



The first Pan-Carettochelys turtle in the Neogene of the American continent and its paleobiogeographical relevance

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ARTICLE INFO

Keywords:

Allaeochelys
Pan-Carettochelys
Mazantic shale
Early miocene
Phylogenetic analysis

ABSTRACT

Turtles of the clade Pan-Carettochelys have a broad fossil record, from the Early Cretaceous to the late Miocene in the Old World, and some records in the Paleogene of North America; however, its distribution in the Neogene of the American continent was unknown. Here we describe a new species of Pan-Carettochelys, *Allaeochelys liliae* sp. nov., based on an incomplete single specimen from the Los Pocitos mine, Mazantic Shale (Lower Miocene, Aquitanian), near Simojovel, State of Chiapas, southern Mexico. A midline keel, plastral kinesis, and a single suprapygal, suggest that the new turtle belongs to Pan-Carettochelys, and the loss of plastral scutes includes it in Carettochelyidae. The new fossil is referred to *Allaeochelys* based on the loss of carapacial and plastral scutes and a large plastron. It differs from other *Allaeochelys* by the following unique combination of characters: carapacial ornamentation slightly marked with small and shallow tubercles and pits, xiphiplastron and hypoplastron ornamented with pits and vermicular grooves uniformly distributed in all the bone surface, single suprapygal with general triangular shape but with five contact edges, and costal eight in contact with the peripherals nine and ten. *Allaeochelys liliae* sp. nov., represent the first record of Pan-Carettochelys in the Neogene of the American continent, and it is the first *Allaeochelys* described for the Aquitanian (Early Miocene) worldwide.

1. Introduction

Pan-Carettochelys Joyce, Parham, and Gauthier 2004, is defined as the most inclusive clade containing *Carettochelys insculpta* Ramsay (1887), but not *Trionyx triunguis* (Forskål 1775), or any other extant turtle species (Joyce et al., 2004a). Pan-Carettochelys comprises the most basal members including the genus *Kizylkumemys* Nessov 1976, from the Early-Late Cretaceous (Aptian-Cenomanian) of central Asia (Uzbekistan), and Carettochelyidae Gill 1889, a clade that ranges from the Paleocene to the Recent (Joyce, 2014). In all Pan-Carettochelys, the shell is formed by an uninterrupted series of seven neurals (except in

C. insculpta), ten pairs of peripherals, eight pairs of costals, one single suprapygal triangular in shape and the pygal (Joyce, 2014). The plastron is formed by a pair of epiplastra, a large entoplastron triangular in shape, a pair of hyoplastra, a pair of hypoplastra, and a pair of xiphiplastra (Joyce, 2014). The plastron varies in form and size between taxa. In *Kizylkumemys* the plastron is thin, and the xiphiplastra are long and posteriorly acuminate. In *Anosteira*, the plastron is medium-size, while in *Allaeochelys* and *Carettochelys* the plastron is wide and extends along the entire ventral part of the shell (Harrassowitz, 1922; Walther, 1922). The plastral scutes are only present in *Kizylkumemys*.

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<https://doi.org/10.1016/j.jsames.2020.102925>

Received 18 July 2020; Received in revised form 23 September 2020; Accepted 23 September 2020

Available online 30 September 2020

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late Miocene in Eurasia and Africa, and some records in the Paleogene of North America. In Eurasia there are records from the Early Cretaceous of Laos and Thailand (Lapparent de Broin, 2004; Tong et al., 2005; Danilov et al., 2017); the Late Cretaceous of France, Mongolia, Uzbekistan, Thailand and Japan (Nessov, 1976; Hirayama and Chitoku, 1994; Hirayama, 1998; Vullo et al., 2010; Danilov et al., 2017); the early Eocene of Belgium, France, Germany, Spain, United Kingdom and Pakistan (Lydekker, 1889a, 1889b; Dollo, 1886; Harrassowitz, 1922; Jiménez Fuentes, 1971; Broin, 1977, 1987; Wesgate, 2001; Alonso-Santiago et al., 2008); the late Eocene of France, United Kingdom, China, Mongolia and Myanmar (Lydekker, 1889c; Gilmore, 1931; Zangerl, 1947; Cheng, 1961; Broin, 1977; Hutchison et al., 2004; Tong et al., 2010); the early and late Oligocene of Germany (Darga et al., 1999; Karl, 2002; Karl et al., 2006; Karl and Müller, 2008); the early Miocene of Saudi Arabia, Libya and Germany (Lapparent de Broin, 2000; Joyce et al., 2004b; Havlik et al., 2014). In Africa they are known from the early Miocene of Egypt and the late Miocene of the Democratic Republic of Congo (Thomas et al., 1981; Hirayama, 1992), and in Oceania in Papua New Guinea (Glaessner, 1942). Today, they are represented by the monospecific taxon *Carettochelys insculpta* from northwestern Australia and southern Papua New Guinea (Bonin et al., 2006).

In North America *Pan-Carettochelys* has been reported from the early Eocene of Canada and USA, and the late Eocene of USA (Hay,

1906; Clark, 1932; Clark et al., 1967; Estes and Hutchison, 1980; Hutchison and Storer, 1998; Eaton et al., 1999; Weems, 2014). None *Pan-Carettochelys* have been described southern from eastern Hanover County, Virginia in North America (Weems, 2014). During the Neogene there are no reports of this clade along the American continent. Here we report the first record of a *Pan-Carettochelys* turtle from the Neogene (Early Miocene-Aquitania) of the American continent, based in a fossil collected from the State of Chiapas, southern Mexico.

2. Geological setting

Simojovel, in the southern Mexican State of Chiapas, is famous for its amber deposits contained in three Cenozoic marine terrigenous units that outcrop in the southern edge of Montañas del Norte (Fig. 1). Allison (1967) informally named Simojovel Formation to 884 m thick sequence that crops out northeast of the La Esperanza syncline and southwest of the Simojovel syncline. Later, Frost and Langenheim (1974) proposed the name La Quinta Formation in substitution of Simojovel Formation, and they divided it in three members formed mainly by sandstone, shale, and limestone: Camino Carretero (in the base), Florida Limestone (in the middle) and Finca Carmito (at the top). La Quinta Formation is covered by a sequence of 310 m of dark-gray shales named Mazantic Shale (Allison, 1967), that contains amber in association with benthic



Fig. 1. Location map of Los Pocitos mine, near of Simojovel de Allende town, Simojovel municipality, State of Chiapas, southern Mexico.

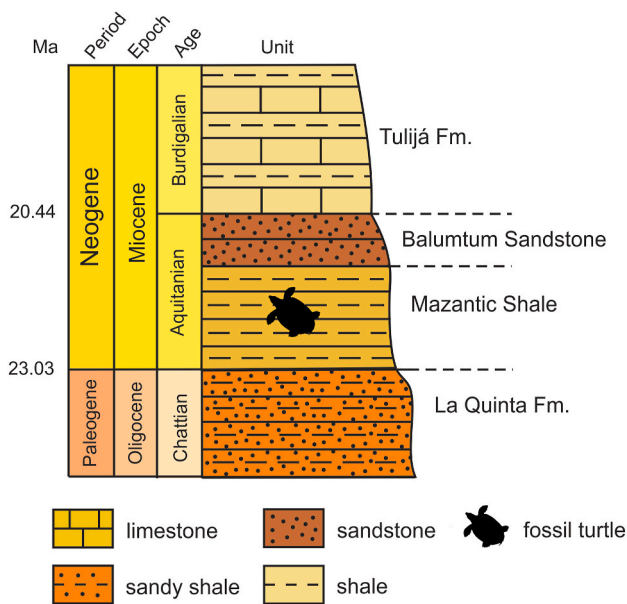


Fig. 2. Generalized stratigraphic chart showing the age and geological divisions of the Simojovel area. Modified from Serrano-Sánchez et al. (2015).

foraminifera, corals, echinoids, bivalves, marine gastropods, crabs and shark teeth (Frost and Langenheim, 1974; Gonzalez-Barba et al., 2002; Vega et al., 2009; Perrilliat et al., 2010). Overlaying Mazantic Shale is the Balumtum Sandstone, conformed by 760 m of gray sandstone bearing amber, gastropods, bivalves, and crustaceans (Frost and Langenheim, 1974; Perrilliat et al., 2010) (see Fig. 2).

The specimen here described was recovered from Los Pocitos amber mines, near Simojovel de Allende village, 125 km northwest of Tuxtla Gutiérrez, Chiapas. Los Pocitos mines are located within the Mazantic Shale. This lithographic deposit has been dated as late Oligocene to middle Miocene (Langenheim et al., 1966; Tomasini-Ortiz and Martínez-Hernández, 1984; Ferrusquía-Villafranca, 2006; Castañeda-Posadas and Cevallos-Ferriz, 2007; Solorzano-Kraemer, 2007, 2010; Solorzano-Kraemer and Mohrig, 2007). Vega et al. (2009) dated the deposit with an absolute age of 23 Ma for the Mazantic Shale based on $^{87}\text{Sr}/^{86}\text{Sr}$ isotopes of a sample taken from a well-preserved shell of the gastropod *Turbinella maya* from Los Pocitos, placing it in the early Miocene (Aquitanian). A similar age (22.8 Ma) was obtained by the same radiometric method from the amber deposits in Las Granjas mines that outcrop in the Balumtum Sandstone (Serrano-Sanchez et al., 2015). These results suggest that the radiometric age of ~23 Ma represents an accurate age for the amber deposits. This age is consistent throughout the upper part of La Quinta Formation–Mazantic Shale–Balumtum Sandstone lithographic units.

3. Material and methods

3.1. Studied material

The turtle was collected by a local miner at Los Pocitos amber mine, in 2004. It preserves the posterior part of carapace with an incomplete plastron, embedded on a dark-gray sandy shale matrix. Latter, the specimen was acquired by Luis Zúñiga Mijangos, who housed it at the Museum of Amber Lilia Mijangos (MALM) in San Cristobal de Las Casas, State of Chiapas, Mexico, with collection number MALM-401. The fossil collection of MALM is formally certified by the Instituto Nacional de Antropología e Historia (INAH), the federal agency that protects the paleontological heritage in Mexico.

3.2. Preparation

The specimen was prepared using a scribe, dental needles, and soft bristle brushes to remove rock matrix. It was hardened with Butvar-B90, and the broken parts were joined with water-proof commercial glue.

3.3. Comparative materials

The specimen was compared with valid Pan-Carettochelys taxa according to Joyce (2014). It includes the basal species *Kizylkumemys schultzi* Nessov (1976), *K. khoratensis* Tong, et al. (2005), *Anosteira manchuriana* Zangerl (1947); *An. maomingensis* Chow and Liu (1955), *An. mongoliensis* Gilmore (1931), *An. ornata* Leidy (1871); *An. pulchra* (Clark, 1932) and all species within *Allaeochelys* Noulet, 1867. Additionally, we compared it to the extant *Carettochelys insculpta* Ramsay (1887) (see Appendix A). The morphological nomenclature for the bony plates follows Zangerl (1969).

3.4. Phylogenetic analysis

To establish the phylogenetic relationships of the new taxa within Pan-Carettochelys, we scored MALM-401 features in a modified dataset (Appendix B) based on Joyce (2007), Havlik et al. (2014) and Danilov et al. (2017), using Mesquite 3.61 (Maddison and Maddison, 2019). We eliminated character 82 from Joyce (2007) (retaken by Havlik et al., 2014) and Danilov et al., 2017, because it is redundant with the character 81 from the same data matrix; in consequence, we added a new character state (see note in Appendix C, character 98). A data matrix with 153 morphological characters and 81 taxa was used in the phylogenetic analysis.

We conducted a Maximum Parsimony Analysis in TNT 1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016), considering all characters with equal weight. For analysis we deactivate phylogenetic uninformative characters using the command *xinact*. The characters were treated as unordered. We used the New Technology search option with 100 random seeds, with the Sectorial search, Ratchet, Drift and Tree fusing default options activated. The final tree was obtained by strict consensus. We estimated tree robustness using bootstrap with 1000 replicates (Groups present/Contradicted, GC; Goloboff et al., 2003) (Appendix D; Fig. S2) and we calculated Statistical Support Values (Bremer Index, Consistence Index and Retention Index) with the command scripts included in TNT.

3.5. Institutional abbreviations

MALM: Museum of Amber Lilia Mijangos, San Cristóbal de Las Casas, Chiapas, Mexico.

4. Results

4.1. Systematic paleontology

Testudines Batsch, 1788.
Cryptodira Cope, 1868.
Trionychoidea Fitzinger, 1826.
Pan-Carettochelys Joyce (2004a).
Carettochelyidae Gill, 1889.
Carettochelyinae Williams, 1950.
Allaeochelys Noulet, 1867.
Allaeochelys liliae sp. nov.
Zoobank: urn:lsid:zoobank.org:act:819C03FB-1E74-406C-A11F-A7A913724DA7.

Holotype. MALM-401, posterior part of the carapace and partial plastron. Museum of Amber Lilia Mijangos, San Cristóbal de Las Casas, Chiapas, Mexico.

Etymology. The specific epithet *liliae* is to honor the memory of Mrs.

Lilia Mijangos. Her effort has safe a great number of Simojovel fossils. Her interests in scientific research has facilitated many paleontologists to study these fossils.

Type locality and horizon. Los Pocitos mines, municipality of Simojovel de Allende, State of Chiapas, southern Mexico. Mazantic Shale, Lower Miocene (Aquitanian).

Diagnosis. *Allaeochelys liliae* sp. nov. differs from other species of *Allaeochelys* in the following combination of characters: carapacial ornamentation slightly marked with small and shallow tubercles and pits; xiphiplastron and hypoplastron ornamented with pits and vermicular grooves uniformly distributed in all bone surface; single suprapygal with general triangular shape, but with five contact edges, and costal eight in contact with the peripherals nine and ten.

4.2. Description

General aspect of carapace and plastron. The specimen is dark-brown and is embedded in a dark-gray sandy shale matrix. Only the posterior portion of the carapace is preserved, suggesting a drop-like general shape. The carapace preserves part of neural seven, the left and right costals six, seven and eight, the pygal and suprapygal, the right and left peripheral ten, and the left peripheral nine. The carapace has a midline keel from peripheral seven to the pygal bones and there is no evidence of a bridge with the plastron, suggesting that the connection was ligamentous, as in another soft-shell turtles. The plastron preserves both xiphiplastra and the left hypoplastron and lacks plastral fontanels. The surface of the carapace and plastron are ornamented with slighty marked pits and grooves. There is no evidence of scute sulci neither in the carapace nor the plastron.

Neurals. Only neural seven is preserved. It is semi-rectangular and longer than width. The lateral side contacts costal six, but posteriorly barely touches costal seven. The surface of the neural is almost smooth with no evident ornamentation.

Costals. Costal bones six, seven and eight are preserved. All costal bones are completely ossified showing no lateral fontanels. Costal six is longer than width, slightly curved posteriorly, and medially it contacts neural seven. Costal seven is longer and more curved than costal six and laterally it reaches peripheral seven. Costal eight is posteriorly curved contacting the suprapygal and distally the peripherals nine and ten. Both costals seven and eight are in contact medially. All costal bones are ornamented with slighty marked grooves and slight irregular bumps.

Peripherals. Only the anterior part of the left peripherals nine and ten, and proximal part of the right peripheral ten are preserved. Peripheral nine contacts costal seven, but their shape cannot be defined. Peripheral ten is rectangular in shape. Lateral side of the peripheral contacts costal eight and the pygal, while the anteromedial side contacts the suprapygal. The surface of both conserved peripherals is sculpted with small pits.

Suprapygal. There is only one suprapygal with a general triangular shape, but with five edges. Anterolaterally it contacts costal eight, posterolaterally peripherals ten, and posteriorly the pygal.

Pygal. The pygal is incomplete and only preserves de anterior part, which contacts the suprapygal with a straight suture. The general shape cannot be established.

Hypoplastron. The specimen preserves a nearly complete left hypoplastron and a portion of the right hypoplastron. In the left hypoplastron the “wing” is missing. The bone surface is ornamented with small and shallow pits and tubercles, more abundant in the distal portion.

Xiphiplastron. Both xiphiplastra are preserved. The xiphiplastron is semitriangular, longer than wide, narrowing posteriorly. The left xiphiplastron contacts the left hypoplastron with a straight suture, condition not seen in the right xiphiplastron because the bone is displaced to the right from the original position. There is a clear evidence of a hinge indicating that was some degree of plastral kinesis between these two bones. Both xiphiplastra are ornamented with pits and vermicular

grooves uniformly distributed in all their bone surface.

5. Discussion

5.1. Taxonomic assessment and comparison

Following Joyce (2014), the specimen MALM-401 can be referred to Pan-Carettochelys by the following synapomorphies: presence of a midline keel, plastral kinesis and a single suprapygal; it can be referred to Carettochelyinae by the loss of plastral scutes and is referred to *Allaeochelys* by the loss of vertebral scutes and a large-size plastron (see Fig. 4).

Allaeochelys liliae sp. nov. is considered a new species of *Allaeochelys* because of a unique combination of characters compared to previously described species of the genus. *Allaeochelys liliae* sp. nov. differs from the Eocene species *Al. delheidi* (Dollo, 1886), *Al. crassesculpta* (Harrassowitz, 1922) and *Al. parayrei* Noulet (1867) in the contact of the last neural. While in the new species the neural seven contacts the suture between the costals six and seven, in *Al. delheidi*, *Al. crassesculpta* and *Al. parayrei* the neural seven reaches the middle part of the costal seven (Fig. 5). Similarly, *Al. liliae* sp. nov. shows differences with *Al. delheidi* and *Al. crassesculpta* in the contact of the posterior costals and peripherals. In *Al. liliae* sp. nov. costal eight contact peripherals nine and ten, and costal seven contact peripherals nine, contrary to *Al. delheidi* in which costal eight only contact peripheral ten, and costal seven contact peripheral nine and barely peripheral ten (Fig. 5B). In *Al. crassesculpta* costal eight contact peripheral nine, and costal seven contact peripheral eight (Fig. 5C).

Also, in *Allaeochelys liliae* sp. nov. the suprapygal have five contact sides, similar to that of *Al. delheidi* (Alonso-Santiago et al., 2008; Fig. 6), differing to the middle Eocene *Al. magnifica* (Hutchison et al., 2004), and the late Eocene *Al. parayrei* that have a triangular suprapygal, with three contact sides (Fig. 5D and E). Additionally, the new species is considerably smaller than *Al. magnifica*, reaching about 1000 mm (Hutchison et al., 2004) compared to the 350 mm estimated for *Al. liliae* sp. nov.

Allaeochelys liliae sp. nov. has slighty marked carapacial ornamentations, with small and shallow tubercles and pits. Shell ornamentation differs from remaining *Allaeochelys* species. In the early Eocene *Al. lingnanica* Young and Chow (1962) the carapacial sculpturing consists on elongated anteroposterior ridges more prominent along the costals toward the neurals (Joyce, 2014). In the early Eocene and *Al. rouzilhaensis* Lapparent de Broin 2018, carapace ornamentations are less pronounced, fine, with parasagittal pleural margins interrupted, tight, with punctuations in low relief (Godinot et al., 2018). In *Al. liliae* sp. nov. the hypoplastron and xiphiplastron are completely sculpted, differing from the late Eocene *Al. parayrei* where the xiphiplastron is smooth and the hypoplastra exhibit ornamentations conformed by vermicular grooves only in their lateral “wings”. Contrary to the middle Miocene *Al. libyca* Havlik et al. (2014), with hypoplastron ornamentations radially developed, more distinct along the bridge and worn along the main body of the element (Havlik et al., 2014), in the new species, ornamentations are uniformly distributed in all the bone surface, showing no difference between the ornamentation of the bridge area and the rest of the bone surface. Also, the new species differs to the early Eocene *Al. crassesculpta* (Harrassowitz, 1922) and the extant species *Carettochelys insculpta* Ramsay (1887) in which the ornamentation grooves in the hypoplastron and xiphiplastron are radially distributed from the center to the sides of the bone, and not uniformly distributed along the bone surface as are in the new species.

5.2. Phylogenetic analysis

In our Maximum Parsimony analyses, the strict consensus tree shows *Allaeochelys liliae* sp. nov. grouped within Pan-Carettochelys, Carettochelyidae and Carettochelyinae in unresolved polytomies. The analysis recovered four Most Parsimonious Trees (MPTs). The general

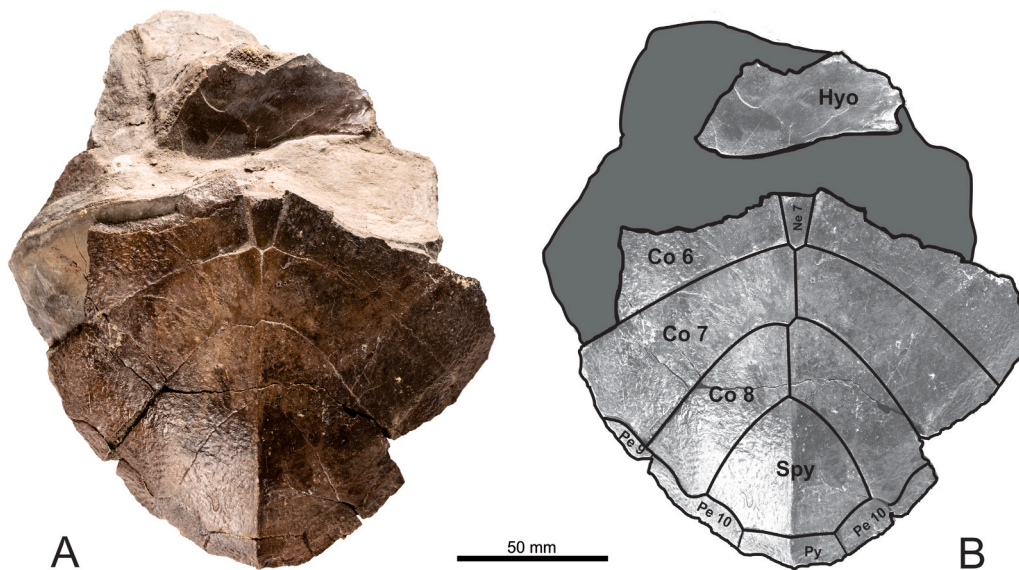


Fig. 3. MALM-401, holotype *Allaeochelys liliae* sp. nov. (dorsal view) from the early Miocene of Simojovel, State of Chiapas. Photograph (A) and schematic draw (B). Abbreviations: Co, costal; Hyo, hyoplastron; Ne, neural; Pe, peripheral; Py, pygal; Spy, suprapygals.

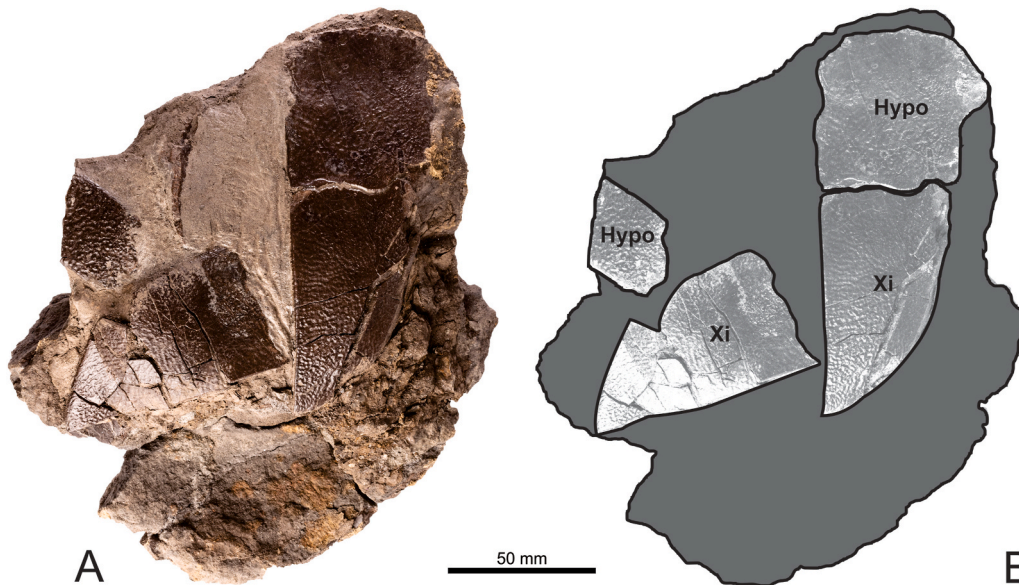


Fig. 4. MALM-401, holotype *Allaeochelys liliae* sp. nov. (ventral view) from the early Miocene of Simojovel, State of Chiapas. Photograph (A) and schematic draw (B). Abbreviations: Hypo, hypoplastron; Xi, xiphiplastron.

topology of Pan-Carettochelys in the strict consensus tree (Fig. 6) is similar to that presented by Joyce (2014, Fig. 3), Havlik et al. (2014, fig. 1) and Danilov et al. (2017, fig. 5B), with the difference that *Kizylkumemys khoratensis* was placed out of Pan-Carettochelys, together with *Sandownia* Meylan, Moody, Walker and Chapman 2000, and *Peltochelys* Dollo 1884, possibly because material on these species is very fragmentary. In Havlik et al. (2014) and Joyce (2014), *Anosteira maomingensis* resulted as the sister taxon of Carettochelyinae, while in our analysis all *Anosteira* species branched together in an unresolved clade here treated as Anosteirinae, according to Nessov (1976), that excludes *K. khoratensis*. *Allaeochelys liliae* sp. nov. is recovered in a polytomy with all *Allaeochelys* species together with *Carettochelys insculpta*, forming the clade Carettochelyinae. This arrangement does not differ from those obtained by Joyce (2014), Havlik et al. (2014) and Danilov et al. (2017).

