A Review of the Fossil Record of Turtles
of the Clade *Pan-Carettochelys*

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Abstract

Turtles of the total clade *Pan-Carettochelys* have a relatively poor fossil record that extends from the Early Cretaceous. The clade is only found in Asia during the Cretaceous, but spreads to Europe and North America during the Eocene. Neogene finds are restricted to Europe, Africa and Australia, whereas the only surviving species, *Carettochelys insculpta*, lives in New Guinea and the Northern Territories of Australia. The ecology of fossil pan-carettochelyids appears similar to that of the extant *C. insculpta*, although more primitive representatives were likely less adapted to brackish water. Current phylogenies only recognize three internested clades: *Pan-Carettochelys*, *Carettochelyidae* and *Carettochelyinae*. A taxonomic review of the group concludes that of 25 named taxa, 13 are nomina valida, 7 are nomina invalida, 3 are nomina dubia, and 2 are nomina nuda.

Keywords

Phylogeny, biogeography, paleoecology, *Pan-Carettochelys, Carettochelyidae, Carettochelyinae*

Introduction

The name *Pan-Carettochelys* is defined as belonging to the most inclusive clade containing the extant turtle *Carettochelys insculpta* Ramsay, 1887, but no other species of extant turtle (Joyce, Parham and Gauthier 2004). The prefix "pan-" is herein used to connote that this clade is the total clade (sensu Jefferies 1979) of *C. insculpta* and I herein informally refer to the representatives of this clade as "pan-carettochelyids." Morphological and molecular synapomorphies generally place *Pan-Carettochelys* as sister to *Pan-Trionychidae* (i.e., the total clade of *Trionychidae*) to form the clade *Trionychia* (e.g., Hummel 1929; Meylan 1988; Shaffer et al. 1997; Joyce 2007), but a long list of morphological, ecological and behavioral features nevertheless distinguishes all currently known species from their closest relatives (Meylan 1988). Although the long list of apomorphic features makes it easy to identify extinct pan-carettochelyids as such, their fossil record is notably poor and little is known about the early evolution of the group.

Pan-Carettochelys is the only primary group of living turtles that was first known by its fossil rep-

resentatives. Noulet (1867) described a fossil taxon, *Allaeochelys parayrei,* from the Eocene of France, but his description was brief, was not accompanied by figures, and therefore received only little attention. Leidy (1871a, 1871b) soon after described another stem species, *Anosteira ornata*, from the Eocene of North America, but the fragmentary nature of his find, combined with the puzzling combination of characters it displayed, made it difficult for him to assess its phylogenetic relations. Leidy (1873) later described more complete material of this species and speculated that it was intermediate between *Pleurodira* and *Chelydridae*. Cope (1882, 1884), by contrast, felt that *An. ornata* is "intermediate" between *Plastomenidae*, *Chelydridae* and *Dermatemys mawii*, but ultimately placed it in *Chelydridae*. Dollo (1886) soon after figured and described another species, *Allaeochelys delheidi*, this time from the Eocene of Belgium, noted similarities with the American *An. ornata*, and followed Cope by placing these taxa in *Chelydridae*. In the same year, the Australian zoologist Ramsay (1887) described a new species of extant turtle, *Carettochelys insculpta*, from the lowland swamps of New Guinea, which he placed in *Trionychidae* because it lacks keratinous scutes. It is

unlikely that Ramsay (1887) had access to the relevant paleontological literature and he therefore missed obvious similarities with the previously described fossils. However, as soon as news of the strange new turtle from New Guinea arrived in Europe, Boulenger (1887) recognized these similarities and coined the name "Carettochelyididae" for the group. Boulenger (1887), furthermore, mistakenly placed his new family within *Pleurodira*, but biogeographic considerations apparently dominated that decision.

Early difficulties with placing *Pan-Carettochelys* in the phylogenetic system of turtles were based on misconceptions and missing data. Leidy (1871a, 1871b, 1873) erroneously reported *Anosteira ornata* as having 11 pairs of peripherals and lacking scutes. The cranial, vertebral and limb morphology remained unknown and it was unclear whether an entoplastron or mesoplastra was present. Baur (1889a) was later able to ascertain the presence of a reduced number of peripherals (10 pairs) and the presence of carapacial scutes for *An. ornata*, but the presence of an entoplastron and the absence of mesoplastra remained unclear until Hay (1906) described more completely preserved material. Many of these difficulties could have been averted had Noulet (1867) published figures of the beautifully preserved type material of *Allaeochelys parayrei* (e.g., Broin 1977). Similarly, Ramsay's (1887) preliminary description of *Carettochelys insculpta* mostly focused on external characteristics and did not include the osteology of the skull, neck or girdles. These deficiencies were only slowly addressed through a preliminary description of photographs by Baur (1891), the first description of the skull and neck by Waite (1905), and the more comprehensive anatomical description of Walther (1922).

The modern taxonomic consensus was first formulated by Baur (1891), who erroneously though that pan-carettochelyids still possess mesoplastra, but nevertheless reasoned correctly using characteristics from the cranium and shell that the clade is placed closest to *Trionychidae*. This hypothesis was consecutively supported by additional data collected by Waite (1905), Walther (1922), Harrassowitz (1922), Hummel (1929) and Meylan (1987, 1988).

For institutional abbreviations see Appendix 1. Named pan-carettochelyid genera are listed in Appendix 2.

Skeletal Morphology

Cranium

The cranial morphology of *Carettochelys insculpta* was described by Baur (1891), Waite (1905) and Walther (1922) and many additional anatomical details were provided by Gaffney (1979) and Meylan (1987). Fragmentary cranial material is known from *Kizylkumemys schultzi* from the Late Cretaceous of Uzbekistan and was figured by Nessov (1977a, 1977b, 1977c), but a detailed description of this material is still outstanding and many anatomical aspects remain uncertain. Gaffney (1979) provided the reconstruction of a skull from the Eocene of North America under the name *Pseudanosteira*, but this specimen is not accompanied by sufficient postcranial material to allow referral to any particular taxon. My own observations of this specimen revealed significant deviations from the idealized reconstruction published by Gaffney (1979), and I therefore await formal description of this specimen. The Eocene species *Allaeochelys crassesculpta* is known from more than 100 complete, though crushed, skeletons associated with skulls, but no significant description is available beyond the preliminary account of Harrassowitz (1922) based on lesser material. Several skulls are also known from Eocene localities in Spain (pers. obs.), but these too remain to be described in any detail. I agree with Lydekker (1889b, 1889c) that the isolated skull from the Eocene of England that had been figured by Owen (1849–1858) as a pleurodire likely represents a pan-carettochelyid, but this material also awaits more formal description. This summary is therefore based primarily on the cranial anatomy of extant *C. insculpta* and differences with extinct taxa are highlighted when apparent.

The skull of pan-carettochelyids has a broad interorbital region, deep upper temporal emarginations, but only very minor lower temporal emarginations (Figure 1). The prefrontals are large elements that contact one another along the midline and the vomer and palatine within the orbit. The frontals are square elements that contribute to the orbital margin. A foramen orbitonasale is not developed. The parietals are large, partially roof the upper temporal fossae, and form well-developed descending processes that contact the pterygoids and the ascending processes of the palatines ventrally, but lack contacts with the
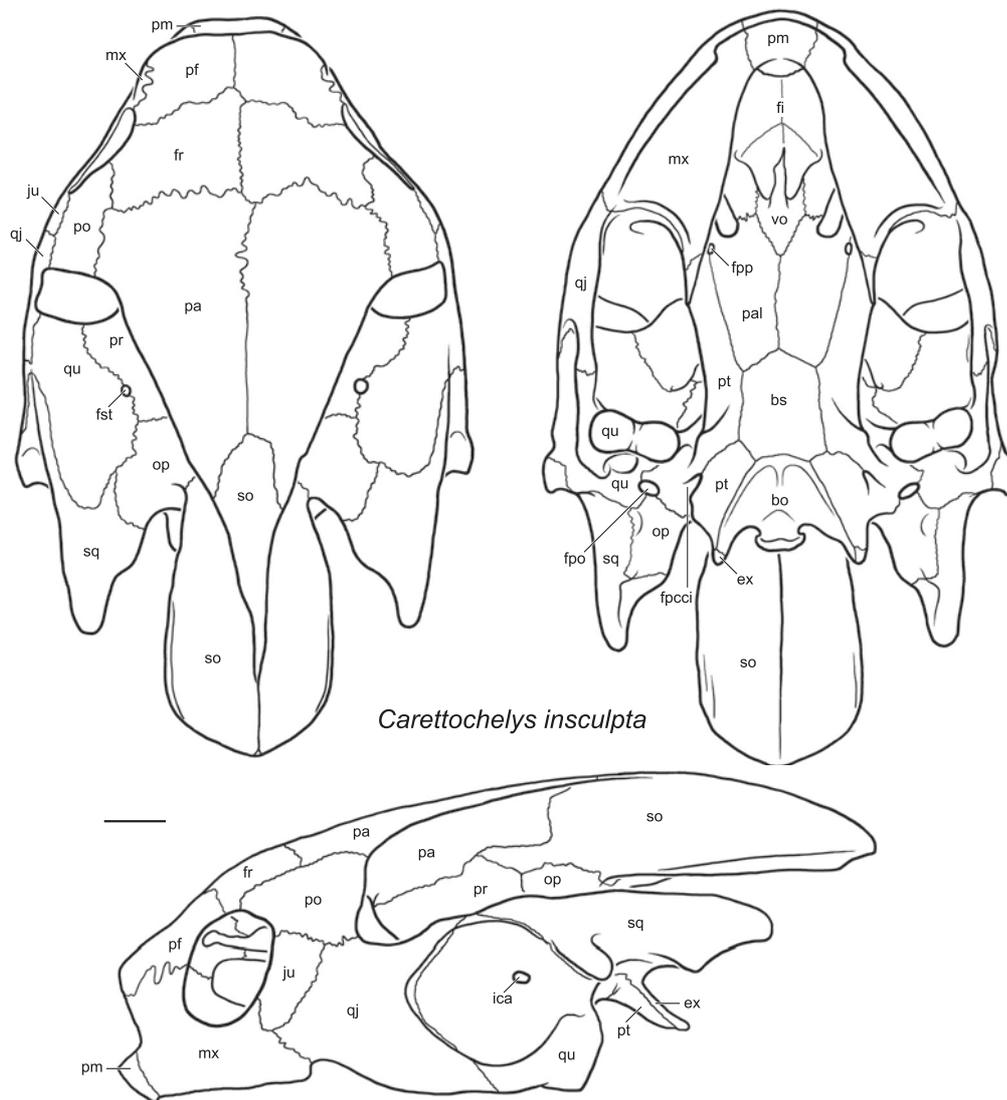
Figure 1. Cranial morphology of *Pan-Carettochelys* as exemplified by *Carettochelys insculpta* (SMF 56626). *Abbreviations*: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fi, fenestra intermaxillaris; fpcci, foramen posterius canalis carotici interni; fpo, fenestra postoticum; fpp, foramen palatinum posterius; fr, frontal; fst, foramen stapedio-temporale; ica, incisura columella auris; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postotic; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. Scale bar approximates 1 cm.

jugals, quadratojugals or squamosals. The postorbitals are small elements that contribute to the margins of the orbits and upper temporal emarginations.

The premaxillae are small and medially fused with one another (Figure 1). The maxilla is short, but high, has a posterior contact with the quadratojugal, but only forms a labial ridge. The jugal is notably small, contributes to the orbit, but not to the upper or lower temporal emarginations. The quadratojugal is a relatively large element that contacts the maxilla anteriorly and frames the anterior margin of the cavum tympani. The squamosal is reduced in size, shows no anterior contacts with the jugal, postorbital or parietal, and forms a long posterior process.

The palate is characterized by a large foramen intermaxillaris (sensu Meylan 1987) that is framed by the premaxillae, maxillae and the descending branches of the prefrontals (Figure 1). The triturating surface consists of a low labial ridge and a flat crushing surface. The vomer is a short element that lacks anterior contacts with the maxilla or premaxilla or a posterior contact with the basisphenoid. The palatines are broad elements that contact one another medially, and the basisphenoid posteriorly, and that contribute to the anterior margins of the lateral walls of the braincase. The foramen palatinum posterius (suborbital foramen) is small and framed by the palatine and the pterygoid. The pterygoids are unusually elongate elements that contact the maxillae and palatines anteriorly, broadly floor the otic areas, reach the posterior margins of the skull, but do not contact one another along the midline. A deep trough within each pterygoid is defined medially by a thin, wing-like lamina of bone that is confluent with the attachment site of the pterygoid musculature. The basisphenoid is a stout element that ranges from a rounded rectangle to the shape of an arrow. The foramen posterius canalis carotici interni is situated at the back of the skull and is formed by the pterygoids only. The basioccipital is a broad element that forms elongate tubercles together with the pterygoids. The fenestra postotica is broadly separated from the posterior jugular foramen.

The quadrate forms the large and subcircular cavum tympani (Figure 1). The antrum postoticum is greatly reduced in early representatives of the group, but completely absent in *Carettochelys insculpta*. The incisura columella auris is fully enclosed by the quadrate. The posterior side of the processus articularis has a cavity, which is relatively small in primitive representatives, but can be very deep in more derived taxa. The parietal and prootic form a shoulder that pushes the temporal musculature laterally, but the actual trochlear surface is formed by the prootic and quadrate. A descending process of the prootic splits the trigeminal foramen into two discrete foramina. The quadrate forms the posterior rim, the epipterygoid the ventral rim, and the parietal the anterior rim of the trigeminal foramen. The basioccipital and exoccipitals together form the occipital condyle, which is fused in adult individuals. The exoccipitals enclose one or two pairs of hypoglossal foramina. The supraoccipital produces an elongate supraoccipital crest with extremely broad shelves that give the crest a T-shaped cross section.

The mandible has a broad, fused symphysis and a single labial ridge. Splenials are absent. The coronoid process is high and retroarticular processes are well developed. The foramen nervi auriculotemporalis is relatively small, but the foramen dentofaciale majus is notably large.

Shell
Most valid fossil taxa recognized herein are known from well-preserved shell material and the evolution of the *Pan-Carettochelys* shell is therefore well understood. The most important descriptions of shells were provided by Hay (1906; *Anosteira ornata*; Figure 2B), Harrassowitz (1922; *Allaeochelys crassesculpta*), Clarke (1932; *Anosteira pulchra*), Zangerl (1947; *Anosteira manchuriana*), Broin (1977; *Allaeochelys parayrei*), Nessov (1977a, 1977b; *Kizylkumemys schultzi*, Figure 2A), Tong et al. (2005; *Kizylkumemys khoratensis*), and Tong et al. (2010; *Anosteira maomingensis*). The morphology of the shell of *Carettochelys insculpta* (Figure 2C) is summarized in Ramsay (1887), Waite (1905) and Walther (1922).

