RESEARCH PAPER

A new kinosternoid from the Late Cretaceous Hell Creek Formation of North Dakota and Montana and the origin of the *Dermatemys mawii* lineage

Georgia E. Knauss · Walter G. Joyce ·
Tyler R. Lyson · Dean Pearson

Abstract A nearly complete turtle shell from the Late Cretaceous (Maastrichtian) Hell Creek Formation of Slope County, North Dakota, represents the most complete remains to date of a Mesozoic kinosternoid turtle and a new species, *Hoplochelys clark* nov. sp. The new taxon is diagnosable from other representatives of *Hoplochelys* by the plesiomorphic placement of the humeral/femoral sulcus behind the hyo/hypoplastral suture and the autapomorphic development of an interrupted median (neural) keel. All six previously named Paleocene (Puercan and Torrejonian) representatives of *Hoplochelys* lack diagnostic characters and are synonymized as *Hoplochelys crassa*. A phylogenetic analysis reveals that *Hoplochelys* spp. and *Agomphus pectoralis* are most parsimoniously placed within Kinosternoidea along the phylogenetic stem of the extant Mesoamerican River Turtle *Dermatemys mawii*, extending that taxon's stem lineage from the early Eocene to the late Maastrichtian. The two primary crown lineages of Kinosternoidea are thus known from the Mesozoic and split prior to the late Campanian. The presence of a thickened cruciform plastron, true costiform processes, only three inframarginals, and the reduction of the medial contact of the abdominals are synapomorphies of Chelydroidea, the clade formed by Chelydridae and Kinosternoidae.

G. E. Knauss
SWCA Environmental Consultants,
Inc., Sheridan, WY 82801, USA
e-mail: gknauss@swca.com

G. E. Knauss
Department of Geoscience, University of Iowa,
121 Trowbridge Hall, Iowa City, IA 52242, USA

W. G. Joyce (✉)
Institut für Geowissenschaften, University of Tübingen,
Sigwartstraße 10, 72076 Tübingen, Germany
e-mail: walter.joyce@uni-tuebingen.de

W. G. Joyce
Division of Vertebrate Paleontology,
Yale Peabody Museum of Natural History,
170 Whitney Avenue, New Haven, CT 06511, USA

T. R. Lyson
Department of Geology and Geophysics, Yale University,
210 Whitney Avenue, New Haven, CT 06511, USA
e-mail: tyler.lyson@yale.edu

T. R. Lyson
Marmarth Research Foundation, Marmarth, ND 58643, USA

D. Pearson
Pioneer Trails Region Museum, 12 First Avenue Northeast,
Bowman, ND 58623, USA

Kurzfassung Eine fast komplette Schildkrötenschale, die in der spätkretazischen (Maastrichtium) Hell Creek Formation in Slope County, Norddakota, gefunden wurde, stellt den bisher vollständigsten mesozoischen Rest einer kinosternoideen Schildkröte dar und wird hier als neue Art *Hoplochelys clark* beschrieben. Anhand der plesiomorphen Lage des humero/femoralen Sulcus hinter der hyo/hypoplastralen Sutur und des autapomorphisch unterbrochenen medianen Kiels kann die neue Schildkröte von anderen Hoplochelys Arten unterschieden werden. Allen sechs bisher bekannten Arten aus dem Paläozän (Puercium und Torrejonium) fehlen diagnostische Merkmale. Daher werden sie als *Hoplochelys crassa* synonymisiert. Die phylogenetische Analyse ergibt, dass es am sparsamsten ist, *Hoplochelys* spp. und *Agomphus pectoralis* entlang der

Stammlinie der heute lebenden Tabascoschildkröte *Dermatemys mawii* zu platzieren. Das Alter dieser Stammliniengruppe wird daher vom Früheozän ins Spätmaastrichtium zurückverlegt. Die zwei primären Stammlinien der Kinosternoidea sind somit aus dem Mesozoikum bekannt und spalteten sich voneinander vor dem Spätcampanium ab. Die Ausbildung eines verdickten, kreuzförmigen Plastrons, echte rippenartige Fortsätze des Nuchale, nur drei Inframarginalschilder und der Verlust des medianen Kontaktes der Abdominalscuta sind Synapomorphien des Monophylums Chelydroidea, welches von Chelydridae und Kinosternoidea gebildet wird.

Schlüsselwörter Hell Creek Formation · Norddakota · Maastrichtium · Oberkreide · Kinosternoidea · *Hoplochelys clark* n. sp. · *Dermatemys mawii*

Introduction

Kinosternoidea is a species-rich clade of turtles that originated in North America during the Cretaceous and is currently endemic to the western hemisphere (Hutchison 1991; Ernst and Barbour 1989). The two primary subgroups of this clade are the lineages leading to the extant Mesoamerican river turtle, *Dermatemys mawii*, and the North American mud turtles, the Kinosternidae (e.g., Meylan and Gaffney 1989; Hutchison 1991; Shaffer et al. 1997).

Although it could be argued that the fossil record of North American turtles is the best worldwide, the detailed origin and evolutionary history of Kinosternoidea remains poorly known. The pre-Pleistocene fossil record of Pan-Kinosternidae only includes four named taxa that range from the early Eocene (Wasatchian) to early Oligocene (Chadronian) (Hutchison 1991). Even older, fragmentary remains of unnamed stem-kinosternids have been reported from the Paleocene Williamsburg Formation of South Carolina (Hutchison and Weems 1998), the Maastrichtian Hell Creek Formation of Montana (Hutchison and Archibald 1986; Holroyd and Hutchison 2002), and the Campanian Kaiparowits Formation of Utah (Hutchison et al. 1998). More recently Brinkman and de la Rosa (2006) figured and described a number of compelling remains from the Campanian Cerro del Pueblo Formation of Mexico that they interpreted as stem-kinosternids.

The fossil record of the stem lineage of *Dermatemys mawii* is similar to that of Kinosternidae in that it includes a number of named fossil taxa from the Eocene, all of which are currently classified as *Baptemys* (Hay 1908a; Hutchison and Bramble 1981; Hutchison 1991). However, even though the presence of a stem-kinosternid in the Campanian predicts the co-occurrence of the *Dermatemys mawii* stem lineage, not a single pre-Eocene fossil has yet

been described, although late Paleocene (Tiffanian) material has been mentioned in the literature (e.g., Hutchison et al. 1998). The Late Cretaceous to Paleocene taxon *Agomphus* is currently interpreted as a stem-kinosternoid (Hutchison and Bramble 1981), whereas all Paleocene *Hoplochelys* spp. are currently interpreted as stem-kinosternids (Hutchison and Bramble 1981; Hutchison 1991; Joyce 2007). Meylan and Gaffney (1989) hypothesized that the Late Cretaceous (Maastrichtian) taxon *Emarginachelys cretacea* is a stem-kinosternoid. However, based on personal observations of the type material by two of the authors (G.E.K. and W.G.J.), we agree with Whetstone's (1978) original assessment that this taxon is a stem-chelydrid because the holotype clearly exhibits an extensive nuchal costiform process that contacts the third peripheral, a character that unambiguously diagnoses Pan-Chelydridae (Hutchison 2008).