The disparity in the available morphological data per taxon was the major source for the weak resolution of the Maximum Parsimony

analyses. For example, of all known *Allaeochelys*, only *Al. crassesculpta* is based in cranial and postcranial anatomy, including carapace, plastron and appendicular skeleton (Harrassowitz, 1922), *Al. libyca* and *Al. rouzilhacensis* are known by their skull, and the description of remaining species are based on incomplete carapace or/and plastral elements.

The complete results of the Maximum Parsimony Analysis can be consulted in Appendix D.

5.3. Character analysis

In our analysis (Fig. 6), Trionychia Humel 1929, is supported by five unambiguous synapomorphies: premaxillae fused (character 24[1]), foramen pre-palatium absent (character 25[2]), vomer-ptyergoid contact in palatal view absent (character 29[1]), ten pairs of peripherals presents (character 73[1]), and posterior cervicals with strongly developed ventral keels absents (character 120[1]). Pan-Carettochelys is

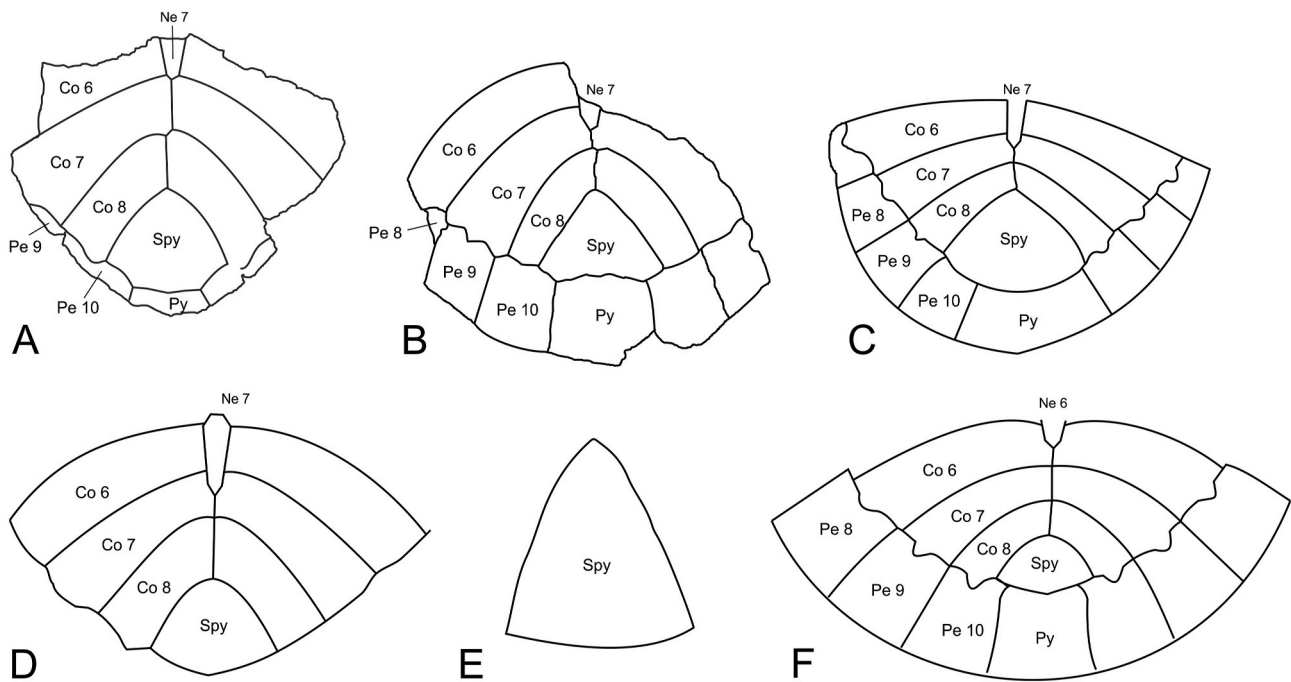


Fig. 5. Schematic draw of the posterior part of the carapace of *Allaeochelys* selected species plus *Carettochelys*. A) *Allaeochelys liliae* sp. nov. (holotype MALM-401); B) *Al. delheidi* (based on specimen STUS 14.132; Alonso-Santiago et al., 2008); C). *Al. crassesculpta* (Harrassowitz, 1922); D) *Al. parayrei* (based on the specimen MHNT-PAL-2010-0-115); E) *Al. magnifica* (illustration of the suprapygal based on the reconstruction by Hutchison et al., 2004, fig. 5); F) *Carettochelys insculpta* (based on the specimen 4800 of the Peter C. H. Pritchard Collection). Not to scale. Abbreviations: Co, costal; Ne, neural; Pe, peripheral; Py, pygal; Spy, suprapygal.

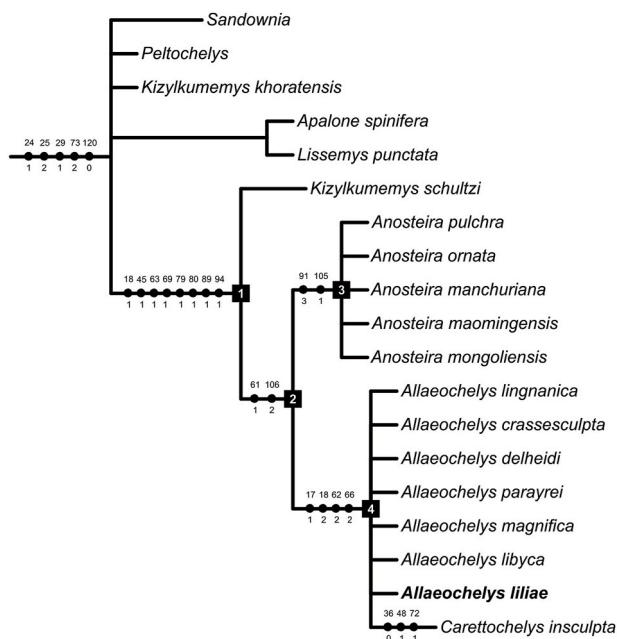


Fig. 6. Phylogenetic hypothesis resulting when including *Allaeochelys liliae* sp. nov. Simplified consensus tree of four MPTs (CI = 0.461, RI = 0.807) resulting from the Maximum Parsimony Analysis showing the position of *Allaeochelys liliae* sp. nov. (in bold). Only unambiguous characters are shown. Numbers in the nodes indicate the Clades: 1, Pan-Carettochelys; 2, Carettochelyidae; 3, Anosteirinae; 4, Carettochelyinae.

supported by eight unambiguous synapomorphies: fossa behind articular process of quadrate absent (character 18[1]), pterygoid-ptyergoid suture between foramen *posterius canalis caroticus interni* and basisphenoid present (character 45[1]), foramen *nervi trigemini* divided into two parts by prootic (character 63[1]), ventral processes of nuchal

paired (character 69[1]), anterior margin of pygal greatly thickened and with visceral groove (character 79[1]), carapace with single midline keel (character 80[1]), absence of sulcus between vertebrals 3 and 4 (character 89[1]), and plastral kinesis because the scute sulci coincide with hyoplastral–epiplastral contact (character 94[1]). Our character distribution differs from previous phylogenetic studies where 11 synapomorphies (Joyce, 2014; Havlik et al., 2014) or one synapomorphy (Danilov et al., 2017) were recovered defining the Pan-Carettochelys clade.

The clade Carettochelyidae (Anosteirinae + Carettochelyinae) is supported by two unambiguous synapomorphies: *antrum postoticum* deep (character 61[1]), and plastral scutes absent (character 106[1]). ACCTRAN optimization added two ambiguous synapomorphies: vertebral 1 partly or completely divided along the midline (characters 86[1]*, and additional vertebral scute between vertebrals 2 and 3 (characters 91[2])*). In the analysis by Danilov et al. (2017), Carettochelyidae is supported by two unambiguous synapomorphies, i) *antrum postoticum* deep, also recovered in our analysis (here character 61[1]) and ii) additional vertebral scute between vertebrals 2 and 2, fused with vertebrals 3 + 4 (here character 91[3]). The additional vertebral scute is present in *Anosteira* (Danilov et al., 2017), but absent in *Allaeochelys* and *Carettochelys*.

Anosteirinae (*Anosteira* spp.) is supported by two unambiguous synapomorphies: an additional vertebral scute between vertebrals 2 and 3 fused with vertebrals 3 + 4 (character 91[3]), and posterior plastral lobe reduced (characters 105[1]). Under the DELTRAN optimization one ambiguous synapomorphies is added: sulcus between cervical and/or marginal and vertebral I absent (characters 87[1])*.

Carettochelyinae (*Allaeochelys* + *Carettochelys*) is supported by four unambiguous synapomorphies: quadratojugal–maxilla contact present (character 17[1]), large fossa behind articular process of quadrate (character 18[2]), foramen *posterius canalis caroticus interni* distant from the posterior border of basisphenoid on the ventral surface of the skull within pterygoids (character 62[2]), and all carapacial scutes absent (character 66[2]). Under ACCTRAN optimization one ambiguous synapomorphies is added: wide posterior plastral lobe (character 105[0]*),

and under DELTRAN optimization two additional ambiguous synapomorphies support the clade: elongate flippers manus (character 150[2])* , and two manual claws (character 153[3])*.

5.4. Paleobiological aspects

The holotype specimen of *Allaeochelys liliae* sp. nov. was an adult female. The carapace and plastron are completely ossified, with no evidence of fontanels between the costals and peripherals bones, expected in juvenile turtle specimens (Suzuki, 2006), and the suture between the hypoplastron and xiphiplastron is almost straight as expected in female *Allaeochelys*, as indicated by Joyce et al. (2012) for *Al. crassesculpta*. The straight hypoplastron/xiphiplastron suture allows plastral kinesis, which is useful in oviposition (Joyce et al., 2012).

The extant species *Carettochelys insculpta* inhabits rivers, billabongs, estuarine reaches and river deltas in Papua New Guinea and Australia (Bonin et al., 2006). Local people of the Purari region mentioned that the hatchling turtles feed on vegetation and fruits of mangroves (Georges et al., 2008). A mangrove estuarine habitat has been proposed for the Simojovel area during the early Miocene (Langenheim et al., 1966; Serrano-Sánchez et al., 2015; Huys et al., 2016) and it is possible that *Allaeochelys liliae* sp. nov. preferred this type of habitat, as in *C. insculpta*. This agree with the discovery of Eocene *Allaeochelys* and Miocene fragmentary carettochelyine specimens in marine, near-shore, or deltaic sediments (Joyce, 2014).

5.5. Paleobiogeography

Kizylkumemys schultzi from the early Cenomanian of Uzbekistan (Fig. 6; Nessov, 1976) and *Kizylkumemys khoratensis* from the Early Cretaceous of Thailand (Tong et al., 2005) has been considered the oldest members of Pan-Carettochelys (Havlik et al., 2014; Joyce, 2014; Danilov et al., 2017). Additional ancient records of Pan-Carettochelys come from the Late Cretaceous of France, Mongolia, and Japan

(Hirayama and Chitoku, 1994; Hirayama, 1998; Vullo et al., 2010). The Euro-Asiatic origin hypothesis for the clade is consistent with the fossil record.

Similarly, the genus *Anosteira* has been recorded from the late Paleocene to the late Eocene of Asia and North America (Hutchison and Storer, 1998; Hutchinson et al., 2004; Tong et al., 2010; Joyce, 2014). Based on its current fossil record, the genus *Anosteira* was restricted in the northern hemisphere of the Earth during the Paleogene. Its sister taxa *Allaeochelys* extends also throughout the Paleogene, but with a broader geographic distribution in Eurasia. The oldest member of the genus is *Al. lignanica* from the Paleocene deposits in Guangdong, China (Young and Chow, 1962; Tang and Zhou, 1965) supporting an Asiatic origin of the genus. The presence of *Al. delheidi*, *Al. crassesculpta*, and *Al. parayrei* in the Eocene of Europe, suggests that the genus *Allaeochelys* reached this continent by the late Paleocene or early Eocene and then it diversified. During the late Eocene or Oligocene *Allaeochelys* extended its distribution range outside Eurasia to Africa and North America (Fig. 7).

The presence of *Allaeochelys* in North America is better explained by dispersion from the Old World. Unfortunately, the unresolved resolution of *Allaeochelys* members in our phylogenetic analysis does not allow us to know which lineage is the closest to *Al. liliae*, and infer whether the genus spread to North America from Europe, Asia or Africa. *Allaeochelys liliae* shares the triangular pygal with five contacts with *Al. delheidi* from the early Eocene of Europe, and it is possible that *Al. liliae* was closer to *Al. delheidi* than to any other *Allaeochelys*. Under this hypothesis, it is highly probable that once European *Allaeochelys* crossed to North America via the Greenland bridge during the global warming of the Paleocene–Eocene Thermal Maximum. This hypothesis agrees with the dispersal of several mammal taxa from Europe to North America during a key event called the Mammalian Dispersal Event, during the Paleogene-Eocene boundary. During this time there was a well-represented faunal correlation in the NALMA Wa-0 of the Tienen Formation of Dormaal, Belgium and the Bighorn Basin, Wyoming, that

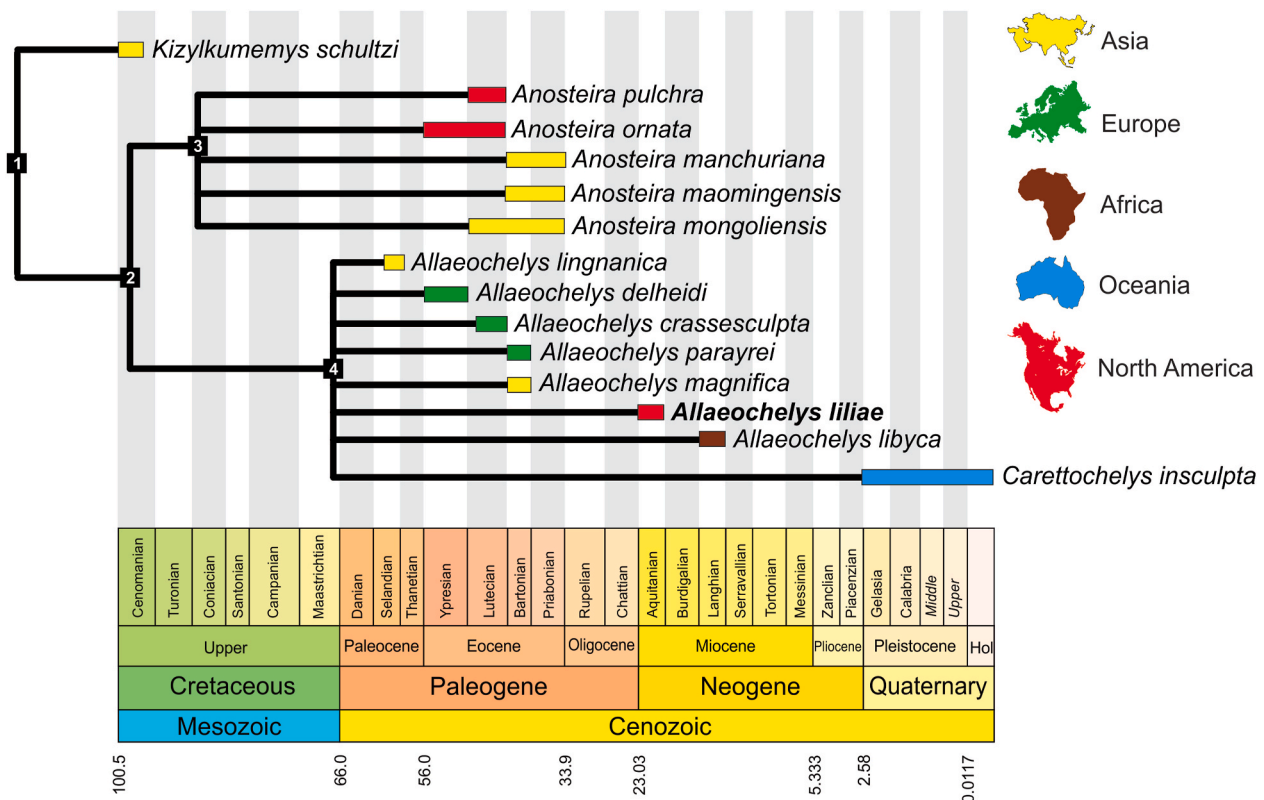


Fig. 7. Simplified cladogram of the Pan-Carettochelys showing the temporal and geographical distribution of the members of this clade.

includes the equiodes *Sifrihippus*, the artiodactyl *Diacodexis*, the hyaenodontid *Hypsodus*, the amphilemurid *Macrocranium* and the primate *Teilhardina* (Smith et al., 2006; Hooker, 2015).

The presence of one fragmentary specimen referred as *Allaeochelys* sp. from the Piney Point Formation (late Lutetian-early Bartonian, middle Eocene) in Pamunkey River, eastern Hanover County, Virginia, USA (Weems, 2014), provide support for the idea that *Allaeochelys* has a pre-Neogene presence in North America. The new species *Allaeochelys liliae* sp. nov. extends the time and spatial distribution of the genus *Allaeochelys* into the Miocene and far south into northern middle América.

If the sister species of *Al. liliae* sp. nov. is an African taxon, a second hypothesis would include a trans-Atlantic dispersion to North America from North Africa or southwestern Europe during the late Oligocene or early Miocene. The arrival of Old-World terrestrial taxa (e.g. platyrrhine primates and caviomorph rodents) to America has been traditionally explained by a trans-Atlantic dispersion during the Oligocene-Miocene interval (Hoffstetter, 1972; Martin, 1994; Poux et al., 2006; Seiffert et al., 2020). This hypothesis suggests that during the earliest Oligocene there was an eustatic drop in the sea level (Miller et al., 2008) favoring the dispersal of terrestrial vertebrates. Although the distance between the two landmasses during the Oligocene-Miocene was still large, the colonization could have occurred by rafting, aided by equatorial paleo-currents (Godinot, 2020). A rafting hypothesis is presented by Peris et al. (2015) to explain the presence of African beetles of the subfamily Platypodinae in the Miocene Mexican and Dominican amber.

6. Conclusions

The morphological characters included in the description of *Allaeochelys liliae* sp. nov. and the phylogenetic analysis presented in this work, support its inclusion as a new species into the Carettochelyidae, increasing the diversity and geographical distribution of this clade. *Allaeochelys liliae* sp. nov. differs from the rest of the species of the genus *Allaeochelys*, mainly in the sculpturing of the carapace and plastron, and some shell structure features.

Allaeochelys liliae sp. nov. is biogeographically important because it expands the geographical range of the genus to the south, into State of Chiapas, Mexico, and represents the only known species of the Pan-Carettochelys in the Aquitanian age (early Miocene) worldwide, and the first Neogene record of the clade in the American continent. The distribution of the genus *Allaeochelys* in the American continent (a very common turtle in the Paleogene and Neogene of Eurasia and Africa), can be better explained by dispersion from Europe to North America via the Greenland bridge during the global warming at the Paleocene–Eocene Thermal Maximum, or in second term by trans-Atlantic dispersion from Africa or southern Europe during the eustatic drop in the sea level in the earliest Oligocene.

The Simojovel area represents the only known early Miocene fossil deposit with continental organisms in Mexico. This locality is better known because of the amber and their biological inclusions. Prior to this work, only two continental vertebrates were formally described for the Simojovel area, the protoceratid *Paratoceras tedfordi* Webb et al (2003) (Webb et al., 2003), and the tayassuid *Simojovelhyus pocitose* Ferrusquía-Villafranca (2006) (Ferrusquía-Villafranca, 2006; Prothero et al., 2013). *Allaeochelys liliae* sp. nov. is the third continental vertebrate formally described from this area, and contribute to the knowledge of middle-American faunas.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank Luis Zuñiga Mijangos, who facilitated the specimen for study. We specially thank France de Lapparent de Broin and Philippe E. Havlik for the bibliography and photographs of specimens of *Allaeochelys* and *Carettochelys* for comparison. This paper constitutes a partial fulfillment of the Doctoral Thesis of the Biodiversity and Conservation of Tropical Ecosystems Graduate Program, Universidad de Ciencias y Artes de Chiapas of G. Carbot-Chanona. We thank The Willi Hennig Society to make TNT freely available and to Instituto de Ciencia, Tecnología e Innovación del Estado de Chiapas for the support to acquire the photographic equipment through the Sistema Estatal de Investigadores (project: Fortalecimiento del estudio de los microinvertebrados y microvertebrados fósiles del Estado de Chiapas, México, a través de la microfotografía digital). Finally, we thanks to the three assigned reviewers for the comments that helped to improve this manuscript.

Appendix E. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jsames.2020.102925>.

Funding

This research was supported by the Biodiversity and Conservation of Tropical Ecosystems Postgrad Program, Instituto de Ciencias Biológicas of the Universidad de Ciencias y Artes de Chiapas.

Author contributions

GCC: Conceptualization; Investigation; Data curation; Methodology; Formal analysis; Writing - original draft; Writing - review & editing. GRV: Funding; Supervision; Writing - review & editing. E.JH: Investigation; Supervision; Writing - submitted draft review & editing. VHR: Supervision; Methodology; Formal analysis; Writing - submitted draft review & editing.

Author statement

The authors of the manuscript “The first Pan-Carettochelys turtle in the Neogene of the American Continent and their paleobiogeographical relevance”, declare that we have no conflict of interest, whether personal or financial, that conflicts with the objectivity with which the research was conducted.

References

- Allison, R.C., 1967. The Cenozoic Stratigraphy of Chiapas, México, with Discussions of the Classification of the Turtellidae and Selected Mexican Representatives. Ph.D. dissertation. University of California, Berkeley, p. 225.
- Alonso-Santiago, L., Alonso Andrés, L., Jiménez Fuentes, E., 2008. Primer espaldar en conexión anatómica de *Allaeochelys casasecai*. Cazorra: nuevo yacimiento del Eoceno de Zamora (España). *Studia Geol. Salamanticensia* 44, 177–186.
- Batsch, A.J.G.C., 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien. Akademische Buchhandlung, Jena, p. 528.
- Bonin, F., Devaux, B., Dupré, A., 2006. Turtles of the World. The Johns Hopkins University Press, Baltimore, Maryland, p. 416.
- Broin, F. de, 1977. Contribution à l'étude des chéloniens: chéloniens continentaux du Crétacé et du Tertiaire de France. Paris: Éditions du muséum. *Mémoires. Muséum Natl. Hist. Natl. Nouv. Sér., Ser. C, Sci.* 38, 366.
- Broin, F. de, 1987. Lower vertebrates from the early-middle Eocene kuldana Formation of Kohat (Pakistan): Chelonia. *Contribut. Museum Paleontol.* 27 (7), 169–185.
- Castañeda-Posadas, C., Cevallos-Ferriz, S.R.S., 2007. *Swietenia* (meliaceae) flower in late oligocene–early Miocene amber from Simojovel de Allende, Chiapas, Mexico. *Am. J. Bot.* 94 (11), 1821–1827.
- Cheng, Z.-W., 1961. A new anostérine turtle from Linchu, Shantung. *Vertebrata Palasiatica*, pp. 273–276, 1961.
- Chow, M.M., Liu, C.-I., 1955. A new anostérine turtle from Maoming, Kwangtung. *Acta Palaeontol. Sin.* 3, 275–282.