The shell of all pan-carettochelyids has a tectiform shape and a pronounced midline keel that is particularly distinct in the posterior half of the carapace (Figure 2). A fin-like midline process furthermore adorns the midline in *Kizylkumemys schultzi*. The surface is typically ornamented with a diagnostic surface texture, which ranges among taxa from distinct need-like protrusions to vermiculate ridges. The carapace of all pan-carettochelyids consists of the nuchal (= cleithrum; Lyson et al. 2013), eight pairs of costals, ten pairs of peripherals, a single triangular suprapygal, and the pygal. All fossil species seem to have an uninterrupted series of seven neurals, whereas *Carettochelys insculpta* often displays an interrupted series, or less than seven neurals. A preneural is present in some individuals of *C. insculpta* and *Allaeochelys parayrei*. The nuchal is universally known to have a pair of processes that seem to be related to the neck retraction mechanism. The bridge includes peripherals IV to VII and the bridge peripherals are C- to V-shaped in cross section. The posterior peripherals and the pygal form a lip on their visceral sides that is useful in
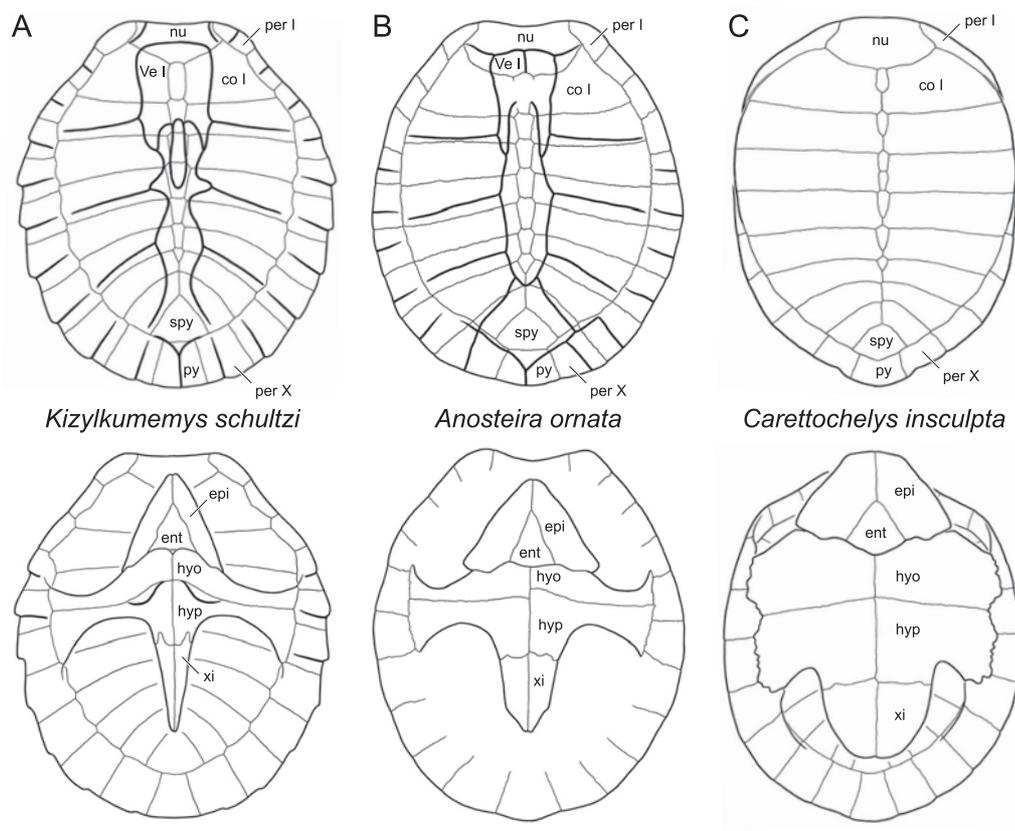
FIGURE 2. Shell morphology of *Pan-Carettochelys* as exemplified by three species. **A,** *Kizylkumemys schultzi* (redrawn from Nessov 1977b). **B,** *Anosteira ornata* (redrawn from Hay 1906). **C,** *Carettochelys insculpta* (CRI 14). *Abbreviations*: co, costal; ent, entoplastron; epi, epiplastron; hyo, hyoplastron; hyp, hypoplastron; nu, nuchal; per, peripheral; py, pygal; spy, suprapygal; Ve, vertebral scute; xi, xiphiplastron. Scale bars approximate 5 cm.

diagnosing these elements in isolation. There is a clear evolutionary trend toward the reduction of carapacial scutes within *Pan-Carettochelys*. Whereas species of *Kizylkumemys* still have vertebrals, pleurals, marginals and a cervical, representatives of *Anosteira* variously lack marginals and pleurals. The adult shell of *Allaeochelys* and *C. insculpta* completely lacks carapacial scutes.

The plastron of pan-carettochelyids consists of a pair of elongate epiplastra (= clavicles), a large and triangular entoplastron (= interclavicle), and a pair of hyoplastra, hypoplastra and xiphiplastra (see Figure 2). All taxa have an anterior plastral hinge with limited mobility between the entoplastron–epiplastron and the hyoplastron. Only the species of *Kizylkumemys* are known to have plastral scutes, whereas all other taxa lack these elements. There is a clear evolu-

tionary trend within *Pan-Carettochelys* in regards to the relative size of the plastron: whereas *Kizylkumemys* species have a highly reduced, cruciform plastron with a narrow bridge, the plastron and bridge is significantly larger in *Anosteira* species, and fully formed in *Allaeochelys* species and *Carettochelys insculpta*.

Postcranium

The cervical region of *Carettochelys insculpta* was described by Waite (1905), Walther (1922) and Williams (1950), but the remaining postcranial anatomy was only described briefly by Walther (1922). Among fossil species, the postcranial anatomy is only known from the many dozens of complete skeletons of *Allaeochelys crassesculpta* (Harrassowitz 1922), but most aspects remain poorly described. My own observations of some

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Al. crassesculpta specimens nevertheless reveals that *C. insculpta* and *Al. crassesculpta* have a similar postcranial morphology.

The cervical column consists of eight vertebrae. The first seven cervicals are opisthocoelous, but the eighth is biconvex. The caudal vertebrae are procoelous and lack chevrons. The tails are significantly longer in males than in females (Joyce et al. 2012). The coracoids form elongate but only moderately expanded blades. The glenoid lacks a distinct neck. The ilium shows a recurved neck and a moderately expanded dorsal process. The pubes have an expanded midline contact, but the thyroid fenestrae are confluent. The forelimbs are developed into extremely elongate, flexible flippers. The medial process of the humerus is well developed and protrudes proximally relative to the humeral head. The lateral process is indistinct and partially displaced distally along the shaft of the humerus. The ectepicondylar foramen is closed. The metacarpus consists of two block-shaped proximal carpals, an enlarged pisiform, and five rounded distal tarsals. The digital formula is 2-3-3-3-3 (Delfino et al. 2010). The articular surfaces between the metacarpals and phalanges of the first digit are poorly developed and the elements often fuse into blocks. The first two digits are also the only ones with claws. The hind limbs are also developed into flexible flippers, but the digits are not as extremely elongated as those of the forelimb. Only the first two digits have claws. The pedal formula is 2-3-3-3-3.

Phylogenetic Relationships

The early history of *Pan-Carettochelys* is still shrouded in mystery, because no taxa are currently known that fill the substantial morphological gap between the total-group of *Carettochelys insculpta* and the total-group of *Trionychidae*. Several extinct species have nevertheless been proposed as possible basal representatives of *Pan-Carettochelys*. Bräm (1973) suggested that a fragmentary fossil from the Late Jurassic of Portugal may represent such a species, but I agree with Lapparent de Broin and Murelaga (1999) that the surface sculpturing of this turtle is more consistent with that of a pleurosternid.

Sinaspideretes wimani Young and Chow (1953) from the Late Jurassic or Early Cretaceous of Sichuan Province, China, was originally described as a trionychid, but Meylan and Gaffney (1992) showed that this taxon is not a trionychid, while speculating that it may be a pan-carettochelyid on the basis of its characteristic surface sculpturing. A more recent reinvestigation of this specimen by Tong et al. (2013), however, has since shown that *S. wimani* is likely synonymous with *Yehguia tatsuensis* (Ye, 1963) and that *S. wimani* is therefore more parsimoniously interpreted as an adocusian or pan-trionychian. Although molecular phylogenies calibrated using fossils indicate that *Pan-Carettochelys* must have originated in the Middle to Late Jurassic (e.g., Joyce et al. 2013), not a single Jurassic representative is currently known.

Nessov (1976) was the first to present a phylogenetic hypothesis for *Pan-Carettochelys*. Using traditional taxonomic arguments he recognized two primary groups: *Anosteirinae* (consisting of *Kizylkumemys* spp. and *Anosteira* spp.) and *Carettochelyinae* (consisting of *Allaeochelys* spp. and *Carettochelys insculpta*). Using cladistics arguments, Meylan (1988) later corroborated this arrangement. However, the justified use of adocid and trionychid turtles as the outgroups led to the unfortunate conclusion that the broad plastron seen in the extant *C. insculpta* is a plesiomorphy and that the extremely narrow plastron of the Cretaceous *Kizylkumemys schultzi* is derived. The stratigraphic order in which these taxa appear, however, seems to contradict this arrangement, because there is a clear temporal trend within the evolution of *Pan-Carettochelys* from a narrow to an expanded plastron. It is unfortunate that no better outgroups have been found since the analysis of Meylan (1988), although several basal eucryptodiran turtles with narrow plastra are now known from the Cretaceous of Asia, particularly sinemydid taxa such as *Sinemys* spp. (Brinkman and Peng 1993; Tong and Brinkman 2013), which show that plastra evolution was highly dynamic during the Early Cretaceous.

The analysis of Havlik et al. (in review) addressed the outgroup problem by integrating all primary pan-carettochelyid taxa into a global phylogeny (Figure 3). The resulting phylogeny is highly consistent with the stratigraphic record (Figure 4). Only three well-supported clades, however, can be recognized within *Pan-Carettochelys*: the *Kizylkumemys*-node (currently the same composition as *Pan-Carettochelys*), the *Anosteira*-node (= *Carettochelyidae*) and the *Allaeo-*
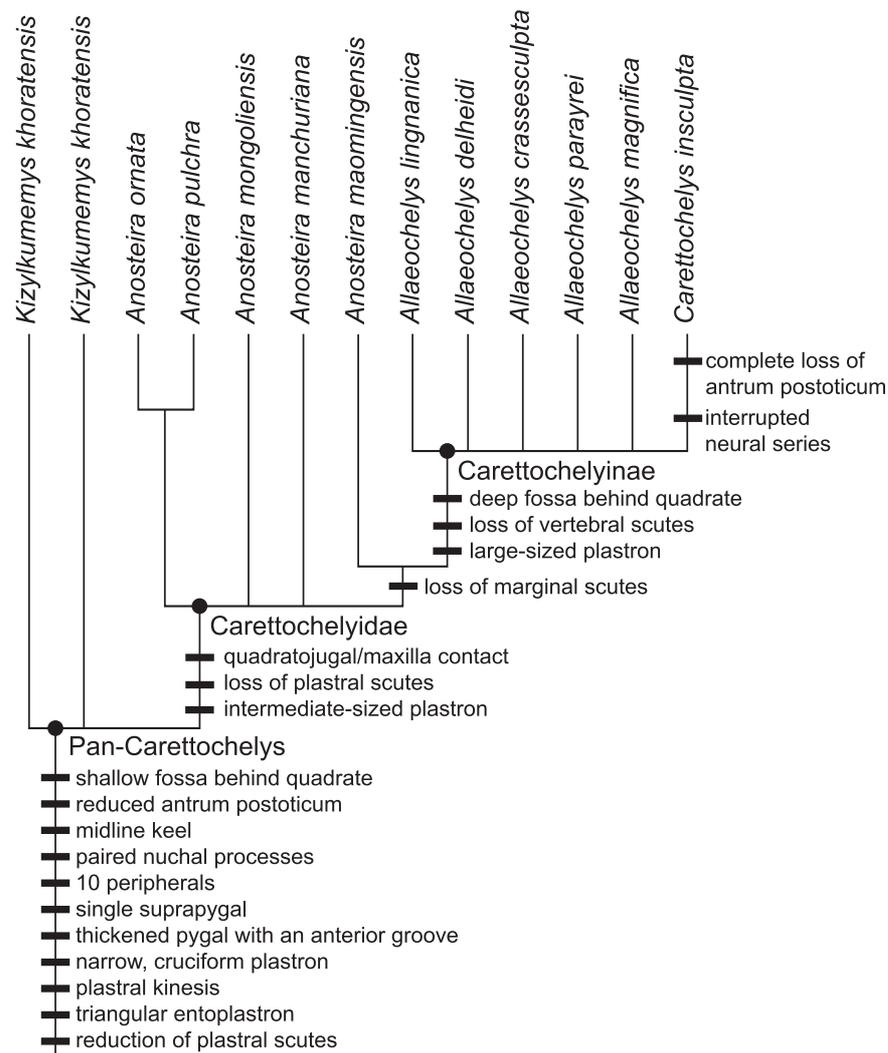
FIGURE 3. A phylogenetic hypothesis of valid pan-carettochelyid taxa with diagnostic characters for the most important clades (Havlik et al. in review).

chelys-node (= *Carettochelyinae*). The diagnostic characteristics of these clades are discussed in the Systematic Paleontology section.

Paleoecology

Not much is known about the paleoecology of fossil pan-carettochelyids, because most of the remains are highly fragmentary. The sole exception to this rule is *Allaeochelys crassesculpta* from the Early Eocene of Germany, which is known from more than 100, often near-complete skeletons (Harrassowitz 1922; Joyce et al. 2012). The limbs of this taxon broadly resemble those of the

extant *Carettochelys insculpta* and it is therefore reasonable to infer that this taxon also swam by symmetrically rowing with its forelimbs (Harrassowitz 1922). The skull of *Al. crassesculpta* also broadly agrees in its morphology with that of *C. insculpta* and is therefore consistent with a generalist feeding strategy.

Allaeochelys crassesculpta is unique, because it is the only known fossil vertebrate to have been fossilized in the act of mating (Joyce et al. 2012). Joyce et al. (2012) reported nine such pairs, but I have since identified two more in the literature (Harrassowitz 1922; Groessens-Van Dyck 1978) leading to a total of at least 11 mating pairs. The primary char-
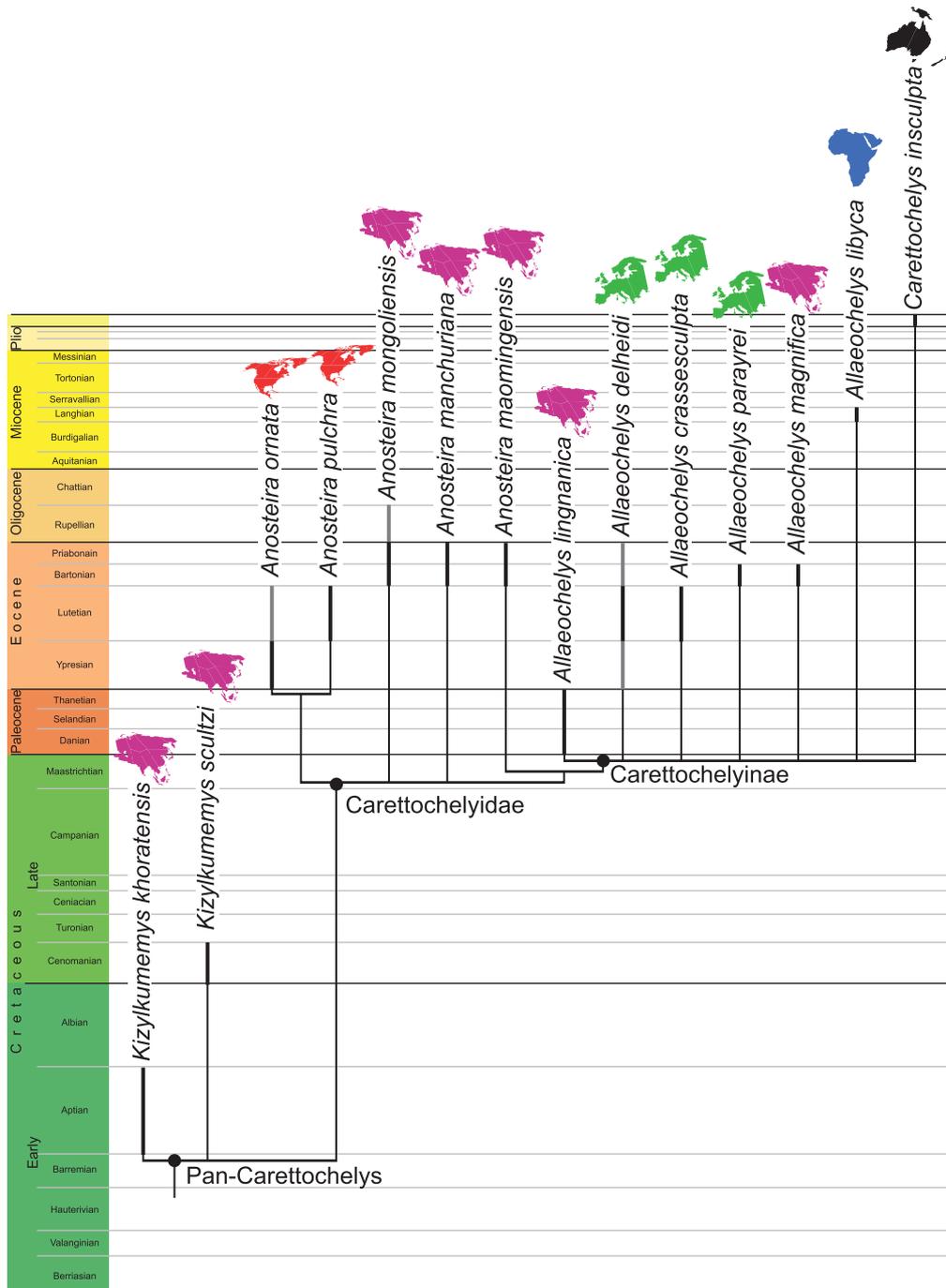
FIGURE 4. The stratigraphic and biogeographic distribution of valid pan-carettochelyid taxa. Black lines indicate temporal distribution based on type material. Gray lines indicate temporal distribution based on referred material.

acter that diagnoses males relative to females is their longer tails. Preservation of the mating pairs in sediments representing the middle of a volcanic lake, combined with the fact that the males are about 20% smaller than the females, indicate that these turtles courted in open water, that females cooperated with males, and that the couples sank while mating into poisonous subsurface layers (Joyce et al. 2012). Finally, the presence of a posterior plastral hinge in females of these species indicates that these small turtles produced large eggs relative to their body size (Joyce et al. 2012). Although not much is known about the mating behavior in *Carettochelys insculpta*, females of this taxon apparently lay relatively smaller eggs and therefore do not need a plastral hinge.

