ISADORA GERHEIM DE VASCONCELLOS MOREIRA

REVISÃO TAXONÔMICA E DO REGISTRO FÓSSIL DE TARTARUGAS MARINHAS NÃO-PROTOSTEGIDAE DO CRETÁCEO

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Biologia Animal, para obtenção do título de *Magister Scientiae*.

VIÇOSA
MINAS GERAIS – BRASIL
2018

Ficha catalográfica preparada pela Biblioteca Central da Universidade Federal de Viçosa - Câmpus Viçosa

T

Moreira, Isadora Gerheim de Vasconcellos, 1990-

M838r
2018

Revisão taxonômica e do registro fóssil de tartarugas marinhas não-Protostegidae do cretáceo / Isadora Gerheim de Vasconcellos Moreira. – Viçosa, MG, 2018.

v, 112 f. : il. (algumas color.) ; 29 cm.

Inclui apêndices.

Orientador: Pedro Seyferth Ribeiro Romano.

Dissertação (mestrado) - Universidade Federal de Viçosa.

Referências bibliográficas: f. 95-112.

1. Tartaruga-marinha. 2. Biologia - Classificação. 3. Paleobiogeografia. 4. Tartarugas fósseis. I. Universidade Federal de Viçosa. Departamento de Biologia Animal. Programa de Pós-Graduação em Biologia Animal. II. Título.

CDD 22. ed. 597.92

ISADORA GERHEIM DE VASCONCELLOS MOREIRA

REVISÃO TAXONÔMICA E DO REGISTRO FÓSSIL DE TARTARUGAS MARINHAS NÃO-PROTOSTEGIDAE DO CRETÁCEO

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Biologia Animal, para obtenção do título de *Magister Scientiae*.

APROVADA: 09 de maio de 2018.

Gustavo Ribeiro de Oliveira

Gisele Mendes Lessa Del Giudice

Pedro Seyferth Ribeiro Romano
(Orientador)

Dedico esse trabalho à minha família, Bia, Maria, Dudu, Giovana e Eduardo.

Resumo

GERHEIM, Isadora Vasconcellos Moreira, M.Sc., Universidade Federal de Viçosa, maio de 2018. **Revisão taxonômica e do registro fóssil de tartarugas marinhas não-Protostegidae do Cretáceo**. Orientador: Pedro Seyferth Ribeiro Romano.

O registro fóssil de tartarugas marinhas do Cretáceo são principalmente do clado Pan-Chelonioidea, mas também engloba algumas espécies sem posição filogenética bem definida, consideradas atualmente como Eucryptodira Indeterminadas. O registro mais antigo de Pan-Chelonioidea é datado do Cretáceo Inferior (Aptiano) da Alemanha, o que desafia a hipótese vigente de que Americhelydia (Pan-Chelonioidea+ Chelydroidea) surgiu na América do Norte durante o Campaniano. Registros de fósseis de tartarugas marinhas do Velho Mundo são escassos, mas na América Norte eles são abundantes e são encontrados em toda a costa do Mar Interior Ocidental, desde o Canadá até o sul dos Estados Unidos. Todas as espécies de Pan-Chelonioidea do Cretáceo possuíam os membros apendiculares modificados em nadadeiras como adaptação ao ambiente aquático, e que permitiam a colonização de pequenos e grandes corpos de água. A dieta era variada, e adaptações na mandíbula para tosquiar e quebrar o alimento estavam presentes em stem Chelonioidea desde o Campaniano Superior. Dentre as 45 espécies nominais de tartarugas marinhas não-Protostegidae do Cretáceo, 13 são nomes válidos de Pan-Chelonioidea, 8 são nomes válidos de Eucryptodira, 12 são nomes inválidos, 5 são nomes nulos, 6 são nomes dúbios e 1 é nome vão.

Abstract

GERHEIM, Isadora Vasconcellos Moreira, M.Sc., Universidade Federal de Viçosa, May, 2018. **A review of the taxonomy and fossil record of non-Protostegidae sea turtles from Cretaceous**. Adviser: Pedro Seyferth Ribeiro Romano.

Fossil records of sea turtles from Cretaceous are found mainly in the clade Pan-Chelonioidea, but it also refers to a few species without a definitive phylogenetic relationship, currently considered Eucryptodira Indeterminate. The oldest record of Pan-Chelonioidea dates from the Aptian (Early Cretaceous) from Germany, which challenges the current hypothesis of the American origin for Americhelydia (Pan-Chelonioidea+ Chelydroidea) during the Campanian (Late Cretaceous). The records of Cretaceous marine turtles from the Old Word are scarce, but the distribution of stem Chelonioidea in North America were very abundant, following the coast of the Western Interior Seaway from Canada to south USA. All species of Pan-Chelonioidea from Cretaceous possessed limbs modified into paddles as adaptation for the marine environment, which allowed them to colonize small and large bodies of water. Their diet was variable, and the jaw specializations to shear and crush the food are present since the Late Campanian in stem Chelonioidea. Among the 45 named non-Protostegidae marine turtles from Cretaceous, 21 are nomina valida of Pan-Chelonioidea, 8 are nomina valida of Eucryptodira, 12 are nomina invalida, 5 are nomina nuda, 6 are nomina dubia, and 1 are nomen vanum.

Sumário

A Review of the Fossil Record of non-Protostegidae Sea Turtles from Cretaceous

Isadora Gerheim[1*], Pedro S. R. Romano[1**]

[1]Departamento de Biologia Animal, Universidade Federal de Viçosa, Viçosa, Minas Gerais, 36570-900, Brazil

*Corresponding author; e-mail: isagvm@gmail.com

**E-mail: psrromano@gmail.com

Acknowledgments: We would like to thank Walter Joyce, Márton Rabi, Püntener Christian, Eric Mulder, Alexander Gehler, Deborah Arbulla, Pernille Richards, Annelise Folie and Cécilia Cousin for all the help during the research and production of this manuscript, and Coordenação de Pessoal de Nível Superior (CAPES) for the scholarship.

Introduction

Marine turtles refer to groups of Testudines that live in the ocean or in the near-shore environment. They can be recognized by the presence of some specializations (such as the paddle-like limbs) and/or by the coastal marine assemblage inferred from the sedimentary matrix found associated to the fossil. Until recently, there was not a consensus if sea turtles comprised a monophyletic group. Gaffney (1975) defined all sea turtles (i.e.: Thalassemydidae, Plesiochelyidae, Eurysternidae, Toxochelyidae, Protostegidae, Cheloniidae and Dermochelyidae) as closely related and nested within Chelonioidea. However, the synapomorphies of Chelonioidea were challenged after the description of '*Thalassemys*' *moseri*, leading to the exclusion of the Late Jurassic coastal marine turtles (Plesiochelyidae, Thalassemydidae and Eurysternidae) from this group (Gaffney and Meylan (1988)). Even though Gaffney and Meylan (1988) suggested a common ancestry for the Late Jurassic coastal sea turtles, further cladistic analysis did not find support to confirm such monophyly (Joyce 2007).

Currently, the name *Pan-Chelonioidea* refers to the total clade of crown *Chelonioidea*, or the most inclusive clade containing the extant turtle *Dermochelys coriacea* (Vandellius, 1761) and *Chelonia mydas* (Linnaeus, 1758) (Joyce et al. 2004). Within Chelonioidea there are one entirely extinct clade named Protostegidae and two crown clades; *Cheloniidae* and *Dermochelyidae* (their total clades are referred as *Pan-Cheloniidae* and *Pan-Dermochelyidae*). We treat all species previously included in "*Toxochelyidae*" solely as stem *Chelonioidea*.

Some of fossil marine turtles were already recognized as such in the 18th century, but the first named non-Protostegidae species was *Allopleuron hofmanni*

(Gray, 1831), followed by *Chelonia cretacea* Keferstein, 1834, *Chelone camperi* Owen, 1851, and *Chelone faujasii* Giebel, 1852, all from Europe. After 1852, the majority of the described species were from the USA, mostly thanks to the reviews of Hay (1908) and Zangerl (1953). Hay (1908) provided the first extensive review on the morphology and taxonomy of fossil turtles of North America, which contributed enormously to the knowledge of the marine species, especially of those now recognized as stem Chelonioidea. Hay (1908) proposed to exclude species without the limbs completely modified into flippers from Cheloniidae, and include them into the family Toxochelyidae, which was supported in several cladistics studies later (Zangerl 1953; Kear and Lee 2006, Brinkman et al. 2006; Joyce 2007; Cadena and Parham 2015). Moreover, Hay (1908) included some genera previously allocated in Cheloniidae into Thalassemydidae, without presenting any reason for it, and declaring it was contrary to the recent studies of that time. This doubtful proposal of Hay (1908) was solved by Zangerl (1953), which invalided some of those genera and transferred others to Toxochelyidae.

R. Zangerl contributed immensely for the amount of named sea turtles from Cretaceous. From 28 species from USA, Zangerl alone described 12 of them. Whereas the review of Hay (1908) focused on the northern states of USA, Zangerl (1953) explored the southern states, and due to the high concentration of stem Chelonioidea in the country, both studies combined result in a comprehensive knowledge of these species. It is important to stress that the disproportion of named Cretaceous species of stem Chelonioidea over crown Chelonioidea can also be a bias due to the amount of descriptions made by Hay (1905) and Zangerl (1953), and it is not necessarily a matter of abundance of the stem lineages.

It was only from 1984 onwards that species of sea turtles from Asia started to be named, thanks to the studies of Nessov and Krassovskaya (1984), Hirayama and Chitoku (1996), Averianov (2002), and Kaddumi (2006). Unfortunately, those species still represent a small portion of the knowledge about Asian sea turtles.

A global analysis of Mesozoic Testudines recovered Pan-Chelonioidea as sister group of all remaining Cryptodira (Joyce 2007), whereas some molecular analyses found it to be more inclusive, as sister group of Kinosternoidea (Shaffer et al. 1997; Fujita et al. 2004), of Testudinoidea (Parham et al. 2006), or of Chelydroidea (Chelydridae + Kinosternidae) (Krenz et al. 2005; Barley et al. 2010; Crawford et al. 2014). The oldest fossil records of Chelydroidea and the oldest definitive Pan-Chelonioidea (*Toxochelys* spp. and *Ctenochelys* spp.) were dated from the Late Cretaceous of North America (Parham and Hutchison 2003; Joyce et al. 2013; Joyce et al. 2013), which led Joyce et al. (2013) to name the clade that originated from the most recent common ancestor of *Chelonia mydas* (Linnaeus, 1758), *Chelydra serpentina* (Linnaeus, 1758), and *Kinosternon scorpioides* (Linnaeus, 1766) as Americhelydia, referring to the supposed origin of this group. The abundance of early stem Chelonioidea in the Late Cretaceous of North America would match such hypothesis; however, currently, the oldest occurrence of a definitive non-Protostegidae Pan-Chelonioidea is from the Early Aptian of Germany (Karl et al. 2012), which not only challenges the American origin, but also expands back the minimum age for Americhelydia from 70.0 (Campanian) to 125 million of years (Aptian). Because the placement within Cryptodira as well as its internal phylogenetic relationships (see Phylogenetic Relationship section) are still a matter of debate, Pan-Chelonioidea is considered one of the most problematic clades of fossil turtles (Cadena and Parham 2015).

For institutional abbreviations, see Appendix 1. Named marine turtles from Cretaceous are listed in Appendix 2.

Skeletal Morphology

Cranium

The following list summarizes the taxa with at least parts of the skull available in the literature: *Allopleuron hofmanni* (Mulder 2003; Figure 1C), *Catapleura repanda* (only a fragmentary lower jaw in Wieland 1904), *Ctenochelys stenoporus* (Hay 1905; Karl and Nyhuis 2012), *Ctenochelys acris* (Gentry 2017), *Corsochelys haliniches* (Zangerl 1960; Figure 1B), *Kimurachelys slobodae* (Brinkman et al. 2015), *Mesodermochelys undulatus* (Hirayama and Chitoku 1996), *Mexichelys coahuilaensis* (Brinkman et al. 2009), *Nichollsemys baieri* (Brinkman et al. 2006), *Oertelia gigantea* (Karl et al. 2012), *Toxochelys latiremis* (Cope 1875; Case 1898; Hay 1905, 1908; Zangerl 1953; Figure 1A), and *Toxochelys moorevillensis* (Zangerl 1953). Zangerl (1953) provided a detailed description of the skull in stem Chelonioidea and Gaffney (1979) described the general morphology for Chelonioidea.

The skulls of stem Chelonioidea are massive, as wide as long, with broad and rounded lateral extremities. The skulls of Cheloniidae and Dermochelyidae are thinner, and longer than wide (Zangerl 1953). The snout of stem Chelonioidea is generally rounded, except in *Nichollsemys baieri* (Brinkman et al. 2006), which is pointed as in Cheloniidae. The orbits face strongly upward in stem Chelonioidea, suggesting a shallow-water habitat (Hirayama 1997). The orbits of Cheloniidae and Dermochelyidae face laterally, similar to extant species, which is associated to aquatic animals adapted to large bodies of water (Hirayama 1997, Kear and Lee 2006).

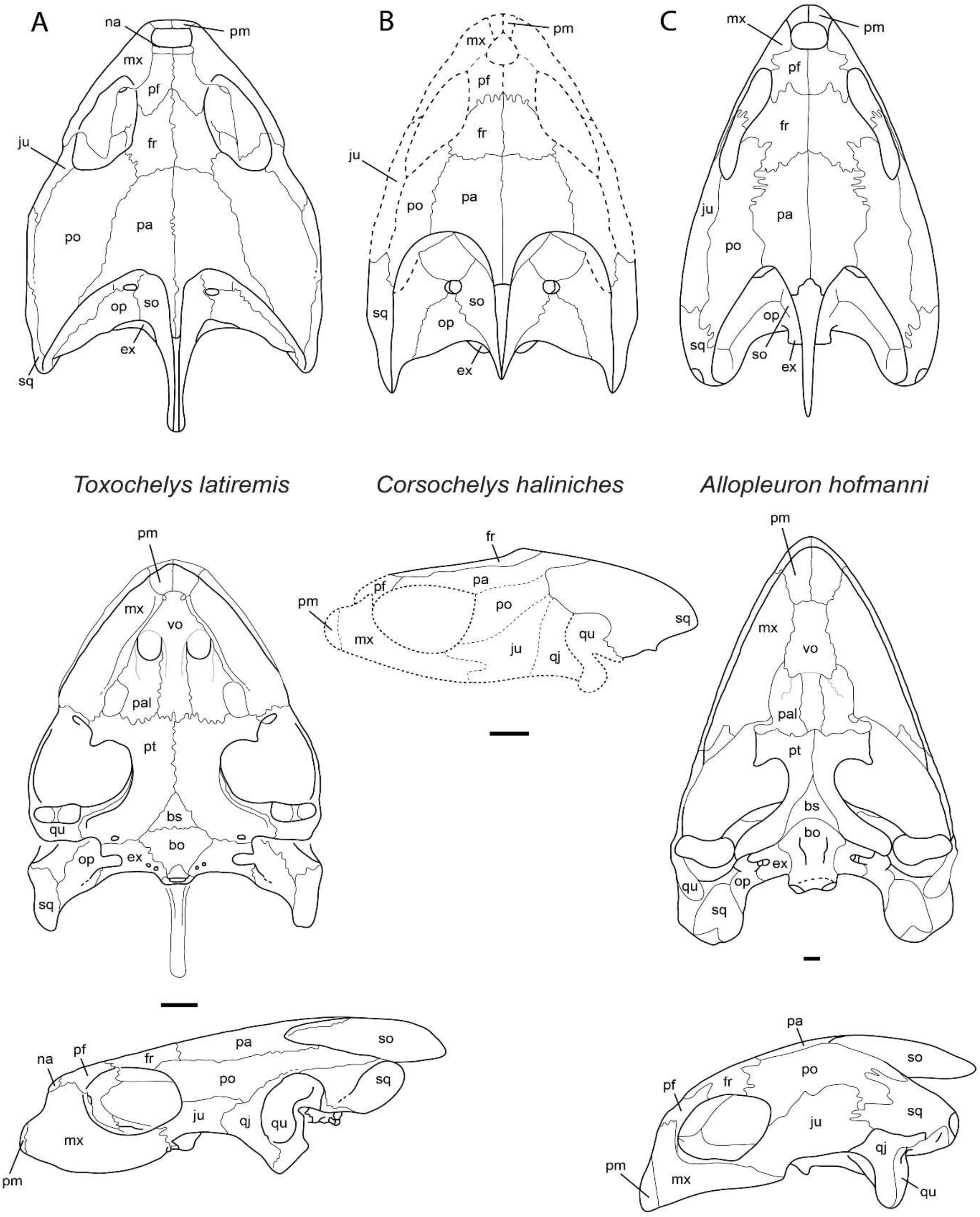

Figure 1. Cranial morphology of marine turtles of Cretaceous as exemplified by three species. A, *Toxochelys latiremis* (redrawn from Gaffney 1979). B, *Corsochelys haliniches* (redrawn from Zangerl 1960). C, *Allopleuron hofmanni* (redrawn from Mulder 2003). *Abbreviations*: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; na, nasal; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. Scale bars approximate 1 cm.

The nasals are absent in fossil and extant Cheloniidae and Dermochelyidae, but they are present in *Toxochelys latiremis* (stem Chelonioidea) and *Porthochelys* *laticeps* (Eucryptodira Indeterminate). In *T. latiremis* they are small and rectangular, with an extense posterior contact with the prefrontals and a short lateral suture with the maxilla (Figure 1A). In *P. laticeps* the nasals are wider and circumvented by the expanded prefrontal, preventing the lateral contact with the maxilla. The anterior portion of the nasal contribute to the apertura narina externa and the posterior suture contacts the prefrontals in both species (Figure 1A). The prefrontals of Pan-Chelonioidea usually contact one another in the midline (Figure 1). The frontals are prominent in Chelonioidea taxa and the downward displacement of the orbits, as seen in *Allopleuron hofmanni*, resulting in a lateral expansion of the frontals (Figure 1C). There is no evidence of contact between parietal and squamosal in all Cretaceous Pan-Chelonioidea, different from that seen in extant Chelonioidea with a well-developed temporal roof. The jugal is reduced in stem Chelonioidea and it contacts only the prootic laterally and the quadratojugal posteriorly. In *A. hofmanni* the jugal is greatly expanded, reaching posteriorly the anterior portion of the squamosal and anteriorly the prefrontal, preventing the maxilla to contribute to the edge of the orbit. The quadratojugal is more reduced in *A. hofmanni* than in other species, also because of the expansion of the jugal (Figure 1C). In stem Chelonioidea the quadratojugal expands dorsally and contacts the prootic, but in *A. hofmanni* the expanded squamosal reduced the area occupied by the quadratojugal and prevents its contact with prootic (Figure 1C). Both premaxilla in stem Chelonioidea have a broad suture with the vomer and the foramen palatinum posterius is observed in the posterior vomer-palatine contact in *T. latiremis* and *Mexichelys coahuilaensis*, but it seems to be lost in crown Chelonioidea. The jugal-palatine contact in crown Chelonioidea prevents the maxilla to contact the pterygoid as seen in stem Chelonioidea. In stem Chelonioidea the maxilla is more expanded, especially in *Mexichelys coahuilaensis*, but a medial contact was not observed in any species from Cretaceous.

The vomer of *Toxochelys latiremis* and *Nichollsemys baieri* is positioned anteriorly in the ventral view, forming a primary palate. However, in most Pan-Chelonioidea the vomer expanded and dislocated to the midline of the palate and it was incorporated into the triturating surface, contributing to the secondary palate. This secondary palate is well developed in crown Chelonioidea, but it varies among stem Chelonioidea from very incipient (seen in *Ctenochelys*) to very extended (seen in *Mexichelys*).

Shell

The following list summarizes the non-Protostegidae Pan-Chelonioidea from Cretaceous with at least parts of the shell available in the literature: *Allopleuron hofmanni* (Winkler 1869; Mulder 2003; Karl et al. 2012), *Catapleura repanda* (Cope 1871a; Hay 1908), *Corsochelys haliniches* (Zangerl 1960), *Ctenochelys acris* (Zangerl 1953; Gentry 2017), *Ctenochelys stenoporus* (Hay 1905; Karl and Nyhuis 2012), *Mesodermochelys undulatus* (Hirayama and Chitoku 1996), *Toxochelys latiremis* (Zangerl 1953, Gentry 2017), *Toxochelys moorevillensis* (Zangerl 1953), and *Zangerlchelys arkansaw* (Schmidt 1944).

The carapace of Pan-Chelonioidea is generally more flatted than in other groups, and it varies in shape, from circular to oval or cordiform (Figure 2). In Cretaceous non-Protostegidae marine turtles, the carapace normally consists of a single nuchal, 8 neurals, 1 to 2 suprapygals, a single pygal, 8 pairs of costals, and 11 pairs of peripherals. The nuchal is a large, trapezoidal element and do not differ greatly among Pan-Chelonioidea, but a rectangular-shaped and protruded nuchal is observed in *C. haliniches*. The neural bones of Pan-Chelonioidea generally are longer than wide, hexagonal and with complete series, i.e. the 8th neural reaches the suprapygal. The number of bones composing the neural series in Cheloniidae are generally supernumerary and it varies; and in *Allopleuron hofmanni* (Figure 2B), for instance, exhibit 9 neural that also differs in shape (square, pentagonal and hexagonal) and in size, with neurals almost with the same width of costal plates, probably due to the reduced ossification of costal series. Among Dermochelyidae, the neurals of *Corsochelys haliniches* is typical of Pan-Chelonioidea excepted by a reduction of the last three posterior bones, and *Mesodermochelys undulatus* (Figure 2C) presents 7 reduced bones and the 7th do not contact the suprapygal because of the medial contact of 10th and 11th costals. Carapacial keels are observed only in the neural series of *Ctenochelys* spp. and *Allopleuron hofmanni* (Figure 2B).

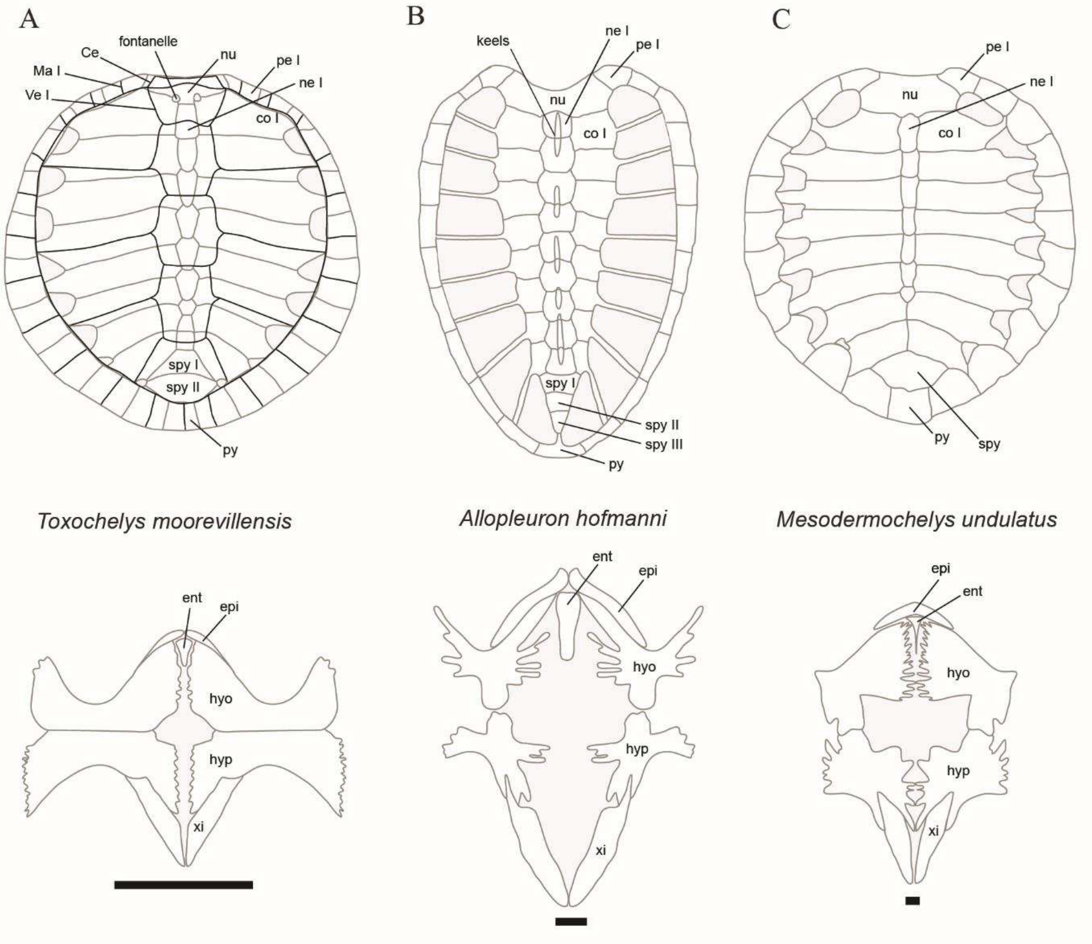

FIGURE 2. Shell morphology of marine turtles from Cretaceous as exemplified by three species. A, *Toxochelys moorevillensis* (redrawn from Zangerl 1953). B. *Allopleuron hofmanni* (redrawn from Mulder 2003). C, *Mesodermochelys undulatus* (redrawn from Hirayama and Chitoku 1996). Gray areas represent fontanelles. *Abbreviations*: Ce, cervical scute; co, costal; epi, epiplastron; ent, entoplastron; hyo, hyoplastron; hyp, hypoplastron; Ma, marginal scute; ne, neural; nu, nuchal; pe, peripheral; py, pygal; spy, suprapygal; Ve, vertebral scute; xi, xiphiplastron. Scale bars approximate 2 cm.