- Clark, J., 1932. A new anosteirid from the Uinta Eocene. *Ann. Carnegie Museum Natl. Hist.* 21, 161–170.
- Clark, J., Beerbower, J.R., Kietzke, K.K., 1967. Oligocene sedimentation, stratigraphy, paleoecology and paleoclimatology in the Big Badlands of South Dakota. *Field Museum of Natural History*, p. 158.
- Cope, E.D., 1868. On the origin of genera. *Proc. Acad. Nat. Sci. Phila.* 1868, 242–300.
- Danilov, I.G., Obratsova, E.M., Chen, W., Jin, J., 2017. The cranial morphology of *Anosteira maomingensis* (Testudines, Pan-Carettochelys) and the evolution of pan-caretochelyid turtles. *J. Vertebr. Paleontol.*, e1335735 <https://doi.org/10.1080/02724634.2017.1335735>.
- Darga, R., Böhme, M., Göhlich, U.B., Rössner, G.E., 1999. Reste höherer Wirbeltiere aus dem Alttertiär des Alpenvorlandes bei Siegsdorf/Oberbayern. *Mittl. Bayer. Staatssamm. Palaontol. Hist. Geol.* 39, 91–114.
- Dollo, L., 1886. Première note sur les chéloniens du Bruxellien (Éocène moyen) de la Belgique. *Bull. Musee R. Hist. Nat. Belg.* 4, 75–100.
- Eaton, J.G., Hutchison, J.H., Holroyd, P.A., Korth, W.W., Goldstrand, P.M., 1999. Vertebrates of the Turtle Basin Local Fauna, Middle Eocene, Sevier Plateau, South-Central Utah, vols. 99–1. *Utah Geological Survey Miscellaneous Publications*, pp. 463–468.
- Estes, R., Hutchison, J.H., 1980. Eocene lower vertebrates from ellesmere island, Canadian arctic archipelago. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 30, 325–347.
- Ferrusquía-Villafraña, I., 2006. The first Paleogene mammal record of Middle America: *Simojovelhyus pocitosense* (Helohyidae, Artiodactyla). *J. Vertebr. Paleontol.* 26 (4), 989–1001.
- Fitzinger, L., 1826. Neue classification der Reptilien nach ihren natürlichen Verwandtschaften. *Verlag J. G. Heubner, Wien*, p. 66.
- Forskål, P., 1775. Descriptions Animalium Avium, Amphibiorum, Piscium, Insectorum, Vermium; Quae in Itinere Orientali Observavit. Möllerus, Haunia, p. 164.
- Frost, S.H., Langenheim, R.L., 1974. Cenozoic Reef Biofacies, Tertiary Larger Foraminifera and Scleractinian Corals from Chiapas. *Northern Illinois University Press, De Kalb, Illinois, Mexico*, p. 388.
- Georges, A., Doody, J.S., Eisemberg, C., Alacs, E.A., Rose, M., 2008. *Carettochelys insculpta* Ramsay 1886 – pig-nosed turtle, fly river turtle. In: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B. (Eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs*. <https://doi.org/10.3854/crm.5.009.insculpta.v1.2008>. No. 5.
- Gill, T., 1889. A remarkable tortoise. In: *Annual Report of the Board of Regents of the Smithsonian Institution, for the Year Ending June 30th, 1887, Pt. 1. Government Printing Office, Washington, DC*, pp. 509–511.
- Gilmore, C.W., 1931. Fossil turtles of Mongolia. *Bull. Am. Mus. Nat. Hist.* 59, 213–257.
- Glaessner, M.F., 1942. The occurrence of the new Guinea turtle (*Carettochelys*) in the Miocene of Papua. *Record Aust. Mus.* 21, 106–109.
- Godinot, M., 2020. Rafting on a wide and wild ocean. *Science* 368 (6487), 136–137. <https://doi.org/10.1126/science.abb4107>.
- Godinot, M., Labarrère, H.-P., Erfurt, J., Franzen, J.L., Lange-Badré, B., de Lapparent de Broin, F., Vidalenc, D., 2018. Un nouveau gisement à vertébrés éocènes, Rouzilhac (MP 10-11), dans la série molassique d'Issel (Aude, France). *Rev. Paléobiol. Genève* 37 (1), 141–333.
- Goloboff, P.A., Catalano, S.A., 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32, 221–238. <https://doi.org/10.1111/cla.12160>.
- Goloboff, P.A., Farris, J.S., Mari Källersjö, M., Oxelman, B., Ramírez, M.J., Szumik, C., 2003. Improvements to resampling measures of group support. *Cladistics* 19, 324–332.
- Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786. <https://doi.org/10.1111/j.1096-0031.2008.00217.x>.
- González-Barba, G., Coutiño, M.A., Ovaldes-Damián, E., 2002. *Carcharocles angustidens* Agassiz, 1843 (Chondrichthyes, Otodontidae) del Oligoceno tardío de la Formación La Quinta, Grupo Simojovel, localidad Los Pocitos, Simojovel, Chiapas. In: VIII Congreso Nacional de Paleontología, Guadalajara, Jalisco, p. 107.
- Harrassowitz, H., 1922. Die Schildkrötengattung *Anosteira* von Messel bei Darmstadt und ihre stammesgeschichtliche Bedeutung. *Abhandlungen der Hessischen Geol. Landesanstalt* 6, 132–239.
- Havlik, P.E., Joyce, W.G., Böhme, M., 2014. *Allaechelys libyca*, a new carettochelyine turtle from the middle Miocene (langhian) of Libya. *Bull. - Peabody Mus. Nat. Hist.* 55 (2), 201–2014.
- Hay, O.P., 1906. On two interesting genera of Eocene turtles, *chisternon* Leidy and *Anosteira* Leidy. *Bull. Am. Mus. Nat. Hist.* 22, 155–160.
- Hirayama, R., 1992. Fossil turtles from the Neogene strata in the sinda basin, eastern zaire. *Afr. Study Monogr. Suppl.* 17, 49–65.
- Hirayama, R., 1998. Fossil turtles from the mifune group (late cretaceous) of kumamoto prefecture, western Japan. In: *Report of the research on the distribution of important fossils in Kumamoto Prefecture. Dinosaurs from the Mifune Group, Kumamoto prefecture, Japan, Mifune*, pp. 85–99.
- Hirayama, R., Chitoku, T., 1994. Fossil turtles from the Japanese Cretaceous marine strata. *Monogr. - Assoc. Geol. Collab. Jpn.* 43, 17–24.
- Hoffstetter, R., 1972. Relationships, origins, and history of the ceboid monkeys and caviomorph rodents: a modern reinterpretation. *Evol. Biol.* 323–347. <https://doi.org/10.1007/978-1-4684-9063-3.11>.
- Hooker, J.J., 2015. A two-phase mammalian dispersal event across the paleocene–eocene transition. *Newsl. Stratigr.* 48 (2), 201–220.
- Hutchison, J.H., Holroyd, P.A., Ciochon, R.L., 2004. A preliminary report on southeast Asia's oldest Cenozoic turtle fauna from the Late Middle Eocene Pondaung Formation, Myanmar. *Asiat. Herpetol. Res.* 10, 38–52.
- Hutchison, J.H., Storer, J.E., 1998. Turtles from the middle Eocene (uintan) of saskatchewan, Canada. *PaleoBios* 18, 36–39.
- Huys, R., Suárez-Morales, E., Serrano-Sánchez, M.L., Centeno-García, E., Vega, F.J., 2016. Early Miocene amber inclusions from Mexico reveal antiquity of mangrove-associated copepods. *Sci. Rep.* 6, 34872. <https://doi.org/10.1038/srep34872>.
- Jiménez Fuentes, E., 1971. Primer Pseudotrionyx español: *Allaechelys casasecai*, nov. sp. del Luteciense de Corrales (Zamora). *Estud. Geol.* 27, 153–166.
- Joyce, W.G., 2007. Phylogenetic relationships of Mesozoic turtles. *Bull. - Peabody Mus. Nat. Hist.* 47, 3–102.
- Joyce, W.G., 2014. A review of the fossil record of turtles of the Clade Pan-Carettochelys. *Bull. - Peabody Mus. Nat. Hist.* 55 (1), 3–33.
- Joyce, W.G., Parham, J.F., Gauthier, J.A., 2004a. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *J. Paleontol.* 78, 989–1013.
- Joyce, W.G., Klein, N., Mörs, T., 2004b. Carettochelyine turtle from the Neogene of Europe. *Copeia* 406–411, 2004.
- Joyce, W.G., Norbert Micklich, N., Schaal, S.F.K., Scheyer, T.M., 2012. Caught in the act: the first record of copulating fossil vertebrates. *Biol. Lett.* 8 (5), 1–3. <https://doi.org/10.1098/rsbl.2012.0361>.
- Karl, H.-V., 2002. Über reptilreste aus dem Alttertiär des nördlichen Alpenvorlandes bei Siegsdorf/Oberbayern. *Joannea - Geol. Paläontol.* 4, 69–81.
- Karl, H.-V., Gröning, E., Brauckmann, C., 2006. New carettochelyine turtle occurrence from the Oligocene in Germany and its palaeozoogeographic importance. *Clausthal. Geowiss.* 5, 51–57.
- Karl, H.-V., Müller, A., 2008. New fossil reptil material (reptilia: chelonii, crocodylia) from the lower Oligocene of borken (Central Germany: hesse). *Studia Geol. Salamanticensia* 44, 41–58.
- Langenheim, J.H., Hackner, B.L., Bartlett, A., 1966. Mangrove pollen at the depositional site of Oligo-Miocene amber from Chiapas, Mexico. *Botan. Museum Leaflets* 21 (10), 289–324.
- Lapparent de Broin, F., 2000. African chelonians from the Jurassic to the present: phases of development and preliminary catalogue of the fossil record. *Palaeontol. Afr.* 36, 43–82.
- Lapparent de Broin, F., 2004. A new shachemydinae (chelonii, cryptodira) from the lower cretaceous of Laos: preliminary data. *Comptes Rendus Palevol* 3, 387–396.
- Leidy, J., 1871. [Remarks on some extinct turtles from Wyoming Territory]. *Proc. Acad. Nat. Sci. Phila.* 102–103, 1871.
- Lydekker, R., 1889a. Preliminary notice of fossil Mesosia. *Ann. Mag. Nat. Hist.* 3, 53–54.
- Lydekker, R., 1889b. On remains of Eocene and mesozoic Chelonia and a tooth of (?) *ornithopsis*. *Q. J. Geol. Soc. Lond.* 45, 227–246.
- Lydekker, R., 1889c. Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History). Part 3. Chelonia, London: Longmans, p. 239.
- Maddison, W.P., Maddison, D.R., 2019. Mesquite: a modular system for evolutionary analysis. Version 3.61. <http://www.mesquiteproject.org>.
- Martin, T., 1994. African origin of caviomorph rodents is indicated by incisor enamel microstructure. *Paleobiology* 20, 5–13. <https://doi.org/10.1017/s00948730001109x> (1).
- Miller, K.G., Browning, J.V., Aubry, M.-P., Wade, B.S., Katz, M.E., Kulpecz, A.A., Wright, J.D., 2008. Eocene-Oligocene global climate and sealevel changes: st. Stephens Quarry, Alabama. *Geol. Soc. Am. Bull.* 120 (1–2), 34–53. <https://doi.org/10.1130/B26105.1>.
- Nessov, L.A., 1976. [On the systematics and phylogeny of two clawed turtles]. *Vestnik Leningradskogo Univ.* 9, 7–17 (in Russian).
- Noulet, J.-B., 1867. Nouveau genre de tortues fossiles proposé sous le nom d'*Allaechelys*. *Mémoires Acad. Impériale. Sci. Inscript. Belles-Lett. Toul.* 5, 172–177.
- Perrilliat, M.C., Vega, F.J., Coutiño, M.A., 2010. Miocene mollusks from the Simojovel area in Chiapas, southwestern Mexico. *J. S. Am. Earth Sci.* 30, 111–119. <https://doi.org/10.1016/j.jsames.2010.04.005>.
- Peris, D., Solórzano Kraemer, M.M., Peñalver, E., Delclós, X., 2015. New ambrosia beetles (Coleoptera: Curculionidae: Platypodinae) from Miocene Mexican and Dominican ambers and their paleobiogeographical implications. *Org. Divers. Evol.* 15, 527–542. <https://doi.org/10.1007/s13127-015-0213-y>.
- Poux, C., Chevret, P., Huchon, D., de Jong, W.W., Douzery, E.J.P., 2006. Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. *Syst. Biol.* 55 (2), 228–244. <https://doi.org/10.1080/10635150500481390>.
- Prothero, D.R., Beatty, B.L., Stucky, R.M., 2013. *Simojovelhyus* is a peccary, not a helohyid (Mammalia, Artiodactyla). *J. Paleontol.* 87 (5), 930–933. <https://doi.org/10.1666/12-084>.
- Ramsay, E.P., 1887. On a new genus and species of fresh water tortoise from the Fly River, New Guinea. *Proc. Linn. Soc. N. S. W.* 158–162, 2nd series 1.
- Seiffert, E.R., Tejedor, M.F., Fleagle, J.G., Novo, N.M., Cornejo, F.N., Bond, M., de Vries, D., Campbell Jr., K.E., 2020. A parapatric stem anthropoid of African origin in the Paleogene of South America. *Science* 368, 194–197. <https://doi.org/10.1126/science.aba1135>.
- Serrano-Sánchez, M. de L., Hegna, T.A., Schaaf, P., Pérez, L., Centeno-García, E., Vega, F.J., 2015. The aquatic and semiaquatic biota in Miocene amber from the Campo LA Granja mine (Chiapas, Mexico): paleoenvironmental implications. *J. S. Am. Earth Sci.* 62, 243–256. <https://doi.org/10.1016/j.jsames.2015.06.007>.
- Smith, T., Rose, K.D., Gingerich, P.D., 2006. Rapid asia–europe–north America geographic dispersal of earliest Eocene primate *Teilhardina* during the paleocene–eocene thermal Maximum. *Proc. Natl. Acad. Sci. Unit. States Am.* 103 (30), 11223–11227. <https://doi.org/10.1073/pnas.0511296103>.
- Solorzano-Kraemer, M.M., 2007. Systematic, Palaeoecology, and Palaeobiogeography of the Insect Fauna from Mexican Amber. *Palaeontographica, Abteilung A*, vol. 282, pp. 1–113.

- Solorzano-Kraemer, M.M., 2010. Mexican amber. In: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 42–56.
- Solorzano-Kraemer, M.M., Mohrig, W., 2007. *Schwenckfeldina archoica* sp. nov. (Diptera, Sciaridae) from the middle Miocene Mexican amber. *Alavesia* 1, 105–108.
- Suzuki, H.K., 2006. Studies on the osseous system of the slider turtle. *Ann. N. Y. Acad. Sci.* 109 (1), 351–410. <https://doi.org/10.1111/j.1749-6632.1963.tb13476.x>.
- Thomas, H., Sen, S., Khan, M., Battail, B., Ligabue, G., 1981. The lower Miocene fauna of Al-sarrar (eastern province, Saudi Arabia). *Atlat* 5, 109–136.
- Tomasini-Ortiz, A.C., Martínez-Hernández, E., 1984. Palinología del Eoceno–Oligoceno de Simojovel, Chiapas, vol. 50. Universidad Nacional Autónoma de México, Instituto de Geología. *Paleontología Mexicana*, pp. 1–60.
- Tong, H., Suteethorn, V., Claude, J., Buffetaut, E., Jintasakul, P., 2005. The turtle fauna from the khok kkuat formation (early cretaceous) of Thailand. In: *Proceedings of the International Conference on Geology, Geotechnology and Mineral Resources of Indochina: Khon Kaen*. Khon Kaen University, Thailand, pp. 610–614.
- Tong, H., Zhang, J.-Y., Li, J.-J., 2010. *Anosteira maomingensis* (Testudines: Carettochelyidae) from the late Eocene of maoming, Guangdong, southern China: new material and re-description. *Neues Jahrbuch Geol. Palaontol. Abhand.* 256, 279–290.
- Vega, F.J., Nyborg, T., Coutiño, M.A., Solé, J., Hernández-Monzón, O., 2009. Neogene Crustacea from southeastern Mexico. *Bull. Mizunami Foss. Mus.* 35, 51–69.
- Vullo, R., de Lapparent de Broin, F., Néraudeau, D., Durrieu, N., 2010. Turtles from the early cenomanian paralic deposits (late cretaceous) of charentes, France. *ORYCTOS* 9, 37–48.
- Walther, W.G., 1922. Die neu-Guinea-schildkröte *Carettochelys insculpta* Ramsay. *Nova Guinea* 13, 607–704.
- Webb, S.D., Beatty, B.L., Poinar jr., G., 2003. New evidence of Miocene Protoceratidae including a new species from Chiapas, Mexico. *Bull. Am. Mus. Nat. Hist.* 279, 348–367.
- Weems, R.E., 2014. Paleogene chelonians from Maryland and Virginia. *PaleoBios* 31 (1), 1–32.
- Wesgate, J.W., 2001. Paleogeology and biostratigraphy of marginal marine Gulf Coast Eocene vertebrate localities. In: Gunnell, G.F. (Ed.), *Eocene Biodiversity: Unusual Occurrences and Rarely Sampled Habitats*. Kluwer Academic/Plenum Publishers, New York, pp. 263–297.
- Williams, E.E., 1950. Variation and selection in the cervical articulation of living turtles. *Bull. Am. Mus. Nat. Hist.* 94, 509–561.
- Young, C.-C., Chow, M., 1962. Some reptilian fossils from the “red-beds” of Kwangtung and Chekiang. *Vertebr. Palasiat.* 130–135, 1962.
- Zangerl, R., 1947. A new anosteirine turtle from Manchuria. *Fieldiana Geol.* 10, 13–21.
- Zangerl, R., 1969. The turtle shell. In: d’Bellairs, A., Parsons, T.S. (Eds.), *Biology of the Reptilia*, vol. 1. Academic Press, London–New York, pp. 311–339.

Appendix A

The first Pan-Carettochelys turtle in the Neogene of the American Continent and its paleobiogeographical relevance

by

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and Víctor Hugo Reynoso

Species of Pan-Charettochelys used for comparison in this study

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; BMNH, Beijing Museum of Natural History, Beijing, China; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; CCMGE, Chernyshev’s Central Museum of Geological Exploration, St. Petersburg, Russia; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MHNT, Muséum d’Histoire Naturelle de Toulouse, Toulouse, France; MNHN, Muséum National d’Histoire Naturelle, Paris, France; NRRU, Collection of the Museum of Petrified Wood and Minerals Resources, Nakhon Ratchasima Rajabhat University, Thailand; TF, Sahat Sakhan Dinosaur Research Centre, Thailand; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

***Kizylkumemys schultzi* Nesso, 1976** – Was described based on right hypoplastron (holotype CCMGE 11180-1) and several isolated scutes from the Khodzhakul

(Chodzhakul) Formation (early Cenomanian), Karakalpakstan Autonomous Republic, Uzbekistan (Nessov, 1976). *Kizylkumemys schultzi* was referred to Pan-Carettochelys by the presence of a shallow fossa behind the quadrate, a reduced antrum postoticum, a midline keel, nuchal articulation facets for the eighth cervical vertebra, ten peripherals, one suprapygal, a thickened pygal with an anterior groove, a triangular entoplastron and the reduction of the plastral scutes (Joyce, 2014), but our analysis concluded this taxon is not part of the clade.

***Kizylkumemys khoratensis* Tong, Suteethorn, Claude, Buffetaut, Jintasakul 2005** – This species was erected based on partial carapaces and plastral fragments from the Early Cretaceous of Ban Saphan Him, Nakhon Ratchasima province, Thailand. The described material includes portion of a carapace with the nuchal and first to fourth neurals, medial portion of the first to fourth costals and right peripheral (holotype NRRU A1861), one peripheral plate (NRRU A1252), one left epiplastron (NRRU A1862); portion of plastra with part of hyoplastron and hypoplastron (NRRU A1251), and one suprapygal (NRRU A1863). Additional material included in the description comprises one incomplete costal plate (TF8001) from Ban Khok Kruat, Nakhon Ratchasima province, Thailand; and one neural plate (TF8002), one peripheral plate (TF8003), and one hypoplastron (TF8004) from Khok Pha Suam, Ubon Ratchathani province, Thailand (Tong *et al.* 2005). This taxon was considered member of Pan-Carettochelys by the presence of a midline keel, a triangular entoplastron, and a single suprapygal (Joyce, 2014), but our analysis concluded this taxon is not part of the clade.

***Anosteira manchuriana* Zangerl 1947** – *Anosteira manchuriana* was described by Rainer Zangerl based on an almost complete shell (holotype FMNH P15102) from Fu-schun coal mine (late Eocene), Fengtien (=Liaoning) Province, China (Zangerl, 1947). *Anosteira manchuriana* was diagnosed as Carettochelyidae by the presence of a midline keel, a triangular entoplastron and the lack of plastral scutes (Joyce, 2014).

***Anosteira maomingensis* Chow and Liu 1955** – This taxon was erected upon two well-conserved specimens from Maoming (Late Eocene), Guangdong Province, China. The holotype IVPP V809, consists of an internal mold of the carapace, external and internal molds of the plastron, and fragmentary marginal and plastral plates of a smaller shell. The paratype IVPP V810, consists of internal molds of the carapace and plastron (Chow and Liu, 1955). Later, Tong *et al.* (2010), extended the description of the species based on new specimens housed in the IVPP and BMNH collections, that included a lower jaw and several shells (see the listed specimens in Tong *et al.*, 2010). *Anosteira maomingensis* was diagnosed as Carettochelyidae by the absence of plastral scutes, the presence of a midline keel, ten peripherals, a single suprapygal, a pygal with an anterior groove, a triangular entoplastron, nuchal articulation sites for the eighth cervical vertebra, and plastral Kinesis (Joyce, 2014).

***Anosteira mongoliensis* Gilmore 1931** – Erected upon two specimens recovered by the Central Asiatic Expedition in 1928 in the Ulan Shireh Formation (Upper Eocene), Chimney Butte locality, North Mesa, Shara Murun region, Inner Mongolia, China (Gilmore, 1931). The specimens consist in a complete nuchal, parts of eight peripheral bones, and the distal end of one costal (holotype AMNH 6666), and the articulated hyoplastron, hypoplastron

and xiphiplastron (paratype AMNH 6697). Joyce (2014) considered *An. mongoliensis* as a member of Carettochelyidae because it has a midline keel, nuchal articulation facets for the eighth cervical vertebra, a thickened pygal with an anterior groove, plastral kinesis, and absence of plastral scutes.

***Anosteira ornata* Leidy 1871** – Erected by Joseph Leidy (1871) based upon isolated plates and fragments of about four different individuals, from Church Buttes and Grizzly Buttes, Wyoming, USA, but the description was very brief. Later, the same Leidy (1873) illustrated and extended the description based in new, better specimens from Bridger Formation (Early Eocene) listed by Gillette (1977). Of the six specimens mentioned, only three are the turtles illustrated by Leidy (ANSP 9801, 9846 and 10225; Joyce, 2014). Of these specimens, Joyce (2014) designated ANSP 9846 as the neotype, because “... not disrupt stability, given that it was the best-preserved specimen known to Leidy (1873) and therefore already served as the quasi-holotype for many years”. *Anosteria ornata* was diagnosed as Carettochelyidae by the absence of plastral scutes, the presence of a midline keel, ten peripherals, a single suprapygal, a pygal with an anterior groove, a triangular entoplastron, nuchal articulation sites for the eighth cervical vertebra, and plastral kinesis (Joyce, 2014). *Anosteria ornata* is the first carettochelyid described for North America.

***Anosteira pulchra* (Clark, 1932)** – Described first as *Pseudanosteira pulchra* by Clark (1932) based on an almost complete shell (holotype CM 11808) collected in Quarry L, Leota Ranch, Uinta Formation (Lutetian, Middle Eocene), Uinta County, Utah, USA. Later, it was placed in *Anosteria* by Broin (1977), although Meylan (1988) considered *Pseudanosteira* as valid genus. *Anosteira pulchra* was considered as carettochelyid based

on the presence of a maxilla-quadratojugal contact, a shallow fossa behind the quadrate, a reduced antrum postoticum, a midline keel, only ten peripherals, a single suprapygal, and loss of plastral scutes (Joyce, 2014). This taxon was the second carettochelyid turtle described to North America.

***Allaeochelys crassesculpta* (Harrassowitz 1922)** – Harrassowitz (1922) described two species of turtles into the genus *Anosteria* based on six specimens from Messel Pit Fossil Site (Lutetian, Early Eocene), State of Hesse, Germany, described as *Anosteria crassesculpta* and *A. gracilis*. Since these two species only differed in size and sculpturing pattern, they were synonymized by Gramann (1956), being *A. crassesculpta* the valid taxa. Later, Nessov (1976) moved the species to genus *Allaeochelys*. *Allaeochelys crassesculpta* is the best-known carettochelyid fossil, thanks to more than 100 specimens that have been recovered from Messel Pit Fossil Site (Joyce, 2014) that have permitted distinguish between males and females, and even observe mating scenes (Joyce *et al.*, 2012).

***Allaeochelys delheidi* (Dollo 1886)** – The taxonomic history of this taxon is complex. It was first described as *Pseudotrionyx delheidi* by Dollo (1886), based on one partial shell (holotype IRSNB-R-19) from the Early Eocene of Melsbrok, Vilvoorde, Belgium. Later Hummel (1929) moved it to *Anosteria*, and later Kuhn (1964) referred it to *Allaeochelys delheidi*. *Castresia munieri* Bergounioux 1935; *Anosteira anglica* Lydekker 1889; *Allaeochelys casasecai* Jiménez Fuentes 1971, and *Allaeochelys jimenezi* Alonso and Alonso 2005, has been synonymized with *Al. delheidi* by Joyce (2014).

***Allaeochelys libyca* Havlik, Joyce, and Böhme, 2014** – Description based on a left hypoplastra (BSPG 1991 II 96 and 97), a bridge peripheral (BSPG 110), an anterior peripheral (BSPG 113), a peripheral I (BSPG 114), a partial skull (BSPG 130) and a partial supraoccipital (BSPG 131) from the Early Miocene (Langhian) of Gebel Zelten (Jabal Zaltan), Libya (Havlik *et al.*, 2014).

***Allaeochelys lingnanica* Young and Chow, 1962** – Description based on a partial carapace (holotype IVPP V 1044), collected in Shaoguan Prefecture, Guangdong, China, maybe Paleocene on age (Young and Chow, 1962; Tang and Zhou, 1965). This turtle is the only evidence of Carettochelyinae in the Paleogene of the east of Asia. Although *Al. lingnanica* lacks all anatomical regions needed to rigorously diagnose a carettochelyid, Joyce (2014) referred it to Carettochelyinae because lack of carapacial scutes.

***Allaeochelys magnifica* (Hutchison, Holroyd and Ciochon, 2004)** – Described first as *Burmemyx magnifica* based on a left hypoplastron (holotype UCMP 61212), and several parts of carapace and plastron referred as paratypes (see Hutchison *et al.*, 2004 for details), from the Pondaung Formation (Late middle Eocene, Bartonian), central Myanmar. Later, the specie was reallocated to *Allaeochelys* genus by Joyce (2014).

***Allaeochelys parayrei* Noulet, 1867** – Erected as the type species of the genus *Allaeochelys*, with specimens collected in Castres, and Vivarié, near of Lafosse, Gironde department, France (Noulet, 1867), late Eocene (Bartonian). In the original description all collected specimens were designated as holotype, but later Broin (1977) designated one specimen as lectotype (specimen MHNT: carapace and partial plastron) and two

paralectotypes (specimen MHNT: dorsal carapace; specimen MHNT: mold of carapace) from syntype series. Additional material illustrated by Bergounioux (1931, 1935) and described by Broin (1977) included a carapace with complete plastron, four plastron fragments and one fragment of a pleural from Lautrec, France, and one partial carapace from La Massale, France.

***Allaeochelys rouzilhacensis* Lapparent de Broin 2018** – Description based on thirteen specimens from Rouzilhac (Early Eocene, Upper Ypresian), Lauragais, Occitanie region, France (Godinot *et al.*, 2018), including an almost complete skull (MNHN.F.RZ 380, holotype), a medial fragment of hyoplastron (MNHN.F.RZ 326), a left ninth peripheral (MNHN.F.RZ 325), a medial fragments of pleural (MNHN.F.RZ 327, MNHN.F.RZ 328, MNHN.F.RZ 329, MNHN.F.RZ 331 and MNHN.F.RZ 334), a mid-lateral pleural fragment (MNHN.F.RZ 330) a worn pleural fragment (MNHN.F.RZ 332), a fragment of small pleural (MNHN.F.RZ 335), a fragment of a scapula (MNHN.F.RZ 333), and s pleural of the middle region without the medial margin (MNHN.F.RZ 369).

