



The Cretaceous Angolan turtle *Angolachelys mbaxi*, description of a new specimen of the postcranial skeleton

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ABSTRACT

The turtle *Angolachelys mbaxi* Mateus et al., 2009, is an enigmatic turtle from the Late Cretaceous of Angola which in its description it was erected a new clade, the Angolachelonia Mateus et al., 2009. The phylogenetic position of *Angolachelys* and Angolachelonia has been questioned and reviewed multiple times since their definition. The new specimen of *Angolachelys mbaxi*, collected from the same locality as the holotype, consists of postcranial material and a skull, which will not be described in this thesis. The postcranial material is described and studied in this thesis, with the objective of reviewing and ascribing the phylogenetic position of *Angolachelys* and confirming the validity of Angolachelonia as a clade, to confirm if *Angolachelys* and the Angolachelonia were in fact of the marine ecology, and therefore suggesting the existence of an evolutionary transition to the marine habit by the Angolachelonia. The paleoecology of *Angolachelys mbaxi* is studied, namely in respect to the adaptations of its feeding habits. *Angolachelys* and the Angolachelonia were found in multiple phylogenetic positions, the most prevalent being found as the sister taxon of the Chelonioidea. *Angolachelys* has been defined as a marine turtle, with features indicative of a more pelagic lifestyle.

Keywords: *Angolachelys mbaxi*, *Angolachelonia*, Marine ecology, Phylogeny, Paleoecology

RESUMO

A tartaruga *Angolachelys mbaxi* Mateus et al., 2009, é uma tartaruga enigmática do Cretáceo Superior de Angola que na sua descrição foi erigida um novo clado, a Angolachelonia. A posição filogenética de *Angolachelys* e Angolachelonia foi questionada e revista várias vezes desde a sua definição. O novo espécime de *Angolachelys mbaxi*, recolhido na mesma localidade do holótipo, constituído por material pós-craniano é descrito e estudado nesta tese, com o objetivo de rever e atribuir a posição filogenética de *Angolachelys* e confirmar a validade de Angolachelonia como clado, confirmar se *Angolachelys* e a Angolachelonia eram de facto da ecologia marinha, sugerindo assim a existência de uma transição evolutiva para o hábito marinho pela Angolachelonia. É estudada a paleoecologia de *Angolachelys mbaxi*, nomeadamente no que diz respeito às adaptações dos seus hábitos alimentares. *Angolachelys* e Angolachelonia foram encontrados em várias posições filogenéticas, a mais prevalente sendo encontrada como o táxon irmão de Chelonioidea. *Angolachelys* foi definida como uma tartaruga marinha, com características indicativas de um estilo de vida mais pelágico.

Palavras-chave: *Angolachelys mbaxi*, *Angolachelonia*, Ecologia marinha, Filogenia, Paleoecologia

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1. INTRODUCTION

1.1 *Angolachelys*, previous studies

Angolachelys mbaxi Mateus et al. 2009, is a turtle from the Upper Cretaceous of Angola. Mateus et al. (2009) described the holotype in detail which consists of a skull, broken dorsally, a dentary, two procoelous cervicals, and an unguis phalanx from the Tadi Beds from the Itombe Formation near Iembe (Mateus et al. 2009). The species exhibits several features of different groups such as from the Trionychidae, such as the absence of the external process of the pterygoid, the reduced vomer, the maxillae meeting on the midline between the premaxilla and the vomer, and partial or complete fusion of the premaxillae, and Chelonioidea, such as a strong parietal-squamosal, the absence of the temporal exposure of the postorbital and the absence of a short postorbital exposed by temporal emargination (Tong & Meylan, 2013).

There have been several phylogenetic studies involving the *Angolachelys* (Mateus et al., 2009; Tong & Meylan, 2013; Cadena, 2015; Evers & Benson, 2019; Evers et al., 2019; Cruz et al., 2019) and its phylogenetic position is still under discussion (e.g. Evers & Benson, 2019) however most phylogenetic studies place it within the Sandownidae Tong & Meylan, 2013, along with *Brachyopsemys tingitana* Tong & Meylan, 2013, *Sandownia harrisi* Meylan et al., 2000 and *Leyvachelys cipadi* Cadena, 2015 (Tong & Meylan, 2013; Cadena, 2015; Evers & Benson, 2019) and some have found it within a clade named Angolachelonia, that was initially defined when the species was described (Mateus et al., 2009) but only included *Angolachelys*, *Sandownia harrisi*, *Solnhofia parsonsi* Gaffney, 1975a and *Leyvachelys cipadi* (then named as “Glenrose turtle”) (Mateus et al., 2009) though now it has been defined as a clade that is formed by the Sandownidae and the Thalassochelydia Anquetin et al., 2017 (Evers & Benson, 2019) in which *Solnhofia parsonsi* is included within the Thalassochelydia and the remaining, previously mentioned, members of Angolachelonia are included in Sandownidae.

When *Angolachelys* was described, the authors (Mateus et al., 2009) defined a new unranked clade to group it, *Sandownia harrisi*, *Solnhofia parsonsi*, and *Leyvachelys cipadi* together, the Angolachelonia. Tong & Meylan (2013), in their study and description of *Brachyopsemys tingitana*, formed a new family which grouped with the previous Angolachelonia members, besides from *Solnhofia parsonsi*, and included *Brachyopsemys*, the Sandownidae, at which point they considered the Angolachelonia as a non-valid clade. Within the Sandownidae, *Angolachelys* was found to be closer to the *Sandownia harrisi* than with the remaining members (Tong & Meylan, 2013; Evers et al., 2019) however the precise relations between the members of the family is yet to be determined (Cadena, 2015; Evers & Benson, 2019).

Cadena (2015) described and studied *Leyvachelys cipadi*, which was informally called *Glenrosechelys* or Glenrose turtle, and placed it within the Sandownidae, however, in their phylogenetic study, besides from *Sandownia harrisi*, the remaining members of Sandownidae were in a polytomy. Both Cadena (2015) and Tong & Meylan (2013) supported positioning the Sandownidae within the Pan-Chelonioidea.

Evers & Benson (2019) did a comprehensive phylogenetic study on the Mesozoic turtle groups especially the marine ones such as the Angolachelonia and they placed the Angolachelonia as the sister taxa of the Testudines and included within the clade the Sandownidae and the Thalassochelydia. Interesting to highlight that they did not include *Angolachelys* in their study since they did not have enough anatomical data for it to be informative in their study and therefore it was not possible to confirm the relationship between the *Angolachelys* and *Solnhofia parsonsi* since they were placed as closely related in the first study but since then have not been placed in the same family until Evers & Benson (2019) which they placed them *Solnhofia* and the rest of the Thalassochelydia within Angolachelonia.

There was another work from Evers et al. (2019) in which they placed the Angolachelonia as the sister taxon of the Pleurodira and within the Testudines, however, this work was more oriented towards the study of the relations within Chelonioida and as such some characters used in their matrix reflexes that and such characters might have influenced negatively the relation of Angolachelonia with Testudines. In this study, they placed *Angolachelys* in the study and it was placed as more closely related to *Sandownia harrisi* than the rest of the sandownids.

1.2 The Angolachelonians

The Angolachelonia clade was first defined by Mateus et al. (2009) with their phylogenetic study following the description of *Angolachelys mbaxi*, the species this group was named after. The clade was defined as “the clade originating from the most recent common ancestor of *Angolachelys mbaxi* Mateus et al, 2009, and *Solnhofia parsonsi* Gaffney, 1972.” a Late Jurassic turtle from Western Europe (Gaffney 1975a; Broin, 1994; de Lapparent de Broin et al., 1996; Joyce, 2000), and it grouped *Angolachelys mbaxi*, *Solnhofia parsonsi*, *Sandownia harrisi* and “Glen Rose turtle” which is now named *Leyvachelys cipadi* Cadena (2015) (Mateus et al., 2009).

The Angolachelonia was first diagnosed by the presence of articulation of quadrate aligned with, or posterior to the occiput; basisphenoid absent or much reduced in ventral view; medial contact of palatines (which is convergent with Trionychidae), expanded secondary palate (which is convergent with *Chelonia* Brongniart, 1800 and *Baptemys* Leidy, 1870) (Mateus et al., 2009).

Evers & Benson (2019) performed a revised phylogenetic approach on several Testudinata groups, including most Mesozoic turtle groups. In their work, the Angolachelonia (Figure 1.1) was positioned as the sister taxa of the modern testudines and grouped the Sandownidae (which includes *Angolachelys*) and the thalassochelydia (which includes *Solnhofia*). It is important to note that they did not include *Angolachelys* in their analysis because of the limitations of the anatomical information available at the time (Evers & Benson, 2019).

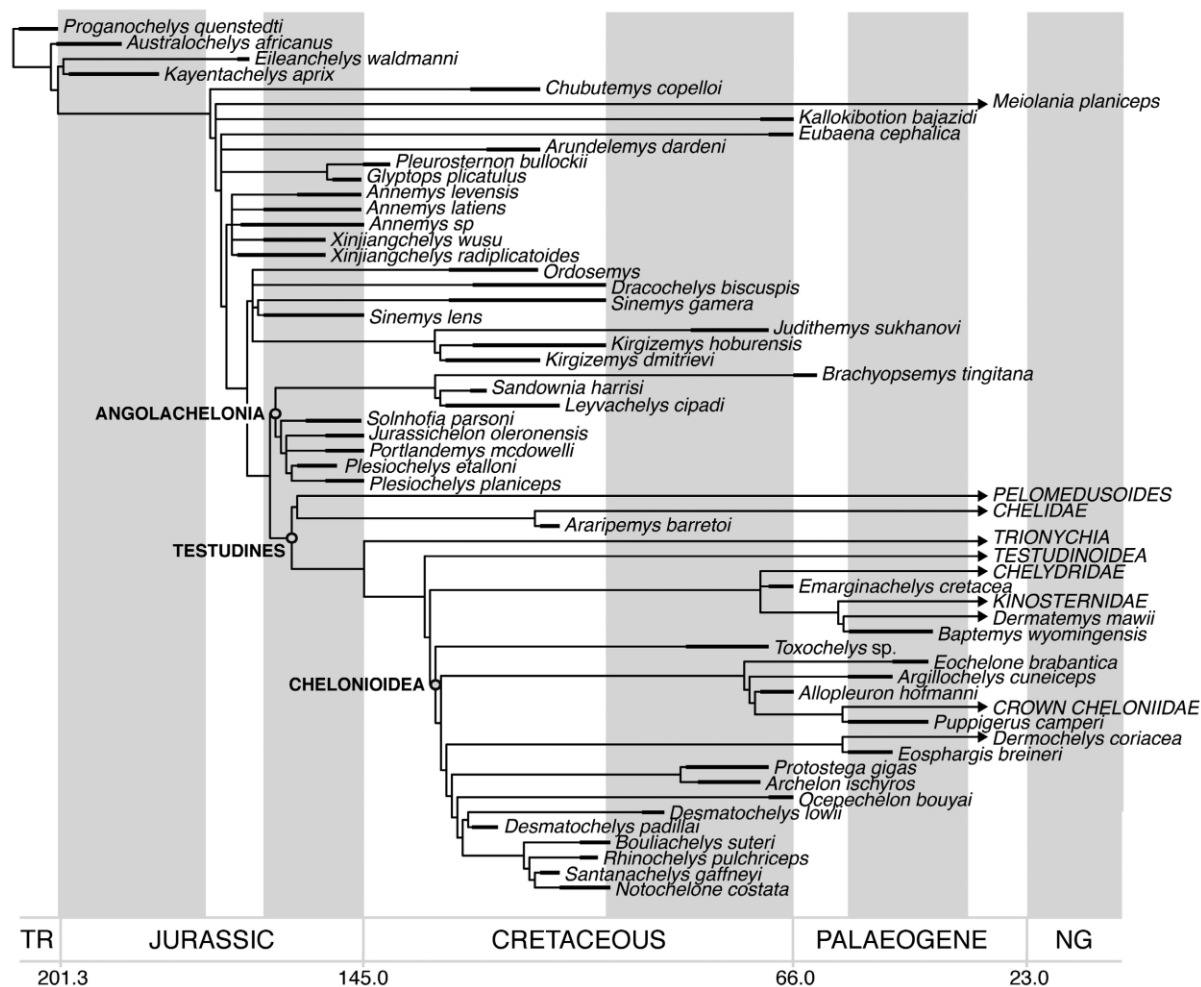


Figure 1.1. A simplified phylogenetic tree scaled to geologic time using range data for turtles, adapted from Evers & Benson (2019). Angolachelonia is presented as the sister-taxa of the Testudines.

The thalassochelydians (sensu Anquetin et al., 2017) are a group of Late Jurassic turtles from central and western Europe (Gaffney, 1975a; de Lapparent de Broin et al., 1996; Anquetin et al., 2017) and possibly from Argentina (de la Fuente & Fernández, 2011). They are divided into three groups: the Eurysternidae, to which *Solnhofia* is assigned (Anquetin et al., 2017); Plesiochelyidae, which is the only one from the three groups whose monophyly can be supported (Anquetin et al., 2015); and the Thalassemydidae (Anquetin, 2017). The thalassochelydians are considered to be marine due to the oxygen isotope signatures from the sediments where they were found (Billon-Bruyat et al., 2005) and to the morphological features such as an expanded foramen interorbitale (indicates the presence of salt glands) and the presence of shell fontanelles (Anquetin et al., 2017). The phylogenetic positions within the Thalassochelydia are uncertain (e.g. Anquetin, 2012; Sterli et al., 2013; Cadena, 2015) and this is mostly due to the uncertainty of the positions of *Jurassichelon* Pérez-García, 2015 (Anquetin, 2017) and *Solnhofia* (e.g. Joyce, 2007; Mateus et al., 2009; Sterli et al., 2013).

Solnhofia parsoni is a turtle from the Upper Jurassic of Western Europe (Gaffney, 1975a; Joyce, 2000). The holotype consists of an isolated cranium from the Solnhofia limestone in Germany (Parsons & Williams, 1961) and since then a very complete specimen has been described (see Joyce, 2000). The phylogenetic of *Solnhofia parsoni* has been changed in several different works having been grouped with non-thalassochelydian taxa such as *Santanachelys* Hirayama, 1998, the early protestegid (Joyce, 2007; Sterli & de la Fuente, 2013; Sterli et al., 2013), and also sandownids (e.g. Mateus et al., 2009). Recently *Solnhofia parsoni* was placed by Evers & Benson, (2019) as sister to plesiochelyids, although the branch support is only moderate (Bremer support = 2).

The Sandownidae is a putative stem-group cryptodires clade erected by Tong & Meylan (2013) whose age range is from the Aptian with *Sandownia harrisi* (Meylan et al., 2000), or possibly Barremian with *Brachyosemis tingitana* (Tong & Meylan, 2013), to the Paleocene with *Leyvachelys cipadi* (Cadena, 2015). The taxa from this group have been recovered as a clade in all phylogenetic studies that included at least two of them (Mateus et al., 2009; Tong & Meylan, 2013; Cadena, 2015; Evers & Benson, 2019; González-Ruiz et al., 2019; Evers et al., 2019). The fossils from these taxa are from shallow marine deposits and they present typical morphological adaptations to marine lifestyle, such as an extensive secondary palate indicative of durophagous diet, therefore, they have been interpreted as being marine adaptations (Mateus et al., 2009; Tong & Meylan, 2013; Cadena, 2015). Although they present marine lifestyle adaptations, the postcranium material of *Leyvachelys cipadi*, which was the only taxa whose postcranium material was recovered, lacks the features present in pelagic marine turtles (cheloniids, dermochelyids, and protostegids) since it presents an unflattened and unexpanded humerus and metacarpal, strongly ossified contact between the plastron and carapace, and lacks the shell fontanelles typical of pelagic turtles (Cadena, 2015). The group is therefore thought to have habited littoral habitats (Cadena, 2015).

The holotype of *Sandownia harrisi* consists of a well-preserved skull and partial lower jaw from the Isle of Wight in England (Meylan et al., 2000) which was placed in the Trionychidae when it was first described by Meylan et al. (2000), however, since then it has been subject to several phylogenetic analysis with differing results with some supporting the initial placement (Anquetin, 2012), while the most supported one is the placement of it as a close relative to the thalassochelydia (Joyce, 2007; Mateus et al., 2009; Sterli et al., 2013; Anquetin et al., 2015). In the study of Tong & Meylan (2013), they placed *Sandownia* as more closely related close to the *Angolachelys* than to *Brachyopsemys* while still placed within the Sandownidae. Recently there has been a re-description of *Sandownia harrisi* by Ever & Joyce (2020) based on computed tomography scans. They concluded that *Sandownia* shares a high number of anatomical similarities with thalassochelydians, particularly with *Solnhofia parsonsi*, and their results implied that there was a rapid morphological evolution during the early history of sandownids and that sandownids likely evolved in central Europe from thalassochelydian ancestors during the Late Jurassic (Ever & Joyce, 2020).

Leyvachelys cipadi is a sandownid from the Early Cretaceous of Colombia and Texas, ranging from the Upper Barremian-lower Aptian of the Paja formation of Colombia to the Albian of the Glen Rose Formation of Texas (Cadena, 2015). The species was informally named "*Glenrosecchelys brooksi*" by Vineyard (2009) however it was later grouped with *Leyvachelys cipadi* by Cadena (2015) due to the absence of any marked morphological differences between the specimens and that the slight variations in size and shape of the skull could be attributed to intraspecific ontogenetic variations, which was also pointed out by Vineyard (2009) (Cadena, 2015). The taxon represents the earliest global record of the sandownids and was the first sandownid that had a large portion of its postcranium described, which allowed the interpretation that the sandownids were not open marine turtles but instead littoral to shallow marine durophagous turtles (Cadena, 2015).

Brachyopsemys tingitana is a sandownid from the Danian of the Ouled Abdoun Basin, in Morocco (Tong & Meylan, 2013). The description of the species was based on skulls and a lower jaw and there are apomorphic features present in these that lead to the association of *Brachyopsemys* with *Sandownia harrisi*, *Angolachelys mbaxi*, and *Leyvachelys cipadi*, and the formation of the Sandownidae (Tong & Meylan, 2013). It ranges in the Paleocene and it is the most recent of the sandownids (Tong & Meylan, 2013).

In another phylogenetic analysis in which a modified version of the data matrix from Evers & Benson (2019) was used, Evers et al. (2019) positioned *Angolachelys mbaxi* within the Angolachelonia and as more closely related to *Sandownia harrisi* than with the remaining angolachelonians. Interestingly the position of *Solnhofia parsonsi* was the same as the analysis from Evers & Benson (2019) and in this study, the Angolachelonia was positioned as the sister taxon of the Pleurodira and within the Testudines contrary to the study from Evers & Benson (2019) in which the Angolachelonia was placed as the sister taxon of the Testudines (Evers et al., 2019).

In the study by Evers et al. (2019), they recovered the Angolachelonia as the sister group of Pleurodira although this relationship was found to be poorly supported in the study (with a Bremer support value of 1). The authors justified this unexpected result due to the uncertainty of the position of the pleurodires in global turtle datasets (e.g. Sterli, 2010; Zhou et al., 2014; Evers et al., 2019) and this uncertain phylogenetic position might explain the resulted relationship between the pleurodires and angolachelonians.

1.3 The locality of Iembe, geology and stratigraphy

1.3.1 Geology, stratigraphy, and age

The locality of Iembe (Figure 1.2) is known for its richness of fishes, mosasaurs, and plesiosaurs (Mateus et al. 2012) and belongs to the Kwanza Basin (Jacobs et al. 2006) in which the most productive formation for vertebrate fossils is the Itombe formation (Mateus et al. 2011).

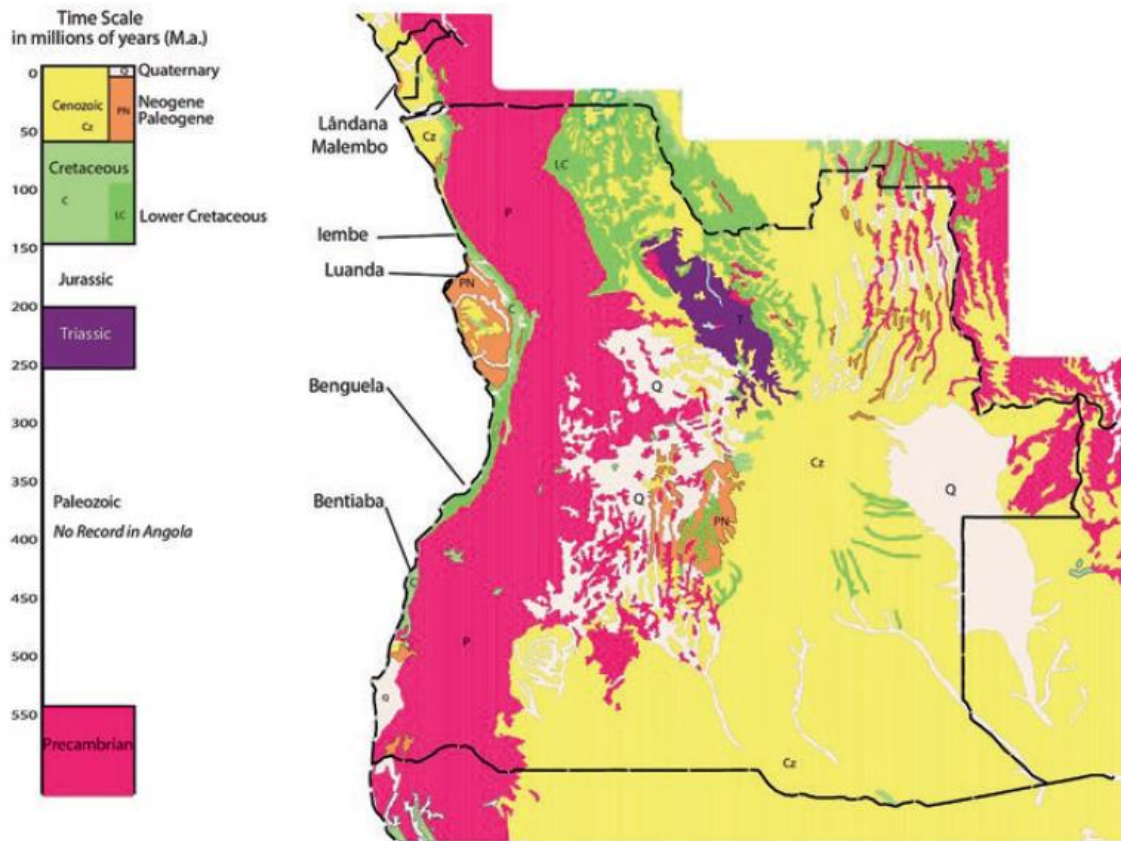


Figure 1.2. The geological map of Angola, with a stratigraphic log (left). Adapted from Mateus et al. (2019).

The Itombe formation, near the village of Iembe in Bengo Province of Angola (Jacobs et al., 2016), is the type locality for mosasaurs *Tylosaurus iembeensis* and *Angolasaurus bocagei* (Antunes, 1964), the first Angolan dinosaur the titanosauriform sauropod *Angolatitan adamastor* (Mateus et al., 2011) and the bizarre durophagous turtle *Angolachelys mbaxi* (Mateus et al., 2009) whose description justified the erection of its clade, the Angolachelonia, however, its phylogenetic position is not entirely confirmed (see Mateus et al., 2009; Tong & Meylan, 2013; Cadena, 2015; Evers et al., 2019). The

Itombe formation ranges from the early Turonian to the late Coniacian, the Turonian layers of the Itombe formation are dominated by silty shale, with the presence of limestone, shale, sandstone, and siltstone in some of the layers (Mateus et al., 2011), the Coniacian layers of the Itombe formation are dominated by silty shale however limestone, shale, sandstone, and siltstone are more abundant in these layers in comparison with the Turonian layers of the formation (Mateus et al., 2011). From this formation the beds that stand-out are the Tadi beds which is the type locality of the aforementioned vertebrate fossils (Jacobs et al., 2016). The Tadi beds are around 50m thick (Antunes, 1964; Mateus et al., 2011) and are placed in the Itombe Formation (Antunes, 1964; Jacobs et al., 2006).

The Tadi beds were first coined in the unpublished study of G. Brognon, G. Verrier, and R Thiers “Géologie du Bassin du Cuanza et du Bas-Congo” in 1960. The term was later accepted and used in Antunes (1964) (Mateus et al., 2011). The Tadi beds were considered to be Coniacian of age in the original work however the study of Antunes (1964) based on the fish fauna determined them to be of late Turonian of age (Mateus et al., 2011). The stratigraphic column of the Tadi beds is presented in figure 1.3.

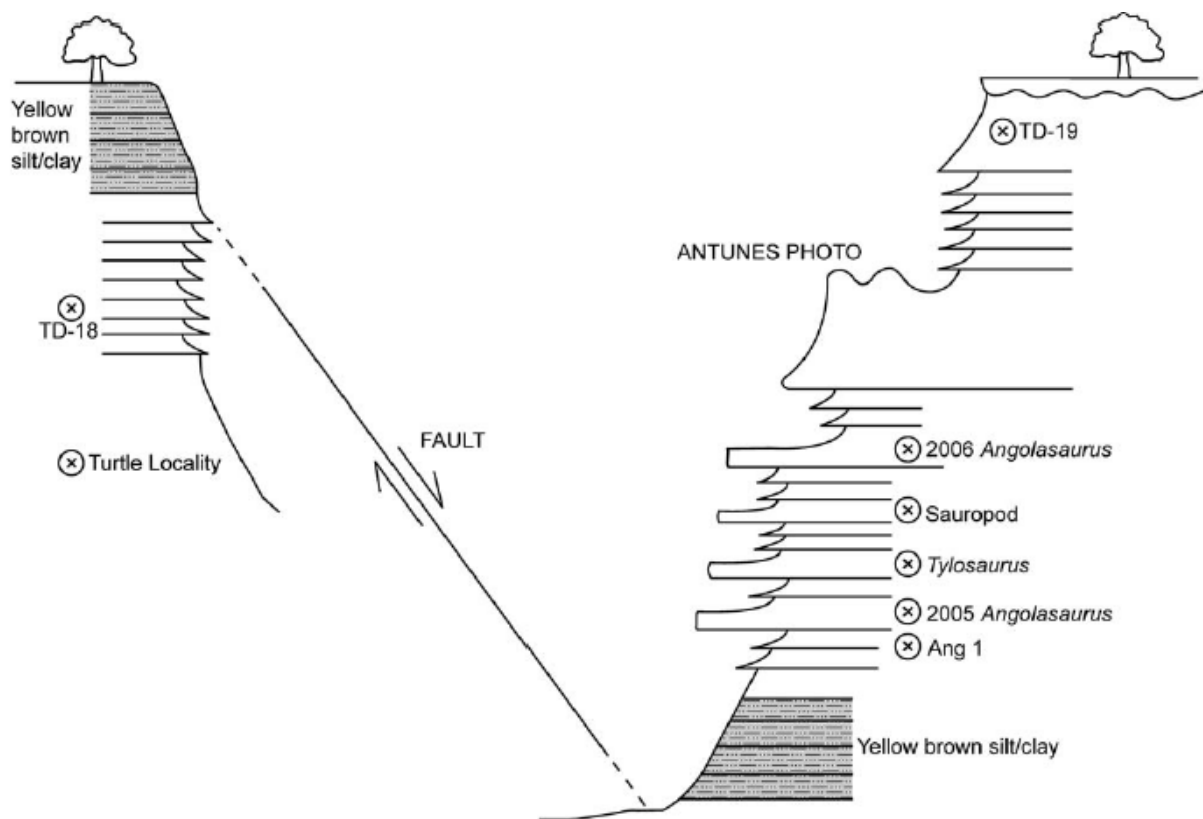


Figure 1.3. Stratigraphic distribution of fossils at the Tadi Beds in Iembe, Angola. “Antunes Photo” refers to an image from Antunes (1964: pl, 1: 2), which shows the locality where the holotype of *Angolasaurus bocagei* was collected. There is a fault separating the type locality of *Angolachelys mbaxi* from that of *Angolasaurus*. The image is not to scale. TD-18, TD-19, and Ang 1 refer to mosasaurs. Adapted from Mateus et al. (2009).

The Tadi beds are very rich in vertebrate fossils especially fishes which occur throughout the section (Mateus et al., 2009). The age of the Tadi beds was once considered to be as late Turonian based on studies on the ichthyofauna by Antunes (1961, 1964; Lingham-Soliar, 1994) and Antunes and Cappetta (2002), however small and distinguishing mosasaur vertebrae along with the sharks found at the top of this section suggest that its age may extend into the Coniacian or possibly to the lower Santonian (Jacobs et al., 2016). The top part of the Itombe Formation corresponds to the Middle Campanian *Globotruncata ventricosa* Zone, and the lower part, the Tadi beds, can be correlated with the Cocaba Beds which contain the ammonite *Coilpoceras* of Turonian and Coniacian age (Jacobs et al., 2006). The upper age limit of the Tadi Beds is constrained by the Pambala Beds, which contains

Texanites of Coniacian to Campanian age (Jacobs et al., 2006), that is included in the N’Golome Formation that contains the Middle Campanian *Globotruncata ventricosa* Zone (Antunes & Cappetta, 2002) but also contains the Late Coniacian *Dicarinella asymerica* Zone (Blake et al., 1996) therefore a similar chronostratigraphic problem present in the Itombe Formation is also present in this formation (Jacobs et al., 2006). The presence of small and distinctive mosasaur vertebrae, as well as shark material at the top of the section of the Tadi Beds, suggest that it may extend into the Coniacian or possibly into the lower Santonian (Jacobs et al., 2016).

The study on the ichthyofauna of the Tadi beds by Antunes & Cappetta (2002), resulted in the recovery and description of multiple shark species, some of which were reported for the first time their presence in Africa (i.e. *Ptychodus whipplei*) (Antunes & Cappetta, 2002). The dating of the Tadi beds by these authors was based on the fauna recovered in the aforementioned study. The species recovered by the authors are indicated in figure 1.4.

Taxa	Late Cretaceous					
	Cenomanian	Turonian	Coniacian	Santonian	Campanian	Maastrichtian
<i>Hexanchus cf. microdon</i> Agassiz, 1843						
<i>Ptychodus mortoni</i> Agassiz, 1843						
<i>Ptychodus cf. paucisulcatus</i> Dixon, 1850						
<i>Ptychodus whipplei</i> Marcou, 1858						
<i>Scapanorhynchus raphiodon</i> Agassiz, 1843						
<i>Scapanorhynchus cf. lewisii</i> Davis, 1887						
<i>Cretoodus semiplicatus</i> Agassiz, 1843						
<i>Enchodus cf. elegans</i>						
<i>Cretoxyrhina mantelli</i> Agassiz, 1843						
<i>Paranomotodon angustidens</i> Reuss, 1845						
<i>Squalicorax falcatus</i> Agassiz, 1843						

Figure 1.4. Diagram indicating taxa recovered by Antunes & Cappetta (2002) and their respective stratigraphic range. Data adapted from the Paleobiology Database and Antunes & Cappetta (2002).

The ichthyofauna list provided by Antunes and Cappetta (2002) lists fauna for the Cenomanian, Late Turonian, and Santonian-to-Lower Campanian, displaying a considerable stratigraphic range.

From excavations, in the Tadi Beds, a specimen of *Protexanites* sp. Matsumoto, 1955 was recovered by the Paleangola group (Mateus et al., 2019). The discovery has led to the definition of the Tadi beds as Coniacian of age (Mateus et al., 2019). The identification of this specimen is detailed in this study.

1.3.2 Associated fauna

There is ammonite material found in the Tadi beds (Mateus et al., 2019), including one with especially good preservation, which will be described here (Figure 1.5). The ammonite is described and identified in order to aid in the determination of the age of the Tadi beds. The ammonite has well-developed ribs, which are trituberculated in the body whorl, with the umbilical (the rib positioned more towards the centre of the ammonite), submarginal (rib positioned towards the centre of the whorl), and lateral nodes (positioned on the lateral side of the whorl). The ammonite is moderately involute and it is medium in size and it presents a depressed whorl section in its shell. Using this

description and cross-referencing with the bibliography, namely Kennedy (1984), the genus of the specimen is identified as *Protexanites*. The genus has a well-defined time range from the Upper Coniacian to the Lower Santonian (Kennedy, 1984). The species of the specimen is, most likely, a *Protexanites bourgeoisi* d'Orbigny, 1850 (Figure 1.6) due to the strong ribs and the strong pointed marginal tubercles, the considerable depression separating the marginal tubercles from a lower and more rounded shaped siphonal keel. The costal whorl breadth to height ratio is 1.6, which is below the maximum costal whorl breadth to height ratio defined by Kennedy (1984) which is 1.7, further indicating that the specimen is a *Protexanites bourgeoisi*. The total number of ribs per whorl is not possible to confirm due to the fragmented nature of the specimen, with a large portion of the ribs not being preserved.

The specimen closely resembles *Protexanites cycni* van Hoepen, 1965, especially in the sense of the small and rounded keel, however it differs from in the ribs. *P. cycni* is ornamented with weak and flattened (Klinger & Kennedy, 1980), whilst *P. bourgeoisi* is ornamented with larger, more sinuous ribs, which are the case that is seen in the specimen, unlike those present in *P. cycni*. *P. cycni* is represented in the Early Coniacian of South Africa, possible to the Late Coniacian of South Africa (Klinger & Kennedy, 1980). *P. bourgeoisi* is represented in the Late Coniacian of France (Kennedy, 1984).



Figure 1.5. Ammonite specimen from the Tadi Beds, identified as *Protexanites bourgeoisi*. Material associated with *Angolachelys mbaxi* material.



Figure 1.6. Ammonite *Protexanites bourgeoisi*. Adapted from Kennedy (1984).

1.4 Marine turtle lineages

Marine turtles have a long and convoluted lineage, with several turtle lineages that evolved secondarily to the marine ecology (Evers & Benson, 2019). The oldest marine adapted turtle being generally understood to be *Odontochelys semitestacea* Li et al., 2008, from the Late Triassic of China, based on its marine depositional environment (Li et al., 2008; Reisz & Head, 2008; Lyson et al., 2010) and for its limb proportions that are characteristic of aquatic turtles (Li et al., 2008).

Odontochelys semitestacea presents a fully developed plastron whilst the carapace seems to be absent, with just the dorsal ribs and neural dermal ossifications present (Li et al., 2008). These features were interpreted by its authors to be that *Odontochelys* represents an early stage in the evolution of the turtle shell (Li et al., 2008) while other authors (e.g. Reisz & Head, 2008) interpreted that the carapace was present but some of its dermal components were not ossified, due to the presence of the expanded lateral bridge that connects the plastron to the carapace (Reisz & Head, 2008). In this interpretation, the reduction of the carapace resulted from the lack of ossification of some of its dermal parts and that it was an adaptation to the marine environment such as in some extant turtles such as the soft-shelled turtles, sea turtles, and snapping turtles (Reisz & Head, 2008). There have been, however, others who claimed that, through the shape of the proximal phalanges which are robust and shortened (Li et al., 2008) and by taking into account the ternary diagram of Joyce and Gauthier (2004), that *Odontochelys semitestacea* was likely a fully terrestrial stem turtle or possibly lived in a swampy freshwater environment (Joyce, 2015), therefore the lifestyle of *Odontochelys* is still up to debate.

There were several lineages in turtles that evolved secondarily to the marine ecology (Evers & Benson, 2019) such as the Angolachelonia (Mateus et al., 2009; Anquetin et al., 2015; Anquetin et al. 2017; Evers & Benson, 2019; González-Ruiz et al. 2019), the pleurodirans Bothremyidae (Gaffney et al., 2006; Rabi et al., 2012) and Stereogyina (Sánchez-Villagra et al., 2000; Winkler & Sánchez-Villagra, 2006; Gaffney et al., 2011), and the extant marine turtle group the Chelonioida (Hirayama, 1994, 1998; Evers & Benson, 2019). Of these groups, the only extant group is the Chelonioida which are highly adapted to the pelagic lifestyle and include modifications in the shell, limbs, and skull adapted to that lifestyle (Zangerl, 1980; Hirayama, 1994).

The Angolachelonia clade composed of the Sandownids and the Thalassochelydians (Tong & Meylan, 2013; Evers et al., 2019), and both groups were considered to be marine (the sandownids references + thalassochelydian references). The Angolachelonians are considered to be an of marine ecology (Mateus et al.2009; Anquetin et al., 2015; Anquetin et al., 2017; Evers & Benson, 2019) and they are considered to be a lineage that developed a marine ecology independently (Evers & Benson, 2019).

Unlike the chelonians, the sandownids do not present the features typical of a pelagic lifestyle specifically they lack the flattened and expanded humerus and metacarpal, strongly ossified contact between the plastron and carapace, and lack the shell fontanelles typical of pelagic turtles (Cadena, 2015) which lead to them being interpreted to being of a littoral habitat (Cadena, 2015). The thalassochelydians, the other group within the Angolachelonia, are considered to be marine because of the oxygen isotope signatures from the sediments where they were found (Billon-Bruyat et al., 2005) and to the morphological features such as an expanded foramen interorbitale (indicative of the presence of salt glands) and the presence of shell fontanelles (Anquetin et al., 2017).

In the Pleurodira, the side-neck turtles, there are considered to be two phylogenetically different lineages that adapted to a marine lifestyle: the Cretaceous till the Oligocene Bothremyidae (Gaffney et al., 2006) and the Eocene until Pleistocene Stereogyina. The Bothremyidae are one of the most abundant pleurodire groups in the fossil record and a proposed peak in the diversity of the pleurodires during the Cretaceous may be related to the diversification of this group (Gaffney et al., 2006). The groups' phylogeny suggests that there could be two independent origins of marine habits since the marine Taphrosphyini does not form a monophyletic group with the freshwater bothremydids (Gaffney et al., 2006; Rabi et al., 2012).

From the Cryptodira Cope, 1868, the hidden-neck turtles, the independent marine lineages of marine turtles are less well understood (Evers et al., 2019). The extant sea turtles are all within the Chelonioida and it represents one unambiguous evolutionary origin to secondary marine ecologies within the Cryptodira (Evers et al., 2019). The chelonioids form a clade of forms that are highly adapted to a marine environment and are characterized by several adaptations to a marine lifestyle such as by the presence of highly modified limbs named flippers, salt glands, or indications of their presence (i.e. expanded foramen interorbitale), and a wide range of modifications of the shell (Hirayama, 1994).

In a study by Evers et al. (2019), they presented that their new phylogenetic hypothesis supports two origins of marine lifestyle in non-pleurodiran turtles, besides from the aforementioned *Odontochelys* which are the Chelonioida, the group that includes the modern sea turtles, and the Angolachelonia, which include the thalassochelydia and the sandownids.

1.5 Objectives

The new specimen of *Angolachelys mbaxi*, an inscrutable turtle from the Late Cretaceous of Angola, was collected from the same locality as the holotype, consisting of postcranial material, and is described and studied in this thesis, with the objective of:

- Reviewing and ascribing the phylogenetic position of *Angolachelys mbaxi*;
- Confirming the validity of Angolachelonia as a clade;

- Confirming if *Angolachelys* and the *Angolachelonia* were of marine ecology;
- The paleoecology of *Angolachelys mbaxi* is studied, namely in respect to the adaptations of its feeding habits;
- Confirming the age of the locality the specimen originated.

2. METHODS

2.1 Photogrammetry

Photogrammetry, or stereophotogrammetry, consists of creating 3D information based on points, lines, and areas of objects or terrain from photographic image sequences (Mallison & Wings, 2014). It is a non-contact technique and it is used as a method for determining the three-dimensional surface topography of an object or area from multiple two-dimensional images acquired at different viewpoints (Sutton et al., 2014).

Photogrammetry involves the measurement of homologous points in two, or more, overlapping images, that are captured at different positions, to reconstruct 3D coordinated of the surface of interest, or a “point cloud”, through triangulation (Sutton et al., 2014). The images used in photogrammetry are normally acquired through the capture of natural light with photography, therefore they integrate information about the colour and texture of the imaged surface, which can then be integrated directly into the point cloud and/or be utilized in the post-processing step in order to grant the photo-texture to the 3D mesh (Sutton et al., 2014).

In palaeontology, the most frequent use of photogrammetry is the three-dimensional digitization of specimens. Until recently the complexity of the required calculations allowed only the measuring of individual points (e.g. Gunga et al., 2008), and the calculation of the entire point clouds was not possible (Mallison & Wings, 2014), however, with the great increase in computing power and advances in programming during the last decade have allowed increasing the forms of data collecting possible.

Due to not needing to handle heavy, fragile, and rare fossil specimens for research and being replaced by digital models allowed computer simulations in palaeontology and allowed to expand the possible research topics (Mallison & Wings, 2014). Often with immobile or considerably heavy specimens require a significant amount of effort and expenses to study, while a highly detailed 3D model that can be transferred, viewed, and measured makes it accessible to practically everybody (Mallison & Wings, 2014). Scans do not decay, while fossils can be damaged by contact with the elements or during the research (Mallison & Wings, 2014). Another great advantage of using digital files of fossils is the capability to save any configuration of several specimens at any time and to compare the numerous configurations directly to each other, without there being any risk involved to the actual physical specimens (Mallison & Wings, 2014). There are possible applications for photogrammetry whilst in the field as well, such as the documentation of progress on excavation and the geospatial relationship of fossils and/ or sites that can be accurately documented (Mallison & Wings, 2014). Maps of fossils in the excavation site can be produced at high accuracy and, through the usage of series of photographs taken at different times, the maps produced can be 3D maps that show the arrangement of the fossils, including the exact distances between them (Mallison & Wings, 2014).

There are numerous research areas in palaeontology in which photogrammetry technology can be utilized such as biomechanics, which include locomotion, ranges of motion and body mass, the reconstruction of soft tissue volumes, along with morphometric studies and ichnology (Mallison & Wings, 2014).

Commonly, a digital camera is utilized to capture photographs of the target, this approach is scale-less, and, therefore, theoretically applicable to surfaces of all sizes (Sutton et al., 2014). In the field of palaeontology, photogrammetry techniques have up until recently been used to document quite large-sized specimens, such as dinosaur skeletons (e.g. Wiedemann et al., 1999; Stoinski, 2011), and tracksites (e.g. Breithaupt & Matthews, 2001; Matthews et al., 2006; Bates et al., 2009), however more recently there have been works that have demonstrated the potential of these methods for the study of a wider variety of fossil taxa (Falkingham, 2012, Sutton et al., 2014).

For the photogrammetry process, it was used the program Agisoft Photoscan. Agisoft Photoscan is a 3D scanning software package, developed by the Russian Agisoft company (Li et al., 2016). Agisoft Photoscan is a cutting-edge 3D modelling package based on image data processing (Li et al., 2016). It utilizes the latest 3D reconstruction technology from multiple different views, which allows it the capability to process any picture taken by non-metric cameras, with data ranges from small sculptures to mass image data taken from a UAV, or Unmanned Aerial Vehicle (Li et al., 2016). 3D scenes have several applications in numerous fields, such as industry, biology, palaeontology, medicine, and also some military applications (Li et al., 2016). There are advantages to utilizing the Agisoft Photoscan software package, however, there are also some disadvantages (Li et al., 2016). Agisoft Photoscan can automatically construct 3D models throughout the whole course, without the need to set any initial values and control points, therefore it is very convenient for users (Li et al., 2016). Photos can be taken at any position and angle, as long as there are corresponding points between two adjacent pictures of the target (Li et al., 2016). Comparing to constructing 3D models of surface features using a 3D Laser Scanner, Agisoft Photoscan is highly efficient and low cost (Li et al., 2016). The disadvantages of this software package are that it requires a high-performance computer that is capable of graphic processing (Li et al., 2016). The construction speed of the 3D model also depends on the number of photos and other parameters, such as the RAM of the processing computer (Li et al., 2016). The larger the amount of data for processing, the longer it takes to build the 3D model (Li et al., 2016). Compared to the 3D Laser Scanner, the Agisoft Photoscan method is less accurate, therefore the 3D Laser Scanner is necessary for 3D measurements that require a great deal of precision (Li et al., 2016).

The photographs used for the photogrammetry, and other pictures in this work, were taken with a Panasonic Lumix DMC-FZ 38 camera. The photo-taking method used was the turntable method, more precisely it was the “Turntable method for small mobile specimens-without turntable” from Mallison & Wings (2014). It consists of the usage of a large piece of cardboard or sandbox (cardboard was used in this case) as a makeshift turntable and takes several photographs from several different positions through the rotation of the makeshift turntable to complete the process of photogrammetry (Mallison & Wings, 2014). The method is used when taking photographs of relatively small specimens.

2.2 TNT

TNT, short for “Tree Analysis Using New Technology” (Giribet, 2005) is a phylogeny program used for the analyses of data under the parsimony criterion and includes in it extensive tree handling and diagnosis capabilities. One of the main features which highlights TNT in comparison with other phylogeny programs (i.e. Hennig 86 (Farris, 1988), PAUP (Swofford, 1990)) is the “New technology” option (Goloboff et al., 2008). The “New technology” from TNT has been implemented with several “fast swappers” in its algorithms which allow the increase in the speed at which the program searches for trees (10 to 50 times faster than PAUP, depending on the size of the analysed data, in which the larger the data size, the greater the difference (Giribet, 2005) as well as having several different options for the specification of driven searches through “New technology” (Giribet, 2005).