Although *Carettochelys insculpta* is never found in regular marine waters, this species seems to tolerate brackish conditions and occurs in intertidal estuaries in addition to their normal riverine habitats (e.g., Schulze-Westrum 1963). *Kizylkumemys* from the Cretaceous of Asia and *Anosteira* from the Paleogene of Asia and North America typically occur in terrestrial (riverine) settings, with the notable exception of *K. schultzi* material, which was found intermixed with terrestrial and marine faunas and therefore interpreted as deltaic (Nessov 1976, 1977b), and it is therefore unlikely that these taxa were adapted to brackish conditions as well. By contrast, many remains of *Allaeochelys* from the Eocene of Europe and most carettochelyine fragments from the Miocene of Africa originated from marine, near-shore, or deltaic sediments. Seemingly, carettochelyines evolved to tolerate brackish water conditions at the beginning of the Paleogene and this helped them to spread more easily among the islands of the European Archipelago during much of the Tertiary and to migrate to the Australian continent in the Miocene (see below).

Paleobiogeography

The oldest unambiguous pan-carettochelyids were recovered from Early Cretaceous sediments in Southeast Asia, including the unkeeled species *Kizylkumemys khoratensis* described on the basis of material from the Aptian of Nakhon Ratchasima and Ubon Ratchathani provinces, Thailand (Tong et al. 2006; Figure 5). Even older fragmentary material was described from the mid Early Cretaceous

of Khon Kaen, Kalasin, and Nong Bu Lam Phu provinces, Thailand, of which some greatly resemble the Central Asian, keeled species *Kizylkumemys schultzi*, although attribution to this taxon remains uncertain (Tong et al. 2006, 2009). Finally, fragmentary remains were reported from the Aptian–Albian of Savannakhet Province, Laos (Lapparent de Broin 2004), but no specimens were figured or listed, so it is not possible to rigorously assess this claim. Fossiliferous rocks farther north in Asia have not yet produced any remains (e.g., Rabi et al. 2010), and it is therefore plausible that the group originated in Southeast Asia.

Pan-carettochelyids only occur farther north in the Late Cretaceous of Asia, but this may be a taphonomic bias. The only described species from this time period is *Kizylkumemys schultzi* from the Cenomanian Karakalpakstan Autonomous Republic, Uzbekistan (Nessov 1977a, 1977b, 1977c, 1985, 1986, 1987; see Figure 5). Additional, fragmentary remains are otherwise known from the Cenomanian–Turonian of Dornogov Province (Aimag), Mongolia (Shuvalov and Chkhikvadze 1979; Nessov 1981; Sukhanov et al. 2008), from the ?lower Turonian of Karakalpakstan Autonomous Republic, Uzbekistan (Nessov 1997), and from the Coniacian–Santonian of Kumamoto Prefecture, Japan (Hirayama and Chitoku 1994; Hirayama 1998). A single fragment was recently reported from the Cenomanian of southwestern France that may represent a pan-carettochelyid (Vullo et al. 2010), but I agree with the authors that the diagnostic value of this fragment is limited. The entire Cretaceous record of *Pan-Carettochelys* is therefore limited to Asia (see Figure 5).

Pan-Carettochelys, in the form of *Carettochelyidae* proper, remained well established in Asia during the Paleogene, and at least two primary lineages are apparent at that time. The less modified and likely paraphyletic *Anosteira* group is particularly well represented in China, with taxa such as *Anosteira mongoliensis* from the Late Eocene of Inner Mongolia (Gilmore 1931) and the Late Eocene–Early Oligocene of Shandong Province (Cheng 1961), *Anosteira manchuriana* from the Late Eocene of Liaoning Province (Zangerl 1947), and *Anosteira maomingensis* Late Eocene of Guangdong Province (Chow and Liu 1955; see Figure 5). Fragmentary remains only attributable to *Anosteira* sp. were otherwise reported from the Eocene of Jiangxi Province, China (Zhou 1959), and Magwe and Mandalay provinces, Myanmar
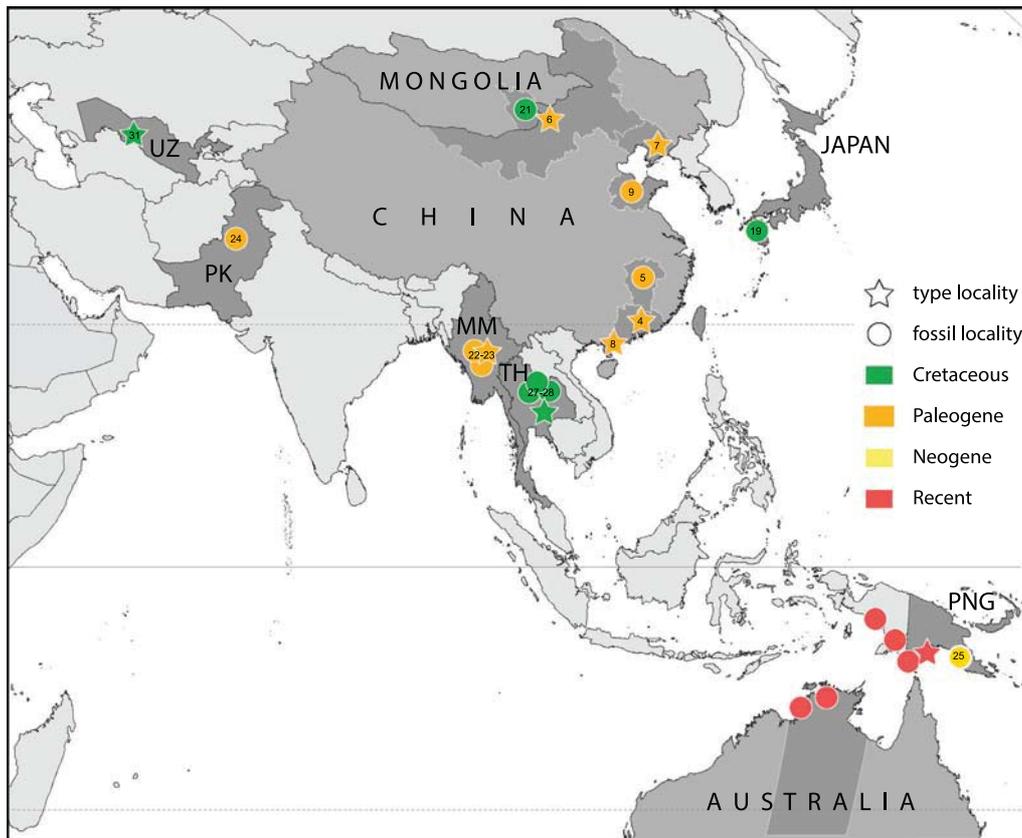
FIGURE 5. The geographic distribution of figured pan-carettochelyid turtles in Asia and Australia. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations*: MM, Myanmar; PK, Pakistan; PNG, Papua New Guinea; TH, Thailand; UZ, Uzbekistan.

(Hutchison et al. 2004). The more derived *Allaeochelys* group is more common along the southern margin of the continent and represented by the Paleocene species *Allaeochelys lingnanica* from Guangdong Province, China (Young and Chow 1962), and by *Allaeochelys magnifica* from the Late Eocene of Magwe and Mandalay provinces, Myanmar (Hutchison et al. 2004). Fragmentary specimens attributable to *Allaeochelys* sp., or at least *Carettochelyinae incertae sedis*, are also described from Khyber Pakhtunkhwa Province, Pakistan (Broin 1987).

After having remained restricted to Asia throughout the Cretaceous, *Carettochelyidae* started to colonize other continents during the Paleogene (Figures 5, 6 and 7; see also Appendix 3). Efimov and Yarkov (1993a, 1993b) reported fragmentary remains from the Upper Paleocene of the Lower Volga Basin, southwestern Russia,

but a later, more thorough review of this material could not confirm the presence of carettochelyids at this locality (Averianov and Yarkov 2000). The oldest unambiguous European carettochelyids are numerous fragmentary finds reported by Broin (1977) from the Early Eocene (Ypresian) of the Paris Basin, northwestern France, that are herein referred to the carettochelyine species *Allaeochelys delheidi* (see Figure 6). This taxon is otherwise known from the type shell from the Early Eocene (Lutetian) of Belgium (Dollo 1886), by abundant herein referred material from the Early Eocene (Lutetian) of northwestern Spain (Jiménez Fuentes 1971; Alonso Santiago and Alonso Andrés 2005; Alonso Santiago et al. 2008), and from isolated material from the Early Eocene (Ypresian) and Late Eocene (Priabonian) of southeastern England (Lydekker 1889c). The world's best-known fossil carettochelyid (and caret-
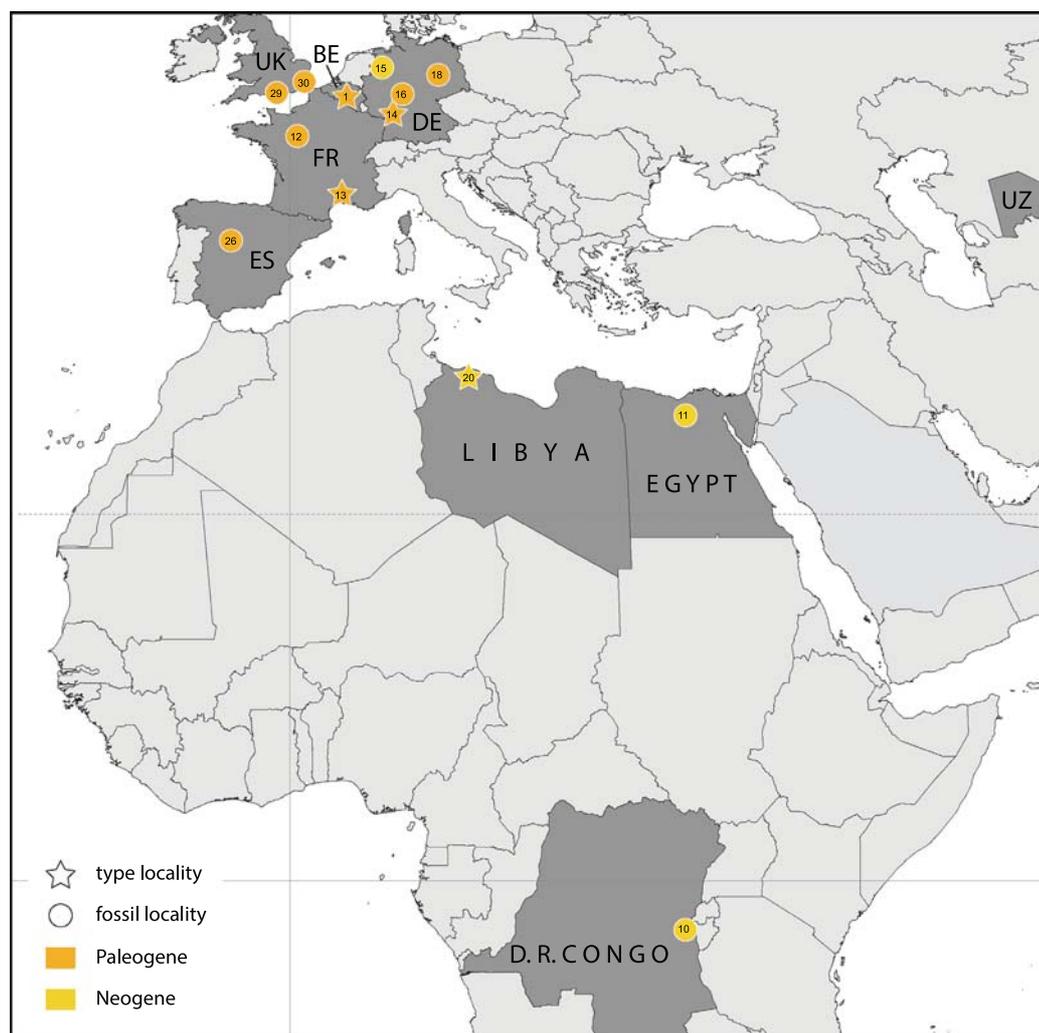
FIGURE 6. The geographic distribution of figured pan-carettochelyid turtles in Africa and Europe. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations*: BE, Belgium; DE, Germany; ES, Spain; FR, France; UK, United Kingdom.

tochelyine) is *Allaeochelys crassesculpta* from the Early Eocene (Lutetian) of Messel Pit in southwestern Germany (Harrassowitz 1922; Weitzel 1949; Groessens-Van Dyck 1978), which is known from more than 100, often near-complete skeletons, of which about a quarter occur as pairs that died while mating (Joyce et al. 2012). The third taxon known from the Paleogene of Europe is *Allaeochelys parayrei*, which is so far restricted to the Late Eocene (Bartonian) of the Aquitaine Basin, southwestern France (Noulet 1867; de Stefano 1902; Bergounioux 1931; Broin 1977). Lapparent de Broin (2001) stated that carettochelyids

disappeared from Europe following the Eocene because of climatic cooling, but several Oligocene sites throughout Germany have yielded fragmentary carettochelyid remains (Gramann 1956; Darga et al. 1999; Karl 2002; Karl et al. 2006; Karl and Müller 2008) and thereby contradict this claim. Notably, all known European carettochelyids belong to the *Allaeochelys* group and likely immigrated from southern Asia along the margins of the closing Paratethys.

North America was colonized by carettochelyids during the Early Eocene as well (see Figure 7). Only two species are currently recognized,
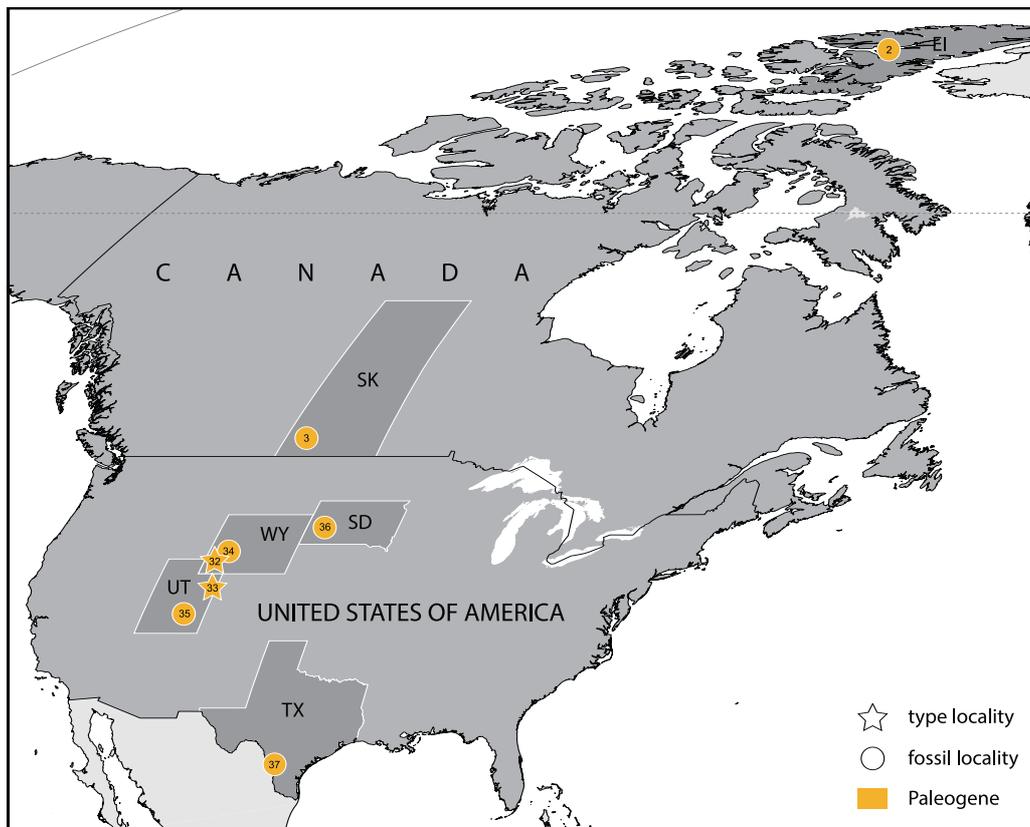
FIGURE 7. The geographic distribution of figured pan-carettochelyid turtles in the North America. Stars mark type localities. Locality numbers are cross-listed in Appendix 3. *Abbreviations*: EI, Ellesmere Island, Canada; SD, South Dakota, USA; SK, Saskatchewan, Canada; TX, Texas, USA; UT, Utah, USA; WY, Wyoming, USA.