***Eulalichelys labarrerei* Lapparent de Broin 2018** – This taxon was erected based on three specimens from a sandstone and clay formation (Early Eocene, Ypresian) in Minervois, Occitanie region, Château Sainte-Eulalie, France (Godinot *et al.*, 2018). The material includes an incomplete skull (MNHN.F. EBA 531, holotype); a left sixth pleural (MNHN.F.EBA 532), and one fragmented plate without a catalog number.

***Carettochelys insculpta* Ramsay 1887** – This species was originally named *Carettochelys insculptus* by Ramsay (1887), and was described based upon an adult female specimen

collected in the Fly River, New Guinea (Ramsay, 1887). Ramsay (1887) mainly used external morphological characters to describe it, Osteological descriptions were provided later by Waite (1905), Walther (1922), Gaffney (1979) and Meylan (1988). Ramsay (1887) placed to *Carettochelys* in Trionychidae and Boulenger (1887) erected the Family Carettochelyidae for this species, based in the following morphological characters: limbs paddle-shaped, the anterior much elongate; first and second digits clawed, no epidermic scutes on the carapace and plastron, and plastron formed by nine bones, without persisting fontanelles. Currently, *Carettochelys insculptus* inhabits in southern Indonesian Papua, Papua New Guinea, and northern of Australia (Georges et al., 2008).

References

- Alonso-Santiago, L., Alonso-Andrés, L., 2005. Diferencias anatómicas entre dos formas de *Allaeochelys* del Eoceno de Corrales (Zamora, España). Nueva especie de tortuga, *Allaeochelys jimenezi* nov. sp. *Studia Geologica Salmanticensia*, 41, 103–126.
- Bergounioux, F.-M., 1931. Le genre *Allaeochelys* et ses caractères adaptatif. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, 61, 161–181.
- Bergounioux, F.-M., 1935. Contribution a l'étude paléontologique des chéloniens: Chéloniens fossiles du Bassin d'Aquitaine. Paris. Société Géologique de France. (Mémoires 25.), 207 pp.
- Boulenger, G.A., 1887. XXII.—On a new family of Pleurodiran turtles. *Annals and Magazine of Natural History*, 19:111, 170-172. DOI: 10.1080/00222938709460223
- Broin, F. de., 1977. Contribution à l'étude des chéloniens: Chéloniens continentaux du Crétacé et du Tertiaire de France. Paris. Mémoires du Muséum National d'histoire naturelle, nouvelle série, Series C, Sciences de la terre, 38, 366 pp.

- Clark, J. 1932., A new anosteirid from the Uinta Eocene. *Annals of the Carnegie Museum of Natural History*, 21, 161–170.
- Chow, M.M., Liu, C.-I., 1955. A new anostesine turtle from Maoming, Kwangtung. *Acta Palaeontologica Sinica*, 3, 275–282. [in Chinese]
- Dollo, L., 1886. Première note sur les chéloniens du Bruxellien (Éocène moyen) de la Belgique. *Bulletin du Musée Royal d’Histoire Naturelle Belgique*, 4, 75–100.
- Gaffney, E.S., 1979. Comparative cranial morphology of Recent and fossil turtles. *Bulletin of the American Museum of Natural History*, 164, 65–376.
- Georges, A., Doody, J.S., Eiseberg, C., Alacs, E.A., Rose, M., 2008. *Carettochelys insculpta* Ramsay 1886 – Pig-nosed turtle, Fly River turtle. *Conservation Biology of Freshwater Turtles and Tortoises, Chelonian Research Monographs*, 5. 1–17.
- Gillette, D.D., 1977. Catalogue of type specimens of fossil vertebrates. *Academy of Natural Sciences, Philadelphia, Part 6: Reptilia, Amphibia, and Tracks. Proceedings of the Academy of Natural Sciences of Philadelphia*, 129, 101–111.
- Gilmore, C.W., 1931. Fossil turtles of Mongolia. *Bulletin of the American Museum of Natural History*, 59, 213–257.
- Godinot, M., Labarrère, H.-P., Erfurt, J., Franzen, J.L., Lange-Badré, B., de Lapparent de Broin, F., Vidalenc, D., 2018. Un nouveau gisement à vertébrés éocènes, Rouzilhac (MP 10-11), dans la série molassique d’Issel (Aude, France). *Revue de Paléobiologie, Genève*, 37(1), 141–333.
- Gramann, F., 1956. Schildkröten aus dem Melanienton von Borken (Niederhessische Senke) (*Trionyx, Anosteira*). *Notizblatt des hessischen Landes-Amtes für Bodenforschung*, 84, 16–20.

- Harrassowitz, H., 1922. Die Schildkrötengattung *Anosteira* von Messel bei Darmstadt und ihre stammesgeschichtliche Bedeutung. Abhandlungen der Hessischen Geologischen Landesanstalt, 6, 132–239.
- Havlik, P.E., Joyce, W.G., Böhme, M., 2014. *Allaeochelys libyca*, a new Carettochelyine turtle from the Middle Miocene (Langhian) of Libya. Bulletin of the Peabody Museum of Natural History, 55(2), 201–2014.
- Hummel, K., 1929. Die fossilen Weichschildkröten (Trionychia). Geologische und Palaeontologische Abhandlungen, 16, 359–487.
- Hutchison, J.H., Holroyd, P.A., Ciochon, R.L., 2004. A preliminary report on southeast Asia's oldest Cenozoic turtle fauna from the Late Middle Eocene Pondaung Formation, Myanmar. Asiatic Herpetological Research, 10, 38–52.
- Joyce, W.G., 2014. A review of the fossil record of turtles of the Clade Pan-Carettochelys. Bulletin of the Peabody Museum of Natural History, 55(1), 3–33,
- Joyce, W.G., Norbert Micklich, N., Schaal, S.F.K., Scheyer, T.M., 2012. Caught in the act: the first record of copulating fossil vertebrates. Biology Letters, 8(5), 1–3.
<https://doi.org/10.1098/rsbl.2012.0361>
- Kuhn, O., 1964. Fossilium Catalogus. Volume 1, Animalia, Part 107, Testudines. Gravenhage, Ysel Press, 299 pp.
- Leidy, J., 1871. Remarks on extinct turtles from Wyoming territory. Proceedings of the Academy of Natural Sciences of Philadelphia, 23(2), 102–103.
- Leidy, J., 1873. Contributions to the extinct vertebrata fauna of the western territories. In: F.V. Hayden (Ed.), Report of the United States Geological Survey of the Territories, Volume 1, Part 1, 358 pp.

- Lydekker, R., 1889. Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History), Part 3, Chelonia. London, Longmans, 239 pp.
- Meylan, P.A., 1988. *Peltochelys* Dollo and the relationships among the genera of the Carettochelyidae (Testudines:Reptilia). *Herpetologica*, 44(4), 440–450.
- Nessov, L.A., 1976. [On the systematics and phylogeny of two clawed turtles]. *Vestnik Leningradeskogo Universiteta*, 9, 7–17. [in Russian]
- Noulet, J.-B., 1867. Nouveau genre de tortues fossiles proposé sous le nom d'*Allaeochelys*. *Mémoires de l'Académie Impériale des Sciences, Inscriptions et Belles-Lettres de Toulouse*, 5, 172–177.
- Ramsay, E.P., 1887. On a new genus and species of fresh water tortoise from the Fly River, New Guinea. *Proceedings of the Linnaean Society of New South Wales*, 2nd series, 1, 158–162.
- Tang, X., Zhou, M.-Z., 1965. The vertebrate-bearing early Tertiary of South China: a review. *International Geology Review*, 7, 1338–1352.
- Tong, H., Suteethorn, V., Claude, J., Buffetaut, E., Jintasakul, P., 2005. The turtle fauna from the Khok Kruat Formation (Early Cretaceous) of Thailand. In: *Proceedings of the International Conference on Geology, Geotechnology and Mineral Resources of Indochina*. Khon Kaen, Thailand, Khon Kaen University, 610–614.
- Tong, H., Zhang, J.-Y., Li, J.-J., 2010. *Anosteira maomingensis* (Testudines: Carettochelyidae) from the Late Eocene of Maoming, Guangdong, southern China: new material and re-description. *Neues Jahrbuch für Geologie Paläontologie, Abhandlungen*, 256, 279–290.
- Waite, E.R., 1905. The osteology of the New Guinea turtle (*Carettochelys insculpta*, Ramsay). *Records of the Australian Museum*, 6(2), 110–118.

Walther, W.G., 1922. Die Neu-Guinea-Schildkröte *Carettochelys insculpta* Ramsay. Nova Guinea, 13, 607–704.

Young, C.-C., Chow, M. 1962. Some reptilian fossils from the “red-beds” of Kwangtung and Chekiang. *Vertebrata Palasiatica*, 1962, 130–135. [in Chinese with English summary]

Zangerl, R., 1947. A new anosteirine turtle from Manchuria. *Fieldiana Geology*, 10, 13–21.

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Baptemys 1--110011111110000300110000101112021011110000[0 1]-1001?00-
21302100101100001000000120211001000000111001210000001-1001000111101111112?11113110101-

-11100011?

Dermatemys 1--110011[0 1]111100003001100001011120210111100001-1001000-21302-0010010[0
1]001001000120211001000000111001201000001-11010001111111111201111110101--011000110
Hoplochelys ???
0210100100000020211001000000111000200010001-1001100??
Staurotypus 1--110011011110103001100011011120210111100001-1001000111302-0010210100210[0
1]010020211001000001111000200010001-10012001111011111211111111010?--111000110
Sternotherus odoratus 1--1100110111100103001100001011120210111100001-1001000111302-
001011010021110100202110010000011120020000001-11120011110111112111111110101--111000110
Kinosternon 1--1100110111100103001100001011120210111100001-1001000111302-
001011010021110100202110010000011120020000001-1112001111011111211111111010?--111000110
Zangerlia neimongolensis 1--11?0110?1?1?0003001100001?1?1120[1 2]?2?111100000-1001?001013?21?
0100?0?101?00?00?21100?000000111000200000100210000001111100000012??1??110101--011100?1?
Basilemys 1--1?01111?1?10000300110?00?1?1?12022?111?0?????????1?????????2??010010010100[0
1]000020211001000000111000200000100[0 2]10000001111000000?????????11?101--011100??0
Adocus 1--1100111111?0003001100001011120210111100001-
1001000101302100100100101001000020211001000000111000200000100010000001111100000002?11??
110101--011000110
Sandownia 1--11001110111000000011[0 1]?0011111120[1 2]2111110100--0001000101302-?
01??
Apalone spinifera 1--1110111111110003001112101111120120111100011-10010001013021001201000?3-01-
--02-2-----11-1111-0200-02----1-----110110000002201-111110101--011001112
Lissemys punctata 1--1110111111110003001112101111120120111100011-10010001013021001201000?3-
01---02-2-----11-1111-0200-02----1-----110110000002201-111110101--011001112
Peltochelys ???
1]00000000011100?20000000001000000??
Kizylkumemys schultzi ???
200101112-2-10[0 1]-111101111000200021??
Kizylkumemys khoratensis ???
00?01??-2-101-011??
Anosteira pulchra 1--11001111?1000130011?200111?112022?111100?1[0 1]?1001?0?1013?10??00???
00200101?1?-2-111-112101111000200012---?-----????????????????????????????????????
Anosteira ornata ???
2-111-113101111000200012---1-----??
Anosteira manchuriana ???
-2-10?-113101111000200012---?-----??
Anosteira maomingensis 1--11001111?10001300111200111?112022?111100110010?1?0?1013?
11101101100020010111?-2-1[0 1]?-113101111000200012---1-----????????????????????
Anosteira mongoliensis ???
-?-??-1?3101?????0200012---?-----??
Allaeochelys lingnanica ???
-2-----1??????020??2----?-----??
Allaeochelys crassesculpta 1--11001111110012300112001111120220111100?11?100100?1013?1??
012011000200101112-2-----101111000200002---1-----110110000001201111110101--011002113
Allaeochelys delheidi ???
2-----101111000200002---1-----??
Allaeochelys parayrei ???
2011000200101112-2-----101111000200002---1-----????????????????????????
Allaeochelys magnifica ???
-2-----101????0020??02----?-----??
Allaeochelys libyca 1--1?01111?1100?230011200?????11202201111??1?0100100?1013?1210?2??0??
0?????1?-2-----?0????????2??02---?-----????????????????????????????????
Allaeochelys liliae ???
-----10??????2?0002---?-----??
Carettochelys insculpta 1--110011111100123001120011111200201111001101100100010130[0
1]2101201100120[0 1]101112-2-----101111000200002---1-----110110000001201111110101--011002113

;

cnames
{0 Nasals present absent;
{1 Medial_contact_of_nasals nasals_contact_one_another_medially_along_their_entire_length
medial_contact_of_nasals_partially_or_fully_hindered_by_long_anterior_frontal_process;
{2 Size_of_nasals dorsal_exposure_of_nasals_large
dorsal_exposure_of_nasals_greatly_reduced_relative_to_that_of_the_frontals;
{3 Medial_contact_of_prefrontals_on_dorsal_skull_surface absent present, prefrontal_contact_with_frontal_absent;
{4 Prefrontal-vomer_contact absent present;
{5 Prefrontal?palatine_contact present absent;
{6 Dorsal_prefrontal_exposure large reduced absent_or_near_absent;
{7 Prefrontals_heavily_sculptured_with_prominences_and_bosses present absent;
{8 Lacrimal present absent;
{9 Frontal_contribution_to_orbit absent, prefrontal_contacts_postorbital present;
{10 Parietal?squamosal_contact present, upper_temporal_emargination_absent_or_only_poorly_developed
absent, upper_temporal_emargination_well_developed;
{11 Parietal_contact_with_the_ptyergoid, epiptyergoid, or palatine
absent, trigeminal_foramen_only_developed_as_a_notch
present, trigeminal_foramen_clearly_formed_by_the_descending_process_of_the_parietal;
{12 Length_of_anterior_extension_of_the_lateral_braincase_wall
short, inferior_parietal_process_only_produces_a_narrow_strut_anterior_to_trigeminal_foramen, palatine_contact_absent
elongate, inferior_parietal_process_produces_an_extended_process_anterior_to_trigeminal_foramen, palatine_contact_commonly_present;
{13 Jugal?squamosal_contact present absent, contact_between_postorbital_and_quadratejugal_commonly_present;
{14 Jugal_participation_to_upper_temporal_rim absent present, upper_temporal_emargination_extensive.;
{15 Quadratejugal present absent, due_to_the_presence_of_a_deep_lower_temporal_emargination;
{16 Quadratejugal-maxilla_contact absent present;
{17 Fossa_behind_articular_process_of_quadrate absent small large;
{18 Squamosal-postorbital_contact present absent, temporal_roofing_well_developed, but_postorbital_short
absent, due_to_lower_temporal_emargination absent, due_to_upper_temporal_emargination;
{19 Squamosal_supraoccipital_contact absent present;
{20 Postorbital?palatine_contact absent
present, foramen_palatinum_posterius_situated_posterior_to_the_orbital_wall;
{21 Supratemporal present absent;
{22 Subdivision_of_external_nares_by_internarial_process_of_premaxilla present absent;
{23 Fusion_of_premaxillae absent present;
{24 Foramen_praepalatinum present absent, premaxillae_well_ossified absent, foramen_intermaxillaris_present;
{25 Exclusion_of_premaxillae_from_apertura_narium_externa absent present;
{26 Distinct, medial_premaxillary_hook_along_the_labial_margin_of_the_premaxillae absent present;
{27 Vomer paired single single, greatly_reduced_or_absent;
{28 Vomer-pterygoid_contact_in_palatal_view present absent, medial_contact_of_palatines_present;
{29 Vomerine_and_palatine_teeth present absent;
{30 Palatine_contribution_to_anterior_extension_of_lateral_braincase_wall absent present, well_developed;
{31 Flooring_of_cavum_acustico-jugulare_and_recessus_scalae_tympani absent
fully_or_partially_present, produced_by_the_posterior_process_of_the_ptyergoid
fully_or_partially_present, produced_by_the_ventral_process_of_the_quadrate_or_the_prootic, or_both;
{32 Central_constriction_of_the_middle_ear absent present, formed_by_quadrate;
{33 Cavum_tympani absent partially_developed fully_developed;
{34 Precolumellar_fossa absent large_and_deep;
{35 Antrum_postoticum absent present, quadrate_does_not_fully_enclose_the_anterior_perimeter_of_the_antrum
present, quadrate_fully_encloses_the_anterior_perimeter_of_the_antrum;
{36 Incisura_columellae_auris absent, stapes_articulates_along_the_medial_side_of_the_quadrate
present, but_open_posteroventrally present_and_closed, but_only_enclosing_the_stapes
present_and_closed, enclosing_stapes_and_the_Eustachian_tube;
{37 Epiptyergoid present absent;
{38 Pterygoid_teeth present absent;
{39 Basipterygoid_articulation open fused;

{40 Interpterygoid_vacuity present absent;

{41 Pterygoid-basioccipital_contact absent present;

{42 Processus_trochlearis_ptyergoideus absent present;

{43 Foramen_palatinum_posterius present present, _but_ open_laterally absent;

{44 Pterygoid-ptyergoid_suture_between_foramen_posterius_canalis_caroticus_interni_and_basisphenoid absent present;

{45 Medial_contact_of_ptyergoids
ptyergoids_in_medial_contact_with_one_another_for_at_least_part_of_their_length
absent, _contact_of_the_basisphenoid_with_the_vomer_or_palatines, _or_both, present;

{46 Pterygoid_contribution_to_foramen_palatinum_posterius present absent;

{47 Pterygoid_trough opened_ventrally closed_ventrally;

{48 Crista_supraoccipitalis poorly_developed protruding_significantly_posterior_to_the_foramen_magnum;

{49 Large_supraoccipital_exposure_to_dorsal_skull_roof absent present;

{50 Medial_contact_of_exoccipitals_dorsal_to_foramen_magnum absent present;

{51 Processus_paroccipitalis loosely_articulated_to_squamosal_and_quadrate
tightly_sutured_to_squamosal_and_quadrate;

{52 Rostrum_basisphenoidale flat_rod-like, _thick, _and_rounded;

{53 Paired_pits_on_ventral_surface_of_basisphenoid absent present;

{54 Path_of_hyomandibular_branch_of_the_facial_nerve
hyomandibular_nerve_passes_through_cranioquadrate_space_parallel_to_vena_capitis_lateralis
hyomandibular_nerve_runs_independent_from_vena_capitis_lateralis;

{55 Position_of_stapedio-temporal_canal posterior_to_fenestra_ovalis_between_paroccipital_process_and_quadrate
anterior_to_fenestra_ovalis_between_quadrate_and_prootic;

{56 Size_of_foramen_stapedio-temporale relatively_large_significantly_reduced_in_size absent;

{57 Anterior_and_posterior_jugular_foramina_defined_by_bone absent present;

{58 Foramen_posterius_canalis_caroticum_internus formed_by_basisphenoid_only
formed_by_both_basisphenoid_and_ptyergoid_halfway_along_the_basisphenoid?ptyergoid_suture
formed_by_prootic_only
formed_mostly_or_fully_by_ptyergoid, _foramen_positioned_near_the_posterior_end_of_the_basisphenoid;

{59 Fenestra_perilymphatica large_reduced_in_size_to_that_of_a_small_foramen;

{60 Depth_of_antrum_postoticum absent shallow deep;

{61
Position_of_the_foramen_posterius_canalis_caroticus_interni_on_the_ventral_surface_of_the_skull_within_ptyergo
ids near_middle_part_of_basisphenoid near_posterior_border_of_basisphenoid
distant_from_posterior_border_of_basisphenoid;

{62 Foramen_nervi_trigemini_is_divided_into_two_parts_by_prootic no yes;

{63 Medial_contact_of_dentaries fused sutured_only_;

{64 Splenial present absent;

{65 Carapace_scutes all_carapacial_scutes_present marginal_scutes_absent all_carapacial_scutes_absent;

{66 Tricarinate_carapace absent present, _but_only_poorly_developed present_and_pronounced;

{67 Articulation_of_nuchal_with_neural_spine_of_eighth_cervical_vertebra
cervical_articulates_with_nuchal_along_a_blunt_facet articulation_absent
cervical_articulates_with_nuchal_along_a_raised_pedestal;

{68 Paired_ventral_processes_of_nuchal absent present;

{69 Elongate_costiform_processes_of_nuchal absent
present, _process_crosses_peripheral_I_to_contact_peripheral_II_and_sometimes_even_peripheral_III;

{70 Neural_formula_6>4<6<6<6<6 absent present;

{71 Neural_series more_or_less_continuous
neural_series_often_disrupted_by_irregular_midline_contacts_of_costals;

{72 Number_of_peripherals more_than_11_pairs_of_peripherals_present 11_pairs_of_peripherals_present
10_pairs_of_peripherals_present less_than_10_pairs_of_peripherals_present;

{73 Anterior_peripherals_incised_by_musk_ducts absent present;

{74 Medial_contact_of_costal_I absent present;

{75 Medial_contact_of_posterior_costals absent medial_contact_of_up_to_three_posterior_costals_present
medial_contact_of_all_costals_present;

{76 Reduction_of_costal_ossification
absent, _costals_fully_or_almost_fully_ossified, _costal_fontanelles_small_or_absent

present, costals ossified only two thirds the length of the costal ribs, costal fontanelles well developed;
 {77 Number_of_suprapygals two_or_more one;
 {78 Shape_of_pygal;
 {79 Carapace_with_single_midline_keel absent present;
 {80 Cleithra present_and_in_contact_with_the_carapace present, osseous_contact_with_carapace absent absent;
 {81 Cervical one_cervical_present cervicals_absent, carapacial_scutes_otherwise_present
 more_than_one_cervical_present;
 {82 Supramarginals complete_row_present, fully_separating_marginals_from_pleurals
 partial_row_present, incompletely_separating_marginals_from_pleurals absent;
 {83 Number_of_vertebrals four_present five_or_more_present;
 {84 Shape_of_vertebrals vertebrals_II_to_IV_significantly_broader_than_pleurals
 vertebrals_II_to_IV_as_narrow_or_narrower_than_pleurals;
 {85 Vertebral_I undivided partly_or_completely_divided_along_the_midline;
 {86 Sulcus_between_cervical_and/or_marginal_and_vertebral_1 present absent;
 {87 Position_of_vertebral_II-III_sulcus_in_taxa_with_five_vertebrals sulcus_positioned_on_neural_VI
 sulcus_positioned_on_neural_V;
 {88 Sulcus_between_vertebrals_3_and_4 present absent;
 {89 Vertebral_2_extended_anteriorly_to_occupy_part_of_the_nuchal no yes;
 {90 Additional_vertebral_scute_between_vertebrals_2_and_3 absent present, but_small_present_and_large
 fused_with_vertebrals_3+4;
 {91 Connection_between_carapace_and_plastron osseous ligamentous;
 {92 Central_plastral_fontanelle absent_in_adult_individuals present, even_in_adult_individuals;
 {93 Plastral_kinesis absent, scute_sulci_and_bony_sutures_do_not_overlap
 present, scute_sulci_coincide_with_hyoplastral?epiplastral_contact;
 {94 Anterior_entoplastral_process present, medial_contact_of_epiplastra_absent
 absent, medial_contact_of_epiplastra_present;
 {95 Size_of_posterior_entoplastral_process posterior_process_long posterior_process_reduced_in_length;
 {96 Distinct_posterolateral_entoplastral_processes present absent;
 {97 Entoplastron massive_and_cross-to_diamond-shaped strap_like_and_V-shaped absent;
 {98 Shape_and_contacts_of_epiplastra epiplastra_squarish_in_shape, minor_posterior_contact_with_hyoplastra
 epiplastra_elongate_in_shape, long_posteromedial_contact_with_hyoplastra;
 {99 Contacts_of_axillary_buttresses_with_the_hyoplastron peripherals_only peripherals_and_first_costal;
 {100 Number_and_size_of_mesoplastra
 one_or_two_pair_of_mesoplastra_present_that_fully_hinder_any_contact_between_the_hyoplastra_and_hypoplastra
 a_one_reduced_pair_of_mesoplastra_present_that_allows_partial_contact_between_the_hyoplastra_and_hypoplastra
 mesoplastra_absent;
 {101 Contacts_of_axillary_buttresses_with_the_hypoplastron peripherals_only peripherals_and_costal_V
 peripherals, costal_V, and_costal_VI;
 {102 Distinct_anal_notch_in_the_xiphiplastron absent present;
 {103 Xiphiplastral_shape elongate_rectangles narrow_struts_that_frame_a_xiphiplastral_fontanelle;
 {104 Width_of_posterior_plastral_lobe wide reduces narrow;
 {105 Plastral_scutes present reduced absent;
 {106 Midline_sulcus_in_plastral_scutes straight distinctly_sinuuous;
 {107 Plastral_scale_set_1, gulars one, medially_situated_pair_of_scutes_present
 one, medially_situated_scute_present;
 {108 Plastral_scale_set_2, extragulars present absent;
 {109 Medial_contact_of_plastral_scale_set_2, extragulars absent
 present, contacting_one_another_anterior_to_gular(s) present, contacting_one_another_posterior_to_gular(s);
 {110 Anterior_plastral_tuberosities present absent;
 {111 Plastral_scale_set_8, intergulars absent present;
 {112 Plastral_scale_set_3, humerals one_pair_present two_pair_present, subdivided_by_a_plastral_hinge;
 {113 Plastral_scale_set_4, pectorals present absent;
 {114 Plastral_scale_set_5, abdominals present, in_medial_contact_with_one_another
 present, medial_contact_absent absent;
 {115 Plastral_scale_set_7, anals only_cover_parts_of_the_xiphiplastra anteromedially_overlap_onto_hypoplastra;
 {116 Inframarginal_scutes more_than_two_pair_present, plastral_scutes_do_not_contact_marginals
 two_pair_present (axillaries_andinguinals), limited_contact_between_plastral_scutes_and_marginals_present