To test the phylogenetic relationships of *Angolachelys mbaxi* among turtles, the matrixes from Evers & Benson (2019) and Evers et al. (2019) were used. These matrixes were chosen because they were

the most up-to-date matrixes available at the time for phylogenetic analysis of turtles. The matrix of Evers et al. (2019) is similar to that of Evers & Benson (2019) with the revision and addition of some characters related to the postcranium, to try and code the variation of parts of the skeleton that were interpreted as being important for the marine lifestyle within the chelonoids (Evers et al., 2019). All the characters and states defined in the aforementioned publications were kept. The resulting matrix based on Evers & Benson (2019) has 81 taxa coded and 345 characters and the matrix based on Evers et al. (2019) resulted in 96 taxa coded and 355 characters. The data set was analysed in TNT V1.5 (Goloboff and Catalano, 2016) in order to conduct parsimony analysis and obtain the most parsimonious trees (MPTs). Like in the case of the study of Evers & Benson (2019), a backbone constraining extant taxa was utilized (Pereira et al., 2017), the fossil taxa were left unconstrained to fit wherever they could within the topology. *Proganochelys quenstedti* Baur, 1887 was set as the outgroup. Searching was conducted with new technologies search (NTS) with default settings, with tree drifting as well as parsimony ratchet enabled. The initial level of the driven search was set to 30 with 30 hits for minimum length, just like it was used in Evers & Benson (2019). Using the NTS allows the usage of several searching algorithms at the same time. All of the algorithms were selected (i.e. sectorial search, ratchet, drift, tree fusing) and the minimum length was set to be hit 30 times. The resulting MPTs were subjected to a final round of tree bisection and reconnection (TBR). For the second case, since some of the strict consensus tree topology was unresolved, it was executed an iterative PCR (Pol & Escapa, 2009) in TNT to identify the “wildcard” taxa that occupied multiple separate phylogenetic positions among the MPTs.

Between the matrixes of Evers & Benson (2019) and Evers et al. (2019) they added, to the latter, they added 16 taxa, *Adocus lineolatus* Cope, 1874, *Angolachelys mbaxi*, Cabindachelys *landanensis* Myers et al., 2018, *Calcarichelys gemma* Zangerl, 1953a, *Chelosphargis advena* Hay, 1908, *Corsochelys halinches* Zangerl, 1960, *Erquelinnesia gosseleti* Dollo, 1886, *Nichollsemys baieri* Brinkman et al., 2006, *Ctenochelys sp.* Zangerl, 1953b, *Galianemys whitei* Gaffney et al., 2002, *Oligochelone rupelensis* Dollo, 1909, *Peritresius martini* Gentry et al., 2018, *Petrochelys kyrgyzensis* Nessov, 1995, *Plesiochelys bigleri* Puntener et al., 2017, *Procolpochelys charlestonensis* Weems & Sanders, 2014, and *Rhinochelys nammourensis* Tong et al., 2006, as well as modified and added characters pertaining to the postcranial skeleton. To test the possible implications these new taxa had to the phylogenetic results, it was done a modified matrix, defined here as “combination” matrix, which it was used the characters from Evers & Benson (2019) but with the added taxa from Evers et al., (2019). The methodology was used in this was the same as the first matrix. It resulted in 96 taxa coded and 345 characters.

It was used the characters added and modified in Evers et al. (2019) with the taxa of Evers & Benson (2019), with the inclusion of *Angolachelys mbaxi*, to test the possible impact of the “new” characters in Evers et al. (2019) over the differences of the results between the previous tests.

The Bremer supports were calculated using the bremmer.run script in TNT and the Consistency and retention indices (CI, RI) were calculated with the stats.run script.

2.3 Materials

The materials of the specimen consist of 16 carapace fragments, which include peripherals, neurals, and costals; three plastral fragments; four cervical vertebrae; two dorsal vertebrae; four caudal vertebrae; one complete left humerus; one fragment of a fibula; a fragment of a metacarpal or metatarsal; one fragment of a femur; one coracoid; two pelvis fragments and several uninformative fragments. The identification number of the specimen is MGUAN-PA 296 (Figure 2.1).

The photographs of the images of the described material were taken with a Panasonic Lumix DMC-FZ 38 camera.

The material was collected by the team of “Projecto PaleoAngola” (Mateus et al., 2011) on 12 of July 2009. The specimen was found in the following coordinates: 8°15'27.58"S; 13°19'18.62"E in the locality of Iembe.



Figure 2.1. *Angolachelys mbaxi* paratype specimen (MGUAN-PA 296) in plaster jacket. Photo taken by Octávio Mateus.

3. RESULTS

3.1 Systematic Palaeontology

Testudines Batsch, 1788

Angolachelonia Mateus et al., 2009

Definition: The clade originating from the most recent common ancestor of *Angolachelys mbaxi* Mateus et al., 2009 and *Solnhofia parsonsi* Gaffney, 1975a.

Revised diagnosis: *Angolachelonia* can be diagnosed based on the subsequent unambiguous synapomorphies: The absence of a quadrate-basisphenoid contact (character 83.1); presenting an infolding ridge on the posterior surface of the quadrate ventral to the incisura columella auris (character 84.1); absence or incipience of a ventral median ridge in pterygoid (character 104.0); coronoid contributes to the triturating surface (character 182.1); coronoid process principally formed by coronoid (character 185.0). The characters used in this diagnosis are the characters used by Evers et al. (2019).

Sandownidae Tong & Meylan, 2013

Definition: The clade that includes *Sandownia harrisi* Meylan et al., 2000 but not *Pelomedusa subrufa* Bonnaterre, 1789, *Testudo graeca* Linnaeus, 1758, *Solnhofia parsonsi* Gaffney, 1975a, *Eurysternum wagleri* Meyer 1839, *Plesiochelys etalloni* Pictet & Humbert, 1857, *Thalassemys hugii* Rüttimeyer, 1873 or *Protostega gigas* Cope, 1871.

Genus *Angolachelys* Mateus et al., 2009

Etymology: *Angolachelys* means “Angola turtle” in classic Greek (Mateus et al., 2009)

Type species: *Angolachelys mbaxi* (Mateus et al., 2009).

Diagnosis – Same as for the type and only species

Angolachelys mbaxi Mateus et al., 2009

Etymology: Mbaxi means “turtle” in the Angolan Nyaneka-Nkumbi and Kimbundo languages (Mateus et al., 2009)

Holotype: The holotype (identification number MGUAN-PA 002) consists of an almost complete skull, an ungual phalanx, two cervical vertebrae, the proximal part of the ilium, shell parts, and a few uninformative fragments (Mateus et al., 2009).

Paratype: The paratype (identification number MGUAN-PA, the number varying depending on the specimen) consists of 16 carapace fragments, including peripherals, neurals, and costals, three plastral fragments, four cervical vertebrae, two dorsal vertebrae, four caudal vertebrae, one complete left humerus, one fragment of a fibula, a fragment of a metacarpal or metatarsal, one fragment of a femur, one coracoid, two pelvis fragments, and several uninformative fragments.

Associated material: Ammonite specimen recovered in the same locality.

Type locality and horizon: Tadi Beds, member of Itombe Formation, near Iembe, Bengo Province, Angola. Upper Turonian according to Antunes & Cappetta (2002), Jacobs et al. (2006), and Mateus et al. (2009). Considered Coniacian in age in this work (discussed in “the locality of Iembe” section and further in this work) in concordance with Mateus et al. (2019).

Revised diagnosis: *Angolachelys* can be diagnosed based on the subsequent unambiguous synapomorphies: presence and development of a medial process of jugal ventral to orbit, jugal contacts maxilla as well as the palatine and/or pterygoid (character 28.1); teeth in premaxilla, maxilla, and dentary are absent (character 47.1); the presence of a subdivision of the apertura narium externa by an internarial process of the premaxilla (character 48.0); absence of the contact between the pterygoid with the exoccipital (character 98.0); the pterygoid is at the same level on the ventral surface in respect to the basisphenoid (character 103.0); pterygoid presents a ventral median ridge that spans nearly the full length of the pterygoids (character 104.1); the extent of the pterygoid ridge on the palatal surface lateral to the skull midline, each ridge extends only along the posterior part of the pterygoid, along with the level of the parabasisphenoid (character 107.1); pterygoid/quadrato forking of cavum acustico-jugulare and recessus scalae tympani present, produced by the ventral process of the quadrato or prootic or a posterolateral expansion of the parabasisphenoid (character 108.2); pterygoid process posterior of pterygoid present but very short, process extends posteriorly to cover the posterior foramen for the canalis cavernosus (i.e. the modified cranioquadrato space) but the cavum-acustico jugulare remains largely exposed ventrally (character 109.1); absence of a development of a posteromedial wing covering partially to completely the basisphenoid and sometimes the basioccipital (character 110.0); foramen nervi hypoglossi (XII) exposed in ventral view (character 118.0); fenestra ovalis is ventrally closed by the prootic and opisthotic (character 130.0); carotid artery/Pterygoid interpterygoid vacuity is reduced to an interpterygoid slit (character 147.1); embedding of carotid artery and its bifurcation, internal carotid artery system is partially embedded, a foramen posterius canalis carotici interni is present, and the split into palatine and cerebral artery occurs at the fenestra carotica and is thus ventrally exposed (character 149.1); exposure of the palatine artery and/or anterior parts of the internal carotid artery absent, the split of the internal carotid

artery is dorsally covered by bone, and the palatine artery exits the basicranium into the cavum cranii via the foramen arterius canalis carotici palatinum (character 152.0); size of foramen stapedio-temporale relatively large (size of a large blood foramina, $\geq 5\text{mm}$ diameter (character 159.0); cranial scutes, scute J formed by several scutes (character 173.0); medial contact of dentaries open suture (character 174.1); width triturating surface vs. jaw length narrow triturating surface, symphysis less the 1/3 of jaw length (character 175.0); dentary, symphyseal ridge present (character 176.1). The characters used in this diagnosis are the characters used by Evers et al. (2019).

3.2 Description

The new postcranial specimen was identified as being *Angolachelys mbaxi* because it was recovered alongside a new specimen of a skull that was identified as *Angolachelys mbaxi* based on the similarities with the holotype skull (Figure 3.1). The specimen number is MGUAN-PA 296. The paratype skull will not be discussed in this work.

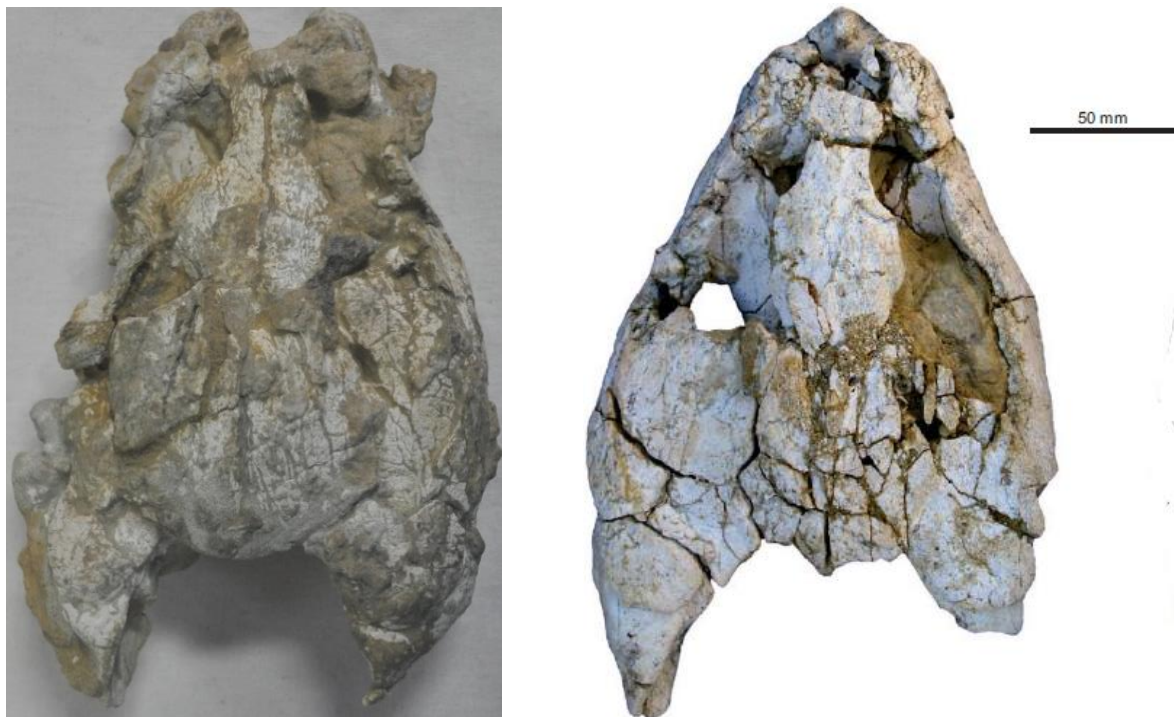


Figure 3.1. *Angolachelys* skull specimen, left is the paratype skull (photo taken by Octávio Mateus) and on the right is the holotype skull (adapted from Mateus et al., 2009).

3.2.1 Carapace

The carapace material consists of 16 separate fragments, some of which are articulated with other parts. There are specimens in a considerably low state of preservation (e.g. Figure 8, 9, 10, 11, 12, and 23) however the majority present a good state of preservation. Several of the fragments were positioned in the medial, posteromedial sections of the carapace.

The majority of the fragments consist of neural fragments with fifteen fragments, the majority of which are articulated with costal fragments (Figure 3.3, 10, 11, 13, 14, 23). There is a total of eleven costal fragments (Figure 3.2, 10, 11, 13, 14, 17, 18, 20, 21, 22) and four peripherals (Figure 3.9, 16).

There is only one scute well preserved, it being a vertebral scute. The remaining scutes are unknown.

Costal fragment,

The fragment specimen consists of a portion of the lateral side of a costal, as well as a free rib articulated with the aforementioned fragment, likely positioned in the left side of the carapace (Figure 3.2).

The majority of it is missing being only a small part of the lateral most side of the costal preserved, therefore it is not possible to confirm the overall size nor shape of the costal nor which costal it consists of.

The costal shows no sculpturing nor any differentiating characteristics on the surface. The free rib extends considerably laterally from the costal fragment, it ends with a small curve that extends posterior-laterally. The fragment is tentatively positioned in the medial portion of the costals of the carapace, due to the size and length of the free rib.



Figure 3.2. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in ventral (left) and dorsal (right) views.

Neural fragment,

Seems to consist of four neural plates (Figure 3.3). The largest one might be the first neural plate, with each successive one is the next neural plate. The edges of the neurals are degraded, though overall is in decent preservation except for the fourth neural that is missing a portion. The neurals are tentatively positioned more anteriorly in the carapace, though it is not certain.

Neural 1 is rhombus-like in shape, being longer than wide. The posterior end of neural 1 is curved posteriorly, the margin that contacts neural 2 is curved anteriorly.

Neural 2 is considerably smaller in size than neural 1, it presents a rectangular-like shape, being longer than wide. The anterior end of the neural is slightly curved anteriorly.

Neural 3 is wider than long, presents a rectangular-like shape, being wider than long.

Neural 4 is missing a significant portion of its posterior portion of the neural, its shape and overall size are unknown due to the damage.



Figure 3.3. *Angolachelys mbaxi* neural elements (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Costal fragment,

The fragment consists of two neural fragments and possibly the fragment of a costal (Figure 3.4). The neurals and the costal are poorly preserved, with costal missing the great majority of it with the only portion intact is the portion articulated with the two neurals. It is not possible to determine, with confidence, the position of the fragments within the carapace.

From the two neurals, one is quite degraded and it is not possible to determine the shape or overall size of it, whilst the other neural is more complete and seems to have a rhombus-like shape, though it is missing a part of the left distal portion of the neural.

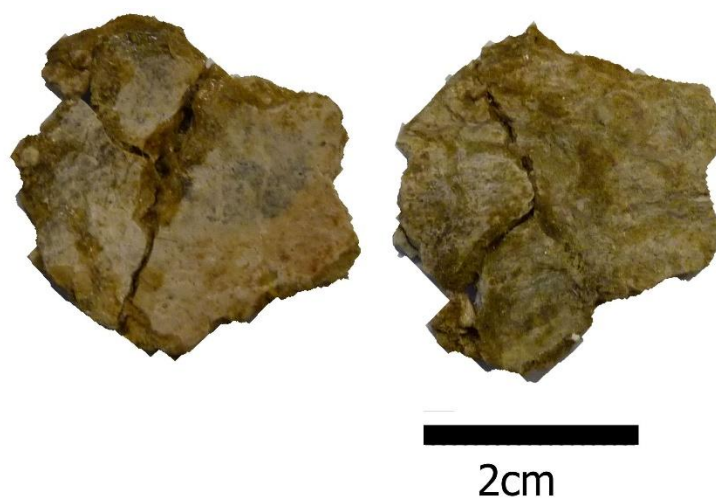


Figure 3.4. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in ventral (left) and dorsal (right) views.

Costal fragment,

Most likely consists of a neural and portion of a costal articulated with it (Figure 3.5). The costal is poorly preserved with the majority of it missing, the neural is better preserved although the edges are somewhat degraded. It is not possible to determine, with confidence, the position of the fragments within the carapace.

There is visible rugosity present in the dorsal side of the specimen. It is not possible to determine the overall size and shape of the costal plate and no other noticeable characteristics.

The neural presents a rhombus-like shape being longer than wide and is around 3cm in size, the dorsal side shows no pitting nor any other noticeable characters.



Figure 3.5. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Costal fragment,

The fragment consists of a vertebral scute articulated with two pleural fragments (Figure 3.6). The pleural fragments are very degraded, with the great majority of them missing, whilst the vertebral scute is better preserved with the posterior section is missing a small portion.

It is not possible to determine the overall size, shape nor position of these pleural fragments.

The vertebral scute displays an ovoid-like shape, being longer than wide. It shows a distinct thickening in the posterior side of the fragment.

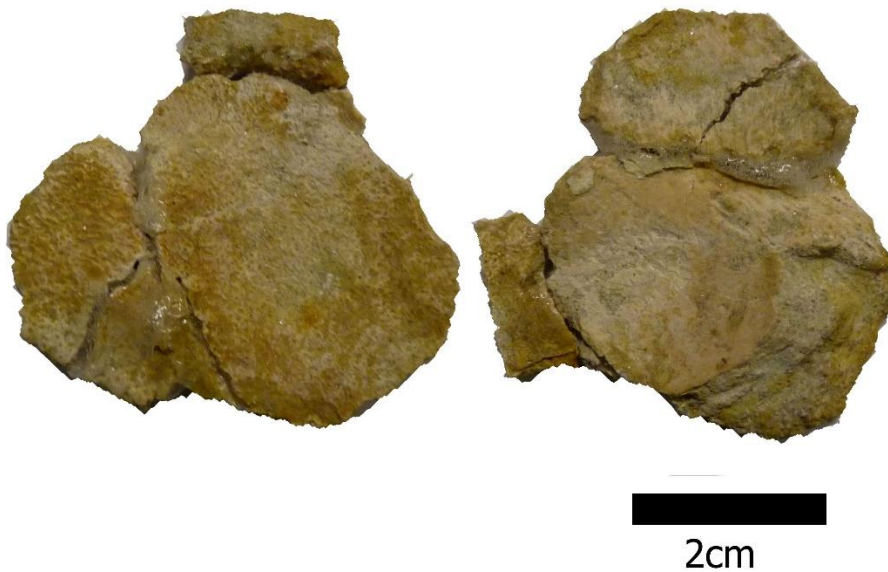


Figure 3.6. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Costal fragment,

The fragment consists of two well-preserved neurals articulated, as well as a third less preserved neural, with a well preserved costal articulated with the neurals (Figure 3.7). The third neural is poorly preserved with the majority of it missing, the section that is articulated with one of the aforementioned neurals is preserved whilst the rest is missing.

The neurals are rhombus-like in shape, being longer than wide, and are somewhat sizeable. They are smooth and do not display any kind of sculpturing, measuring around 3cm in length. The third neural is poorly preserved and, due to the deterioration, it is not possible to determine the overall shape nor size.

The costal presents a distinct curve in the proximal portion, it is connected with the aforementioned neurals on its lateral side that extends proximally and seems to present a small rib on the lateral side that extends distally. The free rib is poorly preserved with a small part extending from the posterolateral side of the costal, the majority is missing, it is not possible to determine the overall size or shape of the free rib. The costal presents no other determining characteristics.

The fragment is likely positioned on the right side of the carapace, with the costal likely consisting of costal 5.



Figure 3.7. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Costal fragment,

The fragment consists of four neurals and three costals, though possibly a fourth one covered in the matrix (Figure 3.8). A portion of the specimen is very fragmentary and is somewhat covered in matrix so its through identification is complicated. The first of the neurals has deteriorated with a portion of it missing, the anterior-most portion of the neural is missing therefore it is not possible to determine, whilst the remaining three neurals are well preserved. The costals are poorly preserved with the majority of the distal portion missing.

The overall shape of the first neural seems to be rhombus in shape, longer than wide, though it is not conclusive. The second neural has a rhombus-like shape, being longer than wide, and it measures around 2,5cm in length, it has a smooth surface and does not present any form of sculpturing. The third neural is smaller in size in comparison to the other present neurals, it presents a rhombus-like shape, being longer than wide, measures around 1cm in length, and presents a smooth surface and it does not present any form of sculpturing. The fourth neural is the longest of the preserved neurals, it has a rhombus-like shape similar to the aforementioned neurals, being longer than wide, it measures around 3cm in length and it presents a smooth surface and does not have any form of sculpturing present.

The surface of the costals is smooth, asides from the marks of the taphonomical process, and there no form of sculpturing present. The posterior portion of the fragment is very fragmentary and covered in matrix, it is not possible to determine, with confidence, the different pieces present that are covered by the matrix.



Figure 3.8. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in ventral (left) and dorsal (right) views.

Peripheral fragment,

Seems to consist of two peripherals, with the anterior-most peripheral being tentatively identified as peripheral II and the other one as peripheral III (Figure 3.9). Peripheral II is preserved in the posterior-most portion, whilst the anterior portion is missing. The posterior section of the peripheral III is not fully preserved, missing a portion in the posterior-most area. The specimen is likely positioned on the left side of the carapace.

Peripheral II presents a rhombus-like shape, being wider than long. It shows marking most likely from the taphonomical process, it is otherwise smooth and shows no other sculpturing.

Peripheral III displays distinct curvature in the distal portion, it is longer than wide. Akin to the rest of the preserved peripherals it displays markings from the taphonomical process on the surface of the peripheral, it is smooth asides from the marking and shows no sculpturing except for the posterior portion which presents markings that resemble striations, which extend slightly anteriorly. The peripheral extends significantly proximally, especially at around the first half of its length, and has what seems to be an emargination in the posterior portion of it.

The peripherals display noticeable emarginations in their proximal side, similar to what *Caretta caretta* presents in the proximal portion of its peripheral II (Valente et al., 2007).



Figure 3.9. *Angolachelys mbaxi* peripheral element (MGUAN-PA 296) in ventral (left) and dorsal (right) views.

Peripheral fragment,

The fragment consists of two peripheral plates, tentatively identified as being the seventh and eighth peripheral plates positioned on the left side of the carapace (Figure 3.10). The peripherals are well preserved, with the fragments being almost complete. The dorsal surface of the peripheral is smooth and shows no sculpturing. The proximal portion of the peripheral VII plate is slightly deteriorated and is missing a rather small part of its anterior portion but is otherwise complete.

The proximal portion of peripheral VIII is deteriorated and, similarly to peripheral VII, it is missing a part of the proximal portion of the peripheral.

Peripheral VII is rectangular-like in shape, being longer than wide. The surface of the peripheral is smooth and there are no signs of sculpturing present. In the ventral side of the peripheral, there is a single slight depression located in the medial area of the peripheral, possibly a result of the taphonomical process. There is a distinct emargination in the medial area of the proximal side of the peripheral.

Peripheral VIII is rectangular-like in shape, being slightly longer than wide. The dorsal surface of the peripheral is smooth and does not display any form of sculpturing. The posterior-proximal portion of the peripheral is inclined and extends slightly dorsally. There is an emargination located in the posterior-medial area on the medial side, similar to the one present in Peripheral VII. In the ventral side of the peripheral, there is a single slight depression located in the medial area of the peripheral, possibly a result of the taphonomical process.

The position of the emarginations in the peripherals resembles the position of the emarginations in the peripherals of *Caretta caretta* (Valente et al., 2007) and *Toxochelys latiremis* Cope, 1873 (Hirayama, 1994).

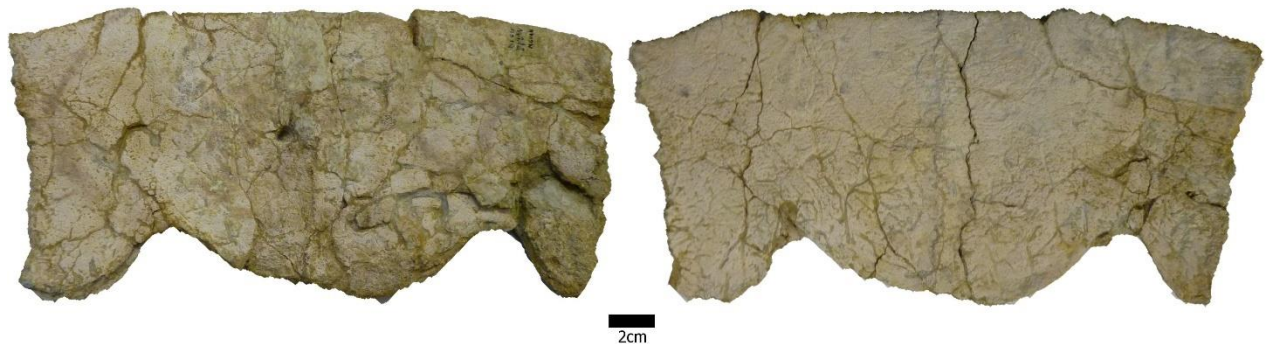


Figure 3.10. *Angolachelys mbaxi* peripheral element (MGUAN-PA 296) in ventral (left) and dorsal (right) views.

Costal fragment,

The fragment consists of a fragment of a costal, most likely one of the most posterior ones such as costal 5 or 6 and positioned in the right side of the carapace (Figure 3.11). The edges of the costal are somewhat degraded, with a portion of the distal and proximal sections missing. Along in the fragment, there are two vertebrae, one costal and one caudal vertebra, that were misplaced during the taphonomical process, and a portion of a rib. The neural arch of the dorsal vertebra is not preserved and the vertebra seems to have suffered some flattening in the taphonomical process. The caudal vertebra is missing a portion of the distal section.

The costal would have a similar outline to the previously described nearly fully preserved costal, it is longer than wide. The surface of the costal is smooth, showing no sculpturing. The costal shows no other special characteristics, asides from the possible free rib possibly articulated in the lateral side of the costal fragment.

Along in the fragment, there are two vertebrae, one costal and one caudal vertebra, that were misplaced during the taphonomical process, and a portion of a rib. The caudal vertebra seems to be one of the anterior halves of the caudal column considering its size although the most posterior (or anterior must determine) portion of it is buried in the fragment. The only one of the prezygapophysis is preserved, it extends slightly dorsally. The cotyle of the centrum is presently displaying an ovoid-like shape. The neural arch seems to be longer than high and has a sub-triangular shape. The anterior surface of the centrum is concave, making the vertebra opistocoelous. The transverse process extends laterally and slightly distally.

The dorsal vertebra does not show any transverse processes nor any prezygapophysis or postzygapophysis. It is not possible to determine the shape or size of the centrum originally due to the flattening. The neural arch is not preserved.

The rib does not show any special characteristics, it is considerably thick, and it exhibits some striations on the distal end.

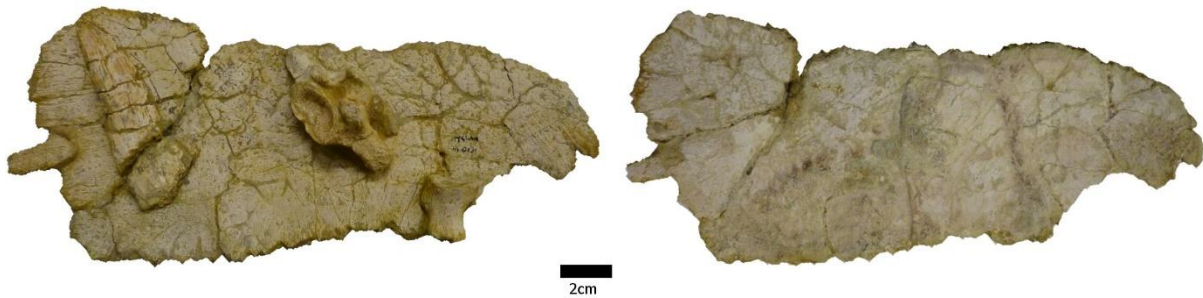


Figure 3.11. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Costal fragment,

The fragment consists of a portion of a costal plate, the extremities of the costal are degraded and a portion seems to be missing, it is not possible to determine the exact shape and size of the costal (Figure 3.12). It is likely positioned on the left side of the carapace.

It has some small pittings on the surface of the costal, these are most likely due to the taphonomical process, it is otherwise smooth. It seems to be considerably thinner on the distal edge of the fragment. The fragment of a costal is most likely a portion that is more distally positioned within the costal considering the thinning edge of the fragment.

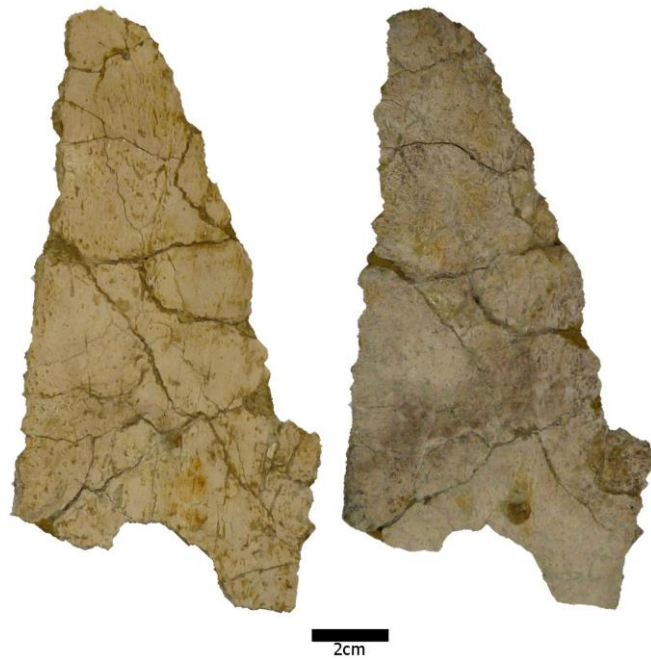


Figure 3.12. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Costal fragment,

The fragment consists of a portion of a costal plate. The extremities of the fragment have deteriorated. The distal portion of the plate is partially preserved, with evidence of the presence of the free rib. The proximal portion of the plate is not preserved. There is no evidence of sculpturing in the dorsal or ventral surface. There is a considerable thickening in the distal end. Presents a rhombus-like shape.

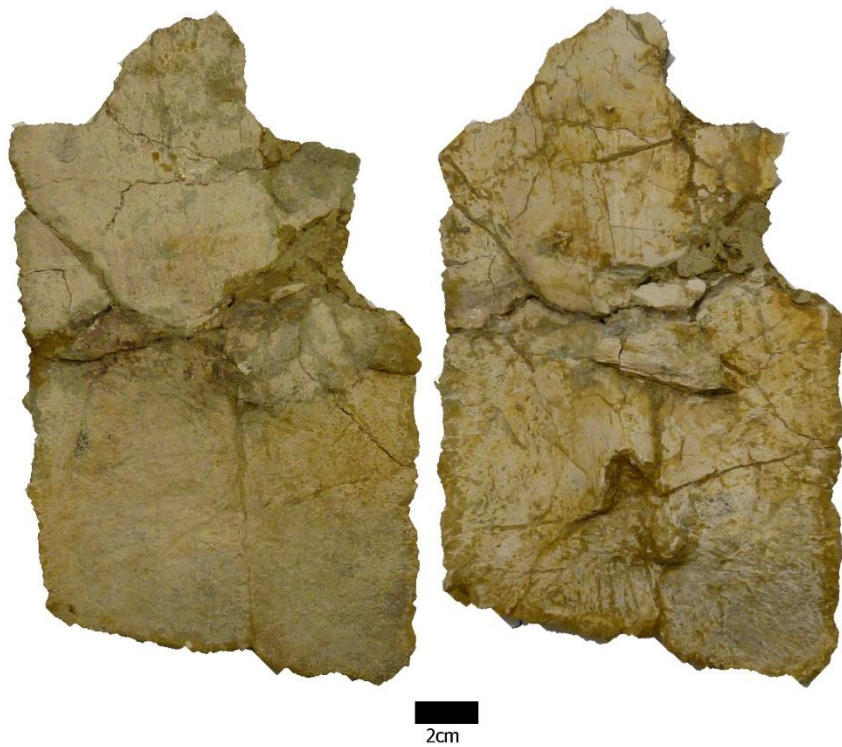


Figure 3.13. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Costal fragment,

The fragment consists of a costal plate, and possibly fragments of a neural or neurals (Figure 3.14). It is well preserved with the majority of it preserved except for the most distal end.

The costal has a distinct curve in the proximal portion, being longer than wide. The most proximal end may have some neural plates articulated with it, but it is covered in matrix. The surface is smooth, some parts are covered by a layer of matrix and do not show any sculpturing.

Most likely consists of costal 2 on the left side of the carapace. It is unknown if the costal would have a free rib since the most distal end is not preserved. The possible neural fragments are covered by matrix, impeding the identification of the fragments.



Figure 3.14. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in ventral (left) and dorsal (right) views.

Costal fragment,

The fragment consists of a costal fragment (Figure 3.15). The distal portion of the costal is degraded and missing, with the majority of the proximal portion preserved. It is likely positioned on the right side of the carapace.

The overall shape of the costal resembles the previously described costal fragment, displaying a more subtle curvature compared to the aforementioned fragment. The proximal portion of the fragment displays two protrusions, connected to each other and displaying a small fontanelle. One of the protrusions extends considerably dorsally whilst the second protrusion extends considerably ventrally. The first protrusion would connect to the neural whilst the other would connect with the vertebra. There are slight markings in the dorsal most likely resulting from the taphonomical process, the surface is otherwise smooth and shows no sculpturing. There are two foramina located in the medial section of the costal, likely resulting from the taphonomical process.

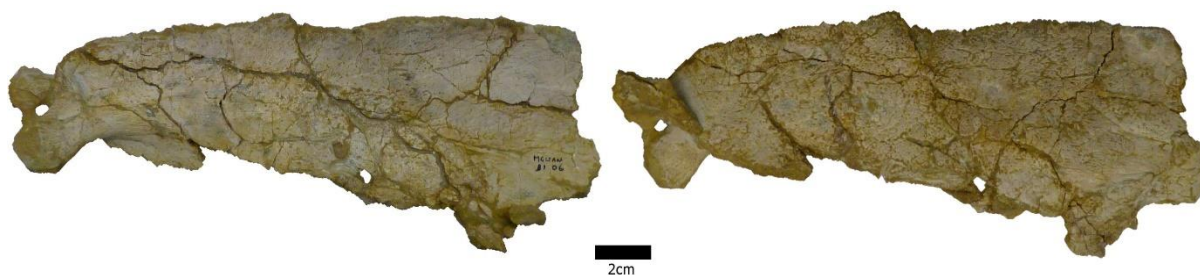


Figure 3.15. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in ventral (left) and dorsal (right) views.

Costal fragment,

The fragment consists of a portion of a costal with a free rib articulated (Figure 3.16). The costal is poorly preserved with most of the proximal portion of it missing, it is not possible to determine the overall shape or size of the costal. It is difficult to identify the number of this costal fragment due to

the damage, though it is likely positioned more posteriorly in the carapace, possibly costal VI or VII. It is likely positioned on the left side of the carapace.

Contrary to the costal plate, the free rib is nearly completely preserved, extending considerably distally and slightly anteriorly, ending with a sharp curve and the tip of the free rib extends considerably more anteriorly. The extremity of the free rib may be articulated with a part of a peripheral considering the difference in texture and inclination between the tip and the remaining of the free rib. The free rib is quite considerable in size.

The costal most probably would have a similar shape to the previously described ones, though the presence of the free ribs leads to the abrupt end of the costal distally, something that differs from the previously described plates.

The presence of this large free rib is a clear indication that the carapace of *Angolachelys* had costoperipheral fontanelles, most likely similar to those present in *Solnhofia parsonsi* (Joyce, 2000).



Figure 3.16. *Angolachelys mbaxi* costal element (MGUAN-PA 296) in ventral (left) and dorsal (right) views.

Neural fragment,

The fragment consists of two neurals (Figure 3.17). The edges of both neurals are degraded, with a portion missing in one of the neurals.

The overall size and shape of the neurals are unknown. The surface of the neurals presents some pitting-like structures, these structures are likely due to the taphonomical process.



Figure 3.17. *Angolachelys mbaxi* neural element (MGUAN-PA 296) in ventral (left) and dorsal (right).

3.2.2 Plastron

Plastron fragment,

The plastron is very fragmented, with a considerable portion of it missing (Figure 3.18). The largest fragment of the plastron is partially encased in a plaster jacket to avoid it from breaking further. The fragments may consist of the entoplastron (possibly part of the epiplastron as well) and the rest might be part of the hyoplastron.

The possible entoplastron has a triangular shape and it displays sculpturing that resembles a form of pitting, it expands considerably posteriorly, gradually getting narrower towards the posterior.

The hyoplastron has deteriorated edges and the posterior portion is quite fractured, the hyoplastron shows the same pitting sculpturing shown by the entoplastron. It presents a sort of half-circle shape.

Only considering the shape of the hyoplastron fragments the plastron could have had a central fontanelle found in aquatic turtles such as *Solnhofia parsonsi* (Joyce, 2000), however due to the fragmented status of the plastron it is not possible to confirm with certainty if the central plastral fontanelle would be present or not nor its overall dimensions.

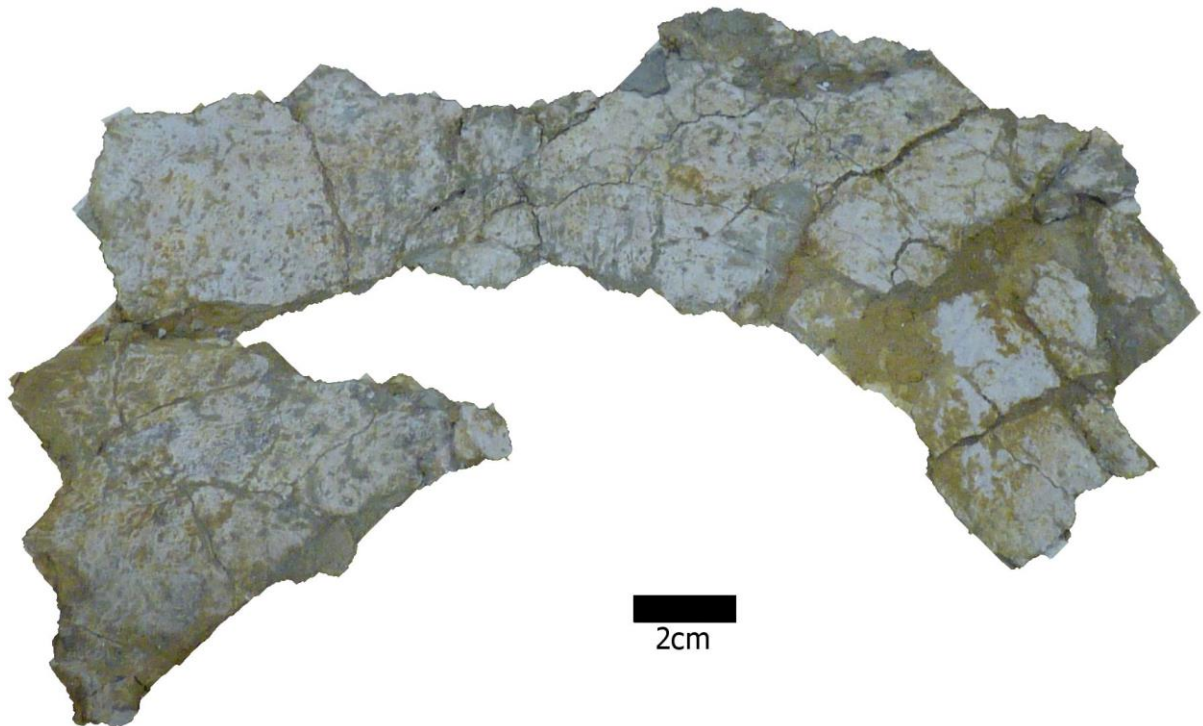


Figure 3.18. *Angolachelys mbaxi* plastral element (MGUAN-PA 296) in ventral view. Only one view is available due to the specimen being encased in a plaster jacket.

Plastron fragments,

The two fragments may consist of pieces of the hyoplastron (Figure 3.19 & 3.20). Their edges have deteriorated, and they are both missing most of their proximal and distal portions. The fragments are likely located on the left side of the plastron.

They both display a sort of fan-like shape, the edges have deteriorated. One of them displays a curvature on one of its edges which could be similar to that of the fontanelles present in some turtle

plastron (check Gaffney (2006) for more examples on these types of plastron). The presence of this curvature may be indicative of these fontanelles.

If these are part of the hyoplastron as it is suspected then the fragments pertain to the distal portions of the hyoplastron, having the fontanelles located in the distal portions of the hyoplastron such as where the fontanelles are located in *Solnhofia parsonsi* (Joyce, 2000).

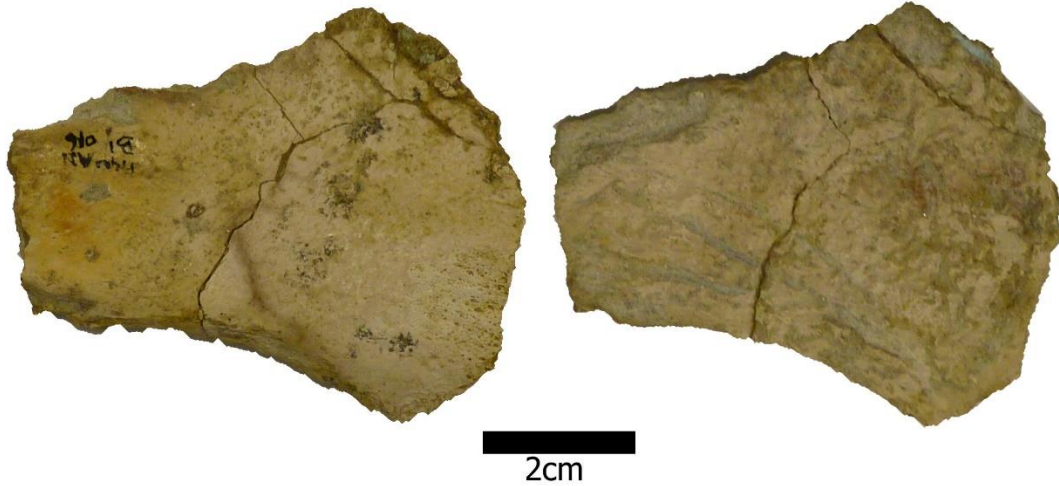


Figure 3.19. *Angolachelys mbaxi* plastral element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

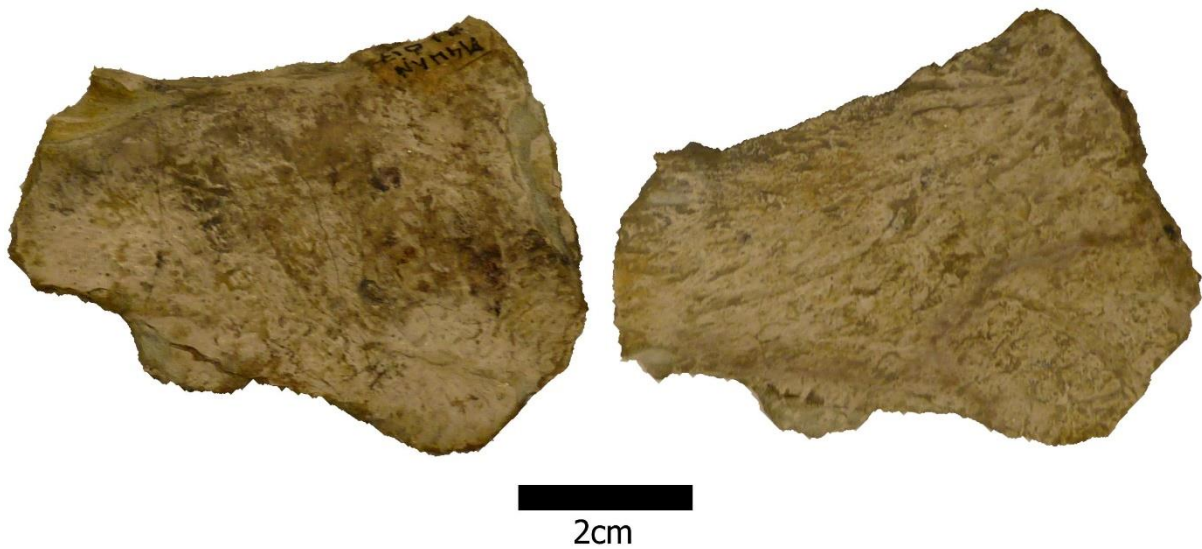


Figure 3.20. *Angolachelys mbaxi* plastral element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

3.2.3 Vertebra

Cervical vertebra

The specimen consists of a cervical vertebra that has a large portion of its degraded (Figure 3.21). It is in a poor state of preservation, with a large portion missing.

The vertebra is most likely procoelous, with the anterior surface of the centrum being convex. The ventral portion of the centrum cotyle is missing, the condyle of the centrum is preserved and has an ovoid-like shape, with the dorsal edge of it displaying a sub-triangular-like shape. The neural arch has

a sub-triangular shape, extends considerably dorsally, and is higher than wide. The neural canal is ovoid in shape and is higher than wide. None of the transverse processes are preserved in the specimen.



Figure 3.21. *Angolachelys mbaxi* vertebral element (MGUAN-PA 296) in posterior (left) and anterior (right) views.

Atlas,

The specimen consists of an atlas vertebra, in a considerably good state of preservation (Figure 3.22).

The anterior side of the centrum of the vertebra is flattened, the anterior condyle is not evident. The neural canal is slightly ovoid in shape and is wider than high. The neural arch has an irregular shape, resembling a semi-circle and it extends considerably dorsally while a portion of it extends considerably posteriorly. A part of the neural arch, located directly above the neural canal, extends anteriorly. The first connected intercentrum is well developed and has a large ventral keel. The posterior cotyle is ovoid in shape and is well developed. There is a considerable-sized intercentrum attached to the right side of the cotyle and it extends significantly anterolaterally. The postzygapophysis is robust, sub-triangular in shape, with the articular surfaces facing mediodorsally.

