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An alternative interpretation of the Paleogene turtle *Cardichelyon rogerwoodi* as a hinged kinosternoid

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Abstract.—*Cardichelyon rogerwoodi* is an enigmatic fossil turtle from the late Paleocene to early Eocene of North America. Previous analyses suggested affiliation with Testudinoidea, in particular the big-headed turtle *Platysternon megacephalum*, based on the presence of multiple musk-duct foramina and a large head. We here highlight previously undocumented characteristics for this turtle, notably the presence of short costiform processes, a rib-like axillary process, and a posterior plastral hinge. Phylogenetic analysis places *Cardichelyon rogerwoodi* within Testudinoidea, but the exclusion of testudinoids suggest an affiliation with Dermatemydidae. Using consilience with external data we favor placement within Kinosternoidea. *Cardichelyon rogerwoodi* is therefore an aberrant, hinged kinosternoid that developed in situ in North America during the Paleocene long before the arrival of testudinoids on this continent in the early Eocene.

Introduction

Cardichelyon rogerwoodi Hutchison, 2013 is an enigmatic, big-headed fossil turtle from the Paleogene of the western United States (Hutchison, 2013). Even though this taxon had been noted in the literature under various informal names since the mid 1970s (Estes, 1975; Bartels, 1980, 1983; Hutchison, 1980, 1992, 1998; McCord, 1996; Holroyd and Hutchison, 2000; Holroyd et al., 2001; Hutchison and Frye, 2001), it was only formally named and described recently (Hutchison, 2013). In addition to rich, fragmentary material from the late Paleocene (Clarkforkian) to early Eocene (Wasatchian) of Wyoming, *Cardichelyon rogerwoodi* is known from more complete specimens, including complete shells and a partial skull, that document important anatomical details of systematic value. Estes (1975), Bartels (1980, 1983), Hutchison (1980, 1992, 1998), and McCord (1996) highlighted affinities with pond turtles (Emydidae and Geoemydidae), but did not discuss this assessment. In the type description, Hutchison (2013) referred *Cardichelyon rogerwoodi* to the Asian big-headed turtles (Platysternidae), but only listed the presence of multiple musk-duct foramina and a macrocephalic skull as character evidence. This hypothesis was tentatively confirmed by the phylogenetic analysis of Vlachos (2018). The possible presence of a fossil platysternid in the Paleogene of North America has biogeographic significance because the group has otherwise only been reported from the Tertiary of Asia (see Danilov et al., 2018 for a recent summary).

We here report that the type material of *Cardichelyon rogerwoodi* exhibits characters that were not noted by previous authors and that suggest kinosternoid, rather than testudinoid affinities for this taxon. The purpose of this contribution is to re-describe the shell of this turtle, to discuss the available character evidence, and to provide an alternative phylogenetic assessment.

Materials and methods

The type material of *Cardichelyon rogerwoodi* was collected over the course of the 1930s and 1940s by teams from Princeton University and is now held at YPM. The descriptions provided herein are based on personal observations of this material. Hutchison (2013) described and figured additional material from other localities that is housed at UCMP. Because we did not observe this material in person, we regularly refer to these descriptions as a source of additional information, but cannot comment on their accuracy. The extant turtles utilized in the phylogenetic analyses or for comparisons are housed at AMNH, BMNH, FMNH, and USNM.

Repositories and institutional abbreviations.—Herpetology, American Museum of Natural History (AMNH), New York, New York, USA; Herpetology, Natural History Museum (BMNH), London, United Kingdom; Herpetology, Field Museum of Natural History (FMNH), Chicago, Illinois, USA; University of California Museum of Paleontology (UCMP), Berkeley, California; USA; Herpetology, National Museum of Natural History (USNM), Washington DC, USA; Vertebrate Paleontology, Yale Peabody Museum of Natural History (YPM), New Haven, Connecticut, USA.

Systematic paleontology

Testudines Batsch, 1788
Cryptodira Cope, 1868
Chelydroidea Baur, 1893
Kinosternoidea Hutchison and Weems, 1998
Dermatemydidae Baur, 1888
Cardichelyon Hutchison, 2013

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Type species.—*Cardichelyon rogerwoodi* Hutchison, 2013, by original designation, by monotypy.

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Cardichelyon rogerwoodi Hutchison, 2013
Figures 1–4

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Holotype.—YPM PU14671, a partial skeleton, including a restored shell, a partial skull, and fragments of long bones and girdles (Hutchison, 2013, figs. 26.8, 26.12, 26.13; Figs. 1–3) from Reis Quarry, Park County, Wyoming, USA, Fort Union Formation, Clarkforkian NALMA, Thanetian, late Paleocene (Hutchison, 2013).

Diagnosis.—See Hutchison (2013) and Vlachos (2018).

Occurrence.—Late Paleocene (Clarkforkian NALMA) to early Eocene (Wasatchian) of Wyoming (Hutchison, 2013).

Description.—In addition to the description given below, see Figures 1–4.

Carapacial bones.—The carapace of the holotype (YPM PU14671) is almost completely fused (Fig. 1), we therefore cannot discern the arrangement of neural and costal bones in this specimen. Illustrations of referred specimens provided by Hutchison (2013, fig. 26.8, 26.11), however, suggest that the carapace consists of a nuchal, eight often irregular neurals, two suprapygals, a pygal, eight pairs of costals that lack a midline contact, and 11 pairs of peripherals.

A number of important characters can be observed on the inside of the carapace that have not been highlighted previously (Figs. 1, 2). The attachment site of dorsal rib I is short and the rib heads of dorsal ribs II–IX are notably slender. It is unclear if the proximal end of dorsal rib X was ossified in life because this part of the shell is not preserved. As previously noted by Hutchison (2013), a groove is formed at the junction of costal I with peripherals II and III that holds the rib-like axillary buttress of the hyoplastron (Fig. 2.1). As also noted by Hutchison (2013), the rib of costal I inserts distally into peripheral IV, just below the axillary buttress. However, the nuchal forms a small, previously unnoted costiform process that penetrates the medial third of peripheral I (Fig. 2.1).