The discovery of a near complete shell of a kinosternoid in the Cretaceous Hell Creek Formation of North Dakota provides a rare glimpse into the early evolution of this clade. The purpose of this paper is to describe the new specimen in detail, designate it as a new taxon, review the alpha taxonomy of *Hoplochelys*, and reassess the phylogeny of the base of Kinosternoidea. The shell nomenclature used herein follows Hutchison and Bramble (1981). All names are intended to be clade names and follow the phylogenetic definitions of Joyce et al. (2004).

Institutional abbreviations

AMNH: American Museum of Natural History, New York City, New York
ANSP: Academy of Natural Sciences, Philadelphia, Pennsylvania
FMNH: Field Museum of Natural History, Chicago, Illinois
PTRM: Pioneer Trails Regional Museum, Bowman, North Dakota
SMP: State Museum of Pennsylvania, Harrisburg, Pennsylvania
UCMP: University of California Museum of Paleontology, Berkeley, California
USNM: United States National Museum, Washington, D.C.
YPM: Yale Peabody Museum of Natural History, New Haven, Connecticut

Geological settings

The Hell Creek Formation was deposited during the retreat of the Western Interior Seaway and is comprised of lithologies that represent channels, crevasse splays,
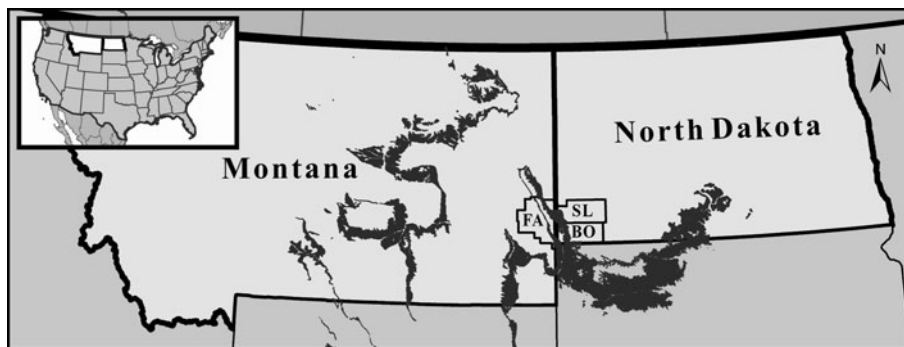
Fig. 1 A map of Montana and North Dakota highlighting the counties from which all material referred to *Hoplochelys clark* n. sp. was recovered. *Dark gray areas* indicate where the Late Cretaceous (late Maastrichtian) Hell Creek Formation is exposed. All localities are located along the northeastern flank of the Cedar Creek anticline. *BO* Bowman County, *FA* Fallon County, *SL* Slope County

floodplain mudstones and siltstones, paleosols, carbonaceous claystones, and occasional lignites (Murphy et al. 2002). All specimens referred to the new taxon were recovered along the erosional drainage basin of the Little Missouri River in Slope and Bowman counties, North Dakota, and Fallon County, Montana (Fig. 1).

The type locality (PTRM V95018) was excavated during the 1996–2000 field seasons by PTRM to remove the remains of associated ceratopsid and hadrosaurid dinosaurs. During the removal of overburden, the stratigraphic positioning of the site was identified, and the depositional sequence was determined as representing channel and floodplain sediments associated with a meander stream environment. The holotype of the new kinosternoid *H. clark* n. sp. (PTRM 16173) was uncovered from within the overlying sediments in the summer of 1999.

The channel sandstone preserving the dinosaur specimens is located 23.44 m below the pollen-defined Cretaceous-Tertiary (K/T) boundary (Johnson 2002). It represents a meander channel preserved as a series of stacked sandstone deposits. The basal portion of this sandstone has large sets of cross-bedding overlain by a horizon of iron-stained planar sandstone with abundant non-armored mud ball inclusions, which in turn lies in contact with the uppermost sandstone, again planar in nature, but containing abundant lignitic clasts and macerated carbonaceous materials. The dinosaur fossils are primarily associated with the mud ball horizon in the middle of the sandstone horizons. The entire excavation is located within a bend of the channel, and most of the specimens are found lying at an inclined angle mirroring the channel margins.

Overlying the channel sands is a nearly 200 cm thick silty mudstone deposit with thin siltstone laminae representing the adjacent floodplain. The lower part of this silty mudstone is 65 cm thick and preserves mud balls along its contact with the sandstone deposit below. The presence of these mud balls indicates an incising current causing stream margin erosion of the flood plain and bank cave-off. This mudstone also represents the adjacent floodplain and preserves leaf impressions from nearby floras within the silty laminae. The plant material represents megaflora remains of "*Dryophyllum*" *tennessensis*, "*Dryophyllum*" *subfalcatum*, *Erlingdorfia montana*, "*Rhamnus*" *cleburni*, *Marmarthia trivialis*, and *Sequoia* sp., all of which are assigned to the HC III Floral Zone known to represent the last floral assemblage of the Hell Creek Formation during warm and wet climates (Johnson 2002). PTRM 16173 was collected from within this silty mudstone, 40 cm above the basal contact, which is 21.10 m below the pollen-defined K/T boundary.

Above the basal 65 cm of silty mudstone is a 4 cm thick interfingering sandstone interpreted to be an overbank deposit of the sandstone channel (containing the dinosaurs of this site below), which remains active in the area adjacent to the floodplain. No vertebrate or plant remains are found in association with this sandstone stringer, which effectively divides the floodplain mudstone into an upper and lower part and also indicates some scale of missing time. The upper part of this floodplain mudstone is 130 cm thick and preserves no vertebrate or plant remains.

Systematic paleontology

Testudines Linnaeus, 1758
Cryptodira Cope, 1868
Chelydroidea Baur, 1893
Kinosternoidea Gaffney and Meylan, 1988
Pan-Dermatemys Joyce et al., 2004
Hoplochelys Hay, 1908a

Type species: *Hoplochelys crassa* (Cope, 1888)
  Diagnosis: Member of Chelydroidea (i.e., the clade consisting of Kinosternoidea and Chelydridae) based on the presence of a thickened cruciform plastron, absence of

extragular scales, reduced abdominal scales that do not contact one another along the midline, reduction of infra-marginal scales to three, and the presence of true costiform processes (sensu Joyce 2007) that cross at least the first peripherals on the visceral shell surface. Member of Kinosternoidea based on the absence of femoral scales and overlap of hyo/hypoplastron sutures by inguinal scales. Member of Pan-Dermatemys based on the presence of rectangular vertebral scales that are at least one and a half times longer than wide, a greatly thickened plastron, and the presence of three distinct keels.