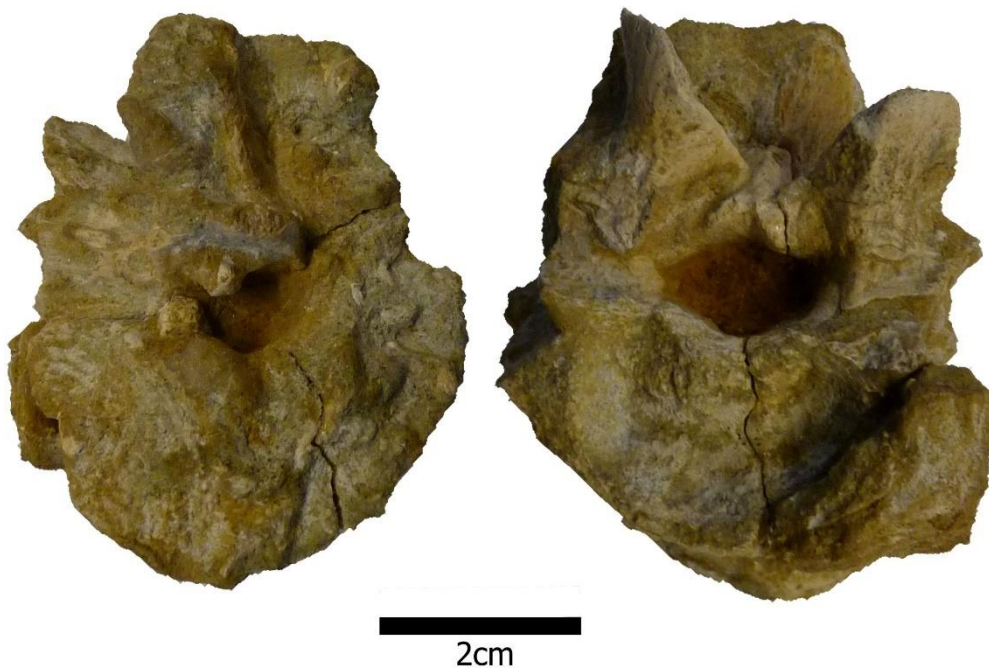


Figure 3.22. *Angolachelys mbaxi* atlas element (MGUAN-PA 296) in posterior (left) and anterior (right) views.

Cervical vertebra,

The specimen consists of a cervical vertebra, it is well preserved with some aspects of the anterior side missing (Figure 3.23). The medial section of the anterior side of the vertebra is mostly covered with matrix, filling the neural canal.

The centrum is procoelous, with the posterior surface of the centrum being concave. The neural canal is ovoid in shape and is higher than wide. The neural arch has a sub-triangular shape, being higher than wide, it extends considerably dorsally and is thin. Only one of the transverse processes is preserved, it extends from the centrum and extends slightly anteriorly. There is a hypapophysis in the ventral side of the centrum, it extends from the posterior edge to the anterior edge. Only one of the postzygapophysis is present, it is robust, sub-rectangular in shape, it extends considerably dorsally, it presents a depression in the medial area of the articular surfaces, which are facing mediodorsally. The prezygapophysis is not preserved.



Figure 3.23. *Angolachelys mbaxi* vertebral element (MGUAN-PA 296) in posterior (left) and anterior (right) views.

Cervical vertebra,

The specimen consists of a cervical vertebra (Figure 3.24), tentatively positioned as cervical vertebra III. The specimen is in a good state of preservation,

The centrum is opistocoelous, with the posterior surface convex. The condyle of the centrum has a small ridge in the medial region of it the extends slightly dorsally. The neural canal is filled with matrix and it has an ovoid shape and it is higher than wide. The neural arch is sub-triangular in shape, being higher than wide. There is a small hypapophysis in the ventral side of the centrum, it extends ventrally and extends from the posterior edge to the anterior edge, in the ventral portion of the anterior side of the vertebra there are two considerable depressions formed with the hypapophysis between them. The postzygapophysis has a sub-rectangular shape, they extend slightly ventrally and slightly posteriorly, the articular surface is facing mediodorsally. Only one of the prezygapophysis is present, it is sub-triangular in shape, it extends slightly anteriorly and considerably dorsally. The articular surface of the prezygapophysis is facing laterodorsally. The overall size of the prezygapophysis is similar to that of the postzygapophysis. There is a considerably large-sized extension connected to the vertebra in the ventral side of it, it may consist of a portion of a cervical rib although it not possible to discern the anatomical aspects of it due to the great majority of it being covered by matrix. It may consist of a ventral keel, however, it is not confirmed.



Figure 3.24. *Angolachelys mbaxi* vertebral element (MGUAN-PA 296) in anterior (left) and posterior (right) views.

Dorsal vertebrae

Dorsal vertebra,

The specimen consists of a dorsal vertebra (Figure 3.25), it is poorly preserved, the neural arch is missing, as well as any transverse processes.

The vertebra seems to have suffered slight flattening, therefore the original size and shape are not possible to determine. The centrum condyle is greatly degraded, with a portion of it missing.



Figure 3.25. *Angolachelys mbaxi* vertebral element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Dorsal vertebra,

The fragment possibly consists of a dorsal vertebra, the fragment is quite degraded. The neural arch is not preserved either are the transverse processes (Figure 3.26).

There is a small extension located in the ventral side of the vertebra, it may be a ventral crest or part of a hypapophysis, however, due to the deterioration of the vertebra it is difficult to confirm. It is difficult to confirm the overall size and shape of the vertebra due to the poor state of preservation of the vertebra. The condyle of the centrum is not preserved.



Figure 3.26. *Angolachelys mbaxi* vertebral element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Caudal vertebrae

Caudal vertebra,

The specimen consists of a caudal vertebra (Figure 3.27). It is in a good state of preservation with only one of the prezygapophysis missing.

The posterior surface of the centrum of the caudal vertebra is convex, making it opistocoelous, the centrum has a small protrusion located in the centre of its concavity that has a circular shape. The neural canal is filled by the matrix, the neural arch is short has it extends slightly dorsally and more considerably laterally, being wider than high, it has a sub-oval shape in the medial area of the vertebra, in the dorsal side of the neural arch there is a protrusion that extends considerably dorsally, displaying a rounded knob-like shape. The transverse processes of the vertebra extend considerably laterally and slightly anteriorly. Only the right prezygapophysis is preserved, it extends considerably anteriorly and ventrally, displaying a curved form in the end portion of it. The articular surface is facing mediodorsally. The postzygapophysis is both preserved, they are short and display a sub-columnar, extending slightly distally and ventrally, their articular surfaces are facing medioventrally. The postzygapophysis is less prominent than the prezygapophysis. There is not any evidence of a hypapophysis in the specimen.



Figure 3.27. *Angolachelys mbaxi* vertebral element (MGUAN-PA 296) in ventral (left) and dorsal (right) views.

Caudal vertebra,

The specimen consists of a caudal vertebra (Figure 3.28). It is in a good state of preservation, with the postzygapophyses missing.

The anterior surface of the centrum is concave, making it opistocoelous. In the condyle of the centrum, there is a small ridge located in the medial section of the ventral side and there are two small extensions on each side of the ridge. The neural canal is filled by the matrix, it has a triangular shape. The neural arch has a triangular shape and extends dorsally, being higher than wide, and it extends anteriorly considerably. The transverse processes of the vertebra extend laterally and slightly posteriorly, they slightly expand in the distal portion. The prezygapophysis are sub-triangular in cross-section, the anterior portion of the prezygapophysis is missing, therefore it is not possible to determine their overall length. The articular surface is facing mediodorsally. The postzygapophysis are poorly preserved, with the majority of it missing, it is not possible to determine the size, shape, or articular surface. A hypapophysis is not evident in the specimen.



Figure 3.28. *Angolachelys mbaxi* vertebral element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Caudal vertebra,

The specimen consists of a well-preserved caudal vertebra (Figure 3.29). The postzygapophysis is not preserved in the specimen neither is the neural arch. The dorsal section of the vertebra is slightly degraded.

The centrum displays a concavity on the anterior surface making it opistocoelous, there is a slight ridge in the centre of the concavity of the centrum that extends slightly laterally, the centrum has an

oblong-like shape, the posterior surface of the centrum displays a small ridge in the medial region which extends slightly dorsally. The transverse processes extend considerably laterally and slightly proximally, they have a small constriction proximally. The prezygapophysis extend considerably anteriorly and slightly ventrally, they do not present such a noticeable curve in the anterior end of the prezygapophysis has the ones from vertebra n°3. Their articular surfaces are facing mediodorsally. The neural arch is not evident in the specimen nor is a hypapophysis.



Figure 3.29. *Angolachelys mbaxi* vertebral (MGUAN-PA 296) in ventral (left) and dorsal (right) views.

Caudal vertebra,

The specimen consists of a caudal vertebra (Figure 3.30). The specimen is in a good state of preservation.

The centrum of this caudal vertebra displays a convexity on the posterior surface, making it opisthocoelous. The transverse processes extend considerably posteriorly and laterally. The neural canal is not well evident in the specimen. The neural arch is reduced, and it extends considerably anteriorly. The prezygapophysis are sub-rectangular in shape, they extend considerably anteriorly and slightly ventrally. Their articular surfaces are facing mediodorsally. The postzygapophysis are very reduced in comparison to the prezygapophysis, they extend slightly posteriorly, they are sub-triangular in shape. The articular surface of the postzygapophysis are facing medioventrally. There is not any evidence of a hypapophysis in the specimen.



Figure 3.30. *Angolachelys mbaxi* vertebral element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Vertebra fragment

The specimen consists of a portion of a vertebra (Figure 3.31). The specimen is in a somewhat poor state of preservation, with the centrum and the majority of the vertebra missing.

It seems to be a part of a vertebra, with the one on the left being a part of the zygapophyses while the upper part is a part of a rib. The specimen is poorly preserved, with the seeming majority of the specimen missing. The fragment does not provide any considerable information about the specimen. The specimen was slightly cleaned using an ultrasonic bath using a “Bandelin Sonorex” equipment from the Departamento de Ciências da Terra of the Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa.



Figure 3.31. *Angolachelys mbaxi* vertebral element (MGUAN-PA 296). Orientation is unknown.

A figure depicting the vertebrae of the specimen together can be seen below (Figure 3.32).



Figure 3.32. *Angolachelys mbaxi* vertebral elements (MGUAN-PA 296).

3.2.4 Forelimb

Humerus,

The specimen consists, most likely, of a left humerus (Figure 3.33).

The specimen is quite well preserved with only the collum humeri region, along with the tuberculum majus and the caput humeri, separated from the rest of the humerus, though they are preserved.

The humerus displays an hourglass-shape, it displays some diagenetic damage on the ventral side of the shaft in the distal portion of the humerus. The tuberositas deltoidea is partially preserved in the form of a distinct curve in the proximal-most area of the humerus and is missing the proximal portion of it.

The caput humeri is considerably large in size, it is strongly convex and pitted and presents a circular shape. The anatomical neck is small in size in comparison with the caput humeri and it is not possible to determine the total length of it.

The tuberculum majus is quite larger in size than the caput humeri, on the dorsal side, it presents striations and considerably less pitting than the caput humeri. It extends and thickens proximally, the medial section of it flattens and has a slight concavity in ventral view whilst it is slightly convex in dorsal view. It further constricts distally.

The shaft is a great deal thicker in the proximal-most portion, in the medial portion it constricts considerably, decreasing its width and thickness. In the distal portion of the humerus, the humeral shaft increases its width considerably whilst decreasing its thickness.

The distal portion of the humerus is slightly deteriorated and fractured but still in a good condition of preservation. The condyles are quite noticeable and well preserved. The epicondylus lateralis extends slightly laterally and presents an ovoid-like shape. The epicondylus medialis extends slightly laterally, it presents a somewhat ovoid shape and its preservation is worse than the preservation of the epicondylus lateralis. The capitulum humeri is preserved, located medially to the epicondylus lateralis, it is considerable in size and it presents an ovoid shape, it extends distally, and it presents a small ridge in the distal side of it. Proximally to the capitulum humeri, there is a small fossa radialis that extends slightly medially. There is a small elevation medial to the epicondylus medialis that is poorly preserved. The elevation could be the trochlea humeri which would make the concavity between this and the capitulum humeri the sulcus capitulo-trochlearis, for the rotation surface of the humerus. Directly proximal to the trochlea humeri is the coronoid fossa. The condylus radialis and the condylus ulnaris are well preserved and well evident in the specimen. The condylus ulnaris is considerably larger than the condylus radialis, presents a somewhat ovoid shape, extending distally.

The dorsal side of the distal portion of the humerus is flat and presents slight pitting.

The tuberositas deltoidea does not seem to be well developed, contrary to what it is seen in, for example, on the leatherback turtle *Dermochelys coriacea* Vandelli, 1761, and it would be positioned quite proximally in the humeral shaft, relatively close to the tuberculum majus, unlike the tuberositas deltoidea in the Chelonioidea that is positioned relatively far distally on the humeral shaft, which is considered a synapomorphy of the total-group Chelonioidea (Gaffney & Meylan, 1988; Hirayama, 1994).

The shape of the humerus is similar to the “humerus morphotype 1” from Evers et al. (2019) which is similar to the humeri of protostegids (e.g. *Chelosphargis advena* Hirayama, 1994) and of some cheloniids (e.g. *Eoachelone brabantica* Hirayama 1994), due to the humerus shaft being moderately flattened with the distal end of the humerus being broadened, the caput humeri being rounded and positioned on the proximal surface of the humerus, being separated from the medial process by a shallow notch and because an ectepicondylar foramen is not evident (Evers et al., 2019). It is however significantly different in the distal portion of the humerus, especially in the noticeable condyles which differ from the “humerus morphotype 1” from Evers et al. (2019) which lack these well noticeable condyles. The humerus of *Chelonia mydas* somewhat resembles proximally that of *Angolachelys* as well as the overall shape of the humerus, namely in the size and positioning of the tuberculum majus, caput humeri, and the tuberositas deltoidea, however distally it differs from *Angolachelys* due to the lack of distinctly visible condylus radialis and condylus ulnaris and the due to the larger sized epicondylus medialis compared to that of *Angolachelys* (Koolstra et al., 2019). The humerus of *Caretta caretta* is considerably different from the humerus of *Angolachelys*, proximally the tuberculum majus, caput humeri, and the tuberositas deltoidea are smaller than that of *Angolachelys*, whilst distally it lacks the visible condylus radialis and condylus ulnaris present in *Angolachelys* (Koolstra et al., 2019). Compared to small-sized tortoises (e.g. *Testudo hermanni* Gmelin, 1789) the humerus is straighter in *Angolachelys* and does not display the sharp, dorsally oriented curve present in the humerus of small tortoises (Pérez-García et al., 2017).

The humerus of *Angolachelys* resembles the humerus that was designated as “Toxocheilyd type” in Hirayama (1994), except for the absence of noticeable condylus in the “Toxocheilyd type” humerus. In comparison with the humerus of *Apalone spinifera* (Valdes et al., 2017), the proximal portion of the humerus greatly resembles that of *Angolachelys*, in the relative size of the caput humeri and of the tuberculum majus, the tuberositas deltoidea are also similar to each other in the size and location of it (right below the caput humeri). The condylus radialis and the condylus ulnaris are both considerably evident in the humerus of *Apalone spinifera* and they are similar to those preserved in the humerus of *Angolachelys*. The shaft of *Apalone spinifera* however, presents considerable differences with the shaft of the humerus of *Angolachelys*, namely in the curvature, in which it curves considerably laterally and dorsally whilst in the case of *Angolachelys* the humeral shaft is comparatively

significantly straighter. If the similarity of the two humeri would involve a similar adaptation towards movement, namely in consideration of the posterior portion of the humerus with the well-defined condylus radialis and condylus ulnaris, then it would be possible that the locomotion method of *Angolachelys* would be of a similar type as that of *Apalone spinifera*. The *Apalone* present a type of swimming movement termed “rowing” as opposed to the typical swimming movement displayed by marine turtles termed as “flapping” (Rivera et al., 2013). It could be that *Angolachelys* would present a type of swimming more akin to that of *Apalone* than to that of Chelonioidea.

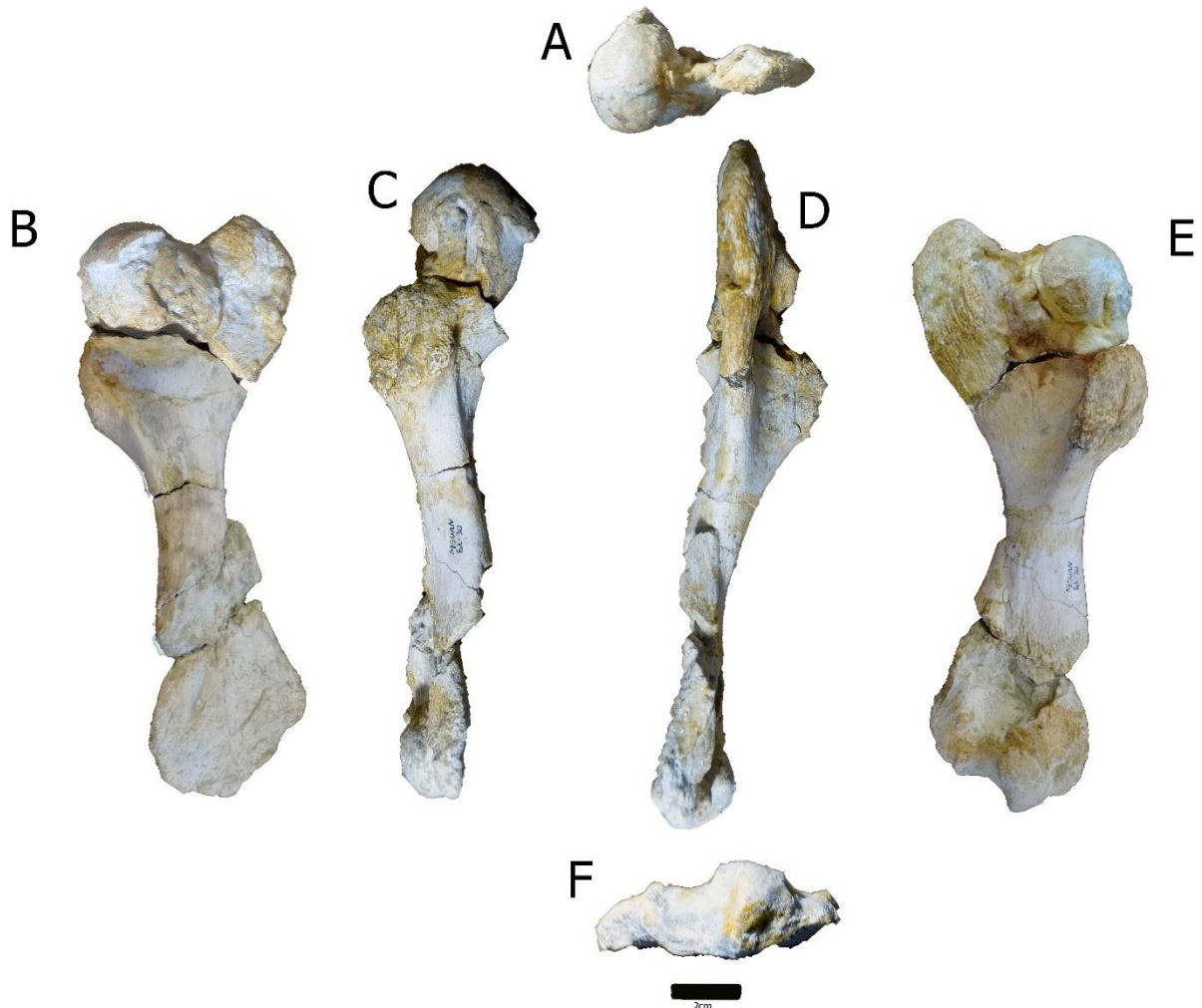


Figure 3.33. *Angolachelys mbaxi* left humerus (MGUAN-PA 296) in proximal (A), dorsal (B) lateral (C & D), ventral (E), and distal (F) views.

Fibula fragment,

The specimen consists of a fragmented, distal portion of a fibula. (Figure 3.34). The specimen is tentatively positioned in the left hindlimb. The specimen is broken and the majority of the proximal end of the specimen is missing.

The distal articulation surface of the fibula is preserved, forming a distinct curve in the distal end. It is not possible to confirm the overall length of the fibula.

The fibula somewhat resembles the fibula of *Solnhofia parsonsi*, though the curve of the distal end of the fibula of *Solnhofia parsonsi* is not as pronounced as the specimens.



Figure 3.34. *Angolachelys mbaxi* fibula element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Fragment of a limb bone,

The specimen may consist of the distal end of a metacarpal or a metatarsal (Figure 3.35). The distal articulation surface is mostly preserved, with one of the condyles preserved. The specimen is broken, with the majority of the proximal portion of the specimen is missing.

It is not possible to confirm how much of the proximal portion is missing, nor the overall size of the specimen. There is a constriction in the proximal section of the specimen and an expansion in the distal portion.



Figure 3.35. *Angolachelys mbaxi* limb bone element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

3.2.5 Hindlimb

Femur,

The specimen consists of a partial right femur, placement based on the position of the medial epicondyle on the specimen (Figure 3.36).

The entire proximal portion of the femur is not preserved, the shaft is fractured in its medial section leaving the proximal portion of the femur absent. The remaining portion is in a good state of preservation.

The femoral shaft is considerably constricted proximally, increasing in width and thickness in the distal portion. The dorsal side of the femoral shaft is slightly fragmented. The femoral shaft is round in cross-section and it is slightly arched dorsally.

The distal articular surfaces are well developed and preserved, the condylus medialis is well developed, extending slightly ventrally and proximally. The medial portion of the condylus medialis has a small concavity that covers the majority of the medial section of the condyle. The condylus lateralis is considerably smaller than the condylus medialis, it extends slightly ventrally and presents a rectangular-like shape. The intercondyle fossa, which extends between the two condyles, extends slightly proximally, reaching a similar length to that of the condylus medialis. There is a small extension in the proximal-most portion of the condylus lateralis that connects it to the condylus medialis, which likely consists of the rotation surface of the femur.

The femur resembles that of *Euclastes hutchisoni* Lynch & Parham, 2003, with the shape and size of the well noticeable condyles and the curvature of the femoral shaft.

In comparison to some large tortoises (i.e. *Titanochelon* sp. (Pérez-García et al., 2017), *Stigmochelys pardalis* (Pérez-García et al., 2017), *Centrochelys sulcata* (Pérez-García et al., 2017), and *Titanochelon gymnesica* (Pérez-García et al., 2017)), both of the condylus are not as large in *Angolachelys* as it is in these tortoises, nor does it present the clear great thickening in the distal-most portion in comparison to the femoral shaft.

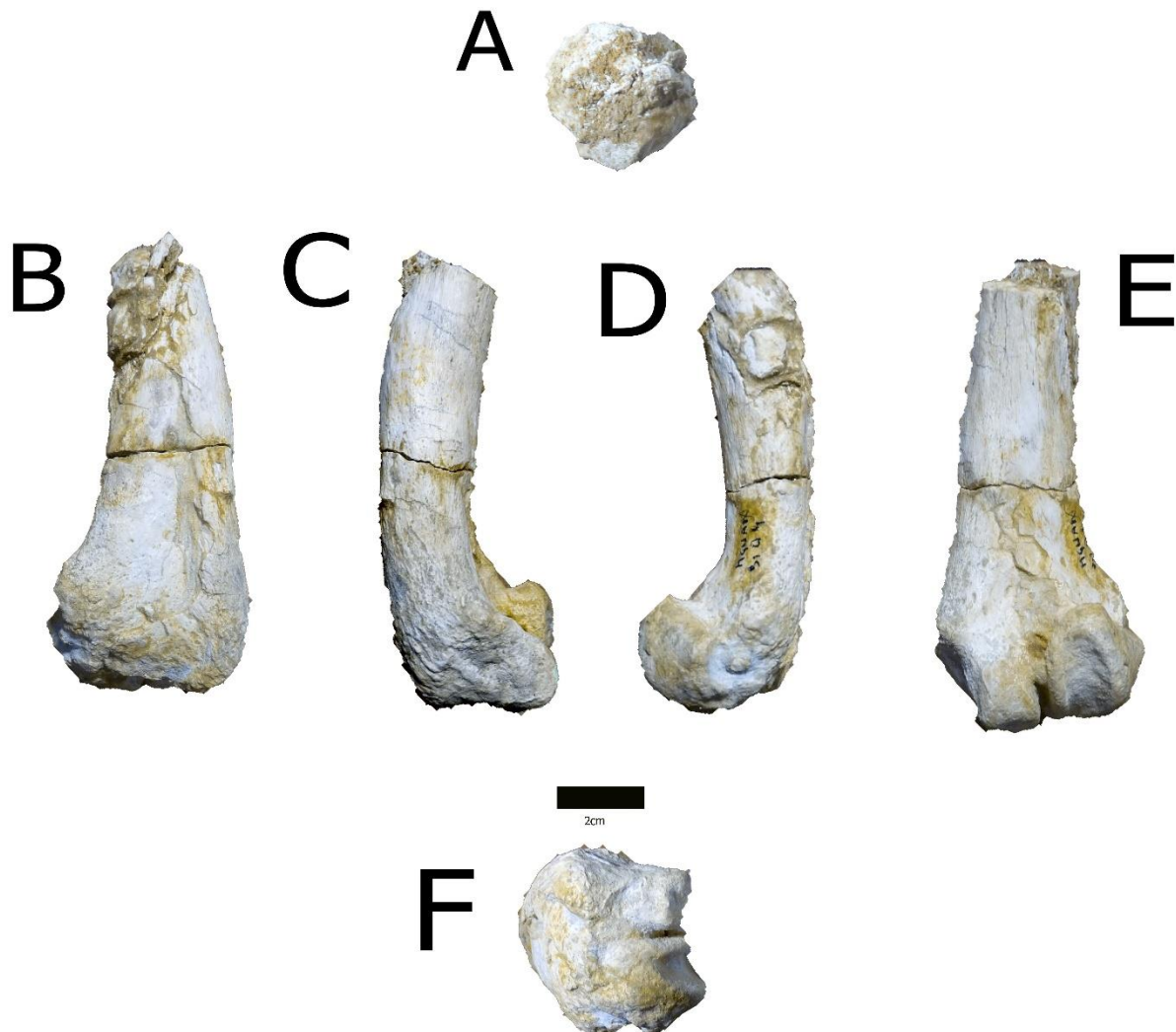


Figure 3.36. *Angolachelys mbaxi* femoral element (MGUAN-PA 296) in proximal (A), dorsal (B), lateral (C & D), ventral (E), and distal (F) views.

3.2.6 Coracoid

Coracoid,

The specimen consists of a left coracoid, articulated with the most proximal portion of the scapula (Figure 3.37). The majority of the scapula and the acromion are not preserved in the specimen. The coracoid is well preserved.

The middle portion of the shaft of the coracoid displays a constriction, giving it a cylindrical shape. The distal portion of the coracoid is large and extends in a fan-like shape, it is quite thin in the distal extremity and it is very wide. The articulation of the coracoid with the scapula is preserved, with a clear glenoid fossa displayed in the proximal end.

The general shape of the coracoid resembles that of *Toxochelys latiremis*, although this specimen displays a greater constriction in the shaft and the posterior portion of the coracoid is wider and displays a more “fan-like” appearance than that of *Toxochelys latiremis* (Parham & Pyenson, 2010). The coracoid slightly resembles that of *Solnhofia parsonsi* though this specimen displays a greater constriction in the shaft and the distal portion of the coracoid is wider than the coracoid of *Solnhofia parsonsi* (Joyce, 2000). The shape of the coracoid resembles the coracoid from *Kinixys* Bell, 1827, which also has a “fan-like shape” and is constricted in the centre and is distally very wide (Depecker et al. 2006). It also resembles the coracoid of the giant land tortoise *Hesperotestudo* (Morgan et al., 2008) in terms of the overall shape.

The coracoid of the Cheloniidae tends to be relatively larger than other turtles and shows large attachment areas for the musculus biceps complex (i.e. musculus biceps superficialis inferior, musculus biceps profundus, musculus biceps superficialis) and musculus coracobrachialis brevis (Walker, 1973; Depecker et al., 2006; Krahl et al., 2019) which matches the specimens, although this shape can also be seen in some cases of land turtles (e.g. *Hesperotestudo* (Morgan et al., 2008).

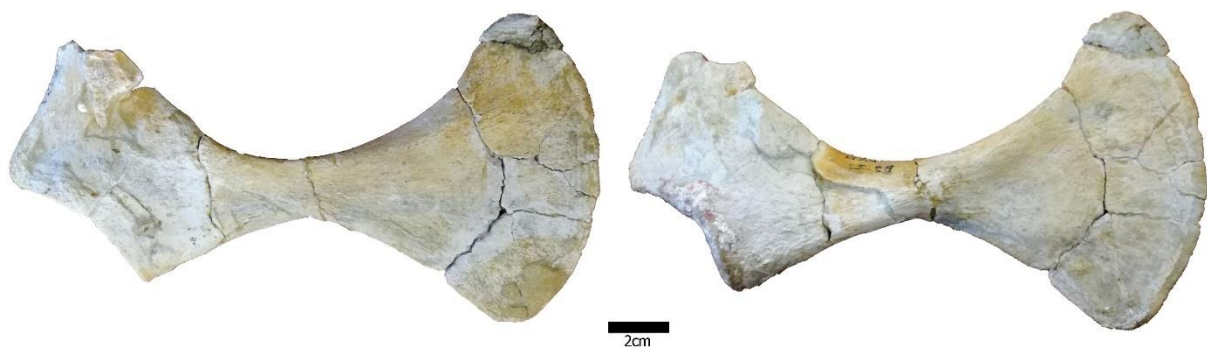


Figure 3.37. *Angolachelys mbaxi* coracoid (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

3.2.7 Pelvis

Pelvic fragment,

The specimen consists of a fragment of the pubis articulated with a fragment of the ischium (Figure 3.38). The anterior portion of the pubis is absent as well as a large portion of the distal portion and the lateral portion of the pubis.

The ventral side of the pubis displays a small groove in the anteromedial region, the dorsal side of the pubis is flattened. The pubis extends slightly laterally and is articulated posteriorly with the ischium. Laterally to the pubis and ischium is a clearly defined thyroid fenestra. The ischium extends considerably laterally on the right. The left side equivalent to the extension of the ischium is missing

in the specimen. On the dorsal side of the ischium, there is a small groove on the left side, which could consist of damage to the specimen or a small portion of the left thyroid fenestra.

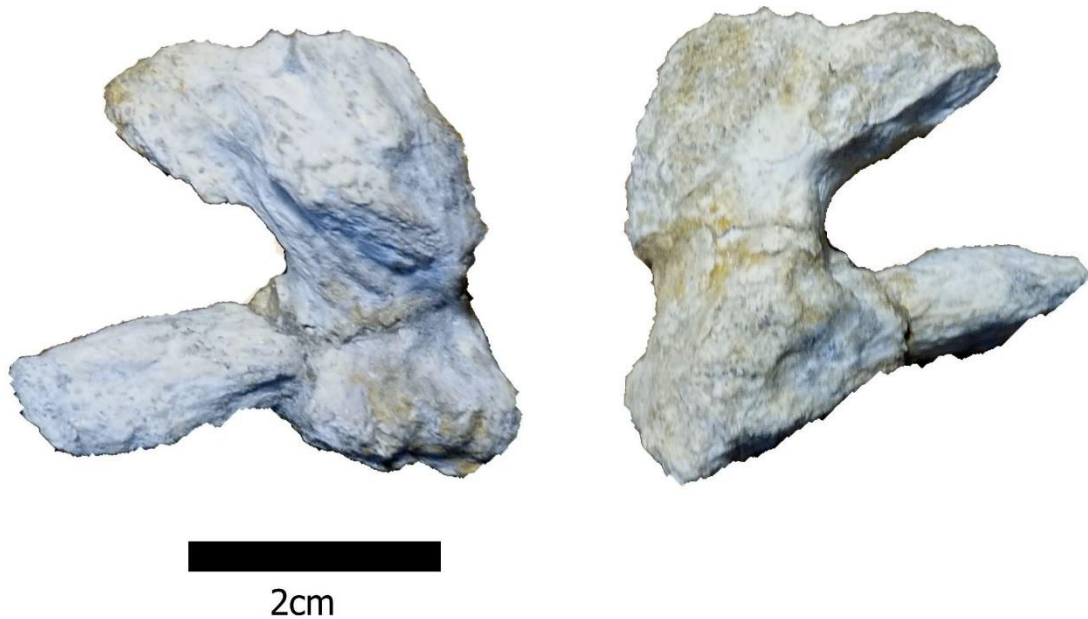


Figure 3.38. *Angolachelys mbaxi* pelvic element (MGUAN-PA 296) in dorsal (left) and ventral (right) views.

Pelvic fragment,

The specimen may consist of a pelvis fragment, with the acetabulum (the articulation surface), the puboischiadic fenestra (next to the acetabulum and pubis), the pubis (the larger sized piece), the ilium (smaller piece “detached” from the acetabulum), and the ischium (directly connected to the acetabulum, beneath it), it is in a decent state of preservation though the majority of it is missing (Figure 3.39).

The acetabulum has a circular-like shape, it is relatively deep. The diameter is around 15mm. The intersection between the pubis, the ilium, and the ischium forms the acetabulum. The pubis is broken in the proximal portion, it is unknown how much is missing. It extends anteroventrally and posteroventrally though the majority is missing. The ilium extends posterodorsally, while proximally it contributes to the acetabulum. It narrows and forms a distinct curvature in its posterodorsal extension, forming a nearly 90° angle in the edge. The anterior portion of the ilium is broken, with a part missing.

The size of the acetabulum would indicate that the caput femoris of the femur of this species would have been significantly small, taking into consideration the overall dimensions of the femur (Figure 3.36). Regrettably, the proximal portion of the femur was not preserved in this specimen, therefore it is not possible to confirm this (Figure 3.36).

The acetabulum of the specimen does not display the same “kidney-shaped” of *Plesiochelys bigleri*, a thalassochelyd from the Late Jurassic of Switzerland. (Püntener et al., 2017), displaying instead a more ovoid-like shape.

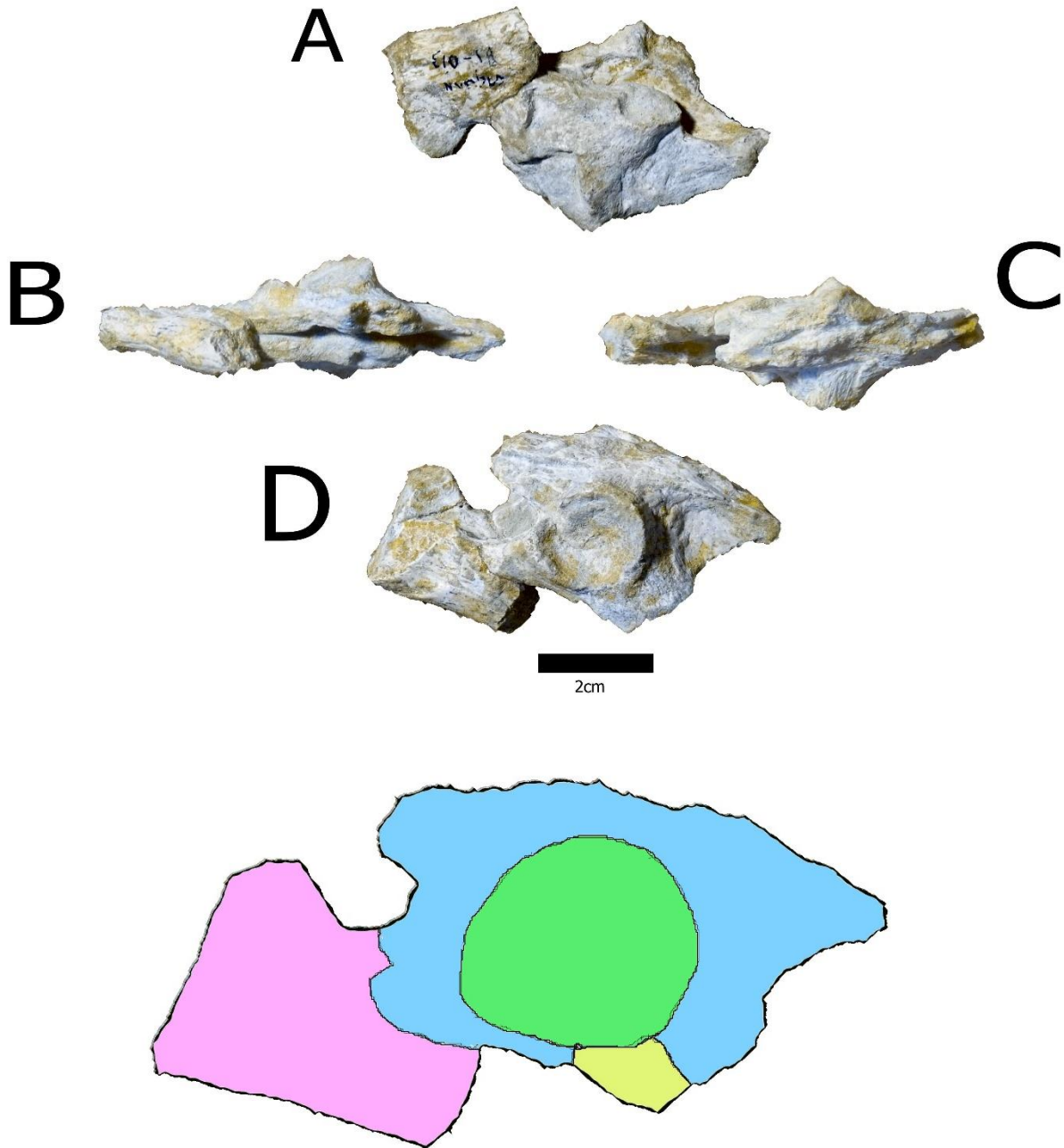


Figure 3.39. *Angolachelys mbaxi* pelvic element (MGUAN-PA 296) in dorsal (A), lateral (B & C), and ventral (D) views. The second image is a rough diagram representing the different parts of the bones preserved in the specimen. In pink is the ilium, in blue is the pubis, in green is the acetabulum and in yellow is the ischium. The diagram is not up to scale.

A reconstruction of the *Angolachelys mbaxi* postcranial skeleton is presented below (Figure 3.40). It has been reconstructed based on the anatomy of *Leyvachelys cipadi*, *Solnhofia parsonsi*, and *Toxochelys latiremis*.

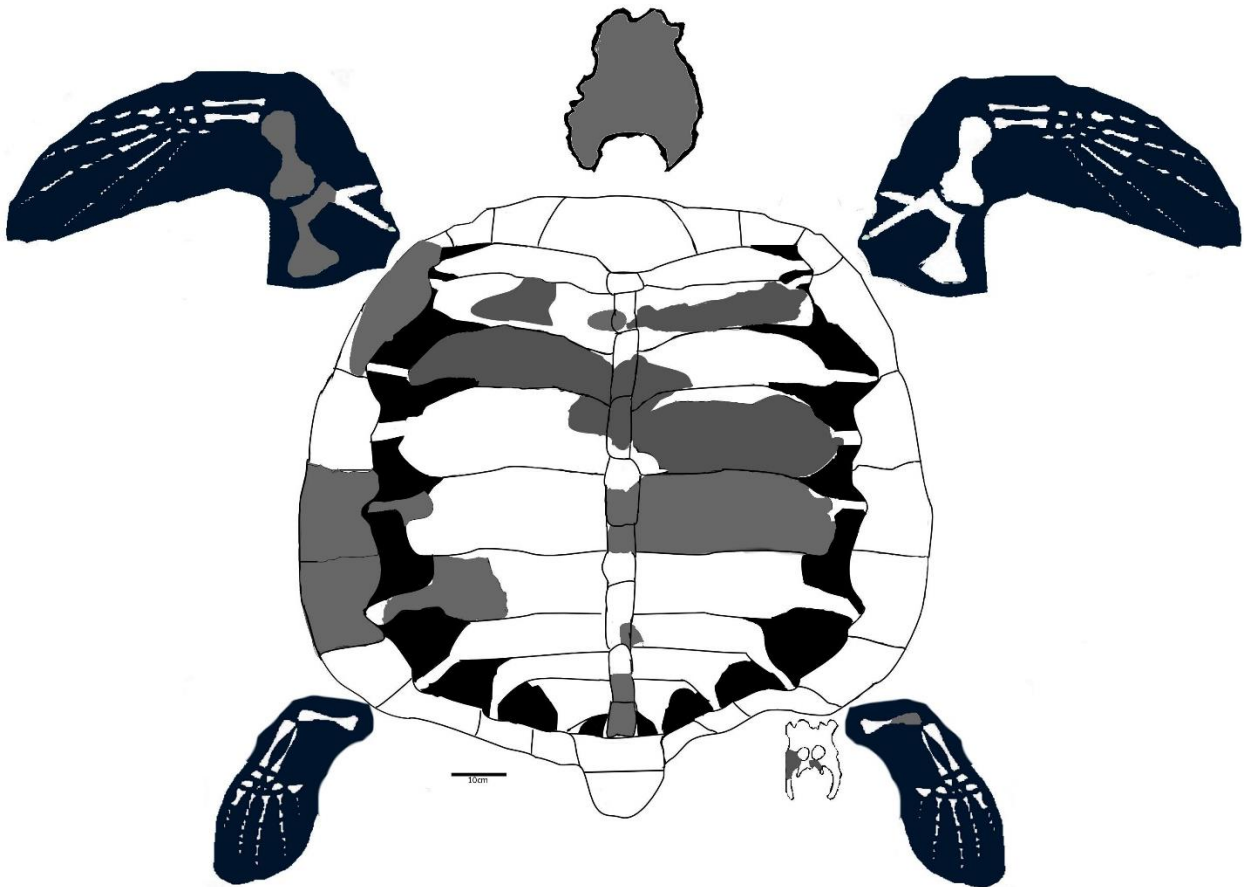


Figure 3.40. Postcranial reconstruction of *Angolachelys mbaxi*. The greyed-out sections are equivalent to the parts that are preserved in the specimen, white corresponds to the bones. Black corresponds to the outline and the shell fontanelles and dark blue correspond to the limbs.

4. DISCUSSION

4.1 The phylogenetic position of Angolachelonia

4.1.1 TNT results

For the TNT analysis, the first analysis was made utilizing a matrix based on the matrix of Evers & Benson (2019), with the difference being the coding of *Angolachelys mbaxi* into the matrix.

The parsimony analysis utilizing “New technology” of the unordered dataset in TNT resulted in a total of 4 most parsimonious trees (MPTs) being produced, each with the tree length (TL) of 1550 steps long. The following TBR branch swapping resulted in 4 MPTs overall. The consistency index (CI) is 0.268, whilst the retention index (RI) is 0.649. The zero-branch lengths were collapsed during the construction of the strict consensus tree (Figure 4.1).

The results from the phylogenetic analysis are similar to those from Evers & Benson (2019), which is to be expected since the matrix used in this study was almost the same as the one, they used. The monophyly of Angolachelonia, which groups the Sandownidae and the Thalassochelydia, is confirmed in this tree and they were positioned as the sister taxa of the Testudines. The members found in the Sandownidae include *Angolachelys mbaxi*, *Sandownia harrisi*, *Leyvachelys cipadi*, and

Brachyopsemis tingitana. The members found within the Thalassochelydia are *Plesiochelys etalloni* Pictet & Humbert, 1857, *Plesiochelys planiceps* Owen, 1842, *Jurassichelon oleronensis* Pérez-García, 2015, *Portlandemys mcdowellii* Gaffney, 1975b and *Solnhofia parsonsi* Gaffney, 1975a.

Angolachelys mbaxi was found to be closely related to *Sandownia harrisi* than with the rest of the Sandownidae. Contrary to the expectations, *Solnhofia parsonsi* was not found to be within the Sandownidae in this tree but instead was found to be at the base of the Thalassochelydia, as was previously positioned in previous works (e.g. Evers & Benson, 2019). In this tree, the Angolachelonia clade is supported by eight synapomorphies, all of which consist of cranial and mandibular characters. The branch support value for Angolachelonia is moderate-high (Bremer support = 3), with the branch support for Sandownidae being high (Bremer support = 4) but the branch support for Thalassochelydia including *Solnhofia parsonsi* is low (Bremer support = 1), however, the branch support for Thalassochelydia excluding *Solnhofia parsonsi* is moderate-high (Bremer support = 3). The Sandownidae is supported by five synapomorphies, all of which consist of cranial characters. The Thalassochelydia share eight synapomorphies, of which four are cranial and mandibular, whilst the remaining four are postcranial.

Other groups are well defined in this tree such as the Sinemydidae/Macrobaenidae clade which was found to be monophyletic and close to the Angolachelonia, and the Protostegidae Cope, 1872 that was found to be monophyletic and within the crown-group Cheloniodea.