Anosteira ornata from the Early Eocene (Bridgerian, Ypresian) of Wyoming (Leidy 1871a; Hay 1906) and *Anosteira pulchra* from the Early Eocene (Uintan, Lutetian) of Utah (Gilmore 1915; Clark 1932). Fragmentary remains referable to *Anosteira* sp. have otherwise been reported from the Early Eocene (Bridgerian, Ypresian) of Ellesmere Island (Estes and Hutchison 1980), Saskatchewan (Hutchison and Storer 1998) and Wyoming (Zonneveld et al. 2000), the Late Eocene (Duchesnian, Bartonian) of Utah (Eaton et al. 1999) and the Late Eocene (Chadronian, Priabonian) of South Dakota (Clark et al. 1967). Isolated carettochelyid fragments have also been reported from the Early Eocene (Uintan, Lutetian) of Texas, but in contrast to all other North American material, they were referred to cf. *Allaeochelys* (Westgate 1989, 2001), likely because of their large size. No carettochelyids have been reported from the Oligocene of North America (Hutchison 1996).

There is disagreement about from which continent North America was colonized by carettochelyids. Hutchison (1998) argued that North American carettochelyids emigrated from Asia during the Early Eocene, but Godinot and Lapparent de Broin (2003) soon after pleaded for a route via Europe. It is apparent from the available data that North American representatives of *Anosteira* must have dispersed from Asia along the Bering Land Bridge, because this taxon is otherwise only known from neighboring northeastern Asia, but is notably absent from Europe. However, it remains possible that North American representatives of *Allaeochelys* dispersed from Europe, although the available material is insufficient to clarify this question at present.

At the beginning of the Neogene, carettochelyids are lacking completely in the New World and Asia, but carettochelyines were still relatively widespread in Europe and Africa (see Fig-

ure 6). The European record is limited to a single fragment from the Early Miocene (Burdigalian) of northwestern Germany (Joyce, Klein and Mörs 2004). A partial shell from the Middle Miocene of Austria (Gemel and Rauscher 2000) is herein reinterpreted to be a cheloniid turtle because it shows well-developed marginal scutes. In contrast to Europe, carettochelyines seem to be well established in northern Africa at this time, with isolated remains reported from the Early Miocene (Burdigalian) of Egypt (Dacqué 1912; Lapparent de Broin 2000), Libya (Havlik et al. in review), and perhaps also Saudi Arabia (Thomas et al. 1981; remains not figured). Fragmentary remains reported from the Miocene of Oman (Roger et al. 1994) have since been reidentified as belonging to a testudinid (Lapparent de Broin 2000). A single carettochelyine fragment from the Late Miocene of the Democratic Republic of Congo (Hirayama 1992) is the last trace of this group west of Wallace's Line. It is unclear whether Africa was colonized from Europe or from Asia (Lapparent de Broin 2000).

Although nearly the entire evolutionary history of *Pan-Carettochelys* took place in the northern hemisphere (see Figures 5, 6 and 7), the only surviving representative of the clade, *Carettochelys insculpta*, lives in southern Papua New Guinea and Northern Territory, Australia (Ernst and Barbour 1989). Fragmentary fossils from the Upper Miocene of Papua New Guinea (Glaessner 1942) reveal that dispersal across Wallace's Line must have taken place no later than the Middle Miocene (see Figure 5). The fragmentary carettochelyid remains reported by Gorter and Nicoll (1978) from the Neogene northern Western Australia are more properly identified as *Testudines* indet. (Gaffney 1981).

Systematic Paleontology

Valid Taxa
See Appendix 4 for the hierarchical taxonomy of *Pan-Carettochelys* as described in this work.

Pan-Carettochelys Joyce, Parham and Gauthier 2004

Phylogenetic definition. Following Joyce, Parham and Gauthier (2004), the name *Pan-Carettochelys* is herein referred to the total-clade that includes *Carettochelys insculpta* Ramsay, 1887 (i.e., all extant populations from Australia and New Guinea), but no other extant turtle species.

Diagnosis. Representatives of *Pan-Carettochelys* are currently diagnosed relative to other turtles by the presence of a shallow fossa behind the quadrate, a reduced antrum postoticum, a midline keel, nuchal articulation sites for the eighth cervical vertebra, presence of only 10 peripherals, a single suprapygal, a thickened pygal with an anterior groove, a narrow, cruciform plastron, plastral kinesis, a triangular entoplastron, and reduction of the plastral scutes (see Figure 3).

Kizylkumemys Nessov, 1976

Type species. *Kizylkumemys schultzi* Nessov, 1976.

Diagnosis. *Kizylkumemys* can be diagnosed as a pan-carettochelyid by the presence of all the apomorphies listed above. *Kizylkumemys* is currently differentiated from all other pan-carettochelyids by retaining some plastral and carapacial scutes, an undivided vertebral I, a narrow vertebral scute that spans neurals II to IV, and a highly reduced, cruciform plastron. Most of these characters appear to be plesiomorphies and this taxon could therefore be paraphyletic relative to later and more derived pan-carettochelyids.

Kizylkumemys khoratensis Tong et al., 2005

Taxonomic history. *Kizylkumemys khoratensis* Tong et al., 2005 (new species).

Type material. NRRU A1861 (holotype), anterior portion of a carapace, including nuchal, neurals I to IV, medial portion of costals I to V, and right peripheral I (Tong et al. 2005, fig. 1; Tong et al. 2006, fig. 4; Tong et al. 2009, fig. 3a, b).

Type locality. Ban Saphan Hin locality, Nakhon Ratchasima Province, Thailand (see Figure 5); Khok Kruat Formation, Aptian, Early Cretaceous (Tong et al. 2005).

Referred material and range. Early Cretaceous (Aptian), Khok Kruat Formation, Ban Saphan Hin Locality (type locality) and Ban Khok Kruat Locality, Nakhon Ratchasima Province, Khok P(h)a Suam Locality, Ubon Ratchathani Province, Thailand (Tong et al. 2005, Tong et al. 2006).

Diagnosis. *Kizylkumemys khoratensis* can be diagnosed as a pan-carettochelyid by the presence of a midline keel, a triangular entoplastron, and a single suprapygal, and as a representative of *Kizylkumemys* by the presence of plastral and carapacial scutes, an undivided vertebral I, a narrow vertebral scute that spans neurals II to IV, and a highly reduced, cruciform plastron. *Kizylkumemys khoratensis* is differentiated from *K. schultzi* in lacking a distinct midline projection formed by neurals II to IV and in the presence of a distinct second vertebral.

Comments. *Kizylkumemys khoratensis* is based on a relatively large carapacial fragment from the Aptian Khok Kruat Formation of Thailand and is well differentiated by several characters relative to the slightly younger species *K. schultzi* from the Cenomanian of Uzbekistan. The most distinctive character that distinguishes these two species is the shark-fin-like dorsal process that is formed by neurals II to IV in *K. schultzi*, in comparison to the relatively smooth anterior region seen in *K. khoratensis*. How-

ever, fragmentary remains from the slightly older Sao Khua Formation of Thailand reveal a *K. schultzi*-like morphology with a distinct midline keel (Tong et al. 2006; Tong et al. 2009). Additional material will hopefully reveal in the future whether two turtle taxa indeed coexisted in the Early Cretaceous of Southeast Asia. It is alternatively possible that only a single taxon existed with strong sexual dimorphism, with males perhaps having the *K. schultzi* morphology for sexual display and females retaining the less modified *K. khoratensis* morphology. Similar variation was already reported by Nessov (1986) for *K. schultzi* and tentatively attributed to sexual dimorphism. It is not possible to distinguish between these two hypotheses with the currently available material. It notable, however, that similar sexual dimorphism has been yet been reported for any other turtle taxon.

Kizylkumemys schultzi Nessov, 1976

Taxonomic history. *Kizylkumemys schultzi* Nessov, 1976 (new species).

Type material. CCMGE 11180-1 (holotype), right hypoplastron (Nessov 1977b, pl. 9, fig. 15).

Type locality. Khodzhakulsay Locality, Sultan-Avays (= Sultanuvais = Sultanuizdag) Range, Karakalpakstan Autonomous Republic, Uzbekistan (see Figure 5); Khodzhakul (Chodzhakul) Formation, early Cenomanian (see Syromyatnikova and Danilov 2009; Danilov et al. 2011).

Referred material and range. Early Cenomanian Khodzhakul (Chodzhakul) Formation of Ayazkala, Karatepa, Sheichdzheili II (= Sheikhdzheili II), and Tçelpyk (Chelpyk) localities, Sultan-Avays (Sultanuvais) Range. All localities are in Karakalpakstan Autonomous Republic, Uzbekistan. Locality information from Nessov (1977a, 1977b, 1985, 1986, 1987); alternative spellings and updated stratigraphic information from Syromyatnikova and Danilov (2009). Referred specimens are figured in Nessov (1976, figs. 1, 2; 1977b, pl. 9, 10, figs. 1–3; 1977c [only figure]; 1986, pl.1.2–8, fig. 13; 1987, pl. 2.11–15; 1995, pl. 4.18; 1997, pl. 27.2–23, pl. 28.1, 2, 8) and Nessov and Krassovskaya (1984, figs. 3, 12).

Diagnosis. *Kizylkumemys schultzi* can be diagnosed as a pan-carettochelyid by a shallow fossa behind the quadrate, a reduced antrum postoticum, the presence of a midline keel, nuchal articulation sites for the eighth cervical vertebra, presence of only 10 peripherals, a single suprapygal, a thickened pygal with an anterior groove, plastral kinesis, a triangular entoplastron and reduction of the plastral scutes; and as a representative of *Kizylkumemys* by the presence of plastral and carapacial scutes, an undivided vertebral I, a narrow vertebral scute that spans neurals II to IV, and a highly reduced, cruciform plastron. *Kizylkumemys schultzi* is differentiated from *K. khoratensis* in the presence of a distinct midline projection formed by neurals II to IV and the absence of a distinct second vertebral.

Comments. *Kizylkumemys schultzi* is based on a collection of several hundred fragments (Nessov 1977a, 1977b) that were collected from several Cenomanian localities in the Kyzyl Kum (Kizylkum) Desert of Uzbekistan. Although the type specimen is only an isolated right hyoplastron, and although the temporal range of the Uzbek localities span a time interval of up to 11 Ma, I herein follow Nessov (1976, 1977a, 1977b, 1977c, 1981, 1985, 1986, 1987, 1995, 1997) in assuming that all material from these three localities indeed represents a single species. A thorough description of this material is nevertheless long overdue to enable a more transparent referral of all material.

Nessov (1981) later created the subspecies *Kizylkumemys schultzi mirabilis* for five shell fragments (type = ZIN PH #T/M78-3) from the Cenomanian–lower Turonian Khara Khutul Locality, Dornogov Province (Aimag), Mongolia (Sukhanov et al. 2008). One of these fragments, a neural IV, was later figured by Nessov (1986, pl. 1, fig. 8) under the name *K. schultzi*. According to Nessov (1981), this taxon can be distinguished from *K. schultzi schultzi* by differences in the shape of neural IV and the morphology of the free edge of the bridge peripherals, but it is impossible to evaluate these claims on the basis of the available literature. I therefore declare *Kizylkumemys schultzi mirabilis* a nomen dubium.

Tong et al. (2006, fig. 3; Tong et al. 2009, fig. 3c–f) reported four neural fragments from the pre-Aptian Phu Wat Locality of the Sao Khua Formation in Khon Kaen Province, Thailand, that resemble those of *Kizylkumemys schultzi* by the presence of distinct fin-like midline projections, and I agree with Tong et al. (2009) that more material is needed to allow a more confident identification. The occurrence of fossil carettochelyids with and without midline projections in the penecontemporaneously deposited Sao Khua and Khok Kruat formations of Thailand either implies the existence of two *Pan-Carettochelys* taxa in southeastern Asia in the late Early Cretaceous or pronounced sexual dimorphism combined with the synonymy of *K. schultzi* and *K. khoratensis*.

Carettochelyidae Gill, 1889

Phylogenetic definition. Following Joyce, Parham and Gauthier (2004), the name *Carettochelyidae* is herein referred to the clade arising from the last common ancestor of *Carettochelys insculpta* Ramsay, 1887 and *Anosteira ornata* Leidy, 1871a.

Diagnosis. Representatives of *Carettochelyidae* are currently diagnosed relative to more basal pan-carettochelyids by a maxilla-quadratojugal contact, absence of plastral scutes, and by the presence of an intermediate to large plastron (see Figure 3).

Comments. At least five family level names have been proposed for the taxon typified by *Carettochelys insculpta* (Joyce, Parham and Gauthier 2004). Although *C. insculpta* had only been named by Ramsay in early 1887, Boulenger (1887) almost immediately noted similarities between this new taxon from New Guinea and the fossil taxa *Anosteira ornata* from North America and *Allaeochelys delheidi* from Europe and proposed the name Carettochelyididae. Soon after, however, Gill (1889) proposed the alternate spelling *Carettochelyidae*, which is now considered by the International Commission on Zoological Nomenclature (ICZN 1999) to be the correctly derived family group name. I herein follow the rationale of Joyce, Parham and Gauthier (2004) and apply authorship of the name *Carettochelyidae* to Gill (1889), because it is logically inconsistent

to refer authorship of a clade to a historical figure, but possible to objectively conclude that he was the first to arrive at that spelling.

Anosteira Leidy, 1871a

Type species. *Anosteira ornata* Leidy, 1871a.

Diagnosis. *Anosteira* can be diagnosed as a carettochelyid by the presence of a maxilla-quadratojugal contact, a shallow fossa behind the quadrate, a reduced antrum postoticum, a midline keel, nuchal articulation sites for the eighth cervical vertebra, presence of only 10 peripherals, a single suprapygal, a thickened pygal with an anterior groove, plastral kinesis, a triangular entoplastron, and absence of plastral scutes. *Anosteira* is differentiated from more derived carettochelyids by the presence of carapacial scutes and an intermediately sized, cruciform plastron. These characters are currently considered to be plesiomorphies and this taxon is therefore likely paraphyletic relative to more derived pan-carettochelyids.

Anosteira manchuriana Zangerl, 1947

Taxonomic history. *Anosteira manchuriana* Zangerl, 1947 (new species).

Type material. FMNH P15102 (holotype), near-complete shell, primarily missing the peripherals and the left epiplastron (Zangerl 1947, figs. 5–8).

Type locality. Fushun (Fu-chun in Zangerl 1947) Coalmine, Fushun Prefecture, Liaoning (Fengtien in Zangerl 1947) Province, China (Figure 5); late Eocene (Zangerl 1947).

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

Diagnosis. *Anosteira manchuriana* can be diagnosed as a carettochelyid by the presence of a midline keel, a triangular entoplastron and lack of plastral scutes, and as a representative of *Anosteira* by the presence of carapacial scutes and an intermediately sized plastron. *Anosteira manchuriana* differs from all other representatives of *Anosteira* by having a broad, yolk-shaped nuchal.

Comments. *Anosteira manchuriana* is based on a single fossil from the late Eocene of Liaoning and I cautiously agree with all previous authors (e.g., Ye 1963, 1994; Kuhn 1964; Mlynarski 1976; Brinkman et al. 2008; Tong et al. 2010) that this taxon can be diagnosed sufficiently by the presence of a narrow, yolk-shaped nuchal, assuming that this morphology is not the result of damage, as was ascertained by Zangerl (1947). The holotype was given to the Field Museum of Natural History with only limited locality information and Zangerl (1947) was therefore only able to report that the holotype had been found in an oil shale in the Fushun Coal Mine. Wang et al. (2010) report that several hundred meters of sediment are exposed at the Fushun Coal Mine. The only lithographic member within this sequence that Wang et al. (2010) report to be an oil shale and the only one that that they report to yield fossil vertebrates (i.e., "fish") is

the Jijuntun Formation. It is reasonable to assert that this fossil may originate from this layer. However, I was unable to find any precise dates for the Jijuntun Formation and the age of *An. manchuriana* therefore remains unconstrained as Late Eocene.

Anosteira maomingensis Chow and Liu, 1955

Taxonomic history. *Anosteira maomingensis* Chow and Liu, 1955 (new species).