Costal fontanelles are always present in the shells in Pan-Chelonioidea, but it varies greatly among the species. In stem Chelonioidea and Dermochelyidae the fontanelles are small, allowing the costals I to VIII to contact the peripherals and suprapygal I, respectively, with broader suture (Figure 2A, C). In *A. hofmanni* the fontanelles are large, sometimes occupying about half the shell area and restricting the contact of costals and peripherals to a tiny suture (Figure 2B). The peripherals are broad, mostly as wide as long in stem Chelonioidea and Dermochelyidae, but in

Cheloniidae they are reduced and elongated throughout. From 6th to 11th peripherals there are a gradual increase in the width of the bones, excepted in *A. hofmanni*, which the peripherals 4th and 5th have the greater width (Figure 2B). The shell scutes sulci of *Mesodermochelys undulatus* are poorly known and can be seen only on the 3th and 5th neural bones.

The plastron of stem Chelonioidea are cruciform and well developed, with a relatively small longitudinal fontanelle that expands around the hyo-hypoplastra suture (Figure 2A). In the Cheloniidae *A. hofmanni* the plastron is greatly reduced, with an oval outline and a large medial fontanelle that prevents the right and left hyo- and hypoplastron to contact each other (Figure 2B). The shape of plastron varies among Dermochelyidae; in *C. haliniches* it is similar to *A. hofmanni*, and in *M. undulatus* it is also oval, but the bones are bigger and with a large central fontanelle. The epiplastron of Chelonioidea varies from narrow and slender in stem Chelonioidea, intermediary size in Dermochelyidae to very expanded in *A. hofmanni* (Figure 2). The hyo- and hypoplastra are reduced in Chelonioidea and has a spread-hand shape (Figure 2B), varying in the amount of projections. Similar to the carapace, the plastron of *M. undulatus* does not preserve evidence of scute sulci.

Postcranium

Non-shell postcranium remaining of non-Protostegidae Pan-Chelonioidea from Cretaceous is rarely found intact and articulated. The few available materials are described and illustrated in the literature for the following taxa: *Allopleuron hofmanni* (Mulder 2003; Karl et al. 2012); *Catapleura repanda* (Hay 1908; Cope 1871a), *Corsochelys haliniches* (Zangerl 1960), *Gigantatypus salahi* (Kaddumi 2006), *Mesodermochelys undulatus* (Hirayama and Chitoku 1996), *Toxochelys latiremis* (Hay 1908; Zangerl 1953), *Toxochelys moorevillensis* (Zangerl 1953), and *Oertelia gigantea* (Karl et al. 2012).

Vertebrae of non-Protostegidae Pan-Chelonioidea from Cretaceous are described in detail only for *Allopleuron hofmanni* (Mulder 2003), *Corsochelys haliniches* (Zangerl 1960), *Mesodermochelys undulatus* (Hirayama and Chitoku 1996) and *Toxochelys latiremis* (Zangerl 1953). *M. undulatus* possesses a procoelous vertebrae from fifth to eighth cervical (Hirayama and Chitoku 1996), whereas in *A. hofmanni* only the fifth is described as procoelous (Mulder 2003) and in *T. latiremis* presents biconvex vertebrae from 5th to 8th cervical (Zangerl 1953). A double central articulation can be found between the seventh and eighth cervical of most Pan-Chelonioidea, including *A. hofmanni* and *T. latiremis*, but not in *M. undulatus* (Hirayama and Chitoku 1996). The caudal vertebrae are generally procoelous in Pan-Chelonioidea, as in *T. latiremis*, *A. hofmanni* and *M. undulatus*.

The limbs of Pan-Chelonioidea from Cretaceous have been reported only for *Gigantatypus salahi* (humerus only; Kaddumi 2006), *Corsochelys haliniches* (almost complete right humerus, carpal bones, tibias, manus and pes; Zangerl 1960), *Mesodermochelys undulatus* (humerus, ulna, carpal bones, femur, tibia, fibula, manus and pes; Hirayama and Chitoku 1996), and *Toxochelys latiremis* (almost complete forelimb; Wieland 1902; Zangerl 1953). Pan-Chelonioidea possess limb bones generally flat and the forelimbs present larger surface than the hindlimbs. In Chelonioidea, the digits also possess great elongation and rigidness, achieved by the loss of all articular condyles between the phalanges (e.g., *M. undulatus* and *A.*

hofmanni). In stem Chelonioidea the digits length resembles more the size seen in Trionychidae, and the articular condyles are present in at least two digits. All Pan-Chelonioidea possesses a lateral process in the humerus, which is incipient and located near the caput humeri in stem Chelonioidea (e.g., *T. latiremis*) and very developed, laterally-oriented and located very distally to the caput humeri in Pan-Dermochelyidae (e.g., *C. haliniches and M. undulatus*). In Pan-Cheloniidae, the lateral process is moderate and located distally to the caput humeri (e.g., *G. salahi*), except for *Allopleuron hofmanni*, which presents a laterally-oriented process, similar to Pan-Dermochelyidae.

The pectoral girdle of Pan-Chelonioidea from Cretaceous consists of the characteristic triradiate structure formed by the coracoid, scapula and acromion. In freshwater turtles (e.g., Chelydridae), the coracoid is generally shorter than the acromion, but in stem Chelonioidea it is longer (e.g., *T. latiremis*), and in Chelonioidea the coracoid is much more elongated (e.g., *A. hofmanni*, *C. haliniches* and *M. undulatus*). The pelvic girdle of stem Chelonioidea is more similar to those of Chelydridae than to Chelonioidea. The ischium of stem Chelonioidea (e.g., *T. latiremis* and *T. moorevillensis*) is large and its posterior process is more pronounced than in Chelydridae, whereas in Chelonioidea the ischium is much small, and the posterior process is poorly developed (e.g., *M. undulatus*) or absent (e.g., *Chelonia mydas*). The lateral process of the pubis is generally pronounced in Pan-Dermochelyidae (e.g., *M. undulatus*), extending anteriorly beyond the medial border, whereas in Pan-Cheloniidae the lateral process is much smaller and extends in the same plane as the pubis. In stem Chelonioidea (e.g., *T. moorevillensis*) such process points ventrally, as in Chelydridae.

Phylogenetic Relationships

Several studies were carried out aiming to explore the phylogenetic relationships of sea turtles, but the placement of many fossil species is still poorly resolved. Based on the features in the basicranium, all clades of sea turtles were hypothesized to share an exclusive common ancestor, and therefore, the fossil lineages (Thalassemydidae+Plesiochelyidae) were placed as sister group of (Dermochelyidae+Cheloniidae), and Toxochelyidae as sister group of all of them (Gaffney 1976). Later, Fastovsky (1985), Hirayama and Suzuki (1985), and Gaffney and Meylan (1988) found that Toxochelyidae are paraphyletic and that some species previously included in this family are closer to (Dermochelyidae+Cheloniidae) than Plesiochelyidae. Thalassemydidae and Plesiochelyidae are currently considered related to Eurysternidae (Gaffney and Meylan 1988, Joyce 2007), and these three clades are nested as a paraphyletic group stem to the exclusive common ancestor of Cryptodira, not directly related to Pan-Chelonioidea (Joyce 2007).

Most authors agree that Pan-Chelonioidea is comprised by Toxochelyidae, Cheloniidae, Protostegidae and Dermochelyidae (Zangerl 1953; Hirayama 1994; Hirayama 1997; Hooks 1998; Brinkman et al. 2006; Kear and Lee 2006; Scavezzoni and Fischer 2018). However, Protostegidae was also recovered as an earlier and independent clade, not closely related to Pan-Chelonioidea (Joyce 2007; Sterli and De La Fuente 2011; Anquetin 2012). Since this hypothesis was not supported in more recent studies (Cadena and Parham 2015; Gentry 2017; Scavezzoni and Fischer 2018), we do not challenge nor confirm the placement of Protostegidae within Pan-

Chelonioidea (Figure 3) but follow the most recent contributions that suggest Protostegidae would be closer to Pan-Dermochelyidae.

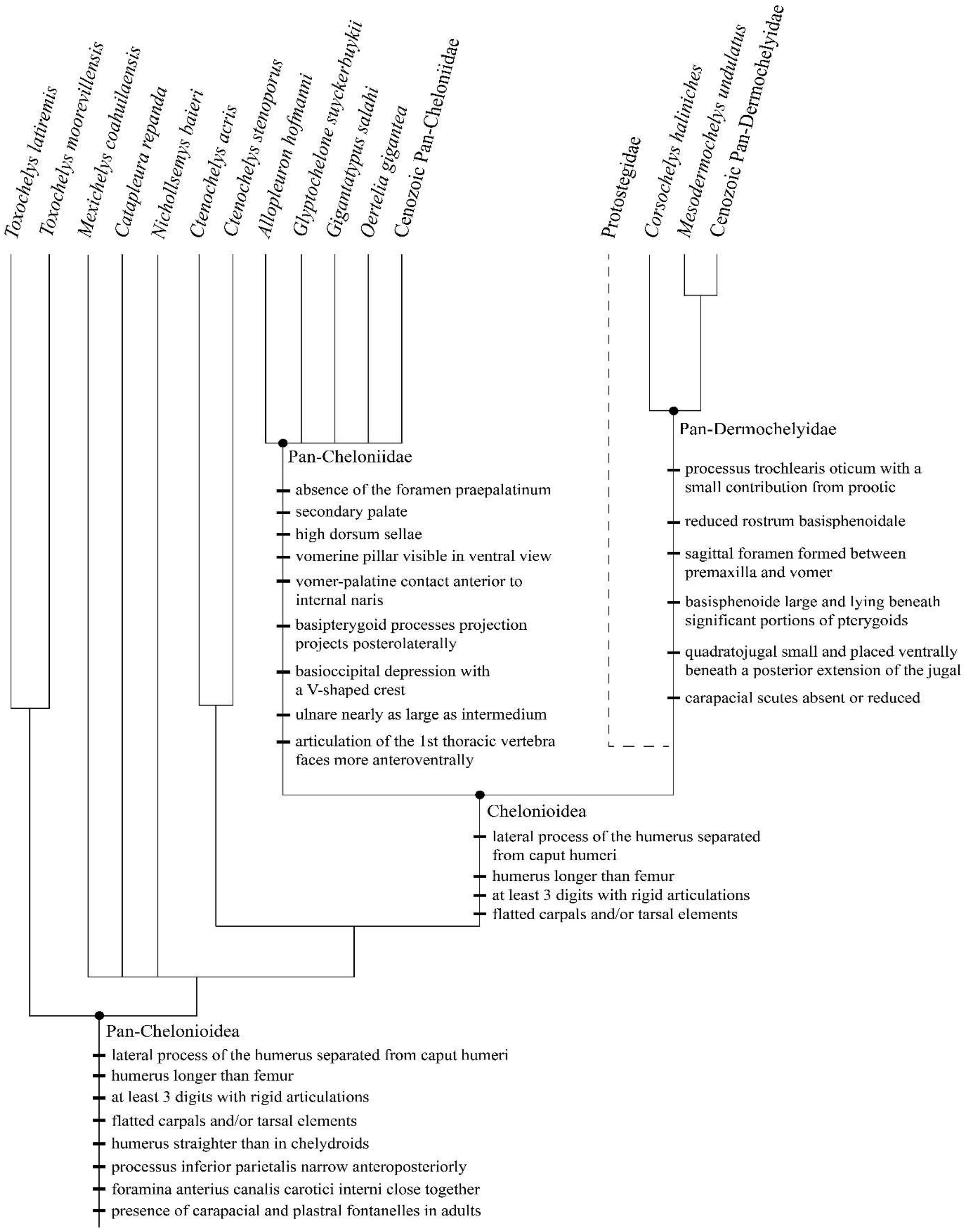

FIGURE 3. A phylogenetic hypothesis of valid Pan-Chelonioidea taxa with diagnostic characters for the most important clades. All valid taxa herein classified as Pan-Chelonioidea Indet. or Eucryptodira Indet. are omitted.

The fossil record of Toxochelyidae were considered one of the earliest registered among Pan-Chelonioidea and it comprised more than 20 named species, but most of them were later synonymized due to the poor state of preservation and/or lack of complete material (Zangerl 1953; Hirayama 1997; see details on Systematic Paleontology section). In some phylogenies, species of Toxochelyidae were formerly recovered as stem-Cheloniidae (Hirayama 1994, 1998; Lynch and Parham 2003), but in most of them as stem-Chelonioidea (Zangerl 1953; Brinkman et al. 2006; Kear and Lee 2006; Joyce 2007; Cadena and Parham 2015; Scavezzoni and Fischer 2018) (Figures 3 and 4). Several studies suggested a paraphyly of Toxochelyidae (Fastovsky 1985; Gaffney and Meylan 1988; Hirayama 1994; Parham and Fastovsky 1997; Hirayama 1998; Gentry 2017; Scavezzoni and Fischer 2018) and therefore, some authors refer those species only as stem-Chelonioidea (Brinkman et al. 2006; Kear and Lee 2006; Brinkman et al. 2015), in agreement with the conversion to phylogenetically defined names (Joyce et al. 2004). The abandonment of Toxochelyidae along with its subfamilies Toxochelyinae and Lophochelyinae, was finally proposed in Gentry (2017) and it is followed herein.

Cheloniidae is the most diverse clade of Pan-Chelonioidea, but most species are from the Cenozoic (Gaffney and Meylan 1988; Hirayama 1997; Parham and Fastovsky 1997; Parham and Pyenson 2010), leaving only three taxa, here identified as Pan-Cheloniidae Indeterminate from the Cretaceous to be discussed in here. A deeper revision of the phylogenetic relationships of Cheloniidae will be addressed in another chapter (W. Joyce, pers. comm.).

Probably due to the pelagic habit and the lack of shell ossification, good fossil records of Dermochelyidae from Mesozoic and Cenozoic are scarce (Hirayama 1997). From the Cretaceous record, *Mesodermochelys undulatus* has abundant material, and it was recovered closely related to *Dermochelys coriacea* (Hirayama 1994; Kear and Lee 2006; Joyce 2007; Cadena and Parham 2015). *Corsochelys haliniches* was first considered a very specialized Cheloniidae (Zangerl 1960), but in more recent phylogenetic analyses it was recovered as sister group of Chelonioidea (Gentry 2017; Scavezzoni and Fischer 2018) or, more consistently, as sister group of (*Mesodermochelys*+*Dermochelys*) (Hirayama 1994, 1998; Brinkman et al. 2006; Kear and Lee 2006; Scavezzoni and Fischer 2018) (Figure 3).

The diagnoses of main Pan-Chelonioidea lineages were verified in published analyses of Cadena and Parham (2015), Gentry (2017), Gaffney and Meylan (1988), Kear and Lee (2006), Hirayama (1994), Joyce (2007), Gaffney (1975), Brinkman et al. (2009), and Parham and Pyenson (2010) and are summarized in Figure 3. Given that many Mesozoic species were never included in any taxon-character matrix for phylogenetic analyses, we tentatively allocated them based on the diagnoses defined for each clade. To establish the broadest position of clades within Pan-Chelonioidea, we relied mainly on Cadena and Parham (2015) and Scavezzoni and Fischer (2018) (Figure 3).

Paleoecology

Pan-Chelonioidea and Protostegidae are the only turtles highly adapted to the marine habitat (Hirayama 1997). The oldest record of Pan-Chelonioidea are dated from the Cretaceous (Kear and Lee 2006; Cadena and Parham 2015), but the

Thalassemydidae, a clade of shallow-water turtles, were already inhabiting the sea in the Late Jurassic (Püntener et al. 2015), suggesting that the invasion from the fresh water to the sea occurred independently at least twice between the eucryptodiran turtles (Parham and Fastovsky 1997). The Pan-Chelonioidea species from Cretaceous exhibit greater diversity in their morphology and ecology than the living ones (Hirayama 1997), and some of them show different specializations to the marine habitat (Zangerl 1980). The stem-Chelonioidea seems to display only a few adaptations to the aquatic environment, and they vary in the degree of this specialization (Zangerl 1953, 1980). The forelimbs of *Toxochelys*, a stem-Chelonioidea, are compared with those of Cheloniidae and the freshwater *Chelydra serpentina*, but more similar to the latter, with three movable digits, but also possessing hindlimbs as reduced as in living sea turtles (Hay 1908). The orbits dorsally-oriented of stem-Chelonioidea resembles more *Chelydra* than Cheloniidae (Hay 1908) and it suggests a condition of shallow-water and/or benthic habits, whereas in Chelonioidea the orbits face more laterally, which is related to a more pelagic habit (Kear and Lee 2006). However, the stem-Chelonioidea show some limb specializations, as a shorter ulna and a longer radius, if compared to *Chelydra* (Hay 1908). Also, the third and fourth fingers are greatly elongated, but not as in *Caretta*; on the other hand, the first and second fingers have the same proportion to the humerus as seen in *Chelydra* (Hay 1908) and it possess movable articulations between the phalanges (Hirayama 1994). The deposition sedimentary environment inferred for the rock where Pan-Chelonioidea are found also varies from near shore environments (e.g., *Kimurachelys, Toxochelys*, *Thinochelys*, *Ctenochelys*) to open marine sediments (e.g., *Nichollsemys*) (Zangerl 1953; Brinkman et al. 2015; Gentry 2017). Although stated that the preferred habitat can be inferred from the depositional sediments, Zangerl (1980) pointed out that it could be a misinterpretation and the distinction between habitat and burial ground should be investigate, perhaps revealing alternative habitats for those species. However, to our knowledge, up to date no study investigated such scenario.

Despite the long evolutionary history of Cheloniidae, dating back from Cretaceous until present, it presents less morphological variation than seen in other Pan-Chelonioidea (Zangerl 1980). Also, even the extant species do not display many highly specializations to the highly aquatic life, as greatly elongated forelimbs, broad and flat humeri and extremely reduced shell scutes as seen in extinct Protostegidae and extinct and living Dermochelyidae (Hirayama 1994; Parham and Fastovsky 1997).

The forelimbs of the Dermochelyidae *Corsochelys haliniches* possess a similar elongation as the extant Cheloniidae (Zangerl 1960), but it does not show other adaptation to the marine habitat of its closely related species of Dermochelyidae (Zangerl 1960). The limb of *Mesodermochelys undulatus* resembles those of *Dermochelys coriacea* in the nearly straight shaft of the humerus, flattened and immovable metacarpals, suggesting a more pelagic habit than *Corsochelys haliniches* (Hirayama and Chitoku 1996).

The feeding variation within the stem-Chelonioidea have not been extensively studied and little is known about their food habits (Zangerl 1953). However, the inferred shearing jaw of *Toxochelys moorevillensis* based on the presence of a thin dentary with significant symphyseal ridges (Parham and Pyenson 2010), indicates the existence of a feeding apparatus specialized to shear the food. The same jaw morphology is found in *Allopleuron hofmanni* and *Mesodermochelys undulatus*, and it has been proposed to have evolved independently at least four times within Pan-Chelonioidea (Parham and Pyenson 2010). It is more likely that the shearing jaw is a specialization for feeding on seagrass, and, in fact, its timing of appearance is highly associated with the evolution of these plants (Bjorndal et al. 1997; Parham and Pyenson 2010).

The durophagous specialization (adaptation for crushing the food) is supported by the presence of flat and wide jaw, and its oldest record in Pan-Chelonioidea is seen in *Mexichelys coahuilaensis*, from the Late Campanian (Parham and Pyenson 2010). It has been hypothesized that this durophagous niche was previously dominated by the Protostegidae, and its extinction released this ecological opportunity, allowing the diversification of Pan-Chelonioidea during the Late Cretaceous (Hirayama 1997; Parham and Pyenson 2010). The evolution of shearing and crushing morphology seen in Pan-Chelonioidea is considered a case of iterative evolution, as suggested by the repeated and independently appearance of ecological traits followed by the extinction of similarly adapted species (Parham and Pyenson 2010).

Paleobiogeography

The fossil record of non-Protostegidae Pan-Chelonioidea from Cretaceous has so far being restricted to the current northern hemisphere of the New and Old Worlds. Except from Japan, the material of the Old World is very scarce. Its diversity is limited to six species confined to Western and Central Europe and four taxa from Asia (see Figures 5 and 6), including the oldest sea turtle, the eucryptodiran *Sontiochelys cretacea* from the Hauterivian-Barremian of Slovenia (Karl et al. 2012) and the oldest Pan-Chelonioidea, *Oertelia gigantea* from the Early Aptian of Germany (Karl et al.

2012). In the Netherlands, the only taxon known is the well-represented *Allopleuron hofmanni* from Maastrichtian (Mulder 2003; Janssen et al. 2011), probably the most abundant sea turtle from Europe in that time (Figure 5). If confirmed the identification of *A.* cf. *hofmanni* from Karl (2012), the distribution of this species would be expanded from Maastrichtian to the Turonian-Late Campanian of Germany. In this case, Germany had at least three Cretaceous taxa, since *Ctenochelys stenoporus* and *Oertelia gigantea* were also found in the north of the country (Zangerl 1953; Karl and Nyhuis 2012; Karl et al. 2012). Fragments from the Coniacian of France were referred to Cheloniidae Indet. (De Lapparent De Broin 2001).