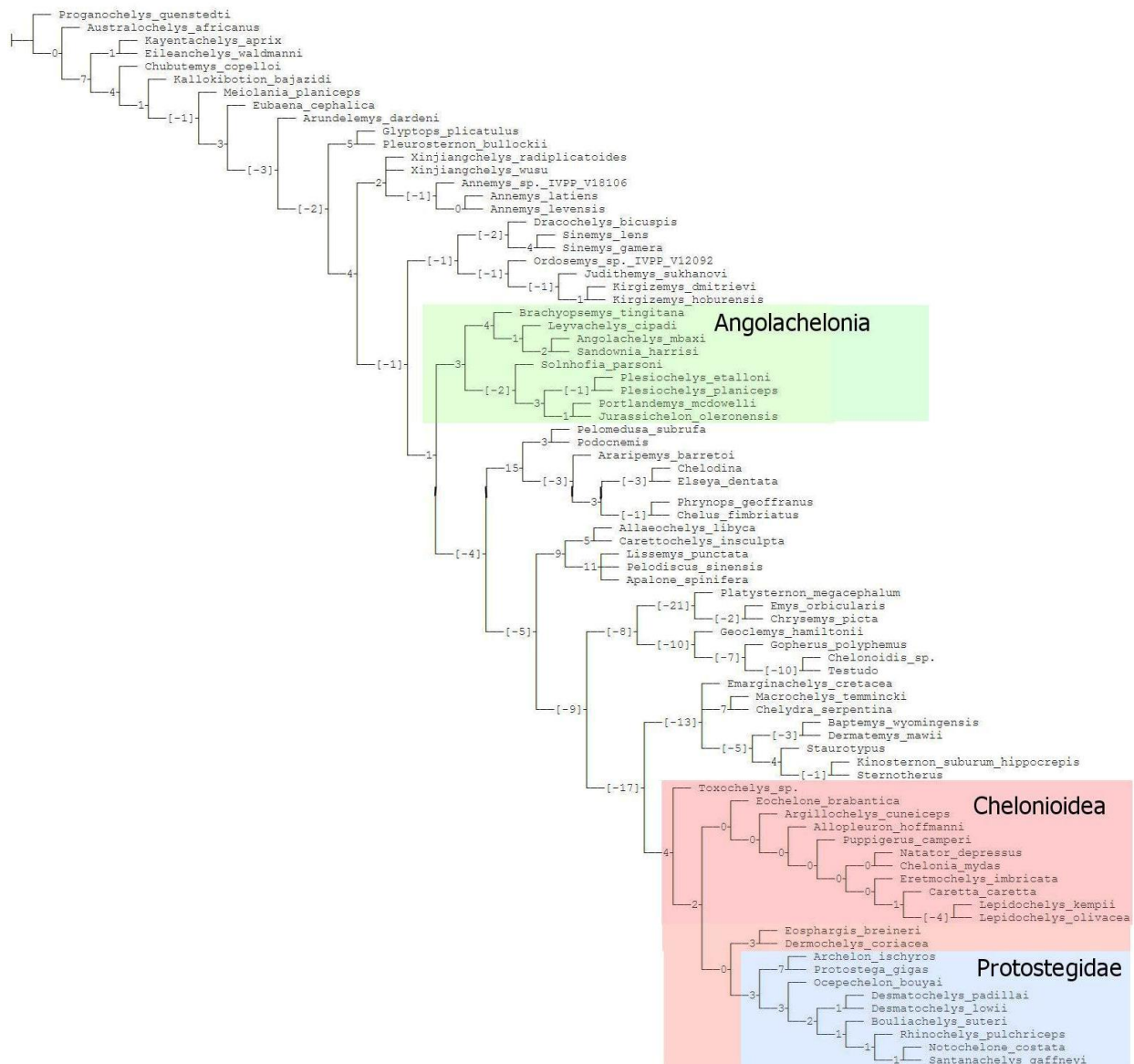


Figure 4.1. Parsimony consensus tree resulted from the phylogenetic analysis. Bremer support presented in the tree. Consensus tree of 4 MPTs. Based on the matrix of Evers & Benson (2019).

The following analysis was made utilizing a matrix based on the matrix of Evers et al. (2019), with the biggest difference being the coding of *Angolachelys mbaxi*, namely the postcranial characters.

The parsimony analysis utilizing “New technology” of the unordered dataset in TNT resulted in a total of 234 MPTs being produced, each with the TL of 1752 steps long. The following TBR branch swapping resulted in >10000 MPTs in total.

The results from the phylogenetic analysis are quite different from those from Evers et al. (2019), which is unexpected since the matrix used in this study was almost the same as the one they used, except for the postcranial characters codification of *Angolachelys*. The monophyly of Angolachelonia, which groups the Sandownidae and the Thalassochelydia, is confirmed in this tree and they were positioned as the sister taxa of the total-group Chelonioidae. The members found in the Sandownidae include *Angolachelys mbaxi*, *Sandownia harrisi*, *Leyvachelys cipadi*, and *Brachyopsemis tingitana*. The members found within the Thalassochelydia are *Plesiochelys etalloni* Pictet & Humbert, 1857, *Plesiochelys planiceps* Owen, 1842, *Jurassichelon oleronensis* Pérez-García, 2015, *Portlandemys mcdowelli* Gaffney, 1975b and *Solnhofia parsonsi* Gaffney, 1975a. A large portion of the tree resulted in a polytomy, contrary to what resulted in Evers et al., (2019), although the monophyly of the

Sinemydidae/Macrobaenidae is not well confirmed in this tree due to the polytomy, therefore the phylogenetic relationship between the members is not ascertained. The Protostegidae are shown to be monophyletic, however, the clade resulted in a polytomy, not confirming well the phylogenetic relationships between the members.

The branch support value for Angolachelonia was found to be low (Bremer support = 0), with the branch support for Sandownidae being low (Bremer support = 0) but the branch support for Thalassochelydia including *Solnhofia parsonsi* is low (Bremer support = 1), however, the branch support for Thalassochelydia excluding *Solnhofia parsonsi* is low (Bremer support = 1). In this case, however, several clades of this tree, including the majority of Chelonioidea, were found to have branch support of 0, causing these results to be put into question. The Sandownidae is supported by five synapomorphies, all of which consist of cranial characters. The Thalassochelydia share ten synapomorphies, of which five are cranial and mandibular, whilst the remaining five are postcranial.

The result from the strict consensus tree topology revealed a large part of it unresolved, therefore, in order to identify the “wildcard” taxa present in this study that occupied multiple different phylogenetic positions in the MPTs, as well as an analysis on the different characters that are influencing these taxa this way, it was executed an iterative Positional Congruence Reduced (PCR) using the IterPCR.run script from Pol & Escapa (2009) in TNT as well as the iterative PCR command from TNT. The IterPCR resulted in the pruning of several taxa which were considered to be “wildcard” taxa, namely: *Rhinochelys pulchriceps* Owen, 1842, *Bouliachelys suteri* Kear & Lee, 2006, *Ocepechelon bouyai* Bardet et al., 2013, *Desmatochelys lowii* Williston, 1894, *Desmatochelys padillai*, *Rhinochelys nammourensis*, *Chelosphargis advena*, *Calcarichelys gemma*, *Corsochelys halinches*, *Oligochelone rupelensis*, *Erquelinnesia gosseleti*, *Emarginachelys cretacea* Whetstone, 1978, *Ordosemys* sp. IVPP V12092 Brinkman & Peng, 1993, *Judithemys sukhanovi* Parham & Hutchison, 2003, *Kirgizemys hoburensis* Sukhanov & Narmandakh, 1974, *Kirgizemys dmitrievi* Nessov & Khozatskii 1981, *Adocus lineolatus*. The resulting consensus tree from the iterPCR found the Angolachelonia to be within the Cryptodire and sister taxa of the total-group Chelonioidea (Figure 4.2).

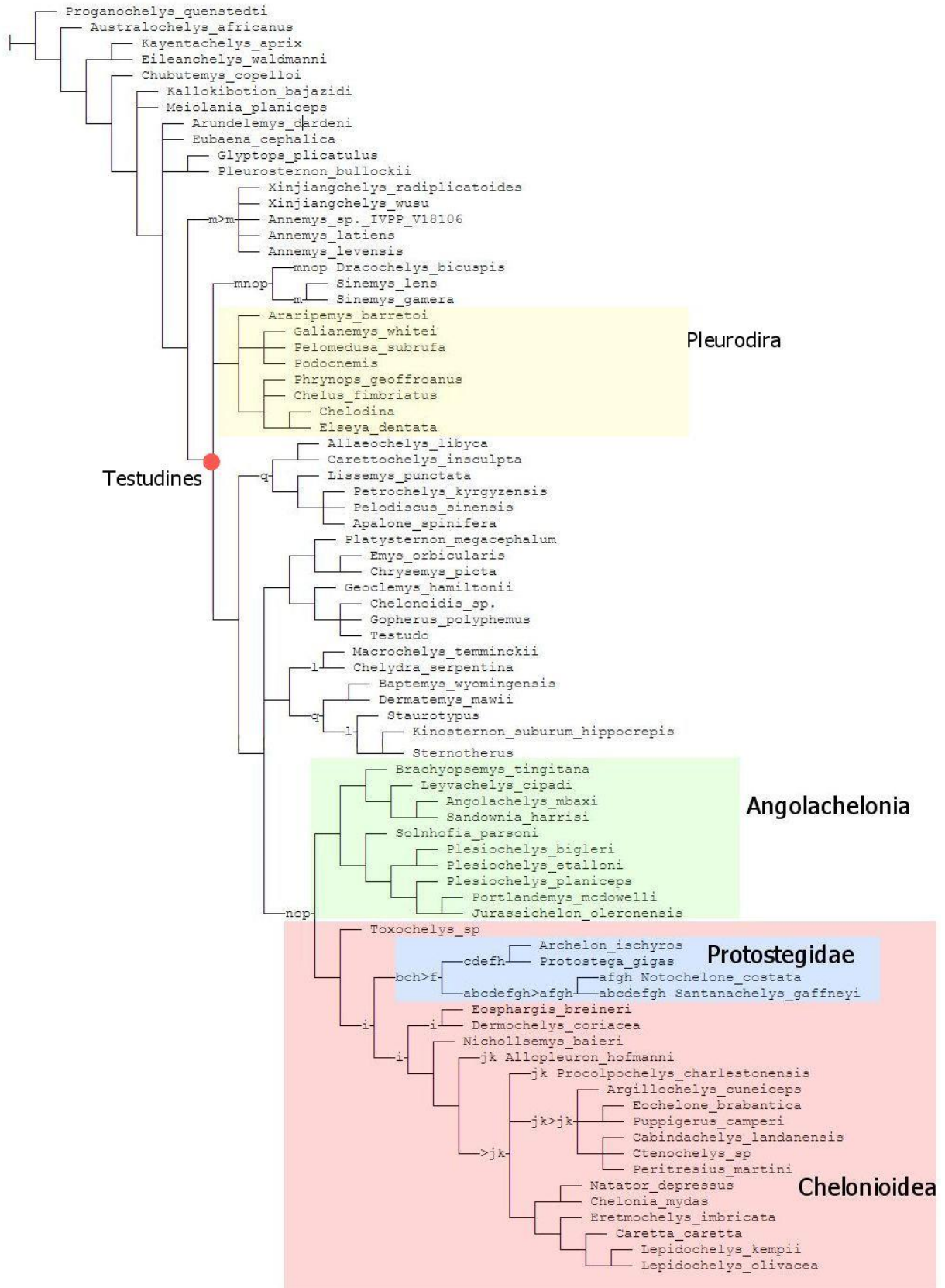


Figure 4.2. Parsimony consensus tree resulted from the phylogenetic analysis. Consensus tree >10000 MPTs, after iterPCR. a: *Rhinochelys pulchriceps*, b: *Bouliachelys suteri*, c: *Ocepechelone bouyai*, d: *Desmatochelys lowii*, e: *Desmatochelys padillai*, f: *Rhinochelys nammourensis*, g: *Chelosphargis advena*, h: *Calcarichelys gemma*, i: *Corsochelys halinches*, j: *Oligochelone rupelensis*, k: *Erquelinnesia gosseti*, l:

Emarginachelys_cretacea, m: *Ordosemys_sp._IVPP_V12092*, n: *Judithemys_sukhanovi* o: *Kirgizemys_hoburensis*, p: *Kirgizemys_dmitrievi*, q: *Adocus_lineolatus*

There are some interesting aspects in the iterPCR results, such as the fact that a good portion of what was classified as the Sinemydidae/Macrobaenidae clade was found to be “wildcard” taxa (i.e. *Ordosemys_sp._IVPP_V12092*, *Judithemys_sukhanovi*, *Kirgizemys_hoburensis*, and *Kirgizemys_dmitrievi*), and were pruned from the resulting tree, even though the monophyly of this group has been previously established in previous works (e.g. Evers & Benson, 2019) and the first phylogenetic tree in this work. In the tree it is seen that this is mostly due to *Judithemys_sukhanovi* (n), *Kirgizemys_hoburensis* (o) *Kirgizemys_dmitrievi* (p) which were disputed, from the results of the interPCR, either in the Sinemydidae/Macrobaenidae clade or in the base of the connection between the Angolachelonia and the total-group Chelonioidea. It would be interesting to check the possible relation these taxa have with these groups.

Several members of the Protostegidae were found to be “wildcard” taxa, however, contrary with the cases with the taxa from the Sinemydidae/Macrobaenidae clade, the “wildcard” protostegids were disputed in different positions only within the Protostegidae clade, somewhat collaborating to the monophyly of the clade, the phylogenetic relationship between the members, however, is not well determined due to these different positioning.

Between the matrixes of Evers & Benson (2019) and Evers et al. (2019), they added, to the latter, multiple taxa as well as modified and added characters on the postcranial skeleton. To test the possible implications these new taxa had to the phylogenetic results, it was done a “modified matrix”, in which it was used the characters from Evers & Benson (2019) but with the added taxa from Evers et al. (2019). The resulting tree is presented below (Figure 4.3).

The parsimony analysis utilizing “New technology” of the unordered dataset in TNT resulted in a total of 64 most parsimonious trees (MPTs) being produced, each with the tree length (TL) of 1550 steps long. The following TBR branch swapping resulted in 118 MPTs overall. The consistency index (CI) is 0.228, whilst the retention index (RI) is 0.640. The zero-branch lengths were collapsed during the construction of the strict consensus tree.

The tree resulted in a considerable polytomy, though smaller and better resolution than in comparison to the second tree. Similar to the second tree, the Angolachelonia was found to be the sister taxon of the total-group Chelonioidea. Interestingly *Rhinochelys_nammourensis* was positioned within the crown-group Chelonioidea not within the Protostegidae, as it was expected to be. Considering that it was found to be within the Protostegidae in Evers et al. (2019), it would be interesting to confirm what would be influencing it in the Evers & Benson, (2019) characters to position it in such a way since it was not included in their phylogenetic test.

The branch support value for Angolachelonia was found to be moderate (Bremer support = 2), with the branch support for Sandownidae being moderate-high (Bremer support = 4) but the branch support for Thalassochelydia including *Solnhofia_parsonsi* was significantly low (Bremer support = -2), however, the branch support for Thalassochelydia excluding *Solnhofia_parsonsi* was high (Bremer support =4).

The Sinemydidae/Macrobaenidae were recovered as a monophyletic group, though due to the small polytomy in it, the relationship between the taxa in this clade is ambiguous.

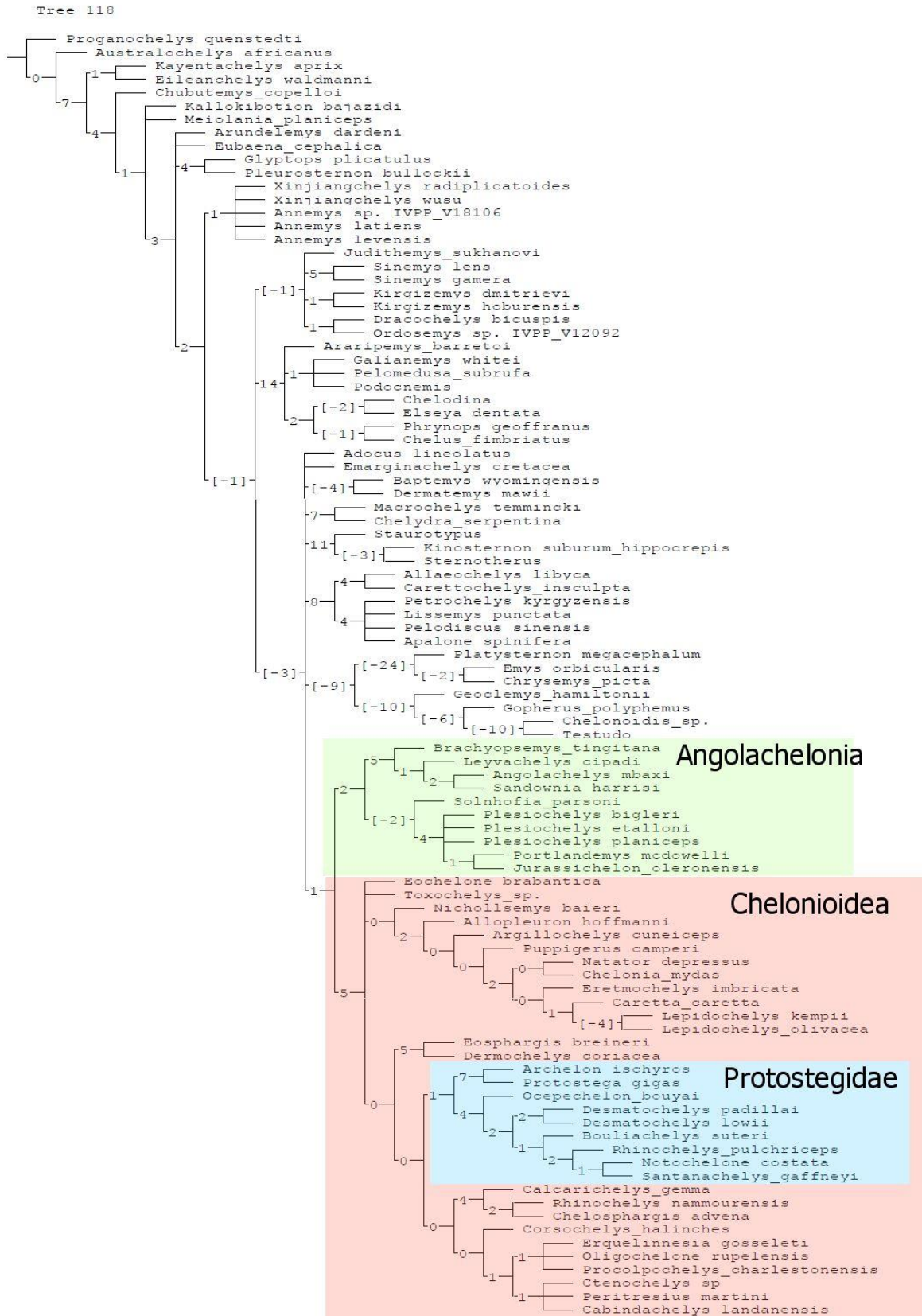


Figure 4.3. Parsimony consensus tree resulted from the phylogenetic analysis. Bremer support presented in the tree. Consensus tree of 118 MPTs. Based on the “modified matrix” with the characters from Evers & Benson (2019) and with the added taxa from Evers et al. (2019).

To further test the influences of the “new” characters from Evers et al. (2019), it was done another test with a second “modified” matrix was included the taxa from Evers & Benson (2019) with the characters from Evers et al. (2019).

The parsimony analysis utilizing “New technology” of the unordered dataset in TNT resulted in a total of 8 most parsimonious trees (MPTs) being produced, each with the tree length (TL) of 1611 steps long. The following TBR branch swapping resulted in 8 MPTs overall. The consistency index (CI) is 0.255, whilst the retention index (RI) is 0.653.

The branch support value for Angolachelonia was found to be moderate (Bremer support = 2), with the branch support for Sandownidae being moderate (Bremer support = 2) but the branch support for Thalassochelydia including *Solnhofia parsonsi* was low (Bremer support = 1), however, the branch support for Thalassochelydia excluding *Solnhofia parsonsi* was moderate (Bremer support =2).

The results of the phylogenetic analysis are similar to that of Evers & Benson (2019) and those from figure 4.1. The monophyly of Angolachelonia, which groups the Sandownidae and the Thalassochelydia, is confirmed in this tree and they were positioned as the sister taxa of the Testudines. The results of this phylogenetic analysis indicate that the differences between the resulted phylogenetic analysis from the previous tests are mainly due to the presence of the added taxa and not due to the modified characters since the results of this analysis were considerably similar to those of the first analysis, in which the only difference in the matrixes used being the characters used (the first analysis is based on the characters from Evers & Benson (2019) whilst this was based on the characters from Evers et al. (2019)).

The synapomorphies of the Angolachelonia and its members are mapped and presented below (Figure 4.4; Table 4.1). The synapomorphies were mapped after the analysis with the matrix based on the matrix of Evers et al., (2019).

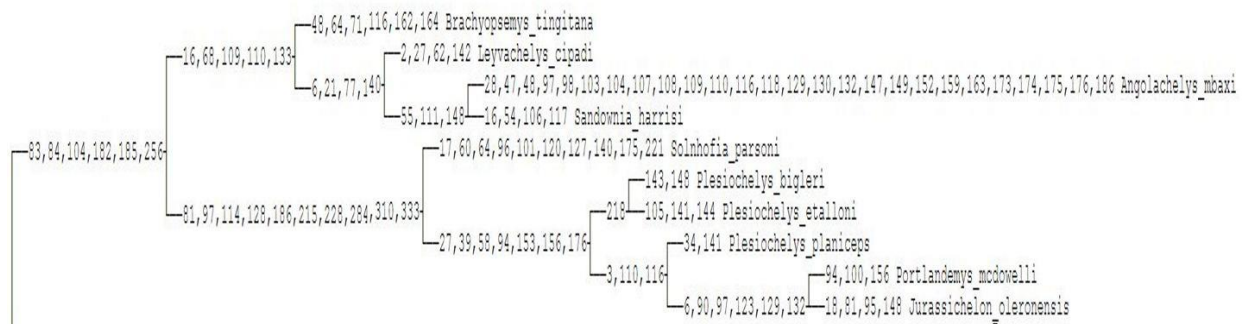


Figure 4.4. Synapomorphies of the Angolachelonia and its members mapped.

Table 4.1. Synapomorphies for the Angolachelonia, Sandownidae, Thalassochelydia, and *Angolachelys mbaxi*.

Taxon	Unambiguous synapomorphies	Sum Total
Angolachelonia	83.0; 84.1; 104.0; 182.1; 185.0; 256.0	6
Sandownidae	16.0; 68.2; 109.2; 110.1; 133.0	5
Thalassochelydia	81.0; 97.0; 114.0; 128.1; 186.1; 215.0; 228.0; 284.0; 310.1; 333.1	10
<i>Angolachelys mbaxi</i>	28.1; 47.1; 48.0; 98.0; 103.0; 104.1; 107.1; 108.2; 109.1; 147.1; 149.1; 152.0; 159.0; 173.0; 174.1; 175.0; 176.1	17

4.1.2 The phylogenetic position of Angolachelonia discussion

The phylogenetic position of Angolachelonia has been under discussion for several years, ever since the group was formed (check the “The Angolachelonians” section for more details).

The Angolachelonia were first found to be Eucryptodira it grouped *Angolachelys mbaxi*, *Solnhofia parsonsi*, *Sandownia harrisi*, and *Leyvachelys cipadi* when it was first erected and formalized by Mateus et al. (2009).

In the study of Tong & Meylan (2013) their results separated the Sandownidae, formed, in their study, by *Angolachelys*, *Sandownia*, and *Brachyopsemys*, from the Thalassochelydia. The Sandownidae were found to be the sister taxa of the Chelonioida, although it was also found to be close to the Trionychidae. It is likely due to the presence of chelonioid and trionychid features shared with the group and present in the character matrix used in the aforementioned study. The Angolachelonia were not found to be monophyletic in Tong & Meylan (2013) and the Thalassochelydia are represented by *Solnhofia* and *Thalassemys* Rüttimeyer, 1859 in Tong & Meylan (2013).

Cadena (2015) recovered the sandownids as sister-taxon to the xingjianchelyids + sinemydids + *Judithemys* as stem-group chelonioids, forming together with *Jurassichelon* and *Solnhofia* a panchelonioid clade. Interestingly in the aforementioned study, Sandownidae was not recovered as sister-taxon of Thalassochelydia but instead recovered them as sister-taxon of the xingjianchelyids + sinemydids + *Judithemys*, and this group is recovered as the sister-taxa of Chelonioida, whilst the Thalassochelydia were recovered as stem-group chelonioids. The Sandownidae were represented by *Sandownia harrisi*, *Angolachelys mbaxi*, *Brachyopsemis tingitana*, and *Leyvachelys cipadi*, while the Thalassochelydia were represented by *Solnhofia parsonsi* and *Jurassichelon oleronensis* (Cadena, 2015).

In the Evers & Benson (2019) study they performed a revised phylogenetic approach on several Testudinata groups, in which the Angolachelonia was positioned as the sister taxa of the modern testudines and grouped the Sandownidae and the Thalassochelydia. Angolachelonia was recovered as a monophyletic group. The Sandownidae were represented by *Sandownia harrisi*, *Brachyopsemis tingitana*, and *Leyvachelys cipadi* while Thalassochelydia was represented by *Plesiochelys etalloni*, *Plesiochelys planiceps*, *Jurassichelon oleronensis*, *Portlandemys mcdowellii*, and *Solnhofia parsonsi* (Evers & Benson, 2019).

The phylogenetic study by Evers et al. (2019) recovered Angolachelonia as a monophyletic group and they were found to be the sister taxon of the Pleurodira and within the Testudines, although this relationship was found to be poorly supported in the study (with a Bremer support value of 1). The authors justified this unexpected result to the uncertainty of the position of the pleurodires in global turtle datasets (e.g. Sterli, 2010; Zhou et al., 2014; Evers et al., 2019) and this uncertain phylogenetic position could explain the resulted unclear relationship between the pleurodires and angolachelonians. The Sandownidae were represented by *Angolachelys mbaxi*, *Sandownia harrisi*, *Brachyopsemis tingitana*, and *Leyvachelys cipadi* while Thalassochelydia were represented by *Plesiochelys etalloni*, *Plesiochelys planiceps*, *Jurassichelon oleronensis*, *Portlandemys mcdowellii*, and *Solnhofia parsonsi* (Evers et al., 2019).

In this study, the Angolachelonia are represented by the Sandownidae, represented by *Angolachelys mbaxi*, *Sandownia harrisi*, *Brachyopsemis tingitana*, and *Leyvachelys cipadi*, and by the Thalassochelydia, that is represented by *Plesiochelys etalloni*, *Plesiochelys planiceps*, *Jurassichelon oleronensis*, *Portlandemys mcdowellii*, and *Solnhofia parsonsi*. The majority of the characters coded of these taxa were based on the characters coded in the matrixes of Evers & Benson (2019) or Evers et al. (2019).

They were recovered as a monophyletic group, grouping the Sandownidae and Thalassochelydia in all of the phylogenetic trees resulted from this study. The phylogenetic relationship with the other groups differs in the resulted of trees.

In the first resulted tree they were found to be sister taxa of the Testudines, similar to the result in Evers & Benson (2019) as was to be expected since the matrix on which it was based is from the aforementioned study.

In the remaining trees, either with the matrix based on Evers et al. (2019) or the combination matrix in which the characters of Evers & Benson (2019) with the taxa of Evers et al. (2019) were used, resulted with the Angolachelonia being found to be monophyletic and recovered as the sister taxon of the Chelonioidea. The result differs from what was to be expected, considering the results of the studies in which the matrixes were based on (i.e. Evers & Benson (2019) they recovered Angolachelonia as the sister taxon of Testudines and Evers et al. (2019), recovered them as Testudines and sister taxa of Pleurodira). The difference between the matrix of Evers et al. (2019) and the matrix used in this study is the codification of *Angolachelys mbaxi*, which in this study some of the postcranial characters are coded whilst in Evers et al. (2019) the postcranial characters were not coded. To attempt to test if this difference is what lead to the Angolachelonia being placed as a sister taxon of the Chelonioidea, the “combination” matrix was made, using the taxa of Evers et al. (2019) with the character matrix of Evers & Benson (2019) with the added codification of the postcranium characters of *Angolachelys*. The results for the Angolachelonia for the “combination” matrix were very similar to the previous matrix, indicating that it is possible that the results using the matrix based on Evers et al. (2019) was not solely based on the codification of the *Angolachelys* postcranium characters but also based on some still unidentified relationship between the Angolachelonia and the added taxa of Evers et al. (2019), which contributed to the placement of Angolachelonia as a sister taxon of the Chelonioidea.

The taxa that were added in Evers et al. (2019) are *Adocus lineolatus*, *Angolachelys mbaxi*, *Cabindachelys landanensis*, *Calcarichelys gemma*, *Chelosphargis advena*, *Corsochelys halinches*, *Erquelinnesia gosseleti*, *Nichollsemys baieri*, *Ctenochelys sp.*, *Galianemys whitei*, *Oligochelone rupelensis*, *Peritresius martini*, *Petrochelys kyrgyzensis*, *Plesiochelys bigleri*, *Procolpochelys charlestonensis*, and *Rhinochelys nammourensis*. The nature of the relationship between the Angolachelonia and *Angolachelys* with these taxa is yet undetermined and it would be interesting to confirm their relationship.

The results of the first phylogenetic study are considerably different from those obtained by Gentry et al. (2019). In the aforementioned study, the Angolachelonia were recovered as a monophyletic group and they were represented by *Sandownia harrisi*, *Brachyopsemis tingitana*, *Leyvachelys cipadi*,

Plesiochelys etalloni, *Plesiochelys planiceps*, *Jurassichelon oleronensis*, *Portlandemys mcdowellii*, and *Solnhofia parsonsi*. They were found to be stem Pan-Chelonioidea and closely related to Protostegidae. In the aforementioned studies result in the Protostegidae were found to be the sister-taxa of the total-group Chelonioidea (Gentry et al., 2019). It is important to note that the aforementioned study did not include *Angolachelys mbaxi* in the matrix, the matrix that was used was based on Evers & Benson (2019) with some modifications, namely the addition of the fossil taxa *Toxochelys latiremis*, *Ctenochelys stenoporus*, *Ctenochelys acris*, *Prionocheles matutina*, *Peritresius ornatus*, *Euclastes wielandi*, and *Asmodochelys parhami*, the addition of two characters, the revision of nine characters and the rescoring of some characters of a few taxa (see Gentry et al., 2019). The aforementioned study found strong support for the placement of the angolachelonians and the protostegids as stem chelonoids (Gentry et al., 2019), which differ considerably from some of the results of this study, in which the Angolachelonia was placed as the sister taxon of the Pleurodira, nevertheless, it does support the result of some of the other phylogenetic results from this study, in which the Angolachelonia was placed as the sister taxa of the total-group Chelonioidea. The Protostegidae were found to be part of the total-group Chelonioidea, which is supportive with the study of Gentry et al. (2019), which placed the Protostegidae as close to the Angolachelonia and the Chelonioidea (Gentry et al., 2019), as well as the study of Evers et al. (2019), which placed the Protostegidae as sister taxa of the crown-group Chelonioidea (Evers et al., 2019).

4.2 Squamosals hypothesis and durophagy hypothesis

One of the most distinctive characteristics of *Angolachelys mbaxi* is the presence of the squamosal projections of its cranium, which extends a large amount of posteriorly, forming a triangular-like shape (Mateus et al., 2009). In its description the authors (Mateus et al., 2009) believed that *Angolachelys* possessed characteristics belonging to the Trionychoidea, including these squamosal projections, however, they were found to be different from the ones present in the Trionychoidea (Mateus et al., 2009). *Angolachelys* has been classified as a durophagous turtle since its first description (Mateus et al., 2009) due to the several common characteristics that it shares with typical durophagous turtles, especially the secondary palate.

The secondary palate is characterized by the bony separation of the narial cavity from the oral cavity (Parham & Pyenson, 2010), forming two separate plates which are commonly complemented by a greater expansion of the trituration surface, due to the secondary palate contributing to the trituration surface (Parham & Pyenson, 2010; Cadena, 2015; Ferreira et al., 2015). The secondary palate is a feature that is commonly linked to the durophagy diet and the marine lifestyle (Parham & Pyenson, 2010; Ferreira et al., 2015).

The large squamosal projections of *Angolachelys* are likely linked to its feeding and, therefore, linked to the durophagy feeding. The exact nature and function of these odd projections have not been fully ascertained and it will be explored in this part.

The squamosal projections of *Angolachelys* are akin to those of the Trionychoidea (Mateus et al., 2009), however, they are considerably different from them as well. The squamosal projections of *Angolachelys* consist of solid posterior projections, lacking the emarginations present in the projections of the Trionychoidea and, therefore, not forming the crista squamosalis. The crista squamosalis, along with the crista supraoccipitalis, consists of the primary origin sites for the musculus adductor mandibulae externus, with the m. adductor mandibulae externus Pars medialis and Pars superficialis attached to the crista squamosalis and the m. adductor mandibulae externus Pars profundus attached to the crista supraoccipitalis (Werneburg, 2012). The crista supraoccipitalis is underdeveloped and nearly non-existent in *Angolachelys* (Mateus et al., 2009). It suggests the underdevelopment of these muscles in this turtle. Such being the case, it may be that such would lead to a decrease in the bite force (Sterli & de La Fuente, 2010, but see Ferreira et al., 2020).

These projections would likely be connected to neck musculature, however, it was shown by Ferreira et al. (2020), that the expanded temporal crests offer a broader attachment site for neck musculature, enabling this way for more complex and stronger neck musculature (Ferreira et al., 2020).

The skull of *Angolachelys* is also considerably flattened, contrary to what would be expected from a turtle with a durophagous diet, since it was suggested by Herrel et al. (2002), that durophagous turtles tend to exhibit higher skulls than others, due to involving a greater bite force (Claude et al., 2004). The flattening could be due to the taphonomical process and crushing as was suggested by the authors (Mateus et al., 2009), but it could also be an adaptation for greater efficiency in skull retraction (Ferreira et al., 2020) although this is closely connected to the expansion and emargination of the temporal crests (Ferreira et al., 2020).

Another interesting aspect of this species is the lower jaw. The dentary of *Angolachelys* is remarkably flat and considerably thin, displaying a sort of “spade” like shape, somewhat similar to that of *Erquelinnesia gosseleti* and *Brachyopsemis tingitana* (Mateus et al., 2009).

The species may display a highly specialized form of feeding and its adaptations. One hypothesis for the nature of these squamosal projections and feeding is the “levy” hypothesis.

The “levy” consists of the usage of the dentary in order to insert in the gaps of the shells of certain, large-sized molluscs and serving as a levy in order to open it by force. The squamosal projections, in this hypothesis, would be used as the attachment sites of neck musculature that would move the posterior portion of the skull in a ventral-dorsal plane, forcing the posterior portion of the skull to move ventrally and, consequently, move the anterior portion of the skull dorsally, displaying force required for the “levying” of the shells of the prey without requiring a large amount of bite force. The hypothesis would entail the lack of squamosal and supraoccipital crests, the thinness and flatness of the dentary, and the possible usage of the squamosal projections as a feeding adaptation. The attachment site for the muscles in the squamosal projections would be in the ventral surface of the projections.

The “levy” hypothesis is supported by the presence of the large-sized clams, *Inoceramus* sp., and other molluscs in the area where the specimen was found (Mateus, personal comm.), the shape and flatness of the dentary, the presence of ventral keels in some of the cervical vertebrae (described above) which could be served as an attachment site for the muscles involved in this process, though this is yet to be confirmed.

The principal flaw of this hypothesis is the lack of identification of the muscles involved in this mechanism, as there is no known muscle in turtles directly attached to the squamosals that are connected to that function (Werneburg, 2011), lacking, therefore, more substantial evidence supporting this hypothesis.

Another hypothesis for the nature of these squamosal projections is that they are horn-like protrusions, akin to those present in *Meiolania* Owen, 1886. In this hypothesis, the projections are horn-like protrusions that, due to the taphonomical process, suffered crushing and were flattened.

The issues with this hypothesis are mainly due to the orientation of the projections and the form of the “horns”. The projections in *Angolachelys* expand posteriorly, whilst the “horns” of the *Meiolania* expand posteriorly, laterally and dorsally (Gaffney, 1992; Sterli, 2015), whilst the squamosal projections of *Angolachelys* expand posterior and slightly ventrally, revealing no obvious signs of sufficient crushing do deform them in such a manner (Mateus et al., 2009).

Of the presented hypotheses, the most probable would be the “levy” hypothesis, however, it remains to be determined.

4.3 Marine nature of *Angolachelys mbaxi*

Angolachelys mbaxi has been interpreted to be marine in its description due to the nature of the sediment which it was found (Mateus et al., 2009), however, due to the absence of postcranial marine-oriented characteristics, it was not confirmed. From the description of the new postcranial material of *Angolachelys*, it is possible to conjecture the exact nature of *Angolachelys*.

Some costals of the carapace of *Angolachelys* are not completely ossified in the distal portion, which results in open peripheral fontanelles, or costo-peripheral fontanelles and uncovered distal ends of the corresponding ribs, known as “free ribs”. These characteristics are commonly found in marine turtles and it is evident in the specimen from the presence of the free ribs that are preserved in some of the costal fragments. It would indicate a reduction of the carapace, a characteristic that is typically present in fully marine turtles. The carapace would have presented costo-peripheral fontanelles along the distal portion of the carapace, formed due to the lack of ossification in the distal portion of the costal. The connection of the costal and the peripheral in the specimen is formed by the free ribs of the costals. The peripherals present emarginations in the locations in which the free rib would connect to the peripherals. Taking into consideration the emarginations of the peripherals, it may be that the carapace would have been somewhat similar to the carapace of *Caretta caretta*, due to the emarginations being located medially in the aforementioned peripherals (Valente et al., 2007). The costals are quite thin, indicating a lack of ossification and a reduction of the carapace, a common feature in marine lifestyle adapted turtles.

The preserved coracoid has a large, “fan”-like expansion on the distal portion of it. The expansion can be seen in both terrestrial and marine turtles, therefore not giving any indication of the nature of *Angolachelys*, as previously mentioned in the description of the coracoid. Another possible feature that could have aided in the identification of the nature of this turtle would have been the angle formed by the coracoid and the scapula, however, the scapula and acromion are not preserved in the specimen and, thus, it is not possible to confirm the angle.

The proximal portion of the femur is not preserved in the specimen, not being possible to confirm the size of the trochanters, however, the curvature formed by the shaft until the distal portion of the femur does not display the distinct accentuated curvature formed by the shafts of femurs belonging to typically terrestrial turtles, which is a way to sustain the heavier and larger size of their bodies. It has also been previously mentioned that the femur resembles the femur of *Euclastes hutchinson* (Lynch & Parham, 2003).

The humerus is large and long, being slightly larger than the coracoid. The humerus is considerably flattened and does not display any sort of distinct curvature in the shaft present in more terrestrial turtles and seems to belong to the morphospace assigned to marine adapted turtles from Dickson & Pierce (2019), based on the aforementioned characteristics. It would designate the forelimb of *Angolachelys* being of a similar morphology as that of determined marine lifestyle turtles, implying the same or similar lifestyle for *Angolachelys*.

The femur, by comparing their distal portions, is relatively smaller than the humerus, complementing the notion that *Angolachelys* is a marine turtle. The condylus of the femur are well distinctive and the shaft does not show any large curvature, a common feature in femurs of land tortoises (e.g. *Titanochelon* sp. (Pérez-García et al., 2017)), indicating and supporting a marine lifestyle hypothesis.

Based on the description of the humerus, as well as the morphotypes formed by Evers et al. (2019), the humerus of *Angolachelys* displays a shape similar to the “humerus morphotype 1” from Evers et al. (2019), which is similar to the humeri of protostegids (e.g. *Chelosphargis advena* Hirayama, 1994) and of some cheloniids (e.g. *Eochelone brabantica* Hirayama 1994), further supporting the hypothesis that *Angolachelys* is of a marine environment.

The format of the humerus of *Angolachelys* is very interesting, displaying the overall format of that of a typical marine turtle, yet display plesiomorphies uncommon in marine turtles humeri (i.e. the

noticeable condyles). It is possible that *Angolachelys* presented a type of swimming more akin to that of *Apalone*, which is a type of swimming movement termed “rowing”, as opposed to the typical swimming movement displayed by marine turtles termed as “flapping” (Rivera et al., 2013) present in the Chelonioida.

There are some distinct differences between the characteristics of this specimen compared to completely pelagic turtles such as *Dermochelys coriacea*, however, it presents, as previously mentioned, distinct marine adaptations typical of a marine turtle.

It presents more adaptations towards a marine lifestyle than those present in some turtles that were interpreted to be of littoral or coastal adapted such as some bothremydid turtles (Gaffney et al., 2006, Cadena et al., 2012) or *Leyvachelys cipadi*, a member of the same clade as *Angolachelys* however it lacks multiple adaptations for a marine lifestyle that are present in *Angolachelys* (e.g. the lack of shell fontanelles typical of marine turtles (Cadena, 2015)).

Likely, *Angolachelys* did not possess the same pelagic lifestyle presented in some of the dermochelyids or advanced protostegids (Hirayama, 1994) from the resemblance that the humerus presents with not so specialized for a pelagic lifestyle such as *Toxochelys* (Hirayama, 1994).

4.4 Tadi Beds age

The age of the Tadi Beds has been discussed and disputed multiple times (e.g. Antunes & Cappetta, 2002; Jacobs et al., 2006, 2016) with the previous definition of it being of Turonian in age a member of the Itombe formation (Jacobs et al., 2006).

The Itombe formation ranges from the early Turonian to the late Coniacian, the Turonian layers of the Itombe formation are dominated by silty shale, with the presence of limestone, shale, sandstone, and siltstone in some of the layers (Mateus et al., 2011), the Coniacian layers of the Itombe formation are dominated by silty shale however limestone, shale, sandstone, and siltstone are more abundant in these layers in comparison with the Turonian layers of the formation (Mateus et al., 2011). From this formation the beds that stand-out are the Tadi beds which is the type locality of the aforementioned vertebrate fossils (Jacobs et al. 2016). The Tadi beds are around 50m thick (Antunes, 1964; Mateus et al., 2011) and are placed in the Itombe Formation (Antunes, 1964; Jacobs et al., 2006). The top part of the Itombe Formation corresponds to the Middle Campanian *Globo truncata ventricosa* Zone, and the lower part, the Tadi beds, can be correlated with the Cocaba Beds which contain the ammonite *Coilpoceras* of Turonian and Coniacian age (Jacobs et al. 2006). The upper age limit of the Tadi Beds is constrained by the Pambala Beds, which contains *Texanites* of Coniacian to Campanian age (Jacobs et al. 2006), that is included in the N'Golome Formation that contains the Middle Campanian *Globo truncata ventricosa* Zone (Antunes & Cappetta, 2002) but also contains the Late Coniacian *Dicarinella asymetrica* Zone (Blake et al. 1996) therefore a similar chronostratigraphic problem present in the Itombe Formation is also present in this formation (Jacobs et al. 2006). There is also the presence of small and distinctive mosasaur vertebrae, as well as shark material at the top of the section of the Tadi Beds, which suggest that it may extend into the Coniacian or possibly into the lower Santonian (Jacobs et al., 2016).

The Tadi Beds can be correlated with the Cocaba Beds, which contain the ammonite *Coilpoceras* of Turonian and Coniacian in age (Jacobs et al., 2006). The upper age limit of the Tadi Beds is constrained by the Pambala Beds, which contain *Texanites* ammonites of Coniacian to Campanian in age (Jacobs et al., 2006). The presence of small and distinctive mosasaur vertebrae, as well as shark material at the top of the section of the Tadi Beds, indicate the possibility that the age of the Tadi Beds may extend into the Coniacian or, possibly, into the lower Santonian (Jacobs et al., 2016).

The study on the ichthyofauna of the Tadi beds by Antunes & Cappetta (2002) resulted in the attribution of the age of Turonian to the Tadi Beds based on the ichthyofauna that was collected and

classified, however, this attribution may be conflicting due to the presence of other fauna, especially ammonitic fauna, as well as the fact that the authors did not provide a locality or faunal list for Early Turonian or Coniacian ichthyofauna, increasing the difficulty to defend the accuracy of a Late Turonian based on the strict comparison with other Angolan sites (Jacobs et al., 2006).

It was stated by Lingham-Soliar (1994) that the Pambala Beds contain the ammonites *Hemitissotia* and *Romaniceras*, however, it was clarified by Antunes (1964) and Antunes & Cappetta (2002) that these ammonites were found in the Tadi Beds instead (Jacobs et al., 2006).

The ammonite *Hemitissotia* is characteristic of the Upper Coniacian in Europe (Gräfe & Wiedmann, 1998), whilst the *Romaniceras* ammonite can be a potential marker for the Upper Turonian, with *Romaniceras deverianum* Ogg et al., 2004, or the Coniacian, with *Romaniceras hispanicum* Gräfe & Wiedmann, 1998 (Jacobs et al., 2006).

A *Protexanites* sp. ammonite specimen was recovered from the Paleoangola groups' excavations in the Tadi Beds (Mateus et al., 2019). The finding has led to the definition of the Tadi beds as Coniacian of age (Mateus et al., 2019). The ammonite specimen was described in this study to aid in the determination of the age of the Tadi Beds.

Through the description above and cross-referencing with bibliography, namely Kennedy (1984), the genus of the specimen is identified as *Protexanites* Matsumoto, 1955, which has a well-defined time range from the Upper Coniacian to the Lower Santonian (Kennedy, 1984), and the species is *Protexanites bourgeoisi* d'Orbigny, 1850, which is well defined in the Upper Coniacian of France (Kennedy, 1984).

Taking into consideration the time range of the *Protexanites* specimen, as well as the other, previously mentioned, ammonitic fauna (i.e. *Hemitissotia* and *Romaniceras*), the ichthyofauna presented by Antunes & Cappetta (2002), which contain several taxa whose time range cover or are close to the Coniacian, the correlation of the Tadi Beds with the Cocaba Beds, that contain the ammonite *Coilpoceras* of Turonian and Coniacian in age (Jacobs et al., 2006), the upper age limit of the Tadi Beds that is constrained by the Pambala Beds, which themselves contain *Texanites* ammonites of Coniacian to Campanian in age (Jacobs et al., 2006) and the presence of the previously mentioned small and distinctive mosasaur vertebrae and shark material at the top of the section of the Tadi Bed, which indicate that its time range may increase into the Coniacian or possibly into the lower Santonian (Jacobs et al., 2016), it is possible to confidently claim that the age of the Tadi Beds is defined as Coniacian in age, in concordance with Mateus et al. (2019).

5. CONCLUSIONS

5.1 Marine nature of *Angolachelys*

Angolachelys was defined as being of marine nature when it was first described (Mateus et al., 2009) due to the marine sediments in which it was recovered. Here it was given more evidence that the species present several morphological aspects linked to marine adaptations. The assertion of the marine nature of *Angolachelys* and the Sandownidae clade indicates that since that Thalassocheilydia has been previously ascertained to be of a marine nature (Anquetin et al., 2017), that the *Angolachelonia* clade is a clade formed by marine turtles, similar to how Chelonioida is.