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absent, unrestricted_contact_between_plastral_scutes_and_marginals_present;
{117 Cervical_ribs_large_cervical_ribs_present_cervical_ribs_reduced_or_absent;
{118 Position_of_transverse_processes_in_cervical_vertebrae_middle_of_the Centrum
anterior_end_of_the_Centrum;
{119 Posterior_cervicals_with_strongly_developed_ventral_keels absent present;
{120 Cervical_Centrum_VIII_significantly_shorter_than_VII absent present;
{121 Cervical_central_articulations articulations_not_formed articulations_formed;
{122 Cervical_articulation_between_cervical_II_and_III 2(3 2)3;
{123 Cervical_articulation_between_cervical_III_and_IV 3(4 3)4;
{124 Cervical_articulation_between_cervical_IV_and_V 4(5 4)5;
{125 Cervical_articulation_between_cervical_V_and_VI 5(6 5)6;
{126 Cervical_articulation_between_cervical_VI_and_VII 6(7 7)8;
{127 Cervical_articulation_between_cervical_VII_and_VIII 7)8 7(8;
{128 Cervical_articulation_between_cervical_VIII_and_the_first_dorsal 8(dorsal 8)dorsal
none, vertebrae_only_meet_at_zygapophyses;
{129 Length_of_first_dorsal_rib
long_extends_full_length_of_first_costal_and_may_even_contact_peripherals_distally
intermediate_in_contact_with_well-developed_anterior_bridge_buttresses
intermediate_to_short_extends_less_than_halfway_across_first_costal;
{130 Contact_of_dorsal_ribs_IX_and_X_with_costals present absent;
{131 Dorsal_rib_X_dorsal_rib_X_long_spanning_full_length_of_costals_and_contacting_peripherals_distally
dorsal_rib_X_short_not_spanning_further_distally_than_pelvis;
{132 Anterior_articulation_of_first_dorsal_Centrum_faces_at_most_slightly_anteroventrally
faces_strongly_anteroventrally;
{133 Chevrons_present_on_nearly_all_caudals absent_or_only_poorly_developed_along_the_posterior_caudals;
{134 Tail_club present absent;
{135 Caudal_centra_all_centra_amphicoelous_all_centra_more_or_less_pronounced_procoelous
all_centra_more_or_less_pronounced_opisthocoelous
anterior_few_centra_procoelous_posterior_centra_predominantly_opisthocoelous;
{136 Length_of_acromial_process_less_than_one_half_length_of_scapular_process
more_than_one_half_length_of_scapular_process;
{137 Acromial_ridge present_contacts_the_glenoid_proximally absent;
{138 Glenoid_neck_present_on_scapula absent present;
{139 Coracoid_foramen present absent;
{140 Sutural_articulation_of_pelvis_to_shell absent present;
{141 Elongated_iliac_neck absent present;
{142 Iliac_scar_extends_from_costals_onto_the_peripherals_and_pygal positioned_on_costals_only;
{143 Shape_of_iliac_articular_site narrow_and_pointed_posteriorly oval;
{144 Posterior_notch_in_acetabulum absent present;
{145 Ischial_contacts_with_plastron contact_by_way_of_a_large_central_tubercle
contact_by_way_of_two_separate_ischial_processes;
{146 Hypoischium present absent;
{147 Phalangeal_formula_of_manus_and_pes most_digits_with_three_elongate_phalanges
most_digits_with_two_short_phalanges;
{148 Manus_paddles absent short_paddles_present elongate_paddles_present;
{149 Manus_flippers absent short_flippers_present elongate_flippers_present;
{150 Pes_claw_of_fifth_digit present absent;
{151 Pes_metatarsal_V_and_functional_metatarsal_V metatarsal_V_functions_as_true_metatarsal
metatarsal_V_functions_as_a_tarsal_with_the_first_phalanx_of_digit_V_functioning_as_a_metatarsal;
{152 Manual_claws five four three two one zero;
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ccode + 0.152 *;
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proc /;
comments 0
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Appendix C

The first Pan-Carettochelys turtle in the Neogene of the American Continent and its paleobiogeographical relevance

by

Gerardo Carbot-Chanona, Gustavo Rivera-Velázquez, Eduardo Jiménez-Hidalgo

and Víctor Hugo Reynoso

Character list, modified from Joyce (2007), Havlik et al. (2014), and Danilov et al. (2017).

Skull

1. Nasals (Joyce, 2007, character 1): 0 = present; 1 = absent.
2. Medial contact of nasals (Joyce, 2007, character 2): 0 = nasals contact one another medially along their entire length; 1 = medial contact of nasals partially or fully hindered by long anterior frontal process
3. Size of nasals (Joyce, 2007, character 3): 0 = dorsal exposure of nasals large; 1 = dorsal exposure of nasals greatly reduced relative to that of the frontals.
4. Medial contact of prefrontals on dorsal skull surface (Joyce, 2007, character 4): 0 = absent; 1 = present, prefrontal contact with frontal absent.
5. Prefrontal–vomer contact (Joyce, 2007, character 5): 0 = absent; 1 = present.
6. Prefrontal–palatine contact (Joyce, 2007, character 6): 0 = present; 1 = absent.
7. Dorsal prefrontal exposure (Joyce, 2007, character 7): 0 = large; 1 = reduced; 2 = absent or near absent.
8. Prefrontals heavily sculptured with prominences and bosses (Joyce, 2007, character 8): 0 = present; 1 = absent.
9. Lacrimal (Joyce, 2007, character 9): 0 = present; 1 = absent.
10. Frontal contribution to orbit (Joyce, 2007, character 10): 0 = absent, prefrontal contacts postorbital; 1 = present.

11. Parietal–squamosal contact (Joyce, 2007, character 11): 0 = present, upper temporal emargination absent or only poorly developed; 1 = absent, upper temporal emargination well developed.
12. Parietal contact with the pterygoid, epipterygoid, or palatine (Joyce, 2007, character 12): 0 = absent, trigeminal foramen only developed as a notch; 1 = present, trigeminal foramen clearly formed by the descending process of the parietal.
13. Length of anterior extension of the lateral braincase wall (Joyce, 2007, character 13): 0 = short, inferior parietal process only produces a narrow strut anterior to trigeminal foramen, palatine contact absent; 1 = elongate, inferior parietal process produces an extended process anterior to trigeminal foramen, palatine contact commonly present.
14. Jugal–squamosal contact (Joyce, 2007, character 14): 0 = present; 1 = absent, contact between postorbital and quadratojugal commonly present.
15. Jugal participation to upper temporal rim (Joyce, 2007, character 15): 0 = absent; 1 = present, upper temporal emargination extensive.
16. Quadratojugal (Joyce, 2007, character 16): 0 = present; 1 = absent, due to the presence of a deep lower temporal emargination.
17. Quadratojugal–maxilla contact (Joyce, 2007, character 17): 0 = absent; 1 = present.
18. Fossa behind articular process of quadrate (Havlik et al., 2014, character 137): 0 = absent; 1 = small; 2 = large.
19. Squamosal–postorbital contact (Joyce, 2007, character 18): 0 = present; 1 = absent, temporal roofing well developed, but postorbital short; 2 = absent, due to lower temporal emargination; 3 = absent, due to upper temporal emargination.
20. Squamosal supraoccipital contact (Joyce, 2007, character 19): 0 = absent; 1 = present.
21. Postorbital–palatine contact (Joyce, 2007, character 20): 0 = absent; 1 = present, foramen *palatinum posterius* situated posterior to the orbital wall.
22. Supratemporal (Joyce, 2007, character 21): 0 = present; 1 = absent.
23. Subdivision of external nares by internarial process of premaxilla (Joyce, 2007, character 22): 0 = present; 1 = absent.
24. Fusion of premaxillae (Joyce, 2007, character 23): 0 = absent; 1 = present.
25. Foramen prepalatinum (Joyce, 2007, character 24): 0 = present; 1 = absent, premaxillae well ossified; 2 = absent, *foramen intermaxillaris* present.
26. Exclusion of premaxillae from *apertura narium externa* (Joyce, 2007, character 25): 0 = absent; 1 = present.
27. Distinct, medial premaxillary hook along the labial margin of the premaxillae (Joyce, 2007, character 26): 0 = absent; 1 = present.

28. Vomer (Joyce, 2007, character 27): 0 = paired; 1 = single; 2 = single, greatly reduced or absent.
29. Vomer–pterygoid contact in palatal view (Joyce, 2007, character 28): 0 = present; 1 = absent, medial contact of palatines present.
30. Vomerine and palatine teeth (Joyce, 2007, character 29): 0 = present; 1 = absent.
31. Palatine contribution to anterior extension of lateral braincase wall (Joyce, 2007, character 30): 0 = absent; 1 = present, well developed.
32. Flooring of *cavum acustico-jugulare* and *recessus scalae tympani* (Joyce, 2007, character 31): 0 = absent; 1 = fully or partially present, produced by the posterior process of the pterygoid; 2 = fully or partially present, produced by the ventral process of the quadrate or the prootic, or both.
33. Central constriction of the middle ear (Joyce, 2007, character 32): 0 = absent; 1 = present, formed by quadrate.
34. Cavum tympani (Joyce, 2007, character 33): 0 = absent; 1 = partially developed; 2 = fully developed.
35. Precolumellar fossa (Joyce, 2007, character 34): 0 = absent; 1 = large and deep.
36. *Antrum postoticum* (Joyce, 2007, character 35): 0 = absent; 1 = present, quadrate does not fully enclose the anterior perimeter of the antrum; 2 = present, quadrate fully encloses the anterior perimeter of the antrum.
37. *Incisura columellae auris* (Joyce, 2007, character 36): 0 = absent, stapes articulates along the medial side of the quadrate; 1 = present, but open posteroventrally; 2 = present and closed, but only enclosing the stapes; 3 = present and closed, enclosing stapes and the Eustachian tube.
38. Epipterygoid (Joyce, 2007, character 37): 0 = present; 1 = absent.
39. Pterygoid teeth (Joyce, 2007, character 38): 0 = present; 1 = absent.
40. Basipterygoid articulation (Joyce, 2007, character 39): 0 = open; 1 = fused.
41. Interpterygoid vacuity (Joyce, 2007, character 40): 0 = present; 1 = absent.
42. Pterygoid–basioccipital contact (Joyce, 2007, character 41): 0 = absent; 1 = present.
43. *Processus trochlearis pterygoideus* (Joyce, 2007, character 42): 0 = absent; 1 = present.
44. Foramen *palatinum posterius* (Joyce, 2007, character 43): 0 = present; 1 = present, but open laterally; 2 = absent.
45. Pterygoid-pterygoid suture between foramen *posterius canalis caroticus interni* and basisphenoid (Danilov et al. 2017, character 148): 0 = absent; 1 = present.

46. Medial contact of pterygoids (Joyce, 2007, character 44): 0 = pterygoids in medial contact with one another for at least part of their length; 1 = absent, contact of the basisphenoid with the vomer or palatines, or both, present.
47. Pterygoid contribution to foramen *palatinum posterius* (Joyce, 2007, character 45): 0 = present; 1 = absent.
48. Pterygoid trough (Danilov et al. 2017, character 149): 0 = opened ventrally; 1 = closed ventrally.
49. *Crista supraoccipitalis* (Joyce, 2007, character 46): 0 = poorly developed; 1 = protruding significantly posterior to the foramen magnum.
50. Large supraoccipital exposure to dorsal skull roof (Joyce, 2007, character 47): 0 = absent; 1 = present.
51. Medial contact of exoccipitals dorsal to *foramen magnum* (Joyce, 2007, character 48): 0 = absent; 1 = present.
52. *Processus paroccipitalis* (Joyce, 2007, character 49): 0 = loosely articulated to squamosal and quadrate; 1 = tightly sutured to squamosal and quadrate.
53. *Rostrum basisphenoidale* (Joyce, 2007, character 50): 0 = flat; 1 = rod-like, thick, and rounded.
54. Paired pits on ventral surface of basisphenoid (Joyce, 2007, character 51): 0 = absent; 1 = present.
55. Path of hyomandibular branch of the facial nerve (Joyce, 2007, character 52): 0 = hyomandibular nerve passes through cranioquadrate space parallel to *vena capitis lateralis*; 1 = hyomandibular nerve runs independent from *vena capitis lateralis*.
56. Position of *stapedio-temporal* canal (Joyce, 2007, character 53): 0 = posterior to fenestra ovalis between paroccipital process and quadrate; 1 = anterior to *fenestra ovalis* between quadrate and prootic.
57. Size of foramen *stapedio-temporale* (Joyce, 2007, character 54): 0 = relatively large (the size of a large blood foramina); 1 = significantly reduced in size (the size of a nerve foramina); 2 = absent.
58. Anterior and posterior jugular foramina defined by bone (Joyce, 2007, character 55): 0 = absent, 1 = present.
59. Foramen *posterius canalis caroticum internus* (Joyce, 2007, character 56): 0 = formed by basisphenoid only; 1 = formed by both basisphenoid and pterygoid halfway along the basisphenoid–pterygoid suture; 2 = formed by prootic only; 3 = formed mostly or fully by pterygoid, foramen positioned near the posterior end of the basisphenoid.
60. *Fenestra perilymphatica* (Joyce, 2007, character 57): 0 = large; 1 = reduced in size to that of a small foramen.

61. Depth of *antrum postoticum* (Havlik et al., 2014, character 138): 0 = absent; 1 = shallow; 2 = deep.
62. Position of the foramen *posterius canalis caroticus interni* on the ventral surface of the skull within pterygoids (Danilov et al. 2017, character 150): 0 = near middle part of basisphenoid; 1 = near posterior border of basisphenoid; 2 = distant from posterior border of basisphenoid.
63. Foramen *nervi trigemini* is divided into two parts by prootic (Danilov et al. 2017, character 151): 0 = no; 1 = yes.

Lower jaw

64. Medial contact of dentaries (Joyce, 2007, character 58): 0 = fused; 1 = sutured only (symphysis).
65. Splenial (Joyce, 2007, character 59): 0 = present; 1 = absent.

Carapace bones

66. Carapace scutes (Joyce, 2007; Havlik et al., 2014, character 60): 0 = all carapacial scutes present; 1 = marginal scutes absent; 2 = all carapacial scutes absent.
67. Tricarinate carapace (Joyce, 2007, character 61): 0 = absent; 1 = present, but only poorly developed, 2 = present and pronounced.
68. Articulation of nuchal with neural spine of eighth cervical vertebra (Joyce, 2007, character 62): 0 = cervical articulates with nuchal along a blunt facet; 1 = articulation absent; 2 = cervical articulates with nuchal along a raised pedestal.
69. Paired ventral processes of nuchal (Havlik et al., 2014, character 139): 0 = absent; 1 = present.
70. Elongate costiform processes of nuchal (Joyce, 2007, character 63): 0 = absent; 1 = present, process crosses peripheral I to contact peripheral II and sometimes even peripheral III.
71. Neural formula $6 > 4 < 6 < 6 < 6 < 6$ (Joyce, 2007, character 64): 0 = absent; 1 = present.
72. Neural series (Havlik et al., 2014, character 146): 0 = more or less continuous; 1 = neural series often disrupted by irregular midline contacts of costals.
73. Number of peripherals (Joyce, 2007, character 65): 0 = more than 11 pairs of peripherals present; 1 = 11 pairs of peripherals present; 2 = 10 pairs of peripherals present; 3 = less than 10 pairs of peripherals present.

74. Anterior peripherals incised by musk ducts (Joyce, 2007, character 66): 0 = absent; 1 = present.
75. Medial contact of costal I (Joyce, 2007, character 67): 0 = absent, 1 = present.
76. Medial contact of posterior costals (Joyce, 2007, character 68): 0 = absent, 1 = medial contact of up to three posterior costals present; 2 = medial contact of all costals present.
77. Reduction of costal ossification (Joyce, 2007, character 84): 0 = absent, costals fully or almost fully ossified, costal fontanelles small or absent; 1 = present, costals ossified only two thirds the length of the costal ribs, costal fontanelles well developed.
78. Number of suprapygal (Havlik et al., 2014, character 144): 0 = two or more; 1 = one.
79. Anterior margin of pygal greatly thickened and with visceral groove (Havlik et al., 2014, character 145): 0 = absent, 1 = present
80. Carapace with single midline keel (Havlik et al., 2014, character 147): 0 = absent; 1 = present.
81. Cleithra (Joyce, 2007, character 120): 0 = present and in contact with the carapace; 1 = present, osseous contact with carapace absent; 2 = absent.

Carapace scutes

82. Cervical (Joyce, 2007, character 70): 0 = one cervical present; 1 = cervicals absent, carapacial scutes otherwise present; 2 = more than one cervical present.
83. Supramarginals (Joyce, 2007, character 71): 0 = complete row present, fully separating marginals from pleurals; 1 = partial row present, incompletely separating marginals from pleurals; 2 = absent.
84. Number of vertebrae (Joyce, 2007, character 72): 0 = four present; 1 = five or more present.
85. Shape of vertebrae (Joyce, 2007, character 73): 0 = vertebrae II to IV significantly broader than pleurals; 1 = vertebrae II to IV as narrow or narrower than pleurals.
86. Vertebral I (Havlik et al., 2014, character 140): 0 = undivided; 1 = partly or completely divided along the midline.
87. Sulcus between cervical and/or marginal and vertebral I (Danilov et al. 2017, character 152): 0 = present; 1 = absent.
88. Position of vertebral II–III sulcus in taxa with five vertebrae (Joyce, 2007, character 74): 0 = sulcus positioned on neural VI; 1 = sulcus positioned on neural V.

89. Sulcus between vertebrals III and IV (Danilov et al. 2017, character 153): 0 = present; 1 = absent.
90. Vertebral II extended anteriorly to occupy part of the nuchal: 0 = no; 1 = yes.
91. Additional vertebral scute between vertebrals II and III (Danilov et al. 2017, character 155): 0 = absent; 1 = present, but small (narrower than neurals II–III and not extending on to neural I); 2 = present and large (wider than neurals 2–3 and extending on to neural I); 3 = fused with vertebrals III+IV.

Plastral bones

92. Connection between carapace and plastron (Joyce, 2007, character 75): 0 = osseous; 1 = ligamentous.
93. Central plastral fontanelle (Joyce, 2007, character 76): 0 = absent in adult individuals; 1 = present, even in adult individuals.
94. Plastral kinesis (Joyce, 2007, character 77): 0 = absent, scute sulci and bony sutures do not overlap; 1 = present, scute sulci coincide with hyoplastral–epiplastral contact.
95. Anterior entoplastral process (Joyce, 2007, character 78): 0 = present, medial contact of epiplastra absent; 1 = absent, medial contact of epiplastra present.
96. Size of posterior entoplastral process (Joyce, 2007, character 79): 0 = posterior process long; 1 = posterior process reduced in length.
97. Distinct posterolateral entoplastral processes (Joyce, 2007, character 80): 0 = present; 1 = absent.
98. Entoplastron (Joyce, 2007, character 81 and 82): 0 = massive and cross- to diamond-shaped; 1 = strap like and V-shaped; 2 = absent. Note: Joyce (2007) coding two characters referring to entoplastron (characters 81 and 82). Character 81 has the character states that refer to the shape of the entoplastron, which makes evidence its presence. On the other hand, the character 82 refers the presence/absence of the entoplastron. This causes more weight to character of the entoplastron because is coding twice. For this reason, we add a new state of character (absent) in the character 81 from Joyce (2007) and eliminate the character 82.
99. Shape and contacts of epiplastra (Joyce, 2007, character 83): 0 = epiplastra squarish in shape, minor posterior contact with hyoplastra; 1 = epiplastra elongate in shape, long posteromedial contact with hyoplastra.
100. Contacts of axillary buttresses with the hyoplastron (Joyce, 2007, character 84): 0 = peripherals only; 1 = peripherals and first costal.
101. Number and size of mesoplastra (Joyce, 2007, character 85): 0 = one or two pair of mesoplastra present that fully hinder any contact between the hyoplastra and

- hypoplastra; 1 = one reduced pair of mesoplastra present that allows partial contact between the hypoplastra and hypoplastra; 2 = mesoplastra absent.
102. Contacts of axillary buttresses with the hypoplastron (Joyce, 2007, character 86): 0 = peripherals only; 1 = peripherals and costal V; 2 = peripherals, costal V, and costal VI.
103. Distinct anal notch in the xiphiplastron (Joyce, 2007, character 87): 0 = absent; 1 = present.
104. Xiphiplastral shape (Joyce, 2007, character 88): 0 = elongate rectangles; 1 = narrow struts that frame a xiphiplastral fontanelle.
105. Width of posterior plastral lobe (Havlik et al., 2014, character 141): 0 = wide; 1 = reduced; 2 = narrow.

Plastral scutes

106. Plastral scutes (Havlik et al., 2014, character 89): 0 = present; 1 = reduced; 2 = absent.
107. Midline sulcus in plastral scutes (Joyce, 2007, character 90): 0 = straight; 1 = distinctly sinuous.
108. Plastral scale set 1, gulars (Joyce, 2007, character 91): 0 = one, medially situated pair of scutes present; 1 = one, medially situated scute present.
109. Plastral scale set 2, extragulars (Joyce, 2007, character 92): 0 = present; 1 = absent.
110. Medial contact of plastral scale set 2, extragulars (Joyce, 2007, character 93): 0 = absent; 1 = present, contacting one another anterior to gular(s); 2 = present, contacting one another posterior to gular(s).
111. Anterior plastral tuberosities (Joyce, 2007, character 94): 0 = present; 1 = absent.
112. Plastral scale set 8, intergulars (Joyce, 2007, character 95): 0 = absent; 1 = present.
113. Plastral scale set 3, humerals (Joyce, 2007, character 96): 0 = one pair present; 1 = two pair present, subdivided by a plastral hinge.
114. Plastral scale set 4, pectorals (Joyce, 2007, character 97): 0 = present; 1 = absent.
115. Plastral scale set 5, abdominals (Joyce, 2007, character 98): 0 = present, in medial contact with one another; 1 = present, medial contact absent; 2 = absent.
116. Plastral scale set 7, anals (Joyce, 2007, character 99): 0 = only cover parts of the xiphiplastra; 1 = anteromedially overlap onto hypoplastra.
117. Inframarginal scutes (Joyce, 2007, character 100): 0 = more than two pair present, plastral scutes do not contact marginals; 1 = two pair present (axillaries and inguinals), limited contact between plastral scutes and marginals present; 2 = absent, unrestricted contact between plastral scutes and marginals present.

Vertebrae and ribs

118. Cervical ribs (Joyce, 2007, character 101): 0 = large cervical ribs present; 1 = cervical ribs reduced or absent.
119. Position of transverse processes in cervical vertebrae (Joyce, 2007, character 102): 0 = middle of the centrum; 1 = anterior end of the centrum.
120. Posterior cervicals with strongly developed ventral keels (Joyce, 2007, character 103): 0 = absent; 1 = present.
121. Cervical centrum VIII significantly shorter than VII (Joyce, 2007, character 104): 0 = absent; 1 = present.
122. Cervical central articulations (Joyce, 2007, character 105): 0 = articulations not formed; 1 = articulations formed.
123. Cervical articulation between cervical II and III (Joyce, 2007, character 106): 0 = 2(3; 1 = 2)3.
124. Cervical articulation between cervical III and IV (Joyce, 2007, character 107): 0 = 3(4; 1 = 3)4.
125. Cervical articulation between cervical IV and V (Joyce, 2007, character 108): 0 = 4(5; 1 = 4)5.
126. Cervical articulation between cervical V and VI (Joyce, 2007, character 109): 0 = 5(6; 1 = 5)6.
127. Cervical articulation between cervical VI and VII (Joyce, 2007, character 110): 0 = 6(7; 1 = 6)7.
128. Cervical articulation between cervical VII and VIII (Joyce, 2007, character 111): 0 = 7(8; 1 = 7)8.
129. Cervical articulation between cervical VIII and the first dorsal (Joyce, 2007, character 112): 0 = 8 (dorsal; 1 = 8) dorsal; 2 = none, vertebrae only meet at zygapophyses.
130. Length of first dorsal rib (Joyce, 2007, character 113): 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.
131. Contact of dorsal ribs IX and X with costals (Joyce, 2007, character 114): 0 = present, 1 = absent.
132. Dorsal rib X (Joyce, 2007, character 115): 0 = dorsal rib X long, spanning full length of costals and contacting peripherals distally; 1 = dorsal rib X short, not spanning farther distally than pelvis.

133. Anterior articulation of first dorsal centrum (Joyce, 2007, character 116): 0 = faces at most slightly anteroventrally; 1 = faces strongly anteroventrally.
134. Chevrons (Joyce, 2007, character 117): 0 = present on nearly all caudals; 1 = absent, or only poorly developed, along the posterior caudals.
135. Tail club (Joyce, 2007, character 118): 0 = present; 1 = absent.
136. Caudal centra (Joyce, 2007, character 119): 0 = all centra amphicoelous; 1 = all centra more or less pronounced procoelous; 2 = all centra more or less pronounced opisthocoelous; 3 = anterior few centra procoelous, posterior centra predominantly opisthocoelous.