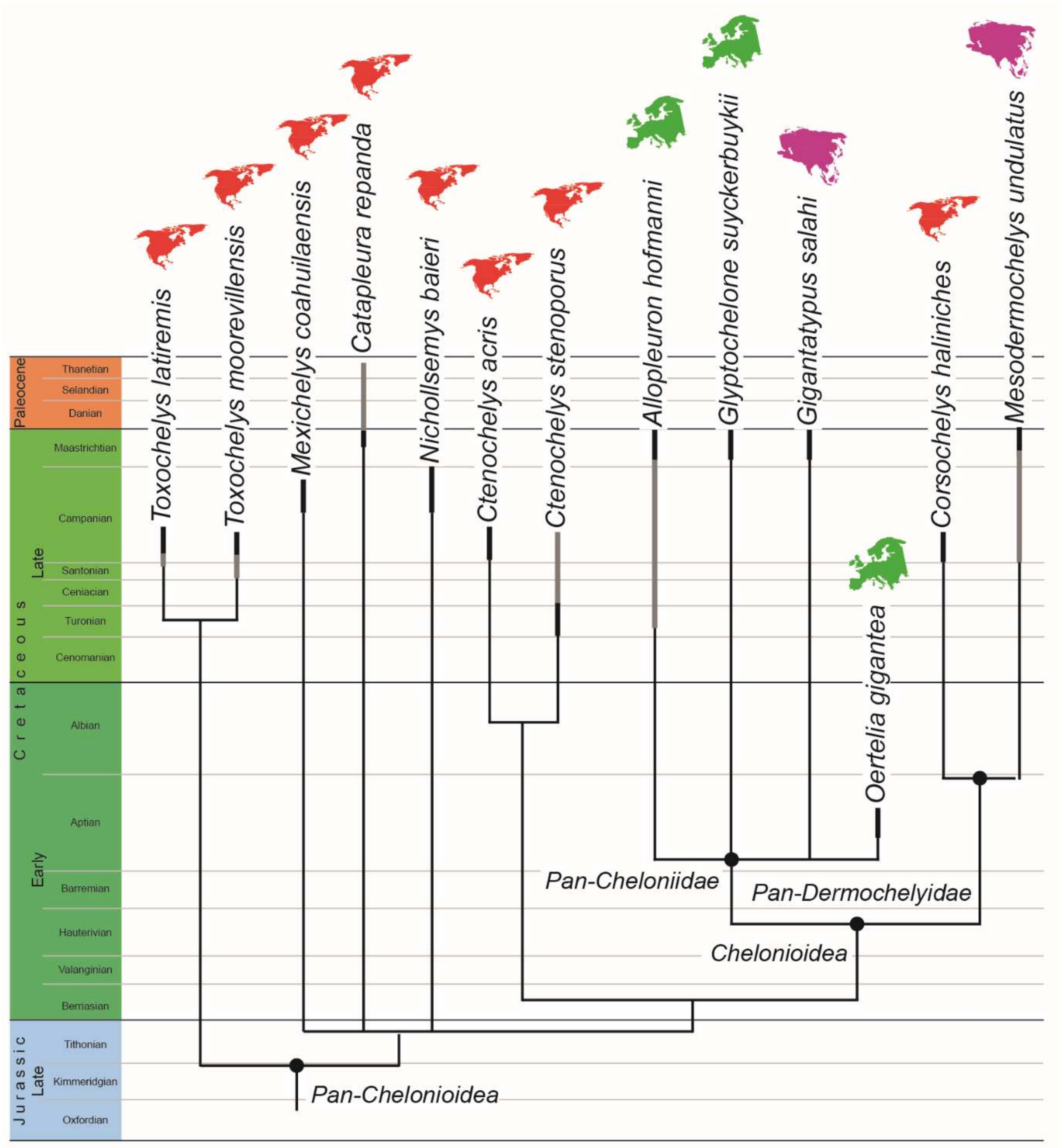

FIGURE 4. The stratigraphic and biogeographic distribution of valid marine turtles taxa. Black lines indicate temporal distribution based on type material. Grey lines indicate temporal distribution based on referred material.

Slovenia and Belgium are represented by the shell material of the eucryptodiran *Sontiochelys cretacea* and the Pan-Cheloniidae *Glyptochelone suyckerbuykii*, respectively (Dollo 1903; Stache 1905; Dollo 1909). The only record of Cretaceous Pan-Chelonioidea from the Middle East is a single humerus assigned to *Gigantatypus salahi* found in Jordan (Averianov 2002; Kaddumi 2006). The eucryptodiran marine turtles *Thalassemys cava* and *Turgaiscapha kushmurunica* were found in Uzbekistan and Kazakhstan, expanding back the occupation of Asia by marine turtles to possibly Late Albian (Averianov 2002).

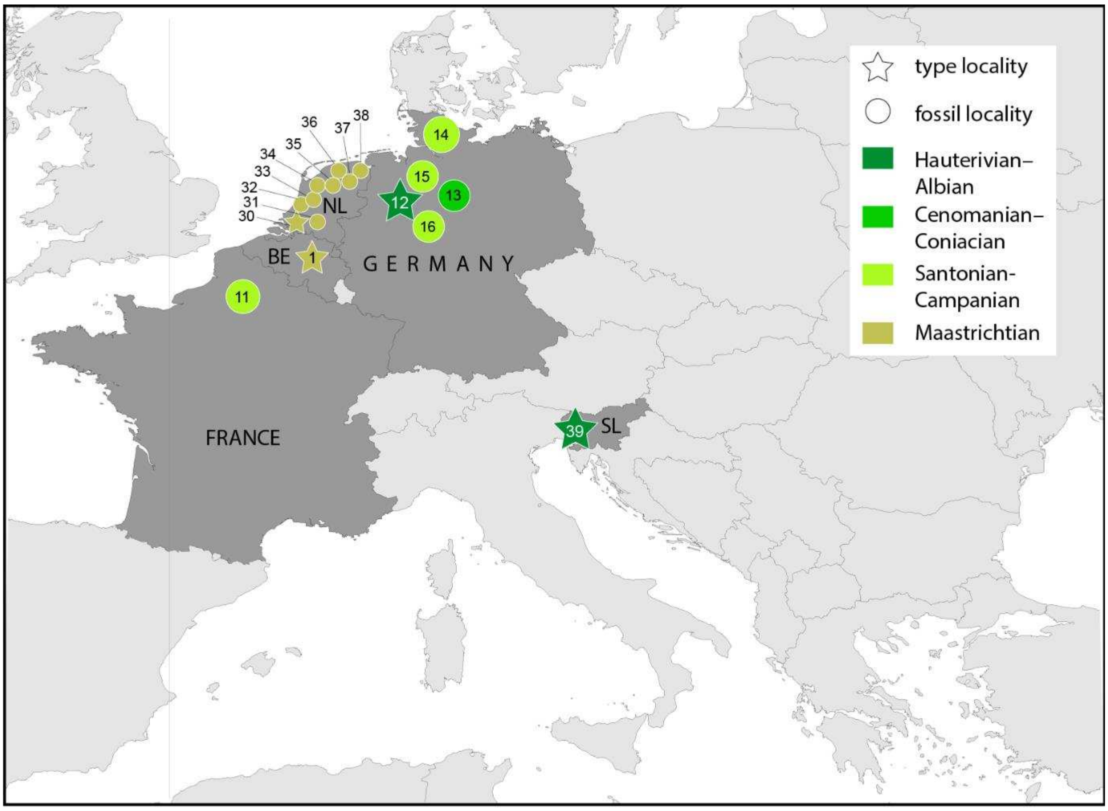

FIGURE 5. The geographic distribution of figured sea turtles non-prototegids from Cretaceous from Europe. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations:* BE, Belgium; NL, Netherlands; SL, Slovenia.

From Japan, the only described species is *Mesodermochelys undulatus*, but it has abundant material from Maastrichtian of Central Hokkaido (Hirayama and Chitoku 1996). The presence of other Pan-Dermochelyidae from Cretaceous outside Japan is rare, with the only exception of *Corsochelys haliniches* from North America (Zangerl 1960). The abundance of *Mesodermochelys undulatus* in Japan led Hirayama (1997) to propose a strong endemism of Pan-Chelonioidea during Cretaceous, which would be the cause of a higher diversity of this group in the past compared to today. Hirayama

(1996) also proposed Japan as the source of radiation of Pan-Dermochelyidae, but this may be a taphonomic bias of the fossil record, and specially because all specimens belong to the same species. Analyses of endemicity of fossil vertebrates are often weakly supported, because they are more prone to error due to the small sample size (Nicholls and Russell 1990).

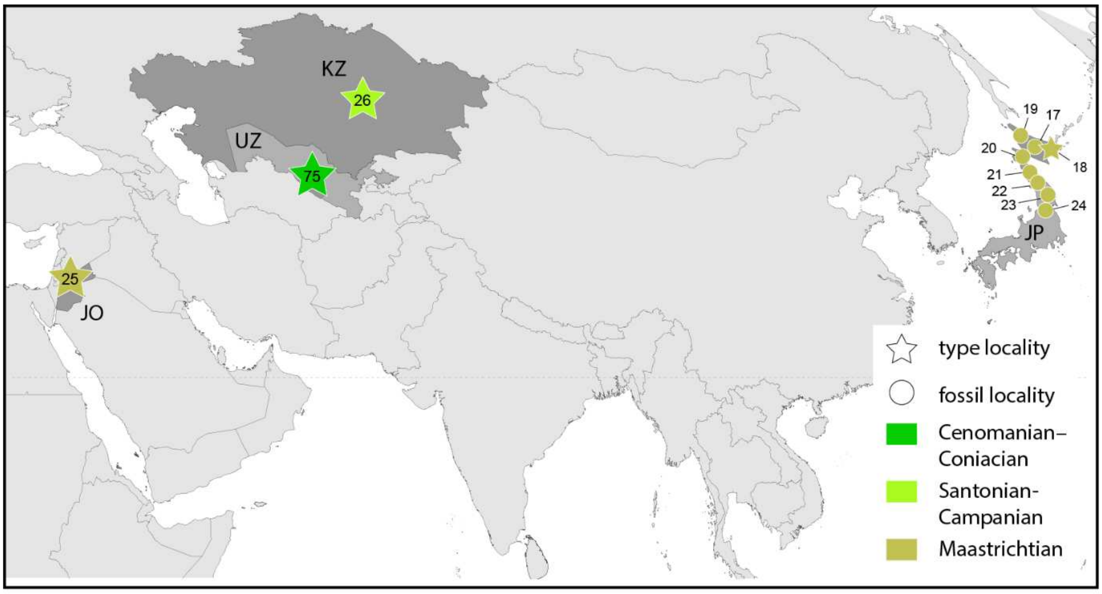

FIGURE 6. The geographic distribution of figured sea turtles non-prototegids from Cretaceous from Asia. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations:* JP, Japan; JO, Jordan; KZ, Kazakhstan; UZ, Uzbekistan.

In Canada, Manitoba Province has only one record assigned to Chelonioidea Indet. (Nicholls et al. 1990), but Alberta Province has occurrences of *Nichollsemys baieri*, *Toxochelys latiremis*, *Kimurachelys slobodae*, and two Pan-Chelonioidea Indet., all from Late Campanian (Nicholls et al. 1990; Brinkman et al. 2006; Brinkman et al. 2015). In the USA, the non-Protostegidae Pan-Chelonioidea records are most found in assemblages from the Mooreville Chalk of Alabama and the Niobrara Chalk of Kansas (Hay 1908; Zangerl 1953). The peak of diversity and abundance of stem Chelonioidea was during the Late Cretaceous in USA, demonstrated by the amount of types found in the South-Central states, referred today to *Catapleura repanda*, *Ctenochelys stenoporus*, *Ctenochelys acris*, *Toxochelys latiremis* and *Toxochelys moorevillensis*. The Eucryptodira Indet. taxa *Porthochelys laticeps*, *Thinochelys lapisossea*, *Zangerlchelys arkansaw*, and *Prionochelys nauta*, are also found in the South Central of USA. The distribution of those species, summed to those of stem Chelonioidea and the Pan-Dermochelyidae *Corsochelys haliniches* from Alabama, reveal the South Central of USA as the region of highest concentration of sea turtles during the Cretaceous. The south-most occurrence is *Mexichelys coahuilaensis*, from the Late Campanian of Mexico (Brinkman et al. 2009). There is no record of non-Protostegidae Pan-Chelonioidea from Cretaceous in South America until the date.

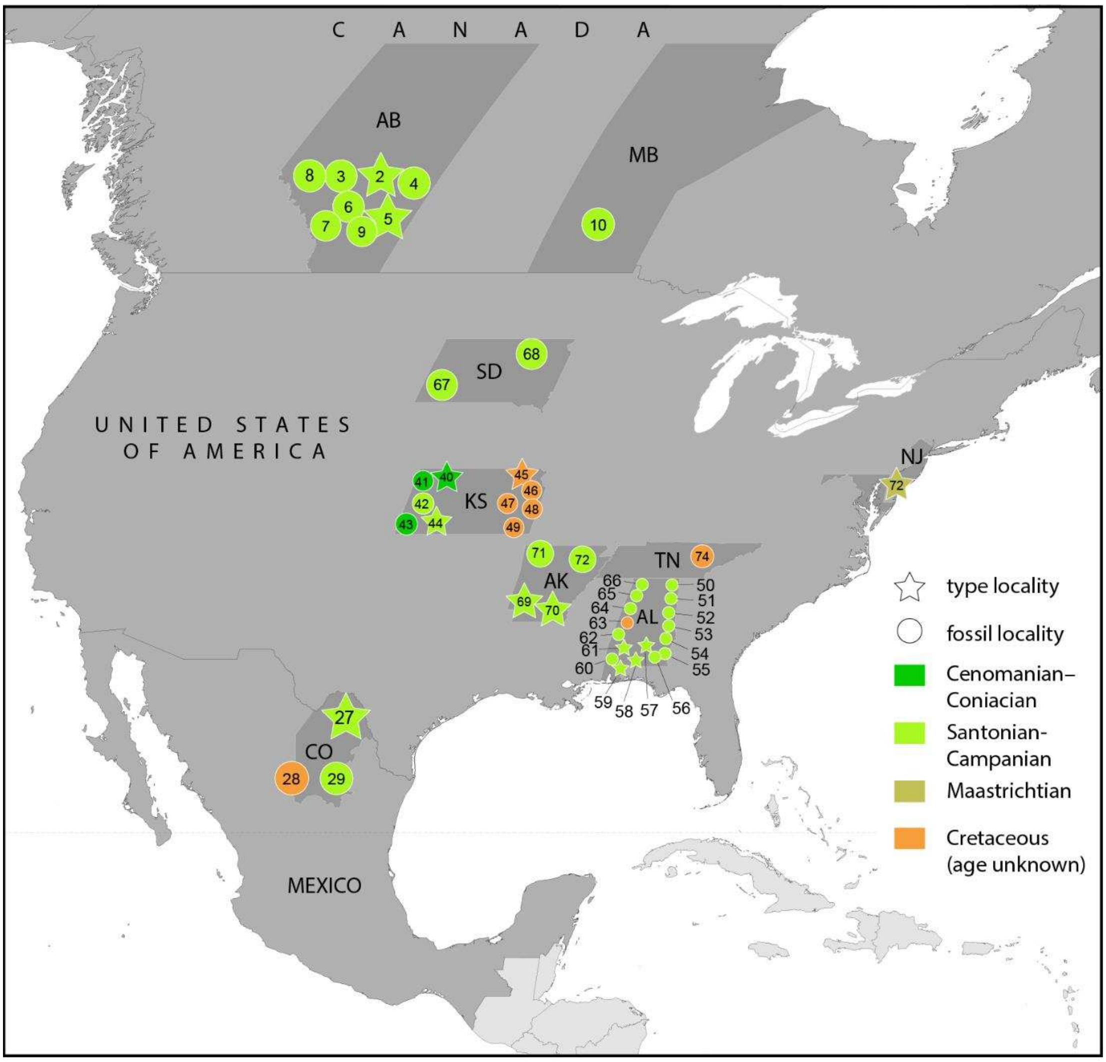

FIGURE 7. The geographic distribution of figured sea turtles non-prototegids from Cretaceous from North America. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations:* AL, Alabama; AB, Alberta; AK, Arkansas; CO, Coahuila; KS, Kansas; MB, Manitoba; NJ, New Jersey; SD, South Dakota; TN, Tennessee.

The geographical distribution of sea turtles in North America (Figure 7) follows the Western Interior Seaway bank (KWIS), an epicontinental inland seaway with deep marine and shallow estuarine environments, that connected the Artic Ocean with the Gulf of Mexico, passing through the center of North America during the Cretaceous (Gill and Cobban 1973; Petersen et al. 2016). A decrease of abundance and diversity of sea turtles with the increase of latitude in North America was noticed by

Nicholls and Russel (1990), and they proposed the existence of two distinct assemblages along the KWIS, the northern and the southern. The north portion of the KWIS had more influence of temperature from the Artic Sea, which limited the occurrence of turtles, whereas the warm to subtropical temperature of the south portion favored the high abundance of Pan-Chelonioidea in the area (Nicholls and Russell 1990). The synonymization of stem Chelonioidea from the North America (Hirayama 1997) resulted in a reevaluation of the sea turtle diversity in North America, with fewer species richness than previously considered, but those species showing the wider distributions seen in Pan-Chelonioidea (see Appendix 3). This widely-spread nature of sea turtle distribution is common among marine vertebrates, as a result of their ability to migrate long distances and their high tolerance to a variety of conditions (Nicholls and Russell 1990).

Systematic Paleontology

Valid Taxa

See Appendix 4 for the hierarchical taxonomy of non-Protostegidae Sea Turtles from Cretaceous as described in this work.

Pan-Chelonioidea Joyce et al., 2004

Phylogenetic definition. Following Joyce et al. (2004), the term *Pan-Chelonioidea* is herein referred to the total-clade (stem + crown) of *Chelonioidea* (see *Chelonioidea* below).

Diagnosis. Representatives of *Pan-Chelonioidea* are currently diagnosed relative to other hide-necked turtles by the presence of a lateral process of the humerus at least slightly separated from caput humeri, humerus longer than femur, at least 3 digits with rigid articulations, flatted carpals and/or tarsal elements, humerus straighter than in chelydroids, processus inferior parietalis narrow anteroposteriorly, foramina anterius canalis carotici interni close together, and presence of carapacial and plastral fontanelles in adults. It can be differentiated to crown-Chelonioidea by the orbits facing dorsolaterally, and the lateral process of humerus slightly separated from caput humeri.

Comments. A large number of species described until the middle of the 20th century was placed traditionally into Toxochelyidae. Several phylogenetic analyses failed to recover the monophyly of this family (Fastovsky 1985; Gaffney and Meylan 1988; Hirayama 1994; Parham and Fastovsky 1997; Hirayama 1998; Gentry 2017) and the present study also failed to define an exclusive set of diagnostic characters for Toxochelyidae. Thus, even a putative definition of this group seems to be unfeasible. We therefore follow the suggestion of Gentry (2017) in abandon the name Toxochelyidae. The species we could assign as the earliest definitive total-group of Chelonioidea, we classified as stem-Chelonioidea in agreement with the conversion of ranking-names to phylogenetically defined names (Joyce et al. 2004).

Catapleura repanda (Cope, 1868)

(= *Toxochelys atlantica* Zangerl, 1953 = *Lytoloma angusta* Cope 1871 = *Lytoloma wielandi* Hay 1908; = *Dollochelys atlantica* (Zangerl, 1953) = *Dollochelys casieri* Zangerl, 1971 = *Dollochelys coatesi* Weems, 1988)

Taxonomic history. *Osteopygis repandus* Cope, 1868 (new species); *Propleura repanda* Cope 1868 (new combination and probably change of epithet in agreement for plural flexion); *Catapleura repanda* Cope 1870 (new combination); *Catapleura repanda* = *Toxochelys atlantica* Hirayama 1997 (senior synonym); *Catapleura repanda* = *Dollochelys atlantica* = *Dollochelys casieri* = *Dollochelys coatesi* Hirayama 2006 (senior synonym).

Type material. AMNH 2353 (holotype); part of the nuchal bone, the following three peripherals, part of the fourth (right side), part of the first (left side), four other peripherals, some costal (one nearly complete) and a portion of a femur (Cope 1870; Hay 1908, fig. p. 185–188).

Type locality. West Jersey Marl Company Pit, Barnsboro, Gloucester County, New Jersey, USA (Cope 1868, 1870); Navesink or Hornerstown Formation, Late Maastrichtian? - Danian?, Late Cretaceous?- Paleogene?.

Referred material and range. Late Cretaceous (Late Maastrichtian), type locality (type material of *Toxochelys atlantica*; Zangerl 1953); Late Cretaceous (Late Maastrichtian), type formation, Sewell, Gloucester County, New Jersey, USA (Zangerl 1953); Late Paleocene, Landen Formation, Erquelinnes, Hainaut, Belgium (type material of *Dollochelys casieri*; Zangerl 1971); Late Paleocene, Aquia Formation, Liverpool Point, eastern bank of Potomac River, Charles County, Maryland, USA (type material of *Dollochelys coatesi*; Weems 1988); Paleogene, Barnersboro Formation, near Barnsboro, New Jersey, USA (type material of *Lytoloma angusta*; Cope 1870); Paleogene, Hornerstown Formation, Mullica Hill, New Jersey, USA (type material of *Lytoloma wielandi*; Hay 1908).

Diagnosis. *Catapleura* can be diagnosed as Pan-Chelonioidea by the presence of carapacial and plastral fontanelles in adults and the presence of the lateral process of the humerus separated from caput humeri. *Catapleura* can be differentiated from

Chelonioidea by the lateral process of humerus only slightly separated from caput humeri. *Catapleura* can be differentiated from *Toxochelys* by the mandible with a greater posterior protrusion of chin shelf beyond border of triturating surface and the absence of post-nuchal fontanelles, and it can be differentiated from *Ctenochelys* and *Mexichelys* by the absence of a developed secondary palate, and from *Kimurachelys* by the narrower triturating surface.

Comments. *Catapleura repanda* is based on several fragments from Barnsboro city, New Jersey (Cope 1868, 1870), where two formations can be found, the Navesink and the Hornestown (Gaffney et al. 2006). Both have been reported as Late Cretaceous in the literature and, therefore, *C. repanda* has been considered from the Maastrichtian of New Jersey (Hay 1908; Hirayama 2006); however, the Hornerstown Formation was reclassified to Paleogene (Miller Jr 1955, 1956). Miller (1956) proposed the "middle greensand" unit between the Navesink and the Hornerstown Formations, to belong to the Red Bank Formation (Cretaceous). The accurate formation of *C. repanda* is unknown, and although it has been tentatively assigned to the Hornerstown Formation (Hirayama 2006), it could be incorrect, since it is almost indistinguishable to the Red Bank Formation (Cretaceous), since both are formed by nearly pure greensand (Miller Jr 1956). We included *C. repanda* as representative of Cretaceous, but we are aware that this may change with future discoveries. Except for the synonymization, none additional specimens have been referred to this species since its first description. Due to the similarity of *Lytoloma angusta* and *L. wielandi* with *Toxochelys latiremis*, Zangerl (1953) synonymized the first two and erected a new species, *Toxochelys atlantica*, based on the carapace of *L. angusta* as the type and a fragment of mandible as the referred material. The mastigatory surface of this mandible resembles *Porthochelys laticeps*, but because of the confinement of *Porthochelys* to Kansas and the great variation of this feature in turtles, this similarity was considered result of a convergent specialization of the skull and jaw of *T. atlantica* and *P. laticeps*. Later, Zangerl (1971) erected a new genus and species from Early Eocene, *Dollochelys casieri*, and recognized its similarity to *Toxochelys atlantica*. Despite the similarity of *T. atlantica* to *Toxochelys* spp., the oval outline of the carapace is different from all other species of the genus, which led Zangerl (1971) to erect a new combination, *Dollochelys atlantica*. The diagnoses that used to distinguish the species *D. casieri*, *D. atlantica* and *D. coatesi* seems to vary according to Parris et al (1986), and since the first costal and the pygal of *Dollochelys* spp. are similar to those of *Catapleura repanda*, Hirayama (2006) proposed the subjective synonymization of those species. In the revision of the genera, Hirayama (2006) placed *Catapleura* within Cheloniidae based on the presence of more than eight neurals, but both this synapomorphy and the inclusion of "Toxochelyidae" into Cheloniidae were not recovered in most of published phylogenies (Kear and Lee 2006; Joyce 2007; Cadena and Parham 2015; Gentry 2017), it is not followed herein.

Ctenochelys Zangerl, 1953

<u>Type species</u>. *Ctenochelys stenoporus* (Hay, 1905).