The definition of a marine nature in *Angolachelys* further establishes the *Angolachelonia* as a marine turtle clade, since the Thalassocheilydia have previously been defined as a marine turtle (i.e. Anquetin et al., 2017) and now the Sandownidae are confirmed as well with *Angolachelys*. It complements with the “independent marine lifestyle transitions” within turtles that were studied by Evers & Benson

(2019) which acknowledged that the *Angolachelonia* represented an independent transition to a marine lifestyle and that they were marine (Evers & Benson, 2019).

Although *Angolachelys* presents adaptations for marine lifestyle, it does not present the same adaptations for the highly pelagic lifestyle adaptations that some modern marine turtles present, with the case of *Dermochelys coriacea* being extreme in such adaptations, however, it is possible that it presented a pelagic lifestyle although not presenting more extreme adaptations such as the ones present in *Dermochelys coriacea* (Hirayama, 1994).

It was shown in this study clear evidence indicating the marine nature of *Angolachelys*, with sustainable evidence to support that it was not a littoral or coastal adapted turtle as it presents more adaptations towards a marine lifestyle than those present in some turtles that were interpreted to be of littoral or coastal adapted such as some bothremydid turtles (Gaffney et al., 2006, Cadena et al., 2012) or *Leyvachelys cipadi* (Cadena, 2015).

It likely presented a marine lifestyle, yet not the same pelagic lifestyle presented in some of the dermochelyids or advanced protostegids (Hirayama, 1994).

It would be interesting to confirm in future studies if the meant that the turtle did not display a pelagic lifestyle or if it presented a pelagic lifestyle whilst not displaying more pelagic lifestyle-oriented adaptations such as in the case of the aforementioned example.

5.2 Age of the Tadi Beds

The age of the Tadi Beds has long been under discussion, with the placement of the Tadi Beds in the Itombe Formation, with an age of Late Turonian being the previously established for the Tadi Beds (Antunes & Cappetta, 2002).

From this study, it was determined that the age of the Tadi Beds from Iembe, Angola, is of Coniacian of age, a result that is concordance with Mateus et al. (2019) mainly from the presence of the ammonite *Protexanites*, but also due to the presence of other ammonitic fauna (i.e. *Hemitissotia* and *Romaniceras*), the ichthyofauna presented by Antunes & Cappetta (2002), containing several taxa whose time range cover or are close to the Coniacian, the correlation of the Tadi Beds with the Cocaba Beds that contain the ammonite *Coilpoceras* of Turonian and Coniacian in age (Jacobs et al., 2006) and due to the upper age limit of the Tadi Beds being constrained by the Pambala Beds, which themselves contain *Texanites* ammonites of Coniacian to Campanian in age (Jacobs et al., 2006). These elements indicate that the age of the Tadi Beds is of Coniacian of age, contrary to what was previously estimated age (Antunes & Cappetta, 2002).

By defining the Tadi Beds as Coniacian in age, it changes the formerly defined ages of the previously described specimens and taxa from the Tadi Beds (see Mateus et al., 2012, 2019, for more details), as well as alter other possible correlations with other formations, either possibly worsening or complicating the correlations, or possibly aiding in the correlations.

It would be interesting to confirm if the definition of this age for the Tadi Beds would change the definition of them belonging to the Itombe formation and if they do not belong to the aforementioned formation, which formation they would belong to. It would also be interesting to confirm in future studies if this definition would change any possible correlations with other formations.

5.3 Phylogenetic position

The phylogenetic position of Angolachelonia and *Angolachelys* is convoluted and has been under discussion since the establishment of the clade. In this study, there were different results for the phylogenetic position of the Angolachelonia. They were found, in some results of this study, to be sister taxa of the Pleurodira and within the Testudines, in concordance with the results from Evers & Benson, 2019. They were also found, in other results, to be sister taxa of the total-group Chelonioida, within the Cryptodira Cope, 1868, considerably different from the results of the study in which the matrix that was used was based on, namely Evers et al., (2019). The main difference for the disparity between the tests seems to reside in the taxa that were added in Evers et al., (2019), in comparison with Evers & Benson (2019) and the still not defined relationship between these and *Angolachelys mbaxi*.

The phylogenetic position of the Angolachelonia has not been ascertained, although it is likely that they are closely related to the total-group Chelonioida, even though the exact nature of the relationship between these groups is yet to be determined. It has been shown that, regardless of which of the matrixes were used in this work that the Angolachelonia were always found together, demonstrating that it is a well-instituted clade.

It has further supported the positioning of the Protostegidae as closely related to the Chelonioida, being recovered as stem chelonioids, in concordance with Evers et al., (2019), indicating that they are likely to belong to the stem of the total-group Chelonioida, as opposed to Evers & Benson (2019), in which they were placed as crown-group chelonioids, as well as Gentry et al., (2019), where they were placed as sister-taxa of the total-group Chelonioida.

A possible future study could be considered in the subject of studying the exact relationship that *Angolachelys* has with the aforementioned taxa, namely *Adocus lineolatus*, *Cabindachelys landanensis*, *Calcarichelys gemma*, *Chelosphargis advena*, *Corsochelys halinches*, *Erquelinnesia gosseleti*, *Nichollsemys baieri*, *Ctenochelys sp.*, *Galianemys whitei*, *Oligochelone rupelensis*, *Peritresius martini*, *Petrochelys kyrgyzensis*, *Plesiochelys bigleri*, *Procolpochelys charlestonensis*, and *Rhinochelys nammourensis*.

Another interesting question is the positioning of the two *Rhinochelys* species in this study, as they were found to be farther apart from each other in some of the results than it would be expected. The precise nature of why these were found to be this way, namely if it was due to a yet unknown relationship between some of the taxa used in these studies or if it was due to a yet unknown factor, would be interesting to verify.

5.4 Squamosal projections

The squamosal projections of *Angolachelys* represent a very remarkable and unique feature of this species. The exact nature of these projections has been questioned since the species was first described (Mateus et al., 2009). They had previously been thought to be similar to the projections present in the Trionychidae, however, as it has been previously discussed in this study, these projections seem to present significant differences compared to those from the Trionychidae or those seen in modern marine turtles.

The function of these projections are likely connected to the distinctive design of the lower jaw of the species and likely related to neck movement, however, it was not possible to positively confirm any muscle originating from this area that would display such functions from the muscle anatomy of modern marine turtles (Werneburg, 2011, 2012). The exact muscles associated with these projections are yet to be determined nor the exact function of these muscles and these projections. The primary functions of these projections were previously discussed in the “Squamosals hypothesis and durophagy hypothesis” section, however, their functions could only be estimated and conjectured due

to the lack of information about the muscles connected to the squamosal projections and that would be related to the aforementioned actions.

The most likely of the hypotheses presented in this work is the “levy” hypothesis (discussed in the “Squamosals hypothesis and durophagy hypothesis” section), however, the validity of this hypothesis is yet to be confirmed, leaving it as only conjecture for now.

The squamosal projections of *Angolachelys* remain as perplexing structures, with their function still unknown.

It would be interesting to confirm if there could be muscles that are homologous to these in marine turtles or homoplastic in nature. The precise nature of the function of these projections is yet to be confirmed and it may be that they cannot be undoubtedly confirmed if these muscles are not researched.

6. Unresolved questions/future studies

6.1 Marine nature section:

Confirmation of the pelagic nature of *Angolachelys* despite seemingly lacking the adaptations common in modern pelagic turtles and, if it is, what other adaptations it presents for this lifestyle.

6.2 Age of Tadi Beds section:

Support on the definition of the age for the Tadi Beds.

6.3 Phylogenetic position section:

Studying the potential relationship between *Angolachelys mbaxi* has with some of the added taxa from Evers et al. (2019), namely *Adocus lineolatus*, *Cabindachelys landanensis*, *Calcarichelys gemma*, *Chelosphargis advena*, *Corsochelys halinches*, *Erquelinnesia gosseleti*, *Nichollsemys baieri*, *Ctenochelys sp.*, *Galianemys whitei*, *Oligochelone rupelensis*, *Peritresius martini*, *Petrochelys kyrgyzensis*, *Plesiochelys bigleri*, *Procolpochelys charlestonensis*, and *Rhinochelys nammourensis*.

6.4 Squamosal section:

Verification if there would be muscles that would be homologous, or perhaps homoplastic in nature, to those that would have attached to the squamosal projections of *Angolachelys* in modern marine turtles.

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APPENDICES

Appendices 1- Character list

CRANIUM

Character 1 (Evers & Benson (2019): character 1). Nasals: 0 = present; 1 = absent.

Character 2 (Evers & Benson (2019): character 2). Nasal, medial contact of nasals: 0 = nasals contact one another medially along their entire length; 1 = medial contact of nasals partially or fully hindered by long anterior frontal process.

Character 3 (Evers & Benson (2019): character 3). Nasal, size of nasals: 0 = dorsal exposure of nasals large; 1 = dorsal exposure of nasals greatly reduced relative to that of the frontals.

Character 4 (Evers & Benson (2019): character 4). Prefrontals, medial contact of prefrontals on the dorsal skull surface: 0 = absent; 1 = present, absence of contact between the nasal or apertura narium externa and the frontal.

Character 5 (Evers & Benson (2019): character 5). Prefrontal, prefrontal-vomer contact: 0 = present; 1 = absent.

Character 6 (Evers & Benson (2019): character 6). Prefrontal, prefrontal-palatine contact: 0 = present; 1 = absent.

Character 7 (Evers & Benson (2019): character 7). Prefrontal, dorsal prefrontal exposure: 0 = present, large; 1 = reduced; 2 = absent or near absent.

Character 8 (Evers & Benson (2019): character 8). Prefrontal, cranial scutes on the prefrontal: 0 = one pair; 1 = two pairs or more.

Character 9 (Evers & Benson (2019): character 9). Prefrontal, sculpturing: 0 = heavily sculptured; 1 = sculpturing absent.

Character 10 (new character): Prefrontal, preorbital bulge formed between the prefrontal and premaxilla: 0 = absent; 1 = present.

Character 11 (Evers & Benson (2019): character 10). Lacrimal: 0 = present; 1 = absent.

Character 12 (Evers & Benson (2019): character 11). Frontal, frontal contribution to orbit: 0 = absent, contact between prefrontal and postorbital; 1 = present.

Character 13 (Evers & Benson (2019): character 12). Frontals, both frontals medially fused: 0 = absent; 1 = present.

Character 14 (Evers & Benson (2019): character 13). Frontal, direction of the orbits in dorsal view of the skull: 0 = laterally facing, with a very narrow to almost complete absent dorsal exposure of the maxilla and jugal; 1 = dorsolateral facing, with portions of the maxilla and jugal dorsally exposed.

Character 15 (Evers & Benson (2019): character 14). Frontals, development of crista cranii: 0 = crista cranii on ventral surface of frontals very shallow, sulcus olfactorius developed is a low trough; 1 = crista cranii developed as moderately deep parasagittal ridges on the ventral surface of each frontal, forming a ventrally open, median trough (the sulcus olfactorius) that extends from the anterior margin of the cavum cranii posteriorly to the fissura ethmoidalis anteriorly; 2 = crista cranii very deep anteriorly, forming extended processes that meet along the midline of the cranium and are sutured to one another, forming an ossified olfactory canal.

Character 16 (Evers & Benson (2019): character 15). Parietal, parietal-squamosal contact: 0 = present, upper temporal emargination absent or poorly developed; 1 = absent, upper temporal emargination well developed.

Character 17 (Evers & Benson (2019): character 16). Parietal, posterodorsal margin of the temporal fossa roofed by an overhanging process of the skull roof: 0 = absent; 1 = present.

Character 18 (Evers & Benson (2019): character 17). Parietal, contribution to the processus trochlearis oticum: 0 = absent; 1 = present.

Character 19 (Evers & Benson (2019): character 18). Parietals, foramen stapedio-temporalis: 0 = absent or weak, foramen stapedio-temporale concealed in dorsal view; 1 = moderate foramen stapedio-temporale, partial exposition of the processus trochlearis in dorsal view; 2 = strong, entire exposition of the processus trochlearis in dorsal view.

Character 20 (Evers & Benson (2019): character 19). Parietal, pineal foramen located medially between parietals: 0 = absent; 1 = present.

Character 21 (Evers & Benson (2019): character 20). Parietal, processus inferior parietalis: 0 = weak or absent, parietal does not contact the pterygoid, epipterygoid, and/or palatine; 1 = present and well developed, the parietal contacts the pterygoid, epipterygoid, and/or palatine.

Character 22 (Evers & Benson (2019): character 21). Parietal, closure of foramen nervi trigemini and the length of the anterior extension of the lateral braincase wall: 0 = foramen nervi trigemini anteriorly open, anterior extension of lateral braincase wall absent; 1 = foramen nervi trigemini anteriorly closed, processus inferior parietalis only produces a narrow strut anterior to the foramen nervi trigemini, usually absence of contact with palatine; 2 = foramen nervi trigemini anteriorly closed, processus inferior parietalis produces an extended process anterior to the foramen nervi trigemini, contact with palatine commonly present.

Character 23 (Evers & Benson (2019): character 22). Parietal, posterior ramus of processus inferior parietalis forming the posterior margin of the trigeminal foramen: 0 = absent; 1 = present.

Character 24 (Evers & Benson (2019): character 23). Posterior ramus of processus inferior parietalis of the parietal: 0 = short; 1 = long, excludes the prootic from the trigeminal foramen. This character is scored inapplicable for taxa that lack the process altogether.

Character 25 (Evers & Benson (2019): character 24). Parietal, ridge on lateral surface of processus inferior parietalis: 0 = absent; 1 = present, a ridge between the ventral surface of the parietal and the lateral surface of the descending process marks the border between the temporal and orbital fossae.

Character 26 (Evers & Benson (2019): character 25). Jugal, jugal-squamosal contact: 0 = present; 1 = absent.

Character 27 (Evers & Benson (2019): character 26). Jugal, jugal participation in the margin of the upper temporal emargination: 0 = absent; 1 = present, upper temporal emargination extensive.

Character 28 (Evers & Benson (2019): character 27). Jugal, medial process of jugal ventral to orbit: 0 = weakly developed or absent, jugal contacts only the maxilla; 1 = present and well developed, jugal contacts the maxilla as well as the palatine and/or pterygoid.

Character 29 (Evers & Benson (2019): character 28). Jugal, contact with the palatine: 0 = absent; 1 = present. This character is scored as inapplicable when the jugal lacks a medial process (ch 27.0).

Character 30 (Evers & Benson (2019): character 29). Jugal, contact with the pterygoid: 0 = absent; 1 = present. This character is scored as inapplicable when the jugal lacks a medial process (ch 27.0).

Character 31 (Evers & Benson (2019): character 30). Jugal, jugal-parietal contact: 0 = absent; 1 = present.

Character 32 (Evers & Benson (2019): character 31). Quadratojugal: 0 = present; 1 = absent.

Character 33 (Evers & Benson (2019): character 32). Quadratojugal, quadratojugal-maxilla contact: 0 = absent; 1 = present, jugal does not contribute to lower temporal emargination.

Character 34 (Evers & Benson (2019): character 33). Quadratojugal, quadratojugal-squamosal contact below the cavum tympani: 0 = absent; 1 = present.

Character 35 (Evers & Benson (2019): character 34). Quadratojugal, lower temporal emargination: 0 = weak to no emargination, the margin of the lower temporal emargination is formed by the quadratojugal or quadratojugal and jugal; 1 = moderate emargination, the margin of the lower temporal emargination is principally formed by the quadratojugal and jugal, but the maxilla is included in the anterior section of the margin and/or the quadrate is included in the posterior section of the margin; 2 = large emargination, the postorbital and/or squamosal and parietal are included in the margin of the lower temporal emargination.

Character 36 (Evers & Benson (2019): character 35). Squamosal, squamosal-postorbital contact: 0 = present; 1 = absent.

Character 37 (Evers & Benson (2019): character 36). Squamosal, squamosal-supraoccipital contact: 0 = absent; 1 = present.

Character 38 (Evers & Benson (2019): character 37). Squamosal, posterolateral protuberances developing horns: 0 = absent; 1 = present.

Character 39 (Evers & Benson (2019): character 38). Squamosal, very long posterior process, formed exclusively by the squamosal and protruding beyond condyles occipitalis: 0 = absent; 1 = present.

Character 40 (Evers & Benson (2019): character 39). Squamosal, squamosal-quadrate contact: 0 = tightly sutured; 1 = wide open.

Character 41 (Evers & Benson (2019): character 40). Squamosal, posterodorsal margin of cavum tympanum: 0 = the squamosal forms the posterodorsal margin of the cavum tympanum; 1 = the squamosal is excluded from the posterodorsal margin of the cavum tympanum.

Character 42 (Evers & Benson (2019): character 41). Postorbital, postorbital-palatine contact: 0 = absent; 1 = present, foramen palatinum posterius situated posterior to the orbital wall.

Character 43 (Evers & Benson (2019): character 42). Postorbital, contact with the quadratojugal: 0 = present; 1 = absent.

Character 44 (Evers & Benson (2019): character 43). Postorbital, postorbital-maxilla contact preventing the jugal from entering the orbital margin: 0 = absent; 1 = present.

Character 45 (Evers & Benson (2019): character 44). Postorbital, dorsal margin of orbit: 0 = continuously and concavely curved margin between frontals and jugal; 1 = frontal margin relatively narrow, with lateral bulge of postorbital.

Character 46 (Evers & Benson (2019): character 45). Supratemporal: 0 = present; 1 = absent.

Character 47 (Evers & Benson (2019): character 46). Teeth in premaxilla, maxilla, and dentary: 0 = present; 1 = absent.

Character 48 (Evers & Benson (2019): character 47). Premaxilla, subdivision of the apertura narium externa by an internarial process of the premaxilla: 0 = present; 1 = absent.

Character 49 (Evers & Benson (2019): character 48). Premaxilla, fusion of premaxillae: 0 = absent; 1 = present.

Character 50 (Evers & Benson (2019): character 49). Premaxilla, foramen praepalatium: 0 = absent; 1 = present.

Character 51 (Evers & Benson (2019): character 50). Premaxilla, foramen intermaxillaris: 0 = absent; 1 = present.

Character 52 (Evers & Benson (2019): character 51). Premaxilla, exclusion of the premaxillae from the apertura narium externa: 0 = absent; 1 = present.

Character 53 (Evers & Benson (2019): character 52). Premaxilla, distinct, median premaxillary hook along the labial margin of the premaxillae: 0 = absent; 1 = present.

Character 54 (Evers & Benson (2019): character 53) Premaxilla, cusps developed on the labial ridge in conjunction with maxilla: 0 = absent; 1 = present.

Character 55 (Evers & Benson (2019): character 54). Palatine, contribution to the anterior extension of the lateral braincase wall: 0 = absent; 1 = present.

Character 56 (Evers & Benson (2019): character 55). Palatine, contribution to the upper triturating surface: 0 = absent or less than 30% of the total width of the triturating surface; 1 = present, at least 30% or more of the total width of the triturating surface.

Character 57 (Evers & Benson (2019): character 56). Palatine, secondary palate: 0 = absent; 1 = present, complete separation of the narial cavity from the oral cavity.

Character 58 (Evers & Benson (2019): character 57). Palatine, vomer-palatine contact anterior to internal naris (apertura narium interna): 0 = absent; 1 = present.

Character 59 (Evers & Benson (2019): character 58). Maxilla, triturating surface definition: 0 = triturating surface with labial ridge only; 1 = triturating surface with labial and lingual ridge; 2 = triturating surface with labial, lingual, and accessory ridge(s).

Character 60 (Evers & Benson (2019): character 59). Maxilla, accessory ridge(s): 0 = accessory ridge(s) on maxilla present along the triturating surface; 1 = accessory ridge(s) only in some sectors of the triturating surface.

Character 61 (Evers & Benson (2019): character 60). Maxilla, median contact between right and left maxilla on the palate: 0 = absent; 1 = present.

Character 62 (Evers & Benson (2019): character 61). Vomer, number of vomer(s): 0 = paired; 1 = single, but large; 2 = single and greatly reduced or absent.

Character 63 (Evers & Benson (2019): character 62). Vomer, vomer-ptyergoid contact in palatal view: 0 = present; 1 = absent, medial contact of palatines present.

Character 64 (Evers & Benson (2019): character 63). Vomer, vomerine and palatine teeth: 0 = present; 1 = absent.

Character 65 (Evers & Benson (2019): character 64). Vomer, vomer-premaxilla contact in ventral view: 0 = present; 1 = absent.

Character 66 (Evers & Benson (2019): character 65). Vomer, ventral median crest: 0 = absent, ventral surface of vomer is smooth; 1 = present, shallow ridge extends along the ventral surface posterior to ventral process of the vomer, ridge becomes shallower posteriorly; 2 = narrow and tall ventral crest present all along the vomer.

Character 67 (Evers & Benson (2019): character 66). Vomer, shape of the palate roof: 0 = flat; 1 = domed.

Character 68 (Evers & Benson (2019): character 67). Vomer, shape of anterior end contacting the maxillae and praemaxillae: 0 = flat, near horizontal contact with maxillae; 1 = the anterior end of the vomer is anteroventrally directed and laterally expanded; 2 = the anterior end of the vomer is ventrally expanded to form a horizontal footplate with a flat ventral surface.

Character 69 (Evers & Benson (2019): character 68). Vomer, contribution to the upper triturating surface: 0 = absent, triturating surface narrow to absent; 1 = present.

Character 70 (Evers & Benson (2019): character 69). Vomer, median trough on dorsal surface posterior to sulcus vomeri: 0 = absent, dorsal surface of vomer flat or transversely convex; 1 = present, dorsal surface bears a median trough that extends posteriorly from the sulcus vomeri.

Character 71 (Evers & Benson (2019): character 70). Foramen orbito-nasale: 0 = formed as true foramen that is surrounded by bone from all sides; 1 = foramen orbito-nasale is not completely surrounded by bone and coalescent with the passage between the fossa orbitalis and the fossa nasalis.

Character 72 (Evers & Benson (2019): character 71). Foramen orbito-nasale, contribution of vomer: 0 = absent; 1 = present.

Character 73 (Evers & Benson (2019): character 72). Foramen orbito-nasale, contribution of the maxilla: 0 = absent; 1 = present.

Character 74 (Evers & Benson (2019): character 73). Quadrate, precolumellar fossa: 0 = absent; 1 = present.

Character 75 (Evers & Benson (2019): character 74). Quadrate, development of the cavum tympani: 0 = shallow, but not developed anteroposteriorly; 1 = shallow, but anteroposteriorly developed; 2 = deep and anteroposteriorly developed.

Character 76 (Evers & Benson (2019): character 75). Quadrate, anterior margin of the cavum tympanum: 0 = formed entirely by the quadrate; 1 = formed by the quadratojugal, which overlaps the lateral surface of the quadrate, reaching the anterior margin of the cavum tympanum.

Character 77 (Evers & Benson (2019): character 76). Quadrate, antrum postoticum: 0 = absent; 1 = incipient, the antrum postoticum is completely formed within quadrate (irrespective of the elements involved in forming the margin of the cavum tympanum); 2 = antrum postoticum fully developed, and extending posterodorsally into the squamosal (i.e. there is a large posterodorsal fenestra in the quadrate that leads to a pocket within the squamosal). This character is scored as inapplicable for turtles without a cavum tympanum.

Character 78 (Evers & Benson (2019): character 77). Quadrate, incisura columellae auris: 0 = absent, stapes extends posteroventrally to quadrate body; 1 = present, but open posteroventrally; 2 = present and closed, but only enclosing the stapes; 3 = present and closed, enclosing stapes and the Eustachian tube.

Character 79 (Evers & Benson (2019): character 78). Quadrate, formation of incisura columella auris: 0 = formed exclusively by quadrate; 1 = formed by quadrate and squamosal and/or quadratojugal.

Character 80 (Evers & Benson (2019): character 79). Quadrate, processus trochlearis oticum: 0 = absent; 1 = present, very reduced; 2 = present, large forming a well defined musculatory facet.

Character 81 (Evers & Benson (2019): character 80). Quadrate, contribution to the musculatory facet of the processus trochlearis oticum: 0 = extensive contribution; 1 = small contribution, facet formed principally by the protic and/or parietal. This character is scored as inapplicable when a processus trochlearis oticum is absent (ch 79.0).

Character 82 (Evers & Benson (2019): character 81). Quadrate, width of processus trochlearis oticum: 0 = the otic process spans all the mediolateral space between the braincase wall and the lateral surface of the skull; 1 = the otic process is limited to the medial part of the otic chamber, and there is a deep recess laterally. This character is scored as inapplicable when a processus trochlearis oticum is absent (ch 79.0).

Character 83 (Evers & Benson (2019): character 82). Quadrate, quadrate-basisphenoid contact: 0 = absent; 1 = present.

Character 84 (Evers & Benson (2019): character 83). Quadrate, infolding ridge on the posterior surface of the quadrate ventral to the incisura columella auris: 0 = absent; 1 = present.

Character 85 (Evers & Benson (2019): character 84). Quadrate, direction of cranial articular process: 0 = ventrolaterally directed; 1 = with strong posterior inclination.

Character 86 (Evers & Benson (2019): character 85). Posterior quadrate fossa: 0 = absent; 1 = present.

Character 87 (Evers & Benson (2019): character 86). Stapes, lateral articulation: 0 = stapes articulates with medial surface of the quadrate, quadrate has stapedial pit; 1 = stapes articulates with tympanic membrane, pit on medial surface of quadrate is absent.

Character 88 (Evers & Benson (2019): character 87). Epipterygoid: 0 = present; 1 = absent.

Character 89 (Evers & Benson (2019): character 88). Epipterygoid, shape: 0 = rod-like element; 1 = laminar element. This character is scored as inapplicable if an epipterygoid is absent (ch 87.1).

Character 90 (Evers & Benson (2019): character 89). Pterygoid, pterygoid teeth: 0 = present; 1 = absent.

Character 91 (Evers & Benson (2019): character 90). Pterygoid, basipterygoid process and basipterygoid articulation: 0 = basipterygoid process present with a movable basipterygoid articulation; 1 = basipterygoid process present with a sutured basipterygoid articulation; 2 = basipterygoid process absent and sutured basipterygoid articulation.

Character 92 (Evers & Benson (2019): character 91). Pterygoid, pterygoid-basioccipital contact: 0 = absent; 1 = present.

Character 93 (newly added from Hooks [1998]: character 10): Basioccipital, anterolateral edge of basioccipital with knob-like processes fitting into sockets on the posterior processes of the pterygoids: 0 = absent; 1 = present.

Character 94 (Evers & Benson (2019): character 92). Pterygoid, processus trochlearis pterygoideus: 0 = absent; 1 = present.

Character 95 (Evers & Benson (2019): character 93). Pterygoid, foramen palatinum posterius: 0 = present; 1 = present, but open laterally; 2 = absent.

Character 96 (Evers & Benson (2019): character 94). Pterygoid, medial contact of pterygoid: 0 = present, pterygoids in a very long medial contact with one another, longer than the basisphenoid total length in midline; 1 = present, pterygoids in medial contact with one another, contact length equal or shorter than the basisphenoid total length in midline; 2 = absent, contact of the basisphenoid with the vomer and/or palatines present.

Character 97 (Evers & Benson (2019): character 95). Pterygoid, pterygoid contribution to foramen palatinum posterius: 0 = present; 1 = absent. This character is scored inapplicable when the foramen palatinum posterius is absent (ch. 66.0).

Character 98 (Evers & Benson (2019): character 96). Pterygoid, contact with the exoccipital: 0 = absent; 1 = present.

Character 99 (Evers & Benson (2019): character 97). Pterygoid, fossa podocnemidoidea or cavum pterygoidei: 0 = absent; 1 = present.

Character 100 (Evers & Benson (2019): character 98). Pterygoid, lateral margin: 0 = a processus pterygoideus externus is developed as a process that projects into the subtemporal fenestra; 1 = the lateral margin of the pterygoid is gently expanded laterally and/or expanded dorsoventrally; 2 = absent, i.e. the lateral margin of the pterygoid forms a straight or concave outline that forms the medial margin of the subtemporal fenestra. Scored inapplicable for pleurodires.

Character 101 (Evers & Benson (2019): character 99). Pterygoid, processus pterygoideus externus: 0 = forming an extensive process that contacts the maxilla anterolaterally at the posteromedial end of the triturating surface, is anteriorly sutured to the anterior palate, and has a posterior projection into the subtemporal fenestra; 1 = forming a large lateral wing that projects as a free process into the subtemporal fenestra; 2 = forming a pointed triangular process that projects laterally into the subtemporal fenestra. Scored inapplicable for taxa that lack a processus pterygoideus externus (i.e. ch 98.1 or 98.2)

Character 102 (Evers & Benson (2019): character 100). Pterygoid, vertical flange on anterolateral margin of the pterygoid: 0 = absent; 1 = present. Zhou *et al.* (2014) & Joyce (2007: ch 67) (Pterygoid I).

Character 103 (Evers & Benson (2019): character 101). Pterygoid, level of the position of the pterygoid respect to basisphenoid: 0 = both bones are at the same level on ventral surface; 1 = two different levels, creating a step between the two bones.

Character 104 (Evers & Benson (2019): character 102). Pterygoid, ventral median ridge: 0 = incipient to absent; 1 = present, ridge spans nearly the full length of the pterygoids, sometimes reaching the most posterior portion of the vomer. This character is scored as inapplicable for taxa in which the pterygoids lack a midline contact.

Character 105 (Evers & Benson (2019): character 103). Pterygoid, extending laterally almost reaching the mandibular condyle facet: 0 = absent; 1 = present, the pterygoid contacts the medial edge of the mandibular condyle when is seen in ventral view; 2 = present, the pterygoids extends not only laterally to reach the outline of the mandibular condyle facet, but also posteriorly far from the level of the condyles.

Character 106 (Evers & Benson (2019): character 104). Pterygoid, ventral ridge on the palatal surface lateral to skull midline. 0 = absent; 1 = present, each pterygoid has a parasagittal ridge on its ventral surface.

Character 107 (Evers & Benson (2019): character 105). Pterygoid, extent of ventral ridge on the palatal surface lateral to skull midline: 0 = each ridge extends along most of the ventral surface of the pterygoid, from the anteromedial margin of the pterygoid fossa to the processus pterygoideus externus; 1 = each ridge extends only along the posterior part of the pterygoid, along the level of the parabasisphenoid. This character is scored inapplicable in turtles in which ventral pterygoid ridges are absent (ch 104.0).

Character 108 (Evers & Benson (2019): character 106). Pterygoid/Quadrate, flooring of cavum acustico-jugulare and recessus scalae tympani: 0 = absent; 1 = present, formed primarily by the posterior part of the pterygoid; 2 = present, produced by the ventral process of the quadrate or prootic or a posterolateral expansion of the parabasisphenoid.

Character 109 (Evers & Benson (2019): character 107). Pterygoid, posterior process: 0 = posterior process of pterygoid is absent, the cranioquadrate space or posterior foramen for the canalis cavernosus is not covered by the pterygoid; 1 = posterior process of pterygoid present but very short, process extends posteriorly to cover the posterior foramen for the canalis cavernosus (i.e. the modified cranioquadrate space), but the cavum-acustico jugulare remains largely exposed ventrally; 2 = posterior process of the pterygoid present and developed as an extensive sheet that projects posteriorly and covers large parts of the cavum acustico-jugulare.

Character 110 (Evers & Benson (2019): character 108). Pterygoid, development of a posteromedial wing covering partially to completely the basisphenoid and sometime the basioccipital too, seen in ventral view of the skull: 0 = absent; 1 = present.

Character 111 (Evers & Benson (2019): character 109). Pterygoid, pterygoid fossa: 0 = weakly developed; 1 = developed as a deep concavity between the articular process of the quadrate and the basicranium.

Character 112 (Evers & Benson (2019): character 110). Supraoccipital, crista supraoccipitalis: 0 = poorly developed; 1 = protruding significantly posterior to the foramen magnum.

Character 113 (Evers & Benson (2019): character 111). Supraoccipital, large supraoccipital exposure on dorsal skull roof: 0 = absent; 1 = present.

Character 114 (Evers & Benson (2019): character 112). Supraoccipital, horizontal crest in the crista supraoccipitalis: 0 = absent or poorly developed anteriorly; 1 = present, along the entire crista supraoccipitalis.

Character 115 (Evers & Benson (2019): character 113). Supraoccipital, fossa on the posterodorsal surface of the floor of the supratemporal fossa: 0 = absent; 1 = present, fossa is formed on the lateral surface of the supraoccipital, dorsal to the contact area between exoccipital, opisthotic, and supraoccipital.

Character 116 (Evers & Benson (2019): character 114). Exoccipital, medial contact of exoccipitals dorsal to foramen magnum: 0 = absent; 1 = present.

Character 117 (Evers & Benson (2019): character 115). Exoccipital, median contact of exoccipitals in the floor of the foramen magnum, excluding the basioccipital from the latter: 0 = absent; 1 = present.

Character 118 (Evers & Benson (2019): character 116). Foramen nervi hypoglossi (XII), ventral covering: 0 = exposed in ventral view; 1 = covered in ventral view by an extension of the pterygoid and the basioccipital; 2 = covered in ventral view an extension of the basioccipital; 3 = covered in ventral view by an expansion of the exoccipital and basioccipital.

Character 119 (Evers & Benson (2019): character 117). Exoccipital, foramina nervi hypoglossi: 0 = the foramina nervi hypoglossi exit the exoccipital on the occipital surface posteriorly to the margin of the fenestra postotica; 1 = at least one foramen nervi hypoglossi opens within the recessus scalae tympani anterior to margin of the fenestra postotica, and the others exit the exoccipital on the occipital surface; 2 = all foramina nervi hypoglossi open within the recessus scalae tympani anterior to the margin of the fenestra postotica.

Character 120 (Evers & Benson (2019): character 118). Basioccipital, morphology of the anteriormost part of the basioccipital: 0 = with two or one ventral tubercle; 1 = tubercle absent.

Character 121 (Evers & Benson (2019): character 119). Basioccipital, deep C-shaped concavity between basioccipital tubera: 0 = absent; 1 = present.

Character 122 (Evers & Benson (2019): character 120). Basioccipital, basal tubera: 0 = the basal tubera are completely formed by the basioccipital; 1 = the exoccipitals and the basioccipital form the basal tubera; 2 = the pterygoids and the basioccipital form the basal tubera; 3 = the basal tubera are formed by the exoccipitals, basioccipital and pterygoids.

Character 123 (Evers & Benson (2019): character 121). Prootic, dorsal exposure: 0 = large; 1 = very reduced or absent.

Character 124 (Evers & Benson (2019): character 122). Prootic, lateral semicircular canal enclosure by bone: 0 = canal only formed by bone of the opisthotic, the prootic portion of the canal is not ossified and is instead medially confluent with the recessus labyrinthicus prooticus; 1 = prootic and opisthotic both contribute to the formation of the lateral semicircular canal.

Character 125 (Evers & Benson (2019): character 123). Prootic, ventral process: 0 = ventral process is short and without extensive posterior contact with the pterygoid; 1 = ventral process is large, with a broad contact with the pterygoid along a posteriorly expanded footplate, forming parts of the floor of the inner ear cavity; 2 = ventral process is extensive, and forms parts of the floor of the basicranium so that it is visible on the ventral surface of the skull. This character is scored as inapplicable for taxa that lack an anatomically modern middle ear chamber.

Character 126 (Evers & Benson (2019): character 124). Prootic, unnamed foramen exiting into the subtemporal fossa from the canalis cavernosus: 0 = absent; 1 = present.

Character 127 (Evers & Benson (2019): character 125). Prootic/pterygoid, posteroventral elongation of the trigeminal foramen: 0 = absent, the trigeminal foramen is approximately circular or oval, but the ventral margin of the foramen is positioned above the level of the canalis/sulcus cavernosus; 1 = the trigeminal foramen is oval, anterodorsally-posteroventrally elongate and anteroventrally-posterodorsally narrow, and the ventral margin is level with the canalis/sulcus cavernosus. This character is scored inapplicable for turtles without a trigeminal foramen (i.e. without a neomorphic secondary lateral wall of the braincase formed by the parietal and pterygoid).

Character 128 (Evers & Benson (2019): character 126). Prootic, recess on posterior surface of the element anterodorsolaterally to the fenestra ovalis: 0 = absent; 1 = present.

Character 129 (Evers & Benson (2019): character 127). Prootic, position of the geniculate ganglion and the split of the facial nerve into the hyomandibular and palatine branches: 0 = the geniculate ganglion is positioned with the canalis cavernosus; 1 = the geniculate ganglion is positioned within the facial nerve canal; 2 = the geniculate ganglion is positioned in the canalis carotici interni.

Character 130 (Evers & Benson (2019): character 128). Prootic/opisthotic, enclosure of fenestra ovalis: 0 = the fenestra ovalis is ventrally enclosed by the prootic and opisthotic; 1 = the prootic and opisthotic do not have a contact ventrally to the fenestra ovalis.

Character 131 (Evers & Benson (2019): character 129). Opisthotic, wide transverse occipital plane with depression for the nuchal musculature: 0 = absent; 1 = present.

Character 132 (Evers & Benson (2019): character 130). Opisthotic, processus interfenestralis: 0 = developed as a robust ridge that does not form a ventrally projecting process and does not reach closely to the floor of the basicranium; 1 = incipient, developed as a ventrally low and mediolaterally broad, robust structure that separates the cavum labyrinthicum anteriorly from an incipient recessus scalae tympani posteriorly; 2 = present, developed as a ventrally directed process that separates the cavum labyrinthicum anteriorly from the recessus scalae tympani posteriorly.

Character 133 (Evers & Benson (2019): character 131). Opisthotic, development of the processus interfenestralis: 0 = developed as a ventrally directed process that separates the cavum labyrinthicum anteriorly from the recessus scalae tympani posteriorly, the process is not expanded at its ventral end, and almost or just about reaches the floor of the basicranium, but a small gap (hiatus postlagenum) usually remains; 1 = developed as a ventrally directed process that separates the cavum labyrinthicum anteriorly from the recessus scalae tympani posteriorly, but the process has a horizontally expanded footplate at its ventral end that is sutured to elements of the basicranium; 2 = developed as a ventrally directed process that separates the cavum labyrinthicum anteriorly from the recessus scalae tympani posteriorly, and the ventral surface of the process is integrated into the basicranium to form parts of the ventral surface of the cranium. This character is scored as inapplicable if an anatomically modern processus interfenestralis is absent (i.e. ch 131.0 or 131.1).

Character 134 (Evers & Benson (2019): character 132). Opisthotic, posterior surface of paroccipital process: 0 = the occipital side of the paroccipital process is developed as a posteriorly exposed, broad, planar or gently concave surface; 1 =

the occipital side of the paroccipital process is dorsoventrally flattened and forms a posterior ridge that traverses the paroccipital process mediolaterally; 2 = the paroccipital process has a dorsoventrally convex surface.

Character 135 (Evers & Benson (2019): character 133). Fenestra perilymphatica: 0 = large; 1 = reduced in size to that of a small foramen.

Character 136 (Evers & Benson (2019): character 134). Parabasisphenoid, paired pits on ventral surface of basisphenoid: 0 = absent; 1 = present.

Character 137 (Evers & Benson (2019): character 135). Parabasisphenoid, ventral surface: 0 = flat to slightly convex, with posterior margin straight or slightly concave; 1 = V-shaped crest, with posterior margin forming the basipterygoid process projected posterolaterally.

Character 138 (Evers & Benson (2019): character 136). Parabasisphenoid, rough surface between basisphenoid and basioccipital: 0 = absent; 1 = present.

Character 139 (Evers & Benson (2019): character 137). Parabasisphenoid, posterolateral processes lapping onto the ventral surface of the basioccipital: 0 = absent; 1 = present.

Character 140 (Evers & Benson (2019): character 138). Parabasisphenoid, rostrum basisphenoidale: 0 = flat; 1 = flat base, but with trabeculae contact one another medially forming a short rod at the anterior end of the parabasisphenoid; 2 = singular median, rod-like, thick and rounded process.

Character 141 (Evers & Benson (2019): character 139). Parabasisphenoid, dorsum sellae: 0 = deep, i.e. the dorsal surface of parabasisphenoid between the clinoid processes is a transversely concave floor forming a trough between the posterior part of the dorsal surface of the parabasisphenoid, which is usually cup-like, and the anterior portion of the parabasisphenoid forming the rostrum basisphenoidale and sella turcica; 1 = low, i.e. the dorsum sellae is formed as a transverse ridge between the clinoid processes that projects anteriorly at a low angle from posterodorsal surface of the parabasisphenoid; 2 = high, i.e. a transverse ridge or wall of bone between the clinoid processes is present that projects dorsally at a high angle from the posteriorly positioned cup, separating the cup very clearly from of the anteriorly positioned rostrum basisphenoidale and sella turcica.

Character 142 (Evers & Benson (2019): character 140). Parabasisphenoid, anterior surface of dorsum sellae: 0 = anterior surface of the dorsum sellae is flat and smooth; 1 = vertical median ridge on anterior surface of dorsum sellae between the clinoid processes is present, ridge may have a small anterodorsal projection.

Character 143 (Evers & Benson (2019): character 141). Parabasisphenoid, retractor bulbi pits on anterolateral surface: 0 = absent; 1 = present.

Character 144 (Evers & Benson (2019): character 142). Parabasisphenoid, foramina anterius canalis carotici cerebralis: 0 = widely separated; 1 = close together; 2 = right and left cerebral arteries converge within the parabasisphenoid and run within a short joint canal, and exit anteriorly into the cavum cranii via a single foramen within the sella turcica.

Character 145 (Evers & Benson (2019): character 143). Parabasisphenoid, prootic foramen in primary lateral wall of the braincase: 0 = present, the clinoid process of the parabasisphenoid and parts of the prootic, an ossified pila antotica, the laterosphenoid, and/or parts of the parietal form a foramen medially to the cavum epiptericum; 1 = the prootic foramen is reduced, and the clinoid processes are free structures.

Character 146 (Evers & Benson (2019): character 144). Parabasisphenoid, crista tuberculi basalis developed on posterior part of dorsal surface: 0 = absent, parabasisphenoid dorsal surface is relatively flat or gently concavely excavated; 1 = present as median, dorsally high projecting tubercle or ridge.

Character 147 (Evers & Benson (2019): character 145). Carotid artery/Pterygoid, interpterygoid vacuity: 0 = large opening, triangular in shape; 1 = reduced to an interpterygoid slit; 2 = entirely closed, no foramina posterius canalis carotici palatinum present. Scored inapplicable for taxa with a bony canal for the palatine artery (ch 146.1)

Character 148 (Evers & Benson (2019): character 146). Embedding of the palatine division of carotid artery: 0 = the palatine artery is not encased in a bony canal (artery enters the skull through the interpterygoid cavity, interpterygoid slit, or possibly other skull openings); 1 = the palatine artery is encased in a bony canal (irrespective of the exposure or embedding of the internal carotid artery split).

Character 149 (Evers & Benson (2019): character 147). Embedding of internal carotid artery and its bifurcation: 0 = Internal carotid arterial system is not embedded by bone, a foramen posterius canalis carotici is absent, and the split into palatine and cerebral artery occurs extracranially; 1 = internal carotid arterial system is partially embedded, a foramen posterius canalis carotici interni is present, and the split into palatine and cerebral artery happens at the fenestra carotica and is thus ventrally

exposed; 2 = internal carotid arterial system is ventrally fully embedded by bone, a foramen posterius canalis carotici interni is present and the split into palatine and cerebral artery is ventrally covered by bone.

Character 150 (Evers & Benson (2019): character 148). Position of the foramen posterius canalis carotici interni (fpcci): 0 = the fpcci is located at the ventral surface of the skull in a position far anterior to the margin of the fenestra postotica; 1 = the fpcci is located at the posterior end of the skull, either on the ventral surface of the skull close to the margin of the fenestra postotica, or on the posterior surface of the skull at the ventral margin of the fenestra postotica. This character is scored inapplicable for taxa that lack a foramen posterius canalis carotici interni.

Character 151 (Evers & Benson (2019): character 149). Entry of the internal carotid artery into skull relative to cavum acustico-jugulare: 0 = internal carotid enters the skull ventrally to the level of the cavum acustico-jugulare; 1 = internal carotid artery enters the skull within the cavum acustico-jugulare, artery lies in dorsally open through on dorsal surface of pterygoid and only becomes dorsally covered within the cavum acustico-jugulare.

Character 152 (Evers & Benson (2019): character 150). Dorsal exposure of the palatine artery and/or anterior parts of the internal carotid artery: 0 = absent, the split of the internal carotid artery is dorsally covered by bone, and the palatine artery exits the basicranium into the cavum cranii via the foramen anterius canalis carotici palatinum; 1 = the internal carotid artery exits the braincase anterodorsally into the sulcus cavernosus where it continues on the floor of the sulcus cavernosus (= sulcus caroticus of Gaffney 1979), and the split into cerebral and palatine arteries occurs within the sulcus cavernosus. The cerebral artery enters the parabasisphenoid medially, whereas the palatine artery continues in the sulcus cavernosus anteriorly without ever being embedded in a canal. This character is scored as inapplicable when the carotid split is ventrally exposed (i.e. ch 148.0 or 148.1).

Character 153 (Evers & Benson (2019): character 151). Formation of the foramen posterius canalis carotici interni, pterygoid involvement: 0 = present; 1 = absent.

Character 154 (Evers & Benson (2019): character 152). Formation of the foramen posterius canalis carotici interni, parabasisphenoid involvement: 0 = present; 1 = absent.

Character 155 (Evers & Benson (2019): character 153). Formation of the foramen posterius canalis carotici interni, quadrate involvement: 0 = present; 1 = absent.

Character 156 (Evers & Benson (2019): character 154). Formation of the foramen posterius canalis carotici interni, prootic involvement: 0 = present; 1 = absent.

Character 157 (Evers & Benson (2019): character 155). Hyomandibular branch of the facial nerve: 0 = contained within the canalis cavernosus; 1 = contained in a sulcus or separate canal paralleling the canalis cavernosus.