Appendicular skeleton

137. Length of acromial process (Joyce, 2007, character 121): 0 = less than one half length of scapular process; 1 = more than one half length of scapular process.
138. Acromial ridge (Joyce, 2007, character 122): 0 = present, contacts the glenoid proximally; 1 = absent.
139. Glenoid neck present on scapula (Joyce, 2007, character 123): 0 = absent; 1 = present.
140. Coracoid foramen (Joyce, 2007, character 124): 0 = present; 1 = absent.
141. Sutural articulation of pelvis to shell (Joyce, 2007, character 125): 0 = absent; 1 = present.
142. Elongated iliac neck (Joyce, 2007, character 126): 0 = absent; 1 = present.
143. Iliac scar (Joyce, 2007, character 127): 0 = extends from costals onto the peripherals and pygal; 1 = positioned on costals only.
144. Shape of ilium articular site (Joyce, 2007, character 128): 0 = narrow and pointed posteriorly; 1 = oval.
145. Posterior notch in acetabulum (Joyce, 2007, character 129): 0 = absent; 1 = present.
146. Ischial contacts with plastron (Joyce, 2007, character 130): 0 = contact by way of a large central tubercle; 1 = contact by way of two separate ischial processes.
147. Hypoischium (Joyce, 2007, character 131): 0 = present; 1 = absent.
148. Phalangeal formula of manus and pes (Joyce, 2007, character 132): 0 = most digits with three elongate phalanges; 1 = most digits with two short phalanges.
149. Manus: paddles (Joyce, 2007, character 132): 0 = absent; 1 = short paddles present; 2 = elongate paddles present.

150. Manus: flippers (Joyce, 2007, character 134): 0 = absent; 1 = short flippers present; 2 = elongate flippers present.
151. Pes: claw of fifth digit (Joyce, 2007, character 135): 0 = present; 1 = absent.
152. Pes: metatarsal V and “functional metatarsal V” (Joyce, 2007, character 136): 0 = metatarsal V functions as true metatarsal; 1 = metatarsal V functions as a tarsal, with the first phalanx of digit V functioning as a metatarsal.
153. Manual claws (Havlik et al., 2014, character 142): 0 = five; 1 = four; 2 = three; 3 = two; 4 = one; 5 = zero.

References

- Danilov, I.G., Obraztsova, E.M., Chen, W., Jin, J., 2017. The cranial morphology of *Anosteira maomingensis* (Testudines, Pan-Carettochelys) and the evolution of pan-carettochelyid turtles. *Journal of Vertebrate Paleontology*, e1335735. DOI: 10.1080/02724634.2017.1335735.
- Havlik, P.E., Joyce, W.G., Böhme, M., 2014. *Allaeochelys libyca*, a new Carettochelyine turtle from the Middle Miocene (Langhian) of Libya. *Bulletin of the Peabody Museum of Natural History*, 55(2), 201-214.
- Joyce, W.G., 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History*, 47, 3–102.

Appendix D

The first Pan-Carettochelys turtle in the Neogene of the American continent and its paleobiogeographical relevance

by

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and Víctor Hugo Reynoso

Additional resulting trees obtained from the Maximun Parsimonious Analysis

To establish the phylogenetic relationships of *Allaeochelys liliae* sp. nov, we conducted a Maximun Parsimonious Analysis in TNT 1.5 (Goloboff et al., 2008), using a modified dataset based in Joyce (2007), Havlik et al. (2014) and Danilov et al. (2017). Here, we present additional resulting trees from this analysis including the complete consensus tree, the bootstrap tree, the Bremer support tree, and map trees of the unambiguous synapomorphic characters.

Figure S1. Strict consensus tree obtained from four most parsimonious trees resulting in the Maximum Parsimonious Analysis in TNT (TL=425, CI=0.461, RI=0.807).

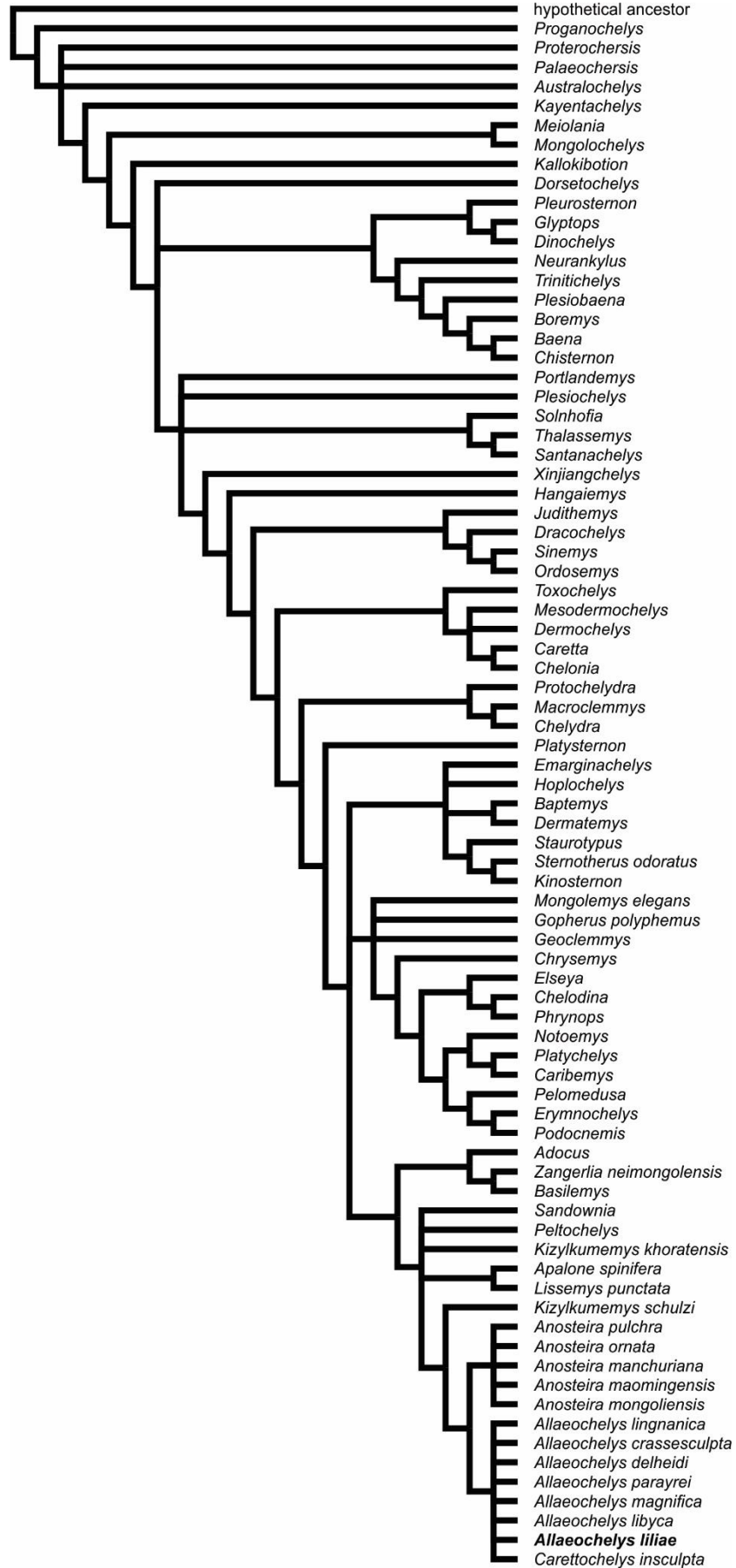


Figure S2. Bootstrap tree resulted from the Maximum Parsimonious Analysis in TNT.

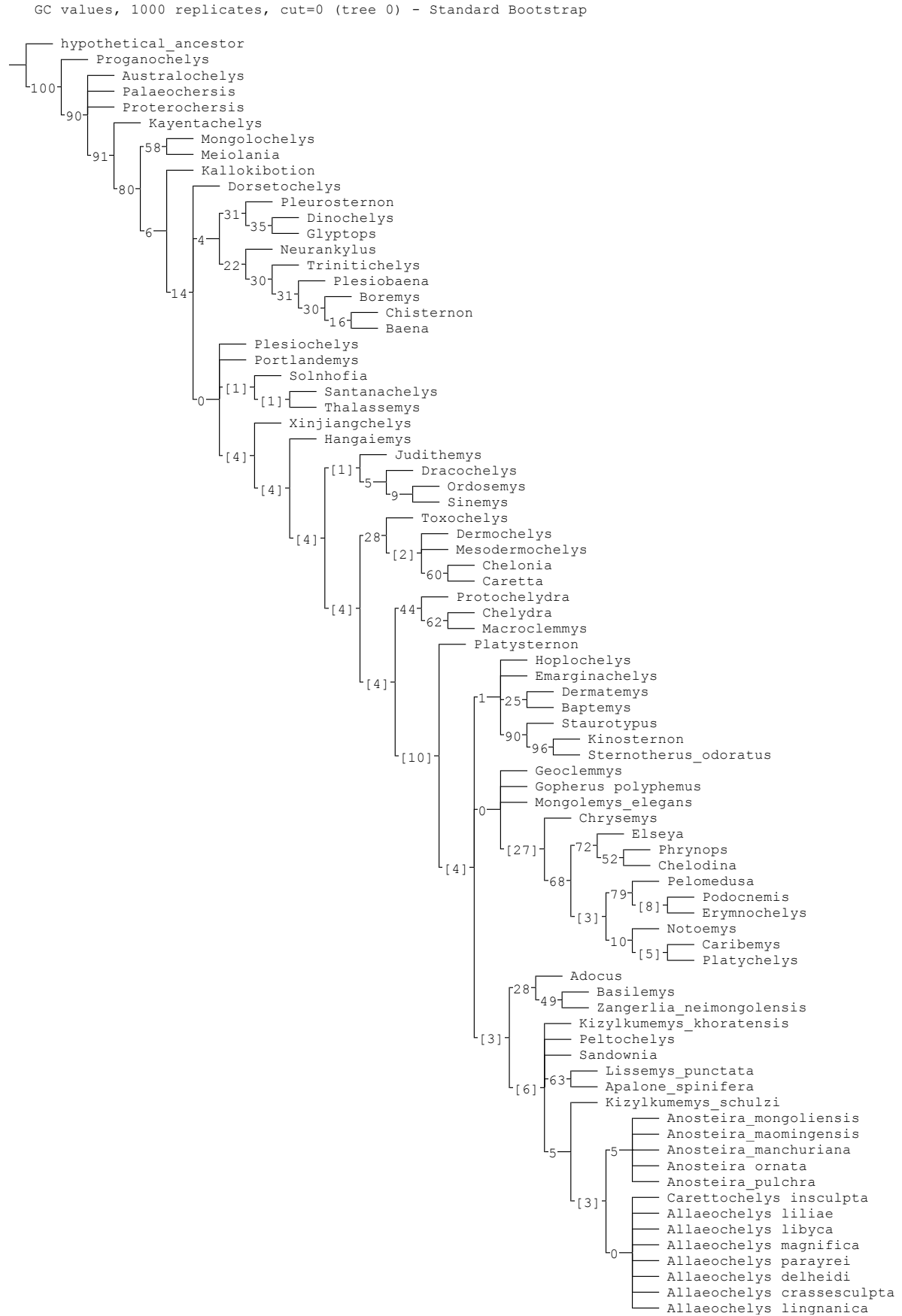


Figure S3. Bremer support values resulting for the Maximun Parsimonious Analysis in TNT.

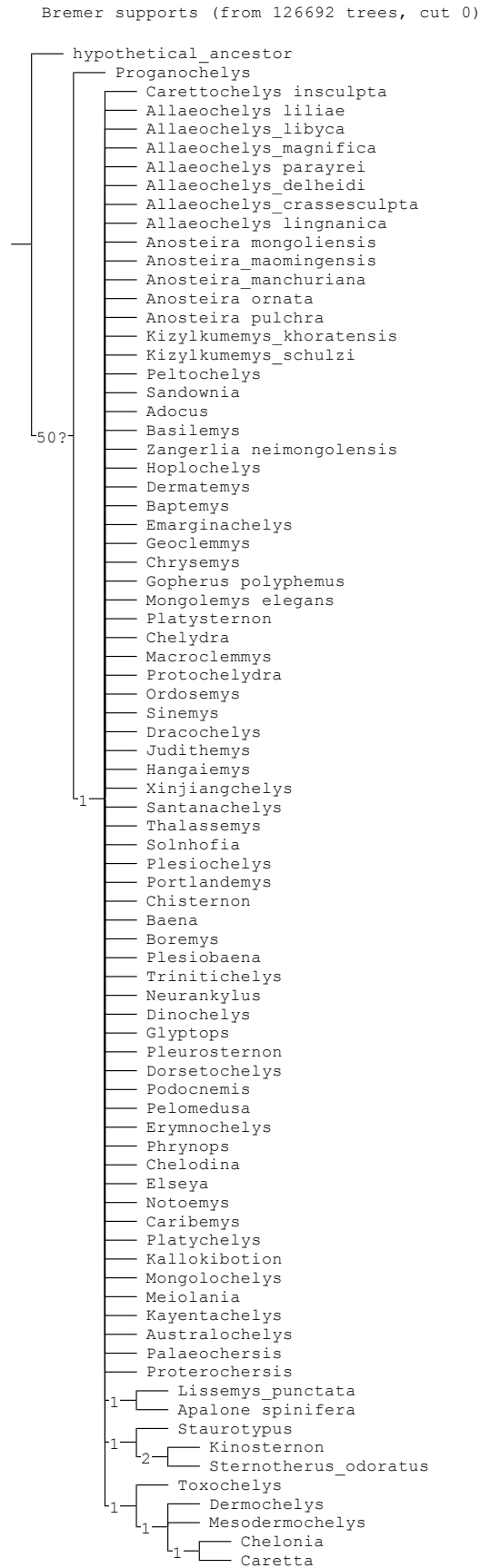


Figure S4. Unambiguous character 18 mapped in the Most Parsimonious Tree supporting the clade Pan-Carettochelys.

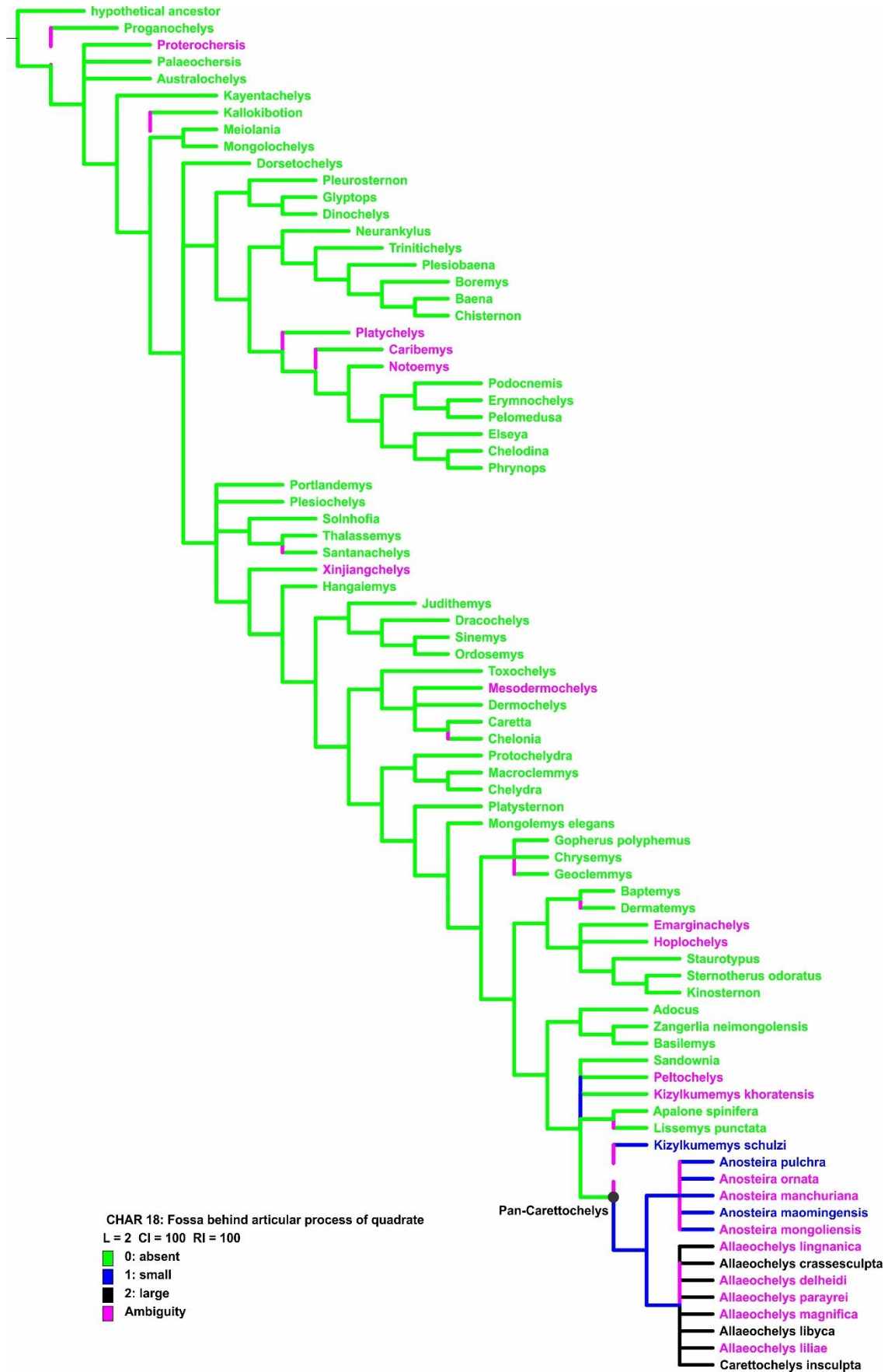


Figure S5. Unambiguous character 45 mapped in the Most Parsimonious Tree supporting the clade Pan-Carettochelys.

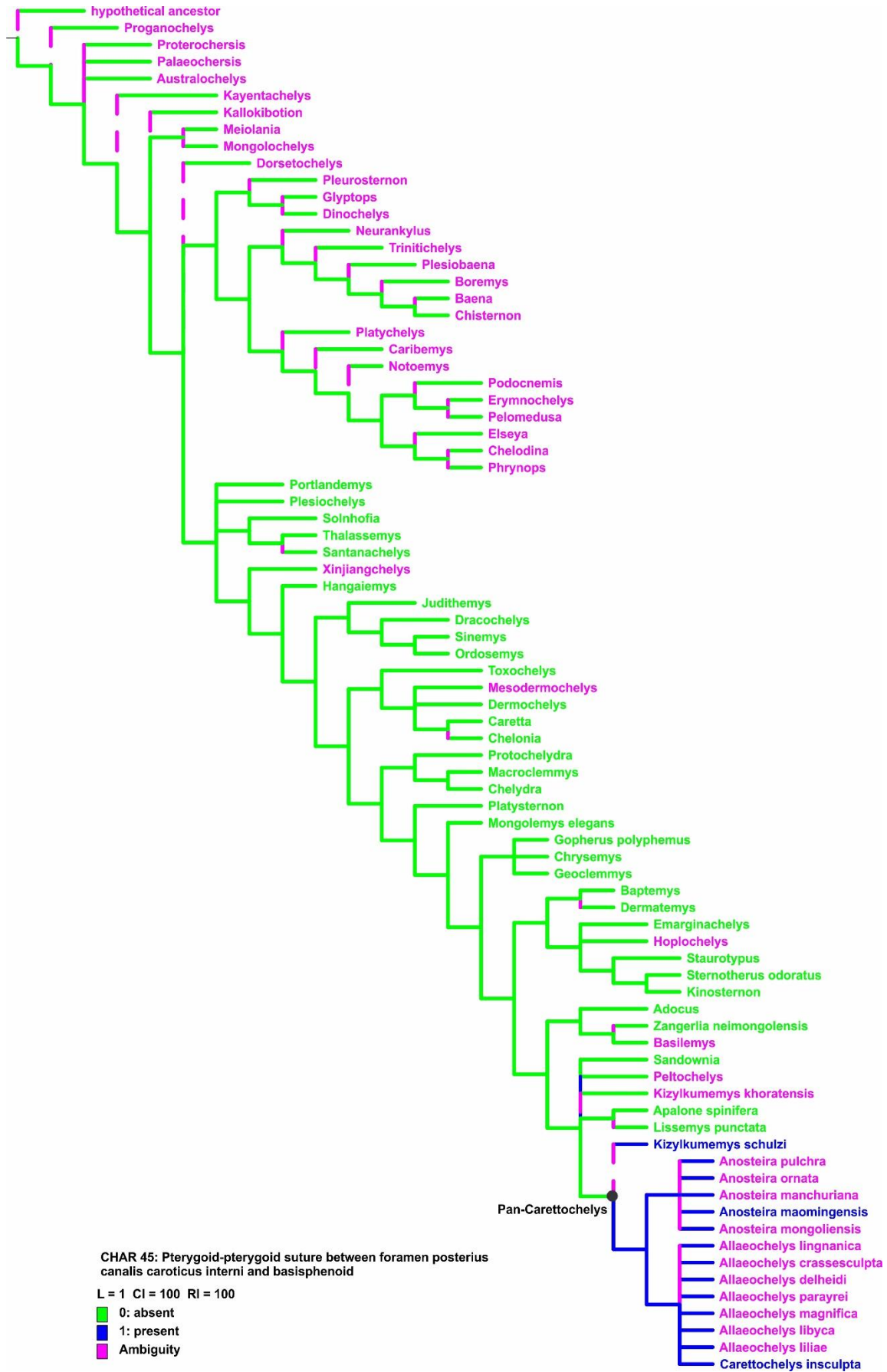


Figure S6. Unambiguous character 63 mapped in the Most Parsimonious Tree supporting the clade Pan-Carettochelys.

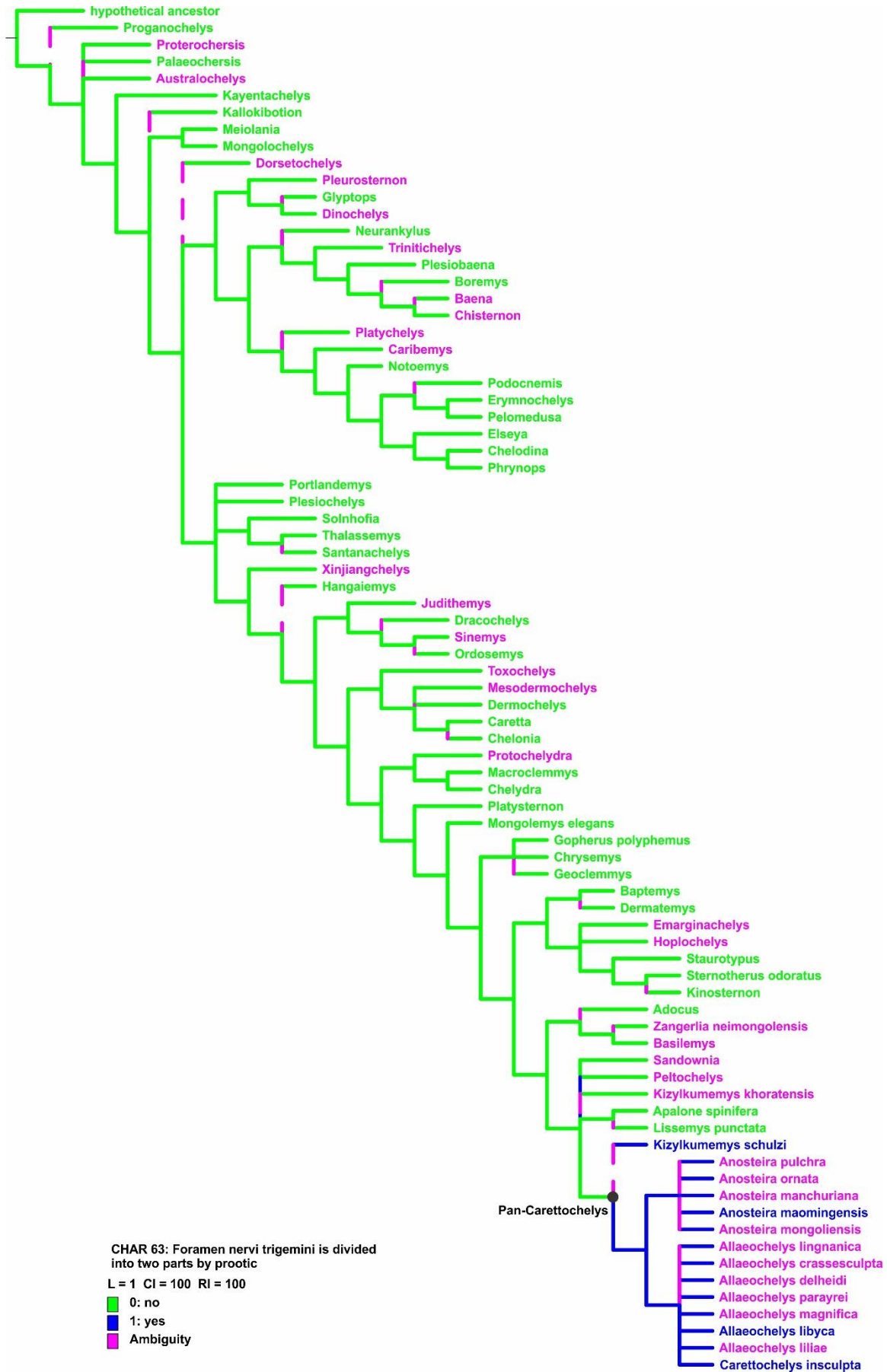


Figure S7. Unambiguous character 69 mapped in the Most Parsimonious Tree supporting the clade Pan-Carettochelys.