<u>Diagnosis</u>. *Ctenochelys* can be diagnosed as *Pan-Chelonioidea* by most characters of the list given above for that clade. *Ctenochelys* can be differentiated to crown-Chelonioidea by the presence of orbits facing dorsolaterally, the lateral process of humerus slightly separated from caput humeri (in *C. stenoporus*), and the presence of

the foramen palatinum posterius (in *C. acris*). *Ctenochelys* is currently differentiated primarily from other stem-Chelonioidea by the presence of a medially expanded triturating surface of the maxillae, dentary with pronounced labial and lingual ridges, anteroventral portion of the vomer narrow and rugose, triturating surface involving significant contributions from the ventral portions of the palatines, raised articulation for the neural spine of the eighth cervical vertebrae on the visceral surface of the nuchal, the presence of keeled neurals with epineural ossifications between neurals 2–3, 4–5 and 6–7; peripherals with a moderately serrated lateral edge; and the presence of significant plastral and costal fontanelles even in juvenile forms.

<u>Comments</u>. *Ctenochelys* has been always considered closer to Cheloniidae than *Toxochelys* (Fastovsky 1985; Hirayama 1994; Hirayama 1997; Hirayama 1998; Parham and Pyenson 2010; Gentry 2017; Scavezzoni and Fischer 2018), however, in some phylogenetic studies it was recovered within a polytomy of stem-Chelonioidea (Brinkman et al. 2006; Kear and Lee 2006). The placement of *Ctenochelys* as Pan-Cheloniidae is doubtful, because they share the well-developed secondary palate, but it lacks the diagnosis of Chelonioidea defined herein. The new diagnoses of *Ctenochelys* found in Gentry (2017) is followed herein.

Ctenochelys acris Zangerl, 1953

<u>Taxonomic history</u>. *Ctenochelys acris* Zangerl, 1953 (new species); *Ctenochelys stenoporus* = *Toxochelys serrifer* (in part) = *Toxochelys procax* = *Toxochelys elkader* = *Lophochelys natatrix* = *Lophochelys venatrix* = *Ctenochelys tenuitesta* = *Ctenochelys acris* Hirayama 1997 (junior synonym); *Ctenochelys acris* Gentry 2017 (revalidation).

Type material. FMNH P27354 (holotype); fragmentary carapace and fragments of the plastron (Zangerl 1953, fig. 112).

Type locality. Moore Brothers Farm, Harrel Station area, Dallas County, Alabama, USA; Mooreville Chalk, Selma Formation, Early Campanian, Late Cretaceous (Zangerl 1953; Nicholls and Russell 1990).

Referred material and range. Late Cretaceous (Early Campanian), type locality (Zangerl 1953); Late Cretaceous (Early Campanian), Greene County, Alabama, USA (Gentry 2017).

Diagnosis. *Ctenochelys acris* can be diagnosed as *Ctenochelys* by the full list of characters given to that clade. It can be differentiated from *C. stenoporus* by the nearly dorsally facing orbits, with length equals about 30% of the total length of the skull, significant contribution to the orbital margin by the lateral edge of the frontals, prominent serrations located at or near the lateral midpoint of peripheral elements 3-11, minimal width of pterygoid bridge equal to or greater than the length of the basisphenoid total length in midline, lack of vomer-palatine contact anterior to the internal nostril, irregularly pentagonal posterior peripherals with concave lateral margins anterior to the furrow point, and posterior peripherals 8–10 as wide as long.

Comments. *Ctenochelys acris* were first described based on fragments of carapace and plastron from the Early Campanian of Alabama (Zangerl 1953; Gentry 2017). All species assigned to *Ctenochelys* were later synonymized to *C. stenoporus*, resulting in a monotypic genus (Hirayama 1997; Matzke 2007). However, the discovery of nearly complete specimens also from the Campanian of Alabama led to the re-description and revalidation of *C. acris* by Gentry (2017).

Ctenochelys stenoporus (Hay, 1905)

(= *Toxochelys elkader* Hay, 1908 = *Toxochelys bauri* Wieland, 1905 = *Toxochelys procax* (in part) Hay, 1905; *Ctenochelys tenuitesta* Zangerl, 1953 = *Toxochelys serrifer* Cope, 1875)

Taxonomic history. *Toxochelys stenoporus* Hay, 1905 (new species); *Toxochelys stenoporus* = *Toxochelys serrifer* (in part) Hay 1905 (senior synonym); *Toxochelys stenoporis* Wieland 1905 (misspelled species epithet); *Toxochelys stenopora* Hay 1908 (misspelled species epithet); *Ctenochelys stenopora* Zangerl 1953 (new combination); *Ctenochelys stenopora* = *Toxochelys elkader* = *Toxochelys bauri* = *Toxochelys procax* (in part) Zangerl 1953 (senior synonym); *Ctenochelys stenoporus* = *Toxochelys serrifer* (in part) = *Toxochelys procax* = *Toxochelys elkader* = *Lophochelys natatrix* = *Lophochelys venatrix* = *Ctenochelys tenuitesta* = *Ctenochelys acris* Hirayama 1997 (senior synonym).

Type material. YPM 1786 (holotype); a fragmented skull, marginals and hyoplastron (Hay 1905; Karl and Nyhuis 2012, fig. 8–9).

Type locality. Near the Monument Rocks, Gove County, Kansas, USA; Smoky Hill Chalk Member, Niobrara Formation, Turonian, Late Cretaceous (Hay 1902; Wieland 1905; Nicholls and Russell 1990).

Referred material and range. Late Cretaceous (Turonian), type formation, Gove County, Kansas, USA (Matzke 2007); Late Cretaceous (Ceniacian), type formation, Butte Creek, Logan County, Kansas, USA (Hay 1909); Late Cretaceous (Late Santonian-Early Campanian), Lägerdorf, Lägerdorf Formation, Schleswig-Holstein, Germany (Karl and Nyhuis 2012); Late Cretaceous (Campanian), Mooreville Chalk Formation, Crawford Farm, Hale County, Alabama, USA (Gentry 2017); Cretaceous, type formation, Russell Springs, Logan County, Kansas, USA (Zangerl 1953); Cretaceous, type formation, Smoky Hill River, Kansas, USA (part of type material of *Toxochelys procax*; Hay 1905); Cretaceous, type formation, near Elkader, Logan County, Kansas, USA (type material of *Toxochelys elkader*; Hay 1908); Late Cretaceous (Turonian), type locality (type material of *Toxochelys bauri*; Hay 1908); Late Cretaceous, Selma Formation, Moore Brothers Farm, Harrell Station area, Dallas County, Alabama, USA (type material of *Ctenochelys tenuitesta*; Zangerl 1953).

Diagnosis. *Ctenochelys stenoporus* can be diagnosed as *Ctenochelys* by the full list of characters given to that clade. It can be differentiated from *C. acris* by the presence of a skull with slender snout region, mandible foremost pointed, nuchal with a broad emargination, and orbits slight further away from the tip of the snout and facing more dorsally.

Comments. *Ctenochelys stenoporus* was based on fragments of cranial and post-cranial elements that were first assigned to *Toxochelys serrifer* Cope, 1875 by Case (1898). Hay (1905) recognized they do not belong to the same species and relocated its type material as belonging to a new species named *Toxochelys stenoporus*. Several new species of *Toxochelys*, *Lophochelys* and *Ctenochelys* were described by Zangerl (1953), but most of them were based on fragmentary and incomplete material. Later, Hirayama (1997) considered all dubia species as junior synonym of *Ctenochelys stenoporus*, leading to a monotypic genus until the revalidation of *C. acris* based on new specimens from Alabama (Gentry 2017).

Mexichelys coahuilaensis (Brinkman et al., 2009)

Taxonomic history. *Euclastes coahuilaensis* Brinkman et al., 2009 (new species); *Mexichelys coahuilaensis* Parham and Pyenson 2010 (new combination).

Type material. CPC 257 (SEPCP 9/721) (holotype); skull (Brinkman et al. 2009, fig. 2).

Type locality. La Parrita area, Coahuila State, Mexico; Cerro del Pueblo Formation, Late Campanian, Late Cretaceous (Brinkman et al. 2009).

Referred material and range. Late Cretaceous (Late Campanian), type locality (Brinkman et al. 2009); Late Cretaceous, General Cepada area, exact locality uncertain, Mexico (Brinkman et al. 2009); Late Cretaceous (Late Campanian), Turtle Paradise Locality, Cerro del Pueblo Formation, Mexico (Brinkman et al. 2009).

Diagnosis. *Mexichelys* can be diagnosed as Pan-Chelonioidea by the foramina anterior canalis carotici interni close together and the absence of post-nuchal fontanelles and it can be differentiated from crown-Chelonioidea by the presence of a narrow foramen palatinum posterius. *Mexichelys* can be differentiated from *Ctenochelys* by the greater extent of the secondary palate, the presence of a narrow foramen palatinum posterius, and orbits facing more laterally.

Comments. *Mexichelys coahuilaensis* is based only on descriptions of a skull from the Late Campanian of Mexico (Brinkman et al. 2009). Since the diagnoses of Pan-Chelonioidea are mostly from the appendicular skeleton, the placement of *M. coahuilaensis* as stem-Chelonioidea is supported only by the presence of narrow foramen palatinum posterius, as confirmed by Parham and Pyenson (2010) based on a cladistic inference.

Nichollsemys baieri Brinkman et al., 2006

Taxonomic history. *Nichollsemys baieri* Brinkman et al., 2006 (new species);

Type material. TMP 97.99.1 (holotype), skull with lower jaws (Brinkman et al. 2006, fig. 2–5).

Type locality. Chin Coulee Valley, south of the city of Taber, Alberta, Canada; Bearpaw Formation, Late Campanian, Late Cretaceous (Brinkman et al. 2006).

Referred material and range. Late Cretaceous (Late Campanian), type formation, South of Lethbridge, Alberta, Canada (Brinkman et al. 2006); Late Cretaceous (Late Campanian), type formation, East of Manyberries, Alberta, Canada (Brinkman et al. 2006); Late Cretaceous (Late Campanian), Pierre Shale Formation, Hyde County, South Dakota, USA (Brinkman et al. 2006).

Diagnosis. *Nichollsemys* can be diagnosed as Pan-Chelonioidea by the foramen anterior canalis carotici interni close together and the presence of the foramen palatinum posterius. *Nichollsemys* can be differentiated from crown-Chelonioidea by the large orbits facing strongly dorsally. *Nichollsemys* can be differentiated from *Ctenochelys* by the absence of secondary palate and the presence of relatively narrower triturating surfaces of the upper jaw that do not include the vomer and a larger foramen palatinum posterius. *Nichollsemys* differs also from *Porthochelys* by exhibiting a relatively narrower skull that is more triangular-shaped in dorsal view and by the small exposure of the basisphenoid on the ventral surface of the palate. It can be distinguished from *Kimurachelys* by the narrow triturating surface of the upper jaw and from *Toxochelys* by the absence of nasals.

Comments. *Nichollsemys baieri* is based on a skull with lower jaw from the Late Campanian of Canada (Brinkman et al. 2006). Because of the presence of *Lophochelys niobrarae* in the Bearpaw Formation and the sister-group relationship of *N. baieri* holotype and *L. baieri*, this skull and jaw were first informally assigned to *Lophochelys* sp. by Brinkman (2000). However, *Lophochelys niobrarae* was based solely on shell material, without cranial elements associated to it. Thereafter, the discovery of a carapace of moderate size (indeterminated species) in the Bearpaw Formation indicated that *Lophochelys* was not the only Pan-Chelonioidea genera from this Formation (Brinkman et al. 2006). To avoid problems by assigning cranial material to a shell-only taxon, Brinkman (2006) attributed these materials to *Nichollsemys baieri* but recognized that it can belong to one of the shell-based taxa. The phylogenetic analyses of Brinkman (2006) recovered *Nichollsemys* as sister group of *Ctenochelys*, mostly because of the derived braincase features.

Toxochelys Cope, 1873

Type species. *Toxochelys latiremis* Cope, 1873.

Diagnosis. *Toxochelys* can be diagnosed as Pan-Chelonioidea by most of the characters of the list given above for that clade and it can be differentiated from crown-Chelonioidea by the orbits facing outward and upward, and the lateral process of humerus slightly separated from caput humeri. *Toxochelys* can be differentiated from other stem-Chelonioidea by the carapace oval or more or less circular, moderate to extensive costo-peripheral fontanelles, a pair of post-nuchal fontanelles, narrow upper mandible triturating surfaces, slightly or not involving the palatine bones, dorsal exposure of nasals although greatly reduced relative to that of the frontals, and absence or little development of secondary palate.

Toxochelys latiremis Cope, 1873

(= *Toxochelys browni* (Hay, 1905) = *Toxochelys serrifer* Cope, 1875 = *Toxochelys brachyrhina* Cope, 1898 = *Porthochelys browni* Hay, 1905 = *Toxochelys weeksi* Collins, 1951 = *Toxochelys barberi* Schmidt, 1944; = *Lophochelys niobrarae* Zangerl, 1953)

Taxonomic history. *Toxochelys latiremis* Cope, 1873 (new species); *Toxochelys latiremis* = *Cynocercus incisus* Hay 1908 (senior synonym); *Toxochelys latiremis* = *Toxochelys browni* Schultze 1985 (senior synonym); *Toxochelys latiremis* = *Toxochelys browni* = *Toxochelys serrifer* = *Toxochelys brachyrhina* = *Porthochelys browni* = *Toxochelys weeksi* = *Toxochelys barberi* Nicholls 1988 (senior synonym); *Toxochelys latiremis* = *Lophochelys niobrarae* Hirayama 1997 (senior synonym).

Type material. AMNH 2362 (holotype); lower jaw, right ilium and a coracoid (Hay 1908, fig. 200, 202–206).

Type locality. Near the forks of the Smoky Hill River, Saline County, Kansas, USA; Smoky Hill Chalk Member, Niobrara Formation, Early Campanian, Cretaceous (Cope 1873; Wieland 1902; Hay 1908; Nicholls and Russell 1990; Matzke 2009). However, the above type locality is more likely to have been described erroneously by Cope (1873) as the geological structure of the sedimentary matrix is more similar to the Early Campanian of Pierre Shale of Logan County, also Kansas (Nicholls 1988; Nicholls and Russell 1990; Brinkman et al. 2006).

Referred material and range. Late Cretaceous (Late Santonian – Early Campanian), Niobrara Formation, near Castle Rock, Gove County, Kansas, USA (Nicholls 1988); Late Cretaceous, type formation, two miles south of Russell Springs, Logan County, Kansas, USA (Matzke 2008); Late Cretaceous (Early Campanian), Pierre Shale, Twenty miles southeast of Edgemont, South Dakota, USA (type material of

Toxochelys browni; Zangerl 1953); Late Cretaceous, Niobrara Formation, Kansas, USA (type material of *Toxochelys serrifer*; Cope 1875); Late Cretaceous, Ripley Formation, Dave Weeks place, Coon Creek, McNairy County, Tennessee, USA (type material of *Toxochelys weeksi*; Zangerl 1953); Late Cretaceous (Campanian), Marlbrook Formation, Cox Farm, road to Arkadelphia, Clark County, Arkansas, USA (type material of *Toxochelys barberi*; Schmidt 1944; Benson and Tatro 1964); Late Cretaceous (Late Campanian), Pierre Shale Formation, Cardston County, Alberta, Canada (Nicholls et al. 1990; Brinkman et al. 2015); Late Cretaceous (Early Campanian), Mooreville Chalk, Sumter County, Alabama, USA (Gentry and Ebersole 2018).

Diagnosis. *T. latiremis* can be diagnosed as *Toxochelys* by the full list given above for that taxon. *T. latiremis* can be differentiated from *T. moorevillensis* by the well-developed costo-peripheral fontanelles in carapace, the width of peripherals never exceeding their lengths, vertebral scutes wider than long, plastron with well-developed medial and lateral fontanelles, and mastigatory surface of mandible flat, without sagittal or lingual ridges.

Comments. The holotype of *Toxochelys latiremis* was first described based on a lower jaw from the Niobrara Formation (Cope 1873). Later, there was three recognized species of *Toxochelys* in North America: *T. latiremis* from Niobrara Formation, *T. browni* from Pierre Shale Formation and *T. moorevillensis* from the Mooreville Chalk. Inconsistencies on the geological features on the sedimentary matrix adhered in the type of *T. latiremis* material suggested that this lower jaw probably came from the Pierre Shale Formation (Schultze et al. 1985; Nicholls 1988; Brinkman et al. 2006). Schultze et al. (1985) agreed with this new Formation attributed to *T. latiremis*, and since it equals the one of *T. browni* and the species are morphologically very similar, he proposed their synonymization. In that case, the name *Toxochelys latiremis* Cope, 1873 has priority over *Toxochelys browni* (Hay, 1905) (Schultze et al. 1985) and the morphological differences between the specimens should be considered a plastic variation rather than a differential feature (Nicholls 1988). However, even if they belong to the same Formation, Brinkman et al. (2006) questioned if the type of *T. latiremis* and *T. browni* belong to the same species. The solution for this issue requires a deeper look into the sedimentary matrix of *T. latiremis* and a morphological comparation between the types, so we reinforce the need for a species-level revision of *Toxochelys* suggested by Brinkman et al. (2006).

Toxochelys moorevillensis Zangerl, 1953

Taxonomic history. *Toxochelys moorevillensis* Zangerl, 1953 (new species).

Type material. FMNH P27330 (holotype), almost complete shell, girdle and vertebral fragments (Zangerl 1953, fig. 76).

Type locality. Moore Brothers Farm, Harrel Station area, Dallas County, Alabama, USA; Mooreville Chalk, Selma Formation, Early Campanian, Late Cretaceous (Zangerl 1953).

Referred material and range. Late Cretaceous (Santonian), Eutaw Formation, Eutaw area, Greene County, Alabama, USA (Zangerl 1953); Late Cretaceous, type formation, Burkville area, Lowndes County, Alabama (Zangerl 1953); Late Cretaceous, type formation, Clinton area, Greene County, Alabama, USA (Zangerl 1953); Late Cretaceous (Early Campanian), type formation, Harrel Station area, Dallas County, Alabama, USA (Zangerl 1953); Late Cretaceous (Campanian), type formation, Crawford Farm, Hale County, Alabama, USA (Zangerl 1953); Late Cretaceous, type formation, West Greene area, Greene County, Alabama, USA (Zangerl 1953); Late Cretaceous, type formation, Mt. Hebron area, Greene County, Alabama, USA (Zangerl 1953); Late Cretaceous, type formation, Boligee area, Greene County, Alabama, USA (Zangerl 1953).

Diagnosis. *T. moorevillensis* can be diagnosed as *Toxochelys* by the full list given above for that taxon. *T. moorevillensis* can be differentiated from *T. latiremis* by the small costo-peripheral fontanelles in carapace, peripherals wider than lengthy, vertebral scutes as wider as long, small plastral fontanelles, and mastigatory surface of mandible with sharp sagittal ridge.

Comments. Despite the doubts concerning *Toxochelys latiremis* and *T. browni* discussed above, the validity of *T. moorevillensis* has never been challenged.

Chelonioidea Baur, 1893

Phylogenetic definition. Following Joyce et al., (2004), the term *Chelonioidea* is herein referred to the most inclusive clade that includes the last common ancestor of *Chelonia mydas* (Linnaeus, 1758) and *Dermochelys coriacea* (Vandellius, 1761). *Chelonioidea* is the crown clade of Pan-Chelonioidea.

Diagnosis. Representatives of *Chelonioidea* are currently differentiated relative to stem Chelonioidea by the orbits facing laterally, small or absent lateral process of ischium or metischial process, lateral process of humerus located away from the caput humeri, and the presence of an opened laterally or absent foramen palatinum posterius.

Pan-Cheloniidae Joyce et al., 2004

Phylogenetic definition. Following Joyce et al. (2004), the term *Pan-Cheloniidae* is herein referred to the total clade that includes crown-*Cheloniidae* and stem-*Cheloniidae*. The crown-*Cheloniidae* refers to the clade arising from the last common ancestor of *Chelonia mydas* (Linnaeus, 1758), *Caretta caretta* (Linnaeus, 1758), *Eretmochelys imbricata* (Linnaeus, 1758); *Lepidochelys kempii* (Garman, 1880); *L. olivacea* (Eschscholtz, 1829); *Natator depressus* (Garman, 1880).

Diagnosis. *Pan-Cheloniidae* can be diagnosed as *Chelonioidea* by the full list of characters given above for that taxon. Representatives of *Pan-Cheloniidae* can be distinguished to other Chelonioidea by the absence of the foramen praepalatinum, basioccipital depression with a V-shaped crest, high dorsum sellae, vomerine pillar visible in ventral view, sometimes obscured by the posterior extension of the triturating surface of the vomer (absent in *A. hofmanni*), vomer-palatine contact anterior to internal naris (apertura narium interna) (absent in *A. hofmanni*), basipterygoid processes of basisphenoid projection projecting posterolaterally, anterior articulation of the first thoracic vertebra ventrally or anteroventrally faced, ulnare nearly as large as intermedium and presence of secondary palate.

Comments. *Cheloniidae* is a diverse clade, specially considering the Cenozoic record (Gaffney and Meylan (1988); Parham and Pyenson (2010)). The fossil species assigned to Cheloniidae revel abundant shell-only material, but only fragments of limbs and skull and even more rare vertebra (Parham and Fastovsky 1997), unlike other Pan-Chelonioidea. Given that most of the diagnoses features of Pan-Chelonioidea are found on the skull, the inclusion of *Allopleuron hofmanni*, *Gigantatypus salahi* and *Glyptochelone suyckerbuyki* as and within Cheloniidae is merely tentatively, because such species do not possess all diagnostic features of the group. Therefore, we assign those species from the Cretaceous as Pan-Cheloniidae Indet., to avoid overlap with the diagnoses proposed for *Cheloniidae* in the review of the Cenozoic Pan-Cheloniidae.

Allopleuron hofmanni (Gray, 1831)

(= *Chelone faujasii* Giebel, 1852)

Taxonomic history. *Chelonia Hofmanni* Gray, 1831 (new species); *Allopleuron Hoffmanni* Baur 1888 (new combination and misspelled species epithet); *Chelone Hofmanni* = *Chelone Faujasii* = *Chelone cretacea* Winkler 1869 (senior synonym); *Allopleuron hoffmanni* = *Chelone camperi* Lydekker 1889 (senior synonym and misspelled species epithet); *Allopleuron hoffmanni* Hay 1908, Dollo 1909, Hirayama 1997 (misspelled species epithet).

Type material. MNHNP AC 8324, 8556 (types), NHMM 000001 (cotype by Mulder 2003; fragmentary carapace (Mulder 2003, pl. 5–6).

Type locality. Limburg, southern of Netherlands; Maastrichtian, Late Cretaceous (Janssen et al. 2011).