Character 158 (Evers & Benson (2019): character 156). Stapedial artery, foramen stapedio-temporale: 0 = present; 1 = absent.

Character 159 (Evers & Benson (2019): character 157). Stapedial artery, size of foramen stapedio-temporale: 0 = relatively large (the size of a large blood foramina, ≥ 5 mm diameter); 1 = significantly reduced in size (the size of a nerve foramina, ≤ 3 mm diameter). This character is scored as inapplicable for taxa without a foramen stapedio-temporale (i.e. ch 156.1).

Character 160 (Evers & Benson (2019): character 158). Stapedial artery, foramen stapedio-temporale location in the otic chamber: 0 = on dorsal part and pointing dorsally; 1 = on the anterior wall of the otic region, pointing anteriorly. This character is scored as inapplicable for taxa without a foramen stapedio-temporale (i.e. ch 156.1).

Character 161 (Evers & Benson (2019): character 159). Stapedial artery, formation of the foramen stapedio-temporale, contribution of the quadrate: 0 = absent; 1 = present. Scored inapplicable for taxa without a foramen stapedio-temporale. This character is scored as inapplicable for taxa without a foramen stapedio-temporale (i.e. ch 156.1).

Character 162 (Evers & Benson (2019): character 160). Stapedial artery, formation of the foramen stapedio-temporale, contribution of the prootic: 0 = absent; 1 = present. Scored inapplicable for taxa without a foramen stapedio-temporale. This character is scored as inapplicable for taxa without a foramen stapedio-temporale (i.e. ch 156.1).

Character 163 (Evers & Benson (2019): character 161). Stapedial artery, formation of the foramen stapedio-temporale, contribution of the opisthotic: 0 = absent; 1 = present. Scored inapplicable for taxa without a foramen stapedio-temporale. This character is scored as inapplicable for taxa without a foramen stapedio-temporale (i.e. ch 156.1).

Character 164 (Evers & Benson (2019): character 162). Stapedial artery, formation of the foramen stapedio-temporale, contribution of the supraoccipital: 0 = absent; 1 = present. Scored inapplicable for taxa without a foramen stapedio-temporale. This character is scored as inapplicable for taxa without a foramen stapedio-temporale (i.e. ch 156.1).

Character 165 (Evers & Benson (2019): character 163). Foramen jugulare posterius, relationship with the fenestra postotica: 0 = separate from fenestra postotica; 1 = coalescent with fenestra postotica.

Character 166 (Evers & Benson (2019): character 164). Foramen jugulare posterius, formation of lateral bar separating foramen from fenestra postotica: 0 = formed by pterygoid; 1 = formed by opisthotic and/or exoccipital. The character is scored inapplicable for taxa in which the foramen jugulare posterius is coalescent with the fenestra postotica (ch. 163.1).

Character 167 (Evers & Benson (2019): character 165). Recessus scalae tympani: 0 = almost nonexistent, not surrounded by bone; 1 = well developed.

Character 168 (Evers & Benson (2019): character 166). Cranial scutes, scute D meeting in midline: 0 = absent; 1 = present.

Character 169 (Evers & Benson (2019): character 167). Cranial scutes, scute X much smaller than scute D: 0 = absent; 1 = present.

Character 170 (Evers & Benson (2019): character 168). Cranial scutes, scute X partially separates scutes G: 0 = absent; 1 = present.

Character 171 (Evers & Benson (2019): character 169). Cranial scutes, scutes A, B, and C forming a continuous posterolateral shelf: 0 = absent; 1 = present.

Character 172 (Evers & Benson (2019): character 170). Cranial scutes, scute F: 0 = formed by several scutes; 1 = formed by a single scute.

Character 173 (Evers & Benson (2019): character 171). Cranial scutes, scute J: 0 = formed by several scutes; 1 = formed by a single scute.

Character 174 (Evers & Benson (2019): character 172). Dentary, medial contact of dentaries: 0 = fused; 1 = open suture.

Character 175 (Evers & Benson (2019): character 173). Dentary, width triturating surface vs. jaw length: 0 = narrow triturating surface, symphysis less than 1/3 of jaw length; 1 = broad triturating surface, symphysis \geq 1/3 jaw length.

Character 176 (Evers & Benson (2019): character 174). Dentary, symphyseal ridge: 0 = absent; 1 = present.

Character 177 (Evers & Benson (2019): character 175). Dentary, lingual (tomial) ridge: 0 = prominent; 1 = weak or absent.

Character 178 (Evers & Benson (2019): character 176). Dentary, size of foramen dentofaciale majus: 0 = small, size of a small vessel; 1 = enlarged, foramen is several mm in diameter.

Character 179 (Evers & Benson (2019): character 177). Dentary-Surangular arrangement: 0 = lack of a posterior expansion of dentary and anterior projection of surangular; 1 = posterior expansion of dentary present almost reaching the articular surface, covering the dorsal half of the surangular in lateral view, surangular with anterior projection.

Character 180 (Evers & Benson (2019): character 178). Surangular, with anteromedial process forming a vertical lamina that projects anteriorly into the fossa meckelii: 0 = absent; 1 = present.

Character 181 (Evers & Benson (2019): character 179). Coronoid, anteromedial process: 0 = absent; 1 = present.

Character 182 (Evers & Benson (2019): character 180). Coronoid, contribution to triturating surface: 0 = absent; 1 = present.

Character 183 (Evers & Benson (2019): character 181). Coronoid, notch on posterior margin of coronoid: 0 = absent; 1 = present.

Character 184 (Evers & Benson (2019): character 182). Coronoid, foramen at anterior end, leading from fossa meckelii into space between mandibular rami: 0 = absent; 1 = present.

Character 185 (Evers & Benson (2019): character 183). Coronoid process, principally formed by: 0 = coronoid; 1 = dentary; 2 = surangular.

Character 186 (Evers & Benson (2019): character 184). Coronoid process: 0 = relatively low, dorsally well rounded; 1 = relatively high, process is dorsally or posterodorsally pointed.

Character 187 (Evers & Benson (2019): character 185). Splenial: 0 = present; 1 = absent.

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Character 188 (Evers & Benson (2019): character 186). Carapace, carapacial scutes: 0 = present; 1 = absent.

Character 189 (Evers & Benson (2019): character 187). Carapace, carapacial scutes: 0 = present, fully covering the carapace; 1 = reduced not fully covering the carapace.

Character 190 (Evers & Benson (2019): character 188). Carapace, continuous keel on costals: 0 = absent; 1 = present.

Character 191 (Evers & Benson (2019): character 189). Carapace, continuous keel on neurals: 0 = absent; 1 = present.

Character 192 (Evers & Benson (2019): character 190). Shell, sculpturing of dorsal surface (carapace) and ventral surface (plastron): 0 = absent, smooth to slightly rugose; 1 = present, development of striations, vermiculations, striations, or pitting.

Character 193 (Evers & Benson (2019): character 191). Shell, pattern of sculpturing of the dorsal surface (carapace) and ventral surface (plastron): 0 = parallel to radial striations; 1 = vermiculation; 2 = highly dense pattern of pitting combined with striations; 3 = dichotomic striations; 4 = spread pitting without marked striation pattern; 5 = granules (positive relief).

Character 194 (Evers & Benson (2019): character 192). Carapacial Sutures: 0 = carapacial elements finely sutured or the contact is smooth; 1 = carapacial sutures strongly serrated in adult stage.

Character 195 (Evers & Benson (2019): character 193). Nuchal, articulation of nuchal with neural spine of eighth cervical vertebra: 0 = articulation via a blunt facet is present; 1 = articulation along a blunt facet absent.

Character 196 (Evers & Benson (2019): character 194). Raised pedestal on the visceral surface of the nuchal for the articulation with the neural spine of the eighth cervical vertebra: 0 = absent; 1 = present.

Character 197 (Evers & Benson (2019): character 195). Nuchal, elongate costiform process: 0 = absent; 1 = present.

Character 198 (Evers & Benson (2019): character 196). Nuchal, length of costiform process: 0 = crosses peripheral 1; 1 = reaches peripherals 2 or 3. This character is scored inapplicable for taxa without a costiform process on the nuchal (ch. 195.0).

Character 199 (Evers & Benson (2019): character 197). Nuchal, length versus width: 0 = wider than long; 1 = longer than wide or as long as wide.

Character 200 (Evers & Benson (2019): character 198). Nuchal, posteriomedial fontanelles: 0 = absent; 1 = present.

Character 201 (Evers & Benson (2019): character 199). Neurals, neural formula $6 > 4 < 6 < 6 < 6$: 0 = absent; 1 = present.

Character 202 (Evers & Benson (2019): character 200). Neurals, shape of neurals: 0 = very irregular in shape, wider than long or squared; 1 = regular, often perfectly hexagonal or pentagonal, longer than wide.

Character 203 (Evers & Benson (2019): character 201). Neurals: 0 = present; 1 = absent.

Character 204 (Evers & Benson (2019): character 202). Neurals, number of neurals: 0 = ten or more; 1 = nine or less.

Character 205 (Evers & Benson (2019): character 203). Peripheral Gutter: 0 = peripheral gutter absent or only anteriorly developed; 1 = peripheral gutter extensively developed along anterior and bridge peripherals.

Character 206 (Evers & Benson (2019): character 204). Peripherals: 0 = present; 1 = absent.

Character 207 (Evers & Benson (2019): character 205). Peripherals, number of peripherals: 0 = more than 11 pairs of peripherals present; 1 = 11 pairs of peripherals present; 2 = 10 pairs of peripherals present. This character is scored as inapplicable when peripherals are absent (ch. 204.1).

Character 208 (Evers & Benson (2019): character 206). Peripherals, anterior peripherals incised by musk ducts: 0 = absent; 1 = present.

Character 209 (Evers & Benson (2019): character 207). Costals, medial contact of the first pair of costals: 0 = absent; 1 = present.

Character 210 (Evers & Benson (2019): character 208). Costals, medial contact of posterior costals: 0 = absent; 1 = present.

Character 211 (Evers & Benson (2019): character 209). Costals, number of costals involved in medial contact: 0 = medial contact of up to three posterior costals; 1 = medial contact of all costals. This character is scored as inapplicable for turtles without a medial contact of posterior costals.

Character 212 (modified from Evers & Benson (2019): character 210): Costals, lateral ossification: 0 = all costals fully ossified laterally with strong sutural contact with peripherals, lack of dorsal exposure of distal end of costal ribs and absence of costo-peripheral fontanelles; 1 = lateral sutural contact between costals and peripherals absent in at least parts of

the costo-peripheral series, resulting in the presence of costo-peripheral fontanelles and/or the exposure of the distal rib ends.

Character 213 (modified from Evers & Benson (2019): character 210): Costals, position of costo-peripheral fontanelles and exposure of dorsal rib ends: 0 = limited to parts of the carapace; 1 = fontanelles and exposed rib ends present and retained in adults between all costals and along the anterior margin of the first costal. Scored as inapplicable for taxa that lack costo-peripheral fontanelles (character 212.0).

Character 214 (new character): Costal, fontanelle along anterior margin of costal 1: 0 = anterior margin of first costal positioned very close to nuchal and/or anteriormost peripherals, reducing the fontanelle to an anteroposteriorly narrow, slot-like opening; 1 = extensive fontanelle between first costal and anterior margin of carapace. Scored inapplicable for taxa without costo-peripheral fontanelles (character 212.0) or when costo-peripheral fontanelles are absent along the first costal.

Character 215 (new character): Posterior costals, shape: 0 = rectangular, much wider mediolaterally than long anteroposteriorly; 1 = square or hexagonal, as wide as long.

Character 216 (Evers & Benson (2019): character 211). Rib free peripherals: 0 = absent; 1 = present.

Character 217 (Evers & Benson (2019): character 212). Position of rib free peripherals: 0 = only present anterior and posterior to ribs; 1 = present between sixth and seventh ribs. This character is scored as inapplicable for taxa that lack rib free peripherals (ch. 211.0).

Character 218 (Evers & Benson (2019): character 213). Costals, alternative short and long ends in the lateral part of costals: 0 = absent; 1 = present.

Character 219 (Evers & Benson (2019): character 214). Costals, costal 9: 0 = present; 1 = absent.

Character 220 (Evers & Benson (2019): character 215). Costals, shape of Costal 3: 0 = tapering towards the lateral side of the shell or with parallel anterior and posterior borders; 1 = broadens towards the lateral side of the shell.

Character 221 (Evers & Benson (2019): character 216). Suprapygals: 0 = present; 1 = absent.

Character 222 (Evers & Benson (2019): character 217). Suprapygals, number of suprapygals: 0 = one; 1 = two; 2 = more than two.

Character 223 (Evers & Benson (2019): character 218). Suprapygals, size between suprapygals 1 and 2: 0 = suprapygals 1 smaller than suprapygals 2; 1 = suprapygals 1 larger. Reworded from KL (ch 88). Turtles with only one suprapygals or suprapygals absent are coded as inapplicable.

Character 224 (Evers & Benson (2019): character 219). Cervical scutes: 0 = present; 1 = cervical scutes absent.

Character 225 (Evers & Benson (2019): character 220). Number of cervical scutes: 0 = more than one cervical scute present; 1 = one cervical scute present. This character is scored as inapplicable when cervical scutes are absent (ch. 219.1)

Character 226 (Evers & Benson (2019): character 221). Pygal, posterior notch: 0 = present; 1 = absent.

Character 227 (Evers & Benson (2019): character 222). Supramarginals: 0 = present; 1 = absent.

Character 228 (Evers & Benson (2019): character 223). Supramarginals, separating marginal and pleurals: 0 = complete row present, fully separating marginals from pleurals; 1 = partial row present, incompletely separating marginals from pleurals. This character is scored as inapplicable for turtles in which supramarginals are absent.

Character 229 (Evers & Benson (2019): character 224). Vertebrae, shape of the vertebrae: 0 = vertebrae 2 to 4 significantly broader than pleurals; 1 = vertebrae 2 to 4 as narrow as, or narrower than, pleurals.

Character 230 (Evers & Benson (2019): character 225). Vertebrae, position of vertebral 3-4 sulcus in taxa with five vertebrae: 0 = sulcus positioned on neural 6; 1 = sulcus positioned on neural 5.

Character 231 (Evers & Benson (2019): character 226). Vertebrae, vertebral 3-4 sulcus with a wide posteriorly oriented medial embayment: 0 = absent; 1 = present.

Character 232 (Evers & Benson (2019): character 227). Vertebrae, vertebral 1: 0 = vertebral 1 does not enter anterior margin of carapace; 1 = enters anterior margin.

Character 233 (Evers & Benson (2019): character 228). Marginals, marginal scutes overlap onto costals: 0 = absent, marginals restricted to peripherals; 1 = present.

Character 234 (Evers & Benson (2019): character 229). Pleurals, at least one pair of additional pleural scutes located laterally of vertebral scute 1, with anterior contact with cervical scute: 0 = absent; 1 = present.

Character 235 (Evers & Benson (2019): character 230). Plastron, connection between carapace and plastron: 0 = osseous; 1 = ligamentous.

Character 236 (Evers & Benson (2019): character 231). Plastron, central plastral fontanelle: 0 = absent; 1 = present.

Character 237 (Evers & Benson (2019): character 232). Plastron, posterior plastral fontanelle, posterior plastral fontanelle between the xiphiplastra and/or the hypoplastra: 0 = absent in adult stage; 1 = retained in adult stage.

Character 238 (Evers & Benson (2019): character 233). Plastron, plastral kinesis: 0 = absent, scutes sulci and bony sutures do not overlap; 1 = present, scutes sulci coincide with epiplastral-hyoplastral contact.

Character 239 (Evers & Benson (2019): character 234). Plastron, plastral kinesis: 0 = between hyoplastron and hypoplastron; 1 = between hyoplastron and epiplastron- entoplastron.

Character 240 (Evers & Benson (2019): character 235). Plastron, hyo-hypoplastra contact: 0 = contact between hyo-hyoplastra absent or reduced; 1 = extensive contact between hyo-hyoplastra (even for those taxa with plastral kinesis).

Character 241 (modified from Evers & Benson (2019): character 236): Plastron, hyo-hypoplastra serrations: 0 = serrations on the lateral and medial margins absent or weakly developed; 1 = strong serrations present along the surfaces that face other bones, but serrations are absent along the margin of the central fontanelle and the lateral contact area of hyo- and hypoplastron; 2 = strong serrations along all margins but the anterolateral margin of the hyoplastra and the posterolateral margin of the hypoplastra present, giving these elements a 'star-shaped' appearance.

Character 242 (Evers & Benson (2019): character 237). Axillar and inguinal notches: 0 = deep U or V-shaped axillar and inguinal notches; 1 = very shallow axillar and inguinal notches, and long lateral edges.

Character 243 (Evers & Benson (2019): character 238). Entoplastron: 0 = present; 1 = absent.

Character 244 (Evers & Benson (2019): character 239). Entoplastron, anterior entoplastral process: 0 = present, medial contact of epiplastra absent; 1 = absent, medial contact of epiplastra present.

Character 245 (Evers & Benson (2019): character 241). Entoplastron, distinct posterolateral process: 0 = present; 1 = absent.

Character 246 (modified from Evers & Benson (2019): characters 240 & 242): Entoplastron, shape of the entoplastron: 0 = 'dagger-shaped', with dorsoventrally thick anterior end and long posterior process that extends along the dorsal surface of the plastron and sometimes reaches the mesoplastra; 1 = plate like and diamond-shaped or hexagonal in ventral view, with all margins of subequal length; 2 = T-shaped or triangular, i.e. entoplastron has a mediolaterally expanded anterior end and a progressively narrowing posterior process; 3 = strap like and V-shaped, with posterolateral processes diverging from the midline of the plastron.

Character 247 (new character): Entepiplastron: 0 = absent, entoplastron and epiplastra are separate elements; 1 = present, entoplastron is fused with epiplastra, resulting in a laterally extremely expanded entepiplastron wings.

Character 248 (Evers & Benson (2019): character 243). Entoplastron, suture with hyoplastra: 0 = tightly sutured; 1 = lightly sutured to almost absent contact between both.

Character 249 (modified from Evers & Benson (2019): character 244): Epiplastra, shape: 0 = epiplastra squarish in shape and forming parts of the anterior plastral lobe; 1 = epiplastra elongate, become narrower posteriorly along the anterolateral margin of the hyoplastron, and with gently convex lateral margin; 2 = epiplastra are laterally strongly expanded to a wing-like shape; 3 = epiplastra rod-like and anteriorly as narrow as posteriorly, with concave lateral margin.

Character 250 (Evers & Benson (2019): character 245). Epiplastra, very thick anterior lip in dorsal view: 0 = present; 1 = absent.

Character 251 (Evers & Benson (2019): character 246). Hyoplastra, contacts of axillary buttresses: 0 = absent to slightly contacting peripherals only; 1 = peripherals and costal 1.

Character 252 (Evers & Benson (2019): character 247). Hyoplastra, axillary buttresses: 0 = present; 1 = ossified axillary buttresses absent.

Character 253 (Evers & Benson (2019): character 248). Hyoplastra, termination of axillary buttresses: 0 = terminates on peripheral 1 or 2; 1 = terminates on peripheral 3; 2 = terminates on peripheral 4 or 5 level. This character is scored as inapplicable for turtles without axillary buttresses (ch. 247.1).

Character 254 (Evers & Benson (2019): character 249). Mesoplastron: 0 = present; 1 = absent.

Character 255 (Evers & Benson (2019): character 250). Number of mesoplastra: 0 = two; 1 = one. This character is scored as inapplicable when mesoplastra are absent (ch. 249.1).

Character 256 (Evers & Benson (2019): character 251). Mesoplastron, medial contact of mesoplastra: 0 = present, or virtually present when a central plastral fontanelle is present, absence of contact between hyoplastron and hypoplastron; 1 = absent, partial contact between hyoplastron and hypoplastron present.

Character 257 (Evers & Benson (2019): character 252). Hypoplastra, contacts of inguinal buttresses: 0 = absent to slightly contacting peripherals; 1 = peripheral and costal 5; 2 = peripheral, costals 5 and 6; 3 = peripherals and costal 4.

Character 258 (Evers & Benson (2019): character 253). Hypoplastra, termination of inguinal buttresses: 0 = peripheral 8; 1 = peripheral 7; 2 = peripheral 6.

Character 259 (Evers & Benson (2019): character 254). Xiphiplastra, distinct anal notch: 0 = absent; 1 = present.

Character 260 (modified from Evers & Benson (2019): character 255): Xiphiplastra, shape of xiphiplastra: 0 = triangular, trapezoidal, or rectangular plate-like element; 1 = anteroposterior elongate rods.

Character 261 (modified from Evers & Benson (2019): character 255): Xiphiplastra, articulation with hypoplastron: 0 = the xiphiplastra articulate with the hypoplastra along an anteriorly facing margin, forming a mediolaterally broad suture; 1 = the xiphiplastra have an elongate anterolateral process articulating along the posterolateral margin of the hypoplastron, resulting in an oblique suture, and the hypoplastra extend posteriorly along the anteromedial margin of the xiphiplastra.

Character 262 (modified from Evers & Benson (2019): character 255): Xiphiplastra, posteriorly in contact with one another, often sutured along the midline and forming a plastral lobe: 0 = present; 1 = absent.

Character 263 (Evers & Benson (2019): character 256). Plastral scutes: 0 = present; 1 = absent.

Character 264 (Evers & Benson (2019): character 257). Plastral scutes, midline sulcus: 0 = straight; 1 = distinctly sinuous, at least for part of its length.

Character 265 (Evers & Benson (2019): character 258). Gular, number of gulars: 0 = one pair of scutes; 1 = only one scute.

Character 266 (Evers & Benson (2019): character 259). Extragulars: 0 = present; 1 = absent.

Character 267 (Evers & Benson (2019): character 260). Extragulars, medial contact: 0 = absent; 1 = present, contacting one another anterior to gular(s); 2 = present, contacting one another posterior to gular(s).

Character 268 (Evers & Benson (2019): character 261). Extragulars, anterior plastral tuberosities: 0 = present; 1 = absent.

Character 269 (Evers & Benson (2019): character 262). Extragulars, restricted to epiplastra: 0 = present; 1 = absent, extragulars reach the entoplastron.

Character 270 (Evers & Benson (2019): character 263). Intergulars: 0 = absent; 1 = present.

Character 271 (Evers & Benson (2019): character 264). Humeral, number of pairs: 0 = one pair present; 1 = two pairs present, subdivided by a plastral hinge.

Character 272 (Evers & Benson (2019): character 265). Humeral, humero-pectoral sulcus: 0 = restricted to hypoplastra; 1 = crossing the posterior portion of entoplastron.

Character 273 (Evers & Benson (2019): character 266). Pectorals: 0 = present; 1 = absent.

Character 274 (Evers & Benson (2019): character 267). Pectorals, antero-posteriorly developed: 0 = present; 1 = absent, very short antero-posterior development.

Character 275 (Evers & Benson (2019): character 268). Abdominals: 0 = present; 1 = absent.

Character 276 (Evers & Benson (2019): character 269). Abdominals, medial contact to one another: 0 = present; 1 = absent. This character is scored as inapplicable for turtles that lack abdominals.

Character 277 (Evers & Benson (2019): character 270). Anal: 0 = only cover parts of the xiphiplastra; 1 = overlap anteromedially onto the hypoplastra.

Character 278 (Evers & Benson (2019): character 271). Inframarginals: 0 = present; 1 = absent.

Character 279 (Evers & Benson (2019): character 272). Number of inframarginals: 0 = more than two pair present, plastral scales do not contact marginals; 1 = two pair present (axillaries and inguinals), limited contact between plastral scales and marginals present. This character is scored as inapplicable when inframarginals are absent (ch. 271.1).

Character 280 (Evers & Benson (2019): character 273). Cervical ribs: 0 = large cervical ribs present; 1 = cervical ribs reduced or absent.

Character 281 (Evers & Benson (2019): character 274). Cervicals, position of the transverse processes: 0 = middle of the centrum; 1 = anterior end of the centrum.

Character 282 (Evers & Benson (2019): character 275). Cervicals, posterior cervicals with strongly developed ventral keels: 0 = absent or slightly developed in all vertebrae; 1 = present, more developed on posterior vertebrae.

Character 283 (Evers & Benson (2019): character 276). Cervicals, cervical 8 centrum significantly shorter than cervical 7: 0 = absent; 1 = present.

Character 284 (Evers & Benson (2019): character 277). Cervicals, triangular diapophyses: 0 = absent; 1 = present.

Character 285 (Evers & Benson (2019): character 278). Cervicals, central articulations of cervical vertebrae: 0 = articulations not formed, cervical vertebrae am- phicoelous or platycoelous; 1 = articulations formed, cervical vertebrae procoelous or opisthocelous.

Character 286 (Evers & Benson (2019): character 279). Cervicals, articulation between cervical 8 and dorsal vertebrae 1: 0 = 8 (dorsal 1; 1 = 8) dorsal 1; 2 = vertebrae articulate along zygapophyses only.

Character 287 (Evers & Benson (2019): character 280). Cervicals, biconvex cervical vertebrae in the middle of the neck: 0 = absent; 1 = present.

Character 288 (Evers & Benson (2019): character 281). Cervicals, biconvex cervical vertebra in the middle of the neck: 0 = cervical 2; 1 = cervical 3; 2 = cervical 4; 3 = cervical 5.

Character 289 (Evers & Benson (2019): character 282). Cervicals, biconcave cervical vertebrae: 0 = absent; 1 = present.

Character 290 (Evers & Benson (2019): character 283). Cervicals, double articulation between cervical 5 and 6: 0 = absent; 1 = present.

Character 291 (Evers & Benson (2019): character 284). Cervicals, double articulation between cervical 6 and 7: 0 = absent; 1 = present.

Character 292 (Evers & Benson (2019): character 285). Cervicals, central articulation between cervical 6 and 7: 0 = cervical 6 concave cervical 7 convex; 1 = platycoelous, cervical 6 II cervical 7.

Character 293 (Evers & Benson (2019): character 286). Cervicals, double articulation between cervical 7 and 8: 0 = absent; 1 = present.

Character 294 (Evers & Benson (2019): character 287). Cervicals, height versus length of centra and neural arch: 0 = total height of centra and neural arch longer than the anteroposterior length of the cervical centra; 1 = total height of centra and neural arch much shorter than the anteroposterior length of the cervical centra.

Character 295 (Evers & Benson (2019): character 288). Cervicals, modification of neural arch on cervical 8: 0 = neural arch without modification of postzygapophyses; 1 = neural arch with postzygapophyses pointing anteroventrally.

Character 296 (Evers & Benson (2019): character 289). Cervicals, postzygapophyses united in midline: 0 = absent; 1 = present.

Character 297 (Evers & Benson (2019): character 290). Cervicals, ventral process on cervical 8: 0 = absent; 1 = present, well developed (as tall or taller than the height of the centrum).

Character 298 (Evers & Benson (2019): character 291). Cervicals, shape of central articulation of cervicals 7 and 8: 0 = as high as wide; 1 = much wider than high.

Character 299 (Evers & Benson (2019): character 292). Ribs, length of first dorsal rib: 0 = long, extends full length of first costal and may even contact peripherals distally; 1 = intermediate, in contact with well-developed anterior bridge buttresses; 2 = intermediate to short, extends less than halfway across first costal.

Character 300 (Evers & Benson (2019): character 293). Ribs, contact of dorsal ribs 9 and 10 with costals: 0 = present; 1 = absent.

Character 301 (Evers & Benson (2019): character 294). Dorsal rib 10: 0 = long, spanning full length of costals and contacting peripherals distally; 1 = short, not spanning father distally than pelvis.

Character 302 (Evers & Benson (2019): character 295). Dorsals, anterior articulation of the first dorsal centrum: 0 = faces at most slightly anteroventrally; 1 = faces strongly anteroventrally.

Character 303 (Evers & Benson (2019): character 296). Caudals, tail club: 0 = present; 1 = absent.

Character 304 (Evers & Benson (2019): character 297). Caudals, anterior caudal centra: 0 = amphicoelous; 1 = procoelous or platycoelous; 2 = opisthocoelous.

Character 305 (Evers & Benson (2019): character 298). Caudals, posterior caudal centra: 0 = amphicoelous; 1 = procoelous or platycoelous; 2 = opisthocoelous.

Character 306 (Evers & Benson (2019): character 299). Caudals, chevrons: 0 = present on nearly all caudal vertebrae: 1 = absent, or only poorly developed, along the posterior caudal vertebrae.

Character 307 (Evers & Benson (2019): character 300). Caudals, tail ring: 0 = absent; 1 = present.

Character 308 (Evers & Benson (2019): character 301). Scapula, anterodorsal ridge of acromion: 0 = present; 1 = absent.

Character 309 (Evers & Benson (2019): character 302). Scapula, ventral ridge of acromion: 0 = present; 1 = absent developed proximally near glenoid.

Character 310 (Evers & Benson (2019): character 303). Scapula, horizontal ridge of acromion: 0 = well-developed, coracoid foramen present; 1 = reduced, only developed along distal portion of acromion.

Character 311 (Evers & Benson (2019): character 304). Scapula, glenoid neck on scapula: 0 = absent; 1 = present.

Character 312 (Evers & Benson (2019): character 305). Scapula, lamina between the dorsal process of the scapula and the acromion: 0 = well developed; 1 = reduced; 2 = absent.

Character 313 (Evers & Benson (2019): character 306). Scapula, internal angle between acromion process and scapular process $\geq 110^\circ$: 0 = absent; 1 = present.

Character 314 (Evers & Benson (2019): character 307). Coracoid, coracoid vs humerus length: 0 = shorter than humerus; 1 = at least as long as humerus.

Character 315 (Evers & Benson (2019): character 308). Coracoid, foramen: 0 = present; 1 = absent.

Character 316 (Evers & Benson (2019): character 309). Cleithrum: 0 = present; 1 = absent.

Character 317 (Evers & Benson (2019): character 310). Cleithrum, contact with carapace: 0 = present; 1 = osseous contact with carapace absent.

Character 318 (Evers & Benson (2019): character 311). Pelvis, pelvis-shell attachment: 0 = pelvis-shell attachment by ligaments; 1 = pelvis attached by strong sutural contact of the ischium and pubis with the plastron, and illium with the carapace.

Character 319 (Evers & Benson (2019): character 312). Pelvis, thyroid fenestra: 0 = coalescent; 1 = two separated fenestra completely or partially separated.

Character 320 (Evers & Benson (2019): character 313). Ilium, elongated iliac neck: 0 = absent; 1 = present.

Character 321 (Evers & Benson (2019): character 314). Ilium, iliac scar: 0 = extends from costals onto the peripherals and pygal; 1 = positioned on costals only.

Character 322 (Evers & Benson (2019): character 315). Ilium, shape of the ilium articular site on the visceral surface of the carapace: 0 = narrow and pointed posteriorly; 1 = oval.

Character 323 (Evers & Benson (2019): character 316). Ilium, posterior notch in acetabulum: 0 = absent; 1 = present.

Character 324 (Evers & Benson (2019): character 317). Ilium, thelial process: 0 = absent; 1 = present.

Character 325 (Evers & Benson (2019): character 318). Pubis, lateral process: 0 = small, poorly developed, columnar; 1 = well developed and flat.

Character 326 (Evers & Benson (2019): character 319). Pubis, epipubis process: 0 = osseous or calcified; 1 = cartilaginous or absent.

Character 327 (Evers & Benson (2019): character 320). Ischium, ischial contacts with plastron: 0 = contact via a large central tubercle; 1 = contact via two separate ischial processes.

Character 328 (Evers & Benson (2019): character 321). Ischium, lateral process of ischium or metischial process: 0 = absent; 1 = present.

Character 329 (Evers & Benson (2019): character 322). Hypoischium: 0 = present; 1 = absent.

Character 330 (Evers & Benson (2019): character 323). Humerus, ectepicondylar foramen: 0 = in a channel; 1 = only a groove.

Character 331 (Evers & Benson (2019): character 324). Humerus, proximal articular surface of humerus: 0 = with shoulder on preaxial side, upturned; 1 = without shoulder, not upturned.

Character 332 (Evers & Benson (2019): character 325). Humerus, lateral process of humerus: 0 = abuts caput humeri; 1 = slightly separated from caput humeri; 2 = located distal to caput humeri but along proximal end of shaft; 3 = located at middle of humeral shaft.

Character 333 (Evers & Benson (2019): character 330). Humerus, prominent anterior projection of lateral process: 0 = absent; 1 = present.

Character 334 (new character): Humerus, distal articulation: 0 = articular surface forms distinct trochlea; 1 = rounded epiphyseal surface without clearly defined articulation facets.

Character 335 (Evers & Benson (2019): character 331). Humerus, length of the humerus versus the width of the proximal end: 0 = two times or less the width of the proximal end; 1 = more than two times the width of the proximal end.

Character 336 (Evers & Benson (2019): character 332). Humerus, scar for Muscle latissimus dorsi and Muscle teres major: 0 = located anterior to humeral shaft; 1 = located at middle of shaft.

Character 337 (Evers & Benson (2019): character 333). Humerus, humerus length vs femur length: 0 = shorter than femur; 1 = longer than femur.

Character 338 (Evers & Benson (2019): character 334). Ulna, contact with radius through rugosity and ridge: 0 = absent; 1 = present.

Character 339 (Evers & Benson (2019): character 335). Radius, curves towards anterior: 0 = absent; 1 = present.

Character 340 (Evers & Benson (2019): character 336). Manus, phalangeal formula of the manus: 0 = most digits with two shortened phalanges; 1 = most digits with three elongated phalanges.

Character 341 (Evers & Benson (2019): character 337). Manus, rigid articulations in 1st and 2nd digit: 0 = absent; 1 = present.

Character 342 (Evers & Benson (2019): character 338). Manus, rigid articulations in 3rd to 5th digit: 0 = absent; 1 = present.

Character 343 (Evers & Benson (2019): character 339). Manus, flippers: 0 = absent; 1 = short flippers present; 2 = elongate flippers present. Joyce (2007: ch 134, Manus C).

Character 344 (Evers & Benson (2019): character 340). Ulnare, size of the ulnare vs the intermedium: 0 = smaller than intermedium; 1 = nearly as large as intermedium; 2 = much larger than intermedium.

Character 345 (new character): Size of proximal carpals vs. distal carpals: 0 = proximal carpals are of similar size with respect to distal carpals; 1 = proximal carpals are much larger than distal carpals.

Character 346 (new character): Relative lengths of manual phalanges on the 3rd and 4th digit: 0 = the 1st phalanx is longer than or equally long as the 2nd phalanx; 1 = the 2nd phalanx is longer than the 1st phalanx. This character is scored as inapplicable when the manus digits only have two phalanges (i.e. the second phalanx is an ungual).

Character 347 (new character): 3rd phalanx on 5th manual digit: 0 = absent; 1 = present.

Character 348 (new character): Longest digit in the manus: 0 = 4th digit; 1 = 3rd digit. This character is scored as inapplicable when the 3rd and 4th digits are equally long.

Character 349 (Evers & Benson (2019): character 341). Pes, number of digits: 0 = five; 1 = four.

Character 350 (Evers & Benson (2019): character 342). Manus and Pes, flattening of carpals and tarsal elements: 0 = absent; 1 = present.

Character 351 (Evers & Benson (2019): character 343). Manus and Pes, hyperphalangy manus digits 4 and 5, pes digit 4: 0 = absent; 1 = present.

Character 352 (modified from Evers & Bensons (2019): character 344): Femur, femoral trochanters: 0 = distinct, and separated from one another; 1 = connected by a ridge.

Character 353 (modified from Evers & Bensons (2019): character 344): Femur, intertrochanteric ridge: 0 = ridge is low and concave, creating a notch between the major and minor trochanter; 1 = ridge is high and obliterates intertrochanteric notch, and the proximal surface of the trochanters and their connecting ridge forms a continuous surface. This character is scored as inapplicable when an intertrochanteric ridge is absent (character 352.0)

Character 354 (new character): Femur, the connection between femoral head surface and the major trochanter: 0 = the femoral head and major trochanter have distinct proximal surfaces separated by a deep notch; 1 = the femoral head surface slopes toward the major trochanter and forms a continuous proximal surface with it.

Character 355 (Evers & Benson (2019): character 345). Tibia, tibial pit for pubotibialis and flexor tibialis internus muscles: 0 = absent; 1 = present.

Appendices 2- matrix based on the matrix of Evers & Benson (2019)

nstates 8;
xread
345 81

Rhinochelys_pulchriceps 001000011100210000110-0100--000000001100001110000000001-
0111010100001020[1 2]10201000011-121011010011001111200?00000201000000001020200002200210-
121000011000011001-1?????00110[0
1]1?00000??
??

Santanachelys_gaffneyi 0010000?11100?10?00110-?100--000000000?00001110?00000000?-
011101010?001021?1020?0?0011-121010000011001101200100?0??10????0????2???0000??????-
1200?0011?????????1?????00?0?????00000?0?0-000101001?00-20-0100--??01-0000?01100-0110111211?0011--
0?00?0?????????????11?????????0?????0?1?1????111021????0?--0??1?1??2?0---?010110102?1???

Bouliachelys_suteri 0011000?010001?0000110-0100--000?00?0?1?0?0011100000000001-
011101010000102010201010011-12101011001100111120010000020100010000010202100002210210-
12100011100001101-
1?????0011011100?001??
??

Notochelone_costata ???000?111002??0?0110-0?00--00?000??1?0000111000?0000001-
?1110100010010???102000?0?11-121010000011001111200??1?????0000010010200000?02210210-
121000011000011001-
1?????0011??
?????????????0??

Ocepechelon_bouyai 0000?01011101?0?00011???100--000000001?10000111100000?0000-
011101000?00?0201020?0?00101121020-100110010-120000?0120100?????002??00000221?1??-
1210?0111?000????1-
1??
??

Desmatochelys_lowii 001000101110011[0 1]001111?0100--0000000010000011101000000001-
011101010?001020110201000011-121000110011001??12001000??0??0?001?0002120000221021?-
121000111000011101-1?????0001?0???????10000-0100-0101010?001120-010??01?1-?100001110-0110111211101-1-
-0-0000??????????????1011011120?0010000201?????111021111-0?1--0011101112001101011111102?1?1?

Desmatochelys_padillai 0010??1?11100?10011?????100--
000000000?100001110?000?000??01110??0?0010201102??0?001??12101001002?00111200100?01201000??????02?2
?0000??????-1210?0011?00011101-1?????00??0??0?00?0000-0100-0001010?00??2??0?0??01?1-

????0001??10110111200000100002?10?????1110211????????????????????11200110
1??11?1102?1???

Protostega_gigas 1--0??0011000??0?00?0??0?100--000000?0??00001110?001000001-
011100000??02?21?21?0?0?1??1?102?-102-1011??1?0?100?0?0?1000?????02??000??????-
1200?0011?000?????1?????000100?00?0001-010-0100-000101001000-20-00000-1-11----0--1110-0110111312101-1--0-
021-----111?011120????1000020101110111021111-001--0011101112001101111111020101?

Archelon_ischyros 1--0??0011000?00?001????100--0000?0001000011110?001000001-
011100000??021210??0?0?101121020-102-?011??1200100?0?0?10?0?????02??000??????-
?????????000?????1?????0001?0?????11-010-0100-00011-001000-20-00000-1-11----0--1110-0110111312101-1--0-
021-----101?011?????????0??201?1110111021111-001--0011101112001101111111020101?

Dermochelys_coriacea 1--1010011000001-00100-0000--00000000010010011101000100010-
0101010000011021210100000011-121021-002--0000-1200000[0 1]00001030-01-0010202000000210111-
1211?0111000011101-1-----0001011--0-2011--0-?0110--00-1--1-00-----0--1--1-----111-?0011-----1101-1--0-021-----
-----111101112000110000120-011110111021111-011--0011-01113010011010011102?1?10

Eosphargis_breineri 1--1??0?11000??1?00?????100--000000????0001110?0001?0011-
010101010??02??10??000?1??120020-002-?1000-1200000?00?0111???????0??0110??????-1211?011?????????1-
1??
?????????????0??

Lepidochelys_olivacea 1--1010111000101000110-01011000000000010000111100000001110-
0101000211011021210201000011-121020-100201100-1201100[0 1]0000110000010010201001002210210-
121010111000011001-1?????011111100100100010-0110-00011-00?000-2110100110111-1100?11110-0000111211101-
1--0-020001---0[0 1]000000011101112000111000120111110111020111-001--00111011120100011101110101020

Caretta_caretta 1--1010111000101000110-01011000000000010000111100000001110-
110110021001102121020100[0 1]011-121020-101-11100-12011100000011-000011010202001002210211-
121010111000011101-1?????000111100100100010-0110-000101000000-3110100100111-1100011110-0000111211101-
1--0-020001---[0 1]0[0 1]000000011101112000111000120111110111020111-001--00111011120100011101110101020

Chelonia_mydas 1--1010?11100101000110-
010111000000000100001111000000011120010100021000102121010100001[0 1]1121020-102-00000-
1201100101001110001110102000010020-0111-121010111000011001-1?????0011110100000100010-0110-0[0 1]011-
001000-310010011011-1100001110-0000111211101-1--0-020001---10[0 1]00000001110111200011100[0
1]120111110111021111-001--00111011120100011101110101?10

Eretmochelys_imbricata 1--1010111100101000110-
0101100000000001000011110000000111200101000211011021210201000011-121020-100211100-
120110000010111000010010200001002210111-121010111000011001-1?????000011100000100000-0110-0[0 1]011-
001000-2110100110101-1100001110-0000111211101-1--0-020001---10[0
1]000000011101112000111000120111110111021111-001--00111011120100011101110101020

Lepidochelys_kempii 1--1010111100101000110-01011100000000010000111100001001112-
0101000211011021210201000011-121020-100211000-1201100[0 1]0000110000011010202001002210110-
121010111000011001-1?????0011101100000100000-0110-00011-00?000-2110100110111-1100011110-0000111211101-
1--0-020001---0[0 1]000000011101112000111000120111110111020111-001--00111011120100011101110101020

Natator_depressus 1--1010011100101000110-
0101110000000001000011110000000111200101000211011020210101000011-121020-100211100-
120110010000110000010010202001002210211-121010111000011001-1?????0010110100100100000-0110-
000101001000-2110100110101-1100001110-0000111211101-1--0-020001---10[0
1]000000011101112000111000120111110111021111-001--0011101112010001?1101110101011

Puppigerus_camperi 1--1010011100100000110-0101110000000010000111100000001110-
010101021001102121021?000011-121020-100211100-120110010000110000001010202001001200110-
121100111000011001-1?????0111101100?00100000-0100-000101001000-2100100110111-1100001110-0000111211101-
1--0-02000????????000?1111011120001110001201?????111021111-0?????????112000010110?1101?1?1

Argillochelys_cuneiceps 1--1000011100101000110-0101110000000010000111100000001111-
01010002100010212102010000101121020-1002?1100-120110010100110000010010202001002210111-
121100110000011001-
1?????0011101100?001??11
11011120001110001?010??

Allopleuron_hoffmanni 1--10000111001?1000110-00011?0000000010010011101000001110-
010100021?001021110111001010112100011002?1100-1201???1000011000010000212001002210111-
12100011100001100011?????0000???10000001-010-0100-000101001000-20-0100111-01-1100001110-0100111211101-
1--0-021-----1111011120001110001201011110111021111-001--00111011120000010110111010101?

Toxochelys_sp. 0011000?1110111001011??101010000000011?00001110100000[0 1]011-01010001[0
1]00010212102000000101121000010001000111200100000001000?000?0?0202001000200111-121000111000011001-
1?????1001[0 1]11100100100000-0110-010101001000-20-0100110111-11000011[0 1]0-0000111211101-1--0-
0200???1???1011011?10111200?0?0??1?0101?001110?00??000?--0??111??100---?01101010?1?00

Eachelone_brabantica 1--1000011100100000110-010111000000001000011110000000001-
01010001100010212101000000101121020-100210000-120110000100112000011010200001001200011-
12100011100001100101?????00011?11000001??
??

Solnhofia_parsonsi 0011000?111011??100111101010100001?00?000?0011100000000100-
11111002000010202102010101011210001001-000101100???100201110[0 1]0000110200000000100110-
121000111000011001-1?????011100111101000000-0?????0101001?01121-01002?01?1-0100?01100-
0000???111?0001--000000?????000?000?110?00-----???????1?1???111020???0?0?--?0?1?1??000---
1?0?01000?0000?

Jurassichelon_oleronensis 0010001?1110110001011110100--00001000010000011101000000001-
0111000000001021210200011010111101101001100110120100010?00100010001100212000000200110-
111000011100011001-1?????011100111101000000-0?????0100-0001010????0?????10?????????????????1?0-000?????1?1?1001--
????00?????0?0?00??11?000-----0?0?1????????????????????????????????1????????????????????????

Portlandemys_mcdowellii 0010001?111011??00011110?00--??0?0000100?0011101000000001-
010100000000102?210201011010111100001000100?101201?0010100100010001[0 1]00212000000200110-
121000011000011001-
1?????000000?1001010??
??

Plesiochelys_planiceps ???0000?111011?00?011110100--0?0?2?00?100?0?11?0100?000001-
011100000000102?210201011010112101000001100110110110010120100000001110202000000210110-
121000011100011001-
1?????00000011011010??
??

Plesiochelys_etaloni 0011000?111011?00?011110100--00001000010000111101000000001-
0101000000001020210201011010112?0100000110010-1200?????????0000001110202000000210100-
121000011100011001?1?????000000010110100000?0100-000101001?01121-0100100001-0100000[0 1]00-
000011101?1?1--10000000100000010010?????????????????0010?????1110?????0?1--0?????1?000---
10?001000???????

Sandownia_harrisi 0111001?111011?0000121101010100000000?0?000011100000011110-
01010002100010202020001101011110001101--00110121100000010-0?010001010201000-00000010-

110110?0???1?00?0???020?000001?0?0-121100110?0001100??------????????????0011?01011?0?0001?00-00-
?10?????1-1100001000-10001111?1?0??1--0?000001-1-00??010?11??111????????????1?????11102?????0?1--
01????1?????????0?1000??????

