemyx lusitania and Compemys spp.),  
by having a midline contact of the mesoplastra (in contrast to  
Riodevemys inumbragigas and most baenids), by apomorphically  
lacking a cervical (as in Selenemyx lusitania and Toemys cassinipes),  
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 Plate-  
mys (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 initially distin- 
}
Mesochelys durletensis was indeed a junior synonym of Pleurosternon bullockii (Milner 2004). Pleurosternon bullockii was reported from the Tithonian of northern France (Sauvage 1894a, 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 Olition, 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 entoplastic 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 Arzo-bispo 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, Lourinhá 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 cassiopea).

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

_Referenced 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 _Compsemys victa_) 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._ _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 uluaos_ Carpenter and Bakker, 1990

_Taxonomic history._ _Uluops uluaos_ Carpenter and Bakker, 1990 (new species).

_Type material._ UCM 53971 (holotype), a partial skull (Carpenter and Bakker 1990). The type skull has not yet been described, 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 uluaos_ 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 uluaos_.

_The name _Uluops uluaos_ is somewhat unusual for a recently proposed name by being an absolute tauonym (i.e., a bimomial 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 and incorrectly spelled species epithet); _Ballerstedtia bueckebergensis_ is somewhat unusual for a recently proposed name by being an absolute tauonym (i.e., a bimomial 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).

_Diagnosis._ _Uluops uluaos_ can be diagnosed as a paracryptodire by the full list of cranial characters provided for that clade above. _Uluops uluaos_ can readily be differentiated from _Dorsetochelys typocardium_, _Glyptops ornatus_, and _Pleurosternon bullockii_ by having a relatively 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 uluaos_ 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 uluaos_ 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 uluaos_.

_The name _Uluops uluaos_ is somewhat unusual for a recently proposed name by being an absolute tauonym (i.e., a bimomial 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 Problematical 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 delatiri_ = _Thalassemys rue-timeyeri_ 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; Bückeburg Formation, late Berriasian, Early Cretaceous (Karl, Gröning, et al. 2012).

_Comments._ See _Dorsetochelys typocardium_ (above) for discussion.

_Chelys blakii_ Mackie, 1863 _nomen dubium_ (junior synonym of _Protochelys striklandii_ = _Chelys? blakei_ (Lydekker 1889a) (junior synonym and incorrectly spelled species epithet).
Protochelys blakii = Testudo stricklandii 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 stricklandii (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 stricklandii (see below), has been considered by some authors to belong to pleurosternids (Bergounioux 1955; Anquetin and Claude 2008). 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 puerensis** = **Compsemys torrejonensis** = **Compsemys vafer** Gaffney 1972 (junior synonym); **Compsemys victa** = **Compsemys parva** = **Compsemys puerensis** = **Compsemys torrejonensis** = **Compsemys vafer** = **Emys obscurus** = **Glyptops depressus** Lyson and Joyce 2011 (junior synonym). **Comments.** See **Compsemys victa** (above) for discussion.

**Compsemys puerensis** Gilmore, 1919

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

**Taxonomic history.** **Compsemys puerensis** Gilmore, 1919 (new species); **Compsemys victa** = **Compsemys parva** = **Compsemys puerensis** = **Compsemys torrejonensis** = **Compsemys vafer** Gaffney 1972 (junior synonym); **Compsemys victa** = **Compsemys victa** = **Compsemys puerensis** = **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 puerensis** = **Compsemys torrejonensis** = **Compsemys vafer** Gaffney 1972 (junior synonym); **Compsemys victa** = **Compsemys victa** = **Compsemys puerensis** = **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).

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

Compsemys vafer Hay, 1910
nomem 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 NALMA, Danian, early Paleocene (Gaffney 1972; Sullivan and Lucas 1986).

Comments. See Compsemys victa (above) for discussion.

Desmemys bertelsmanni Wegner, 1911
nomem dubium

Taxonomic history: Desmemys bertelsmanni Wegner, 1911 (new species); Desmemys bertelsmanni Karl, Nyhuis, et al. 2012 (unjustified neotype designation); Desmemys bertelsmanni 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. Gerdermann 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 confidently 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 fragmented 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, Pleurosterion bullockii, and Rodevemys innumbragens.

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

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

Type material. DORMC 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
nomem 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. *Dorosuchelys 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 obscurus* Hay 1890b (alternative spelling of species epithet); *Compsemys victa* = *Compsemys parva* = *Compsemys puercensis* = *Compsemys tortuosephus* = *Emys obscurus* = *Glyptops depressus* Lyon and Joyce 2011 (junior synonym).