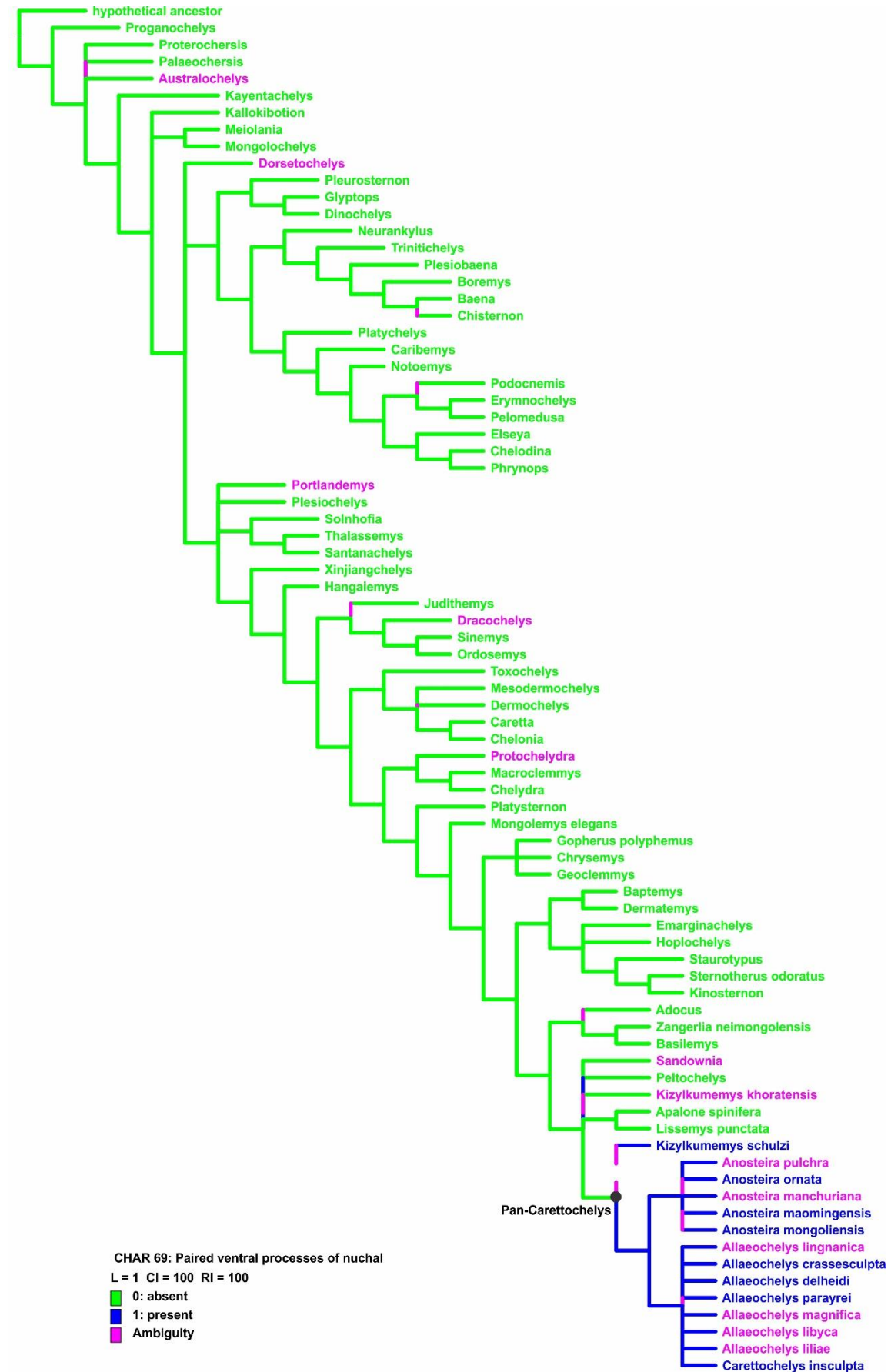


Figure S8. Unambiguous character 75 mapped in the Most Parsimonious Tree supporting the clade Pan-Carettochelys.

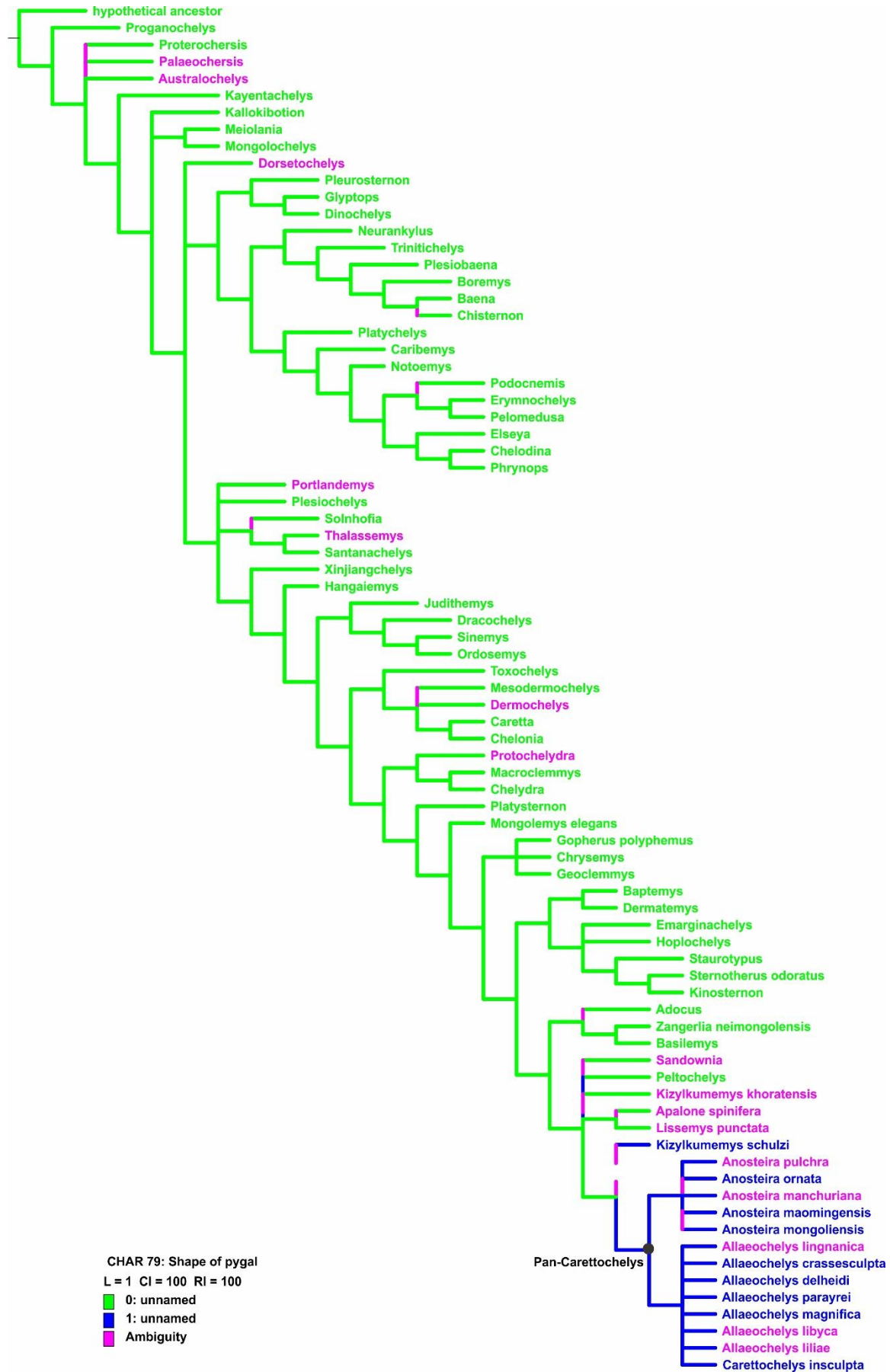


Figure S9. Unambiguous character 80 mapped in the Most Parsimonious Tree supporting the clade Pan-Carettochelys.

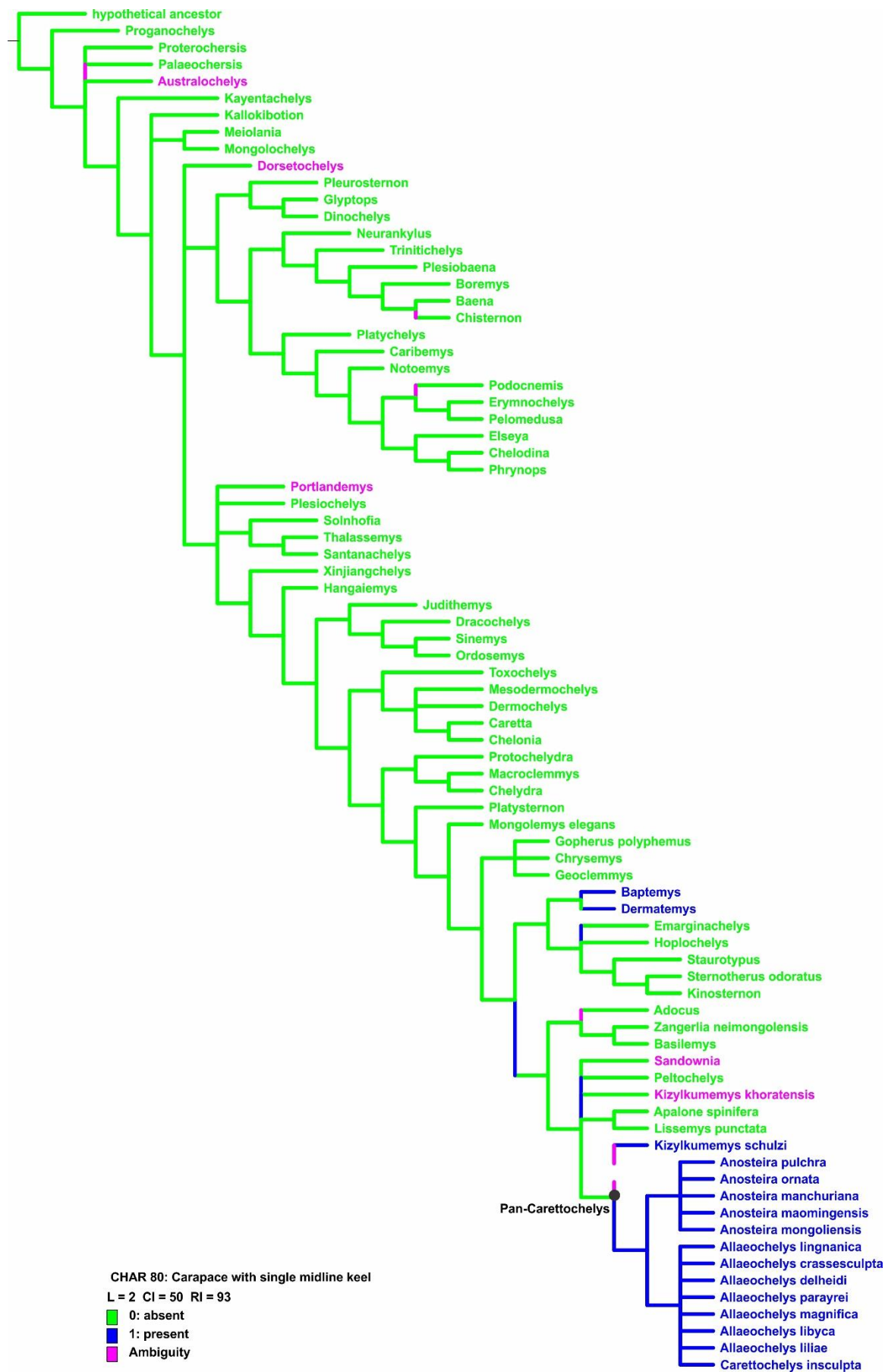


Figure S10. Unambiguous character 89 mapped in the Most Parsimonious Tree supporting the clade Pan-Carettochelys.

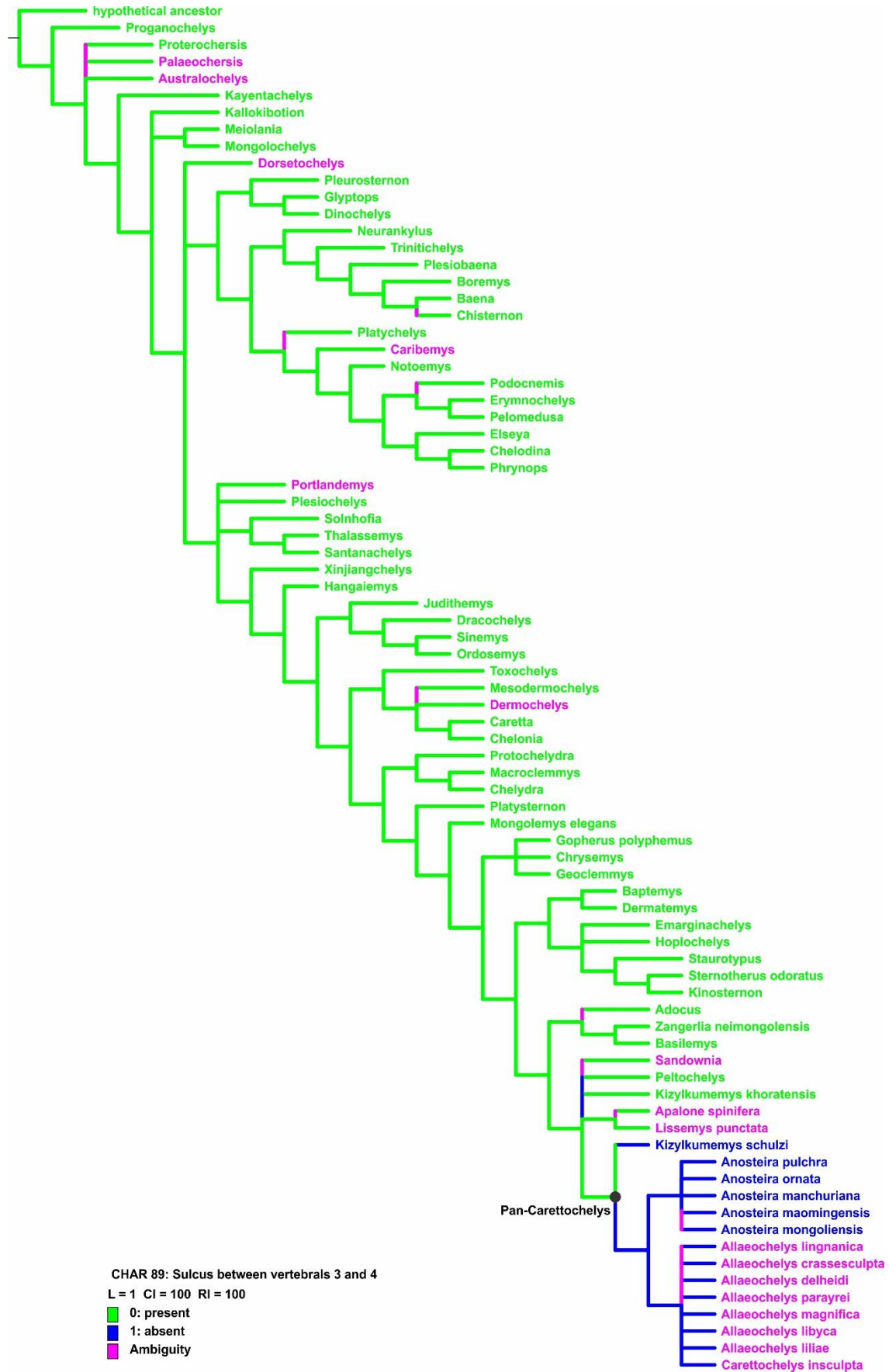


Figure S11. Unambiguous character 95 mapped in the Most Parsimonious Tree supporting the clade Pan-Carettochelys.

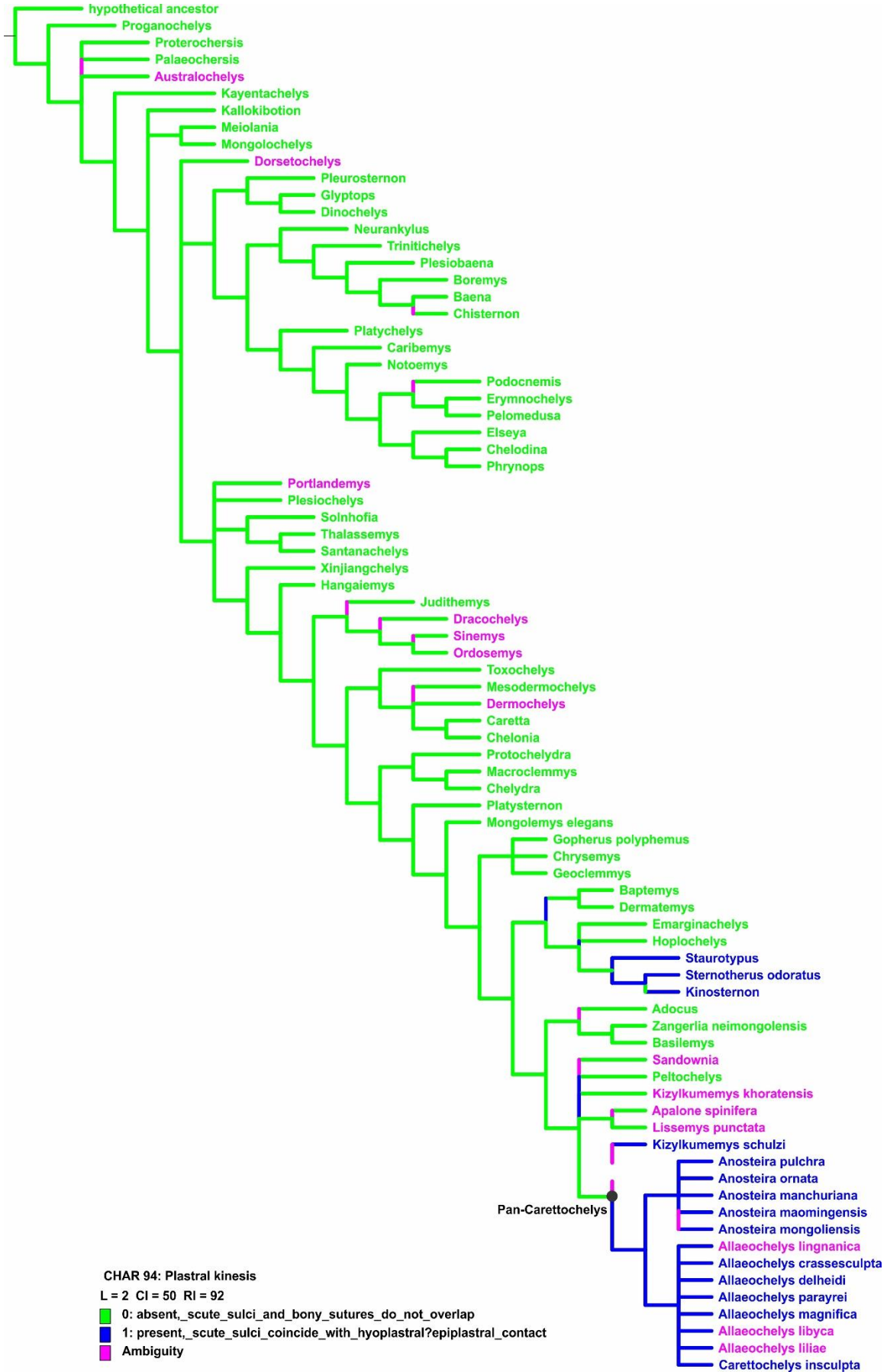


Figure S12. Unambiguous character 61 mapped in the Most Parsimonious Tree supporting the clade Carettochelyidae (Anosteirinae + Carettochelyinae).

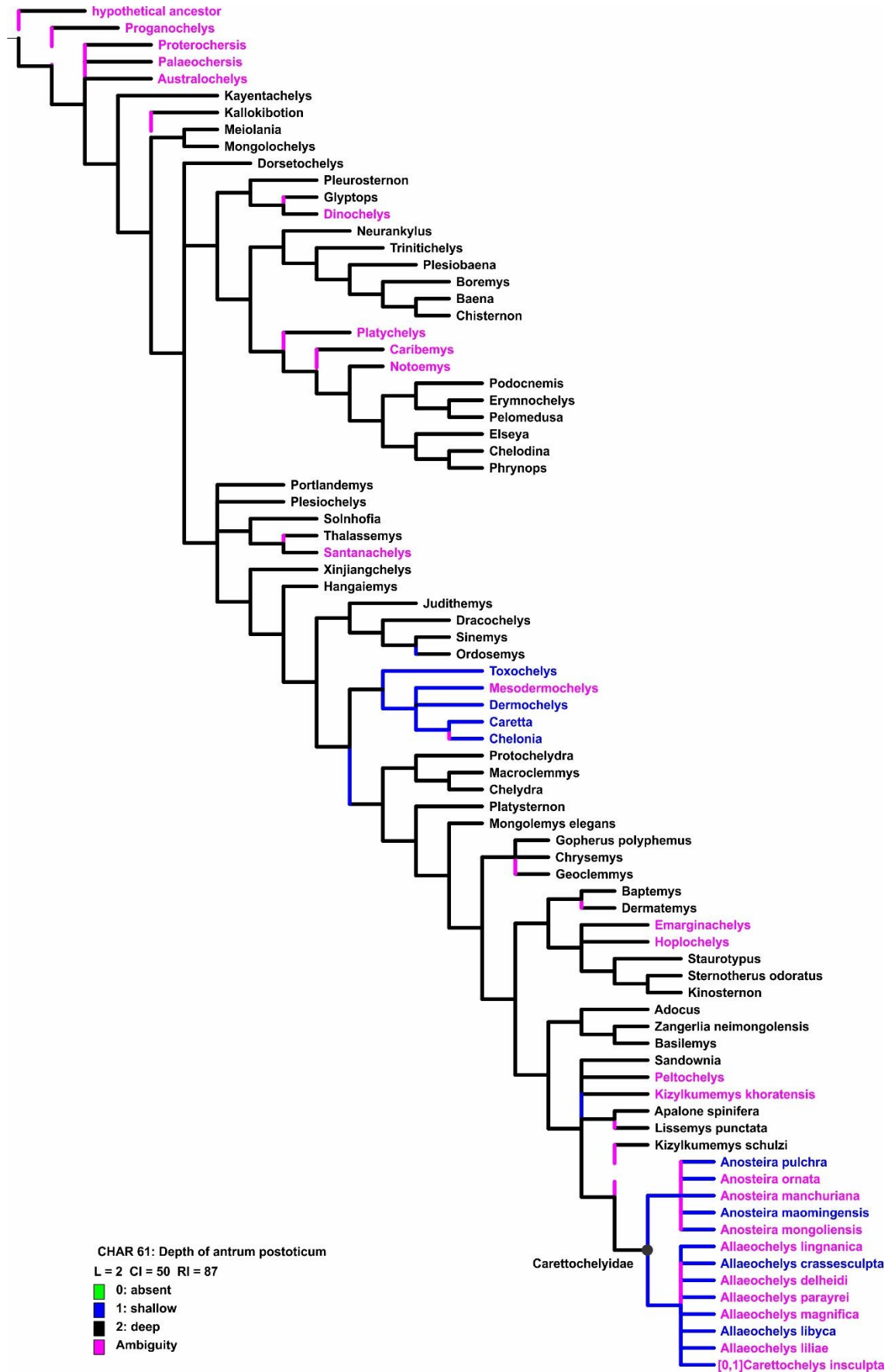


Figure S13. Unambiguous character 106 mapped in the Most Parsimonious Tree supporting the clade Carettochelyidae (Anosteirinae + Carettochelyinae).

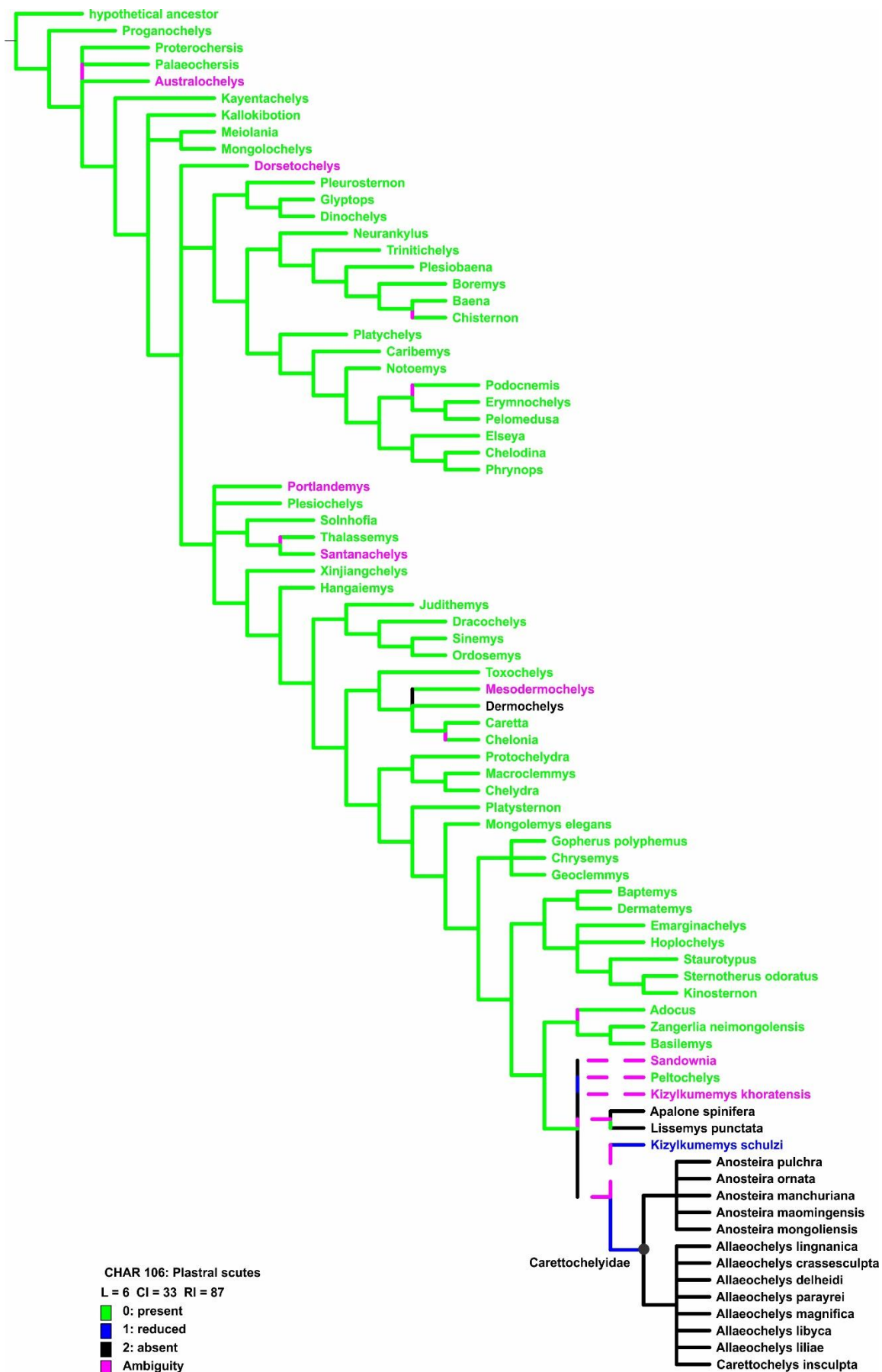


Figure S14. Unambiguous character 91 mapped in the Most Parsimonious Tree supporting the clade Anosteirinae (*Anosteira* spp.).