Chrysemys_picta 1--100001110[0 1]110020110-
010111000011001010000111010000000020010102001100102121020000001011210011000210000-
120010010020101111000010200000000100010-12110011000001100011-----0000101110000100000-0100-
100101001000-00-01000-0101-1100000000-100011110111011--10100001-1-
0000100001111101112111011101020111110111020011-011--000111110010---1?000100010000?

Emys_orbicularis 1--1000011000110020111101010100001100001000011101000000000-
010100000100002121010000001011200011000210000-120010000120100101001010200000000101011-
121100110?0001100011-----0000?0?????100000-0100-100101001000-00-01000-0101-11000010010100010110110011-
?01000001-1-00100000?111101112101011101020111111?111020011-011--00?11?110010---1?000100010000?

Geoclemys_hamiltonii 1--10000110001101201111011110000100001010011101000000000-
0101021111000021210200000010112100110002100010120010000020103101001010200000000100010-
12110011110001100011-----000010?010000100110-0100-100101001100-00-0100100111-1100000000-
100011110101011--11100001-1-001010000111101112101011101020111110111020011-011--000111110010---
1?000100010000?

Testudo 1--100001110011012011110100--
000011000010100111010000000020010102000100002012010000001011210011000200000-
120010010100100101001010200000000101010-12110011010001100011-----0000000000010100000-0100-
100001001000-00-1100100111-1100000000-100011110101001--00100001-1-
0000100001111101112101011101020111110111020011-011--000111110010---1?000000011000?

Gopherus_polyphemus 1--1000011100110020120-0100--0000110000[0
1]0000111010000100020010102100101002112010000001011210010000210100-1200100001001000-
11000102200000000-1010-12110011010001100011-----0000100010000100000-0100-100001001000-00-1100100111-
1100000000-100011110101001--10100001-1-0000100001111101112101011101020111110111020011-011--
000111100010---1?000000011000?

Chelonoidis_sp. 1--1000011101[1 2]1012011110100--
00001100000000011101000000002001010210010000201201000000101121001000021000111200100001001000-
1001010220[0 1]00000101010-12110011010001110011-----000000000000100000-0100-000001001100-00-0100100101-
1100001000-1000111101101-1--02100001-1-00000000001101011121010111000201111200111020011-001--
000111100000---1?0001000100?0?

Platysternon_megacephalum 1--1000011000[1 2]11000111001011100100000000001011101001000001-
01010100010010220210000010112100010002010010120110000201000011110102000000020-0110-
121100111000001001-1-----0000001[0 1]01001100000-0100-000001001100-00-0100100101-1100001000-
1000111101101-1--02100001-1-00000000001101011121010111000201111200111020011-001--000111100000---
1?0001000100?0?

Apalone_spinifera 1--1010011101110120120-1111110000100100010011110110010001-
11112000101102122021000001011210020101-10-10-120010110110100000011010201000000100010-
120000111000011001-1-----000100011100111-00120100-000101-1-001000-0101--1--1-----11[0 1]0-1000111411101-1--
0-001----1-----11010120-0010111000201-11110111020011-001--001110111010---1?000100110010?

Pelodiscus_sinensis 1--1010011101110120120-1111110000100100010011110110010000-
11112000101102122021000001011210021101-10-10-120010110110100010011010201000000100010-
12000011100001100[0 1]11-----000100011100111-00120100-000101-1-001000-0101--1--1-----1110-10001114111-1-1--
--001-----110?0120-00?011100020--1??10??0010?

Lissemys_punctata 1--1010011101110120120-11111010000100100010011110110010000-
11112000001102122021000001011210021101-00-20-120010110110100000011010201000000100010-

Judithemys_sukhanovi

??1??0?11?01??0?101????101??0001?001000?00111??0?00?000??010102000?0??021210??0?001??1210010100010001
01200100?0100100??????0??1000010101?-1110-0111?000????1-1????000100?????0?00000?0100-000101001?00-
00-01001001?1-1100001000-100011211?0001--0000001-1?000000[0 1]00?111011120[0 1]0001[0
1]0102?10112101110200?1-0?1--00??1?100000---1?0??1000?00?0?

Annemys_levensis

00110000111011?00201110?101?10000200010[0 1]000011101000000000-
010102000?0??02021010000001011100010?0001000??1101100001001000?01??020000010??????1?110-
0?11?00011001-1011?0?000000?100000000000-0100-000101101101000-0100100111-1010101000-100011110110001--
000001000100000000100?????????????????0?00?????11102001010?1--?0????00000---1?0???????????

Annemys_latiens

0010??1?11101??00201110?10??0?0??0?????01?1??0??0?????????????????????101000?0010011?0?1??0?
??0?????0?0?0?????0?1??????2??00?0?????0[0 1]110-0?11?0001100?????????????????????00000-0100-
000101101?0[0 1]?00-0100100111-1[0 1]10101000-100011110110001--
000001000100000000100?????????????????????????????????????0?1--?????00000---1?0???????????

Annemys_sp_IVPP_V18106

0110001?1110110002011??01010100002000101000?11101000000000-
010102000000102021010100?0101110001000001000101101100?0?201000?10111?0210?00000101100-1110-
0011100011001-
1??
??

Xinjiangchelys_wusu

0110?01011101?00020????101??0000100010?00001110?0000?????01?1?2?00??0211101000?001??11000101000100?
??1201100?0?201000?????0200?0000?????0[0 1]110-0111?00011001-1011??00??0?1????0000000-
0?0??00010110110[0 1]?00-0100100111-1100101000-10001?110110001--00000000010000000010000??0?-----
1?0?????????????????????????????????0?000---1?0??100000000?

Xinjiangchelys_radiplicatoides

0110??1?111011?00?011????0??0????0????00111?00?0?0?????11?????????02111010?0?0?1011110?2??0
??0-?1012?0?00001201000?001??0200000000201110-1110-0011000011001-1??????0?1?????????100000-0100-
000??101?00-00-0100100111-1100??000-10001?110110001--
000001000100000000100?????????????????0?0?????111?200101?????????00000---1?????????????

Dracochelys_bicuspis

???1000?11101??0?01???1010100001?0????000111010001?0001-
010100000?0?020?101010000101111001010001000101201?0?0?2010?????????02??0000??????10110-
0?11?0001100?1?????000?00?0?0010000??1100-000101001?00-10-0110101-0??1101?01100-1000??211?0001--
00000?????????????????0111?110-000001000?0010????01110200??0?????????0?000---1?0??000?????

Kirgizemys_hoburensis

0011000?1110110001011110101010?0020001010?0011101000000000-
010102000?001020?1010000001011110010?0001000101100100100100001001??02?0?100001010?0-1111-
0110?0001100011?????0001?0??????00000-0100-000101101?00-00-010??0111-1100001000-100011121110001--
0?000001-1?000000[0 1]10?111?111200000110?2?10?????????2??1-0?1?????????0?000---1?????????????

Kirgizemys_dmitrievi

???1000?111001?001?111??101010000200010000001110?0000?0001-
000101000?001020?00001011?100100000?000??00100?0??01000?00??02?0?1000?1110??-1111-
0?1??00011101-
??????000100?000000??
??

Sinemys_gamera

01100?1?1110111002011??1101010?02100?000?0011??0?0?0?0-
0????????????120220100000010111000?00000100010120110010?001000?00?00220?1000??????-1110-
0111?00011001-1?????????????????00001?0??????1?????100-2??010?????1-
?10??1????100?????01?00??00?0?0??1?????00??0000???1??
????????????

Sinemys_lens

0010??1?11101?100201????101??0??02?0000??00111??0000??0??????0??????202201000?0?1??1?000100000?00010
110110?????10?0?????022??1000?????-1110-0111?0001100??1?????00?????????0000?0100-000101001100-20-
0100101--1-1101001[0 1]00-100011121010001--
000100??1?0?0000?10?1?0????0????????0??1????????????0????????????????????????????????1000?000??

Meiolania_planiceps

0000000011000101000110-

000101000100110000000110010000000020010102100000102103110000[0 1]0101121001[0 1]100000000-12001100000[0
1]11211100110020?0000000-101010111-0111100001101-1111110000000000100000000-?100-00??001000-00-
?1????0101-0?00101100-0000101001?0011--000000001000????????01000111200000000000?0022011110000101011--
00001??00000--0?000000010000?

Chubutemys_copelloi

??1000?11000?01?0011??10000000?000?00000011??0?000000-

011102000????0202101?000001??1100011000000001?010010000?00110?????0020??0000??????100-----???????1-
1????????????????00??0??0????????0??0????????0????????0????????0????????0????????0????????0????????0????
?1?1????????0????0????1110?0??

Eubaena_cephalica

0000002?1100011002011??1011100001000000001011101000000001-

0101020001000021210100000011-12100101000?000101201100000201020?00??1210?0001010?110200-----
?00011011-
1?????0000?0?????0??
??

Arundelemys_dardeni

0100001?111001??020110-1?01?1?0??0??0?10?1101000000001-

0101000000?0?02??101000000101111001010001000111201?000000010200101110020?000000101110200-----
0000????1-
1??
??

Pleurosternon_bullockii

0110001?111001001001?1?110111000011000000010111010000?0000-

01??00000??020110110000010111?0020?00010-0101101?00?0?????01100111022110001010111[0 1]200---
???00001100??1????????????????????0000130??0-0?0101001?00-00-01000-1-11-0100100000-
00001??101?010101000001001000000000000??0-----?0?000?0?????????????0?1--
00????????????????????????

Glyptops_plicatulus

01100?1?111001?0?0011??101?100?0100000?0010111??0?0?00?1-

0101000?0??0201101?000001011110020?00010-0101101?0?002?100?1100??0211?000101011?0200---
???0000?????1?????00?0?0??0?00000100100-000101001?00-00-0100100111-0100100000-
00001111011101010100000000100000000000?00010-----?0?000101??01112001010?1--00??1?100000---
1?0???????????

Kallokibotion_bajazidi

0000??0?1110010100011??10??0000000000?001100100000?00??110102??0??0202102000?00101111?0?

?00??0001?1200?00?00-111211100010120000000101111-10-----000011001-1?????00?1??????00?00000-0000-
000101??0000-00-010011??1?00?000?000-00001?1101?00011?200000001000?000000?00000-----0?0??????-
001110100101011--0000??00000--0????????????

Eileanchelys_waldmanni

00000?1?1110??0?-001???1011?0000?00?0?00??11010000??0??01?100000??020?100-

000001??0?0??00??0?0?0?01010?00000[0 1]1000010?01002010?000????????????????100011001-
1?????10????????????00?0-0??000001101?00-00-01001001?1-0000??000-
00001?000?????????0?0?00??00?0??00??
?

Kayentachelys_aprix

0000001011100101-00000-11011100000000000000?110?000000001-

010100000??0201100--0010100010001000000000-0101000?0?001000?-0??001-101000-11111[0 1]000-----
?0001100--0?????1000?0?00000000000-0000-0000000?100-00-00000-0111-0000001000-
0000001000?000010000000000100000000000?0?00-----?0000000100001010?00101011--00001?10?000---
?????000????0?

Australochelys_africanus ???10?00?0101-00000-1?0???0000?000?0000?10?00?000001-0?01?01000??01?00-0--
000?1??11000?000000000-0000?01??0?0?0?-??0?010-1-00?0-211?10000-----??????-
0??
??

Proganochelys_quenstedti 0000100?00000101-00000-0001010000000000-010001000000000001-000000100100000--0-
0--00000?0000010000000000-000-0001000000-0?-0-0?000-0-0000-200100000-----?0001010--
0?????000000000000000000[0 1]00000-?0?00000001000-??0??010000-00?00000-
000000000?0??0100?0000000100000000?010000-----0000000000000000000000010--00000?000000---
0?0000000000000?
force/(Proganochelys(((Pelomedusa_subrufa Podocnemis)((Chelus_fimbriatus Phrynops_geoffranus)(Chelodina
Elseya_dentata)))(Carettochelys_insculpta (Lissemys_punctata (Pelodiscus_sinensis
Apalone_spinifera)))(Platysternon_megacephalum(Emys_orbicularis Chrysemys_picta))(Geoclemys_hamiltonii
(Gopherus_polyphemus (Testudo_Chelonoidis_sp.)))(Macrochelys_temmincki Chelydra_serpentina)(Dermatemys_mawii
(Staurotypus (Kinosternon_suburum_hippocrepis Sternotherus)))(Dermochelys_coriacea ((Chelonia_mydas
Natator_depressus) (Eretmochelys_imbricata (Caretta_caretta (Lepidochelys_olivacea Lepidochelys_kempii)))))))))
;constrain=;

Appendice 3- matrix based on matrix of Evers et al. (2019)

nstates 8;
xread
355 96

Rhinochelys_pulchriceps 00100000111100211000110-0100--00000000011000011100000000001-
0111010100001020[1 2]10201000011-1211011010011001111200?000002010000000001020200002200210-
121000011000011001-1?????00110[0
1]1?000000??
??

Santanachelys_gaffneyi 0010000?010100?11?00110-?100--000000000?00001110?00000000?-
011101010?001021?1020?0?0011-121?010000011001101200100?0??10????0?????0000??????-
1200?0011?????????1?????00??0??????00000?0?0-000101001?00-11100-01000-??01-0000?01100-0110112012?01-
1--0?0010?0?????????????11?????????0??????1?1????111021??????--0??1?1?2-??0101101021010?1?1???

Bouliachelys_suteri 0011000?0010001?0000110-0100--000?00?0?1?0?0011100000000001-
0111010100001020010201010011-121101011001100111120010000020100010000010202100002210210-
12100001100001101-
1?????0011011100?001??
??

Notochelone_costata ???000?0101002??0?0110-0?00--00?000??1?0000111000?0000001-
?1110100010010??102000?0?11-121?010000011001111200??1??0??0000010010200000?02210210-
121000011000011001-
1?????0011??
?????????????????0??

Ocepechelon_bouyai 0000?010101101?0000011??100--00000001?1000011110000?0000-
011101000?00?0201020?0?001011210020-100110010-1200000?0120100?0?????002??00000221?1??-
1210?0111?000????1-
1??
??

Desmatochelys_lowii 00100010101100110001111?0100--0000000010000011101000000001-
011101010?00102010201000011-121?0000110011001??12001000??0??0?001?00021200000221021?-
12100001100001101-1?????0001?0??????10000-0100-0101010?001111100-010??01?1-?100001110-
021011201?101-1--0-011000?????????????1011011120?0010000201?????111021111-0?1--
00110111201101111102?????1?101?

Desmatochelys_padillai 0010??1?101100?10011????100--
00000000?100001110?000?000?01110??0?0010201102??0?001??121101001002?001111200100?01201000?????02?
2?0000??????-1210?0011?00011101-1?????00??0??0?00?00000-0100-0001010?00??1110??0?0??01?1-
????0001??10110111200000100002?10?????1110211????????????????112011?
?11?11021????1?????

Rhinochelys_nammourensis 0010??00111100?10?00????100--
00000000??0001110?0?0??1000????????????????????????
??00010-0?0-000101001?00-10-00-00000-????1100?01110-
0110112012101-1--0-
0010????????????????????????????????????01????????????????????????????????1?2??1?11111021010?1?????

Chelosphargis_advena 0010??0?1011001110?01??0100--00000000??00?01110?0000?0?01-
01??????????0?0?10??0?01??1?1????????????120??0??020????????????????????????1?0-1210?0011????????1-
??????0011?????0?010?010-??0-0001??01000-11100-01?00-?01-110?0?11?000110112012101-1--0-
0110??0????????????????????????????????????

Calcarichelys_gemma 1--1??0?101?00??0?011?????????00?000?????0?1110?00000??1-[0
1]1??0????????02?21020100001??12110?0?00??0010-1200100?00201000?0?????020?000022??210-
1210?0011?0001100??1?????0011?????????0?010-?110-000101?01000-11100-01?00-1-?1-110?0011?0-0110112112101-
1--0-011?0001---?0?0000????????????????????201?????????????????0?????????1????????????????????????

Protostega_gigas 1--0??00101000?0?00????100--000000?0??00001110?001000001-
011100000??102?21?21?0?0?1??1?1102?-102-1011??1?0?100?0?0?1000??????02??000?????2??-
1200?0011?000?????11?????000100?00?0001-010-0100-000101001000-11110-00000-1-11----0--1110-0210112112101-
1--0-01101-----111?011120????1000020101110111021111-001--0011101113011111111021010010101?

Archelon_ischyros 1--0??00101000?0?001????100--00000?0001000011110?001000001-
011100000??021210????0?0?1011211020-102-?011??1200100?0?0?10?0??????02??000??????-
?????????000?????1?????0001?0?????11-010-0100-000101001000-11110-00000-1-11----0--1110-0210112112101-1--
0-01101-----101?011?????????0??201?1110111021111-011--0011101113011111111021010010101?

Dermochelys_coriacea 1--10100101000001-00100-0000--0000000010010011101000100010-
0101010000011021210100000011-1210021-002--0000-1200000[0 1]00001030-01-0010202000000210111-
1211?0111000011101-1-----0001011--0-2011--0-?0110--00-1--1-00-----0---1--1-----111-?0011-----1101-1--0-01111--
-----111101112000110000120-011110111021111-001--0011-010131110100111021001?1?1110

Eosphargis_breineri 1--1??0?101000??1?00????100--0000000??0001110?0001?0011-
010101010????02??10?0000?1??1200020-002-?1000-1200000?00?0111?????????0??0110??????-1211?011?????????1-
1?????????????????1-01??0?????00?0?0????1111?????????????????????11?011?????????????????1111-----
?11?01?????????0?0?????????????????1????01?????1?010131111?1??1110?1????1?101?

Lepidochelys_olivacea 1--10101101000101000110-0101100000000010000111100000001110-
0101000211011021210201000011-1210020-100201100-1201100[0 1]0000110000010010201001002210210-
121010111000011001-1?????0111111100100100010-0110-00010000?000-1110110100110111-1100?11110-
0100112011101-1--0-01110001---[0 1]0[0 1]000000011101112000111000120111110111020111-001--
00111011120111110111011010101110

Caretta_caretta 1--10101101000101000110-0101100000000010000111100000001110-
110110021001102121020100[0 1]011-1210020-101-11100-12011000000011-000011010202001002210211-
121010111000011101-1?????0001111100100100010-0110-000101000000-1110110100100111-1100011110-
0100112011101-1--0-01110001---[0 1]0[0 1]000000011101112000111000120111110111020111-001--
00111011120111110111011010101110

Chelonia_mydas 1--1010?101100101000110-
01011100000000100001111000000011120010100021000102121010100001[0 1]11210020-102-00000-

1201100101001110001110102000010020-0111-121010111000011001-1?????0011110100000100010-0110-0[0
1]0101001000-1110100100110111-1100001110-0100112011101-1--0-01110001---10[0 1]000000011110111200011100[0
1]120111110111021111-001--001110111201111011101110101?1110

Eretmochelys_imbricata 1--10101101100101000110-
01011000000000100001111000000111200101000211011021210201000011-1210020-100211100-
120110000010111000010010200001002210111-121010111000011001-1?????0000111100000100000-0110-0[0
1]0101001000-1110110100110101-1100001110-0100112011101-1--0-01110001---10[0
1]0000000111101112000111000120111110111021111-001--001110111201111101110111010101110

Lepidochelys_kempii 1--10101101100101000110-0101110000000010000111100001001112-
0101000211011021210201000011-1210020-100211000-1201100[0 1]0000110000011010202001002210110-
121010111000011001-1?????0011101100000100000-0110-00010000?000-1110110100110111-1100011110-
0100112011101-1--0-01110001---00[0 1]0000000111101112000111000120111110111020111-001--
001110111201111101110111010101110

Natator_depressus 1--10100101100101000110-
01011100000000100001111000000111200101000211011020210101000011-1210020-100211100-
120110010000110000010010202001002210211-121010111000011001-1?????0010110100100100000-0110-
000101001000-1110110100110101-1100001110-0100112011101-1--0-01110001---10[0
1]0000000111101112000111000120111110111021111-001--0011101112011?1101110111010101111

Puppigerus_camperi 1--10000101100101000110-1101110000000010000111100000001110-
0101000210001021210201000011-1200020-100201100-12011000010011100001?010202001002200110-
121100111000011001-1?????01110110000010000-0??0-000101001000-0--0120100100111-1100001100-
0000112011101-1--0-0010000?????????000??1111011120001?0000120???????111021111-
001??0010?1111201101?0?1101?????1?1??1

Argillochelys_cuneiceps 1--10000101100101000110-0101110000000010000111100000001111-
010100021000102121020100001011210020-1002?1100-120110010100110000010010202001002210111-
121100110000011001-
1?????0011101100?001??
??1111011120001110001?010??

Allopleuron_hofmanni 1--100001011001?0000110-00011?0000000010010011101000001110-
010100021?0010211101110010101121000011002?1100-1201???10000110000010000212001002210111-
12100011100001100011?????0000??10000001-010-0100-000101001000-1111?0100111-01-1100001110-
0100112011101-1--0-01111-----11101112000111000120101110111021111-011--
00111010120110110111011101010?1?

Nichollsemys_baieri 1--1000?1011001?0010110-0101010000100001000001110?000000010-
0111000100001021210201000011-021?0000100010110-1201100?0000110001011?00202001002210111-
121010111?00011001-
1?????0001?????0?00??
??

Eochelone_brabantica 1--10000101100101000110-110111000000001000011110000000000-
010101011000102121020100001011210020-100211000-12011000010011200001?010200001001200111-
121000111000011001-1?????0001101100000100000-0110-0?010?001000-1110120100110111-1100001100-
0000112011101-1--0-
0110?????????????????11?1?????????0??20??1??111021?????0?1??0?????01201101??110?1??01?1011

Corsochelys_halinches
?????????1011000?0111?0?????????0000?0??
??0?0-1200100100?1??0000001?02?200000121?210-12??00?11100011101-1?????????????????????????000-0??0-
00??01001??0-11001001?011??????????110-01??1?011101-1--0-?????????????????????????11?00-----
0?00?????????11102111?????1??00?????01011?????????2???????????

Procolpochelys_charlestonensis 1--1000?101100101?001????1011000000000100001111000000?1110-
010100021?0?1021210??00001??12?0020-?01-01100-1201100????11????????2??010022????-121??0111??????1-
1?????0101111?00?00100000-0??0-100100001000-10-01201000-??1??11????1110-010011201??01-1--0-
0111??????????????11??1????01????1????1?????2111????????????0120110????????????101?

Peritresius_martini
??
??00110-0010-010101001000-
???120100110101-1000001110?010?????1101-1-
?0?011000?????000000?01?1?1?????1??11201?????????????011?001?1????????????????????

Ctenochelys_sp 1--1010?10110111000011??110111000000001000001110?000001111-
010101111?00102?21020100001011210000110001000111201100101001100?00??02??01001210111-
121000111?00011111-1?????0011111?00?00100110-0010-010101001000-1110100100110101-1100001110-
0100112011101-1--0-0100001---?000000?00111??1012000111000120101????11?21110-001--
001??1?1100110110?1101????1????1

Cabindachelys_landanensis 1--1000?1011011?100012??110111000000????000011100000001110-
01010002100?1021210201000011-121?0000100010000-1201100?0?001100?000?0?????01002200111-
12100011100001100??1?????????????????001110-
0??????1??
??

Oligochelone_rupelensis
??
??00000-0??0-000101001000-
11101?0100110111-1100001110-0100112011101-1--0-0111?????????????????1??1?????11?0?1?0?????111021?11-
0?1?0010??0120110????????????????

Erquelinnesia_gosseleti 1--10?0?1011011??001??0?0??00?0?????00?0?1111?0000?1110-
01?1000210??021?1020?0001??1??0?????????0??
????0101101100000100000-0??0-0[0 1]0101001000-110012010011??11-10000011?0-010?????????01-1--0-
011?????????????????1?1?11??0011??01?0?????????????????011?0010??012001?1??????????1?1010

Toxochelys_sp 0011000?10110111001011??10101000000011?000011101000000011-01010001[0
1]00010212102000001011210000100010001120010000001000?000?0?0202001000200111-121000111000011001-
1?????1001[0 1]1100100100000-0110-010101001000-11000-0100110111-11000011[0 1]0-0100112011101-1--0-
001000??1?0?0?1011011?10111200?0?0??1?0101?001110?00?00?--0??11110200?01101010?0010?1?0-00

Solnhofia_parsonsi 0011000?1011011??100111101010100001?00?000?001110000000100-
1111100200001020210201011010112100001001-0001101100??100201110[0 1]0000110200000000100110-
121000111000011001-1?????011100111110100000-0????0?0101001?00010-01-01002?01?1-0100?01100-
100??????1001--1000000?????000?000??110?00-----0?0??1?1??11120??0??--
??0?1?1?00011?0?01000?0??0000-1?

Jurassichelon_oleronensis 0010001?10110110001011110100--0000100001000001110100000001-
01110000000010212102000110101111001101001100110120100010?00100010001100212000000200110-
111000011100011001-1?????????????????0000?0100-0001010??0??????10??????????0??1?0-
100??10??1001--?????00?????0?00??11?00-----
0?0?1?????????????????1?????????????????0-1?

Portlandemys_mcdowellii 0010001?1011011?00011110?00--??0??000100?001110100000001-
010100000000102?210201011010111100001000100?101201?0010100100010001[0 1]00212000000200110-
121000011000011001-
1?????00000?1001010??
??

Plesiochelys_planiceps 00110000000102202010110101121001000001100110110110010120100000001110202000000210110-
121000011100011001-
1????00000011011010??
??

Plesiochelys_etalloni 0011000000010220201011010112100100000110010-1200????????0000001110202000000210100-
121000011100011001?1?????000000010110100000?0100-000101001?0100--01-0000100011-0100000[0 1]00-
1000111000?10?1--100000010010000000000????????????????????010?????111?????0?1--
0?????1?00110?001000????????????

Plesiochelys_bigleri 0011000000010220201011010112100100?0011001101100?00100?0100000001110202000000200010-
111000011100011001-1????????????????????00000-0?0-00010100100100--0?0000100011-01000?0[0 1]00-
1000111000110?1--
1?000000100100000000000????????????????????????????????1111?0?????1?0?1??1?0000?0?0?0?????????0-10

Sandownia_harrisi 0111001?011011?0000121101010100000000?0?000011100000011110-
01010002100010202202000110101111?0001101--00110121100000010-0?010001010201000-00000010-
111000111000011001-
1?????01010?1111011??
??

Brachyopsemys_tingitana 0111000?010110110100011??010101000000000?000011110000000110-
010110021001102?21020001101??1?1?0000101-10011112111000010010?0?0????0201?--0?2??0?0-
121000111?0001110011?????010100?1111011??
??

Leyvachelys_cipadi 0001??1?0110110100012??100--0000000001000011101000000110-
0111000?1?0?102022020?01101011?1?0000?01-?001111211100?00?0-010??????0?1?1?--000011?0-
1210?0111?000?????-1?????01??0?0??0?1????00?0-?0??001?0?0?0-00-
0??????1?1????0????????????????????1????????????????????11?01????????1?0?201?????????2?0??0??--
0?0??1000?1?0??000??????????

Angolachelys_mbaxi 001100000001022020101101011210010000011001101000001110-?101?0021???02?22020?011010?1?1000-?01---
010-1210000?0?1010????????02?2??000?????-1210?0111?00011?01-
1?????01010????????00?0000??????00??0????10?0?????????????????????????????0?0?????????????????0??????????
????11?01????????0?0????????1?????0?11????0?????????11?01????????????????????
Chelydra_serpentina 1--100000100011002011101101010000000001000011101001000001-
0101010001001021220201000101121?00011000100010120010[0 1]1010010000101101020000000101010-
12110011000001100011?????0011011000000100000-01012000001001000-10-00-01002?0101-1100001100-
?000112012101-1--0-01100001-1-0010?01100111101120010111010201111200111020011-001--
00011?110001?00010001001-??????

Macrochelys_temminckii 1--100001010001100201110010111000000000000001110100100000-
0101000001001021220200000101121?00011000100010120010[0 1]10110100000011010200000000-0110-
12100011100001100011?????0011011000000100000-01011000001001000-10-00-01000-0111-110000000111001--??-
1000112012101-1--0101100001-1-00?0001100111101120010111010201112200111020011-001--
00001111000?1?00010001001-10????

Sternotherus 1--10000101000110120120-11[0 1]11100100100001000011101000010000-
0101010211001021220200000101121?0011001-10001012001000000102001001000210000010100010-
12110011000010100011-----00000?01001110011010101100010100211110--00-01000-0111-110000000111001--??-
010021--010000001-1-11-1-1-00111101111001011101021-11110111020011-011--11101011000?1?00010001101-
000????

Staurotypus 1--1000010100[0 1]110120120-011110010010010[0 1]01001110000010000-
01010102110010212202010000101121?00111002000011200100001201020100101021?0000000-0010-
12110011000101100011-----000100?010010100110101100010100210[0 1]?0--00-01000-0111-
11?00000011100011101010021--010000001-1-00-1-1-00111101111001011101021-111?10111020011-001--
1110101100001?00010001??????????

Kinosternon_suburum_hippocrepis 1--10000101000110120120-11111100100100001010011101001010000-
01010101010010212102000000101121?0011100200001012000000120100001011010210000000101010-
12110011000100100011-----000100?001011100110101100010100201100--00-01000-0111-110000000111001--??-
010021--010000001-1-11-1-1-001111011110???11101021-11110111020011-011--1111011000?1?00010001????00?0-
0?

Dermatemys_mawii 1--10000101[0 1]00110020120-010111000011000010000111010000100020[0
1]1011101010010212101000000101121?0011000210000-1200100000201000110000102[0 1]00000000-0010-
12110011001-----011-----000010?010010100000-0101100010100110100--00-01000-0111-1100000000-
1000111000?1011--0010000001-1-100100000011110110-001011101020111??10111020011-011--
00101?11000?1?0001000?001-0000-0?

Baptemys_wyomingensis 1--1000?10110?110020120-
010111000011000000000111010000100021010101010?0010212101000?00101121?001[0
1]0002?000101200100001201120?????020000000010?1?0-121000111?1-----?1-----100010?000001100110-
01011000101001?00-0--00-010??0111-1100000000-100011100011011--1?00000001-1-
001100000011?1?111??????????2?111?1?111020?11-011--1???1?1???0?0?10001??????0-0?

Emarginachelys_cretacea 1--
1000?1011001100201????10110000001000?00000111010000?00?21010101?10????021?102010?001??121?0011?0021000
10110110?0???1?00?0?????020??000001?0?0-121100110?0001100??------????????????0011??01011??0??001?00-0-
-00-?10?????1-1100001000-100011102?0?1--0?00000001-1-00??010?11??111????????????1?????11102?????0?1-
-01????1??????0?1000?101-??0-0?

Chrysemys_picta 1--1000010110[0 1]110020110-
01011100001100101000011101000000002001010200110010212102000000101121?0011000210000-
120010010020101111000010200000000100010-12110011000001100011-----0000101110000100000-0100-
100101001000-0--00-01000-0101-1100000000-100011100011011--1010000001-1-
000010000111101112111011101020111110111020011-011--00011111000?1?00010001????000???

Emys_orbicularis 1--10000101000110020111101010100001100001000011101000000000-
01010000010000212101000000101120?0011000210000-120010000120100101001010200000000101011-
121100110?0001100011-----0000?0?????100000-0100-100101001000-0--00-01000-0101-
11000010010100011100010011-?0100000001-1-00100000?11101112101011101020111111?111020011-011--
00?11?1100001?00010001100-0000-0?

Geoclemys_hamiltonii 1--10000101000110120111101111100000100001010011101000000000-
01010211110000212102000000101121?00110002100010120010000020103101001010200000000100010-
12110011110001100011-----000010?010000100110-0100-100101001100-0--00-0100100111-1100000000-
100011100001011--1110000001-1-001010000111101112101011101020111110111020011-011--
0001111100011?00010001????0000-1?

Testudo 1--1000010110011012011110100--
00001100001010011101000000002001010200010000201201000000101121?0011000200000-
120010010100100101001010200000000101010-12110011010001100011-----0000000000010100000-0100-
100001001000-0--00-1100100111-1100000000-100011100001001--0010000001-1-
000010000111101112101011101020111110111020011-011--0001111100001?0000001????100???

Gopherus_polyphemus 1--10000101100110020120-0100--0000110000[0
1]000011101000010002001010210010100211201000000101121?0010000210100-1200100001001000-
11000102200000000-1010-12110011010001100011-----0000100010000100000-0100-100001001000-0--00-1100100111-

1100000000-100011100001001--1010000001-1-0000100001111101112101011101020111110111020011-011--
0001111000001?00000001001-100????

Chelonoidis_sp. 1--10000101101[1 2]1012011110100--
00001100000000011101000000002001010210010000201201000000101121?001000021000111200100001001000-
1001010220[0 1]00000101010-12110011010001110011-----000000000000100000-0100-000001001100-0--00-
0100100101-1100001000-1000111000101-1--0210000001-1-00000000001101011121010111000201111200111020011-
001--0001111000001?00010001001-00?????

Platysternon_megacephalum 1--10000101000[1 2]11000111001011100100000000001011101001000001-
01010100010010212202100000101121?000100020100101201100000201000011110102000000020-0110-
121100111000001001-1-----0000001[0 1]01001100000-0100-000001001100-0--00-0100100101-1100001000-
1000111000101-1--0210000001-1-00000000001101011121010111000201111200111020011-001--
0001111000001?00010001101-00?0-0?

Apalone_spinifera 1--10100101101110120120-1111110000100100010011110110010001-
11111200010110212202100000101121?0020101-10-10-120010110110100000011010201000000100010-
120000111000011001-1-----000100011100111-00120100-000101-1-001011000-0101--1--1-----11[0 1]0-
1000113013101-1--0-00001----1-----11010120-0010111000201-1110111020011-001--
001101110011?00010011100-0010-0?

Pelodiscus_sinensis 1--10100101101110120120-1111110000100100010011110110010000-
11111200010110212202100000101121?0021101-10-10-1200101101101000010011010201000000100010-
12000011100001100[0 1]11-----000100011100111-00120100-000101-1-001011000-0101--1--1-----1110-10001130131-
1-1----00001-----110?0120-00?011100020--1??10??101-0010-0?

Lissemys_punctata 1--10100101101110120120-11111010000100100010011110110010000-
1111120000010212202100000101121?0021101-00-20-120010110110100000011010201000000100010-
12000011100001100001-----000?00??0?0011-00120100-000101-1-00100--00-0101--1--1-----1110-1000113013101-1--
0-00001----1-----11010120-0010111000201-1--10111020011-001--0111101110011?0??1001?101-001????

Carettochelys_insculpta 1--10100101100110120120-11011100100100101000011110000010001-
01111010010110210202000?01101121?0021101-10-11[0 1]120010110120113000111010201000010100010-
12100011100001100011-----000010111100110100120000-00010100000100--00-01000-1-11-----1000-
100011100010021--0100001----1-----??11010110-001011100020111110111020011-001--
0111101000011?0001002211000000-0?

Allaechelys_libyca 1--
1??0?1?110?1101201??11??200?0?10??1????1?????????????????????????????????0211202000001101121?0??10??0?11[0
1]1201??1101201130001?0010201?0001?10?010-
12100011100001100011??
??

Chelus_fimbriatus 1--0101010110110[0 1]-20110-01011101--21000011-0011111000000000-01010000001-
00202300--000011-120?101000---0000-200-00001132101012001200201000000100010-120001110-0010100011-----
1001?0??????00011[0 3]0100-100001001100-0--00-01000-0101-1100000000-100011100011011--
3110000010211001000001-1011111131000010100201011110111120011-101110001101100001?00010001101-0000-0?

Phrynops_geoffroanus 0110111010110110[0 1]-20111011011101--21000011-0011101000000000-
01010000001-00202300--000011-120?101000---0010-200-00001132101012001210201000000101010-121001100-
0011100011-----1001?0?10?100000000-0100-10010110110100--00-01000-0111-1100000000-100011100011011--
1010000010010000000001-100011113100001000201011110111120011-101110001101100001?0001000100?0000-0?

Eelseya_dentata 01101110101101101-00111111011101--21000011-0011101000000002011010000001-
00202300--000011-120?101000---0000-200-10000120100012001210201000000100010-1[1 2]1001110-00111001-1-----
001000010011000000?0100-100-01001?1110--00-010??1-11-1-00000000-1000111000?1001--
101000001001?00?000001-10?0111131000010?0020101??10111120011-1?11100??101??001?000010001110-??0-0?

Xinjiangchelys_radiplicatoides

0110??1?1011011?00?011????0??0??0??0??0??00111?00?0?0??????11??????02111010?0?0?101111?0?2?
?0??0?-?1012?0?00001201000?001??020000000201110-1110-0011000011001-1?????0?1????????10000-0100-
000??101?00-0--00-0100100111-1100??000-100011100010001--
00000001000100000000100?????????????????0?????????111?200101?????????000001?????????????0?

Dracochelys_bicuspis

??1000?101101?0?01????1010100001?0????000111010001?0001-
010100000?00?020?101010000101111?001010001000101201?0??0?2010????????02??00000??????10110-
0?11?0001100??1?????000?00?0?0010000?1100-000101001?00-10-00-0110101-0?1101?01100-1000????1??0001--
0000000?????????????0111?110-000001000?0010????01110200??0?????????0?0001?0??0000???????????

Kirgizemys_hoburensis

0011000?10110110001011110101010?0020001010?0011101000000000-
010102000?001020?101000000101111?0010?000100010110010010100100001001??02?0?100001010?0-1111-
0110?0001100011?????0001?0??????00000-0100-000101101?00-0--00-010??0111-1100001000-100011201110001--
0?00000001-1?0000000[0 1]10?111?111200000110?2?10????????2??1-0?1????????0001?????????????????

Kirgizemys_dmitrievi

??1000?1011001?001?111??101010000200010000001110?0000?0001-
000101000?00102021020?00001011?1?00100000?000??00100?0?01000?000??02?0?1000?1110??-1111-
0?1??00011101-?????000100?000000????????????????????-
0????????????????????????20?1??
????????????????????????????

Sinemys_gamera

01100?1?10110111002011??1101010?02100?000?0011??0??0?0?0-
0????????????1202201000000101110?00?00000100010120110010?001000?000?00220?1000??????-1110-
0111?00011001-1????????????????00001?0??????1?????100-10-0?010?????1-
?10??1????100?????1?00??00??0??1?????00??001001??
????????????????

Sinemys_lens

0010??1?101101?100201????101?0?0?02?0000??00111?0000?0?0??????0??????202201000?0?1??1?0?00100000?000
10110110?????10?0?????022??1000??????-1110-0111?0001100??1?????00?????????0000?0100-000101001100-
10-00-0100101--1-1101001[0 1]00-1000112?1010001--
00001000??1?0?0000?10?1?0????0????????0??1????????????0????????????????????1000????0000???

Meiolania_planiceps

00000000101000101000110-
000101000100110000000110010000000020010102100000102103110000[0 1]0101121?001[0 1]100000000-
12001100000[0 1]11211100110020?0000000-101010111-0111100001101-111111000000000100000000-?100-
00??001000-0--00-?1????0101-0?00101100-0000110000?0011--
000000000001000????????01000111200000000000?0022011110000101011--00001?000000?000000010-0-0000-0?

Chubutemys_copelloi

??1000?101000?01?0011??10000000?000?000000011??0??000000-
011102000??0202101?000001??110?0011000000001?010010000?00110?????0020?0000??????100-----??????1-
1????????????????00??0????????0??0????????0????????0????????0????????0????????0????????0????????
??????1?1??????0????0?????1110?0??

Eubaena_cephalica

0000002?10100011002011??1011100001000000001011101000000001-
0101020001000021210100000011-121?00101000?000101201100000201020?00??1210?0001010?110200-----
?00011011-
1?????0000?0?????0??
??

Arundelemys_dardeni

0100001?1011001?020110-1?01?1?0??0??0?10?1101000000001-
0101000000?0?02??101000000101111?001010001000111201?000000010200101110020?000000101110200-----
0000????1-
1??
??

Pleurosternon_bullockii 0110001?1011001001001?1?110111000011000000010111010000?0000-
01??00000??020110110000010111??0020?00010-0101101?00?0??01100111022110001010111[0 1]200---
???00001100??1????????????????????0000130??0-0?0101001?00-0--00-01000-1-11-010010000-
00001?1000?01010100000001001000000000000??0-----?0?000????????????????0?1--
00????????????????????????????????

Glyptops_plicatulus 01100?1?1011001?0?0011??101?100?010000?0010111??0?0?00?1-
0101000?0??0201101?00000101111?0020?00010-0101101??0?002?100?1100??0211?000101011?0200---
???0000?????1?????00?0?0??0?00000100100-000101001?00-0--00-0100100111-010010000-
00001110001101010100000000010000000000?00010-----?0?000101??011112001010?1--
00??1?10000?1?0????????????????????

Kallokibotion_bajazidi 0000??0?10110010100011??10??0000000000?00110010000?00?110102??0??0202102000?00101111??0?00??0
001?1200?00?00-111211100010120000000101111-10-----000011001-1?????00?1??????00?00000-0000-
000101??000-0--00-010011??1?00?000?000-0000111000?00011?20000000001000?000000?00000-----0?0?????--
001110100101011--0000??000000????????????????????

Eileanchelys_waldmanni 00000?1?10110??0?-
001??1011?0000?00??0?00??11010000??0??01?100000??020?100-000001????0??0??00??0?0?01010?00000[0
1]1000010?01002010?000????????????????100011001-1?????10????????????00?0-0??000001101?00-0--00-
01001001?1-0000??00-
00001?0000????????0??0?00??00?0??00?0??00??
??????

Kayentachelys_aprix 00000010101100101-00000-11011100000000000000?110?000000001-
010100000??0201100--0010100010?0010000000000-0101000?0?001000?-0??001-101000-11111[0 1]000-----
?0001100--0?????1000?0?00000000000-0000-0000000?100-0--00-00000-0111-0000001000-
0000010000?0000100000000000001000000000000?0?00-----?0000000100001010?001010111--
00001?10?000?????000??????0-1?

Australochelys_africanus ???10?000?0101-00000-1?0??0000?0000?0000?10?00?000001-0?01?01000??01?00-
0--000?1??110?00?0000000000-00000?01??0?0?0?-??0?010-1-00?0-211?10000-----??????--
0??
??

Proganochelys_quenstedti 0000100?000000101-00000-0001010000000000-010001000000000001-000000100100000--
0-0--00000?000?0010000000000-000-0001000000-0?-0-0?000-0-0000-200100000-----?0001010--
0?????000000000000000000[0 1]00000-?0?00000000100--00-??0??010000-00?00000-
0000000000?0?0100?00000000010000000?010000-----0000000000000000000000010--
0000?000000?000000000-0-0000-1?

Adocus_lineolatus 1--1000?101100110120120-
?10111000011001010000111010000100021010102000?0010202102010?00101121?00111002100010120110000?1011?0??
?????020000000010?1?0-111000111?00011000-1?????000?101110001100000-0100-101101001?0[0 1]?0--00-
010??0111-110010000-100011100010001--0000001000100010100010111?100-00101110102?111????111020011-
011--0101111000001?0??10001001-??????

Petrochelys_kyrgyzensis
?????????0?????101201?????????????????0?????????1?????????????????1?????????02?22021?00001??21??2?101-?0-?0-
120010?101101000000?0?020100000?????0-1200?0111?00011001-1-----
??
??

Galianemys_whitei 1--11100101101110-2012101101110010010000110101110100001[0 1]000-011100000?1-
10202200--101011-120?101001---0010-200-0001010010001000?11021100000210?010-120000011-00111001-1-----

Protostega_gigas 1--0?00101000?0?00????100--00000?0??00001110?001000001-
011100000???02?21?21?0?0?1??1?1102?-102-1011??1?0?100?0?0?1000?????02??000????2??-
1200?0011?000?????1?????000100?00?0001-010-0100-000101001000-11110-00000-1-11----0--1110-0210112112101-
1--0-01101-----111?011120????1000020101110111021111-001--0011101113011111111021010010101?

Archelon_ischyros 1--0?00101000?00?001????100--00000?0001000011110?001000001-
011100000???021210??0?0?1011211020-102-?011??1200100?0?0?10?0?????02??000???????-
?????????000?????1?????0001?0?????11-010-0100-000101001000-11110-00000-1-11----0--1110-0210112112101-1--
0-01101-----101?011??????0?201?11110111021111-011--00111011130111111111021010010101?

Dermochelys_coriacea 1--10100101000001-00100-0000--0000000010010011101000100010-
0101010000011021210100000011-1210021-002--0000-1200000[0 1]00001030-01-0010202000000210111-
1211?0111000011101-1-----0001011--0-2011--0-?0110--00-1--1-00-----0--1-1-----111-?0011-----1101-1--0-01111-
-----111101112000110000120-011110111021111-001--0011-010131110100111021001?1?1110

Eosphargis_breineri 1--1??0?101000?1?00????100--000000????0001110?0001?0011-
010101010??02??10??000?1??1200020-002-?1000-1200000?00?0111??????0??0110??????-1211?011?????????1-
1?????????????????1-01??0?????00?0?????11111?????????????????11?011?????????????????1111-----
?11?01??????0?0?????????????1??01????11?01013111?1??110?1????1?101?