We agree with Hutchison (2013) that the bridge reaches from the anterior part of peripheral IV to the midpoint of peripheral VI, but we note a previously undocumented shift in the articulation with the plastron at peripheral VI (Figs. 1, 2.2). In particular, while the articular site with the anterior plastral lobe protrudes medially, is notably thick, and shows evidence of a former sutural contact with the hyoplastron, the articular site with the posterior plastral lobe is recessed, has a granular texture, and lacks interdigitations with the hypoplastron. This morphology is consistent with a kinetic posterior plastral lobe, which is confirmed by the morphology of the plastron (see below). We agree with Hutchison (2013) that peripherals III–VI form four pairs of musk duct foramina. The first musk duct is located on peripheral III at the intersection of marginals III and IV with the skin sulcus. The second and third musk duct foramina are positioned on peripherals IV and V at the intersections of marginals IV, V, and VI with the bridge. The fourth

musk duct foramen on peripheral VI is only poorly developed because it coincides with the hinge line of the plastron.

Carapacial scutes.—We agree with Hutchison (2013) that the carapace of *Cardichelyon rogerwoodi* is covered by five vertebrals, four pairs of pleurals, and 12 pairs of marginals (Fig. 1). The holotype and a referred specimen figured by Hutchison (2013, fig. 26.9) apparently lack a cervical. Hutchison (2013) noted that a minute cervical may be present in unfigured specimens, but we are not able to confirm this observation for the moment. Vertebral I is a narrow, pentagonal element with short anterolateral contacts with marginal I, broad lateral contacts with pleural I, and a straight posterior contact with vertebral II. Vertebrals II and III are hexagonal and slightly broader than long. Vertebral IV is pentagonal, with longer posterolateral sides. Vertebral V is hexagonal, but the anterior sulcus with vertebral III is much broader than the posterior sulcus with vertebral V. Vertebral V is the broadest scute in the vertebral series. It has a short anterior contact with vertebral IV, a broad anterolateral contact with pleural IV, a point contact with marginal X, and broad posterior contacts with marginals XI an XII. The location of the intervertebral sulcus relative to the neural column is obscured in the holotype, but illustrations of referred specimens provided by Hutchison (2013, fig. 26.11) suggest that the vertebral I/II sulcus is located on neural I, the vertebral II/III sulcus on neural III, the vertebral III/IV sulcus on neural V or VI, and the vertebral IV/V sulcus on neural VIII or suprapygal I. The low and narrow nature of the marginals suggests that they are restricted to the peripherals.

Plastral bones.—We generally agree with the morphology of the plastron as presented by Hutchison (2013, fig. 26.12). As in all other cryptodires, the plastron consists of an entoplastron, and a pair of epi-, hyo-, hypo-, and xiphiplastra (Figs. 3, 4). The plastron is notable for being relatively thick (∼7 mm at the center) and for having deep and thick lips along the margins of the anterior and posterior lobes (up to 1.5 cm). In anterior view, the epiplastra jointly form a deep trough (Fig. 3.3).

The hyoplastron has a sutural contact with the posterior three-quarters of peripheral IV, peripheral V, and the anterior third of peripheral VI and forms an elongate axillary buttress that is located along the suture of costal I with peripherals II and III. The anterior plastral lobe was therefore fully immobilized. The hypoplastron, by contrast, forms a short inguinal buttress that ligamentously attached to the posterior two-thirds of peripherals VI and the anterior half of peripheral VII. The posterior plastral lobe was therefore kinetically articulated with the rest of the shell. The type plastron is reconstructed as having a broad posterior plastral lobe and a blunt anal notch (Fig. 3), but a previously unfigured plastron from the type locality (YPM PU16443; Fig. 4) highlights a more distinct anal notch. Although we cannot exclude intraspecific variation, large amounts of plaster lead us to believe that the anal notch of the type specimen was reconstructed incorrectly. We note the presence of paired fields of crenulations with unknown function on the visceral side of the hypoplastron anteromedially to the inguinal notches in the type specimens (Fig. 3).
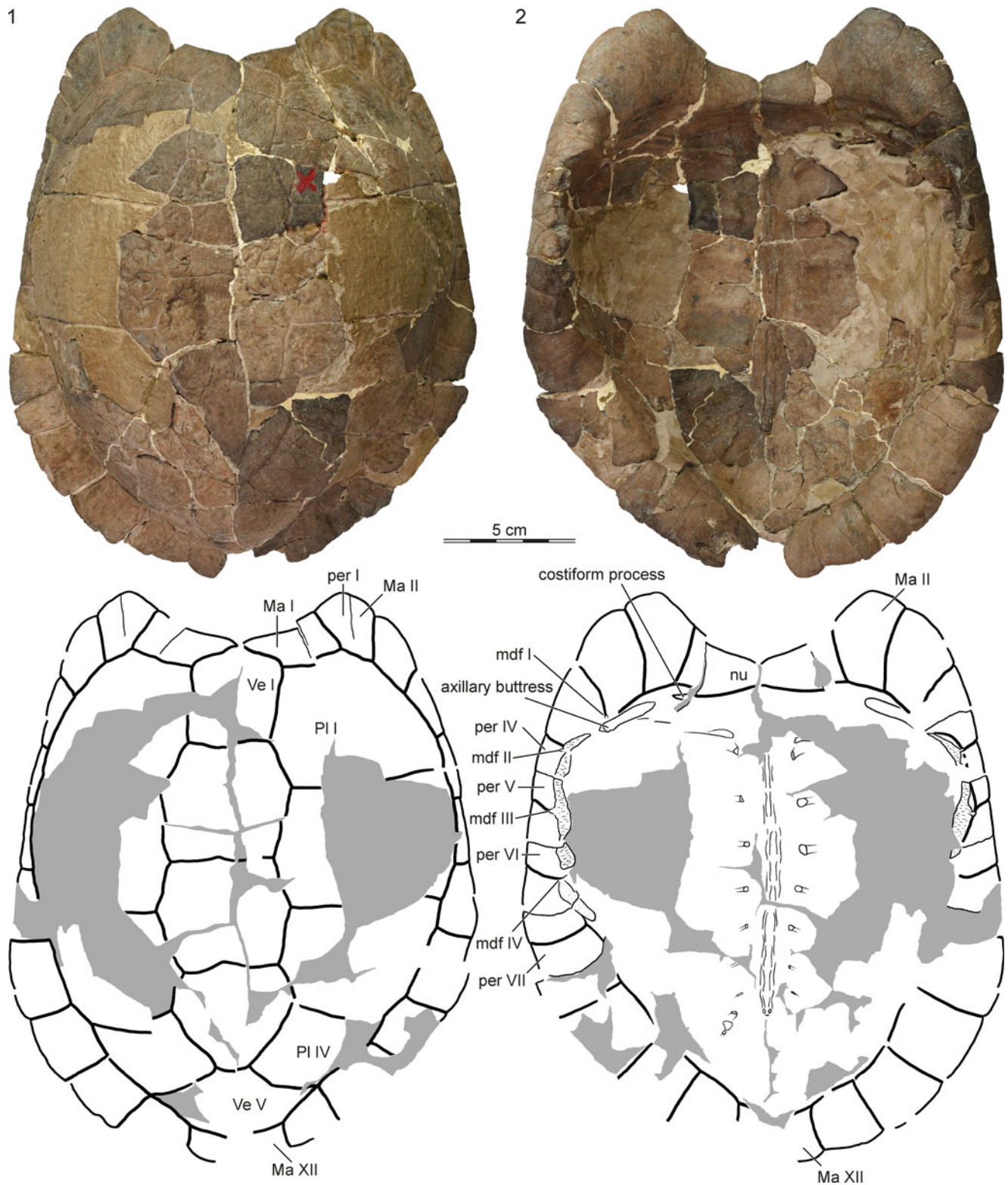
Figure 1. YPM PU14671, holotype of *Cardichelyon rogerwoodi*, late Paleocene (Clarkforkian) of Wyoming. Reconstructed carapace in (**1**) dorsal and (**2**) ventral view. Gray areas highlight reconstruction. Abbreviations: Ma = marginal scute; mdf = musk duct foramen; nu = nuchal; per = peripheral; Pl = pleural scute; Ve = vertebral scute.