Referred material and range. Late Cretaceous (Late Maastrichtian), type locality (Mulder 2003); Late Cretaceous (Late Maastrichtian), Nekum Member, Maastricht Formation, Maastricht, Limburg, Netherlands (Mulder 2003); Late Cretaceous (Late Maastrichtian), Maastricht Formation, Kanne, Limburg, Belgium (Mulder 2003); Late Cretaceous (Late Maastrichtian), Lanaye Member, Maastricht Formation, Visé, Liège, Belgium (Mulder 2003); Late Cretaceous (Late Maastrichtian), Maastricht Formation, Neerkanne, Limburg, Belgium (Mulder 2003); Late Cretaceous (Late

Maastrichtian), Lanaye Member, Gulpen Formation, Eben Emael, Belgium (Mulder 2003); Late Cretaceous (Late Maastrichtian), Maastricht Formation, Gülickerberg Quarry, Voerendaal, Limburg, Belgium (Mulder 2003); Late Cretaceous (Late Maastrichtian), Nekum Member, CBR-Romontbos, Eben-Emael, Belgium (Mulder 2003); Late Cretaceous (Maastrichtian), Kunrade Chalk, Benzenrade, Limburg, Belgium (Mulder 2003); Late Cretaceous (Late Maastrichtian), Maastricht Formation, Nederkanne, Limburg, Belgium (Mulder 2003); Late Cretaceous (Turonian), Oerlinghausen Formation, Raunschweig-Broitzem, Germany (*Allopleuron* cf. *hofmanni*) (Karl et al. 2012); Late Cretaceous (Late Campanian), Quarry "Heidelberg Nord" (former "Teutonia Nord") of "Heidelberg Zement" in Hannover-Misburg, Lower Saxony, Germany (*Allopleuron* cf. *hofmanni*) (Karl et al. 2012); Late Cretaceous (Early Campanian), Sehnde-Höver, SE Hanover, Lower Saxony, Germany (*Allopleuron* cf. *hofmanni*) (Karl et al. 2012); Late Cretaceous (Maastrichtian), Limburg, Netherlands (type material of *Chelone faujasii*, Winkler 1869).

<u>Diagnosis</u>. *Allopleuron hofmanni* can be diagnosed as Pan-Cheloniidae by most of the list given for that clade. *Allopleuron* can be differentiated from other Pan-Cheloniidae by the loss of the vomer-palatine anterior contact to internal naris, vomerine pillar not visible in ventral view, pterygoid do not contributing to form the foramen palatinum posterius, absence of shell scutes, first peripherals with a curved anterior edge protruding prominently beyond the suture with the strongly incurved nuchal, distinct delimitations between pleurals and ribs, fourth to seventh peripherals with marginal keel and distinct vertical rim.

Comments. *Allopleuron* shows many adaptations for the marine life, and it indicates the presence of a very specialized sea turtle by the Late Cretaceous, when the Cheloniidae are starting their radiation into the sea (Hay 1908; Parham and Pyenson 2010). For this reason, Hay (1908) argued that the timing of the rise of *Allopleuron* does not match the inferred time for the emergence of the Cheloniidae. Gaffney and Meylan (1988), Weems (1988) and Hirayama (1992) suggested that *Allopleuron* share more resemblance with Protostegidae and Dermochelyidae, but according to Pritchard (1979), Zangerl (1980), Hirayama (1994; 1997), Hirayama and Chitoku (1996), Lapparent de Broin (2001) and Mulder (2003) it shares more similarities with Cheloniidae. The placement of this taxon is still a matter of debate, but since the most comprehensive and recent phylogenetic hypotheses (cited above) has been recovering closer affinities to Cheloniidae, *A. hofmanni* is currently placed into Pan-Cheloniidae.

Gigantatypus salahi Kaddumi, 2006

Taxonomic history. *Gigantatypus salahi* Kaddumi, 2006 (new species).

Type material. Deposited in the private collection of H. Kaddumi under the number ERMNH 1076; right humerus (Kaddumi 2006, fig. 3–7).

Type locality. Muwaqqar town, 30 km west of AlHarrana area, Jordan, Asia; Muwaqqar Chalk Marl Formation, Maastrichtian, Late Cretaceous (Kaddumi 2006).

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

Diagnosis. *Gigantatypus* can be diagnosed as Pan-Chelonioidea by the presence of the lateral process of the humerus separated from caput humeri, and humerus straighter than in Chelydridae. *Gigantatypus* can be diagnosed as Chelonioidea by the lateral process of humerus located away from the caput humeri. *Gigantatypus* can be distinguish from Pan-Dermochelyidae by the small anterior projection of lateral process of humerus and from other Pan-Cheloniidae by the more prominently enlarged lateral process of humerus, and capitellum ventrally situated.

Comments. *Gigantatypus salahi* is based on a single humerus from the Maastrichtian of Jordan (Kaddumi 2006). The placement of this species as Chelonioidea is supported by the lateral process, but its affinities within Cheloniidae is difficult to establish since the lack of preserved material. We agree with Kaddumi (2006) to recognize *G. salahi* as Cheloniidae given the lack of prominent anterior process of the humerus, a diagnostic feature of Dermochelyidae.

Oertelia gigantea (Oertel, 1914)

Taxonomic history. *Toxochelys gigantea* Oertel, 1914 (new species); “*Toxochelys*” *gigantea* Nicholls 1988 (incertae sedis); *Oertelia gigantea* Karl et al. 2012 (new combination).

Type material. Holotype is lost, fragments of the skull (Karl et al. 2012, pl. 1); GZG.V.5000 (lectotype), trunk vertebra (Karl et al. 2012, pl. 2).

Type locality. Near Garbsen close to Hannover, Germany; *Hoplites Deshayesi*–Zone of Kastendamm, Early Aptian, Late Cretaceous (Oertel 1914; Zangerl 1953; Karl et al. 2012).

Referred material and range. Late Cretaceous (Early Aptian), type locality (Karl et al. 2012).

Diagnosis. *Oertelia* can be diagnosed as Pan-Chelonioidea by the flatted carpals and tarsal elements. *Oertelia* can be differentiated from others stem-Chelonioidea by the presence of vomer extending further posteriorly to the level of the developed pterygoidal processus, smaller exoccipital angle, relatively long skull in relation to the width of mandibular joints. *Oertelia* can be differentiated from *Toxochelys latiremis* by the absence of palatinate contact of the vomer and it can be differentiated from *Ctenochelys acris* by the ratio of vomer/condylobasal length of 3 (in *C. acris* it is lesser than 3). Although the similarity of palate area between them, the roughness on the anterior choanal edge is much stronger pronounced in *Oertelia gigantea*. *Oertelia gigantea* can be diagnosed as Pan-Cheloniidae by the basioccipital depression with a V-shaped crest.

Comments. *Oertelia gigantea* is based on an incomplete and crushed skull from the Early Aptian of Germany (Karl et al. 2012). *Oertelia gigantea* was never included in a phylogenetic analysis and we tentatively place it as Pan-Chelonioidea based on the presence of one diagnosis of this group.

Pan-Dermochelyidae Joyce et al., 2004

Phylogenetic definition. Following Joyce et al. (2004), the term *Pan-Dermochelyidae* is herein referred to the Panstem clade that includes the crown *Dermochelyidae* but not the lineages that contain the *Protostega gigas* Cope, 1871 nor *Chelonia mydas* (Linnaeus, 1758).

Diagnosis. *Pan-Dermochelyidae* can be diagnosed as *Chelonioidea* by the full list of characters given above for that taxon. Representatives of *Pan-Dermochelyidae* can be distinguished to other Chelonioidea by the processus trochlearis oticum with a small contribution from prootic, reduced rostrum basisphenoidale, sagittal foramen formed between premaxilla and vomer, basisphenoide large and lying beneath significant portions of pterygoids, quadratojugal small and ventrally placed beneath a posterior extension of the jugal, prominent anterior projection of lateral process of humerus, and carapacial scutes absent or reduced.

Corsochelys haliniches Zangerl, 1960

Taxonomic history. *Corsochelys haliniches* Zangerl, 1960 (new species).

Type material. FMNH PR249 (holotype), fragments of the skull, partial shell, three ribs, parts of plastron, portions of shoulder girdle, pelvis, hindlimbs and forelimbs, possibly a young individual (Zangerl 1960, fig. 126–145).

Type locality. Near West Greene, Greene County, Alabama, USA; Mooreville Chalk, Selma Formation, Early Campanian, Late Cretaceous (Zangerl 1960).

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

Diagnosis. *Corsochelys haliniches* can be diagnosed as Pan-Chelonioidea by the presence of carapacial and plastral fontanelles, lateral process of the humerus separated from caput humeri, and diagnosed as Chelonioidea by the presence of lateral process of humerus located away from the caput humeri and the orbits facing laterally. *C. haliniches* can be diagnosed as Pan-Dermochelyidae by the reduced rostrum basisphenoidale, but it can be differentiated from other Pan-Dermochelyidae by the unusual small size of the skull and the nuchal with a strongly forward projection. *C. haliniches* can be differentiated from Dermochelyidae by the absence of the crista supraoccipitalis.

Comments. *Corsochelys haliniches* is based on several fragments from the Early Campanian of Alabama (Zangerl 1960). At the time of its description, *C. haliniches* was classified as Cheloniidae and some putative synapomorphies of this clade, as the basioccipital depression with a V-shaped crest and a high dorsum sellae, can be seen in this holotype. However, it is currently placed as a stem-Dermochelyidae because it also possesses synapomorphies of this group, as reduced rostrum basisphenoidale and very reduced carapacial scutes, leading Weems (1988) to suggest that the similarity with Cheloniidae would have been due to convergence for the marine specialization and not closer phylogenetic affinities. Supporting the uncertainty, Gentry (2017) found low statistical support for its placement, since the strict consensus indicated affinities with stem Chelonioidea whereas the 50% majority-rule consensus suggested more proximity with stem Dermochelyidae. Gentry (2017) suggested that the placement of *C. haliniches* as Pan-Chelonioidea might not be accurate and limiting the analysis with characters specific to sea turtles led *C. haliniches* to group with those taxa, causing low support of its affinities. However, as it shares sinapomorphies with Chelonioidea and we do not have evidences yet to exclude it from Pan-Chelonioidea, we placed *C. haliniches* based on the phylogenetic trees available, which found closer affinities with Dermochelyidae (Hirayama 1994, 1998; Kear and Lee 2006).

Mesodermochelys undulatus Hirayama and Chitoku, 1996

Taxonomic history. *Mesodermochelys undulatus* Hirayama and Chitoku, 1996 (new species).

Type material. HMG 5 (holotype); supraoccipital, series of vertebrae from 4th cervical to caudal, fragments of anterior and posterior limbs, posterior portion of the carapace and plastron (Hirayama and Chitoku 1996, fig. 2–3, 7–17).

Type locality. Shirafunenosawa River, Inasato, Hobetsu district of Mukawa Town, Hokkaido, Japan, Asia; Hakobuchi Group, Early sandy Siltstone Formation, Late Maastrichtian, Late Cretaceous (Hirayama and Chitoku 1996).

Referred material and range. Late Cretaceous (Early Campanian), Osoushinai Formation, Nakagawa-cho, Hokkaido, Japan (Hirayama and Hikida 1998); Late Cretaceous (Early Maastrichtian), type formation, Ohmagarinosawa River, Hiraoka, Hobetsu, Japan (Hirayama and Chitoku 1996); Late Cretaceous (Early Maastrichtian), type formation, Pankerusanosawa River, Hiraoka, Hobetsu, Japan (Hirayama and Chitoku 1996); Late Cretaceous (Early Maastrichtian), type formation, Pankerusanosawa River, Tomiuchi, Hobetsu, Japan (Hirayama and Chitoku 1996); Late Cretaceous (Early Maastrichtian), type formation, Hobetsu River, Mobetsu, Hobetsu, Japan (Hirayama and Chitoku 1996); Late Cretaceous (Campanian-Maastrichtian), Hobetsu River, Kiusu, Hobetsu, Japan (Hirayama and Chitoku 1996); Late Cretaceous (Early Maastrichtian), Sososhisawa, Inasato, Hobetsu, Japan (Hirayama and Chitoku 1996).

Diagnosis. *Mesodermochelys undulatus* can be diagnosed as Pan-Chelonioidae by the presence of flatted carpals and/or tarsal elements and presence of carapacial and plastral fontanelles in adults. It can be diagnosed as Chelonioidea by the presence of a small lateral process of ischium (metischial process), and a lateral process of humerus located away from the caput humeri. *M. undulatus* can be differentiated from other Pan-Dermochelyidae by the combination of the following characters states: lateral process of the humerus distally located, but still more proximal to caput humeri than all other Pan-Dermochelyidae, well developed bony shell, lower triturating surface with isolated symphyseal and lingual ridges, undulating medial margin of broader peripherals, narrow neurals, and elongate iliac blade with outward curvature.

Comments. *Mesodermochelys undulatus* is based on fragmentary cranial and several post-cranial materials, with more than 10 referred specimens (Hirayama and Chitoku 1996). The type specimens are from the Early Maastrichtian of Japan, but the discovery of a right humerus, also from Japan, extends back the geological range of *M. undulatus* to the Early Campanian (Hirayama and Hikida 1998). Due to the fragmentary nature of the skull remains of *Mesodermochelys*, its phylogenetic relationships within Pan-Dermochelyidae are still unclear, but it is likely that this genus is more related to the Cenozoic species (*Eosphargis*, *Psephophorus* and *Dermochelys*) than *Corsochelys* (Hirayama and Chitoku 1996).

Pan-Chelonioidea Indet.

Comments. Only one sea turtle fossil species can be assigned as Pan-Chelonioidea, but due to the lack of diagnostic features, the phylogenetic placement within major clades is not well supported, thus we considered this species as Pan-Chelonioidea Indeterminate. We followed the last reviewer rule and keep the use of current nomenclature in order to avoid proposing useless nomenclatural acts that inflate the number of names applied to one species or genus.

Zangerlchelys arkansaw (Schmidt, 1944)

Taxonomic history. *Catapleura arkansaw* Schmidt, 1944 (new species); *Catapleura arcansaw* Hirayama 1997 (misspelled species epithet); *Zangerlchelys arkansaw* Hirayama 2006 (new combination).

Type material. FMNH P27045 (holotype), nearly complete carapace and plastron (Schmidt 1944, fig. 24).

Type locality. Gather Brothers Farm, one-mile northeast of Okolona, Clark County, Arkansas, USA (Schmidt 1944); Marlbrook Marl Formation, Late Campanian, Late Cretaceous (Hirayama 2006).

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

Diagnosis. *Zangerlchelys arkansaw* can be diagnosed as Pan-chelonioid by the presence of carapacial and plastral fontanelles in adults.

Comments. *Zangerlchelys arkansaw* is based on a carapace and plastron from the Late Campanian of Arkansas (Schmidt 1944; Hirayama 2006). It was first described as Cheloniidae, named *Catapleura arkansaw*, but the only diagnostic feature pointed out by Schmidt (1944) (a triangular first peripheral with narrow contact with first costal) to include it to *Catapleura* varies within Cheloniidae (Hirayama 2006). Hirayama (2006) detected more differential features and proposed a new combination, *Zangerlchelys arkansaw*. We agree with Hirayama (2006) that due to the lack of cranial and humeral information, the phylogenetic relationship of *Z. arkansaw* within Pan-Chelonioidea still unknown and it is considered as Pan-Chelonioidea Indet. herein.

Eucryptodira Indet.

Comments. In this section, we assigned the marine species from Cretaceous previously allocated within Pan-Chelonioidea and Thalassemydidae but currently do not correspond to the diagnosis proposed for these groups (see each taxon for details). Therefore, we allocate these species to the most conservative related clade formerly assigned, i.e., Eucryptodira Indeterminate.

Cynocercus incisus Cope, 1871

Taxonomic history. *Cynocercus incisus* Cope, 1871 (new species); *Toxochelys latiremis* = *Cynocercus incisus* Hay 1908 (junior synonym); *Cynocercus incisivus* Zangerl 1953 (incertae sedis and misspelled species epithet).

Type material. AMNH 1582 (holotype); two caudal vertebrae and a metapodial (Cope 1871, no figures; Hay 1908).

Type locality. Near to Butte's Creek, south of Fort Wallace, Wallace County, Kansas, USA; probably Niobrara Formation, Late Cretaceous (Cope 1871).

Comments. *Cynocercus incisus* was based on vertebrae and metapodial probably from the Late Cretaceous of Kansas (Cope 1871). It was assigned to Toxochelyidae by Cope (1871), but Zangerl (1953) pointed that its vertebrae differ significantly from those of *Toxochelys* and *Ctenochelys*, suggesting that *C. incisus* might not be Toxochelyidae. Due to the lack of additional material to confirm its phylogenetic relationship, we cannot recognize it as Pan-Chelonioidea, and we consider it as a Eucryptodira Indeterminate.

Kimurachelys slobodae Brinkman et al., 2015

Taxonomic history. *Kimurachelys slobodae* Brinkman et al., 2015 (new species).

Type material. TMP 2010.85.17 (holotype), mandible with both dentaries, partial left angular, and left coronoid (Brinkman et al. 2015, fig. 3); TMP 2012.39.24 (paratype), mandible with both dentaries, articulars and left coronoid (Brinkman et al. 2015, fig. 3).

Type locality. Sage Creek area, southeast of Manyberries, Alberta, Canada; uppermost part of the Dinosaur Park Formation, Campanian, Late Cretaceous (Brinkman et al. 2015).

Referred material and range. Late Cretaceous (Campanian) from the Lethbridge Coal Zone, Dinosaur Park Formation, Alberta, Canada (Brinkman et al. 2006).

Diagnosis. *Kimurachelys slobodae* can be differentiated from *Nichollsemys* and *Toxochelys* by possessing expanded triturating surface, and it can be differentiated from Chelonioidea by the posterior end of the dentary rising sharply and forming a tall coronoid process, and lingual edge of the triturating surface is significantly higher than the labial edge when seen in lateral view. *Kimurachelys* resembles *Ctenochelys* by the expanded triturating surface and well-developed symphyseal ridge but differs by having symphyseal ridge restricted to the posterior third of the symphysis (similar to the Eocene Chelonioidea *Argillochelys*) rather than extending the full length of the symphysis. The dentary of *Kimurachelys* also resembles the living taxa, and it shares with *Lepidochelys olivacea* a deeply concave triturating surface with a distinctive scoop shape and both have a lingual edge that is higher than the labial.

Comments. *Kimurachelys slobodae* is based on mandibles from the Campanian of Canada (Brinkman et al. 2015). Despite the similarities between the triturating surface of *Kimurachelys* with other species (pointed out above), none of them are diagnostic features used to identify major clades. Also, the morphology of triturating surfaces has been related with diet preference (Parham and Pyenson 2010), and such similarities might be due to convergence and, therefore, it is not necessarily related with phylogenetic proximity (Brinkman et al. 2015).

Prionochelys nauta Zangerl, 1953

(= *Prionochelys matutina* Zangerl, 1953)

Taxonomic history. *Prionochelys nauta* Zangerl, 1953 (new species); *Prionochelys nauta* = *Prionochelys matuina* (misspelled species epithet) = *Prionochelys galeotergum* Hirayama 1997 (senior synonym).

Type material. FMNH P26237 (holotype), partial shell, fragments of plastron, costals, neurals and peripheral fragments (Zangerl 1953, fig. 115–117).

Type locality. Devil's Backbone area, Saratoga municipality, Howard County, Arkansas, USA; Marlbrook Marl Formation, Late Campanian, Late Cretaceous (Zangerl 1953).

Referred material and range. Late Cretaceous (Late Campanian), type locality (Zangerl 1953); Late Cretaceous (Late Campanian), type formation, Nick Gaither Farm, road to Arkadelphia, Clark County, Arkansas, USA (Zangerl 1953); Cox Farm, type formation, Clark County, Arkansas, USA (Zangerl 1953); Late Cretaceous (Early Campanian), Selma Formation, Moore Brothers Farm, Harrel Station area, Dallas County, Alabama, USA (type material of *Prionochelys matutina*; Zangerl 1953).

Diagnosis. *Prionochelys* possessed only one differential diagnose of Pan-Chelonioidea, the presence of carapacial and plastral fontanelles in adults. *Prionochelys* can be differentiated from other species by the carapace with keeled neurals (elevations between the neurals 2-3, 5-6 and 8-9).

Comments. *Prionochelys nauta* is based on fragments of carapace and plastron from the Late Campanian of Arkansas (Zangerl 1953). Due to the lack of complete skull material and limbs, the phylogenetic affinity of this species is unknown. The features present in the referred material suggests great resemblance with the pelvic girdle of *Toxochelys* and the xiphiplastra and the skull of *Ctenochelys*, which might stand for a putative placement of *Prionochelys* within stem-Chelonioidea. However, we did not find more diagnoses feature to confirm its assignment as Pan-Chelonioidea, and therefore we consider it as Eucryptodira Indeterminate.

Porthochelys laticeps Williston, 1901

Taxonomic history. *Porthochelys laticeps* Williston, 1901 (new species).

Type material. KU 1204 (holotype), almost complete skull and left side of the carapace, the plastron and right humerus (Williston 1901, pls. 19–21; Hay 1908, fig. 231–233; Zangerl 1953).

Type locality. Saline River, Trego County, Kansas, USA; Niobrara Formation, Late Cretaceous (Williston 1901; Hay 1908).

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

Diagnosis. *Porthochelys* possessed only one differential diagnose of Pan-Chelonioidea, the retention of carapacial and plastral fontanelles in adults, which can also be seen in Pleurodiras. *Porthochelys* can be differentiated from crown-Chelonioidea by the orbits facing dorsally and it can be distinguished from stem-Chelonioidea by the highly ossified carapace and, specially, the plastron, with only small fontanelles, the stoutness of the skull with broad and flattened maxillae, and the curved appendicular elements.

Comments. *Porthochelys laticeps* is based on skull and parts of the post-cranial elements, from the Late Cretaceous of Kansas (Williston 1901; Hay 1908). Despite the similarity with the skull of *Toxochelys latiremis*, *P. laticeps* has little resemblance with Pan-Chelonioidea, and the almost complete shell ossification, summed with the curved appendicular elements, challenge its identification as Pan-Chelonioidea. A detailed revision of its remains with further inclusion in a phylogenetic analysis is needed, and for now we consider it as a Eucryptodira Indeterminate.

"Thalassemys" cava (Nessov, 1984)

Taxonomic history. *Parathalassemys cava* Nessov, 1984 (new species); *Thalassemys carva* Karl et al. 2012 (new combination and misspelled species epithet).

Type material. CCMGE 1/12086 (holotype) (Averianov 2002), fragments of carapace and plastron (Nessov and Krassovskaya 1984, pls. 3–4).

Type locality. Itemir, Bukhara Viloyat, Uzbekistan, Asia; Kulbecke Formation, Late Albian? – early Cenomanian, Early? – Late Cretaceous (Averianov 2002).

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

Diagnosis. "*Thalassemys" cava* can be differentiated from other eucryptodirans by the presence of a deep sulci of horny shields, broad centrals, with folds crossed by concentric lines in the borders, last costal plates with two widely separated free ribheads, two metaneurals, heads of the trunk ribs are strongly developed, and plastron in large specimens moderately developed and shows central fontanelles.

Comments. *"Thalassemys" cava* were originally identified as a Thalassemydidae, but later it was reallocated to Macrobaenidae (Sukhanov et al. 2000), and then considered as Testudines incertae sedis sharing similarities to Plesiochelyidae (Averianov 2002). More recently, it was recognized once again as Thalassemydidae (Karl et al. 2012). However, according to the diagnosis of Thalassemydidae and *Thalassemys* proposed by Püntener (2015), it cannot be identified as belonging to this genus neither this family because their diagnostic features are not seen in "*T*". *cava*. It is hence treated as Eucryptodira Indet. herein.

Thinochelys lapisossea Zangerl, 1953

Taxonomic history. *Thinochelys lapisossea* Zangerl, 1953 (new species).

Type material. FMNH P27453 (holotype), almost complete carapace, partial plastron, posterior shell and anterior caudal vertebrae, and fragments of the girdle (Zangerl 1953, fig. 82).

Type locality. Harrel Station area, one mile east of Harrel Station, south of railroad tracks, Dallas County, Alabama, USA; Mooreville Chalk, Selma Formation, Early Campanian, Late Cretaceous (Zangerl 1953).

Referred material and range. Late Cretaceous (Early Campanian), type locality (Zangerl 1953).

Diagnosis. *Thinochelys* possessed only one differential diagnose of Pan-Chelonioidea, the retention of carapacial and plastral fontanelles in adults. *Thinochelys* can be differentiated from stem-Chelonioidea by the almost complete ossification of the carapace, similar to *Porthochelys*, but it can be distinguished from this genus by the less fontanellization of the plastron and posterior peripherals much longer than wide.