Type material. IVPP V809 (holotype), internal mold of carapace with fragmentary marginal and plastral bones (Chow and Liu 1955, fig. 1); IVPP V910 (paratype), internal mold of carapace and plastron (Chow and Liu 1955, fig. 2).

Type locality. Maoming Prefecture, Guangdong (Kwangtung in Chow and Liu 1955) Province, China (Chow and Liu 1955; Figure 5); Youkanwo Formation, Late Eocene (Tong et al. 2010).

Referred material and range. Late Eocene of Guangdong Province, China (hypodigm of Tong et al. 2010).

Diagnosis. *Anosteira maomingensis* can be diagnosed as a carettochelyid by a midline keel, nuchal articulation sites for the eighth cervical vertebra, presence of only 10 peripherals, a single suprapygal, a thickened pygal with an anterior groove, plastral kinesis, a triangular entoplastron, and absence of plastral scutes, and as a representative of *Anosteira* by the presence of carapacial scutes and an intermediately sized, cruciform plastron. *Anosteira maomingensis* is differentiated from all other representatives of *Anosteira* in sharing the reduction of the marginal scutes with carettochelyines, which is positive evidence for the paraphyly and its exclusion from *Anosteira*.

Comments. Following *Allaeochelys crassesculpta* and *Al. parayrei*, *Anosteira maomingensis* is the third best-known carettochelyid taxon, because it is known from about two dozen described specimens (Chow and Liu 1955; Chow 1956; Ye 1963, 1994; Tong et al. 2010), and because many more remain undescribed in various museums (pers. obs.). Chow and Liu (1955) and Chow (1956) provided the first descriptions of *An. maomingensis* and the validity of this species has been universally accepted (e.g., Ye 1963, 1994; Kuhn 1964; Mlynarski 1976; Brinkman et al. 2008). Tong et al. (2010) recently provided a comprehensive morphological review, including the description of a mandible, and rigorously diagnosed this species relative to all other carettochelyids. *Anosteira maomingensis* has vertebral scutes like other representatives of *Anosteira*, but resembles representatives of *Allaeochelys* and *Carettochelys insculpta* by being relatively large, lacking marginal scutes, and by having a relatively wider bridge region.

Chow and Liu (1955) noted that two different size classes are apparent among the *Anosteira maomingensis* material and Chow (1956) concluded that these size classes were perhaps the result of sexual dimorphism, the female being larger than the male. Although no substantial differences have been reported for the extant *Carettochelys insculpta*, Joyce et al. (2012) recently documented a clear sexual size difference among representatives of *Allaeochelys crassesculpta*, with the female 20% larger than the male, and similar proportions seems to be true for *Al. parayrei* as well (see *Allaeochelys parayrei*). The morphological

review of Tong et al. (2010) documents various types of variation within their sample of *An. maomingensis*, but unfortunately did not investigate possible sexual size dimorphism.

Anosteira mongoliensis Gilmore, 1931
(= *Anosteira shantungensis* Cheng, 1961)

Taxonomic history. *Anosteira mongoliensis* Gilmore, 1931 (new species).

Type material. AMNH 6666 (holotype), nuchal, parts of eight peripherals, distal end of a costal (Gilmore 1931, pl. 1, figs. 1–4); AMNH 6667 (paratype), posterior plastral lobe with attached peripherals (Gilmore 1931, pl. 1, fig. 5).

Type locality. "North Mesa, Shara Murun region" (Gilmore 1931), Inner Mongolia, China (Figure 5); Ulan Shireh Formation, Late Eocene (Gilmore 1931).

Referred material and range. Late Eocene of Inner Mongolia, China (type material of *Anosteira mongoliensis*); Late Eocene–Early Oligocene of Shandong Province, China (holotype of *An. shantungensis*).

Diagnosis. *Anosteira mongoliensis* can be diagnosed as a carettochelyid by the presence of a midline keel, nuchal articulation sites for the eighth cervical vertebra, a thickened pygal with an anterior groove, plastral kinesis, and absence of plastral scutes, and as a representative of *Anosteira* the presence of an intermediately sized, cruciform plastron. *Anosteira mongoliensis* is differentiated from *An. maomingensis* by being significantly smaller and from *An. manchuriana* in the presence of a trapezoidal nuchal and a divided vertebral I. A clear diagnosis is not possible relative to the North American *An. ornata* and *An. pulchra*.

Comments. *Anosteira mongoliensis* is based on two specimens that were collected in the Late Eocene of Inner Mongolia, China (Gilmore 1931), and has been universally accepted as a valid species ever since (e.g., Ye 1963, 1994; Kuhn 1964; Mlynarski 1976; Brinkman et al. 2008). Tong et al. (2010) recently provided a useful table that summarizes differences among Asian and North American representatives of *Anosteira*, particularly in the shape of the plastral lobes or neural formula. However, given the great amount of variation that is otherwise known to occur among turtles, including carettochelyids (Tong et al. 2010), particularly in the precise outline of the plastral lobes or the neural formula, I find it impossible to identify characters that allow consistently distinguishing *An. mongoliensis* from *An. shantungensis*, *An. ornata* and *An. pulchra*. Although a transcontinental distribution of a single *Anosteira* species is possible (see *An. ornata* above), I herein synonymize the Asiatic taxa *An. mongoliensis* and *An. shantungensis* and cautiously maintain *An. mongoliensis* as a valid species relative to *An. ornata* and *An. pulchra*.

Anosteira ornata Leidy, 1871a

Taxonomic history. *Anosteira ornata* Leidy, 1871a (new species); *Anostira ornata* Cope 1871 (incorrect spelling).

Type material. ANSP 9846 (neotype, designated herein), highly fragmented, partial shell, including carapacial and plastral remains (Leidy 1873, pl. 16.1–3).

Type locality. "Near Fort Bridger" (label associated with ANSP 9846), Uinta County, Wyoming, USA (see Figure 7). Hay (1908:279) speculates that all of Leidy's (1871a, 1871b, 1873) original material originates from "the lower portion of level B of the Bridger Eocene," which corresponds to the Early Eocene (Ypresian) Black Fork Member of the Bridger Formation of Murphey and Evanoff (2007).

Referred material and range. Early Eocene (Bridger B, late Ypresian) of Wyoming, USA (neotype of *Anosteira ornata*); Early Eocene (Bridger C, early Lutetian) of Wyoming, USA (referred specimen of Hay 1906).

Diagnosis. *Anosteira ornata* can be diagnosed as a carettochelyid by the presence of a midline keel, nuchal articulation sites for the eighth cervical vertebra, presence of only 10 peripherals, a single suprapygal, a thickened pygal with an anterior groove, plastral kinesis, a triangular entoplastron, and absence of plastral scutes, and as a representative of *Anosteira* by the presence of carapacial scutes and a intermediately sized plastron. *Anosteira ornata* is differentiated from *An. maomingensis* by the presence of marginal scutes and by being significantly smaller and from *An. manchuriana* in the presence of a trapezoidal nuchal and a divided vertebral I. *Anosteira ornata* is provisionally differentiated from *An. pulchra* in the presence of regular, hexagonal neurals and the absence of a differentiated vertebral II. A clear diagnosis is not possible relative to *An. mongoliensis*.

Comments. Leidy (1871a) originally described *Anosteira ornata* on the basis of "about four different individuals" (Leidy 1871a:102) from localities within reach of Fort Bridger in what is today southwestern Wyoming. The original two publications (Leidy 1871a, 1871b), only included brief descriptions of the available material and did not include any figures, but Leidy (1873) soon after provided illustrations of three fossils in his review of the Eocene fossils of Wyoming, of which the most complete (herein designated as the neotype) is explicitly mentioned as not being part of the original type series. Hay (1908) was not able to find the type specimens and speculated that they may be part of USNM 4062; however, Gillette (1977) later listed six specimens (ANSP 23, 102, 9801, 9845, 9846, 10225) in the collections of the Academy of Natural Sciences in Philadelphia as the syntypes of this taxon. A review of these specimens reveals that ANSP 23 and ANSP 102 do not represent turtles (pers. comm. Ned Gilmore) and may have been listed accidentally by Gillette (1977), and that ANSP 9801, 9846 and 10225 can be recognized in Leidy's (1873) figures. However, given that ANSP 9846 is the only specimen to which Leidy (1871a, 1871b; 1873) refers directly, if only to state that it was not part of the type series, it is not possible to identify any of the syntypes with confidence among the available material. Although the ICZN (1999) sets very high standards for showing that no original type is available, I feel that a possibly present, but unidentifiable, type may as well be considered lost. I therefore herein designate ANSP 9846 as the neotype, which should 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. It

is important to note, however, that Leidy's figures (Leidy 1873, pl. 16.1–3) contain errors on several features, particularly the number of peripherals, and should therefore be viewed with caution. The near-complete specimen described by Hay (1906, figs. 2, 3; 1908, pl. 43; figs. 352, 353; AMNH 6132) unfortunately originates from the Bridger C, in contrast to Leidy's type material from the Bridger B, and therefore does not meet the stratigraphic requirements of the ICZN (1999) for a neotype.

The morphology of *Anosteira ornata* was at the center of interest of many publications in the second half of the 19th century, likely because this taxon was the first carettochelyid to be figured in the literature and because its relationship to other turtles was so controversial. Leidy's (1871a, 1871b) original descriptions were based on rather fragmentary material, but he was nevertheless able to deduce correctly that this taxon was exceptionally small (carapace length less than 15 cm), that the posterior elements, including the pygal, have a midline keel, and that the shell was covered by fine, radially arranged ornamentations. Soon after, Leidy (1873) had access to better material, including the neotype designated here, and provided the first figured reconstruction of this taxon (refigured in Cope 1882). This reconstruction caused a storm of speculation as to the phylogenetic relationships of this taxon. Leidy (1873) noted an intermediate morphology of *An. ornata* between pleurodires and chelydrids. Cope (1882, 1884) highlighted shared characters with trionychids (sculpturing, lack of sulci), baenids and emydids (sutured plastron), but nevertheless referred *An. ornata* to *Chelydridae*, likely because of the cruciform morphology of the plastron. Dollo (1886) noted similarities of *An. ornata* with his newly described European species *Pseudotrionyx delheidi* and placed both within *Chelydridae*. All authors had so far operated under the assumption that *An. ornata* lacked carapacial scutes and had 11 pairs of peripherals as reported by Leidy (1871a, 1871b, 1873). Baur (1889a, 1889b, 1889c) corrected these errors using the available material and placed *An. ornata* near *Kinosternidae*, although he noted that this affiliation depended partially on the assumption that the entoplastron was perhaps absent in this taxon. Soon after, Baur (1891) was the first to formally recognize the close relationships of all fossil and living carettochelyids as sister to *Trionychidae*, although he still thought carettochelyids had mesoplastra. Final doubts about the basic shell anatomy of *An. ornata* were disposed of by a new specimen described and figured by Hay (1906, figs. 2, 3; 1908, figs. 352–354, pl. 43) that clearly revealed this species to lack mesoplastra but to have a well-developed entoplastron. No significant new finds have been reported since Hay (1906), with possible exception of the potentially conspecific holotype of *An. pulchra* (see *Anosteira pulchra*).

Only subtle differences exist in the outline of the posterior plastral lobe of *Anosteira ornata* and *An. mongoliensis* and it is indeed possible that both represent the same taxon. Tong et al. (2010) report that these two taxa differ in the depth of the nuchal notch, but I think this to be an illusion created by the nuchal being depicted in different angles. Considering that carettochelyids emigrated from Asia to North American at the beginning of the Eocene (Hutchison 2000), it is possible that a single carettochelyid species once existed for some time that occurred in Asia and North America, and that *An. ornata*–*An. mongoliensis* represents this taxon. However, it is equally plausible that the *An. ornata* originated through a unique dispersal event and became

isolated from its Asiatic parent species immediately. Given that the morphology and temporal distribution of both taxa are not yet fully understood, I provisionally retain *An. mongoliensis* as a valid taxon and expect new material to clarify this question.

It is difficult to rigorously assess the temporal distribution of *Anosteira ornata,* because only one specimen from the Bridger B (the neotype) and another from Bridger C (AMNH 6132) of Wyoming are diagnostic to the species level relative to the two other carettochelyid taxa reported from North America (i.e., *Anosteira pulchra* and cf. *Allaeochelys*). Fragmentary remains reported by Cope (1884) from Bridger A (Hay 1908; AMNH 1059) cannot be considered diagnostic, although it is plausible that they belong to this taxon. A partial shell (CM 2954) from the Lutetian Horizon C of the Uinta Formation that was referred to *An. ornata* by Gilmore (1915) would significantly expand the range of this taxon, but the specimen remains unfigured and undescribed and I therefore cannot assess its taxonomic status.

Anosteira pulchra (Clark, 1932)

Taxonomic history. *Pseudanosteira pulchra* Clark, 1932 (new species); *Anosteira pulchra* Broin 1977 (new combination).

Type material. CM 11808 (holotype), almost complete shell lacking the anterior and posterior plastral lobes (Clark 1932, figs. 1, 2).

Type locality. Quarry L, Leota Ranch, near the village of Ouray, Uinta County, Utah, USA (Clark 1932; Figure 7); "Upper part of Horizon C," (Clark 1932:161), Uinta Formation, Lutetian, Middle Eocene.

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

Diagnosis. *Anosteira pulchra* can be diagnosed as a carettochelyid by a maxilla-quadratojugal contact, a shallow fossa behind the quadrate, a reduced antrum postoticum, a midline keel, presence of only 10 peripherals, a single suprapygal, and absence of plastral scutes, and as a representative of *Anosteira* by the presence of carapacial scutes and an intermediately sized plastron. *Anosteira pulchra* is differentiated from *An. maomingensis* by the presence of marginal scutes and from *An. manchuriana* in the presence of a trapezoidal nuchal and a divided vertebral I. *Anosteira pulchra* is provisionally differentiated from *An. ornata* by the absence of regular, hexagonal neurals and the presence of a differentiated vertebral II.

Comments. The two North American taxa *Anosteira pulchra* and *An. ornata* are nearly identical to one another in general gestalt and differ primarily in that *An. pulchra* has irregular, not regular, hexagonal neurals and that *An. ornata* lacks a differentiated vertebral II. Given that all taxonomic information for both taxa has been gathered from three shells only, and that the midline portions of the carapace are damaged in both known specimens of *An. ornata*, it is unclear whether these differences are due to variation, imperfect preservation, or taxonomic differences. However, considering that *An. pulchra* is slightly younger than *An. ornata*, I would not be surprised if they are eventually

shown to be parts of a single, anagenetic lineage. If so, they could either be synonymized into a single species, or maintained at separate chronotaxa. Two nearly complete shells (YPM VPPU 016317, 016318) collected from the type section of *An. pulchra* could help resolve the identity of this taxon in the future.

Although most authors have followed Clark (1932) in recognizing the taxon *Pseudanosteira pulchra* (e.g., Kuhn 1964; Mlynarski 1976; Meylan 1988), I favor the combination *Anosteira pulchra* as first proposed by Broin (1977), because I wish to suppress the unnecessary proliferation of generic names, especially if they are monotypic.

It is difficult to assess the temporal distribution of *Anosteira pulchra* because the holotype is the only known specimen that displays diagnostic characters. Hutchison (1992) broadly summarized the distribution of "*Pseudanosteira*" to be Uintan (Lutetian) to Chadronian (Priabonian), but this seems to be based on the assumption that all fragmentary material reported after the Uintan, particularly the fragmentary material reported by Clark et al. (1967) from the Chadronian of South Dakota, is attributable to this taxon.

Carettochelyinae Williams, 1950

Phylogenetic definition. The name *Carettochelyinae* is herein referred to the clade arising from the last common ancestor of *Carettochelys insculpta* Ramsay, 1887 and *Allaeochelys parayrei* Noulet, 1867.

Diagnosis. Representatives of *Carettochelyinae* are currently differentiated relative to more basal pan-carettochelyids by the presence of a deep fossa behind the quadrate, absence of carapacial and plastral scutes in adult individuals, and by having a broad plastron (see Figure 3).

Comments. Following the rules of the ICZN (1999), Boulenger (1887) should be considered the author of *Carettochelyinae* because he was the first to name the family-group taxon typified by *Carettochelys insculpta,* even though he most certainly never conceived of this grouping nor intended to name a clade. I therefore follow the rationale of Joyce, Parham and Gauthier (2004) and apply authorship of the name *Carettochelyinae* to Williams (1950), because he was the first to propose that spelling.

Allaeochelys Noulet, 1867

Type species. *Allaeochelys parayrei* Noulet, 1867.