**Type locality.** 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 (Lyon 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; Lyon 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. Lyon and Joyce (2011), on the other hand, synonymized *Emys obscurus* with *Emys victa* but did not provide an explicit rationale. Given that the morphology apparent in *Glyptops depressus* is fully consistent with *Emys 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 Lyon and Joyce (2011) that it seems highly plausible that *Glyptops depressus* is indeed synonymous with *Emys 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])

**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). Lyon and Joyce (2011), on the other hand, synonymized *Glyptops depressus* with *Emys victa* but did not provide an explicit rationale. Given that the morphology apparent in *Glyptops depressus* is fully consistent with *Emys 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 Lyon and Joyce (2011) that it seems highly plausible that *Glyptops depressus* is indeed synonymous with *Emys 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.
Pleurosternon bullockii = Mesochelys durlstonensis = Pleurosternon concinnum = Pleurosternum emarginatum (pro parte) = Pleurosternum ovatum = Pleurosternon ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = Pleurosternum ovatum = 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concinnum = Pleurosternum emarginatum (pro parte) = Pleurosternum ovatum = Pleurosternum oweni = Pleurosternum sedgwicki = Pleurosternum typocardium = Pleurosternum vansittarti [sic] Delair 1958 (junior synonym and incorrect spelling of genus name); Pleurosternon bullockii = Mesochelys darlstonensis = Pleurosternon concinnum = Pleurosternum emarginatum (pro parte) = Pleurosternum ovatum = Pleurosternum 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); Pleurosternon bullockii = Pleurosternon concinnum = Pleurosternum emarginatum (pro parte) = Pleurosternum ovatum = Pleurosternum oweni = Pleurosternum sedgwicki = Pleurosternum typocardium = Pleurosternum vansittarti [sic] Delair 1958 (junior synonym and incorrect spelling of genus name); Pleurosternon bullockii = Mesochelys darlstonensis = Pleurosternon concinnum = Pleurosternum emarginatum (pro parte) = Pleurosternum ovatum = Pleurosternum 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.

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-Fetch 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 known as the Marsh-Fetch 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 blakii (?) Lydekker 1889a (junior 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.
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)
Desmenys Wegner, 1911 (type species: Desmenys bertelsmanni Wegner, 1911)
Digerhium 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 cassiopoeia 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 buckeckenbergensis 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. (Desmenys 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. (Platycheles 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; Riodevenys imunbraggis (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 Brion 2001)
[17] Early Cretaceous, early Albian; Aragon; Torenys 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 plicatus of Hay 1908b), Uluops uluops (TL) (Carpenter and Bakker 1990), Paracryptodira indet. (Glyptops ornatus of Marsh 1890; Glyptops plicatus 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 plicatus 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 plicatus of Cope 1877), Paracryptodira indet. (Probaena sculpta of Hay 1903)
[22] Late Jurassic, Kimmeridgian (Turner and Peterson 1999); New Mexico; Paracryptodira indet. (Glyptops plicatus of Lucas et al. 2006)
[23] Late Cretaceous, Campanian; Utah; Compsemys victa (Lyon and Joyce 2011; Hutchison et al. 2013)
[24] Late Cretaceous, Campanian; New Mexico; Compsemys victa (Lyon 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 (Hutchison and Lyon 2002; Lyon 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; Lyon and Joyce 2011; Holroyd et al. 2014)
[33] Early Paleocene, Torrejonian NALMA; Montana; Compsemys victa (Estes 1976; Lyon 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 (Lyon and Joyce 2011)
[36] Early Paleocene, Puercan NALMA; Denver Basin, Colorado; Compsemys victa (Hutchison and Holroyd 2003)
[37] Late Paleocene, Tiowan–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; Lyon and Joyce 2011; = C. parva and C. vafer of Hay 1910; = C. parva, C. vafer, C. puercensis, and C. torre-jonensis 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-Garcia 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 Lyon [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
Seleneurus lasitanica Pérez-García and Ortega, 2011
Toremys cassinopoea Pérez-García, Espélez, 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: Protocheles from the Middle Jurassic Stonesfield Slate of Stonesfield, Oxfordshire, UK. Geodiversitas 30(2):331–344.

ANQUETIN, J.C. PUNTENER 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.

BAKER, 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.