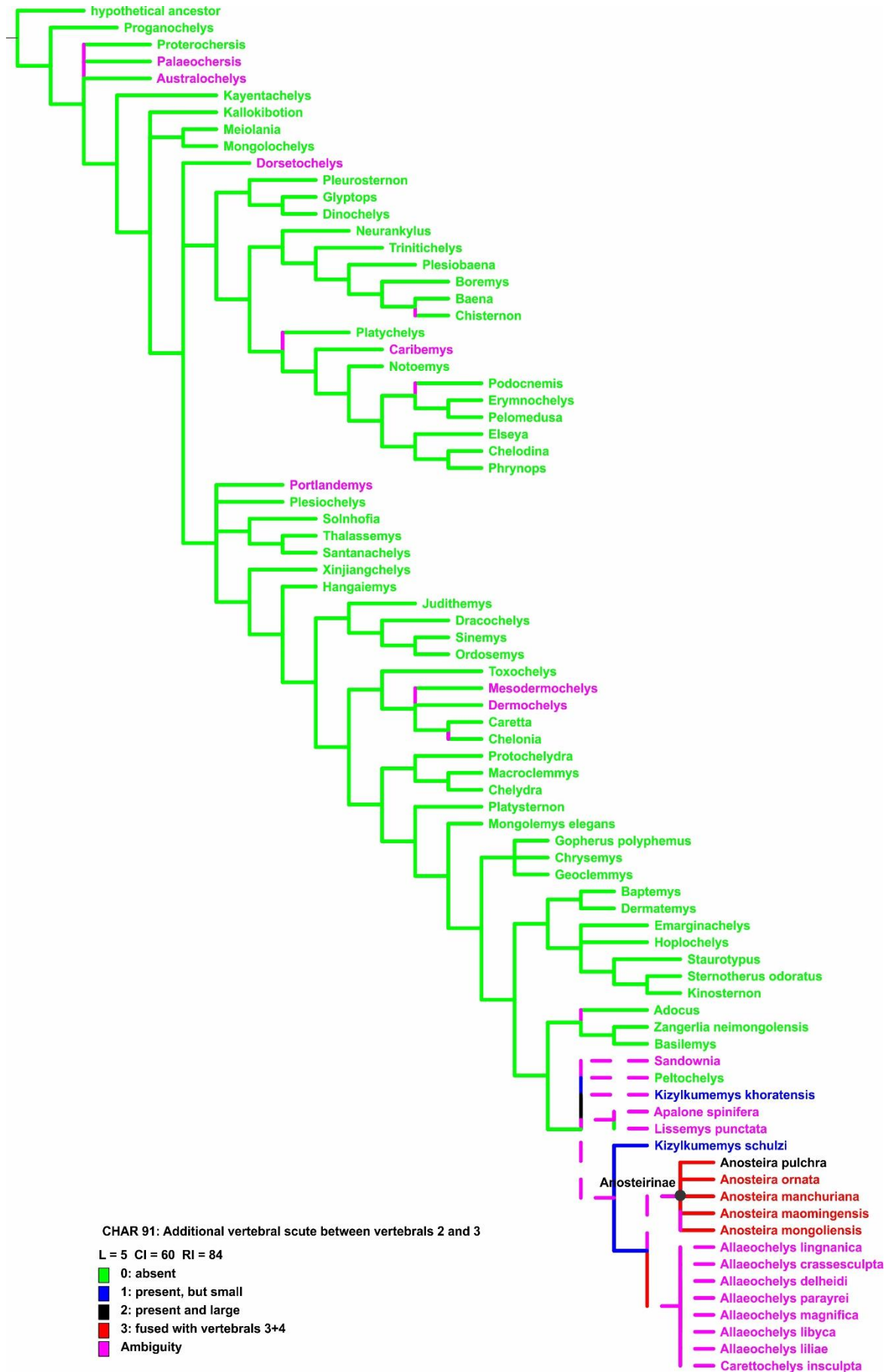


Figure S15. Unambiguous character 105 mapped in the Most Parsimonious Tree supporting the clade Anosteirinae (*Anosteira* spp.).

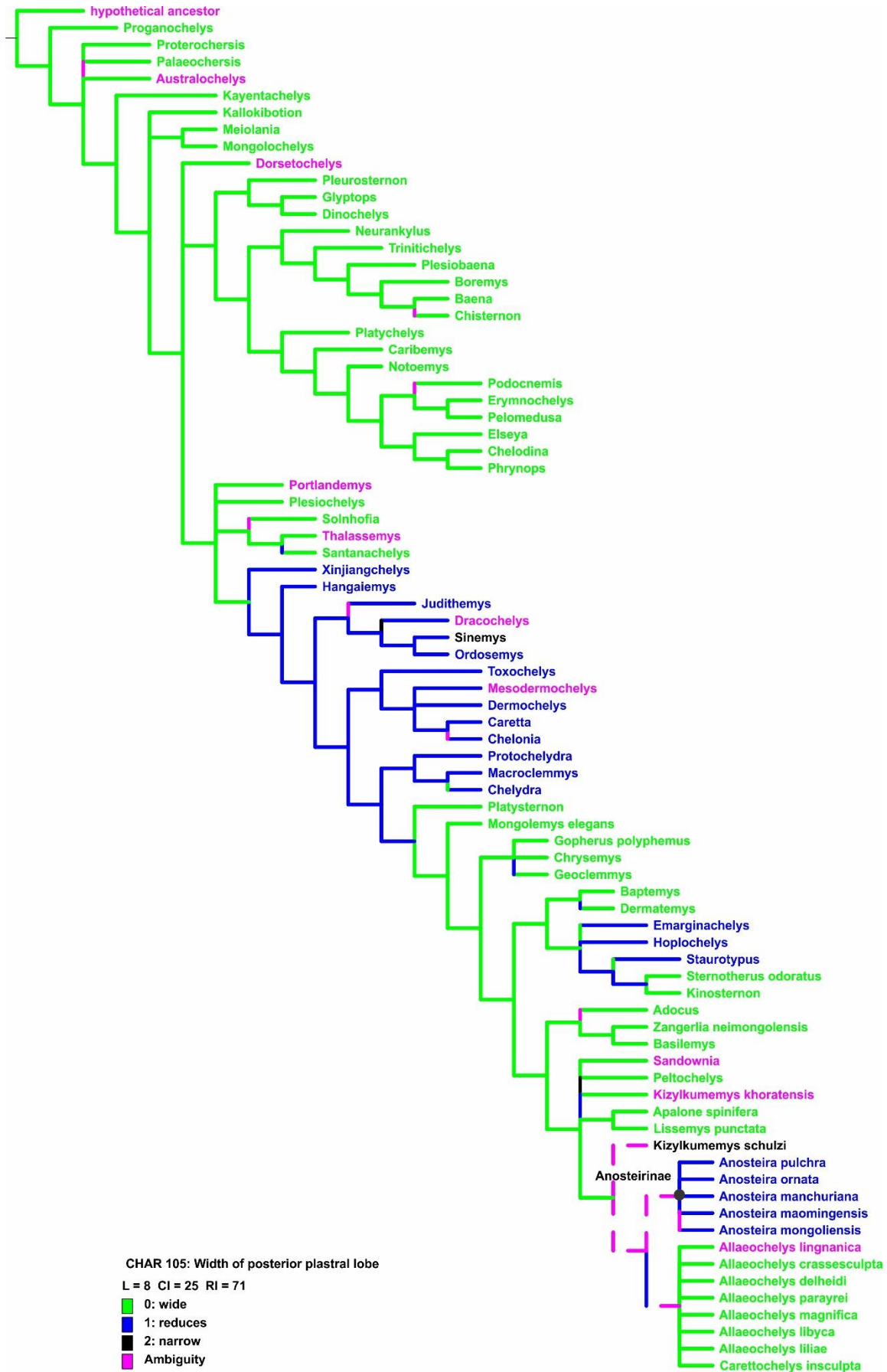


Figure S16. Unambiguous character 17 mapped in the Most Parsimonious Tree supporting the clade Carettochelyinae (*Allaeochelys* + *Carettochelys*).

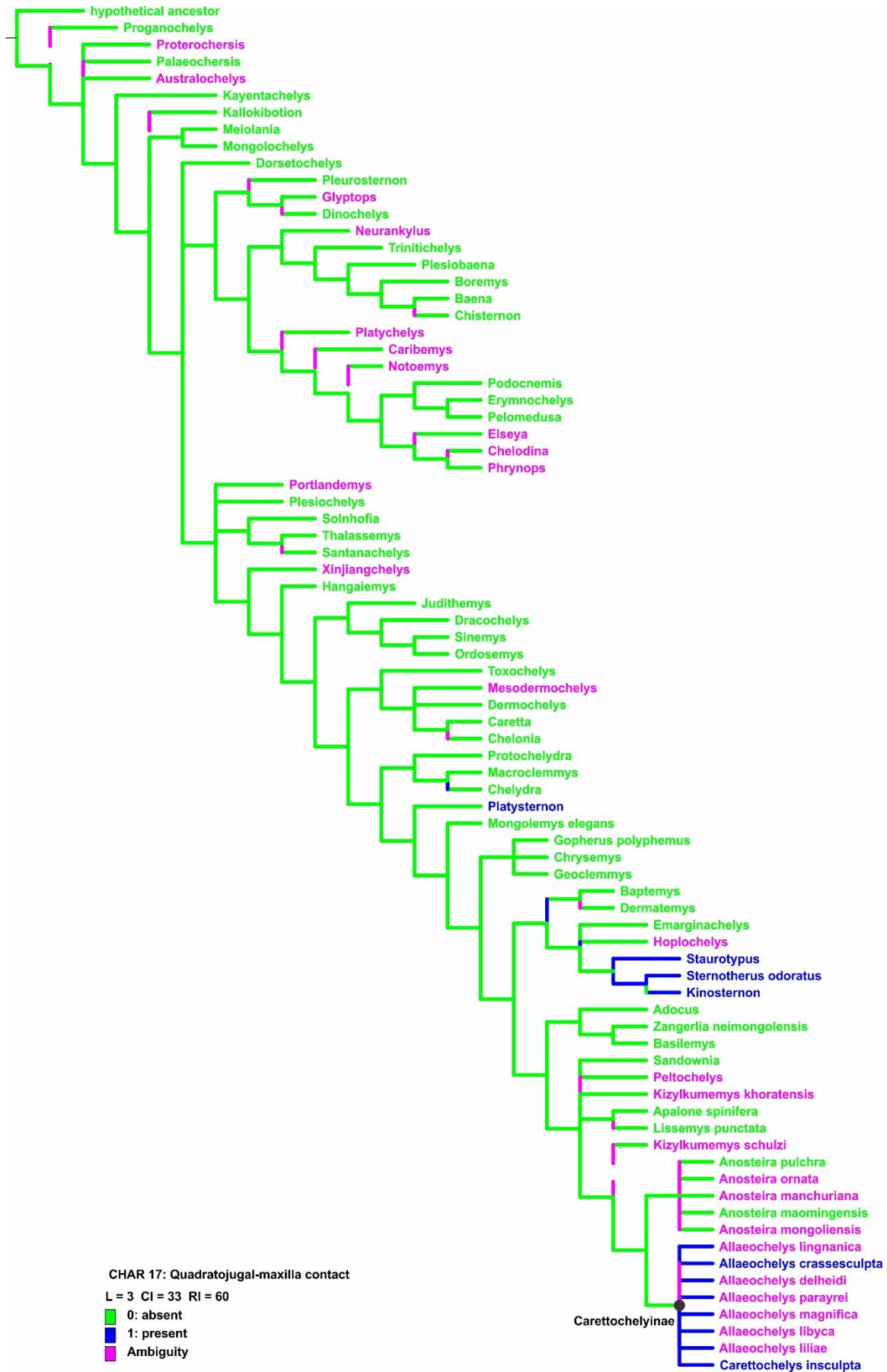


Figure S17. Unambiguous character 18 mapped in the Most Parsimonious Tree supporting the clade Carettochelyinae (*Allaeochelys* + *Carettochelys*).

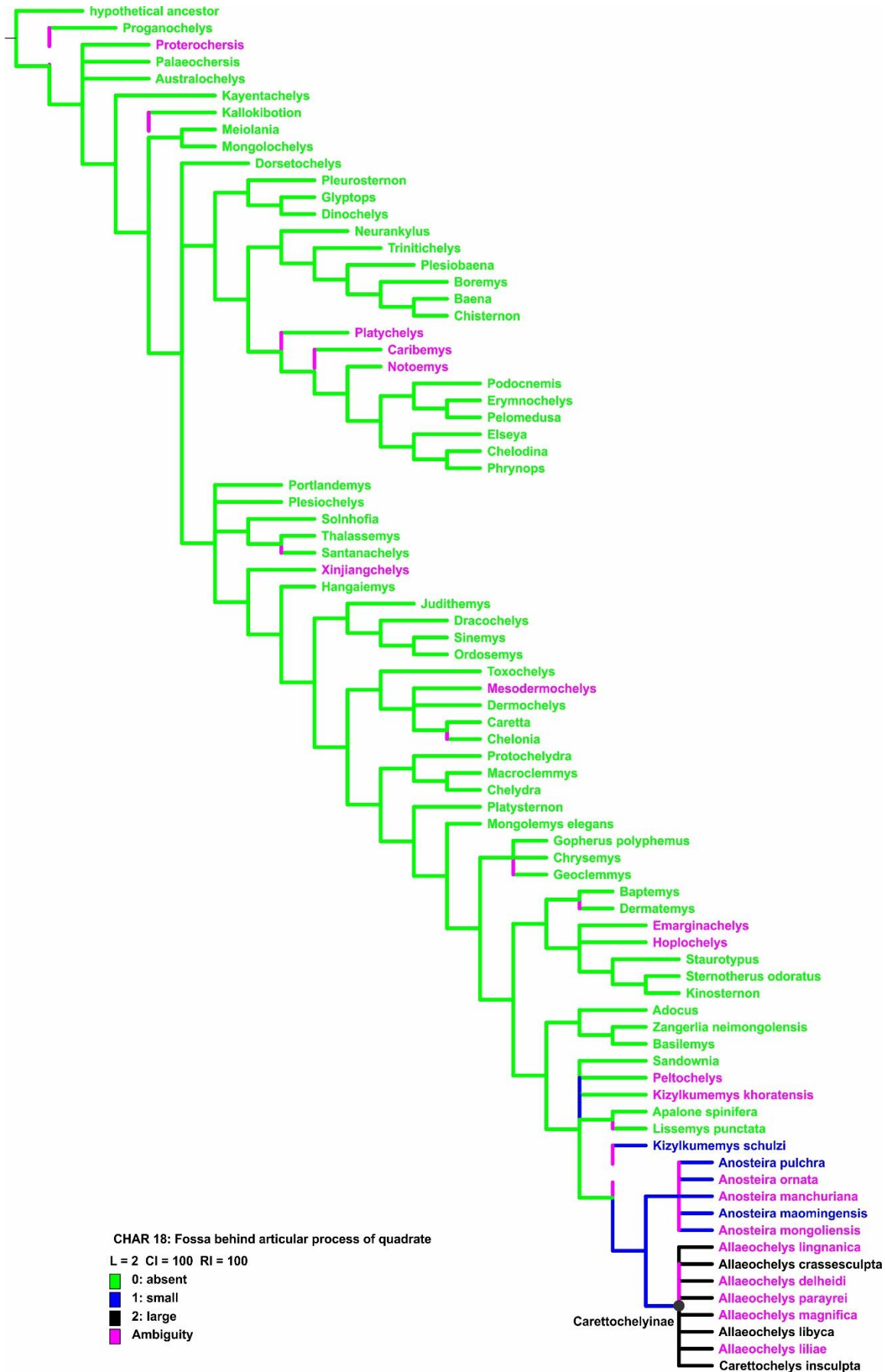


Figure S18. Unambiguous character 62 mapped in the Most Parsimonious Tree supporting the clade Carettochelyinae (*Allaeochelys* + *Carettochelys*).

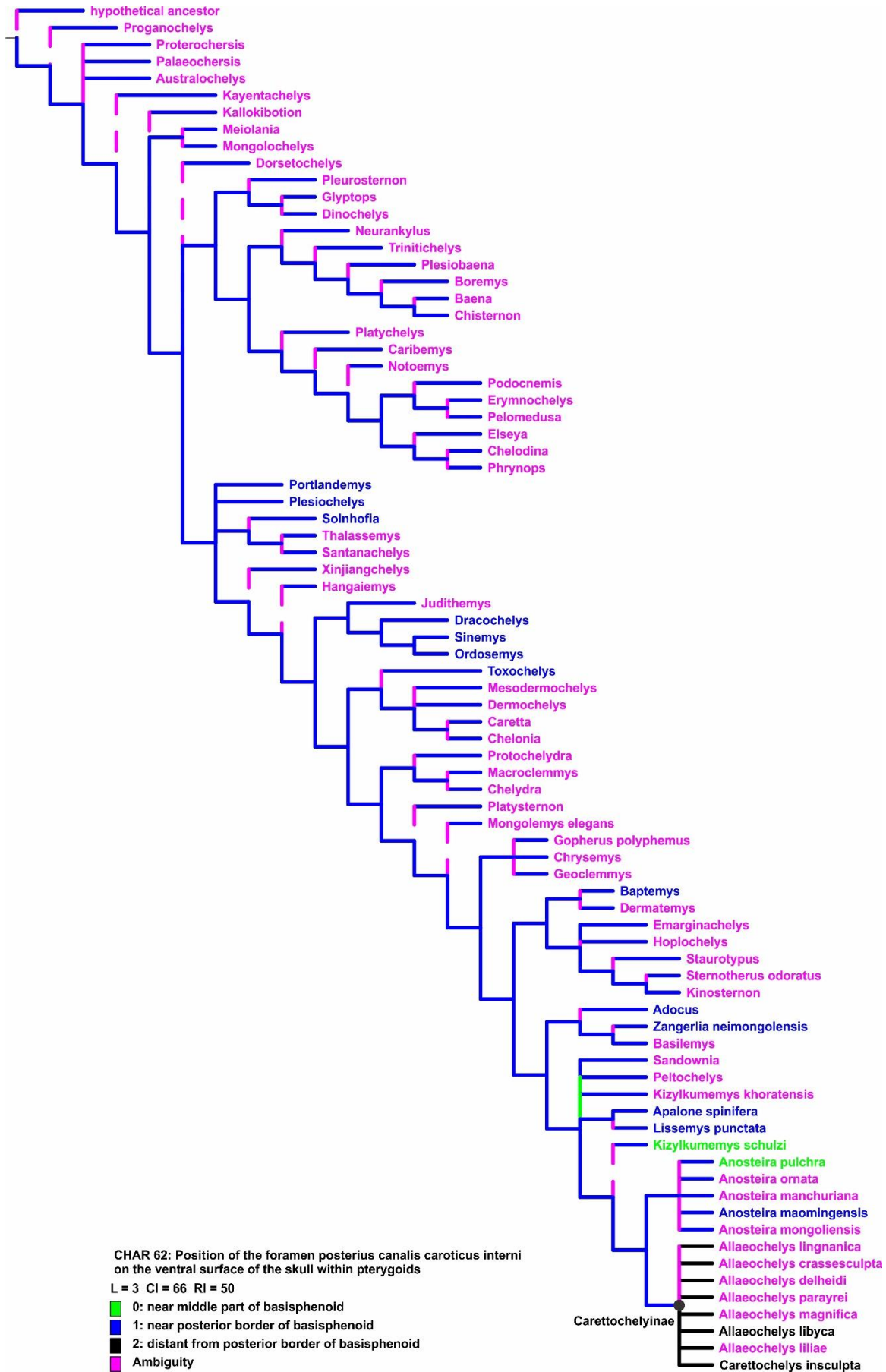
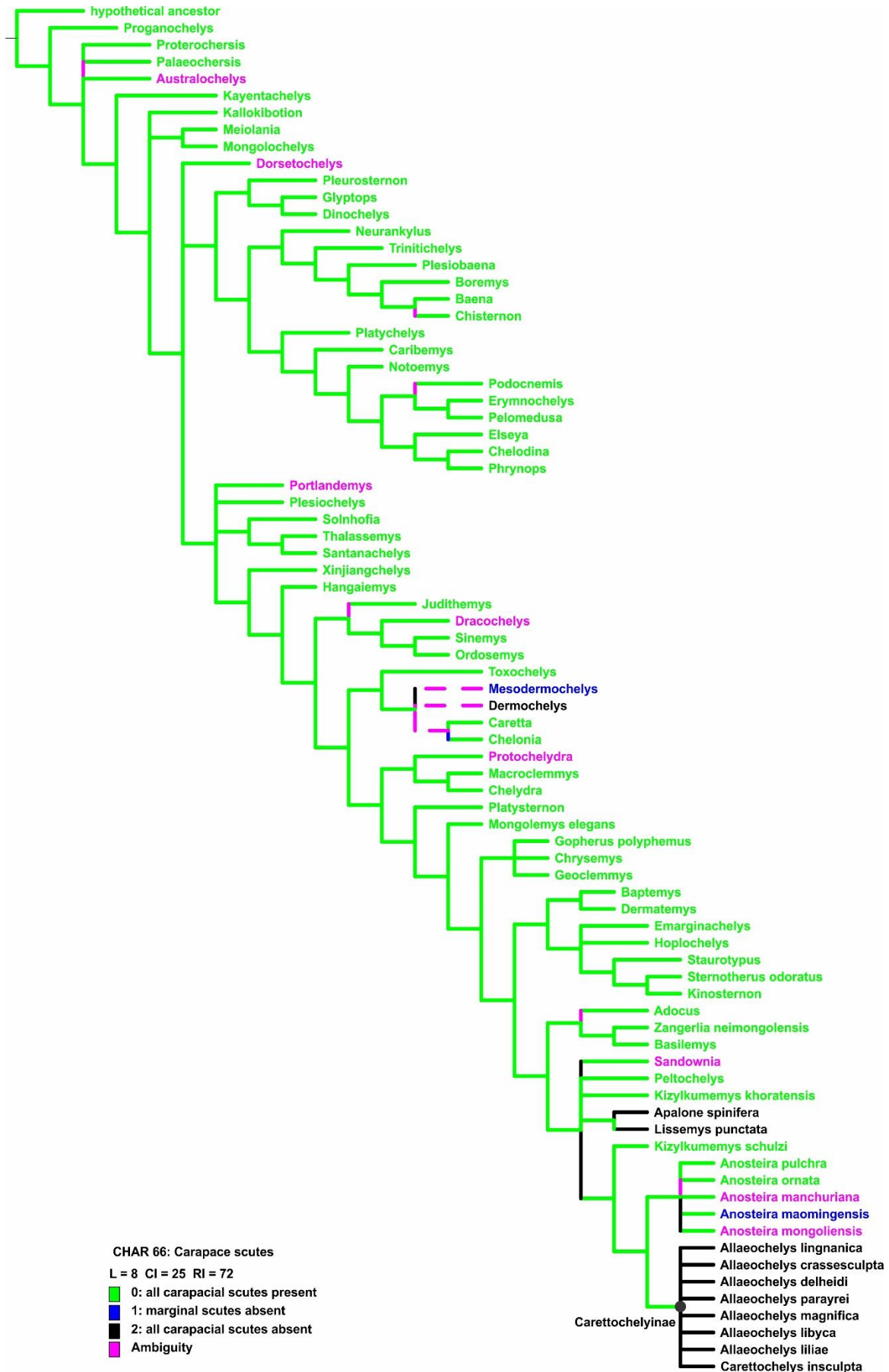


Figure S19. Unambiguous character 66 mapped in the Most Parsimonious Tree supporting the clade Carettochelyinae (*Allaeochelys* + *Carettochelys*).



References

- Danilov, I.G., Obraztsova, E.M., Chen, W., Jin, J., 2017. The cranial morphology of *Anosteira maomingensis* (Testudines, Pan-Carettochelys) and the evolution of pan-carettochelyid turtles. *Journal of Vertebrate Paleontology*, e1335735. DOI: 10.1080/02724634.2017.1335735.
- Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786. Doi: 10.1111/j.1096-0031.2008.00217.x
- Havlik, P.E., Joyce, W.G., Böhme, M., 2014. *Allaeochelys libyca*, a new Carettochelyine turtle from the Middle Miocene (Langhian) of Libya. *Bulletin of the Peabody Museum of Natural History*, 55(2), 201-2014.
- Joyce, W.G., 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History*, 47, 3–102.