Comments. *Thinochelys lapisossea* is based on parts of post-cranial material from the Early Campanian of Alabama (Zangerl 1953). This species was never included into a phylogenetic analysis, and similarly to *Porthochelys*, the almost complete ossification of carapace and plastron challenge the identification as Pan-Chelonioidea. A detailed review of the type material is necessary, but until that we consider *Thinochelys* as Eucryptodira Indeterminate.

Turgaiscapha kushmurunica Averianov, 2002

Taxonomic history. *Turgaiscapha kushmurunica* Averianov, 2002 (new species)

Type material. ZISP PH 1/37 (holotype), pygal (Averianov 2002, fig. 11).

Type locality. Kushmurun, northern Kazakhstan, Asia (Averianov 2002); lower part of

Eginsai Formation, Late Campanian–early Maastrichtian?, Late Cretaceous (Averianov 2002).

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

Diagnosis. *Turgaiscapha* do not possess any diagnoses of Pan-Chelonioidea nor of any clade within it.

Comments. *Turgaiscapha kushmurunica* is based on a single pygal from the Late Cretaceous of Kazakhstan (Averianov 2002). Its placement could not be determined, and it was treated as cf. Dermochelyidae by the similarity with *Corsochelys* and *Mesodermochelys*. Its small size and the presence of well developed shell ossification can be explained as less specialized features (Averianov 2002), but it also makes it dubious to consider this species as a Dermochelyidae. For this reason, it is considered here as Pan-Chelonioidea Indeterminate.

Sontiochelys cretacea Stache, 1905

Taxonomic history. *Sontiochelys cretacea* Stache, 1905 (new species).

Type material. MCST 9959 (plastotype; the holotype is lost); carapace (Karl et al. 2012, fig. 1).

Type locality. Mrzlek, near to Salcano/Solkan at the south–eastern flank of Monte Santo, Nova Gorizia, Slovenia; Hauterivian – Barremian, Early Cretaceous (Stache 1905; Karl et al. 2012).

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

Diagnosis. *Sontiochelys cretacea* can be differentiated to other eucryptodirans by the absence of a neural row, the presence of a metaneural single and wide, free rib end of pleural I alternating between peripheral II and III, presence of a nuchal notch not very deep, and pygal much wider than long.

Comments. This species is considered herein because it displays a high degree of adaptation to the marine life (Karl et al. 2012), although those adaptations are not clearly pointed. After the original description, *Sontiochelys* was scarcely cited in the literature (e.g. Kuhn 1964), until Karl et al. (2012c) figured its plastotype and re described the species, presenting a diagnosis for the genus. Kuhn (1964) and Karl et al. (2012c) classified *Sontiochelys* as Thalassemydidae but following the revised diagnosis of Thalassemydidae (Püntener et al. 2015), this genus does not exhibit diagnostic characters for the group and therefore are classified herein as Eucryptodira Indeterminate.

Invalid and Problematic Taxa

Chelone camperi Owen, 1851

nomen nudum

Taxonomic history. *Chelone camperi* Owen, 1851 (new species); *Chelone hoffmanni* = *Chelone camperi* Lydekker 1889 (junior synonym); *Chelone camperi* this study (nomen nudum).

Type material. Sedgwick Museum of Earth Sciences, unnumbered (Danise and Higgs 2015); two costal bones (Owen 1851, pl. 5).

Type locality. Burham, Kent, United Kingdom; Cenomanian, Late Cretaceous (Owen 1851; Danise and Higgs 2015).

Comments. *Chelone camperi* was based on two costals from the Late Cretaceous of Kent (Owen 1851; Danise and Higgs 2015). It was assigned as junior synonym of *Allopleuron hofmanni* by Lydekker (1889) and later of *Puppigerus camperi* (Karl et al. 2012), but the latter information could not be confirmed. Moody (1974) listed the junior synonyms of *Puppigerus camperi*, and *C. camperi* are not between them, which raises the possibility of confusion due to the name of the epithet. As suggested by Mulder (Karl et al. 2012), *Chelone camperi* should be avoided, and provided the misinformation about its senior synonyms, we proposed to consider it nomen nudum.

Chelone faujasii Giebel, 1852

nomen invalidum

(junior synonym of *Allopleuron hofmanni* [Gray, 1831])

Taxonomic history. *Chelone Faujasii* Giebel, 1852 (new species); *Chelone Hofmanni* = *Chelone Faujasii* = *Chelone cretacea* Winkler 1869 (junior synonym).

Type material. Unknown; carapace (Winkler 1869).

Type locality. Limburg, southern of Netherlands; Maastrichtian, Late Cretaceous (Winkler 1869).

Comments. The nuchal of *Chelone faujasii* presents a strong notch above the neck that led Giebel (1847) to differentiate it from *Allopleuron hofmanni* and refer to a new species (apud Mulder 2003). Later, this difference was considered age-related and *C. faujasii* was synonymized to *A. hofmanni* (Winkler 1869; Mulder 2003).

Chelonia cretacea Keferstein, 1834

nomen nudum

Taxonomic history. *Chelonia cretacea* Keferstein, 1834 (new species); *Chelone Hofmanni* = *Chelone Faujasii* = *Chelone cretacea* Winkler 1869 (junior synonym and misspelled species genera); *Chelonia cretacea* this study (nomen nudum).

Type material. Unknown; incomplete plastron and carapace (Faujas De Saint-Fond 1798, pl. 12–14).

Type locality. Montagne Saint-Pierre, Limburg, Netherlands (Faujas De Saint-Fond 1798); Maastrichtian, Late Cretaceous (Keferstein 1834).

Comments. The literature concerning *Chelonia cretacea* is very scarce. After coined the name without a proper description nor figures, Keferstein (1834) mentioned “Cuvier Vol. 2, p. 239, tab 12, fig. 1”, which seems to be an illustration of the type material, but such reference could not be found. Winkler (1869) compared and synonymized it to *A. hofmanni*, but again without a description and associated figures. Because of the lack of a morphological description of this species and proper identification of the holotype, we propose to consider it a nomen nudum.

Ctenochelys procax (Hay, 1905)

nomen invalidum

(junior synonym of *Ctenochelys stenoporus* [Hay, 1905])

Taxonomic history. *Toxochelys procax* Hay, 1905 (new species); *Ctenochelys procax* Zangerl 1953 (new combination); *Ctenochelys stenoporus* = *Toxochelys elkader* = *Toxochelys bauri* = *Toxochelys procax* (in part) Zangerl 1953 (junior synonym); *Ctenochelys stenoporus* = *Toxochelys serrifer* (in part) = *Toxochelys procax* = *Toxochelys elkader* = *Lophochelys natatrix* = *Lophochelys venatrix* = *Ctenochelys tenuitesta* = *Ctenochelys acris* Hirayama 1997 (junior synonym).

Type material. AMNH 234 (holotype), skull, lower jaw (Hay 1905, fig. 13–14).

Type locality. Along the Smoky Hill River, Kansas, USA; Smoky Hill Chalk member, Niobrara Formation, Early Campanian, Late Cretaceous (Hay 1905; Nicholls and Russell 1990).

Comments. *Ctenochelys procax* was based on a crushed skull and lower jaw from the Niobrara Formation of Kansas (Hay 1905). It was first assigned to *Toxochelys*, but when *Ctenochelys* was coined by Zangerl (1953), mainly because of the features of the lower jaw, *T. procax* and many other *Toxochelys* spp. were transferred to this new genus. Later, Hirayama (1997) synonymized all of them to *Ctenochelys stenoporus*, considering the observed morphological variation as intraspecific.

Ctenochelys tenuitesta Zangerl, 1953

nomen invalidum

(junior synonym of *Ctenochelys stenoporus* [Hay, 1905])

Taxonomic history. *Ctenochelys tenuitesta* Zangerl, 1953 (new species); *Ctenochelys stenoporus* = *Toxochelys serrifer* (in part) = *Toxochelys procax* = *Toxochelys elkader* = *Lophochelys natatrix* = *Lophochelys venatrix* = *Ctenochelys tenuitesta* = *Ctenochelys acris* Hirayama 1997 (junior synonym).

Type material. FMNH P27361 (holotype); partial carapace and plastron, bones of the girdle and the limbs, and vertebrae (Zangerl 1953, fig. 101).

Type locality. Moore Brothers farm, Harrell Station area, Dallas County, Alabama, USA; Mooreville Chalk, Selma Formation, Early Campanian, Late Cretaceous (Zangerl 1953; Nicholls and Russell 1990).

Comments. *Ctenochelys tenuitesta* was based on several fragments, probably the most well-represented specimen of the genus, from the Early Campanian of Alabama (Zangerl 1953; Nicholls and Russell 1990). It was first assigned as the type species of *Ctenochelys* by Zangerl (1953), but later it was synonymized by Hirayama (1997), who also assigned *Ctenochelys stenoporus* (Hay, 1905) as the type of this genus because its description precedes *C. tenuitesta* Zangerl, 1953.

Dollochelys atlantica (Zangerl, 1953)
nomen invalidum
(junior synonym of *Catapleura repanda* Cope, 1868)

Taxonomic history. *Toxochelys atlantica* Zangerl, 1953 (new species); *Toxochelys atlantica* = *Lytoloma angusta* = *Lytoloma wielandi* Zangerl 1953 (senior synonym); *Toxochelys atlantica* = *Dollochelys atlantica* Zangerl 1971 (new combination); *Catapleura repanda* = *Toxochelys atlantica* Hirayama 1997 (junior synonym);

Catapleura repanda = *Dollochelys atlantica* = *Dollochelys casieri* = *Dollochelys coatesi* Hirayama 2006 (junior synonym).

Type material. YPM 625 (holotype); carapace (Zangerl 1953, fig. 79).

Type locality. Barnsboro, Gloucester County, New Jersey, USA (Zangerl 1953); Greensand beds, Late Maastrichtian, Late Cretaceous (Baird 1967).

Comments. *Toxochelys atlantica* was based on an almost complete carapace from the Late Maastrichtian of New Jersey (Zangerl 1953). When Zangerl (1971) erected a new genus, *Dollochelys,* he noticed the resemblance in the carapace of *T. atlantica* and proposed a new combination, *D. atlantica*. Later, the presence of a second suprapygal, a differential diagnosis of *Dollochelys,* was considered a variable feature (Parris et al. 1986; Hirayama 2006) and *D. atlantica* was considered a junior synonym *of Catapleura repanda* Cope, 1868 (Hirayama 1997).

Glaucochelone lonzeensis Dollo, 1909

nomen nudum

Taxonomic history. *Glaucochelone lonzeensis* Dollo, 1909 (new species); *Glaucochelone lonzeensis* Zangerl 1971 (nomen nudum).

Type material. IRSNB Vert-00-494 (holotype); mandible (Dollo 1909, no figures).

Type locality. Lonzée village, province of Namur, near Gembloux, Belgium; "Dark green glauconitic clayey sand", Turonian – Maastrichtian, Late Cretaceous (Dollo 1909).

Comments. *Glaucochelone lonzeensis* was based on a single mandible from the Late Cretaceous of Lonzée (Dollo 1909). Despite the resemblance with the mandible of stem-Chelonioidea, Zangerl (1971) argued that there is not enough material to recognize it as such. Because of the short and vague description and the lack of figures, *G. lonzeensis* was treated as nomen nudum in Zangerl (1971) and it is followed herein.

Lophochelys natatrix Zangerl, 1953

nomen dubium

Taxonomic history. *Lophochelys natatrix* Zangerl, 1953 (new species); *Ctenochelys stenoporus* = *Lophochelys natatrix* = *Lophochelys venatrix* = *Ctenochelys tenuitesta* = *Ctenochelys acris* Hirayama 1997 (junior synonym); *Lophochelys natatrix* this study (nomen dubium).

Type material. FMNH PR220 (holotype); partial carapace and plastron, scapulae, coracoid, limb bones, and vertebrae (Zangerl 1953, fig. 91).

Type locality. One mile north of the Pyramids, Logan County, Kansas, USA; Niobrara Formation, Late Cretaceous (Zangerl 1953).

Comments. *Lophochelys natatrix* was based on several fragments from the Late Cretaceous of Kansas (Zangerl 1953). *Lophochelys natatrix* and *Lophochelys niobrarae* were described based on juvenile individuals and the features that appear to differentiate them from *Lophochelys venatrix* are the degree of ossification of the shell, which is related to difference of age between the individuals (Zangerl 1953). As suggested by Hirayama (1997), it is probably a young individual of a valid species, but the evidences for synonymization have low support because of the difference in size of the specimens (Zangerl 1953). Because it is juvenile, and its features do not match with any other adult species, we propose to consider *Lophochelys natatrix* a nomen dubium.

Lophochelys niobrarae Zangerl, 1953

nomen dubium

Taxonomic history. *Lophochelys niobrarae* Zangerl, 1953 (new species); *Toxochelys latiremis* = *Lophochelys niobrarae* Hirayama 1997 (junior synonym); *Lophochelys niobrarae* this study (nomen dubium).

Type material. FMNH UR1 (holotype); partial carapace (Zangerl 1953, fig. 94).

Type locality. Kansas, USA; Niobrara Formation, Coniacian-Santonian, Late Cretaceous (Zangerl 1953).

Comments. *Lophochelys niobrarae* was based on a partial carapace of a juvenile specimen from the Late Cretaceous of Kansas (1953). See comments for *L. natatrix*. Because the holotype is a juvenile individual (Hirayama 1997) and the diagnostic features do not match with any other adult species, we propose to consider *Lophochelys niobrarae* a nomen dubium. As result, the small shell found in Alberta, Canada and assigned as referred material of *L. niobrarae* by Nicholls (1990) requires careful examination.

Lophochelys venatrix Zangerl, 1953

nomen dubium

Taxonomic history. *Lophochelys venatrix* Zangerl, 1953 (new species); *Ctenochelys stenoporus* = *Lophochelys natatrix* = *Lophochelys venatrix* = *Ctenochelys tenuitesta* = *Ctenochelys acris* Hirayama 1997 (junior synonym).

Type material. FMNH P27355 (holotype), fragments of the carapace and plastron (Zangerl 1953, fig. 95).

Type locality. Moore Brothers Farm, Harrel Station area, Dallas County, Alabama, USA; Mooreville Chalk, Selma Formation, Early Campanian, Late Cretaceous (Zangerl 1953; Nicholls and Russell 1990).

Comments. *Lophochelys venatrix* was based on fragments of carapace and plastron from the Late Cretaceous of Alabama (Zangerl 1953). Hirayama (1997) suggested the holotype would consist on a juvenile specimen and considered this species as a junior synonym of *Ctenochelys stenoporus*. The broadly oval, rounded posteriorly shell, and the degree of specialization in the extremes of the shell differs from those of *Ctenochelys*, *Mexichelys* and *Toxochelys* species, so we do not agree with Hirayama (1997) synonym. On the other hand, we agree that the holotype and only known material is a juvenile specimen, lacking proper diagnostic features to hold a valid species. Therefore, we suggest considering *Lophochelys venatrix* a nomen dubium. Given that the three recognized *Lophochelys* species are nomina dubia and that those species have been diagnosed based on juvenile specimens, this genus is probably inappropriate.

Lytoloma angusta Cope, 1870

nomen invalidum

(junior synonym of *Catapleura repanda* Cope, 1868)

Taxonomic history. *Lytoloma angusta* Cope, 1870 (new species); *Lytoloma angusta* = *Chelone sopita* [in part] Cope 1870 (senior synonym); *Lytoloma wielandi* = *Lytoloma angusta* Hay 1908 (junior synonym); *Toxochelys atlantica* = *Lytoloma angusta* = *Lytoloma wielandi* Zangerl 1953 (junior synonym); *Toxochelys atlantica* = *Dollochelys atlantica* Zangerl 1971 (junior synonym); *Catapleura repanda* =

Toxochelys atlantica Hirayama 1997 (junior synonym); *Catapleura repanda* = *Dollochelys atlantica* = *Dollochelys casieri* = *Dollochelys coatesi* Hirayama 2006 (junior synonym).

Type material. AMNH 1133 (lectotype, Spamer et al. 1995), three peripherals, a fragment of a costal and a lower jaw (Hay 1908, no figures); ANSP 9223 (paralectotype, Spamer et al. 1995), three marginal plates and fragments of a fourth plate (Leidy 1865, plate 19, fig. 5; Spamer et al. 1995).

Type locality. Near Barnsboro, New Jersey, USA; Barnsboro Formation, Late Cretaceous (Cope 1870).

Comments. *Lytoloma angusta* was based on a specimen firstly described as the type of *Chelone sopita* (Leidy, 1865) (ANSP 9223), collected in the Mullica Hill, Gloucester County, New Jersey (Leidy 1865). Later, Hay (1908) declared the AMNH 1133 specimen as the lectotype of *L. angusta*, and the ANSP 9223 the paralectotype (Spamer et al. 1995). Zangerl (1953) revised the *Toxochelys* genus and synonymized several species to *Toxochelys latiremis*, expanding the geographical range of this species. Given the widespread nature of *Toxochelys latiremis*, he concluded that other genera described for the same formations probably belong to *Toxochelys*, and he synonymized *L. angusta* and *L. wielandi* to the latter genus and proposed a new combination, *Toxochelys atlantica*. Later, based on a second suprapygal, Zangerl (1971) erected a new genus for *T. atlantica*, named *Dollochelys*. Such differencial feature was considered variable (Parris et al. 1986), and *Dollochelys* spp. were synonymized to *Catapleura repanda* without further explanation (Hirayama 1997), but possibly because they were found in the same locality. We suggest following Hirayama (1997) and consider *Lytoloma angusta* as a junior synonym of *Catapleura repanda* Cope, 1868.

Osteopygis sopitus (Leidy, 1865)

nomen vanum

<u>Taxonomic history</u>. *Chelone sopita* Leidy, 1865 (new species); *Chelone sopita* [in part] = *Lytoloma angusta* Cope 1870 (junior synonym); *Propleura sopita* Cope 1870 (new combination); *Osteopygis sopitus* Cope 1875 (new combination); *Osteopygis borealis* = *Osteopygis sopitus* [in part] = *Propleura borealis* Hay 1908 (junior synonym); *Osteopygis sopitus* [in part] = *Rhetechelys platyops* Hay 1908 (junior synonym); *Osteopygis emarginatus* = *Osteopygis sopita* = *Osteopygis borealis* = *Propleura sopita* Zangerl 1953 (junior synonym); *Chelone sopita* Zangerl 1953 (nomen vanum).

<u>Type material</u>. RUGM unnumbered (lectotype), four peripherals (Leidy 1865, no figures; Hay 1908, fig. p. 149); ANSP 9223 (paralectotype), three marginal plates and fragments of a fourth plate (Leidy 1865, plate 19, fig. 5; Spamer et al. 1995); AMNH 2361 (paralectotype; Cope 1870), two marginal bones, part of a costal, half a femur, a tarsal and two phalanges (Cope 1870, no figures); AMNH 2351 (paralectotype, Cope 1870), several peripherals, the nuchal, a few costals costal, a number of plastral bones, parts of both humeri, and a complete left femur.

<u>Type locality</u>. Tinton Falls, Monmouth County, New Jersey, USA (Leidy 1865; Spamer et al. 1995); Late Cretaceous (Leidy 1865).

<u>Comments</u>. *Chelone sopita* was based on two specimens from New Jersey (Leidy 1865). The first specimen (RUGM unnumbered) was described unsatisfactorily and

without figures by Leidy (1865), until Hay (1908) provided a drawing. The second specimen (ANSP 9223), collected in the Mullica Hill, Gloucester County, was assigned as type of a new species, *Lytoloma angusta* in Cope (1870). More two specimens were referred to *Chelone sopita* in Cope (1870). The first one was collected at the quarry of Barclay Edwards, near Harrisonville, Salem County, and it is under the identification AMNH 2361. Cope (1870) transferred it to *Propleura* and then to *Osteopygis* in Cope (1875). However, Hay (1908) affirmed it does not belong to *Osteopygis* and transferred it to *Rhetechelys* due to the proximity of localities. The second specimen, AMNH 2351, was transferred to *Osteopygis* in Cope (1868), but Hay (1908) compared *Osteopygis sopita* to *Osteopygis borealis* and concluded that they do not present differential features and he considered *O. sopita* (AMNH 2351) a junior synonym of *O. borealis*. Zangerl (1953) considered *Osteopygis sopitus*, *Propleura sopita*, *Lytoloma angusta* and *Osteopygis borealis* as junior synonym of *Osteopygis emarginatus*. It is not clear if the type specimen (RUGM unnumbered) was reviewed and synonymized in one of those studies. Given the inconsistency and uncertainty of this species and the remaining type material, we agree with Zangerl (1953) to consider it nomen vanum.

Platychelone emarginata Dollo, 1909

nomen nudum

Taxonomic history. *Platychelone emarginata* Dollo, 1909 (new species); *Platychelone emarginata* Mulder et al. 1998 (nomen nudum).

Type material. IRSNB Vert-00000-01681 (holotype); carapace (Dollo 1909, no figures).

Type locality. Belgian Limburg, Belgium; Maastrichtian, Late Cretaceous (Dollo 1909).

Comments. *Platychelone emarginata* was based on a single carapace from the Maastrichtian type area (Mulder et al. 1998). Mulder (1998) proposed to consider it a nomen nudum because it was not formally described nor illustrated.

Prionochelys matutina Zangerl, 1953

nomen dubium

Taxonomic history. *Prionochelys matutina* Zangerl, 1953 (new species); *Prionochelys nauta* = *Prionochelys matuina* = *Prionochelys galeotergum* Hirayama 1997 (junior synonym and misspelled species epithet); *Prionochelys matutina* this study (nomen dubium).

Type material. FMNH P27561 (holotype); a portion of carapace and plastron and elements of the pelvis (Zangerl 1953, fig. 118–120).

Type locality. Moore Brothers Farm, Harrel Station area, Dallas County, Alabama, USA; Mooreville Chalk, Selma Formation, Early Campanian, Late Cretaceous (Zangerl 1953; Nicholls and Russell 1990).

Comments. *Prionochelys matutina* was based on a fragmentary carapace, plastron and pelvis of a juvenile individual from the Early Campanian of Alabama (Zangerl 1953). Apart from the ossification of the carapace keel, it is very similar to *Prionochelys nauta*, which led Hirayama (1997) to identify the holotype of *P. matutina* as young individuals of *P. nauta*. However, Hirayama (1997) did not considered Zangerl (1953)’s observation that younger individuals have more conspicuous ornamental processes than adults, and the young *P. matutina* possess a keel elevation much smaller than the adult of *P. nauta*. There are also differences in the proportions of the neural elements and the plastron of *P. nauta* and *P. matutina*. We, therefore, do not agree with the synonymization of *P. matutina* and *P. nauta*. In addition, because this specimen is a juvenile, very fragmented, and do not present total similarity with another species, it is not appropriated to consider *P. matutina* a valid species. Thence, we propose to consider it a nomen dubium.

Prionochelys galeotergum Zangerl, 1953

nomen dubium

Taxonomic history. *Prionochelys galeotergum* Zangerl, 1953 (new species); *Prionochelys nauta* = ?*Prionochelys matuina* = *Prionochelys galeotergum* Hirayama 1997 (junior synonym); *Prionochelys galeotergum* this study (nomen dubium).

Type material. FMNH PR125 (holotype); portion of the carapace (Zangerl 1953, fig. 122).

Type locality. Gove County, Kansas, USA; Niobrara Formation, Late Cretaceous (Zangerl 1953).

Comments. *Prionochelys galeotergum* was based on a fragmentary carapace of a young individual from the Late Cretaceous (Zangerl 1953). This material was purchased, and the specific locality is unknown, but according to Zangerl (1953) the label seems to indicate it came from Cove County [sic] which we believe is actually Gove County, Kansas. Hirayama (1997) suggested it as junior synonym of *P. nauta* without pointing out a proper justification for the synonym. *P. galeotergum* possess an anal elevation and post-nuchal fontanelles, and both could be an age-dependent feature. The remaining morphological features are also found in other *Prionochelys* species, and therefore are not enough to diagnose a different species. Because the synonymization was not properly justified, the holotype belongs to a juvenile individual, and a keeled carapace formed only by the epithecal ossicles is also seen in *Ctenochelys* spp., we propose to consider it a nomen dubium.