Plastral scutes.—We concur with Hutchison (2013) that the plastron is covered by a pair of gular, humeral, pectoral, abdominal, femoral, and anal scutes with midline contacts (Figs. 3, 4). Inframarginals appear to be absent. In contrast to the referred plastron figured by Hutchison (2013, fig. 26.12.c), the gulars and pectorals of the holotype barely overlap the anterior and posterior tips, respectively, of the entoplastron in the holotype. The pectoral/abdominal sulcus closely
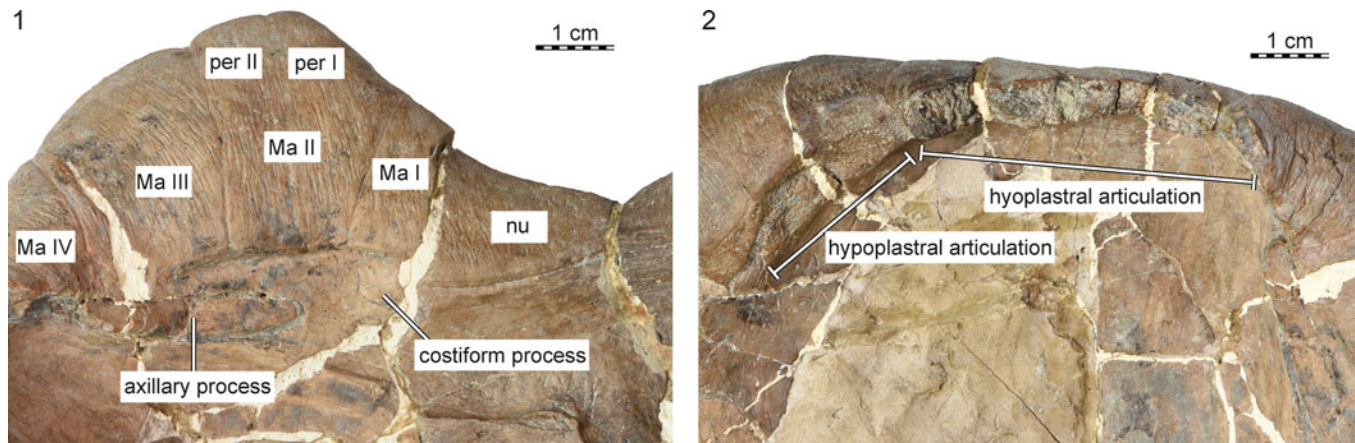
Figure 2. YPM PU14671, holotype of *Cardichelyon rogerwoodi*, late Paleocene (Clarkforkian) of Wyoming. Detailed view of (**1**) the left costiform process and axillary buttress and (**2**) the left bridge peripherals. Abbreviations: Ma = marginal scute; nu = nuchal; per = peripheral.

approximates the hyo/hypoplastral suture. In addition, the portion of the abdominal that overlaps the hyoplastron has a finely crenulated surface. A similar arrangement is found in extant testudinoids with hinges with limited mobility. All scutes jointly cover the visceral side of the plastron to form broad plastral lips (Fig. 3). These lips are at their thickest along the gulars and the femorals.

Remarks.—None.

Phylogenetic analysis

Our character analysis (see Discussion below) highlights that *Cardichelyon rogerwoodi* possesses characters that either suggest relationships with Testudinoidea or Chelydroidea (i.e., the clade consisting of snapping turtles [Chelydridae] and mud and musk turtles [Kinosternoidea]). We are not able to test either position in a global context because no analysis of turtle relationships is currently available that densely samples these two groups of turtles and the characters that diagnose them. Because we herein ultimately favor relationships of this turtle with Chelydroidea (see Discussion below), we inserted *Cardichelyon rogerwoodi* into the chelydroid analysis of Lyson et al. (2017), an expansion of the kinosternoid matrix of Knauss et al. (2011), to investigate its possible placement within the clade Chelydroidea. All characters were scored based on the two specimens described herein (YPM PU14671, the holotype, and YPM PU16443), with exception of the neural and cervical characters, which were scored based on material described by Hutchison (2013). We furthermore added four testudinoids to the matrix to explore their impact on the analysis, in particular the Late Cretaceous *Mongolemys* sp. (based on material referred to *Mongolemys* spp. by Danilov, 2001), the extant emydid *Chrysemys picta* (Schneider, 1783) (AMNH 75250), the extant testudinid *Gopherus agassizii* (Cooper, 1861) (USNM 222094), and the extant platysternid *Platysternon megacephalum* Gray, 1831 (FMNH 51627). The analysis was furthermore expanded to include three additional shell characters that could eventually be relevant for differentiating testudinoids from chelydroids: character 66, number of musk glands (0 = none; 1 = one; 2 = two; 3 = three; 4 = four); character 67, costal contact of