Hoplochelys crassa (Cope, 1888)

- – *Hoplochelys saliens* Hay, 1908a
- – *Hoplochelys paludosa* Hay, 1908a
- – *Hoplochelys bicarinata* Hay, 1910
- – *Hoplochelys elongata* Gilmore 1919
- – *Hoplochelys laqueata* Gilmore, 1919

Type specimen: AMNH 6091, currently consisting of two medial right costals, four peripherals (including the right sixth, a fourth or fifth, a tenth, and a pygal), partial right hyoplastron, and partial left hypoplastron figured in Hay (1908a, plate 38, figs. 4–9 and text-fig. 325), herein designated as the lectotype.

Type locality: Inferred to be "[…] in the neighborhood of Chaco Canyon, San Juan County, New Mexico" (Hay, 1908a, p. 263).

Type horizon: Lower Paleocene beds, Puercan or Torrejonian North American Land Mammal Age (NALMA).

Referred specimens: All material from the Puercan and Torrejonian of New Mexico described by Hay (1908a) and Gilmore (1919) under the name *Hoplochelys*.

Diagnosis: We recognize two differentiating characters: median keel continuous (the usual condition among basal Dermatemydidae but not developed in *H. clark*); humeral/femoral sulcus overlaps with hyo/hypoplastral suture (unique placement among Kinosternoidea).

Comments: *H. crassa* was originally based on two individuals (Cope 1888), one of which was lost by the time Hay (1908a) conducted his review of the fossil turtles of North America. Considering that this syntype appears to be lost and was never figured, we herein designate the second syntype, AMNH 6091, as the lectotype. This specimen was not available for study but was figured by Hay (1908a). Thus, our observations of this specimen are based on the illustrations of Hay (1908a).

Hoplochelys clark n. sp. (Figs. 2, 3, 4).

Type specimen: PTRM 16173, a slightly crushed and nearly complete shell lacking only the anterior portions of the nuchal and much of the pygal regions (Figs. 2, 3).

Type locality: PTRM site V95018 Slope County, North Dakota.

Type horizon: Hell Creek Formation, Late Cretaceous, late Maastrichtian; 21.10 m below the pollen-defined K/T boundary.

Etymology: The new taxon is named after the PTRM volunteer, Merle Clark, who excavated the type specimen and spent numerous hours in the field and at the museum with three of the authors, G.E.K., T.R.L., and D.A.P. The species epithet was formed explicitly as a noun in apposition.

Referred specimens: PTRM site V00009: PTRM 10015 isolated right forth peripheral (Fig. 4e–h) and even numbered posterior neural; PTRM site V01040: PTRM 6794, isolated half non-bridge peripheral; PTRM site V02025: PTRM 8558, even numbered posterior neural; PTRM site V86002: PTRM 2953, even numbered posterior neural, PTRM 2961, isolated right third peripheral (Fig. 4a–d), PTRM 10009, isolated proximal costal; PTRM site V88017: PTRM 9475, even numbered posterior neural; PTRM site V88018: PTRM 2949, isolated proximal half costal five; PTRM site V92003: PTRM 2920, isolated left seventh peripheral (Fig. 4i–l); YPM 57288, isolated proximal portion of even numbered costal; YPM 57648, isolated neural VIII (Fig. 4m–p); YPM 57706, isolated neural VII (Fig. 4p–s). All PTRM specimens originate from late Maastrichtian-age Hell Creek Formation localities in neighboring Slope and Bowman counties, North Dakota. All YPM specimens were also collected from exposures of the Hell Creek Formation, but just west of the PTRM localities in Fallon County, Montana. Detailed locality information will be made available to qualified researchers by PTRM and YPM upon request.

Affiliated specimens: SMP 1578, isolated neural III or V; SMP VP 1650, partial left hypoplastron; SMP VP 2109, isolated peripheral II; SMP VP 2514, proximal costal fragment. All SMP specimens originate from the Naashoibito Member of the Ojo Alamo Formation in San Juan County, New Mexico, and are thus thought to be early Maastrichtian in age.

Diagnosis: We recognize two differentiating characters: median keel not continuous, subdivided into four distinct subkeels (unique among Dermatemydidae); humeral/femoral sulcus placed posterior to the hyo/hypoplastral suture (the usual placement among Kinosternoidea, but not developed in *H. crassa*).

Description of *Hoplochelys clark* n. sp.

Preservation: The holotype is an almost complete shell with no associated cranial or other postcranial remains. The specimen was likely complete in the ground, but was only found by coincidence while overburden was being moved
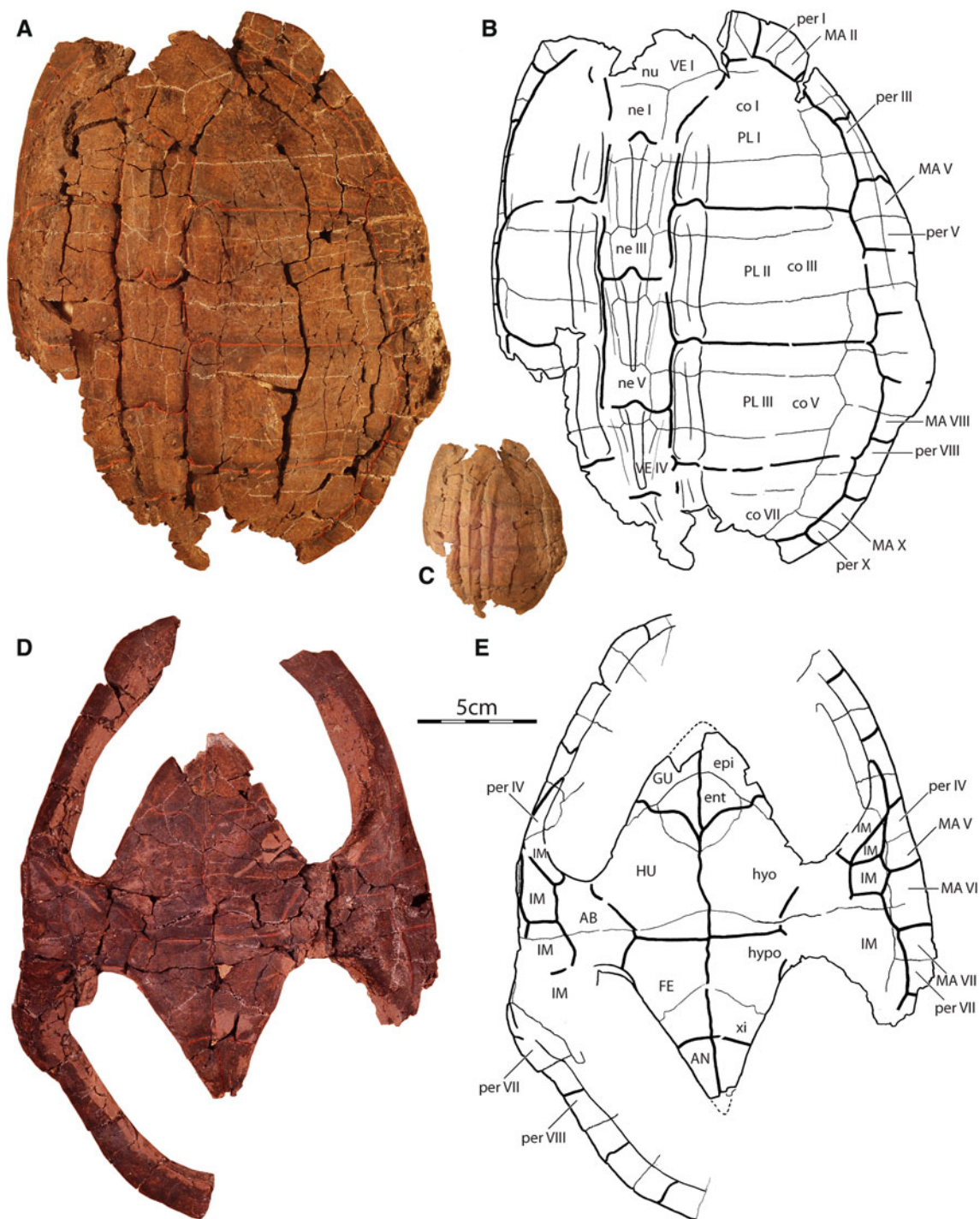
Fig. 2 PTRM 16173, holotype of *Hoplochelys clark* n. sp., from the Hell Creek Formation of Slope County, North Dakota. **a** Photograph and **b** line drawing of carapace in dorsal view. **c** Photograph of carapace under strong cross light highlighting the three dorsal keels. **d** Photograph and **e** line drawing of plastron in ventral view. *Scale bar* applies to **a–b** and **d–e**. *AN* Anal scale, *AB* abdominal scale, *co* costal bone, *ent* entoplastron, *epi* epiplastron, *FE* femoral scale, *GU* gular scale, *HU* humeral scale, *hyo* hyoplastron, *hypo* hypoplastron, *IM* inframarginal scale, *MA* marginal scale, *ne* neural bone, *nu* nuchal bone, *per* peripheral bone, *PL* pleural scale, *VE* vertebral scale, *xi* xiphiplastron