Diagnosis. *Allaeochelys* can be diagnosed as a carettochelyine by the presence of a deep fossa behind the quadrate, a reduced antrum postoticum, maxilla-quadratojugal contact, a midline keel, nuchal articulation sites for the eighth cervical vertebra, 10 peripherals, a single suprapygal, a thickened pygal with an anterior groove, plastral kinesis, a triangular entoplastron, a broad plastron, and the absence of plastral and carapacial scutes in adult individuals. Among carettochelyines, *Allaeochelys* is differentiated from *Carettochelys insculpta* by having a continuous neural series. The last character is currently considered to be plesiomorphic and this taxon may well be paraphyletic relative to *Carettochelys insculpta*.

Allaeochelys crassesculpta (Harrassowitz, 1922) (= *Allaeochelys gracilis* Harrassowitz, 1922)

Taxonomic history. *Anosteira crassesculpta* Harrassowitz, 1922 (new species); *Anosteira crassesculpta = Anosteira gracilis* Gramann 1956 (senior synonym); *Allaeochelys crassesculpta* Nessov 1976 (new combination); *Allaeochelys crassesculptata* Morlo et al. 2004 (incorrect spelling); *Allaeochelys parayrei = Castresia munieri = Allaeochelys nouleti = Anosteira crassesculpta = Anosteira gracilis* Karl and Müller 2008 (junior synonym).

Type material. HLMD 1461 (syntype, no. 6 of Harrassowitz 1922), nearly complete skeleton embedded in a concretion (Harrassowitz 1922, pl. 6.1); HLMD 4283 (syntype, no. 4 of Harrassowitz 1922), hyoplastra, hypoplastra, and xiphiplastra (Harrassowitz 1922, pl. 2.1, pl. 6.4); HLMD 4353b, 4353e, 4353h (syntype, no. 3 of Harrassowitz 1922), poorly preserved shell (Harrassowitz 1922, pl. 2.2).

Type locality. Messel Pit, near the village of Messel, State of Hesse, Germany (Harrassowitz 1922; Figure 6); early Lutetian (ca. 47 Ma), Early Eocene (Joyce et al. 2012).

Referred material and range. Early Eocene (early Lutetian) of Messel, State of Hesse, Germany (material referred by Weitzel [1949], Groessens-Van Dyck [1978] and Joyce et al. [2012], syntype series of *Allaeochelys gracilis*).

Diagnosis. *Allaeochelys crassesculpta* can be diagnosed as a carettochelyine by the presence of a deep fossa behind the quadrate, a reduced antrum postoticum, maxilla-quadratojugal contact, a midline keel, nuchal articulation sites for the eighth cervical vertebra, 10 peripherals, a single suprapygal, a thickened pygal with an anterior groove, plastral kinesis, a triangular entoplastron, a broad plastron, and the absence of plastral and carapacial scutes in adult individuals, and as a representative of *Allaeochelys* by the presence of a continuous neural series. *Allaeochelys crassesculpta* can be differentiated from *Al. delheidi* and *Al. magnifica* by being relatively small (carapace length ca. 20 to 25 cm) and from *Al. parayrei* by the presence of a significantly finer sculpture on the plastron.

Comments. *Allaeochelys crassesculpta* is certainly the best-known carettochelyid, and among the best-known fossil turtle worldwide, because we have more than 100 often near-complete specimens exclusively found at UNESCO protected Messel Pit Fossil Site between Frankfurt and Darmstadt in Germany. Considering the vast quantities of available material, however, surprisingly little is known about the anatomy of this taxon. A monographic description of this species is long overdue.

Harrassowitz (1922) described in detail six specimens that served as the syntypes of *Allaeochelys crassesculpta* (specimens 3, 4 and 6) and *Al. gracilis* (specimens 1, 2 and 5). The primary differences that Harrassowitz (1922) used to diagnose these two species were size and subtleties in the sculpturing pattern, *Al. crassesculpta* being the larger and more coarsely sculpted taxon. Gramann (1956) soon after synonymized these taxa, as he noted that all listed differences are nuanced and

could be explained by ontogeny. Nessov (1976) finally noted similarities with other European carettochelyids and created the new combination *Allaeochelys crassesculpta*. Most authors have since followed these taxonomic suggestions and all Messel material is currently identified as *Al. crassesculpta*. The only exception to this rule is Karl and Müller (2008), who synonymized *Al. crassesculpta* with *Al. parayrei*, but this seems to be from a misreading of Lapparent de Broin (2001), not deeply held convictions based on character evidence (see *Allaeochelys parayrei* for more details).

Allaeochelys crassesculpta* has long been known to often occur in pairs at Messel, but only recently were these finds shown to represent male and female individuals that perished while mating (Joyce et al. 2012). Female individuals are larger and have relatively shorter tails and a posterior plastral hinge, but otherwise show the characteristics highlighted by Harrassowitz (1922) as being diagnostic for *Al. crassesculpta*. By contrast, male individuals are smaller, have a relatively longer tail, lack a plastral hinge, and otherwise show the characteristics thought to be diagnostic of *Al. gracilis*. Indeed, putative syntypes of *Al. crassesculpta* (HLMD 4353b) and of *Al. gracilis* (HLMD 4353a) were found together and represent yet another mating pair (not listed in Joyce et al. 2012). Apparently, Harrassowitz (1922) had used sexually dimorphic character to distinguish his two species.

Gramann (1956) referred fragmentary material from the Early Oligocene (Rupelian) of Borken, State of Hesse, Germany, but this material is not diagnostic to the species level. *Allaeochelys crassesculpta* is therefore known only from the Early Eocene Messel Pit of Germany.

Allaeochelys delheidi (Dollo, 1886)
(= *Anosteira anglica* Lydekker, 1889a
= *Allaeochelys casasecai* Jiménez Fuentes, 1971
= *Allaeochelys jimenezi* Alonso Santiago
and Alonso Andrés, 2005)

Taxonomic history. *Pseudotrionyx delheidi* Dollo, 1886 (new species); *Anosteira delheidi* Hummel 1929 (new combination); *Allaeochelys parayrei* = *Allaeochelys delheidi* = *Castresia munieri* Bergounioux 1935 (junior synonym); *Allaeochelys delheidi* Kuhn 1964 (new combination).

Type material. IRSNB R 19 (holotype), a partial shell consisting of the posterior half of the carapace and the right hyoplastron, hypoplastron, and xiphiplastron (Dollo 1886, pls. 1, 2.1).

Type locality. Village of Melsbroek, Province of Flemish Brabant, Belgium (Dollo 1886; Figure 6); Brussels Formation, Lutetian, Early Eocene (Laga et al. 2001).

Referred material and range. Early Eocene (Lutetian) of Flemish Brabant, Belgium (holotype of *Pseudotrionyx delheidi*); Late Eocene (Priabonian) of Hampshire, United Kingdom (hypodigm of *Anosteira anglica* of Lydekker [1889c]); Early Eocene (Ypresian) of the Isle of Sheppey, Kent County, United Kingdom (part of Lydekker's [1889c] hypodigm of *Pseudotrionyx delheidi*, BMNH 38965, 40099); Early Eocene (Ypresian) of the Paris Basin, France (all material referred to *Allaeochelys* sp. by Broin [1977]); Early Eocene (Lutetian) of Zamora

Province, Spain (all specimens, including types, referred to *Al. casasecai* and *Al. jimenezi* by Jiménez Fuentes [1971], Alonso Santiago and Alonso Andrés [2005] and Alonso Santiago et al. [2008]).

Diagnosis. *Allaeochelys parayrei* can be diagnosed as a carettochelyine by the presence of a midline keel, nuchal articulation sites for the eighth cervical vertebra, 10 peripherals, a single suprapygal, a thickened pygal with an anterior groove, plastral kinesis, a triangular entoplastron, a broad plastron, and the absence of plastral and carapacial scutes in adult individuals, and as a representative of *Allaeochelys* by the presence of a continuous neural series. *Allaeochelys delheidi* can be differentiated from *Al. crassesculpta* and *Al. parayrei* by its significantly larger size and from *Al. magnifica* by having a relatively shorter pygal and a more consistent shell sculpturing consisting of broad vermiculations.

Comments. *Allaeochelys delheidi* is based on a well-figured posterior half of a shell from the Brussels Sands of Belgium. Dollo (1886) reported that the plastral portion of the specimen was originally held in a private collection, but all parts are today housed at the Royal Belgian Institute of Natural Sciences. No additional material was ever referred to this taxon from Belgium, but Lydekker and Boulenger (1887) and Lydekker (1889b, 1889c) referred a few specimens from England. I have been able to examine all shell remains that these authors referred to this species and agree with their assignment. (See below for the proposed synonymy of *Al. casasecai* and *Al. jimenezi* with *Al. delheidi*.)

Allaeochelys libyca Havlik et al., in review

Taxonomic history. *Allaeochelys libyca* Havlik et al., in review (new species).

Type material. BSPG 1991 II 130, an incomplete skull (Havlik et al. in review, figs. 3, 4).

Type locality. Gebel Zelten (Jabal Zaltan), southwestern slopes, localities "MS 2" or "Wadi Shatirat," Al Wahat District, Libya (Figure 6); middle Miocene (Langhian) (Havlik et al. in review).

Referred material and range. Middle Miocene (Langhian) of Al Wahat District, Libya (Havlik et al. in review).

Diagnosis. *Allaeochelys libyca* can be diagnosed as a carettochelyine by the presence of a deep fossa behind the quadrate, a reduced antrum postoticum, maxilla-quadratojugal contact, a broad plastron, and the absence of plastral and carapacial scutes in adult individuals. Given that *Al. libyca* is primarily based on skull material, it is not sufficiently diagnosed relative to all other representatives of *Allaeochelys*, although it notably originates from the Miocene instead of the Eocene. *Allaeochelys libyca* can be differentiated from *Carettochelys insculpta* by the presence of extremely large fossae at the base of the quadrates, close proximity between the foramen posterius canalis carotici interni and the fenestra postotica, the dorsolateral orientation of the tubercula basioccipitale, and the primitive retention of a triangular pterygoid fossa.

Comments. *Allaeochelys libyca* was recently named on the basis of a well-preserved partial skull and a small collection of isolated shell remains from Libya and represents the first-named extinct Neogene pan-carettochelyid. The fragmentary postcranial remains are sufficient to diagnose this taxon as a representative of *Carettochelyinae,* whereas the cranial remains are sufficient to differentiate it from *Carettochelys insculpta.* A partial skull from the Early Miocene of Egypt (Meylan 2009) may be referable to *Al. libyca,* but a formal description of this material is still outstanding.

Allaeochelys lingnanica (Young and Chow, 1962)

Taxonomic history. *Anosteira lingnanica* Young and Chow, 1962 (new species); *Anosteira lignanica* Kuhn 1964 (incorrect spelling); *Allaeochelys lingnanica* Nessov 1976 (new combination).

Type material. IVPP V 1044 (holotype), a partial carapace and the left bridge region (Young and Chow 1962, fig. p. 137).

Type locality. City of Nanxiong (Nanyung in Young and Chow 1962), Shaoguan Prefecture, Guangdong, China (Figure 5); early Paleogene (Paleocene?) (Young and Chow 1962).

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

Diagnosis. *Allaeochelys lingnanica* can be diagnosed as a carettochelyine by the absence of plastral and carapacial scutes, and the presence of an enlarged plastron. *Allaeochelys lingnanica* is differentiated from other representatives of *Allaeochelys* by the presence of a carapacial sculpturing consisting of elongate anteroposterior ridges that become more prominent along the costals toward the neurals.

Comments. *Allaeochelys lingnanica* is based on a highly fragmentary shell that lacks all peripherals, the nuchal, suprapygal, and pygal, and most of the anterior and posterior plastral lobes. Very little locality information is associated with the description of the specimen and Young and Chow (1962) concluded the specimen to originate from "early Paleogene" sediments. Tang and Zhou (1965) briefly reinvestigated the age of the locality and determined a Paleocene age from mammal fossils found in the vicinity, although it remains unclear how close to the type locality these were found.

The holotype of *Allaeochelys lingnanica* lacks all anatomical regions needed to rigorously diagnose a carettochelyid, in particular the skull, the peripherals, the nuchal, suprapygal, pygal and most of the plastral lobes. The lack of carapacial scutes is nevertheless diagnostic of *Carettochelyinae* and the holotype of *Al. lingnanica* is therefore the only evidence of that taxon in the Paleogene of East Asia, justifying its referral in *Allaeochelys* (Nessov 1976). The only character that is truly unique for this taxon is the arrangement of vermiculate, anteroposterior ridges that decorate the carapace and become more prominent along the midline (Young and Chow 1962). I cannot agree with Young and Chow (1962) that the bridge is diagnostic for this taxon, because the type specimen is too poorly preserved to document the width of the lobes and the bridge relative to many other taxa. Additional material from East Asia will hopefully test the validity of this taxon more rigorously.

Allaeochelys magnifica (Hutchison et al., 2004)

Taxonomic history. *Burmemys magnifica* Hutchison et al., 2004 (new species).

Type material. UCMP 61212 (holotype), left hypoplastron (Hutchison et al. 2004, fig. 5a); AMNH 1911, 1919, 1928, 14196, 14197, UCMP 61211, 61218, 128406, 131738, 131739, 131745, 131747, 131748, 131750, 131751, 131753, 142223, 142244, 147001–147003, 147009, 147010, 147012, 147021, 147023, 147027–147029, 154984, 154994, 157443, 157446 (paratypes), a collection of isolated shell remains (Hutchison et al. 2004, figs. 5b–g; 6a–l; see Hutchison et al. 2004 for more details).

Type locality. Holotype and paratypes from multiple localities in the Chindwin-Irrawaddy Basin, Magwe and Mandalay Provinces, Myanmar (Figure 5); Pandaung Formation, Late Eocene (Bartonian), 37.2 ± 1.2 Ma (Hutchison et al. 2004).

Referred material and range. Late Eocene (Bartonian) of Magwe and Mandalay Provinces, Myanmar (hypodigm of *Burmemys magnifica* of Hutchison et al. 2004).

Diagnosis. *Allaeochelys magnifica* can be diagnosed as a carettochelyine by the presence of a midline keel, a single suprapygal, a thickened pygal with an anterior groove, plastral kinesis, a triangular entoplastron, a broad plastron, and the absence of plastral and carapacial scutes in adult individuals, and as a representative of *Allaeochelys* by the presence of a continuous neural series. *Allaeochelys magnifica* can be differentiated from *Al. crassesculpta* and *Al. parayrei* by its significantly larger size and from *Al. delheidi* by having a relatively longer pygal and a less consistent shell sculpturing ranging from distinctly sculptured peripherals to worn neurals.

Comments. *Allaeochelys magnifica* is based on several dozen well-preserved fragments that were collected from the Late Eocene Pandaung Formation of Myanmar. From what can be discerned from the available material, *Al. magnifica* greatly resembles the roughly coeval material reported from Pakistan under the name *Chorlakkichelys shahi* (Broin 1987) and the Pakistani and Burmese material may eventually be shown to be the same species. However, the material from Pandaung is much better preserved and I can therefore reproduce the diagnostic characters outlined by Hutchison et al. (2004) without difficulties, particularly relative to the roughly coeval and similarly sized taxon *Al. delheidi*. This taxon is herein referred to *Allaeochelys* to stop the recent proliferation of monospecific taxa.

Allaeochelys parayrei Noulet, 1867 (= *Castresia munieri* de Stefano, 1902 = *Allaeochelys nouleti* Bergounioux, 1931)

Taxonomic history. *Allaeochelys parayrei* Noulet, 1867 (new species); *Allaeochelys pareyrei* = *Allaeochelys delheidi* = *Cas-*

tresia munieri Bergounioux 1935 (junior synonym and incorrect spelling); *Allaeochelys parayrei = Castresia munieri = Allaeochelys nouleti* Broin 1977 (senior synonym); *Allaeochelys parayrei = Castresia munieri = Allaeochelys nouleti = Anosteira crassesculpta = Anosteira gracilis* Karl and Müller 2008 (senior synonym).

Type material. MHNT, coll. Noulet 1860, uncatalogued (uncat.) (lectotype, designated from syntype series by Broin [1977]), carapace and partial plastron (Bergounioux 1931, figs. 1, 3, 4, 6.1, pls. 12, 13); MHNT, coll. Noulet 1860, uncat. (first paralectotype, designated from syntype series by Broin [1977]), carapace (Bergounioux 1931, fig. 6.2); MHNT, coll. Noulet 1860, uncat. (second paralectotype, designated from syntype series by Broin [1977]), internal mold of carapace (Bergounioux 1931, figs. 2, 6.4).