axillary buttresses (0 = absent; 1 = present); and character 68, costal contacts of inguinal buttresses (0 = absent; 1 = present). All extant taxa were scored for character 66 by reference to Waagen (1972). The remaining characters were scored using the same resources as Knauss et al. (2011) and Lyson et al. (2017). The final characters matrix consisting of 68 characters scored for 29 taxa is provided in Supplementary data set 1.

The matrix was subjected to a parsimony analysis using TNT (Goloboff et al., 2008) with *Judithemys sukhanovi* Parham and Hutchison, 2003 selected as the outgroup. Eleven characters form morphoclines and were run ordered (i.e., characters 4, 10, 16, 22, 25, 29, 34, 40, 44, 45, 66). Following the recommendation of Goloboff et al. (2018), light implied weighting was implemented using a K-factor of 12. The matrix was subjected to 1000 replicates of random addition sequences followed by a second round of tree bisection-reconnection. Two primary analyses were performed that differ in their inclusion of the four testudinoids. Because the testudinoids did not resolve themselves as suggested by recent molecular analyses (e.g., Pereira et al., 2017), we forced the sister group relationship of the fossil *Mongolemys* spp. to all extant testudinoids, and the sister group relationship between the emydid *Chrysemys picta* and *Platysternon megacephalum* relative to *Gopherus polyphemus* through the use of a backbone constraint. All remaining taxa were left to float. The analysis that includes the testudinoids resulted a single tree as well with a score of 8.26752, while the analysis to the exclusion of the four testudinoids resulted in a single tree with a score of 6.49208. These trees are provided in Figure 5.