to uncover a dinosaur. The anterior and posterior ends of the specimen are thus missing, in particular parts of the nuchal bone, first costal, first peripheral, and much of the

pygal region. The plastron is rather complete, only missing the anterior and posterior tips. The specimen is fractured and was slightly crushed during diagenesis. We estimate
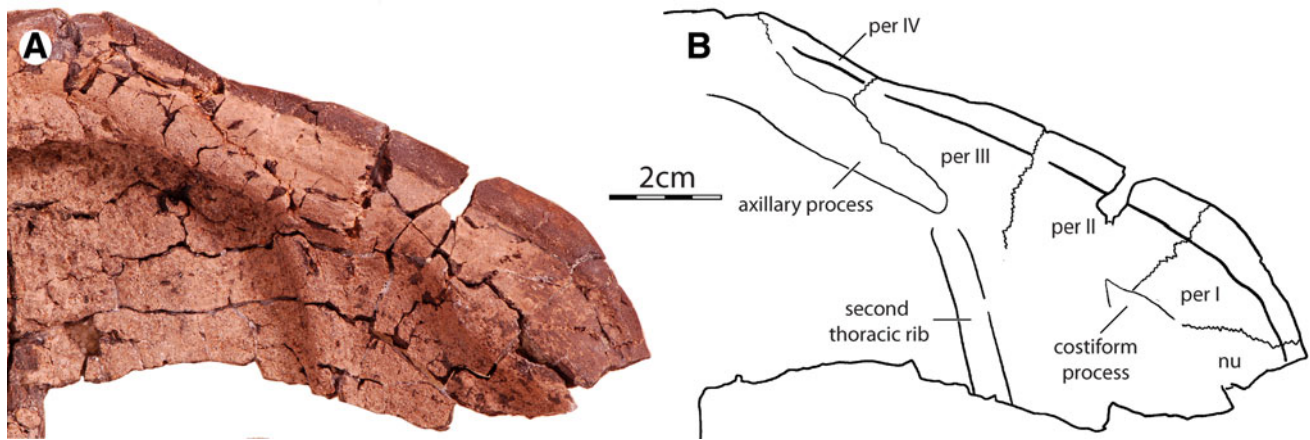
Fig. 3 PTRM 16173, holotype of *Hoplochelys clark* n. sp., from the Hell Creek Formation of Slope County, North Dakota. **a** Photograph and **b** line drawing of right anterolateral portion of carapace in visceral view. *nu* Nuchal bone, *per* peripheral bone

the carapace to have been 30 cm long and the plastron to have been 17 cm long. All sulci are clear, but many carapacial sutures are indistinct (Figs. 2, 3).

Carapace: Although the specimen is slightly crushed, it is apparent that the carapace once had a highly domed oval shape (Fig. 2). The distinct anteroposterior keels are a prominent feature of the carapace (Fig. 2c). The median, neural keel actually consists of four smaller subkeels that do not fully connect to one another. Each of these subkeels is restricted anteriorly and posteriorly by the sulci of vertebral scales II–V. The subkeel of vertebral II is the lowest of all. It originates promptly at the anterior margin of vertebral II and vanishes for the posterior third of this element. The subkeel of vertebral III also originates promptly at the anterior margin of the vertebral. Although the second subkeel is more distinct than the subkeel of vertebral II, it fades for the posterior quarter of vertebral III. The subkeel of vertebral IV also originates at the anterior border of the vertebral but extends posteriorly slightly further before fading away. This subkeel is also the most distinct. Finally, the subkeel of vertebral V is sharp but low, originates promptly at the anterior margin of vertebral V, but the posterior end is unclear, given that the pygal area is missing. In all previously described relatively complete specimens of *Hoplochelys* the median ridge appears to be more or less continuous and never disrupted as in PTRM 16173. Neurals I, III, V, and VII can be identified in isolation, because the intervertebral sulcus runs across these elements. The anterior portion consequently lacks a keel, whereas the posterior portion is strongly keeled. This also occurs in SMP 1578, an isolated neural from the early Maastrichtian of New Mexico.

The lateral costal keels are low rounded structures that run parallel to the vertebral/pleural sulci. Unlike the median keel, these keels are rather continuous, although clear

subdivisions are apparent where the interpleural sulci run across. The costal keels originate low along the posterior half of costal I and become distinct starting at the posterior half of costal II. Given that the posterior end of the costal series is not preserved, the posterior extent of these keels is unclear.

Nuchal bone: The nuchal is present, but was badly damaged during recovery (Fig. 2a–c). The anterior margin is almost completely missing, with exception of the lateral contact with the first peripheral, but the length can be estimated to be twice the size of most peripherals. The posterior portions are present but slightly crushed. From what is preserved, it is apparent that the nuchal was once a rather large bone that formed much of the anterior carapacial margin. As in most turtles, this element expands posteriorly and thus has a trapezoidal shape. On the dorsal surface, the nuchal contacts neural I and costal I posteriorly along a transverse suture and peripheral I laterally along an oblique suture. On the visceral side, the nuchal displays a tapered costiform process that crosses peripheral I and surficially extends onto the medial half of peripheral II (Fig. 3).