Tomochelone lonzeensis Dollo, 1909

nomen nudum

Taxonomic history. *Tomochelone lonzeensis* Dollo, 1909 (new species); *Tomochelone lonzeensis* Zangerl 1971 (nomen nudum).

Type material. IRSNB Vert-00-493 (holotype); mandible (Dollo 1909, no figures).

Type locality. Lonzée village, province of Namur, near Gembloux, Belgium; Dark green glauconitic clayey sand, Turonian – Maastrichtian, Late Cretaceous (Dollo 1909).

Comments. *Tomochelone lonzeensis* was based on a single mandible from the Late Cretaceous of Lonzée (Dollo 1909). Despite the mandible resembles those of stem-Chelonioidea, it could not be truly recognized as such, and, in fact, according to Zangerl (1971) there are some features that are not found in stem-Chelonioidea. Because of the short and vague description and the lack of figures, *T. lonzeensis* was treated as nomen nudum in Zangerl (1971) and it is followed herein.

Toxochelys bauri Wieland, 1905

nomen invalidum

(junior synonym of *Ctenochelys stenoporus* [Hay, 1905])

Taxonomic history. *Toxochelys bauri* Wieland, 1905 (new species); *Ctenochelys stenoporus* = *Toxochelys stenoporus* = *Toxochelys bauri* = *Toxochelys procax* = *Toxochelys elkader* Zangerl 1953 (junior synonym).

Type material. YPM 2823 (holotype); complete carapace and plastron (Wieland 1905, fig. 1–4, 6–7 and pl. 10).

Type locality. Three miles north of Monument Rocks, Gove County, Kansas, USA (Wieland 1905; Karl and Nyhuis 2012); Smoky Hill Chalk Member, Niobrara Formation, Early Campanian, Late Cretaceous (Hay 1902; Wieland 1905; Nicholls and Russell 1990).

Comments. *Toxochelys bauri* was based on a complete plastron and a keeled carapace from the Early Campanian of Kansas (Wieland 1905). Zangerl (1953) recognized that it is possible they actually belong to *Ctenochelys procax*, but since *C. procax* has no associated shell, the synonymization could not be made. Zangerl (1953) argues that it is unlikely that three different species (*Toxochelys latiremis, Ctenochelys stenoporus* and *Toxochelys bauri*) coexisted in the Niobrara area, given the wide distribution of the marine turtles in general. Because *Ctenochelys* are the only known genus with a keeled shell, Zangerl (1953) synonymized *T. bauri* with *C. stenoporus* and we agree with this decision.

Toxochelys barberi (Schmidt, 1944)

nomen invalidum

(junior synonym of *Toxochelys latiremis* Cope, 1873)

Taxonomic history. *Phyllemys barberi* Schmidt, 1944 (new species); *Toxochelys barberi* Zangerl 1953 (new combination); *Toxochelys latiremis* = *Toxochelys barberi* Nicholls 1988 (junior synonym).

Type material. FMNH P27047 (holotype); a portion of the carapace and a nearly complete plastron (Schmidt 1944, fig. 20–22).

Type locality. Marlbrook Marl, Gulf Series, Cox Farm, one-mile northeast of the junction of the Hollywood-Okolona road to Arkadelphia, Clark County, Arkansas, USA; Campanian, Late Cretaceous (Schmidt 1944; Benson and Tatro 1964).

Comments. *Toxochelys barberi* was based on a carapace and plastron from the Campanian of Arkansas (Schmidt 1944). *T. barberi* could be differentiated from *T. latiremis* by the size of the vertebral scutes, which according to Nicholls (1988), are poorly preserved in the holotype of *T. barberi*. They could also be differentiated by the size of carapacial fontanelles, but Zangerl (1953) had already pointed that this feature is probably age-dependent. Therefore, due to the lack of differential diagnoses, Nicholls (1988) considered *T. barberi* as junior synonym of *T. latiremis*.

Toxochelys brachyrhinus Case, 1898

nomen invalidum

(junior synonym of *Toxochelys latiremis* Cope, 1873)

Taxonomic history. *Toxochelys brachyrhinus* Case, 1898 (new species); *Toxochelys latiremis* = *Toxochelys brachyrhina* Hay 1953 (junior synonym and misspelled species epithet).

Type material. KU 1212 (holotype); skull and mandible (Case 1898, fig. 1–2).

Type locality. Kansas, USA; Late Cretaceous (Hay 1902).

Comments. *Toxochelys brachyrhinus* was based on a skull from the Cretaceous of Kansas (Hay 1902). Hay (1905) listed the blunter snout, more parallel lateral outlines of the skull and size differences of *Toxochelys brachyrhinus* as differential features from *Toxochelys latiremis*. Later, those differences were considered a flattening effect due to the poor preservation of the material and Zangerl (1953) assigned *T. brachyrhinus* as junior synonym of *T. latiremis*.

Toxochelys browni (Hay, 1905)

nomen invalidum

(junior synonym of *Toxochelys latiremis* Cope, 1873)

Taxonomic history. *Porthochelys browni* Hay, 1905 (new species); *Toxochelys browni* Zangerl 1953 (new combination); *Toxochelys latiremis* = *Toxochelys browni* Schultze et al. 1985 (junior synonym).

Type material. AMNH 6080 (holotype); nearly complete skull, lower jaw, shoulder girdle, humerus, ulna, radius, pelvis, femur, tibia (Hay 1905, fig. 15–16).

Type locality. Twenty miles south of Edgemont, South Dakota, USA; Pierre Shale Formation, Campanian, Late Cretaceous (Hay 1905).

Comments. *Porthochelys browni* was based of several fragments and one almost complete skull from the Campanian of South Dakota (Hay 1905). The skull is large and broad in the line of the orbits and it becomes narrower around the snout, similar to the skull of *Porthochelys laticeps*. However, the skull of *P. laticeps* is broader than longer, and in *P. browni* it is longer than broader. Zangerl (1953) transferred *P. browni* to *Toxochelys* because the slender snout might be because of the bad preservation of the specimens and its skull is similar to *T. latiremis*. Zangerl (1953) also noticed that the large size of *T. browni* exceeds the size range of all *T. latiremis* from the Niobrara Formation, which led him to retain both as separated species. However, Schultze et al. (1985) proposed their synonymization because they probably belong to the same Formation (see *T. latiremis*'s section) and Nicholls (1988) suggested that the differences of sizes can be a plastic variation in the individuals, rather than a differential feature.

Toxochelys elkader Hay, 1908

nomen invalidum

(junior synonym of *Ctenochelys stenoporus* [Hay, 1905])

Taxonomic history. *Toxochelys elkader* Hay, 1908 (new species); *Ctenochelys stenoporus* = *Toxochelys elkader* = *Toxochelys bauri* = *Toxochelys procax* (in part) Zangerl 1953 (junior synonym).

Type material. AMNH 6137 (holotype); a nearly complete skull and plastron, shoulder girdles, fragments of the pelvis, a few peripherals (Hay 1908, fig. 221–222).

Type locality. Near Elkader, Logan County, Kansas, USA; Niobrara Formation, Late Cretaceous (Hay 1908).

Comments. *Toxochelys elkader* was based on an adult individual with shell and post-cranial elements associated, from the Late Cretaceous of Kansas (Hay 1908). The skull and post-cranial elements of a juvenile specimen from the referred material of *C. stenoporus* do not differ to those of *T. elkader*, which led Zangerl (1953) to consider *T. elkader* a junior synonym of *C. stenoporus*. The shell from the holotype specimen of *C. stenoporus* is, in fact, similar to those of *T. elkader*, but the skull differs (Zangerl 1953). Since the skull and shell from the holotype of *C. stenoporus* were not found associated, there are doubts if the skull really belongs to the same individual or even species (Zangerl 1953). Given the similarity of the post-cranial elements, we agree to consider *T. elkader* a junior synonym of *C. stenoporus*.

Toxochelys serrifer Cope, 1875

nomen invalidum

(junior synonym of *Toxochelys latiremis* Cope, 1873)

Taxonomic history. *Toxochelys serrifer* Cope, 1875 (new species); *Toxochelys stenoporus* = *Toxochelys serrifer* (in part) Hay 1905 (junior synonym); *Toxochelys latiremis* = *Toxochelys serrifer* Zangerl 1953 (junior synonym); *Toxochelys latiremis* = *Toxochelys browni* = *Toxochelys serrifer* = *Toxochelys brachyrhinus* = *Porthochelys browni* = *Phylemys barberi* = *Toxochelys weeksi* = *Toxochelys barberi* Nicholls 1988 (junior synonym).

Type material. AMNH 1835 (holotype); skull and mandible (two individuals) (Cope 1875; Hay 1908, fig. 207–213; Zangerl 1953).

Type locality. Niobrara beds, Kansas, USA; Late Cretaceous (Cope 1875).

Comments. *Toxochelys serrifer* was based on a skull, lower jaw and two peripheral plates from the Late Cretaceous of Kansas (Cope 1875). Case (1898) had also assigned the specimen YPM 1786 to *Toxochelys serrifer* Cope, 1875, but Hay (1905) recognized they do not belong to the same species and made it the type of a new species, *Toxochelys stenoporus* (now *Ctenochelys stenoporus*). Zangerl (1953) and Nicholls (1988) considered *T. serrifer* a junior synonym of *T. latiremis* because their cranial features are identical. However, since the mandible is much smaller than the skull, Zangerl (1953) concluded they do not belong to the same individual. Zangerl (1953) also pointed out that the peripherals were not under the AMNH 1835 identification by the time he examined the specimen, but he did not detail where it could be. However, since serrated peripherals do not correspond with those of neither *Toxochelys* nor *Ctenochelys*, Zangerl (1953) suggested that it belonged to another species and it was mixed with the bones of *T. serrifer* before handed to Professor Cope. Based on the similarity of the skull, we agree with Zangerl (1953) that *T. serrifer* is a junior synonym of *T. latiremis*.

Toxochelys weeksi Collins, 1951

nomen invalidum

(junior synonym of *Toxochelys latiremis* Cope, 1873)

Taxonomic history. *Toxochelys weeksi* Collins, 1951 (new species); *Toxochelys latiremis* = *Toxochelys weeksi* Nicholls 1988 (junior synonym).

Type material. UT K20 (holotype); a partial plastron and three peripherals (Collins 1951, pls. 1–2).

Type locality. Dave Weeks place, Coon Creek, McNairy County, Tennessee, USA; Coon Creek Tongue of Ripley Formation, Late Campanian, Late Cretaceous (Zangerl 1953; Cobban and Kennedy 1994).

Comments. *Toxochelys weeksi* was based on a fragmentary plastron and a few peripherals from the Late Campanian of Tennessee (Zangerl 1953). The diagnostic features that *distinguish T.* weeksi from *T. latiremis* are based on measurements that, according to Nicholls (1988), could have been taken erroneously. Moreover, those variations seem to represent intra-specific variation, and therefore does not characterize a diagnostic feature to support a different species, leading Nicholls (1988) to suggest *T. weeksi* as junior synonym of *T. latiremis*.

Appendix 1

Institutional Abbreviation

AMNH	American Museum of Natural History, New York, New York, USA
ANSP	Academy of Natural Sciences of Philadelphia, USA
CPC	Coleccion Paleontologica de Cohuila, Museo del Desierto, Saltillo, Coahuila, Mexico
ERMNH	Eternal River Museum of Natural History, Jordan, privately owned by Hani F. Kaddumi
FMNH	Field Museum of Natural History, Chicago, USA
GZG	Geoscience Centre of Göttingen, Germany
HMG	Hobetsu Museum at Hobetsu-cho, Hokkaido, JaPan
IGPS	Institut für Geologie und Paläontologie der Universität Salzburg
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Belgium
KU	Property of Kansas University, Kansas, USA
MCST	Museo Civico di Storia Naturale di Trieste, Italy
MIWG	Museum of Isle of Wight Geology, Sandown, Isle of Wight, England
MPEF	Museo Paleontológico Egidio Feruglio de Trelew, Argentina
MSNM	Museo Civico di Storia Naturale di Milano, Italy

OCP	Office Chérifiendes Phosphates, Service Géologique, Khouribga, Morocco
RUGM	Rutgers University Geology Museum, New Jersey, USA
SEPCP	Secretaria de Educacion y Cultura, Coleccion Paleontologica (formerly Secretaria de Educacion Publica de Coahuila), Mexico
TMP	Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada
UT	University of Tennessee
YPM	Yale Peabody Museum, USA

Appendix 2

Named non-Protostegidae Sea Turtles from Cretaceous Genera

Allopleuron Baur, 1888
(type species: *Allopleuron hofmanni* (Gray, 1831))
Catapleura Cope, 1870
(type species: *Catapleura repanda* (Cope, 1868))
Corsochelys Zangerl, 1960
(type species: *Corsochelys haliniches* Zangerl, 1960)
Ctenochelys Zangerl, 1953
(type species: *Ctenochelys stenoporus* (Hay, 1905))
Gigantatypus Kaddumi, 2006
(type species: *Gigantatypus salahi* Kaddumi, 2006)
Glyptochelone Dollo, 1909

(type species: *Glyptochelone suyckerbuyki* (Ubagh, 1879))
Kimurachelys Brinkman et al., 2015
(type species: *Kimurachelys slobodae* Brinkman et al., 2015)
Mesodermochelys Hirayama and Chitoku, 1996
(type species: *Mesodermochelys undulatus* Hirayama and Chitoku, 1996)
Mexichelys Parham and Pyenson, 2010
(type species: *Mexichelys coahuilaensis* (Brinkman et al., 2009))
Nichollsemys Brinkman et al., 2006
(type species: *Nichollsemys baieri* Brinkman et al., 2006)
Oertelia Karl et al., 2012
(type species: *Oertelia gigantea* (Oertel, 1914))
Porthochelys Williston, 1901
(type species: *Porthochelys laticeps* Williston, 1901)
Prionochelys Zangerl, 1953
(type species: *Prionochelys nauta* Zangerl, 1953)
Sontiochelys Stache, 1858
(type species: *Sontiochelys cretacea* Stache, 1905)
Thalassemys Rütimeyer, 1873
Thalassemys hugii Rütimeyer, 1873
Thinochelys Zangerl, 1953
(type species: *Thinochelys lapisossea* Zangerl, 1953)
Toxochelys Cope, 1873
(type species: *Toxochelys latiremis* Cope, 1873)
Turgaiscapha Averianov, 2002

(type species: *Turgaiscapha kushmurunica* Averianov, 2002)

Zangerlchelys Hirayama, 2006

(type species: *Zangerlchelys arkansaw* (Schmidt, 1944))

Appendix 3

Biogeographical Summary of non-Protostegidae Sea Turtles from Cretaceous

Numbers in brackets reference Figures 5–7. TL, type locality.

Belgium

[1] Late Cretaceous, Maastrichtian; Belgium, Limburg; *Glyptochelone suyckerbuykii* (TL) (Dollo 1903; 1909)

Canada

[2] Late Cretaceous, Late Campanian; Alberta, Taber; *Nichollsemys baieri* (TL) (Brinkman et al. 2006)

[3] Late Cretaceous, Late Campanian; Alberta, Lethbridge; *Nichollsemys baieri* (Brinkman et al. 2006)

[4] Late Cretaceous, Late Campanian; Alberta, Manyberries; *Nichollsemys baieri* (Brinkman et al. 2006)

[5] Late Cretaceous, Campanian; Alberta, Manyberries; *Kimurachelys slobodae* (TL) (Brinkman et al. 2015)

[6] Late Cretaceous, Campanian; Alberta, Lethbridge; *Kimurachelys slobodae* (Brinkman et al. 2006)

[7] Late Cretaceous, Late Campanian; Alberta, Cardston County; *Toxochelys latiremis* (Nicholls et al. 1990; Brinkman et al. 2015)

[8] Late Cretaceous, Campanian; Alberta, Lethbridge; stem-Chelonioidea indet. (Brinkman et al. 2015)

[9] Late Cretaceous, Campanian; Alberta, Manyberries; Chelonioidea indet. (Brinkman et al. 2015)

[10] Late Cretaceous, Early Campanian; Manitoba; Chelonioidea indet. (Nicholls et al. 1990)

France

[11] Late Cretaceous, Coniacian; Hellèmes; Cheloniidae indet. (De Lapparent De Broin 2001)

Germany

[12] Late Cretaceous, Early Aptian; near to Hannover; *Oertelia gigantea* (TL) (Zangerl 1953; Karl et al. 2012)

[13] Late Cretaceous, Turonian; Raunschweig-Broitzem; *Allopleuron* cf. *hofmanni* (Karl et al. 2012)

[14] Late Cretaceous, Late Santonian–Early Campanian; Schleswig-Holstein; *Ctenochelys stenoporus* (Karl and Nyhuis 2012)

[15] Late Cretaceous, Late Campanian; Hannover-Misburg; *Allopleuron* cf. *hofmanni* (Karl et al. 2012)

[16] Late Cretaceous, Early Campanian; SE Hanover; *Allopleuron* cf. *hofmanni* (Karl et al. 2012)

Japan

[17] Late Cretaceous, Campanian–Maastrichtian; Hobetsu, Mobetsu, Hobetsu River; *Mesodermochelys undulatus* (Hirayama and Chitoku 1996)

[18] Late Cretaceous, Late Maastrichtian; Hokkaido; *Mesodermochelys undulatus* (TL) (Hirayama and Chitoku 1996)

[19] Late Cretaceous, Early Maastrichtian; Hobetsu, Ohmagarinosawa River; *Mesodermochelys undulatus* (Hirayama and Chitoku 1996)

[20] Late Cretaceous, Early Maastrichtian; Hobetsu, Hiraoka, Pankerusanosawa River; *Mesodermochelys undulatus* (Hirayama and Chitoku 1996)

[21] Late Cretaceous, Early Maastrichtian; Hobetsu, Tomiuchi, Pankerusanosawa River; *Mesodermochelys undulatus* (Hirayama and Chitoku 1996)

[22] Late Cretaceous, Early Maastrichtian; Hobetsu, Inasato; *Mesodermochelys undulatus* (Hirayama and Chitoku 1996)

[23] Late Cretaceous, Early Maastrichtian; Hobetsu, Kiusu, Hobetsu River; *Mesodermochelys undulatus* (Hirayama and Chitoku 1996)

[24] Late Cretaceous, Early Campanian; Nakagawa-cho, Hokkaido, Japan; *Mesodermochelys undulatus* (Hirayama and Hikida 1998)

Jordan

[25] Late Cretaceous, Maastrichtian; Muwaqqar town; *Gigantatypus salahi* (TL) (Kaddumi 2006)

Kazakhstan

[26] Late Cretaceous, Late Campanian-early Maastrichtian?; Kushmurun; *Turgaiscapha kushmurunica* (TL) (Averianov 2002)

Mexico

[27] Late Cretaceous, Late Campanian; Coahuila State; *Mexichelys coahuilaensis* (TL) (Brinkman et al. 2009)

[28] Late Cretaceous; General Cepada area, Mexico; *Mexichelys coahuilaensis* (Brinkman et al. 2009)

[29] Late Cretaceous, Late Campanian; Turtle Paradise, Mexico; *Mexichelys coahuilaensis* (Brinkman et al. 2009)

Netherlands

[30] Late Cretaceous, Maastrichtian; Limburg; *Allopleuron hofmanni* (TL) (Janssen et al. 2011)

[31] Late Cretaceous, Maastrichtian; Limburg, Maastricht; *Allopleuron hofmanni* (Mulder 2003)

[32] Late Cretaceous, Maastrichtian; Limburg, Kanne; *Allopleuron hofmanni* (Mulder 2003)

[33] Late Cretaceous, Maastrichtian; Limburg, Neerkanne; *Allopleuron hofmanni* (Mulder 2003)

[34] Late Cretaceous, Maastrichtian; Limburg, Nederkanne; *Allopleuron hofmanni* (Mulder 2003)

[35] Late Cretaceous, Maastrichtian; Limburg, Voerendaal; *Allopleuron hofmanni* (Mulder 2003)

[36] Late Cretaceous, Maastrichtian; Limburg, Benzenrade; *Allopleuron hofmanni* (Mulder 2003)

[37] Late Cretaceous, Maastrichtian; Liège; *Allopleuron hofmanni* (Mulder 2003)

[38] Late Cretaceous, Maastrichtian; Eben Emael; *Allopleuron hofmanni* (Mulder 2003)

Slovenia

[39] Early Cretaceous, Hauterivian–Barremian; Nova Gorizia; *Sontiochelys cretacea* (TL) (Stache 1905; Karl et al. 2012)

United States of America

[40] Late Cretaceous, Turonian; Kansas, Gove County; *Ctenochelys stenoporus* (TL) (Hay 1902; Wieland 1905)

[41] Late Cretaceous, Coniacian; Kansas, Logan County, Butte Creek; *Ctenochelys stenoporus* (Hay 1909)

[42] Late Cretaceous, Late Santonian-Early Campanian; Kansas, Gove County; *Toxochelys latiremis* (Nicholls 1988)

[43] Late Cretaceous, Coniacian-Santonian; Kansas; *Toxochelys latiremis* (Zangerl 1953)

[44] Late Cretaceous, Early Campanian; Kansas, Logan County; *Toxochelys latiremis* (TL) (Nicholls 1988; Nicholls and Russell 1990)

[45] Late Cretaceous; Kansas; *Porthochelys laticeps* (TL) (Williston 1901; Hay 1908)

[46] Cretaceous; Kansas, Smoky Hill River; *Ctenochelys stenoporus* (Hay 1905)

[47] Cretaceous; Kansas, Logan County, Elkader; *Ctenochelys stenoporus* (Hay 1908)

[48] Cretaceous; Kansas, Logan County, Russell Springs; *Ctenochelys stenoporus* (Zangerl 1953)

[49] Late Cretaceous; Kansas, Logan County, Russel Springs; *Toxochelys latiremis* (Matzke 2008)

[50] Late Cretaceous, Santonian; Alabama, Greene County, Eutaw area; *Toxochelys moorevillensis* (Zangerl 1953)

[51] Late Cretaceous, Early Campanian; Alabama, Greene County, West Greene area; *Toxochelys moorevillensis* (Zangerl 1953)

[52] Late Cretaceous, Early Campanian; Alabama, Dallas County, Harrel Station area; *Toxochelys moorevillensis* (Zangerl 1953)

[53] Late Cretaceous, Early Campanian; Alabama, Greene County, Clinton area; *Toxochelys moorevillensis* (Zangerl 1953)

[54] Late Cretaceous, Early Campanian; Alabama, Greene County, Mt. Hebron area; *Toxochelys moorevillensis* (Zangerl 1953)

[55] Late Cretaceous, Early Campanian; Alabama, Greene County, Boligee area; *Toxochelys moorevillensis* (Zangerl 1953)

[56] Late Cretaceous, Campanian; Alabama, Hale County; *Ctenochelys stenoporus* (Gentry 2017)

[57] Late Cretaceous, Early Campanian; Alabama, Greene County; *Corsochelys haliniches* (TL) (Zangerl 1960)

[58] Late Cretaceous, Early Campanian; Alabama, Dallas County; *Thinochelys lapisossea* (TL) (Zangerl 1953)

[59] Late Cretaceous, Early Campanian; Alabama, Dallas County; *Ctenochelys acris* (TL) (Zangerl 1953)

[60] Late Cretaceous, Early Campanian; Alabama, Greene County; *Ctenochelys acris* (Gentry 2017)

[61] Late Cretaceous, Early Campanian; Alabama, Dallas County; *Toxochelys moorevillensis* (TL) (Zangerl 1953)

[62] Late Cretaceous, Early Campanian; Alabama, Dallas County; *Prionochelys nauta* (Zangerl 1953)

[63] Late Cretaceous; Alabama, Dallas County; *Ctenochelys stenoporus* (Zangerl 1953)

[64] Late Cretaceous, Early Campanian; Alabama, Lowndes County; *Toxochelys moorevillensis* (Zangerl 1953)

[65] Late Cretaceous, Campanian; Alabama, Hale County; *Toxochelys moorevillensis* (Zangerl 1953)

[66] Late Cretaceous, Early Campanian; Alabama, Sumter County; *Toxochelys latiremis* (Gentry and Ebersole 2018)

[67] Late Cretaceous, Early Campanian; South Dakota, Edgemont; *Toxochelys latiremis* (Zangerl 1953)

[68] Late Cretaceous, Late Campanian; South Dakota, Hyde County; *Nichollsemys baieri* (Brinkman et al. 2006)

[69] Late Cretaceous, Late Campanian; Arkansas, Clark County; *Zangerlchelys arkansaw* (TL) (Schmidt 1944; Hirayama 2006)

[70] Late Cretaceous, Late Campanian; Arkansas, Howard County; *Prionochelys nauta* (TL) (Zangerl 1953)

[71] Late Cretaceous, Late Campanian; Arkansas, Clark County; *Prionochelys nauta* (Zangerl 1953)

[72] Late Cretaceous, Campanian; Arkansas, Clark County; *Toxochelys latiremis* (Schmidt 1944; Benson and Tatro 1964)

[73] Late Cretaceous?, Late Maastrichtian?; New Jersey; *Catapleura repanda* (TL) (Cope 1868; Hay 1908)

[74] Late Cretaceous; Tennessee, McNairy County; *Toxochelys latiremis* (Zangerl 1953)

Uzbekistan

[75] Early–Late Cretaceous, Albian?–Cenomanian; Bukhara Viloyat; "*Thalassemys" cava* (TL) (Averianov 2002)

Appendix 4

Hierarchical Taxonomy of non-Protostegidae Sea Turtles from Cretaceous

- *Pan-Chelonioidea* Joyce et al. 2004
  - *Catapleura* Cope, 1870
    - *Catapleura repanda* (Cope, 1868)
  - *Ctenochelys* Zangerl, 1953
    - *Ctenochelys acris* Zangerl, 1953
    - *Ctenochelys stenoporus* (Hay, 1905)
  - *Mexichelys* Parham and Pyenson, 2010
    - *Mexichelys coahuilaensis* (Brinkman et al., 2009)
  - *Nichollsemys* Brinkman et al., 2006
    - *Nichollsemys baieri* Brinkman et al., 2006

Toxochelys Cope, 1873

Toxochelys latiremis Cope, 1873

Toxochelys moorevillensis Zangerl, 1953

Chelonioidea Baur, 1893

Pan-Cheloniidae Joyce et al., 2004

Allopleuron Baur, 1888

Allopleuron hofmanni (Gray, 1831)

Gigantatypus Kaddumi, 2006

Gigantatypus salahi Kaddumi, 2006

Glyptochelone Dollo, 1909

Glyptochelone suyckerbuykii (Ubagh, 1879)

Oertelia Karl et al., 2012

Oertelia gigantea (Oertel, 1914)

Pan-Dermochelyidae et al., 2004

Corsochelys Zangerl, 1960

Corsochelys haliniches Zangerl, 1960

Mesodermochelys Hirayama and Chitoku, 1996

Mesodermochelys undulatus Hirayama and Chitoku, 1996

Pan-Chelonioidea Indet.