Discussion

Cardichelyon rogerwoodi exhibits a number of conflicting characters that either suggest chelydroid or testudinoid affinities. As characters are used to initially assess the phylogenetic affinities of taxa, we list in the first section of this discussion the most notable characters apparent in this turtle and examine their currently known distribution across the tree to assess their phylogenetic significance. In the next section, we then discuss the results of our phylogenetic analysis. In the final section, we
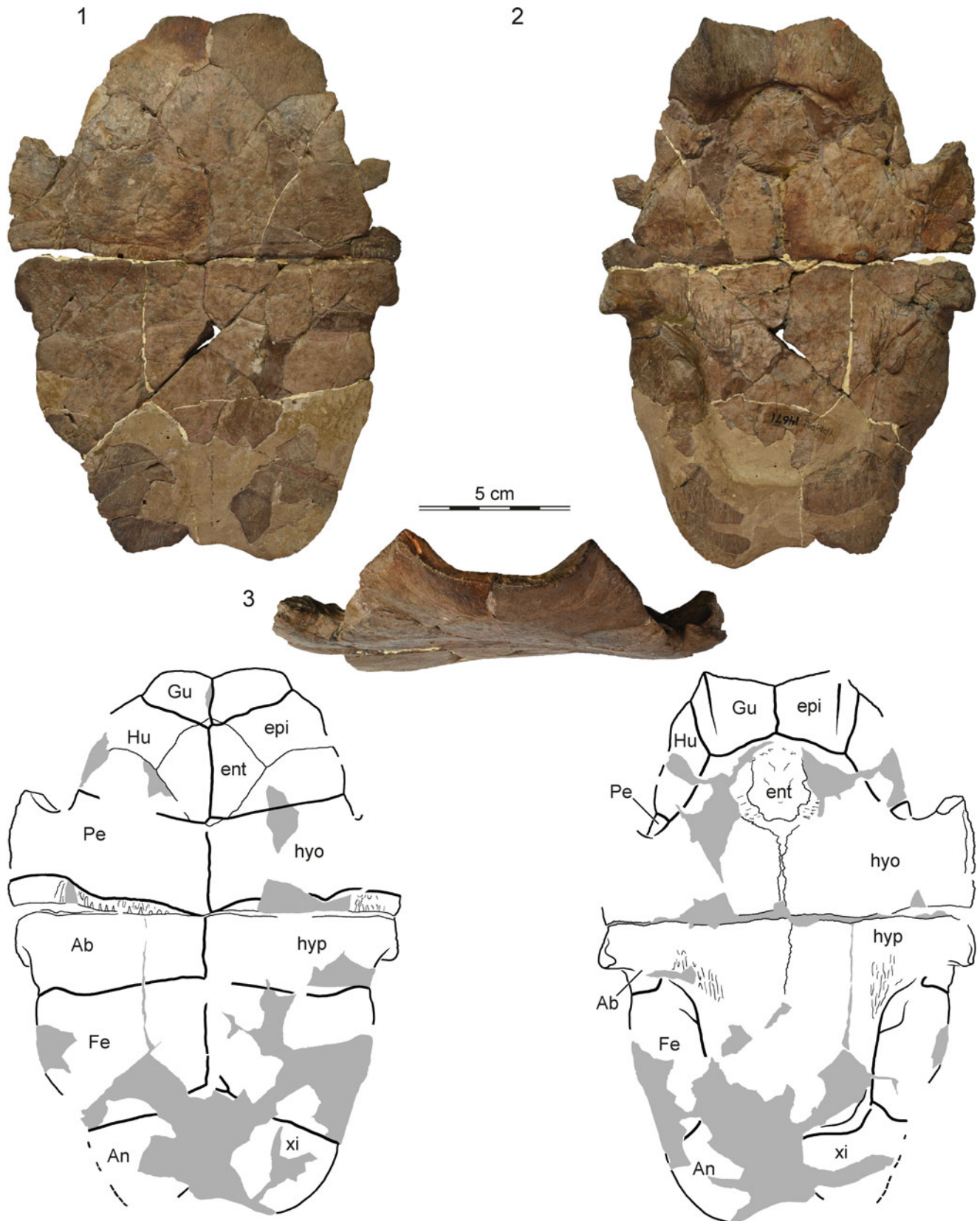
Figure 3. YPM PU14671, holotype of *Cardichelyon rogerwoodi*, late Paleocene (Clarkforkian) of Wyoming. Reconstructed plastron in (**1**) ventral, (**2**) dorsal, and (**3**) and anterior view. Gray areas highlight reconstruction. Abbreviations: Ab = abdominal scute; An = anal scute; ent = entoplastron; epi = epiplastron; Fe = femoral scute; Gu = gular scute; Hu = humeral scute; hyo = hyoplastron; hyp = hypoplastron; Pe = pectoral scute; xi = xiphiplastron.
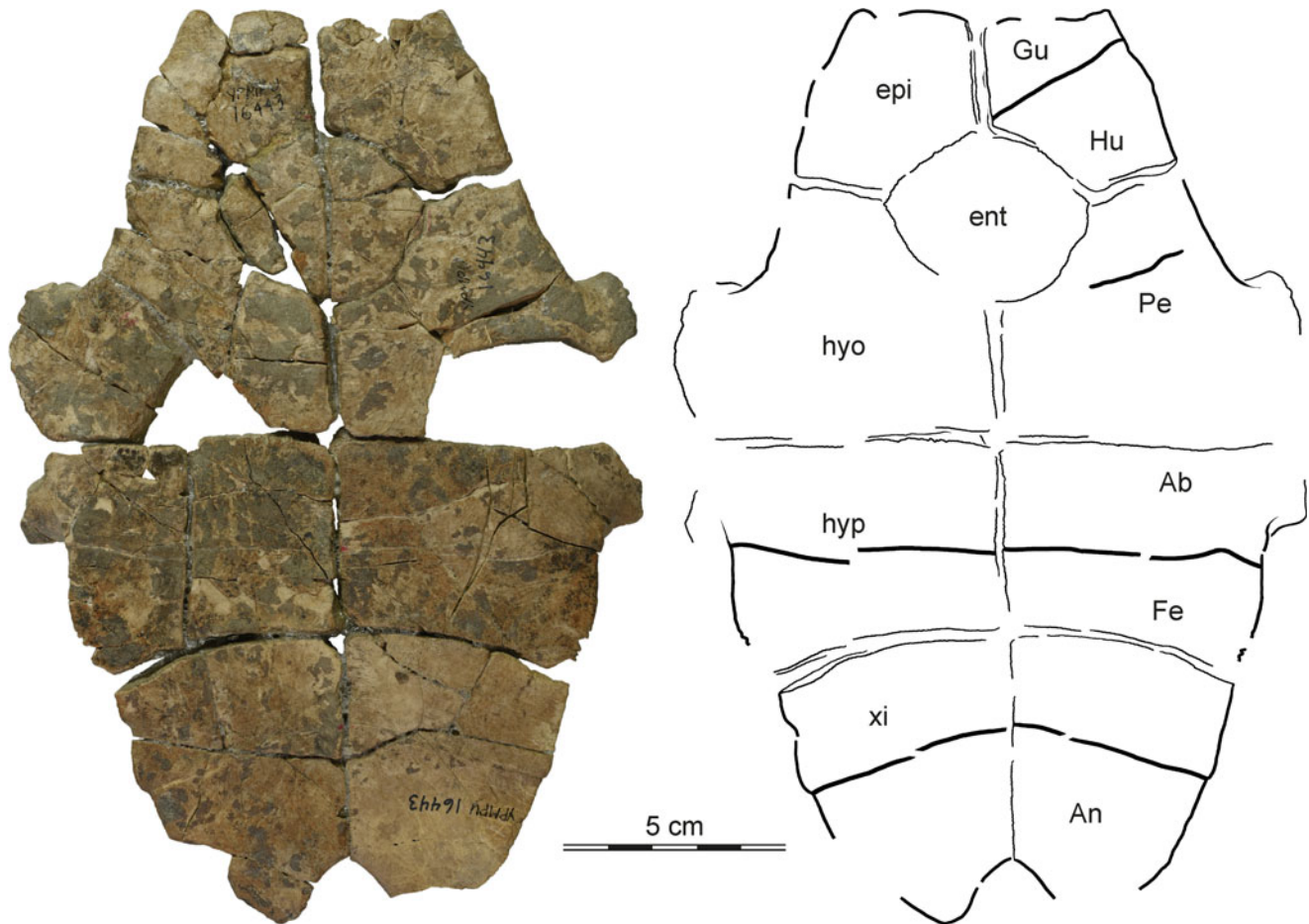
Figure 4. YPM PU16443, *Cardichelyon rogerwoodi*, late Paleocene (Clarkforkian) of Wyoming. Plastron in ventral view. Abbreviations: Ab = abdominal scute; An = anal scute; ent = entoplastron; epi = epiplastron; Fe = femoral scute; Gu = gular scute; Hu = humeral scute; hyo = hyoplastron; hyp = hypoplastron; Pe = pectoral scute; xi = xiphiplastron.

use consilience to argue for the chelydroid affinities of this unusual turtle.

Character analysis.—Prior to its formal description, *Cardichelyon rogerwoodi* was thought to be an emydid or a geoemydid (Estes, 1975; Bartles, 1980, 1983; Hutchison, 1980, 1992, 1998, 2013; McCord, 1996), but no character evidence was provided to support either assessment. Hutchison (2013) suggested platysternid affinities for this taxon based on its macrocephalic nature and presence of multiple musk duct foramina. This was informally accepted by Vlachos (2018), but the format of this contribution prohibited him from exploring the phylogenetic relationships of this enigmatic turtle more extensively. In all cases, however, previous authors presumed this taxon to have testudinoid affinities.

The shell of *Cardichelyon rogerwoodi* possesses a number of characters that indeed are consistent with testudinoid relationships, but also with kinosternoid relationships. We here briefly highlight and discuss the most important ones.