Neural bones: The entire neural column is likely preserved in the type specimen, but the sutures of the posterior elements are obscured making it impossible to assess the presence or shape of neurals VII and VIII (Fig. 2a, b). The first neural is the anteroposteriorly longest and mediolaterally widest of all preserved neural elements. It is hexagonal with short posterior sides. The low subkeel of vertebral II originates along the posterior half of this element. Neural II is shorter than neurals I and III and rectangular in shape. It thus only contacts neurals I and III anteriorly and posteriorly, respectively, and costal II laterally. The low subkeel of vertebral II spans its entire length. Neurals III through VI are hexagonal elements with short anterior sides that decrease in size posteriorly. The posterior half of neural III is dominated by the sharp
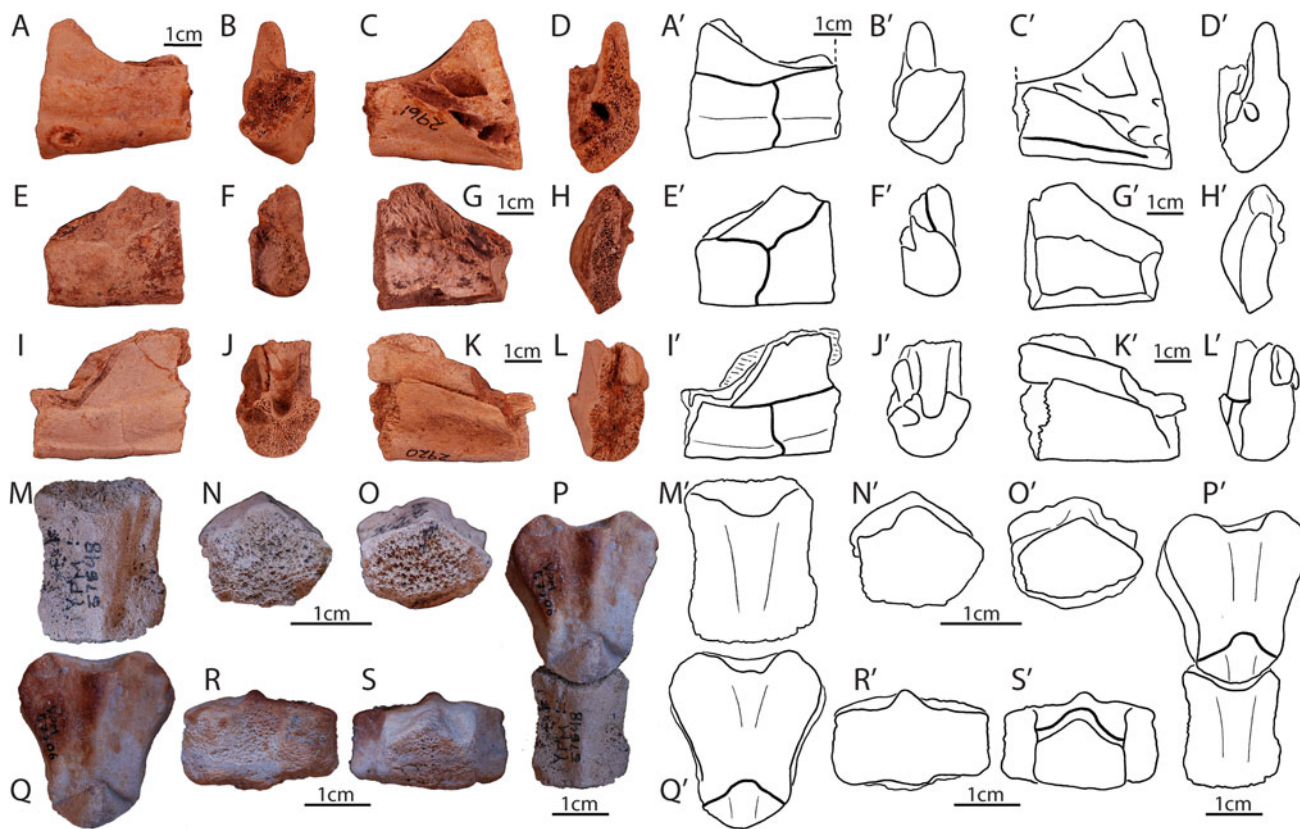
Fig. 4 *Hoplochelys clark* n. sp., from the Hell Creek Formation. **a–d** Photograph and **a′–d′** illustration of dorsal, anterior, ventral, and posterior views of PTRM 2961, a third right peripheral from the Hell Creek Formation of Slope County, North Dakota. **e–h** Photograph and **e′–h′** illustration of dorsal, anterior, ventral, and posterior views of PTRM 10015, a fourth right peripheral from the Hell Creek Formation of Slope County, North Dakota. **i–l** Photograph and **i′–l′** illustration of dorsal, anterior, ventral, and posterior views of PTRM 10015, a seventh left peripheral from the Hell Creek Formation of Slope County, North Dakota. **m–o** Photograph and **m′–o′** illustration of dorsal, anterior, posterior views of YPM 57648, an eighth neural from the Hell Creek Formation of Fallon County, Montana. **p** Photograph of YPM 57648 and YPM 57706 in articulation. **q–s** Photograph and **q′–s′** illustration of dorsal, anterior, posterior views of YPM 57706, a seventh neural from the Hell Creek Formation of Fallon County, Montana

subkeel of vertebral III. The same subkeel distinctly spans the full length of neural IV. The posterior half of neural V is similarly dominated by the sharp subkeel of vertebral IV, whereas neural VI is fully keeled. In the type specimen, we are not able to identify the sutures surrounding neural VII and VIII with any confidence. YPM 57706 (Fig. 4p–s) is an isolated neural that is diagnostic of the new taxon by being relatively thick and lacking a continuous median keel. We interpret this bone as neural VII, because it is much shorter than neurals I, III, or V, as preserved in the type specimen and because it resembles neural VII of *Hoplochelys* spp. Similarly, YPM 57648 (Fig. 4m–p) is an isolated neural that we here interpret as neural VIII because it possesses a low, posteriorly fading keel. Incidentally, although these two neurals were found separately, they fit together nicely, giving further credence to our identification (Fig. 4p). Based on these two specimens, it appears clear that the new taxon possessed a complete neural column of eight elements, that neural II was hexagonal with short anterior

sides, that the subkeel of vertebral V originated at the posterior third of neural VII, and that neural VIII was a short, rectangular element. The broad posterior contact of neural VIII is reminiscent of turtles that have a regular contact of neural VIII with the pygal column.