Type locality. Village of Saïx, Department of Tarn, France (Broin 1977; Figure 6); Bartonian, Late Eocene (Broin 1977).

Referred material and range. Late Eocene (Bartonian) of the Aquitaine Basin, France (hypodigm of *Allaeochelys parayrei* of Broin [1977], including holotypes of *Castresia munieri* and *Al. nouleti*).

Diagnosis. *Allaeochelys parayrei* can be diagnosed as a carettochelyine by the presence of a midline keel, nuchal articulation sites for the eighth cervical vertebra, 10 peripherals, a single suprapygal, a thickened pygal with an anterior groove, plastral kinesis, a triangular entoplastron, a broad plastron, and the absence of plastral and carapacial scutes in adult individuals, and as a representative of *Allaeochelys* by the presence of a continuous neural series. *Allaeochelys parayrei* can be differentiated from *Al. delheidi*, *Al. magnifica*, and *Al. shahi* by being relatively small (carapace length 24 cm) and from *Al. crassesculpta* by having much coarser plastral sculpturing.

Comments. Noulet (1867) was the first to formally name a carettochelyid taxon, but most subsequent authors ignored his work (e.g., Dollo 1886; Lydekker 1889a; de Stefano 1902), likely because he did not provide figures or a detailed description. This situation was remedied by Bergounioux (1931), who relocated the syntype series of *Allaeochelys parayrei* in the collections of the Muséum d'Histoire Naturelle de Toulouse and provided figures and more detailed descriptions of this taxon. Broin (1977) finally provided an even more detailed description of the type material and designated the best-preserved specimen as the lectotype.

Specimens from the immediate vicinity of the type locality of *Allaeochelys parayrei* served as the basis for *Castresia munieri* (de Stefano 1902) and *Allaeochelys nouleti* (Bergounioux 1931), but I agree with Broin (1977) that the presence of a "preneural" is not diagnostic for the presence of a second or third taxon in this region, given that this bone is known to occur polymorphically among taxa such as *Carettochelys insculpta* (Walther 1922). Karl and Müller (2008) furthermore argued that all European carettochelyids are synonymous with *Al. parayrei*, but this conclusion seems to be based on a misreading of Lapparent de Broin (2001), who reported a broad European distribution of the genus *Allaeochelys*, not its type species, *Al. parayrei*.

Karl (2002), Karl et al. (2006), and Karl and Müller (2008) referred several fragmentary carettochelyine specimens from the Early Eocene to Late Oligocene of Germany to *Allaeochelys parayrei* under the assumption that only a single carettochelyid was present in Europe throughout the Tertiary (see above). However, given that three European species are herein designated as valid, it is more prudent to refer these fragmentary remains to *Carettochelyinae* indet.

Invalid and Problematic Taxa

Allaeochelys casasecai Jiménez Fuentes, 1971
nomen invalidum
(junior synonym of
Allaeochelys delheidi
Dollo, 1886)

Taxonomic history. *Allaeochelys casasecai* Jiménez Fuentes, 1971 (new species).

Type material. The holotype consists of the following elements: STUS 27 (partial nuchal), STUS 36, 37, 57, 305 (neurals), STUS 292 (a costal), STUS 1, 2, 4–7, 10, 13, 14, 16, 19, 56, 206, 207, 252, 253, 255–257 (marginals), STUS 15 (partial hyoplastron), STUS 38 (partial hypoplastron), STUS 260 (partial xiphiplastron) (Jiménez Fuentes 1971, figs. 1–8).

Type locality. Corrales del Vino, Zamora Province, Spain (Jiménez Fuentes 1971); MP 13–14, Lutetian, early Eocene (Alonso Santiago and Alonso Andrés 2005).

Comments. The holotype of *Allaeochelys casasecai* was discovered during construction of a well, but the specimen was badly damaged in the process and large portions of the skeleton are missing (Jiménez Fuentes 1971). Substantial amounts of additional material have since been collected in Zamora Province, including complete shells and skulls, that provide further insights into the morphology of this taxon (e.g., Alonso Santiago and Alonso Andrés 2005; Alonso Santiago et al. 2008), but comprehensive description of this material is still wanting.

The description of *Allaeochelys casasecai* provided by Jiménez Fuentes (1971) is sufficient to distinguish it from more primitive carettochelyids (i.e., extensive bridge, lack of scutes), but no differences are listed that would allow it to be distinguished it from all named carettochelyines. Notable exceptions are the large size of this taxon and the development of a relatively broad neural. However, this character combination is also known in the nearly coeval and neighboring taxon *Al. delheidi,* and *Al. casasecai* is therefore herein interpreted as its junior synonym.

Allaeochelys jimenezi
Alonso Santiago and Alonso Andrés, 2005
nomen invalidum
(junior synonym of
Allaeochelys delheidi Dollo, 1886)

Taxonomic history. *Allaeochelys jimenezi* Alonso Santiago and Alonso Andrés, 2005 (new species).

Type material. STUS 12.035 (holotype), a near-complete shell missing most peripherals and the anterior plastral lobe (Alonso Santiago and Alonso Andrés 2005, fig. 4); STUS 12.036–12.039 and 14.056–14.107 (paratypes), a series of additional shell remains, including juvenile material (Alonso Santiago and Alonso Andrés 2005, figs. 5–9).

Type locality. The holotype and the paratypes originate from multiple localities in the vicinity of the town of Corrales del Vino, Zamora Province, Spain; MP 13–14, Lutetian, early Eocene (Alonso Santiago and Alonso Andrés 2005).

Comments. *Allaeochelys jimenezi* is based on several well-preserved shells that were collected in the immediate vicinity of the *Al. casasecai* type locality. The primary differences that distinguish these two taxa are their size and the detailed morphology of the hypoplastral–xiphiplastral suture. In particular, *Al. jimenezi* is about 20% larger than *Al. casasecai* and displays a less complex hypoplastral–xiphiplastral suture (Alonso Santiago and Alonso Andrés 2005; Alonso Santiago et al. 2008). Joyce et al. (2012) recently showed that these very differences reflect sexual dimorphism in *Allaeochelys crassesculpta*. It therefore seems prudent to interpret the Spanish material as a single taxon, with *Al. jimenezi* being the large female with a slightly kinetic posterior plastral lobe and *Al. casasecai* the smaller male lacking shell kinesis. In all other regards, both Spanish taxa fully agree with the near-coeval and neighboring taxon *Allaeochelys delheidi* and are therefore synonymized with it herein.

Allaeochelys nouleti Bergounioux, 1931
nomen invalidum
(junior synonym of
Allaeochelys parayrei Noulet, 1867)

Taxonomic history. *Allaeochelys nouleti* Bergounioux, 1931 (new species); *Allaeochelys parayrei = Castresia munieri = Allaeochelys nouleti* Broin 1977 (junior synonym); *Allaeochelys parayrei = Castresia munieri = Allaeochelys nouleti = Anosteira crassesculpta = Anosteira gracilis* Karl and Müller 2008 (junior synonym).

Type material. A carapace missing most peripherals and the pygal, formerly housed at the Muséum d'Histoire Naturelle de Toulouse, Toulouse, France (Bergounioux 1931, fig. 7, pl. 14), but now considered lost (Broin 1977).

Type locality. La Badaïré locality, near the city of Castres, Department of Tarn, France (Bergounioux 1931; Broin 1977); Bartonian, Late Eocene (Broin 1977).

Comments. Similar to *Allaeochelys munieri*, *Al. nouleti* is based on a near-complete carapace that originated from the general vicinity of the type locality of *Al. parayrei*, is solely diagnosed by the presence of a "preneural," is sufficiently illustrated but now lost, and was argued by Broin (1977) to be a junior synonym of *Al. parayrei*. This conclusion is supported by the observation of Walther (1922) that "preneural" bones occur polymorphically in specimens of the extant *Carettochelys insculpta* (Walther 1922), and I therefore concur with Broin's taxonomic assessment.

Anostira anglica (Lydekker, 1889a)
nomen invalidum
(junior synonym of
Allaeochelys delheidi Dollo, 1886)

Taxonomic history. *Anostira anglica* Lydekker, 1889a (new species, incorrect spelling of genus name); *Anosteira radulina = Anosteira anglica* Baur 1889b (junior synonym, correct spelling of genus name); [*Anosteira anglica*] Hummel 1929 (nomen dubium); *Allaeochelys anglica* Nessov 1976 (new combination).

Type material. BMNH 33198y (holotype), a near complete left xiphiplastron (Lydekker 1889c, fig. 35).

Type locality. Hordle Cliff (formerly Hordwell, Lydekker 1889a), Hampshire, United Kingdom; Headon Hill Formation, Priabonian, Late Eocene (Edwards and Daley 1997).

Comments. *Allaeochelys anglica* is based on an isolated left xiphiplastron from the Late Eocene Hordle Cliffs locality in southern England (Lydekker 1889a, 1889c). The holotype originates from an individual that must have been about the same size as the holotype of the roughly coeval and neighboring taxon *Al. delheidi*, but Lydekker (1889a, 1889c) nevertheless diagnosed a new taxon based on the slightly oblique orientation of the hypoplastral–xiphiplastral suture. The orientation of the hypoplastral–xiphiplastral suture was recently shown to differ between the sexes among representatives of *Allaeochelys crassesculpta* (Joyce et al. 2012) and should therefore not be used to differentiate taxa. Similar sexual variation is herein interpreted to be present among Spanish representatives of *Al. delheidi* (Alonso Santiago and Alonso Andrés 2005). *Allaeochelys anglica* is therefore, at best, a junior synonym of *Al. delheidi*, and at worst a nomen dubium.

Anosteira gracilis (Harrassowitz, 1922)
nomen invalidum
(junior synonym of
Allaeochelys crassesculpta Harrassowitz, 1922)

Taxonomic history. *Anosteira gracilis* Harrassowitz, 1922 (new species); *Anosteira crassesculpta = Anosteira gracilis* Gramann 1956 (junior synonym); *Allaeochelys parayrei = Castresia munieri = Allaeochelys nouleti = Anosteira crassesculpta = Anosteira gracilis* Karl and Müller 2008 (junior synonym).

Type material. HLMD 4000 (syntype, no. 5 of Harrassowitz 1922), posterior half of carapace; HLMD 4282 (syntype, no. 1 of Harrassowitz 1922), near complete skeleton (Harrassowitz 1922, pl. 2.3, pl. 4.2, pl. 6.5, 6); HLMD 4353a, c, d, f, g, i–k (syntype, no. 2 of Harrassowitz 1922), relatively complete skeleton (Harrassowitz 1922, pl. 2.4).

Type locality. Messel Pit, near the village of Messel, State of Hesse, Germany (Harrassowitz 1922); early Lutetian (ca. 47 Ma), Early Eocene (Joyce et al. 2012).

Comments. *Allaeochelys* (orig. *Anosteira*) *gracilis* is based on three individuals found together with the type material of *Al. crassesculpta* at Messel Pit, State of Hesse, Germany (Harrassowitz 1922). The differences that diagnose this taxon were soon after reinterpreted as ontogenetic differences by Gramann (1956), but are now known to represent male characteristics of a sexually dimorphic species (see *Al. crassesculpta* for more details).

Anosteira radulina Cope, 1872b

nomen dubium

Taxonomic history. *Anostira radulina* Cope, 1872b (new species, incorrect spelling of genus name); *Anosteira radulata* Baur 1889b (incorrect spelling); *Anostira radiolina* Lydekker 1889c (incorrect spelling); *Anosteira radulina* Hay 1902 (correct spelling of genus name); [*Anosteira radulina*] Hummel 1929 (nomen dubium).

Type material. USNM 4096 (type series), two marginal bones, one from the front, one from the back (Cope 1884, pl. 18, figs. 18, 19).

Type locality. Upper Green River Basin (Cope 1872b), near Ham's Fork, Lincoln or Sweetwater County, Wyoming. Hay (1908) posits that the types originate from the lowest division of Bridger A, which corresponds to the early Middle Eocene (Ypresian) Black Fork Member of the Bridger Formation of Murphey and Evanoff (2007).

Comments. *Anosteira radulina,* based on two isolated peripheral elements from the Eocene of Wyoming, was primarily diagnosed by Cope (1872b) by its large size relative to all other then known species of *Anosteira*. This size comparison now seems dubious, however, because most *Anosteira* species then known were named by Cope (1872a) and were soon after recognized to be plastomenid trionychids (Cope 1873). An explicit size comparison was not provided by Cope (1872b) relative to *An. ornata.* Cope (1872b) furthermore diagnosed *An. radulina* by differences in the sculpturing, because the sculpturing was as fine as that of other species, even though the material was larger, but Hay (1908) felt this to be irrelevant, because the sculpturing of turtles does not increase in coarseness with size. Hay (1908) instead suggested that *An. ornata* could be diagnosed by differences in the cross-sectional morphology of the peripherals. Not a single specimen has been referred to *An. radulina* to date and the taxonomic validity of this taxon remains uncertain. Hummel (1929) concluded that this taxon is based on insufficient material and that meaningful comparisons with other taxa are not possible. The type specimens of *An. radulina* seem to be lacking a marginal sulcus, which is consistent with the diagnoses of carettochelyines. It is therefore possible that this taxon corresponds to remains of cf. *Allaeochelys* reported from the Eocene of Texas (e.g., Westgate 2001). I herein note that it is possible that two separate carettochelyid lineage could have coexisted during the Eocene of North America, but nevertheless follow Hummel (1929) and consider *An. radulina* to be a nomen dubium, because clearly this isolated peripheral is not sufficient to globally diagnose a taxon.

Anosteira shantungensis Cheng, 1961
nomen invalidum
(junior synonym of
Anosteira mongoliensis Gilmore, 1931)

Taxonomic history. *Anosteira shantungensis* Cheng, 1961 (new species).

Type material. CAGS-IG Vr 32 (holotype), a partial shell and skull in dorsal view, lacking suprapygal, pygal, and peripherals VIII–X (Cheng 1961, figured pp. 273, 277).

Type locality. City of Linqu (Linchu in Cheng 1961), Weifang District, Shandong (Shantung in Cheng 1961) Province, China; Niushan Formation, Late Eocene–Early Oligocene (Cheng 1961).

Comments. *Anosteira shantungensis* is based on a single partial carapace from Shandong Province, China. Cheng (1961) correctly noted that the holotype of *An. shantungensis* differed substantially from that of *An. Manchuriana,* but only found minor differences with other representatives of *Anosteira*, in particular the presence of a square second neural. Variation in the neural counts recently documented by Tong et al. (2010) places doubt on the use of the neural formula in diagnosing carettochelyids, as this character is known to differ among individuals of *An. maomingensis*. I agree with Tong et al. (2010) that *An. shantungensis* is different from *An. maomingensis* in size, but I cannot see any substantial differences with *An. mongoliensis* and therefore synonymize it with that taxon.

Anosteira shuwalovi Chkhikvadze
in Shuvalov and Chkhikvadze, 1979
nomen dubium

Taxonomic history. *Anosteira shuwalovi* Chkhikvadze in Shuvalov and Chkhikvadze, 1979 (new species); *Anosteira shuwalowi = Kizylkumemys schultzi* Nessov and Krassovskaya 1984 (junior synonym, incorrect spelling); *Anosteira shuvalovi* Danilov 1999 (incorrect spelling); *Anosteira shuvalovi = Kizylkumemys schultzi* Sukhanov 2000 (junior synonym, incorrect spelling).

Type material. IP 1-12-14 (holotype), isolated peripheral (Shuvalov and Chkhikvadze 1979, pl. 1.3).

Referred material. IP 11-12-15, right peripheral 9; IP 11-12-16, left peripheral 4; IP, unnumbered, other shell elements.

Type locality. Uryl'b Usu Locality, Dornogovi Province (Aimag), Mongolia; lower part of Bainshire (= Bains15 = Bayanshiree) Formation, Cenomanian–early Turonian, Late Cretaceous (Shuvalov and Chkhikvadze 1979; Danilov 1999).

Comments. *Anosteira shuwalovi* was named on the basis of an isolated peripheral from the Late Cretaceous of Mongolia, but could only be diagnosed using details in the surface sculpture. Although it is possible that future finds from the type locality will support the validity of this taxon, it is apparent that sculpturing alone is not sufficient to diagnose this taxon relative to all other named carettochelyids and that *An. shuwalovi* is best

viewed as a nomen dubium. Indeed, the type specimen is so indistinct that it is not even possible to refer it to either *Anosteira* (Shuvalov and Chkhikvadze 1979) or *Kizylkumemys* (Nessov and Krassovskaya 1984). It is therefore more prudent to identify this fragment as *Pan-Carettochelys* indet.