Kimurachelys Brinkman et al., 2015

Kimurachelys slobodae Brinkman et al., 2015

Zangerlchelys Hirayama, 2006

Zangerlchelys arkansaw (Schmidt, 1944)

Eucryptodira Indet.

- *Prionochelys* Zangerl, 1953
  - *Prionochelys nauta* Zangerl, 1953
- *Porthochelys* Williston, 1901
  - *Porthochelys laticeps* Williston, 1901
- *“Thalassemys”* Rütimeyer, 1873
  - *“Thalassemys” cava* (Nessov, 1984)
- *Thinochelys* Zangerl, 1953
  - *Thinochelys lapisossea* Zangerl, 1953
- *Sontiochelys* Stache, 1905
  - *Sontiochelys cretacea* Stache, 1905
- *Turgaiscapha* Averianov, 2002
  - *Turgaiscapha kushmurunica* Averianov, 2002

Literature Cited

Anquetin, J. 2012. Reassessment of the phylogenetic interrelationships of basal turtles (Testudinata). Journal of Systematic Palaeontology 10(1):3-45.

Averianov, A.O. 2002. Review of Mesozoic and Cenozoic sea turtles from the former USSR. Russian Journal of Herpetology 9(2):137-154.

Baird, D. 1967. Age of fossil birds from the greensands of New Jersey. The Auk 84(2):260-262.

Barley, A.J.; Spinks, P.Q.; Thomson, R.C.; Shaffer, H.B. 2010. Fourteen nuclear genes provide phylogenetic resolution for difficult nodes in the turtle tree of life. Molecular phylogenetics and evolution 55(3):1189-1194.

Baur, G. 1888. Unusual dermal ossifications. Science 11(268):144-144.

Benson, R.H.; Tatro, J.O. 1964. Faunal description of Ostracoda of the Marlbrook Marl (Campanian), Arkansas. Paleontological Contributions 7:1-32.

Bjorndal, K.A.; Lutz, P.; Musick, J. 1997. Foraging ecology and nutrition of sea turtles. In: Lutz, P. L. e Musick, J.,eds. The biology of sea turtles. I. Boca Raton, Florida: CRC Press pp.199-231.

Brinkman, D. A primitive cheloniid from the Campanian (Late Cretaceous) of Alberta, Canada. Sixtieth Annual Meeting, Society of Vertebrate Paleontology. Mexico: Journal of Vertebrate Paleontology. 20**:** 31A p. 2000.

Brinkman, D.; Aquillon-Martinez, M.; De Leon Dávila, C.; Jamniczky, H.; Eberth, D.; Colbert, M. 2009. *Euclastes coahuilaensis* sp. nov., a basal cheloniid turtle from the late Campanian Cerro del Pueblo Formation of Coahuila State, Mexico. PaleoBios 28(3):76-88.

Brinkman, D.; Hart, M.; Jamniczky, H.; Colbert, M. 2006. *Nichollsemys baieri* gen. et sp. nov, a primitive chelonioid turtle from the late Campanian of North America. Paludicola 5(4):111-124.

Brinkman, D.B.; Densmore, M.; Rabi, M.; Ryan, M.J.; Evans, D.C. 2015. Marine turtles from the Late Cretaceous of Alberta, Canada. Canadian Journal of Earth Sciences 52(8):581-589.

Cadena, E.A.; Parham, J.F. 2015. Oldest known marine turtle? A new protostegid from the Lower Cretaceous of Colombia. PaleoBios 32(1):1-42.

Case, E.C. 1898. *Toxochelys*. The University Geological Survey of Kansas IV(6):370-385.

Cobban, W.; Kennedy, W. 1994. Upper Cretaceous ammonites from the Coon Creek Tongue of the Ripley Formation at its type locality in McNairy County, Tennessee. US Geological Survey Bulletin 2073(B):

Collins, R. 1951. A new turtle, *Toxochelys weeksi*, from the Upper Cretaceous of west Tennessee. Journal of the Tennessee Academy of Science 26:262-269.

Cope, E. 1868. On some Cretaceous reptilia. Proceedings of the Academy of Natural Sciences of Philadelphia. 147 pp.

______. 1868. Synopsis of the extinct Reptilia found in the Mesozoic and Tertiary strata of New Jersey. Appendix B of Geology of New Jersey, George H. Cook, State geologist, Newark 1868:733-742.

______. 1870. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. Transactions of the American Philosophical Society 14:1-252.

______. 1873. [Remarks on additional specimens of *Toxochelys latiremis*.]. Philadelphia:Proceedings of the Academy of Natural Sciences of Philadelphia. 10 pp.

______. 1875. The Vertebrata of the Cretaceous formations of the West. Washington:Report of the United States Geological Survey of the Territories. 303 pp.

Cope, E.D. 1871. On a New Testudinate from the Chalk of Kansas. Proceedings of the American Philosophical Society 12(86):308-310.

Crawford, N.G.; Parham, J.F.; Sellas, A.B.; Faircloth, B.C.; Glenn, T.C.; Papenfuss, T.J.; Henderson, J.B.; Hansen, M.H.; Simison, W.B. 2014. A phylogenomic analysis of turtles. Molecular phylogenetics and evolution 83:250-257.

Danise, S.; Higgs, N.D. 2015. Bone-eating *Osedax* worms lived on Mesozoic marine reptile deadfalls. Biology Letters 11(4):20150072.

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

Dollo, L. 1903. Sur l’évolution des chéloniens marins (considérations bionomiques et phylogéniques). Bull. Cl. Sci., Acad. Roy. Belg.,(1903):801-850.

Dollo, L. 1903. *Eochelone brabantica*, tortue marine nouvelle du Bruxellien (Eocène Moyen) de la Belgique et l'évolution des chéloniens marins. Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique:792-850.

______. 1909. The fossil vertebrates of Belgium. Annals of the New York Academy of Sciences 19(1):99-119.

Fastovsky, D.E. 1985. A skull of the Cretaceous chelonioid turtle *Osteopygis* and the classification of the Osteopyginae. New Jersey State Museum. pp.

Faujas De Saint-Fond, B. 1798. Histoire naturelle de la Montagne de Saint-Pierre de Maestricht. Paris:Chez HJ Jansen. 263 pp.

Fujita, M.K.; Engstrom, T.N.; Starkey, D.E.; Shaffer, H.B. 2004. Turtle phylogeny: insights from a novel nuclear intron. Molecular phylogenetics and evolution 31(3):1031-1040.

Gaffney, E.S. 1975. A phylogeny and classification of the higher categories of turtles. Bulletin of the American History Museum 155(5):387-436.

______. 1976. Cranial morphology of the European Jurassic turtles *Portlandemys* and *Plesiochelys*. Bulletin of the American Museum Natural History 157(6):

Gaffney, E.S.; Meylan, P.A. 1988. A phylogeny of turtles. In: Benton, M. J.,eds. The phylogeny and classification of the tetrapods. 1. Oxford: Clarendon Press pp.157-219.

Gaffney, E.S.; Tong, H.; Meylan, P.A. 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. Bulletin of the American Museum of Natural History 300:1-698.

Gentry, A.D. 2017. New material of the Late Cretaceous marine turtle *Ctenochelys acris* Zangerl, 1953 and a phylogenetic reassessment of the ‘toxochelyid’-grade taxa. Journal of Systematic Palaeontology 15(8):1-22.

Gentry, A.D.; Ebersole, J.A. 2018. The first report of Toxochelys latiremis Cope 1873 (Testudines: Panchelonioidea) from the early Campanian of Alabama, USA. PaleoBios 35:

Gill, J.R.; Cobban, W.A. 1973. Stratigraphy and geologic history of the Montana Group and equivalent rocks, Montana, Wyoming, and North and South Dakota.

Hay, O.P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. Buletin of the United States Geological Survey 179:1-868.

______. 1905. A Revision of the Species of the Family of Fossil Turtles Called Toxochelyidae: With Descriptions of Two New Species of *Toxochelys* and a New Species of *Porthochelys*. Bulletin of the American Museum of Natural History. pp.177-185.

______. 1908. The fossil turtles of North America. Carnegie Institution of Washington 75:1-568.

______. 1909. Description of two species of fossil turtles, *Toxochelys stenopora* and *Christernon*? *interpositum*, the latter hitherto unknown. Proceedings of The United States National Museum 36:

Hirayama, R. 1994. Phylogenetic systematics of chelonioid sea turtles. Island Arc 3(4):270-284.

Hirayama, R. 1997. Distribution and diversity of Cretaceous chelonioids. In: Callaway, J. M. e Nicholls, E. L.,eds. Ancient marine reptiles. Academic Press pp.225-241.

Hirayama, R. 1998. Oldest known sea turtle. Nature 392(6677):705-708.

Hirayama, R. 2006. Revision of the Cretaceous and Paleogene sea turtles *Catapleura* and *Dollochelys* (Testudines: Cheloniidae). PaleoBios 26(2):1-6.

Hirayama, R.; Chitoku, T. 1996. Family Dermochelyidae (Superfamily Chelonioidea) from the Upper Cretaceous of North Japan. 日本古生物学會報告・紀事 新編 (184):597-622.

Hirayama, R.; Hikida, Y. 1998. *Mesodermochelys* (Testudines, Chelonioidea, Dermochelyidae) from the Late Cretaceous of Nakagawa-cho, Hokkaido, North Japan. Bulletin of the Nakagawa Museum of Natural History 1:69-76.

Hooks, G. 1998. Systematic revision of the Protostegidae, with a redescription of *Calcarichelys gemma* Zangerl, 1953. Journal of Vertebrate Paleontology 18(1):85-98.

Janssen, R.; Van Baal, R.; Schulp, A. 2011. On the taphonomy of the late Maastrichtian (Late Cretaceous) marine turtle *Allopleuron hofmanni*. Netherlands Journal of Geosciences 90(2-3):187-196.

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

Joyce, W.G.; Parham, J.F.; Gauthier, J.A. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. Journal of Paleontology 78(5):989-1013.

Joyce, W.G.; Parham, J.F.; Lyson, T.R.; Warnock, R.C.; Donoghue, P.C. 2013. A divergence dating analysis of turtles using fossil calibrations: an example of best practices. Journal of Paleontology 87(04):612-634.

Kaddumi, H. 2006. A new genus and species of gigantic marine turtles (Chelonioidea: Cheloniidae) from the Maastrichtian of the Harrana Fauna-Jordan. PalArch 3:1-13.

Karl, H.-V.; Gröning, E.; Brauckmann, C. 2012. New materials of the giant sea turtle *Allopleuron* (Testudines, Chelonioidea) from the marine Late Cretaceous of Central Europe and the Paleogene of Kazakhstan. Studia Geologica Salmanticensia 9:153.

Karl, H.-V.; Nyhuis, C.J. 2012. *Ctenochelys stenoporus* (Hay, 1905) (Testudines: Toxochelyidae) and *Clidastes* sp. (Squamata: Mosasauridae) from the Upper Cretaceous of NW-Germany. Studia Geologica Salmanticensia 9:129.

Karl, H.; Biermann, S.; Tichy, G. 2012. The oldest true sea turtle of the world, *Oertelia gigantea* (Oertel, 1914) n. gen. from the Aptian of Kastendamm near Hanover, Germany Studia Geologica Salmanticensia 9:107.

Karl, H.; Tichy, G.; Valdiserri, D. 2012. *Sontiochelys cretacea* Stache, 1905 y redescripción de las familias Eurysternidae Dollo, 1886 y Thalassemydidae Rütimeyer, 1873 (Testudines: Cryptodira). Studia Geologica Salmanticensia (48):45-76.

Kear, B.P.; Lee, M.S.Y. 2006. A primitive protostegid from Australia and early sea turtle evolution. Biology Letters 2(1):116-119.

Keferstein, C. 1834. Die Naturgeschichte des Erdkörpers in ihren ersten Grundzügen. Zweiter Theil. Die Geologie und Paläontologie. Leipzig: pp.869.

Krenz, J.G.; Naylor, G.J.; Shaffer, H.B.; Janzen, F.J. 2005. Molecular phylogenetics and evolution of turtles. Molecular phylogenetics and evolution 37(1):178-191.

Kuhn, O. 1964. Testudines. In,eds. Fossilium Catalogus. 107. Netherland: Ysel Press, Deventer.

Leidy, J.M.D. 1865. Cretaceous Reptiles of the United States. Smithsonian Contributions to knowledge 192:135.

Lydekker, R. 1889. Part III – Containing the order Chelonia. In,eds. Catalogue of the fossil Reptilia and Amphibia in the British Museum. pp.1-239.

Lynch, S.C.; Parham, J.F. 2003. The first report of hard-shelled sea turtles (Cheloniidae sensu lato) from the Miocene of California, including a new species (*Euclastes hutchisoni*) with unusually plesiomorphic characters. PaleoBios 23(3):21-35.

Matzke, A.T. 2007. An almost complete juvenile specimen of the cheloniid turtle *Ctenochelys stenoporus* (Hay, 1905) from the upper Cretaceous Niobrara Formation of Kansas, USA. Palaeontology 50(3):669-691.

______. 2008. A juvenile *Toxochelys latiremis* (Testudines, Cheloniidae) from the Upper Cretaceous Niobrara Formation of Kansas, USA. Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 249(3):371-380.

Matzke, A.T. 2009. Osteology of the skull of *Toxochelys* (Testudines, Chelonioidea). Palaeontographica Abteilung a-Palaozoologie-Stratigraphie 288(4-6):93-150.

Miller Jr, H.W. 1955. A check-list of the Cretaceous and Tertiary vertebrates of New Jersey. Journal of Paleontology:903-914.

______. 1956. Correlation of Paleocene and Eocene formations and Cretaceous-Paleocene boundary in New Jersey. AAPG Bulletin 40(4):722-736.

Moody, R.T.J. 1974. The taxonomy and morphology of *Puppigerus camperi* (Gray), an Eocene sea-turtle from northern Europe. Bulletin of the British Museum (Natural History), Geology 25:153-186.

Mulder, E. 2003. Comparative osteology, palaeoecology and systematics of the Late Cretaceous turtle *Allopleuron hofmanni* (Gray 1831) from the Maastrichtian type area. Publicaties van het Natuurhistorisch Genootschap in Limburg Reeks XLIV (afl. 1):23-92.

Mulder, E.; Jagt, J.; Kuypers, M.; Peeters, H.; Rompen, P. 1998. Stratigraphic distribution of Late Cretaceous marine and terrestrial reptiles from the Maastrichtian type area. Oryctos 1:55-64.

Nessov, L.; Krassovskaya, T. 1984. Changes in the composition of turtles assemblages of Late Cretaceous of Middle Asia. Vestnik Leningradskogo Gosudarstvennogo Universiteta 3:15-25.

Nicholls, E.L. 1988. New material of *Toxochelys latiremis* Cope, and a revision of the genus *Toxochelys* (Testudines, Chelonioidea). Journal of Vertebrate Paleontology 8(2):181-187.

Nicholls, E.L.; Russell, A.P. 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 79(1-2):149-169.

Nicholls, E.L.; Tokaryk, T.T.; Hills, L.V. 1990. Cretaceous marine turtles from the Western Interior Seaway of Canada. Canadian Journal of Earth Sciences 27(10):1288-1298.

Oertel, W. 1914. *Toxochelys gigantea* nov. sp.; eine neue Schildkröte aus dem Aptien von Hannover. Jahresber. Niedersachs. geol. Ver. 7:91-106.

Owen, R. 1851. Monograph on the fossil Reptilia of the Cretaceous Formations—Part I. Monographs of the Palaeontographical Society 1:80-104.

Parham, J.; Fastovsky, D. 1997. The phylogeny of cheloniid sea turtles revisited. Chelonian Conservation and Biology 2:548-554.

Parham, J.F.; Feldman, C.R.; Boore, J.L. 2006. The complete mitochondrial genome of the enigmatic bigheaded turtle (Platysternon): description of unusual genomic features and the reconciliation of phylogenetic hypotheses based on mitochondrial and nuclear DNA. BMC Evolutionary Biology 6(1):11.

Parham, J.F.; Hutchison, J.H. 2003. A new eucryptodiran turtle from the late cretaceous of North America (Dinosaur Provincial Park, Alberta, Canada). Journal of Vertebrate Paleontology 23(4):783-798.

Parham, J.F.; Pyenson, N.D. 2010. New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the Cretaceous. Journal of Paleontology 84(2):231-247.

Parris, D.C.; Detample, C.; Benton, R.C. 1986. Osteological notes of the fossil turtle ?*Dollochelys atlantica* (Zangerl). The Mosasaur 3:97-108.

Petersen, S.V.; Tabor, C.R.; Lohmann, K.C.; Poulsen, C.J.; Meyer, K.W.; Carpenter, S.J.; Erickson, J.M.; Matsunaga, K.K.; Smith, S.Y.; Sheldon, N.D. 2016. Temperature and salinity of the Late Cretaceous Western Interior Seaway. Geology 44(11):903-906.

Püntener, C.; Anquetin, J.; Billon-Bruyat, J.-P. 2015. *Thalassemys bruntrutana* n. sp., a new coastal marine turtle from the Late Jurassic of Porrentruy (Switzerland), and the paleobiogeography of the Thalassemydidae. PeerJ 3:e1282.

Scavezzoni, I.; Fischer, V. 2018. *Rhinochelys amaberti* (Moret 1935), a protostegid turtle from the Early Cretaceous of France. PeerJ 6:e4594.

Schmidt, K.P. 1944. Two new thalassemyd turtles from the Cretaceous of Arkansas. Field Columbian Museum, Geological series. 8:63-74.

Schultze, H.-P.; Hunt, L.; Chorn, J.; Neuner, A.M. 1985. Type and figured specimens of fossil vertebrates in the collections of the University of Kansas Museum of Natural History. Part II. Fossil amphibians and reptiles. Miscellaneous Publications of the University of Kansas - Museum of Natural History 77:66.

Shaffer, H.B.; Meylan, P.; Mcknight, M.L. 1997. Tests of turtle phylogeny: molecular, morphological, and paleontological approaches. Systematic Biology 46(2):235-268.

Spamer, E.E.; Daeschler, E.; Vostreys-Shapiro, L.G. A study of fossil vertebrate types in the academy of natural sciences of philadelphia: taxonomic, systematic, and historical perspectives. 1995, Academy of Natural Sciences.

Stache, G. 1905. *Sontiochelys*, ein neuer Typus von Lurchschildkröten (Pleurodira) aus der Fischschieferzone der ünteren Karstkreide des Monte Santo bei Görz. Verhandlungen der K. K. geologischen Reichsanstalt 13:285-292.

Sterli, J.; De La Fuente, M.S. 2011. A new turtle from the La Colonia Formation (Campanian–Maastrichtian), Patagonia, Argentina, with remarks on the evolution of the vertebral column in turtles. Palaeontology 54(1):63-78.

Sukhanov, V.B.; Benton, M.; Shishkin, M.; Unwin, D.; Kurochkin, E. 2000. Mesozoic turtles of middle and central Asia. The age of dinosaurs in Russia and Mongolia 17:309-367.

Wieland, G.R. 1902. Notes on the Cretaceous turtles *Toxochelys* and *Archelon*, with a classification of the marine Testudinata. American Journal of Science (80):95-108.

______. 1904. Structure of the Upper Cretaceous turtles of New Jersey: *Adocus*, *Osteopygis* and *Propleura*. American Journal of Science 17(98):112-132.

______. 1905. A new Niobrara *Toxochelys*. American Journal of Science (119):325-343.

Williston, S. A new turtle from the Kansas Cretaceous. Transactions of the Annual Meetings of the Kansas Academy of Science, 1901, Kansas, USA. JSTOR. p.195-199.

Winkler, T.C. 1869. Des tortues fossiles conservées dans le Musée Teyler et dans quelques autres Musées. Héritiers Loosjes. pp.

Zangerl, R. 1953. The vertebrate fauna of the Selma Formation of Alabama. The turtles of the family Toxochelyidae. Fieldiana: Geology Memoirs 3(4):57-132.

______. 1960. The vertebrate fauna of the Selma Formation of Alabama: An advanced cheloniid sea turtle. Chicago:Chicago Natural History Museum. pp.281-312.

______. 1971. Two toxochelyid sea turtles from the Landenian sands of Erquelinnes Hainaut of Belgium. Bruxelles:Institut Royal des Sciences Naturelles de Belgique. 1-32 pp.

______. 1980. Patterns of phylogenetic differentiation in the toxochelyid and cheloniid sea turtles. American Zoologist 20(3):585-596.