Plastral scutes.—Testudinoids are unique among extant turtles by possessing paired gulars, humerals, pectorals, abdominals, femorals, and anals (Hutchison and Bramble, 1981), in contrast to extant chelydrids and kinosternoids, which possess intergulars, but lack pectorals (Joyce, 2016; Joyce and Bourque, 2016). A recent phylogenetic analysis of Americhelydia with focus on Chelydroidea (i.e., the clade consisting of Chelydridae and Kinosternoidea) concluded that the lack of pectorals is a synapomorphy of Chelydroidea, but that pectorals were secondarily reacquired within this clade, for instance in the Paleocene dermatemydid *Agomphus pectoralis* (Cope, 1868) (Lyson et al., 2017). Similarly, although the presence of intergulars may optimize to be a synapomorphy of Americhelydia or Chelydroidea, these scutes are lacking in numerous forms, including most dermatemydids. In addition to *Cardichelyon rogerwoodi*, the testudinoid arrangement of plastral scutes is also found in the tentative kinosternoid *Planetochelys dithyros* Hutchison, 2013 (Joyce and Bourque, 2016). The plastral formula seen in *Cardichelyon rogerwoodi* is therefore consistent with both kinosternoid and testudinoid relationships.

Extensive plastral lips.—In contrast to extant americhelydians, most testudinoids are typically characterized by the presence of extensive plastral lips (i.e., broad margins along the visceral sides of the anterior and posterior plastral lobes covered by scutes). However, extensive plastral lips are also present in
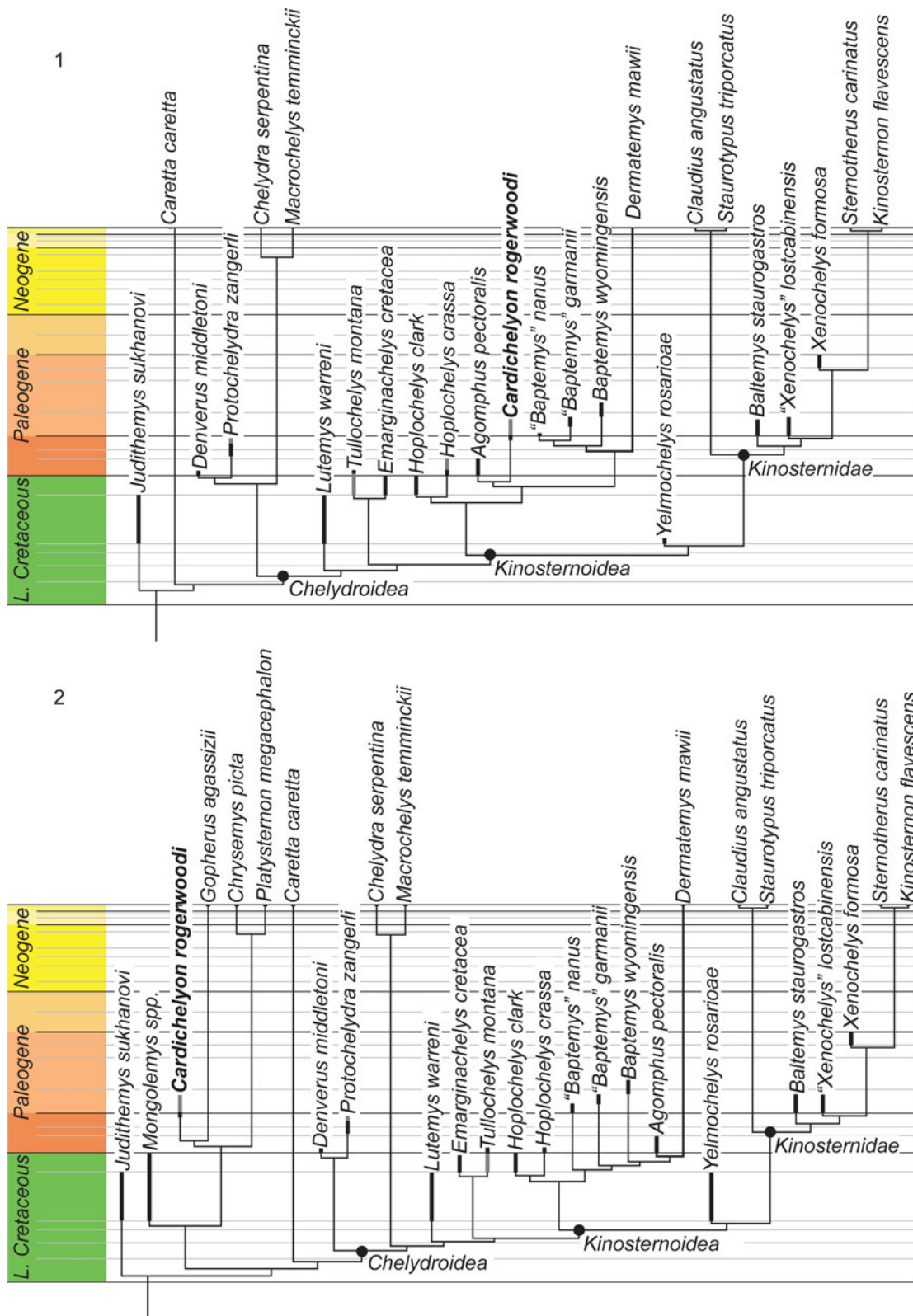
Figure 5. The time calibrated trees retrieved from the phylogenetic analyses performed herein that differ in the (**1**) inclusion and (**2**) exclusion of testudinoids. Thick dark bars denote the type range of a particular species, gray bars connote the range of referred material.

many other turtles, particularly those with broad plastra, including the extant pelomedusid *Pelusios castanoides* Hewitt, 1931 (BMNH 1911.4.7.2), the chelid *Platemys* platycephala (Schneider, 1792) (FMNH 45659), and fossil nanhsiungchelyids, such as "*Zangerlia*" *dzamynchondi* Sukhanov and Narmandkh, 2006 (Danilov et al., 2013). In

addition to *Cardichelyon rogerwoodi*, we also note the presence of plastral lips in the tentative kinosternoid *Planetochelys dithyros* Hutchison, 2013, the stem kinosternid *Xenochelys lostcabinensis* Hutchison, 1991, and the extant kinosternid *Kinosternon flavescens* Agassiz, 1857 (AMNH 73826). This character is therefore consistent with both kinosternoid and testudinoid affiliations.