Costal bones: Costals I–IV are preserved completely on both sides, whereas costals V, VI, and the anterior half of VII are only preserved on the right side (Fig. 2a, b). All costals have parallel transverse sutures and generally decrease in anteroposterior length towards the posterior. Medially, costal I contacts one neural, costal II contacts three neurals, and all remaining costals contact two neurals. Costal I otherwise contacts the nuchal anteriorly, and peripherals I–III laterally. Costal rib I is unique among the costal ribs in that it forms a distinct ridge that runs along the entire visceral length of costal I and deeply inserts into peripheral III. In PTRM 2961, an isolated right peripheral III (Fig. 4a–d), a deep cone shape canal reveals that costal rib I not only inserted into peripheral III, but also continued

for a few millimeters into peripheral IV. Costal II contacts the posterior 10% of peripheral III and all of peripheral IV. The lateral contacts of costal III are unclear, but this element appears to align with peripheral V completely. Costal IV contacts all of peripheral VI and the anterior half of costal VII. Costal V contacts the posterior half of peripheral VII and the anterior 40% of peripheral VIII. Costal VI contacts the posterior 60% of peripheral VIII and the anterior half of peripheral IX. Costal VII contacts at least the posterior half of peripheral IX and appears to contact the full length of peripheral X. In isolation, costal I can be diagnosed by its unique shape, the strong development of the underlying thoracic rib I, but only a hint of a low rounded keel. The lateral keel is clearly developed along the medial sixth of all preserved costal elements. A number of isolated partial costals are referable to the new taxon (see referred specimens), but no new observations can be made from these specimens.

Pygal/suprapygal bones: Although the anterior portion of a suprapygal may be present, the pygal region is not entirely preserved (Fig. 2a, b). It thus is not possible to assess the number of suprapygals or the shape of the pygal. As outlined above, the square shape of neural VIII makes it plausible that the pygal column contacted the neural column.

Peripheral bones: Peripherals I–X are preserved on the right side of the specimen and peripherals II through VI are preserved on the left side of the specimen (Fig. 2a, b). A low gutter is developed from the posterior half of peripheral II to the anterior half of peripheral VI. The elements anterior to the bridge are rather flat and thin, whereas all preserved post bridge elements are greatly thickened. The contacts with the costals are described above. Due to the trapezoidal shape of the nuchal, peripheral I is a wedge-shaped element. In visceral view, peripheral I is crossed by the costiform process of the nuchal. Peripheral II is a rectangular element and contacts peripheral I anteriorly, and peripheral III posteriorly. In visceral view, the costiform process surficially crosses the anterior half of peripheral II and the anterior tip of the axillary buttress barely touches the posterior end of this element (Fig. 3). Peripheral III is a square bone that does not yet contribute directly to the surficial formation of the bridge although it is clearly in contact with the axillary buttress. PTRM 2961 is an isolated right peripheral III that allows detailed study of this element (Fig. 4a–d). In visceral view costal rib I fully pierces this element to deeply contact peripheral IV. Ventral to this contact, peripheral III exhibits a deep groove and a series of pits that hold the anterior buttress dentations of the hyoplastron. The axillary process spans the anterior two-thirds of peripheral IV. In addition, peripheral IV is the first peripheral to contribute directly to the bridge as the posterior third of this element contacts the hyoplastron surficially. These observations are confirmed by PTRM 10015, a partial right peripheral IV (Fig. 4e–h). Peripheral V and VI are bridge peripherals that medially contact the hyoplastron and hypoplastron, respectively. Peripheral VII is the last bridge peripheral and thus the posterior correspondent to peripheral IV. It surficially contacts the hypoplastron along its anterior 25%, and the inguinal process runs along the visceral side to barely contact peripheral VIII. These observations fully overlap with those that can be made from PTRM 2920, an isolated left peripheral VII (Fig. 4i–l). Peripherals VIII through X are rectangular elements that are greatly thickened in the areas overlain by the marginals. Peripheral XI is not preserved. However, the missing posterior shell margin is so large that we are confident that the gap is filled by a regular-sized pygal and peripheral XI, instead of only an extraordinarily large pygal.

Cervical scale: The anterior margin of the carapace is not preserved (Fig. 2a, b). It is thus unclear if a cervical was present.

Vertebral scales: The anterior margin of vertebral I is missing (Fig. 2a, b). From what is preserved, however, it is apparent that this element has a narrow posterior contact with vertebral II and evenly expands anteriorly to contact marginal I. The vertebral I/II sulcus is situated over neural I and displays a distinct anteriorly directed median projection. Vertebrals II and III are elongate rectangles that are about twice as long as wide. The vertebral II/III and vertebral III/IV sulci are situated over neurals III and V, respectively, and also display distinct anteriorly directed median projections. Vertebral IV is as wide as vertebral III, but only one and a half times as long as wide. The vertebral IV/V sulcus again displays a median projection, but it is unclear on the type specimen what neural it crosses. However, an isolated neural VII, YPM 57706 (Fig. 4p–s), preserves the vertebral IV/V sulcus. Unfortunately the shape and posterior placement of vertebral V are not preserved in the type specimen or in the referred material.

Pleural scales: Four pairs of pleurals are present (Fig. 2a, b). Due to the reduced size of the vertebrals, these elements dominate the surface of the carapace. All pleurals contact two vertebrals medially. Pleural I furthermore contacts marginals I–V, pleural II contacts marginals V–VII, pleural III contacts marginals VII–IX, and pleural IV contacts at least marginals IX–XI. Although not preserved, we presume that a 12th pair of marginals covered the posterior rim of the carapace. The interpleural sulci are generally straight, but all show an anteriorly directed inflection where the sulci cross the costal keels.

Marginal scales: Although only 11 pairs of marginals are preserved, we presume that 12 pairs were once present (Fig. 2a, b). The lateral contacts of these elements with the pleurals are described above. In ventral view, the posterior half of marginal IV and the anterior third of marginal V

contact the axillary scale. The posterior two-thirds of marginal V and the anterior one-third of marginal VI contact the (sometimes split) second axillary scale. Finally, the posterior two-thirds of marginal VI, all of marginal VII, and the anterior portion of marginal VIII contact the (sometimes split) inguinal scale. Dorsally, the marginals only cover the peripherals and never lap onto the costals, whereas ventrally marginals V and VI slightly overlap the hyo- and hypoplastra, respectively.

Plastron: The plastron is generally well preserved, but the tips of the epiplastra and xiphiplastra are damaged, and the bridges are heavily fractured at their narrowest point (Fig. 2d, e). As in all kinosternoids, most of the plastron is much thicker than the carapace. Although not entirely preserved, we estimate that the midline length of the plastron is 70% of the midline carapacial length. The anterior plastral lobe is somewhat rounded, but otherwise gently tapers towards the front and likely ended in a tip. The posterior plastral lobe is nearly triangular in shape and likely ended in an apex as well. We estimate that the narrowest portion of the bridge is 25% of the length of the plastron.