<div align="center">

Apholidemys granosa Pomel 1847
nomen nudum
Apholidemys sublaevis Pomel 1847
nomen nudum

</div>

Material. All original material has been reported lost (e.g., Noulet 1867; Hummel 1929; Broin 1977).

Locality. Town of Cuise-la-Motte (Cuis-la-Motte in Pomel 1847; Cuysse-la-Motte in Lydekker 1889c), Department of Oise, France; "Cuisian," late Ypresian, Early Eocene (Broin 1977).

Comments. The name *Apholidemys* was introduced by Pomel (1847) to refer to several fragments from the Early Eocene of the Paris Basin. The original description is brief, focuses mostly on two characters (i.e., the absence of scutes and the presence of surface sculpturing), but is sufficient to diagnose a new genus. However, Pomel (1847) only mentioned the species *Aph. sublaevis* and *Aph. granosa* in passing and did not provide any characters that would allow distinguishing these two species. The original material was not figured and has been reported lost since Noulet (1867).

Various authors have discussed possible links between *Apholidemys sublaevis* and *Aph. granosa* with other fossil and living turtles. Lydekker (1889c) suggested that these taxa could by synonymous with the roughly coeval *Allaeochelys delheidi*. Hummel (1929) agreed that the Cuise-la-Motte material may belong to a carettochelyid, but hinted at the possibility that *Aph. sublaevis* and *Aph. granosa* are nomen dubia. Jimenez-Fuentes (1971) and Broin (1977) agreed that *Aph. sublaevis* and *Aph. granosa* are synonymous with each other and referred both taxa to *Allaeochelys*. Finally, Meylan (1988) argued that both names represent nomen dubia. A close reading of the ICZN (1999) reveals that Pomel's (1847) original descriptions of *Aph. sublaevis* and *Aph. granosa* do not satisfy the availability criteria and should be regarded as nomen nuda, because these species-level taxa are not accompanied by a description or indication (ICZN 1999, Article 12.1). By contrast, although the provisions of the ICZN (1999) support *Apholidemys* as an available taxon name, the brevity of Pomel's (1847) description combined with the loss of the type material render this taxon a nomen dubium.

Interestingly, the locality of Cuise-la-Motte has since yielded unambiguous carettochelyid material that resembles *Allaeochelys delheidi* in size (Broin 1977, pl. 14, figs. 14, 24) and it therefore seems plausible that Pomel's (1847) taxa indeed represent true carettochelyids. However, the lack of type material apparently renders any discussion on possible synonymies complete speculation.

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Castresia munieri (de Stefano, 1902)
nomen invalidum
(junior synonym of
Allaeochelys parayrei Noulet, 1867)

</div>

Taxonomic history. *Castresia munieri* Noulet, 1867 (new species); *Anosteira munieri* Hummel 1929 (new combination); *Allaeochelys parayrei* = *Allaeochelys delheidi* = *Castresia munieri* Bergounioux 1935 (junior synonym); *Allaeochelys parayrei* = *Castresia munieri* = *Allaeochelys nouleti* Broin 1977 (junior synonym); *Allaeochelys parayrei* = *Castresia munieri* = *Allaeochelys nouleti* = *Anosteira crassesculpta* = *Anosteira gracilis* Karl and Müller 2008 (junior synonym).

Type material. A carapace missing most peripherals and the pygal, formerly housed at the University Sorbonne, Paris, France (de Stefano 1902, pl. 16), but now considered lost (Broin 1977).

Type locality. La Massale (Massall in de Stefano 1902) near city of Castres, Department of Tarn, France (Broin 1977); Bartonian, Late Eocene (Broin 1977).

Comments. *Allaeochelys* (orig. *Castresia*) *munieri* was named by de Stefano (1902) on the basis of a near complete carapace that was collected in the immediate vicinity of the type locality of *Allaeochelys parayrei*, but he seems to have been blissfully unaware of the entire carettochelyid literature available at that time and concluded instead that this taxon is a trionychid. Although the holotype is now considered lost (Broin 1977), de Stefano's (1902) description is accompanied with a well-crafted photograph. Hummel (1929) therefore had few difficulties in correctly identifying this taxon as a carettochelyid and referring it to *Anosteira*, a taxon then circumscribed to have a global distribution. The only characteristic that distinguishes *Al. munieri* from *Al. parayrei* is the presence of a "preneural" bone. Hummel (1929) felt that this character was insufficient to diagnose a separate genus, but Broin (1977) concluded that this character is not even sufficient to diagnose a species considering that it is known to occur polymorphically among the extant taxon *Carettochelys insculpta* (Walther 1922). I concur with this assessment.

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Chorlakkichelys shahi Broin, 1987
nomen dubium

</div>

Taxonomic history. *Chorlakkichelys shahi* Broin, 1987 (new species).

Type material. GSP-UM 500.1–26, poorly preserved partial shell, consisting at least of the right hypoplastron, right peripherals I, II, V, VIII, left peripherals II, VII, and fragmentary costals (Broin 1987, pl. 1.1, 1.2).

Type locality. Four km NNW of the village of Chorlakki (also Chorlaki), Kohat District, Khyber Pakhtunkhwa Province, Pakistan; Kuldana Formation, Early Eocene (Lutetian) (Broin 1987).

Comments. *Chorlakkichelys shahi* is based on a dozen fragments that are thought to represent a single, highly incomplete specimen from the Early Eocene of Pakistan (Broin 1987). All preserved elements are poorly preserved and show signs of significant pre- or post-depositional erosion. Although there is no doubt that this specimen represents a carettochelyid, I have significant reservations about the diagnostic value of the type spec-

imen. The costals and neurals are not sufficiently preserved to confirm Broin's (1987) assertion that this taxon can be diagnosed as a carettochelyine by the absence of scutes, but the large size of the type specimens is sufficient to do so. The most significant character presented by Broin (1987) is that the plastron of this taxon has a bridge that is as broad as that of other carettochelyines, but that the plastral lobes are still narrow as in "anosteirines." This character is based on a single plastral fragment (Broin 1987, pl. 1.1, 1.2) that Broin (1987) interprets as a partial hypoplastron. However, the position of the center from which the ornamentation radiates and the general outline of the fragment are more conducive to this fragment being the medial portion of a regular, right hyoplastron. The phylogenetic position of this taxon is therefore vague and its only real apomorphy is obsolete. I therefore suggest that this taxon be disregarded and considered a nomen dubium.

Acknowledgments

Appendix 1
Institutional Abbreviations

AMNH — American Museum of Natural History, New York, New York, USA

ANSP — Academy of Natural Sciences, Philadelphia, Pennsylvania, USA

BMNH — Natural History Museum, London, United Kingdom

BSPG — Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany

CAGS-IG — Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China

CCMGE — Chernyshev's Central Museum of Geological Exploration, St. Petersburg, Russia

CM — Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA

CRI — Chelonian Research Institute, Oviedo, Florida, USA

FMNH — Field Museum of Natural History, Chicago, Illinois, USA

GSP-UM — Geological Survey of Pakistani and University of Michigan Cooperative Paleontological Expeditions, Islamabad, Pakistan

HLMD — Hessisches Landesmuseum Darmstadt, Darmstadt, Germany

IRSNB — Royal Belgian Institute of Natural Sciences, Brussels, Belgium

IP — Institute of Palaeobiology, Georgian National Museum, Tbilisi, Georgia

IVPP — Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

MHNT — Muséum d'Histoire Naturelle de Toulouse, Toulouse, France

NRRU — Collection of the Museum of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, Thailand

SMF — Senckenberg Naturmuseum Frankfurt, Frankfurt am Main, Germany

STUS — Sala de las Tortugas, University of Salamanca, Salamanca, Spain

UCMP — University of California Museum of Paleontology, Berkeley, California, USA

USNM — National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

ZIN PH — Zoological Institute of the Russian Academy of Sciences, Paleoherpetological Collection, St. Petersburg, Russia

Appendix 2
Named Pan-Carettochelyid Genera

Allaeochelys Noulet, 1867
(type species: *Allaeochelys parayrei* Noulet, 1867)

Anosteira Leidy, 1871a
(type species: *Anosteira ornata* Leidy, 1871a)

Burmemys Hutchison et al., 2004
(type species: *Burmemys magnifica* Hutchison et al., 2004)

Carettochelys Ramsay, 1887
(type species: *Carettochelys insculpta* Ramsay, 1887)

Castresia de Stefano, 1902
(type species: *Castresia munieri* de Stefano, 1902)

Chorlakkichelys Broin, 1987
(type species: *Chorlakkichelys shahi*, Broin 1987)

Kizylkumemys Nessov, 1977a
(type species: *Kizylkumemys schultzi*, Nessov 1977a)

Pseudanosteira Clark, 1932
(type species: *Pseudanosteira pulchra*, Clark 1932)

Pseudotrionyx Dollo, 1886
(type species: *Pseudotrionyx delheidi*, Dollo 1886)

Appendix 3
Biogeographical Summary of
Pan-Carettochelyid Turtles

Numbers in brackets reference Figures 5, 6 and 7.

Australia
Neogene; Western Australia; Testudines indet. (non *Carettochelyidae* indet. sensu Gorter and Nicoll 1978)

Austria
Middle Miocene, Badenium; Styria; Chelonioidea indet. (non *Carettochelyidae* indet. sensu Gemel and Rauscher 2000)

Belgium
[1] Early Eocene, Lutetian; Province of Flemish Brabant; *Allaeochelys delheidi* (Dollo 1886)

Canada
[2] Early Eocene, Bridgerian, Ypresian; Ellesmere Island; *Anosteira* sp. (Estes and Hutchison 1980)
[3] Early Eocene, Bridgerian, Ypresian; Saskatchewan; *Anosteira* sp. (Hutchison and Storer 1998)

China
[4] Early Paleogene; Guangdong Province; *Allaeochelys lingnanica* (Young and Chow 1962)
[5] Eocene; Jiangxi Province; *Anosteira* sp. (Zhou 1959)
[6] Late Eocene; Inner Mongolia; *Anosteira mongoliensis* (Gilmore 1931)
[7] Late Eocene; Liaoning Province; *Anosteira manchuriana* (Zangerl 1947)
[8] Late Eocene; Guangdong Province; *Anosteira maomingensis* (Chow and Liu 1955; Chow 1956; Ye 1963, 1994; Tong et al. 2010)
[9] Late Eocene–Early Oligocene; Shandong Province; *Anosteira mongoliensis* (Cheng 1961)

Democratic Republic of Congo
[10] Late Miocene; *Carettochelyinae* indet. (Hirayama 1992)

Egypt
[11] Early Miocene, Burdigalian; *Carettochelyinae* indet. (Dacqué 1912; Lapparent de Broin 2000)

France
Late Cretaceous, Cenomanian; Poitou-Charentes; ?*Carettochelyidae* (Vullo et al. 2010)
[12] Early Eocene, Ypresian; Paris Basin; *Pseudotrionyx delheidi* (?Pomel 1847; Broin 1977)
[13] Late Eocene, Bartonian; Aquitaine Basin; *Allaeochelys parayrei* (Noulet 1867; de Stefano 1902; Bergounioux 1931; Broin 1977)

Germany
[14] Early Eocene, Lutetian; Hesse; *Allaeochelys crassesculpta* (Harrassowitz 1922; Weitzel 1949; Groessens-Van Dyck 1978; Joyce et al. 2012)

[15] Early Miocene, Burdigalian; North Rhine Westphalia; *Carettochelyinae* indet. (Joyce, Klein and Mörs 2004)
[16] Early Oligocene, Rupelian; Hesse; *Carettochelyinae* indet. (Gramann 1956; Karl and Müller 2008)
[17] Late Oligocene; Bavaria; *Carettochelyinae* indet. (Darga et al. 1999; Karl 2002)
[18] Late Oligocene; Saxony-Anhalt; *Carettochelyinae* indet. (Karl et al. 2006)

Japan
[19] Late Cretaceous; Coniacian/Santonian; Kumamoto Prefecture; *Pan-Carettochelys* indet. (Hirayama and Chitoku 1994; Hirayama 1998)

Laos
Early Cretaceous, Aptian/Albian; Savannakhet Province; ?*Pan-Carettochelys* (Lapparent de Broin 2004)

Libya
[20] Early Miocene, Burdigalian; Al Wahat District; *Allaeochelys libyca* (Havlik et al. in review)

Mongolia
[21] Late Cretaceous, Cenomanian/Turonian; Dornogov Province (Aimag); *Pan-Carettochelys* indet. (Shuvalov and Chkhikvadze 1979; Nessov 1981; Sukhanov et al. 2008)

Myanmar
[22] Late Eocene, Bartonian; Magwe and Mandalay provinces; *Anosteira* sp. (Hutchison et al. 2004)
[23] Late Eocene, Bartonian; Magwe and Mandalay provinces; *Allaeochelys magnifica* (Hutchison et al. 2004)

Oman
Early Miocene; Testudinidae indet. (Lapparent de Broin 2000; non *Carettochelyidae* indet. sensu Roger et al. 1994)

Pakistan
[24] Early Eocene, Lutetian; Khyber Pakhtunkhwa Province; *Allaeochelys* sp. (Broin 1987)

Papua New Guinea
[25] Upper Miocene; *Carettochelyinae* indet. (Glaessner 1942)

Russia
Upper Paleocene; Lower Volga Basin; Testudines indet. (Averianov and Yarkov 2000; non *Carettochelyidae* sensu Efimov and Yarkov 1993a, 1993b)

Saudi Arabia
Early Miocene; Eastern Province; ?*Carettochelyinae* indet. (Thomas et al. 1981)

Spain
[26] Early Eocene, Lutetian; Zamora Province, *Allaeochelys delheidi* (Jiménez Fuentes 1971; Alonso San-

tiago and Alonso Andrés 2005; Alonso Santiago et al. 2008)

Thailand

[27] Early Cretaceous, Aptian; Nakhon Ratchasima and Ubon Ratchathani provinces; *Kizylkumemys khoratensis* (Tong et al. 2005; Tong et al. 2006)

[28] Early Cretaceous, Aptian; Khon Kaen, Kalasin and Nong Bu Lam Phu provinces; *Kizylkumemys* sp. (Tong et al. 2006; Tong et al. 2009)

United Kingdom

[29] Late Eocene, Priabonian; Hampshire; *Allaeochelys delheidi* (Lydekker 1889a, 1889c)

[30] Early Eocene, Ypresian; Isle of Sheppey; *Allaeochelys delheidi* (Lydekker 1889c)

United States of America

[32] Early Eocene, Bridgerian, Ypresian; Wyoming; *Anosteira ornata* (Leidy 1871a; Hay 1906)

[33] Early Eocene, Uintan, Lutetian; Utah; *Anosteira pulchra* (Gilmore 1915; Clark 1932)

[34] Early Eocene, Bridgerian, Ypresian; Wyoming; *Anosteira* sp. (Cope 1872b; Zonneveld et al. 2000)

[35] Late Eocene, Duchesnian, Bartonian; Utah; *Anosteira* sp. (Eaton et al. 1999)

[36] Late Eocene, Chadronian, Priabonian; South Dakota; *Anosteira* sp. (Clark et al. 1967)

[37] Early Eocene, Uintan, Lutetian; Texas; cf. *Allaeochelys* (Westgate 1989, 2001)

Uzbekistan

[31] Late Cretaceous, Cenomanian; Karakalpakstan Autonomous Republic; *Kizylkumemys schultzi* (Nessov 1976, 1977a, 1977b, 1977c, 1985, 1986, 1987, 1995, 1997)

Appendix 4
Hierarchical Taxonomy of
Pan-Carettochelys

Pan-Carettochelys Joyce, Parham and Gauthier, 2004

  Kizylkumemys khoratensis Tong et al., 2005

  Kizylkumemys schultzi Nessov, 1977a

  Carettochelyidae Gill, 1889

    Anosteira manchuriana Zangerl, 1947

    Anosteira maomingensis Chow and Liu, 1955

    Anosteira mongoliensis Gilmore, 1931

    Anosteira ornata Leidy, 1871a

    Anosteira pulchra (Clark, 1932)

    Carettochelyinae Williams, 1950

      Allaeochelys crassesculpta (Harrassowitz, 1922)

      Allaeochelys delheidi (Dollo, 1886)

      Allaeochelys libyca Havlik et al., in review

      Allaeochelys lingnanica (Young and Chow, 1962)

      Allaeochelys magnifica (Hutchison et al., 2004)

      Allaeochelys parayrei Noulet, 1867

        Carettochelys insculpta Ramsay, 1887

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