Plastral kinesis.—Plastral kinesis (i.e., a plastral hinge) has evolved multiple times across the turtle tree. The independent acquisition of hinges is suggested in part by the non-homologous structures that are involved. For instance, an epi/hyoplastral hinge is found in the kinosternid *Kinosternon*, an anteriorly mobile hyo/hypoplastral hinge in the pelomedusids *Pelusios*, a posteriorly mobile hyo/hypoplastral hinge in the fossil testudinoid *Ptychogaster*, a fully mobile hyo/hypoplastral hinge in the emydid *Cuora*, and a hypo/xiphiplastral hinge again in the kinosternid *Kinosternon* (e.g., Bramble, 1974; Mlynarski, 1976; Bramble and Hutchison, 1981; Bramble et al., 1984). Although a hyo/hypoplastral suture has not previously been reported for a kinosternoid, with exception of the tentative kinosternoid *Planetochelys dithyros*, the great number of independent acquisitions of this character complex does not provide much support for any particular clade.

Musk glands.—Hutchison (2013) noted that the presence of multiple musk duct glands suggests platysternid relationships for *Cardichelyon rogerwoodi*, but we presume that this assessment was made under the assumption that this fossil is a testudinoid. In general, testudinoids only possess two pairs of musk glands, an axillary gland located near the junction of marginals III and IV and an inguinal gland near the junction of marginals VI and VII (Waagen, 1972). An important exception to the rule is *Platysternon megacephalum*, which possesses doubled axillary glands associated with marginals IV and V, in addition to an inguinal gland, an arrangement also seen in some individuals of *Terrapene* (Waagen, 1972). The musk ducts of *Platysternon megacephalum* do not leave any trace in the bony structures surrounding the ligamentous bridge. The four preserved musk duct foramina of *Cardichelyon rogerwoodi* located at the junctions of marginals III–VII therefore do not align well with those of *Platysternon megacephalum*.

Chelydrids possess four pairs of glands that are situated mid-body associated with marginals V–VII. Kinosternoids, in contrast, possess two pairs of glands, of which the anterior is situated far to the front associated with marginal III and the posterior at the back associated with marginal VII (Waagen, 1972). *Cardichelyon rogerwoodi* appears to possess a condition intermediate between that of extant chelydrids and kinosternoids by possessing more than two pairs of glands, as in chelydrids, of which the most anterior is displaced towards the front, as in kinosternoids. The musk duct foramina of *Cardichelyon rogerwoodi* are therefore overall more consistent with it being a chelydroid.

Costiform processes.—We here note for the first time that *Cardichelyon rogerwoodi* possesses short costiform processes (i.e., lateral projections formed by the nuchal that protrudes laterally into the peripherals). Although one of us (WGJ) previously argued that costiform processes are restricted to chelydroids (Joyce, 2007; Lyson et al., 2017), we here side with Shaffer et al. (1997) by noting the presence of short costiform processes not only in some individuals of the testudinoid *Platysternon megacephalum*, but also some nanhsiungchelyids, such as *Hanbogdemys orientalis* (Sukhanov and Narmandakh, 1975) (Sukhanov, 2000). Costiform processes are therefore typical of chelydroids, but not unique to the group.

Rib-like axillary processes.—The hyoplastron forms elongate axillary processes in a series of turtles to stabilize the bridge, but its shape and contacts have phylogenetic significance. Although the length of the axillary processes varies greatly in testudinoids, if present, it typically curves towards the midline at peripheral III towards dorsal ribs I and II to contact costal I (Joyce and Bell, 2004). Among chelydroids, elongate axillary processes are only present in kinosternoids, particularly those associated with the *Dermatemys* lineage. In these taxa, the axillary buttress forms an elongate, rib-like process that runs along the peripheral/costal contact towards the costiform processes of the nuchal and does not insert distally along the visceral side of costal I (Knauss et al., 2011). In this regard, the rib-like axillary buttress of *Cardichelyon rogerwoodi* more closely matches the axillary buttress of kinosternoids, in particular the *Dermatemys* lineage, rather than that of testudinoids.

Anal notch.—A notable feature of *Cardichelyon rogerwoodi* is its deep anal notch. Among testudinoids, deep anal notches are present in geoemydids and testudinids, but absent in emydids and platysternids. Well-developed anal notches are also present in some kinosternoids, such as the late Eocene *Xenochelys formosa* Hay, 1906 or the extant *Dermatemys mawii* Gray, 1847 (FMNH 98950). This character therefore does not have a strong phylogenetic signal.

In conclusion, the presence of pectorals, extensive plastral lips, hyo/hypoplastral kinesis, a deep anal notch, and the absence of intergulars are typical of testudinoids, but their homoplastic presence among kinosternoids is notable. Costiform processes are consistently developed in kinosternoids, but are known to occur homoplastically elsewhere, including testudinoids. The rib-like axillary process and association of a musk duct foramen with marginal III are typical of kinosternoids, but there are no reasons a priori to conclude that they cannot have developed homoplastically in other groups as well. *Cardichelyon rogerwoodi* is therefore either an unusual testudinoid with supernumerary, anteriorly shifted musk duct foramina, rib-like axillary processes, and costiform processes, or an unusual kinosternoid with hyo/hypoplastral hinge, pectoral scutes, and a deep anal notch.

Phylogenetic relationships.—Our character analysis suggests that *Cardichelyon rogerwoodi* most plausibly represents an unusual testudinoid, or an unusual kinosternoid, but we are not able to test either hypothesis rigorously because we are not aware of an appropriate character/taxon matrix that scores these groups and their characters densely, and because constructing such a matrix is far beyond the scope of this

contribution. We conclude below that consilience favors kinosternoid relationships, therefore we inserted *Cardichelyon rogerwoodi* into the chelydroid matrix of Lyson et al. (2017), but performed two analyses that differ in the inclusion of testudinoids.