Plastral bones: Both epiplastra are present, but much of the right epiplastron is missing as is the anterior tip of the left epiplastron (Fig. 2d, e). The epiplastra contact one another along the midline and posteriorly contact the entoplastron and hyoplastra along straight sutures that are oriented at 120° relative to one another. The entoplastron is a relatively large oval element. It contacts the epiplastra anteriorly and the hyoplastra posteriorly. The visceral side of the specimen is not preserved well enough to determine the placement of the scapular ligament. The hyoplastra and hypoplastra form the majority of the plastron. The hyoplastron contacts the epiplastron and entoplastron anteriorly, surficially contacts peripherals IV and V laterally, and produces an axillary process that crosses along the visceral side of peripherals III and IV to barely reach peripheral II (Fig. 3). The hypoplastra contact the xiphiplastra posteriorly along two straight sutures arranged at 120° relative to one another. Surficially the hypoplastron contacts peripherals VI and VII and produces an inguinal process that runs along the visceral side of peripheral VII to barely insert along the visceral side of peripheral VIII. The xiphiplastra contact one another along their full length and combine to form the posterior tip of the posterior plastral lobe.

Plastral scales: Following Hutchison and Bramble (1981), we interpret the plastral scales of this taxon as being the gular, humeral, abdominal, femoral, and anal. Extragular, intergular, and femoral scales are thus absent (Fig. 2d, e). The gular is a rather large element that contacts its counterpart along the midline. The gular/humeral sulcus is slightly sinuous and crosses the epiplastral/hyoplastron suture and the entoplastron. The humeral is the largest plastral scale and covers much of the anterior plastral lobe. It

contacts the gular anteromedially and the abdominal posterolaterally. The posterior contact with the femoral is transverse and situated posterior to the hyo/hypoplastral suture. SMP VP 1650, an isolated partial left hypoplastron from the early Maastrichtian Ojo Alamo Formation of New Mexico, confirms this arrangement. The femoral contacts the humeral anteriorly and the abdominal anterolaterally. The posterior contact with the anal is transverse and situated halfway down the xiphiplastron. The abdominal contributes to both the axillary and inguinal margins, medially contacts the humeral and femoral, and laterally contacts the inframarginal series. The inframarginal series is irregularly developed in the holotype. The axillary is developed equally on both sides. On the left side, three scales appear to be developed that cover the hyoplastron, but on the right side only two are present. Conversely, on the left side only one scale is developed that covers the hypoplastron, but two are visible on the right side. If only those sulci that are present on both sides are taken into account, one would have to conclude that only three inframarginals are present and that the inguinal crosses the hyo/hypoplastron suture.

Phylogenetic analysis

To determine the phylogenetic affinities of *Hoplochelys clark* n. sp. within Kinosternoidea, we performed a maximum parsimony phylogenetic analysis. For this purpose we built a matrix based on characters presented in Hutchison and Bramble (1981), Meylan and Gaffney (1989), and Hutchison (1991), and developed a number of new characters. In addition to five extant kinosternoids we scored 13 fossil kinosternoid terminals. Following Lucas et al. (1989) and Hutchison (1998), all material previously referred to as *Baptemys garmanii* and *Baptemys tricarinata* (e.g., Hay 1908a) was scored as a single terminal, *Baptemys garmanii* and, following Hutchison and Weems (1998), *Agomphus tardus*, *Agomphus masculinus*, and *Agomphus turgidus* (e.g., Hay 1908a) are synonymized with *Agomphus pectoralis*. We performed two phylogenetic analyses that differed only in the way in which we treated *Hoplochelys* spp. In the first analysis we scored five of the six named taxa as separate terminal taxa based on their holotype specimens only and included as a separate terminal USNM 8525, which was referred by Gilmore (1919) to *H. crassa*. In the second analysis we united all known Paleocene *Hoplochelys* material into a single taxon, *Hoplochelys crassa*. Following recent advances in molecular phylogeny that confirm Williams's theory (1950) in asserting that Chelydridae and Kinosternoidea form a clade Chelydroidea (Near et al. 2005; Parham et al. 2006; Barley et al. 2010), we score the extant chelydrids *Chelydra serpentina* and *Macrochelys temminckii* as our outgroup taxa. After

omitting a number of characters as uninformative or non-reproducible, our final matrix consists of 48 characters with 70 derived character states for 20 terminal taxa. Missing data were scored "?" and not-applicable data were scored "-". A list of all materials and anatomical sources is given in Appendix 1, a list of characters is provided in Appendix 2, and the character matrix is presented in Appendix 3. Eight characters (4, 10, 23, 30, 35, 41, 46, 47) form morphoclines and we ran them ordered. The remaining characters were run unordered and all characters were given equal weight. The parsimony analysis was performed using PAUP 4.0b10 (Swofford 2001). The branch and bound search algorithm was used, and minimum branch lengths were set to collapse. Support for each node was measured by calculating bootstrap (Felsenstein 1985) values with 10,000 bootstrap replicates and 100 random sequence addition replicates. We regard bootstrap values of 70% or greater as strong support and bootstrap values of less than 70% as weak support (Hillis and Bull 1993).

The first analysis in which we scored each *Hoplochelys* spp. separately resulted in 16 trees (TL = 101,

CI = 0.6931, RI = 0.8110, RC = 0.5621). Overall the tree is well resolved except for a large polytomy in the strict consensus tree that includes all species of *Hoplochelys* (Fig. 5a). The 50% majority consensus and Adams consensus show the same topology as the strict consensus. For the second analysis, we united all Paleocene *Hoplochelys* spp. into a single taxon, *Hoplochelys crassa*. This analysis resulted in a single, fully resolved tree (TL = 99, CI = 0.7071, RI = 0.7986, RC = 0.5647; Fig. 5b). Both analyses regard *Baptemys* and *Xenochelys* as paraphyletic.