BARTLES, 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 (Rathonian) Stonesfield Slate of Stonesfield, Oxfordshire, UK. Proceedings of the Geologists’ Association 104(2):123–136.

BRAM, H. 1973. Chelonia from the Upper Jurassic of Guimarota mine (Portugal). Contribuição para o conhecimento da Fauna do Kimeridgiano da Mina de Lignite 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. STAETZMAN AND D. SMITH. 2000. New material of Dinocheles whitiei 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, R.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. BAKER. 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 Bruxellien (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. MESZOREK. 1969. Lower vertebrates from the Late Cretaceous Hell Creek Formation, McCone County, Montana. Breviora 35:1–33.

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 biotratigraphy of the Purbeck and Wealden of southern England. Palaeoecology 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.

FOSE, 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. AND P.A. MEYLAN. 1988. A phylogeny of turtles. Bulletin of the American Museum of Natural History 155:387–436.

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.

GEORGÁIS, G.L. AND W.G. JOYCE. 2017. A review of the fossil record of Old World turtles of the clade Pan-Triomychidae. 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: Arthur Bertrand. 544 pp.

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

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 Amphibians, 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 75:1–588.

—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 L.G. DANILOV. 2000. Distribution and biogeography of non-marine Cretaceous turtles. Russian Journal of Herpetology 7(3):181–198.

HOLBOYT, 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.

HOLBOYT, 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. Palaeoecography, Palaeoclimatology, Palaeoecology 55(1):1–22.

HUTCHISON, J.H. AND P.A. HOLBOYT. 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 (Naasholobito 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 Solemyididae. Special Papers in Palaeontology 86:75–97.

JOYCE, W.G. AND T.R. LISON. 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.

KARL, H.-V., J. LEHMANN AND S. PEITZ. 2007. Systematik der Schildkröten (Anapsida: Chelonii) aus Oberjura und Unterkreide von Nordwestdeutschland. Geol. Mitt. Niedersächs. Geol. Landesamt 2007. 58(1):3–102.

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

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. DUTRICEUX. 1996. Nouvelles découvertes de tortues dans le Jurassique supérieur du Lot (France) et examen du taxon Pleiochelyidae. 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 8:31–312.
—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 Saninia esiriens.] Proceedings of the Academy of Natural Sciences of Philadelphia 22:123–124.
LIGHT, 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
LYDEKKER, R. AND G.A. BOULENGER. 1887. Notes on Chelonia
MEYER, H. VON. 1854. Mittheilung an Professor Bronn
LIGHTIG, A.J. AND S.G. LUCAS. 2015. Paleocene-Eocene turtles of
—1870. [Descriptions of Emys jeanesi, Emys haydeni, Baena arenosa, and Saninia esiriens.] Proceedings of the Academy of Natural Sciences of Philadelphia 22:123–124.
LIGHT, 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
LYDEKKER, R. AND G.A. BOULENGER. 1887. Notes on Chelonia
MEYER, H. VON. 1854. Mittheilung an Professor Bronn
LIGHTIG, 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
LYDEKKER, R. AND G.A. BOULENGER. 1887. Notes on Chelonia
MEYER, H. VON. 1854. Mittheilung an Professor Bronn
LIGHTIG, 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
LYDEKKER, R. AND G.A. BOULENGER. 1887. Notes on Chelonia
MEYER, H. VON. 1854. Mittheilung an Professor Bronn
LIGHTIG, 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.
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 GOMEZ, J. 1926. Los vertebrados del Cretácico español de facies wealdica. 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.
RUTMAYER, L. 1873. Die fossilen Schildkröten von Solothurn und der übrigen Juraf ormation. Neue Denkschriften der allgemeinen schweizerischen naturforschenden Gesellschaft 25:1–185.
SAUVAGE, H.-E. 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.
SCHIEVER, 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 parabasiphenoid complex in Mesozoic turtles and the evolution of the testudinat e 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. Wimbeldon, 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. BALLEVRE, J.-P. BILLON-BRUYAT, R. COURBEAUX, 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 dem 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 rutimeyeri (Lyd.), a chelonian from the Purbeck of Swanage. Geological Magazine 7(7):311–314.
WEGNER, T. 1911. Desmensys Bertelsmanni n. g. n. sp. Ein Beitrag zur Kenntnis der Thalassemydidae Rutimeyer. 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 articular actions 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. 1945. Osteology of the Peabody Museum of Natural History. 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.