Lepidochelys_olivacea 1--10101101000101000110-01011000000000010000111100000001110-
0101000211011021210201000011-1210020-100201100-1201100[0 1]0000110000010010201001002210210-
121010111000011001-1?????0001111100100100010-0110-000101000000-1110110100110111-1100011110-
0100112011101-1--0-01110001---00[0 1]000000011101112000111000120111110111020111-001--
00111011120111101110111010101110

Caretta_caretta 1--10101101000101000110-01011000000000010000111100000001110-
110110021001102121020100[0 1]011-1210020-101-11100-1201100000011-000011010202001002210211-
121010111000011101-1?????0001111100100100010-0110-000101000000-1110110100100111-1100011110-
0100112011101-1--0-01110001---[0 1]0[0 1]000000011101112000111000120111110111020111-001--
00111011120111101110111010101110

Chelonia_mydas 1--1010?101100101000110-
01011100000000010000111100000001120010100021000102121010100001[0 1]11210020-102-00000-
1201100101001110001110102000010020-0111-121010111000011001-1?????00011110100000100010-0110-0[0
1]0101001000-1110100100110111-1100001110-0100112011101-1--0-01110001---10[0 1]00000001110111200011100[0
1]120111110111021111-001--001110111201111011101110101?1110

Eretmochelys_imbricata 1--10101101100101000110-
01011000000000010000111100000001120010100021011021210201000011-1210020-100211100-
120110000010111000010010200001002210111-121010111000011001-1?????0000111100000100000-0110-0[0
1]0101001000-11101100110101-1100001110-0100112011101-1--0-01110001---10[0
1]000000011101112000111000120111110111021111-001--001110111201111101110111010101110

Lepidochelys_kempii 1--10101101100101000110-01011100000000010000111100001001112-
0101000211011021210201000011-1210020-100211000-1201100[0 1]0000110000011010202001002210110-
121010111000011001-1?????0011101100000100000-0110-00010000?000-1110110100110111-1100011110-
0100112011101-1--0-01110001---00[0 1]000000011101112000111000120111110111020111-001--
00111011120111101110111010101110

Natator_depressus 1--10100101100101000110-
01011100000000010000111100000001120010100021011020210101000011-1210020-100211100-
12011001000011000010010202001002210211-121010111000011001-1?????0010110100100100000-0110-
000101001000-1110110100110101-1100001110-0100112011101-1--0-01110001---10[0
1]000000011101112000111000120111110111021111-001--0011101112011?1011101110101011110

Puppigerus_camperi 1--10000101100101000110-11011100000000010000111100000001110-
0101000210001021210201000011-1200020-100201100-12011000010011100001?010202001002200110-
121100111000011001-1?????011101100000100000-0??0-000101001000-0--0120100100111-1100001100-
0000112011101-1--0-0010000????????000?1111011120001?0000120?????111021111-
001?0010?1111201101?0?1101?????1?1??1

Argillochelys_cuneiceps 1--10000101100101000110-01011100000000010000111100000001111-
010100021000102121020100001011210020-1002?1100-120110010100110000010010202001002210111-
121100110000011001-
1?????0011101100?001??
?1111011120001110001?010??

Allopleuron_hofmanni 1--100001011001?0000110-00011?00000000010010011101000001110-
010100021?0010211101110010101121000011002?1100-1201???10000110000010000212001002210111-
12100011100001100011?????0000??10000001-010-0100-000101001000-1111??0100111-01-1100001110-
0100112011101-1--0-01111-----111101112000111000120101110111021111-011--
00111010120110110111011101010?1?

Eochelone_brabantica 1--10000101100101000110-1101110000000001000011110000000000-
010101011000102121020100001011210020-100211000-12011000010011200001?010200001001200111-
121000111000011001-1?????0001101100000100000-0110-0?010?001000-1110120100110111-1100001100-
0000112011101-1--0-
0110????????????????11?1?????????0??20??1???111021???0?1???0????01201101???110?1???01?1011

Toxochelys_sp 0011000?10110111001011???101010000000011?000011101000000011-01010001[0
1]00010212102000000101121000001000100011200100000001000?000?0?0202001000200111-121000111000011001-
1?????1001[0 1]11100100100000-0110-010101001000-11000-0100110111-11000011[0 1]0-0100112011101-1--0-
001000??1?0?0?1011011?10111200?0????1?0101?001110?00??00?--0??11110200?01101010?0010?1?0-00

Solnhofia_parsonsi 0011000?1011011??100111101010100001?00?000?0011100000000100-
1111100200001020210201011010112100001001-0001101100??100201110[0 1]0000110200000000100110-
121000111000011001-1?????0111001111101000000-0????0?0101001?00010-01-01002?01?1-0100?01100-
100??????1001--10000000?????000?000?110?00-----0?0??1?1????111120????0??--
?0?1?1?00011?0?01000?0??0000-1?

Jurassichelon_oleronensis 0010001?10110110001011110100--00001000010000011101000000001-
01110000000010212102000110101111001101001100110120100010?00100010001100212000000200110-
111000011100011001-1?????????????????0000?0100-0001010????????????10??????????0??1?0-
100??10??1001--?????00?????0?00??11?00-----
0?0?1?????????????????????1?????????????????????0-1?

Portlandemys_mcdowellii 0010001?1011011?00011110?00--??0?000100?0011101000000001-
010100000000102?2102010110101111000001000100?010201?0010100100010001[0 1]00212000000200110-
121000011000011001-
1?????000000?1001010??
??

Plesiochelys_planiceps ???0000?1011011?00?011110100--0?0?2?00?100?0?11?0100?000001-
011100000000102?2102010110101121001000001100110110110010120100000001110202000000210110-
121000011100011001-
1?????00000011011010??
??

Plesiochelys_etalloni 0011000?1011011?00?011110100--00001000010000111101000000001-
0101000000001020210201011010112?00100000110010-1200?????????0000001110202000000210100-
121000011100011001?1?????0000000101101000000?0100-000101001?0100--01-0000100011-0100000[0 1]00-

Baptemys_wyomingensis 1--1000?10110?110020120-
01011100001100000000111010000100021010101010?0010212101000?00101121?001[0
1]0002?000101200100001201120??????020000000010?1?0-121000111?1-----?1-----100010?000001100110-
01011000101001?00-0--00-010??0111-1100000000-100011100011011--1?00000001-1-
001100000011?1?111??????????2?111??1?111020?11-011--1??1?1??0?0?0?10001??????0-0?

Emarginachelys_cretacea 1--
1000?1011001100201???10110000001000?00000111010000?00?21010101?10???021?102010?001??121?0011?0021000
10110110?0???1?00?0???020??000001??0?0-121100110?0001100???-----????????????0011??01011??0???001?00-0-
-00-?10?????1-1100001000-10001110?2?0??1--0?00000001-1-00??010?0?11??111????????????1?????11102?????0?1-
-01????1??????0?1000?101-??0-0?

Chrysemys_picta 1--1000010110[0 1]110020110-
010111000011001010000111010000000200101020011001021210200000101121?0011000210000-
1200100100201011100001020000000100010-12110011000001100011-----0000101110000100000-0100-
100101001000-0--00-01000-0101-1100000000-100011100011011--1010000001-1-
00001000011111011121110111010201111110111020011-011--00011111000?1?00010001????000???

Emys_orbicularis 1--10000101000110020111101010100001100001000011101000000000-
01010000010000212101000000101120?0011000210000-120010000120100101001010200000000101011-
121100110?0001100011-----0000?0?????100000-0100-100101001000-0--00-01000-0101-
11000010001011--1110000001-1-00101000001-1-00100000??111101112101011101020111111?111020011-011--
00?11?1100001?00010001100-0000-0?

Geoclemys_hamiltonii 1--10000101000110120111101111100000100001010011101000000000-
01010211110000212102000000101121?0011000210001012001000002010310100101020000000100010-
12110011110001100011-----000010?010000100110-0100-100101001100-0--00-0100100111-1100000000-
100011100001011--1110000001-1-00101000001111101112101011101020111110111020011-011--
0001111100011?00010001????0000-1?

Testudo 1--1000010110011012011110100--
0000110000101001110100000000200101020001000020120100000101121?0011000200000-
1200100101001001010101020000000101010-12110011010001100011-----00000000001010000-0100-
100001001000-0--00-1100100111-1100000000-10001100001001--0010000001-1-
0000100001111101112101011101020111110111020011-011--0001111100001?00000001????100???

Gopherus_polyphemus 1--10000101100110020120-0100--0000110000[0
1]000011101000010002001010210010100211201000000101121?0010000210100-1200100001001000-
1100010220000000-1010-12110011010001100011-----000010001000010000-0100-100001001000-0--00-1100100111-
1100000000-100011100001001--1010000001-1-0000100001111101112101011101020111110111020011-011--
0001111000001?00000001001-100???

Chelonoidis_sp. 1--10000101101[1 2]1012011110100--
0000110000000001110100000000200101021001000020120100000101121?001000021000111200100001001000-
1001010220[0 1]00000101010-12110011010001110011-----00000000000100000-0100-000001001100-0--00-
0100100101-1100001000-1000111000101-1--0210000001-1-0000000001101011121010111000201111200111020011-
001--0001111000001?00010001001-00????

Platysternon_megacephalum 1--10000101000[1 2]1100011100101110010000000001011101001000001-
010101000010010202201000000101121?000100020100101201100000201000011110102000000020-0110-
121100111000001001-1-----000000[0 1]01001100000-0100-000001001100-0--00-0100100101-1100001000-
1000111000101-1--0210000001-1-0000000001101011121010111000201111200111020011-001--
0001111000001?00010001101-00?0-0?

Apalone_spinifera 1--10100101101110120120-11111110000100100010011110110010001-
11111200010110212202100000101121?0020101-10-10-120010110110100000011010201000000100010-

120000111000011001-1-----000100011100111-00120100-000101-1-001011000-0101--1--1-----11[0 1]-
1000113013101-1--0-00001-----1-----11010120-0010111000201-11110111020011-001--
0011101110011?00010011100-0010-0?

Pelodiscus_sinensis 1--10100101101110120120-1111110000100100010011110110010000-
11112000010110212202100000101121?0021101-10-10-120010110110100010011010201000000100010-
12000011100001100[0 1]11-----000100011100111-00120100-000101-1-001011000-0101--1--1-----1110-10001130131-
1-1----00001-----110?0120-00?011100020--1??10??101-0010-0?

Lissemys_punctata 1--10100101101110120120-11111010000100100010011110110010000-
111120000010212202100000101121?0021101-00-20-120010110110100000011010201000000100010-
12000011100001100001-----000?00??0?0011-00120100-000101-1-00100--00-0101--1--1-----1110-1000113013101-1--
0-00001----1-----11010120-0010111000201-1--10111020011-001--011101110011?0??1001?101-001????

Carettochelys_insculpta 1--10100101100110120120-11011100100100101000011110000010001-
01111010010110210202000?01101121?0021101-10-11[0 1]120010110120113000111010201000010100010-
12100011100001100011-----000010111100110100120000-00010100000100--00-01000-1-11-----1000-
100011100010021--0100001----1-----?11010110-001011100020111110111020011-001--
0111101000011?0001002211000000-0?

Allaechelys_libyca 1--
1??0?1?110?1101201??11??00?0?10??1????1????????????????????????????????0211202000001101121?0??10??0?11[0
1]1201??1101201130001?0010201?0001?10?010-
12100011100001100011??
??

Chelus_fimbriatus 1--0101010110110[0 1]-20110-01011101--21000011-0011111000000000-01010000001-
00202300--000011-120?101000---0000-200-00001132101012001200201000000100010-120001110-0010100011-----
1001?0??????000111[0 3]0100-100001001100-0--00-01000-0101-1100000000-100011100011011--
3110000010211001000001-10111113100001010020101111011120011-101110001101100001?00010001101-0000-0?

Phrynops_geoffroanus 0110111010110110[0 1]-20111011011101--21000011-0011101000000000-
01010000001-00202300--000011-120?101000---0010-200-00001132101012001210201000000101010-121001100-
0011100011-----1001?0?10?10000000-0100-10010110110100--00-01000-0111-1100000000-100011100011011--
1010000010010000000001-100011113100001000020101111011120011-101110001101100001?0001000100?0000-0?

Elseya_dentata 01101110101101101-00111111011101--21000011-0011101000000002011010000001-
00202300--000011-120?101000---0000-200-10000120100012001210201000000100010-1[1 2]1001110-00111001-1-----
001000010011000000?0100-100-01001?1110--00-010??1-11-1-00000000-1000111000?1001--
101000001001?0?000001-10?0111131000010?0020101??1011120011-1?11100?101?001?00010001110-??0-0?

Chelodina 01101110101111110-20111001011101--21000011-0011101000000000-01010000001-
00202300--100011-120?101000---0010-200-00001122100012001200201000000100010-121001100-00111001-1-----
100100000000000000130100-100-0100111110--00-01000-0111-1-00000000-100011100011011--
0110000010110000000001-100011113100001010020101111011120011-101110001101110001?00010001100-0000-0?

Araripemys_barrettoi 1--11110101101110-20111001011100001100101100011101000000000-??11?000?1-
01202100--000011-120?102100---0-00-200-??00000101012001210201000000100010-121001100-00111001-1-----
100100000000010011140100-100101001001010-00-01000-1-11-1101001110-000011101111011--0110000011--
000000101-100?1111000000101002??011110111?20011-1?????????11?00?1?0??100010110000-0?

Podocnemis 1--11100101101110-00121111011110001100001110011101000011002002110000001-
11202300--100011-120?101101---0000-200-10000020100010001210201000000100010-120000101-0001100011-----
000000011000010000[0 1]30100-10010100110100--00-01000-1-11-1100000000-00001110001101011101000001001[0
1]001000001-100011110000001000020101111011120011-101110001101110011?00010001110-0000-0?

Kirgizemys_dmitrievi ???1000?1011001?001?111??101010000200010000001110?0000?0001-
000101000?00102021020?00001011?1?00100000?000?00100?0?01000?00??02?0?1000?1110??-1111-
0?1??00011101-??????000100?000000????????????????????-
0????????????????????????????20?1??
????????????????????????????

Sinemys_gamera 01100?1?10110111002011??1101010??02100?000?0011??0?0?0?0?-
0??????????1202201000000101110?00?00000100010120110010?001000?00??00220?1000??????-1110-
0111?00011001-1?????????????????00001?0??????1?????100-10-0?010?????1-
?10??1????100??????1?00??00??0?0??1?????00??001001??
????????????????

Sinemys_lens 0010??1?101101?100201????101??0?02?0000??00111??0000?0????????0??????202201000?0?1??1?0?00100000?000
10110110?????10?0??????022?1000??????-1110-0111?0001100?1?????00??????????0000?0100-000101001100-
10-00-0100101--1-1101001[0 1]00-1000112?1010001--
00001000??1?0?0000?10?1?0????0????????0??1????????????????????????????1000????0000???

Meiolania_planiceps 00000000101000101000110-
000101000100110000000110010000000020010102100000102103110000[0 1]0101121?001[0 1]100000000-
12001100000[0 1]11211100110020?0000000-101010111-0111100001101-11111110000000000100000000-?100-
00????001000-0--00-?1????0101-0?00101100-0000110000?0011--
00000000001000??????01000111200000000000?002201110000101011--00001?000000?00000010-0-0000-0?

Chubutemys_copelloi ???1000?101000?01?0011??1000000?000?00000011??0?0?000000-
011102000??0202101?000001??110?0011000000001?010010000?00110??????0020??0000??????100-----??????1-
1????????????????00????0????????0??0????????0????????0????????????????????????????????????
??????1?1????????0????0?????1110?0??

Eubaena_cephalica 0000002?10100011002011??1011100001000000001011101000000001-
0101020001000021210100000011-121?00101000?000101201100000201020?00??1210?0001010?110200-----
?00011011-
1?????0000?0?????0??
??

Arundelemys_dardeni 0100001?1011001??020110-1?01?1?0?0??0??0?10?1101000000001-
0101000000?0?02?101000000101111?001010001000111201?000000010200101110020?000000101110200-----
0000??1-
1??
??

Pleurosternon_bullockii 0110001?1011001001001?1?110111000011000000010111010000?0000-
01??00000??020110110000010111??0020?00010-0101101?00?0?????01100111022110001010111[0 1]200---
???00001100?1?????????????????0000130?0-0?0101001?00-0--00-01000-1-11-0100100000-
00001?1000?010101000000010010000000000000?00-----?0?000?????????????????0?1--
00????????????????????????

Glyptops_plicatulus 01100?1?1011001?0?0011??101?100?0100000?0010111??0?0?00?1-
0101000?0??0201101?00000101111?0020?00010-0101101?0?002?100?1100??0211?000101011?0200---
???0000?????1?????00?0?0??0?00000100100-000101001?00-0--00-0100100111-0100100000-
000011100011010101000000000100000000000?00010-----?0?000101??011112001010?1--
00??1?10000?1?0???????????????

Kallokibotion_bajazidi 0000?0?10110010100011??10??0000000000?001100100000?00?110102??0??0202102000?00101111??0?00??0
001?1200?00?00-111211100010120000000101111-10-----000011001-1?????00?1??????00?00000-0000-
000101??0000-0--00-010011??1??00?000?000-0000111000?000011?20000000001000?000000?00000-----0?0?????--
001110100101011--0000??000000????????????????

Eileanachelys_waldmanni 00000?1?10110??0-
001????1011?0000?00??0?00??11010000??0??01?100000??020?100-000001??0?0??00??0?0?01010?00000[0
1]1000010?01002010?000????????????????100011001-1?????10????????????00??0-0??000001101?00-0--00-
01001001?1-0000??00-
00001?0000????????0??0?00??00?0??00?0??00?0??
??????

Kayentachelys_aprix 0000010101100101-00000-11011100000000000000?110?000000001-
010100000??0201100--0010100010?001000000000-0101000?0?001000?-0??001-101000-11111[0 1]000-----
?0001100--0?????1000?0?00000000000-0000-0000000?100-0--00-00000-0111-000001000-
0000010000?0000100000000000100000000000?0?00-----?0000000100001010?00101011--
00001?10?000????000??????0-1?

Australochelys_africanus ???10?000?0101-00000-1?0??0000?000?0000?10?00?000001-0?01?01000??01?00-
0-000?1??110?00?000000000-00000?01??0?0?0?-??0?010-1-00?0-211?10000-----??????--
0??
??

Proganochelys_quenstedti 0000100?000000101-00000-0001010000000000-010001000000000001-000000100100000--
0-0--00000?000?0010000000000-000-0001000000-0?-0-0?000-0-0000-20010000-----?0001010--
0?????0000000000000000[0 1]00000-?0?0000000100--00-??0??010000-00?00000-
0000000000?0??0100?0000000000100000000??010000-----00000000000000000000000010--
00000?0000000?000000000-0-0000-1?

force/(Proganochelys(((Pelomedusa_subrufa Podocnemis)((Chelus_fimbriatus Phrynops_geoffroanus)(Chelodina
Elseya_dentata)))(Carettochelys_insculpta (Lissemys_punctata (Pelodiscus_sinensis
Apalone_spinifera)))(Platysternon_megacephalum(Emys_orbicularis Chrysemys_picta)(Geoclemys_hamiltonii
(Gopherus_polyphemus (Testudo_Chelonoidis_sp.)))(Macrochelys_temminckii Chelydra_serpentina)(Dermatemys_mawii
(Staurotypus (Kinosternon_suburum_hippocrepis Sternotherus))))(Dermochelys_coriacea ((Chelonia_mydas
Natator_depressus) (Eretmochelys_imbricata (Caretta_caretta (Lepidochelys_olivacea Lepidochelys_kempii)))))))))
;constrain=;

Appendice 4- “Modified” matrix with taxa of Evers et al, (2019) with characters of Evers & Benson (2019)

nstates 8;
xread
345 96

Rhinochelys_pulchriceps 0010000011100210000110-0100--00000000011000011100000000001-
0111010100001020[1 2]10201000011-121011010011001111200?00000201000000001020200002200210-
121000011000011001-1?????00110[0
1]1?000000??
??

Santanachelys_gaffneyi 0010000?11100?10?00110-?100--000000000?00001110?00000000?-
011101010?001021?1020?0?0011-121010000011001101200100?0??10??0??0??00000?????-
1200?0011?????????1?????00??0??????00000?0?0-000101001?00-20-0100--?01-0000?01100-011011211?0011--
0?00?0?0?????????????11?????????0?????0?1?1????111021?????0?--0??1?1??2?0---?010110102?1??

Bouliachelys_suteri 0011000?010001?0000110-0100--000?00?0?1?0?0011100000000001-
0111010100001020010201010011-12101011001100111120010000020100010000010202100002210210-
1210000111000011101-
1?????0011011100?001??
??

Notochelone_costata ???000?111002??0?0110-0?00--00?000??1?0000111000?0000001-
?1110100010010??102000?0?11-12101000001100111200??1??0?0000010010200000?02210210-
121000011000011001-

Eretmochelys_imbricata 1--1010111100101000110-
0101100000000010000111100000011200101000211011021210201000011-121020-100211100-
1201100001011100001001020001002210111-121010111000011001-1?????0000111100000100000-0110-0[0 1]011-
001000-2110100110101-1100001110-000011211101-1--0-020001---10[0
1]000000011101112000111000120111110111021111-001--001110111201000111101110101020

Lepidochelys_kempii 1--1010111100101000110-0101110000000010000111100001001112-
0101000211011021210201000011-121020-100211000-1201100[0 1]0000110000011010202001002210110-
121010111000011001-1?????0011101100000100000-0110-00011-00?000-2110100110111-1100011110-000011211101-
1--0-020001---00[0 1]000000011101112000111000120111110111020111-001--001110111201000111101110101020

Natator_depressus 1--1010011100101000110-
0101110000000010000111100000011200101000211011020210101000011-121020-100211100-
120110010000110000010010202001002210211-121010111000011001-1?????0010110100100100000-0110-
000101001000-2110100110101-1100001110-000011211101-1--0-020001---10[0
1]000000011101112000111000120111110111021111-001--0011101112010001?1101110101011

Puppigerus_camperi 1--1010011100100000110-010111000000001000011110000001110-
010101021001102121021?000011-121020-100211100-120110010000110000001010202001001200110-
121100111000011001-1?????0111101100?00100000-0100-000101001000-2100100110111-1100001110-000011211101-
1--0-02000???????0000?1111011120001110001201?????111021111-0???????????1120000010110?1101?1?11

Argillochelys_cuneiceps 1--1000011100101000110-010111000000001000011110000001111-
01010002100010212102010000101121020-1002?1100-120110010100110000010010202001002210111-
121100110000011001-
1?????0011101100?001??
11011120001110001?010??

Allopleuron_hoffmanni 1--10000111001?1000110-00011?00000000010010011101000001110-
010100021?001021110111001010112100011002?1100-1201???10000110000010000212001002210111-
12100011100001100011?????0000??10000001-010-0100-000101001000-20-0100111-01-1100001110-0100111211101-
1--0-021-----111011120001110001201011110111021111-001--00111011120000010110111010101?

Toxochelys_sp. 0011000?1110111001011???10101000000011?00001110100000[0 1]011-01010001[0
1]0001021210200000010112100001000100011120010000001000?000?0?0202001000200111-121000111000011001-
1?????1001[0 1]11100100100000-0110-010101001000-20-0100110111-11000011[0 1]0-0000111211101-1--0-
0200??1?0??1011011?10111200?0??1?0101?001110?00??00?--0??111??100---?01101010?1?00

Eocheilone_brabantica 1--1000011100100000110-010111000000001000011110000000001-
01010001100010212101000000101121020-100210000-120110000100112000011010200001001200011-
12100011100001100101?????00011?11000001??
????????????????????????????????0??

Solnhofia_parsonsi 0011000?111011??100111101010100001?00?000?0011100000000100-
111110020000102021020101101011210001001-0001101100??100201110[0 1]0000110200000000100110-
121000111000011001-1?????011100111110100000-0?????0101001?01121-01002?01?1-0100?01100-
0000??111?0001--000000?????000?000?110?00-----??????1?1????111020????0??--?0?1?1?000---
1?0?01000?0000?

Jurassichelon_oleronensis 0010001?1110110001011110100--00001000010000011101000000001-
0111000000001021210200011010111101101001100110120100010?00100010001100212000000200110-
111000011100011001-1????????????????????0000?0100-0001010???0?????10?????????????0??1?0-000??1?1?1001--
????00?????0?00??11?00-----0?0?1?????????????????????????1????????????????????????

Portlandemys_mcdowellii 0010001?111011?00011110?00--??0?000100?001110100000001-
010100000000102?210201011010111100001000100?01201?0010100100010001[0 1]00212000000200110-
121000011000011001-

12110011000100100011-----000100?001011100110101011000101002011000-01000-0111-110000000111001---?-110021-
-01000001-1-11-1-1-0011111011110???11101021-111110111020011-011--111110110010---1?0001000100?0?

Dermatemys_mawii 1--1000011[0 1]00110020120-010111000011000010000111010000100020[0
1]10111010100102121010000001011210011000210000-1200100000201000110000102[0 1]00000000-0010-12110011001-
----011-----000010?010010100000-01011000101001101000-01000-0111-1100000000-1000111101?1011--00100001-1-
100100000011110110-001011101020111??10111020011-011--00101?110010---1?0001000?0000?

Baptemys_wyomingensis 1--1000?1110?110020120-
0101110000110000000001110100001000210101010?0010212101000?00101121001[0
1]0002?000101200100001201120?????020000000010?1?0-121000111?1-----?1-----100010?000001100110-
01011000101001?00-00-010??0111-1100000000-100011110111011--1?000001-1-
001100000011?1?111??????????2?111?1?111020?11-011--1??1?1?????????0??10001?????

Emarginachelys_cretacea 1--
1000?111001100201????1011000001000?00000111010000?00?21010101?10????021?102010?001??1210011?002100010
11010?0??1?00?0??020??000001??0?0-121100110?0001100??------????????????0011??01011??0??001?00-00-
?10?????1-1100001000-10001111?1?0??1--0?000001-1-00??010?211??111????????????1?????11102?????0?1--
01????1?????????0??1000??????

Chrysemys_picta 1--100001110[0 1]110020110-
01011100001100101000011101000000020010102001100102121020000001011210011000210000-
12001001002010111100001020000000100010-12110011000001100011-----0000101110000100000-0100-
100101001000-00-01000-0101-1100000000-100011110111011--10100001-1-
0000100001111101112111011101020111110111020011-011--000111110010---1?000100010000?

Emys_orbicularis 1--1000011000110020111101010100001100001000011101000000000-
01010000010000212101000000101200011000210000-12001000012010010100101020000000101011-
121100110?0001100011-----0000?0?????100000-0100-100101001000-00-01000-0101-11000010010100010110110011-
?01000001-1-00100000??111101112101011101020111111?111020011-011--00?11?110010---1?000100010000?

Geoclemys_hamiltonii 1--1000011000110120111101111100000100001010011101000000000-
0101021111000021210200000010112100110002100010120010000020103101001010200000000100010-
12110011110001100011-----000010?010000100110-0100-100101001100-00-0100100111-1100000000-
100011110101011--11100001-1-0010100001111101112101011101020111110111020011-011--000111110010---
1?000100010000?

Testudo 1--100001110011012011110100--
000011000010100111010000000020010102000100002012010000001011210011000200000-
120010010100100101001010200000000101010-12110011010001100011-----000000000001010000-0100-
100001001000-00-1100100111-1100000000-10001110101001--00100001-1-
0000100001111101112101011101020111110111020011-011--000111110010---1?000000011000?

Gopherus_polyphemus 1--1000011100110020120-0100--0000110000[0
1]0000111010000100020010102100101002112010000001011210010000210100-1200100001001000-
11000102200000000-1010-12110011010001100011-----000010001000010000-0100-100001001000-00-1100100111-
1100000000-100011110101001--10100001-1-000010000111101112101011101020111110111020011-011--
000111100010---1?000000011000?

Chelonoidis_sp. 1--1000011101[1 2]1012011110100--
00001100000000011101000000002001010210010000201201000000101121001000021000111200100001001000-
1001010220[0 1]00000101010-12110011010001110011-----000000000000100000-0100-000001001100-00-0100100101-
1100001000-10001111010101-1--02100001-1-00000000001101011121010111000201111200111020011-001--
000111100000---1?0001000100?0?

Platysternon_megacephalum 1--1000011000[1 2]11000111001011100100000000001011101001000001-
010101000100102022010000001011210001000201001012011000002010000111101020000000020-0110-

121100111000001001-1-----0000001[0 1]01001100000-0100-000001001100-00-0100100101-1100001000-
1000111101101-1--02100001-1-00000000001101011121010111000201111200111020011-001--000111100000---
1?0001000100?0?

Apalone_spinifera 1--1010011101110120120-1111110000100100010011110110010001-
11111200010110212202100000101121002101-10-10-120010110110100000011010201000000100010-
120000111000011001-1-----000100011100111-00120100-000101-1-001000-0101--1--1-----11[0 1]0-1000111411101-1--
0-001----1-----11010120-0010111000201-11110111020011-001--001110111010---1?000100110010?

Pelodiscus_sinensis 1--1010011101110120120-1111110000100100010011110110010000-
111112000101102122021000001011210021101-10-10-120010110110100010011010201000000100010-
12000011100001100[0 1]11-----000100011100111-00120100-000101-1-001000-0101--1--1-----1110-10001114111-1-1--
--001-----110?0120-00?011100020--1??10??0????????????????0010?

Lissemys_punctata 1--1010011101110120120-11111010000100100010011110110010000-
11112000001102122021000001011210021101-00-20-120010110110100000011010201000000100010-
12000011100001100001-----000?00??0?0011-00120100-000101-1-001000-0101--1--1-----1110-1000111411101-1--0-0-
1----1-----11010120-0010111000201-1--10111020011-001--011110111010---1?0??1001?001??

Carettochelys_insculpta 1--1010011100110120120-11011100100100101000011110000010001-
01111010010110210202000?011011210021101-10-11[0 1]120010110120113000111010201000010100010-
12100011100001100011-----000010111100110100120000-000101000001000-01000-1-11-----1000-100011110110021--
01001----1-----??11010110-001011100020111110111020011-001--011110100000---1?000100220000?

Allaechelys_libyca 1--
1??0?1110?1101201???11??00?0?10??1??1??1?????????????????????????????????02112020000011011210??10??0?11[0
1]1201??1101201130001?0010201?0001?10?010-
12100011100001100011??
??
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Chelus_fimbriatus 1--010101110110[0 1]-20110-01011101--21000011-0011111000000000-01010000001-00202300--
000011-120101000---0000-200-00001132101012001200201000000100010-120001110-0010100011-----
1001?0??????00011[0 3]0100-100001001100-00-01000-0101-1100000000-100011110111011--31100010211001000001-
101111131000010100201011110111120011-10111000110110000---1?000100010000?

Phrynops_geoffranus 011011101110110[0 1]-20111011011101--21000011-0011101000000000-01010000001-
00202300--000011-120101000---0010-200-00001132101012001210201000000101010-121001100-0011100011-----
1001?0?10?100000000-0100-100101101101000-01000-0111-1100000000-100011110111011--10100010010000000001-
100011131000010000201011110111120011-10111000110110000---1?000100010000?

Elseya_dentata 0110111011101101-0011111011101--21000011-0011101000000002011010000001-
00202300--000011-120101000---0000-200-10000120100012001210201000000100010-1[1 2]1001110-00111001-1-----
001000010011000000?0100-100-1-001?11100-010??1-1-1-00000000-1000111101?1001--1010001001?00?000001-
10?0111131000010?0020101??10111120011-1?11100??101??0?0---??00010001??0?

Chelodina 011011101111110-20111001011101--21000011-0011101000000000-01010000001-
00202300--100011-120101000---0010-200-00001122100012001200201000000100010-121001100-00111001-1-----
1001000000000000000130100-100-1-001111100-01000-0111-1-00000000-100011110111011--01100010110000000001-
100011131000010100201011110111120011-10111000110111000---1?000100010000?

Araripemys_barretoii 1--1111011101110-20111001011100001100101100011101000000000-??11?000?1-
01202100--000011-120102100---0-00-200-??00000101012001210201000000100010-121001100-00111001-1-----
100100000000010011140100-100101001001020-01000-1-11-1101001110-000011111111011--01100011---000000101-
100?1111000000101002?011110111?20011-1?????????1?000---1?0??100010000?

Podocnemis 1--1110011101110-00121111011110001100001110011101000011002002110000001-
11202300--100011-120101101---0000-200-10000020100010001210201000000100010-120000101-0001100011-----
000000011000010000[0 1]30100-100101001101000-01000-1-11-1100000000-000011110111010111010001001[0
1]001000001-1000111100000010000201011110111120011-10111000110111000---1?000100010000?

Pelomedusa_subrufa 1--1110011101110-20120-01011100001100101100011101000010002002110-0---1-
11202300--100011-120101000---0010-200-10000100100012101210201000000101000-121001110-0011100011-----
0000?0?110000100000-0100-100101001101000-01000-1-11-1100000000-0000111101110101110100010010000000001-
1000111100000010000201011110111020011-10111000110110000---1?000100010000?

Ordosemys_sp._IVPP_V12092 0010000-111011?0010111?0?0101000?1?001?0?00011101000000000-
010102000?00102021011101[0 1]010111?00101002?00?101201?00100201?00?0011002?0?1000??1??-1110-
0011?000??1-
1??
??

Judithemys_sukhanovi
??1??0?11?01??0?101??101??0001?001000?00111??0?00?000?0?010102000?0?021210??0?001??1210010100010001
01200100?0100100??????0??1000010101?-1110-0111?000??1-1?????000100?????0?00000?0100-000101001?00-
00-01001001?1-1100001000-1000111211?0001--00000001-1?0000000[0 1]00?111011120[0 1]0001[0
1]0102?10112101110200?1-0?1--00?1?100000---1?0??1000?00?0?

Annemys_levensis 00110000111011?00201110?101?10000200010[0 1]000011101000000000-
010102000?0??02021010000001011100010?0001000??1101100001001000??01??020000010??????1?110-
0?11?00011001-1011?0?000000?10000000000-0100-000101101101000-0100100111-1010101000-100011110110001--
000001000100000000100?????????????????0?00????11102001010?1--?0????00000---1?0???????????

Annemys_latiens
0010??1?11101?00201110?10??0?0??0?0??0?1?1?0??0?0????????????????????101000?0010011?0?1?0?
??0?????0?0?0??0?1??????2??00?0?????0[0 1]110-0?11?0001100?????????????????????00000-0100-
000101101?0[0 1]?00-0100100111-1[0 1]10101000-100011110110001--
000001000100000000100?????????????????????????????????????0?--?????00000---1?0???????????

Annemys_sp._IVPP_V18106 0110001?1110110002011??01010100002000101000?11101000000000-
010102000000102021010100?0101110001000001000101101100?0?201000?10111?0210?00000101100-1110-
0011100011001-
1??
??

Xinjiangchelys_wusu
0110?01011101?00020????101??0000100010?00001110?0000?????01?1?2?00???0211101000?001??11000101000100?
??1201100?0?201000?????0200?0000?????0[0 1]110-0111?00011001-1011??00??0?1????0000000-
0?0??0001011010[0 1]?00-0100100111-1100101000-10001?110110001--0000000010000000010000??0?-----
1?0?????????????????????????????????0?000---1?0??100000000?

Xinjiangchelys_radiplicatoides
0110??1?111011?00?011????0??0????0????00111?00?0?0?????11??????02111010?0?0?1011110?2??0
??0?-?1012?0?00001201000?001??0200000000201110-1110-0011000011001-1?????0?1?????????100000-0100-
000??101?00-00-0100100111-1100??000-10001?110110001--
000001000100000000100?????????????????0?0?????111?200101?????????00000---1?????????????

Dracochelys_bicuspis ???1000?11101??0?01??1010100001?0????000111010001?0001-
010100000?00?020?101010000101111001010001000101201?0?0?2010??????02??0000?????10110-
0?11?0001100??1?????000?00?0?0010000??1100-000101001?00-10-0110101-0??1101?01100-1000??211?0001--
00000?????????????0111?110-000001000?0010??01110200??0?????????0?000---1?0??000?????

Kirgizemys_hoburensis 0011000?1110110001011110101010?0020001010?0011101000000000-

010102000?001020?1010000001011110010?000100010110010010100100001001?02?0?100001010?0-1111-
0110?0001100011?????0001?0???????00000-0100-000101101?00-00-010??0111-1100001000-100011121110001--
0?000001-1?0000000[0 1]10?111?111200000110??2?10??2??2??2??21-0?1??????0?000---1???????????

Kirgizemys_dmitrievi ???1000?111001?001?111??101010000200010000001110?0000?0001-
000101000?00102021020?00001011?100100000?000??00100?0?01000?00??02?0?1000?1110?-1111-
0?1??00011101-
??????000100?000000??
??

Sinemys_gamera 01100?1?1110111002011??1101010?02100?000?0011??0?0?0?0?-
0??????????120220100000010111000?00000100010120110010?001000?00?00220?1000??????-1110-
0111?00011001-1????????????????00001?0?????1?????100-2??010?????1-
?10??1????100?????01?00??00??0??1?????00??0000????1??
???????????

Sinemys_lens
0010??1?11101?100201????101??0?02?0000??00111?0000?0?0??????0??????202201000?0?1??1?00010000?00010
110110?????10?0??????022??1000??????-1110-0111?0001100??1?????00????????????0000?0100-000101001100-20-
0100101--1-1101001[0 1]00-100011121010001--
000100??1?0?0000?10?1?0????0??????0??1??????????0????????????????????????????1000?000??

Meiolania_planiceps 0000000011000101000110-
000101000100110000000110010000000020010102100000102103110000[0 1]0101121001[0 1]10000000-12001100000[0
1]11211100110020?000000-101010111-0111100001101-11111100000000010000000-?100-00??001000-00-
?1????0101-0?00101100-0000101001?0011--000000001000??????01000111200000000000?0022011110000101011--
00001?00000---0?000000010000?

Chubutemys_copelloi ???1000?11000?01?0011??10000000?000?00000011??0?000000-
011102000??0202101?000001??1100011000000001?010010000?00110??????0020?0000??????100-----??????1-
1????????????????00????0????????0??0????0????????0????????0????????????????????????????????
?1?1????????0????0????1110?0??

Eubaena_cephalica 0000002?1100011002011??1011100001000000001011101000000001-
0101020001000021210100000011-12100101000?000101201100000201020?00??1210?0001010?110200-----
?00011011-
1?????0000?0??????0??
??

Arundelemys_dardeni 0100001?111001?020110-1?01?1?0?0??0??0?10?1101000000001-
0101000000?0?02??101000000101111001010001000111201?000000010200101110020?000000101110200-----
0000????1-
1??
??

Pleurosternon_bullockii 0110001?111001001001?1?110111000011000000010111010000?0000-
01??00000??020110110000010111?0020?00010-0101101?00?0?????01100111022110001010111[0 1]200---
????00001100??1????????????????0000130??0-0?0101001?00-00-01000-1-11-010010000-
00001?101?010101000001001000000000000??0-----?0?000?????????????????0?1--
00????????????????????????

Glyptops_plicatulus 01100?1?111001?0?0011??101?100?0100000?0010111??0?0?00?1-
0101000?0??0201101?000001011110020?00010-0101101?0?002?100?1100??0211?000101011[0 1]200---
????00001100??1??????00?0?0??0?00000100100-000101001?00-00-0100100111-010010000-
00001111011101010100000000100000000000?00010-----?0?000101??011112001010?1--00??1?100000---
1?0???????????

Kallokibotion_bajazidi

0000??0?1110010100011??10??0000000000??001100100000?00??110102??0??0202102000?00101111?0?
?00??0001?1200?00?00-1112111000101200000000101111-10-----000011001-1?????00?1?????00?00000-0000-
000101??000-00-010011??1??00?000?000-00001?1101?00011?20000001000?000000?00000-----0?0??????-
001110100101011--0000??00000--0?????????????

Eileanchelys_waldmanni 00000?1?1110?0?-001????1011?0000?00??0?00??11010000?0??01?100000??020?100-
000001?????0??00??0?0?01010?00000[0 1]1000010?01002010?000????????????????100011001-
1?????10??????????00?0-0??000001101?00-00-01001001?1-0000??00-
00001?00?????????0?0?00??00?0??00?0??00?0??00?0??00?0??00?0??00?0??00?0??00?0??00?0??00?0??00?0??00?
?

Kayentachelys_aprix 0000001011100101-0000-11011100000000000000?110?000000001-
010100000??0201100--0010100010001000000000-0101000?0?001000?-0??001-101000-11111[0 1]000-----
?0001100--0?????1000?0?00000000000-0000-00000000?100-00-00000-0111-0000001000-
0000001000?000010000000000100000000000?0?00-----?0000000100001010?00101011--00001?10?000--
?????000?????

Australochelys_africanus ???10?00??0101-0000-1?0??0000??000?0000?10?00?000001-0?01?01000??01?00-0--
000?1??11000?0000000000-00000?01?0?0?0?0?-??0?010-1-00?0-211?10000-----????????-
0??
??

Adocus_lineolatus 1--1000?11100110120120-
?10111000011001010000111010000100021010102000?0010202102010?0010112?00111002100010120110000?1011?0??
????02000000010?1?0-111000111?00011000-1?????000?101110001100000-0100-101101001?0?000-010??0111-
1100100000-10001100010001--00000001000100010100010111?100-00101110102?111??0?11020011-011--
010111100?001?0??10001?????

Petrochelys_kyrgyzensis
?????????????101201?????????????0??????1??????????????1?????????02?22021?00001??????2?101-?0-?0-
120010?10110100000?0?020100000?????0-1200?0111?00011001-1-----
??
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Galianemys_whitei 1--1110011101110-2012101101110010010000110101110100001?000-011100000?1-10202200--
101011-12?101001---0010-200-0001010010001000?11021100000210?010-120000011-00111001-1-----
??
??

Cabindachelys_landanensis 1--1000?111011?100012??110111000000????000011100000001110-
01010002100?1021210201000011-12?0000100010000-1201100?0?001100?000?0?????01002200111-
12100011100001100??1????????????????????00110-
0??????1??
??

Procolpochelys_charlestonensis 1--1000?11100101?001??10110000000000100001111000000?1110-
010100021?0?1021210??00001?120020-?01-01100-1201100????11?????????2??010022????-121?0111??????1-
1?????0101111?00?00100000-0?0-100100001000-101201000-??1??11??0?1110-01001101?01-1--0-
0111??????????????11?1????01????1????1?????2111????????????01?2110?????????10?

Peritresius_martini
??
??
??120100110101-1000001110?010????1101-1-
?0?011000?????000000?01?1?1?????1??11201?????????????011?001?1????????????????????

Ctenochelys_sp 1--1010?1110111000011?110111000000001000001110?000001111-
010101111?00102?210201000010112000011000100011201100101001100?00??02??01001210111-

12100011100011111-1?????0011111?00?00100110-0010-010101001000-10100100110101-1100001110-01001101101-1--0-01100001---?000000?00111??1012000111000120101?????11?21110-001--001?1?10110110?1101?1???1

Corsochelys_halinches

?????????1011000?0111?0?????????0000?0???2??????0?101120?0?10??
00?0-1200100100?1???0000001?02?200000121?210-12?00?11100011101-1?????????????????????????000-0?0?
00?01001??0-101001?011?????????????110-01??1?011101-1--0-?????????????????????????1?00-----
0?00?????????11102111????1?00?????0?111????????2?????

Chelosphargis_advana

0010?0?111001110?01??0?100--0000000?000?01110?0000?0?1-
01?????????0?0?10?????0?1??1?1?????????????120?0??020?????????????????????????1?0-1210?0011?????????1-
??????0011?????0?010?010-??0-0001??01000-100-01?00-?01-110?0?11?00011011012101-1--0-
0110??

Calcarichelys_gemma

1--1?0?11?00??0?011?????????00?000??0?1110?0000??0?1-
?1?0?????????02?21020100001??1210?0?00??0010-1200100?00201000?0???020?00002??210-
1210?0011?0001100??1?????0011?????????010-?110-000101?01000-100-01?00-1-?1-110?0011?0-011011112101-1--
0-011?0001---?0?0000????????????????????201?????????????????0????????1????????????????????

Nichollsemys_baieri

1--1000?111001?0010110-0101010000100001000001110?000000010-
0111000100001021210201000011-02?0000100010110-1201100?0000110001011?00202001002210111-
121010111?00011001-
1?????0001?????0?00??
??

Oligochelone_rupelensis

??
??00000-0?0-000101001000-
101?0100110111-1100001110-010011011101-1--0-0111?????????????????1??1?????11?0?1?0??????111021?11-
0?1?0010??01?2110?????????????

Plesiochelys_bigleri

?????????????????0?11110100--0000??0010000?1????????000?1-
?101?????????02021020101101011200100?0011001101100?00100?0100000001110202000000200010-
111000011100011001-1?????????????????????00000-0?0-000101001001000?0000100011-01000?0?00-100011000110?1-
-1?0000001001000000000000?????????????????????????111?0?????1?0?1??1?0?0?0?0?0?????????0

Rhinochelys_nammourensis

0010?0011100?10?00?????100--
000000000??0001110?0?0???1?????0?????????????????1000????????????????????
???00010-0?0-000101001?00-100-0000-?????1100?01110-
011011012101-1--0-
0010?????????????????????????????????????01?????????????0?????????1??2?1?1111102?1????

Erquelinnesia_gosseleti

1--10?0?111011????001??0?0??00?0?????00?0?1111?0000?1110-
01?1000210??021?1020?0001??1?0?????????0??
??010110110000010000-0?0-0?0101001000-1012010011??11-10000011?0-010?????01-1--0-
011??????????????????1?1?11??0011??01?0?????????????????011??0010??01?201?1?????????1?100

Proganochelys_quenstedti 0000100?00000101-00000-0001010000000000-010001000000000001-000000100100000--0-
0-00000?0000010000000000-000-0001000000-0?-0-0?000-0-0000-20010000-----?0001010--
0?????000000000000000000[0 1]00000-?0?00000001000-??0??010000-00?00000-
0000000000?0?0100?0000000100000000??010000-----00000000000000000000000010--00000?000000--
0?000000000000?;

force/(*Proganochelys*((*Pelomedusa_subrufa* *Podocnemis*)((*Chelus_fimbriatus* *Phrynops_geoffranus*)(*Chelodina* *Elseya_dentata*)))(*Carettochelys_insculpta* (*Lissemys_punctata* (*Pelodiscus_sinensis* *Apalone_spinifera*)))(*Platysternon_megacephalum*(*Emys_orbicularis* *Chrysemys_picta*))(*Geoclemys_hamiltonii* (*Gopherus_polyphemus* (*Testudo* *Chelonoidis_sp.*))))((*Macrochelys_temmincki* *Chelydra_serpentina*)(*Dermatemys_mawii* (*Staurotypus* (*Kinosternon_suburum_hippocrepis* *Sternotherus*)))(*Dermochelys_coriacea* ((*Chelonia_mydas* *Natator_depressus*)) (*Eretmochelys_imbricata* (*Caretta_caretta* (*Lepidochelys_olivacea* *Lepidochelys_kempii*))))))))))
;constrain=;