The analysis including testudinoids retrieves *Cardichelyon rogerwoodi* outside of Americhelydia within Testudinoidea, in particular as sister to *Gopherus agassizii*, not *Platysternon megacephalum*, as had been suggested previously (Fig. 5.1). However, because the matrix of Lyson et al. (2017) was developed specifically to explore chelydroid relationships, we do not give weight to this particular placement within Testudinoidea. Interestingly, every single testudinoid by itself is sufficient to force the alternative topology. The placement of *Cardichelyon rogerwoodi* as sister to *Gopherus agassizii* is suggested by a single character, the presence of a relatively domed shell (21). Three additional characters (presence of a transverse epi/hyoplastral suture [32], presence of a reduced cervical [60], and presence of a costal contact of the axillary buttress [67]) support placement within Testudinoidea. *Cardichelyon rogerwoodi* itself possess seven autapomorphies (4, 8,12, 13, 21, 47, 66), none of which is a reversal of testudinoid characters. The result of this analysis differs from that of Lyson et al. (2017) by placing *Denverus middletoni* Hutchison and Holroyd, 2003 and *Protochelydra zangerli* Erickson, 1973 at the base of Chelydroidea and not as sister to Chelydridae.

The second analysis excluding testudinoids results in a single tree that resembles the result of Lyson et al. (2017) by hypothesizing an extended dermatemydid lineage consisting not only of *Hoplochelys* and *Baptemys*, but also of *Agomphus pectoralis* and *Cardichelyon rogerwoodi* (Fig. 5.2). In contrast to Lyson et al. (2017), however, *Baptemys* is reconstructed as monophyletic, which implies an extended ghost lineage for *Dermatemys mawii*. The sister group relationship of *Agomphus pectoralis* and *Cardichelyon rogerwoodi* is supported by the insertion of costal rib I into peripheral VI (8) and the presence of pectorals (28). *Cardichelyon rogerwoodi* is placed well within the pan-kinosternoid clade in this analysis. In particular, it is placed within Dermatemydidae, supported by five characters (13, 22, 29, 30, 67). More generally, its placement within Pan-Kinosternoidea is supported by another 11 characters (26, 27, 40, 44–47, 52, 53, 62, 64). *Cardichelyon rogerwoodi* itself exhibits seven autapomorphies (12, 15, 18, 20, 23, 29, 32), but none of these is a reversal of the characters that nest it within Pan-Kinosternoidea. This final observation is consistent for taxa naturally nested deep within the tree because terminal taxa incorrectly pulled into the tree by homoplasy display high numbers of reversals.

Consilience.—Even though parsimony suggests that *Cardichelyon rogerwoodi* has testudinoid relationships (see previous section), three external lines of evidence (time, biogeography, and phylogenetic context) favor chelydroid relationships instead.

Time and biogeography.—As currently understood, a number of Asian lineages (carettochelyids, testudinids, geoemydids, and, perhaps, emydids) appeared in North American nearly instantaneously at the Paleocene/Eocene boundary, likely as a response to a sudden shift in biomes during the Paleocene/Eocene Thermal Maximum (PETM; Hutchison, 1998; Joyce et al., 2016; Vlachos, 2018). Although the Behring Land Bridge consistently existed during the Paleogene, unknown barriers apparently hindered turtles from crossing it. Asian faunas arrived in Europe either directly from Asia or from North America following the PETM as well (e.g., Claude and Tong, 2004; Lourenço et al., 2012; Smith et al., 2014). This general pattern would not hold true if *Cardichelyon rogerwoodi* were a testudinoid because this turtle would have crossed the Behring Land Bridge long before the climatic event that allowed the coordinated dispersal of its relatives (Vlachos, 2018), as early as the Tiffanian (Hutchison, 2013). In contrast, if *Cardichelyon rogerwoodi* is a chelydroid, no uncoordinated dispersal event is needed to explain its presence in the Paleocene fossil record of North America because this clade was endemic to this continent for most of its history (Joyce, 2016; Joyce and Bourque, 2016).

Phylogenetic context.—Our phylogenetic analyses suggest two primary hypotheses for the placement of *Cardichelyon rogerwoodi*: either within Testudinoidea or as sister to *Agomphus pectoralis* at the base of Dermatemydidae. Either hypothesis is made more meaningful by the biogeographic and temporal patterns it explains and the character evolution it implies. The testudinoid hypothesis does not have much explanatory power because it suggests the isolated occurrence of a hinged testudinoid in the late Paleocene of North America that fortuitously shares numerous unusual characteristics (e.g., costiform processes, rib-like axillary processes, supernumerary musk glands) with unrelated, but contemporary turtles from North America. The dermatemydid hypothesis, on the other hand, embeds *Cardichelyon rogerwoodi* in the kinosternoid tree in a meaningful way because this turtle is placed in close association with *Agomphus pectoralis* or *Hoplochelys crassa* (Cope, 1888), two roughly coeval taxa from North America that happen to share the abovementioned characteristics. We therefore favor this hypothesis herein.

Outlook.—Our conclusion that consilience favors *Cardichelyon rogerwoodi* as a kinosternoid provides testable predictions in regards to the morphology of elements not yet found. The skeleton of chelydroids differs most consistently perhaps from that of testudinoids in the morphology of the cervical vertebrae. Although much variation is apparent, testudinoids typically show double articulations between cervicals V–VIII and they have a biconvex cervical IV and a biconcave cervical VII. In the cervical column of chelydroids, by contrast, double articulations are restricted to cervicals VI–VIII, and cervical II or III are often, though not always, biconvex, particularly in dermatemydids, and the posterior cervicals are consistently procoelous (Williams, 1950). These two groups of turtles further differ in the morphology of their pectoral and pelvic girdles because many kinosternoids exhibit an accessory process on the scapula, a true thelial process, and a deep ilial notch (Lyson et al., 2017), although we suspect that the pelvis of *Cardichelyon rogerwoodi* is modified to accommodate for the biomechanical demands of a posterior plastral hinge (Bramble, 1974). Even a complete skull of *Cardichelyon*

rogerwoodi may not provide much useful data, given that the partial skull described by Hutchison (2013) appears to be highly modified, much as the highly modified skull of the testudinoid *Platysternon megacephalum*, which was incorrectly argued to be a chelydrid based on skull characters (Gaffney, 1975; Parham et al., 2006; Joyce and Sterli, 2012).

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sn02v6×0t.

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