Discussion

Monophyly of Chelydroidea

One of the more surprising results of recent molecular phylogenies has been support of a clade consisting of Chelydridae and Kinosternoidea (Barley et al. 2010). Using morphological characteristics, chelydrids and kinosternids were united during the 19th century by the English scientist
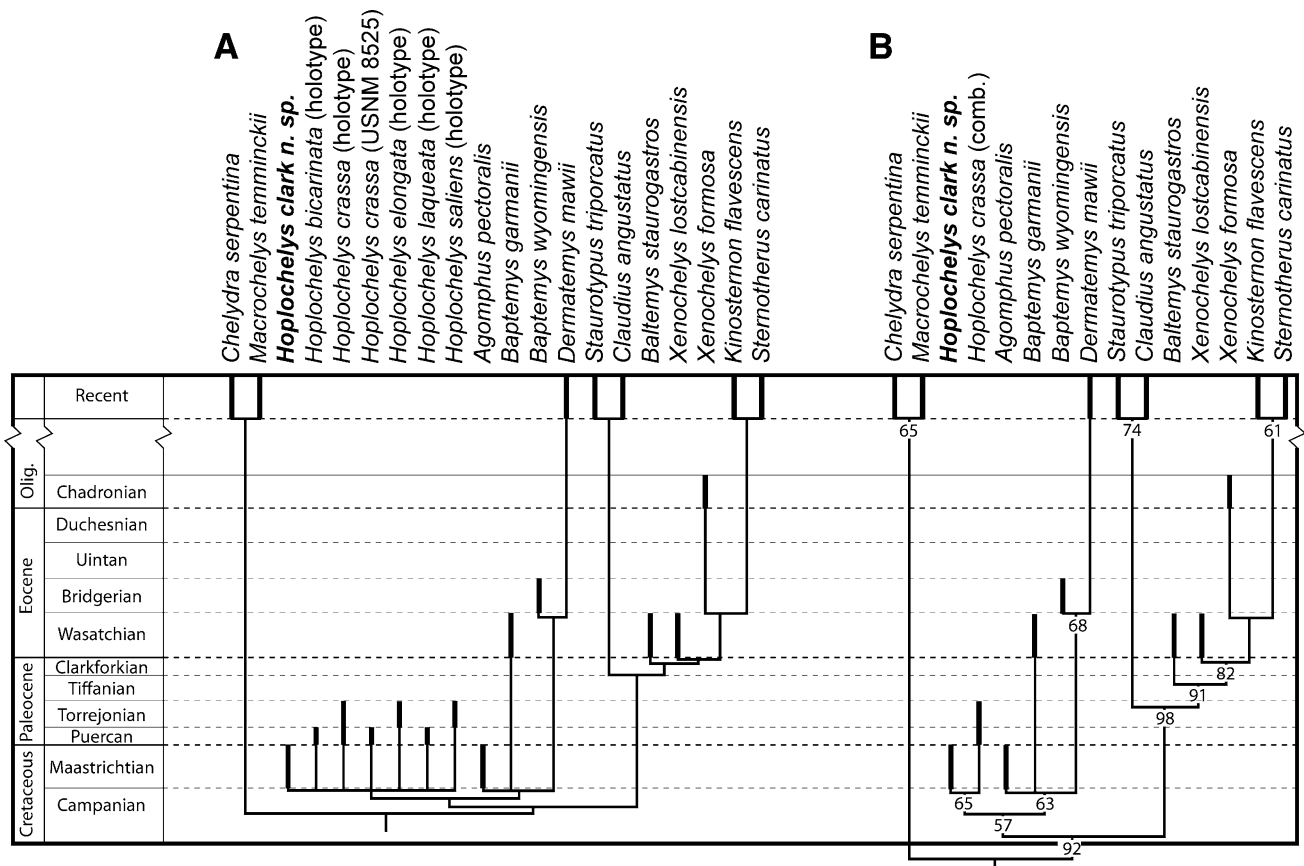

Fig. 5 Phylogenetic analysis of Kinosternoidea. **a** Strict consensus cladogram of the 16 most parsimonious trees resulting from the first analysis, which includes all sufficiently known species of *Hoplochelys* as separate terminals, mapped onto a simplified stratigraphic scheme. **b** The single most parsimonious tree resulting from the second analysis, for which all previously described Paleocene material of *Hoplochelys* was combined into a single terminal, *Hoplochelys crassa*. Bootstrap support is shown at each node

J. E. Gray, though always to the exclusion of *Dermatemys mawii* (e.g., Crucisterna Gray, 1869; Chelydradae Gray, 1870). Baur (1893) was the first to unite all chelydrids and kinosternoids under the term Chelydroidea, and we consequently follow his terminology for that clade. Although Gray (1869, 1870) did not list any explicit morphological traits, Baur (1893) noted the following diagnostic traits (reworded): no parietal/squamosal contact, foramen palatinum posterius present and located between the palatine and maxilla, articular surface between the sixth and seventh cervicals not platycoelous, raised pedestal on the visceral surface of the nuchal for articulation with cervical vertebrae VIII, costiform process present, one biconvex cervical, a complete series of inframarginals. Williams (1950), also favoring this phylogenetic arrangement, confirmed the biconvex centrum as a diagnostic trait, and added that the eighth cervical is procoelous. From a modern phylogenetic perspective, this list of diagnostic traits represents a mixture of plesiomorphies and synapomorphies. If the topology of Barley et al. (2010) is imposed upon the character matrix of Joyce (2007), most characters must be considered symplesiomorphies, given that all occur in basal chelonioids as well. Of the traditionally recognized characters, the only character that remains as an unambiguous synapomorphy is the presence of true costiform processes (see Joyce 2007 for discussion of similarly named, but nonhomologous structures in Trionychidae).

Our review of basal kinosternoids and basal chelydrids adds a number of characters to this list, all of which pertain to the plastron. With the exception of *Agomphus pectoralis*, all basal chelydroids possess reduced abdominal scales that do not contact one another along the midline. The plastron is extremely reduced in size and greatly thickened along the midline and along the bridge. Finally, the inframarginal series is complete (i.e., does not allow contact between the midline plastral scales and the marginals) but reduced to three. This clade can thus be identified using these four unambiguous synapomorphies.

Alpha taxonomy of *Hoplochelys*

Although our understanding of the evolution of North American turtles is generally good, the fossil record of the New World clade Kinosternoidea remains notably poor and mostly restricted to the Eocene (Hutchison 1991). The first nearly complete remains of a Mesozoic kinosternoid thus provides a unique insight into the early evolution of the group.

Six species names were previously available for *Hoplochelys*, of which *Hoplochelys* (orig. *Chelydra*) *crassa* Cope (1888) is the oldest. A seventh taxon, "*Hoplochelys*" *caelata* Hay, 1908b, was recently referred to the stem

lineage of Chelydridae by Hutchison and Holroyd (2003) and we agree with that taxonomic assessment.

For our first phylogenetic analysis, we a priori score five of the six previously named *Hoplochelys* species as distinct Operation Taxonomic Units (OTU). Unfortunately, the outcome of this analysis does not assist us with resolving the alpha taxonomy of kinosternoids, as most stem taxa along the phylogenetic stem of *Dermatemys mawii* collapsed into a polytomy in the strict consensus tree (Fig. 5a).

For our second phylogenetic analysis, we further resolve the alpha taxonomy of *Hoplochelys* using traditional alpha taxonomic techniques. Hutchison and Holroyd (2003) synonymized *H. crassa* with *H. bicarinata* and *H. laqueata*, noting that all specimens are based on material from the Puercan and that the differentiating characters are trivial (i.e., shell shape, neural formula) and should be interpreted as individual variation. We note that the type locality of *H. crassa* is unclear and that this taxon may by typified in the Puercan or Torrejonian. Nevertheless, we fully agree with the assessment of Hutchison and Holroyd (2003) that the characteristics used to differentiate *H. crassa* from *H. bicarinata* and *H. laqueata* are not taxonomically significant and instead should be treated as intraspecific variation. Gilmore (1919) primarily used differences in shell shape to diagnose various species of *Hoplochelys* among Puercan and Torrejonian material. We note, however, that none of the known material preserves the original shell shape because all specimens were collected as disarticulated fragments that had to be reassembled in the lab. The exact width to length proportions, nuchal shape, and the posterior slope of the shell are therefore unknown for all *Hoplochelys* specimens. More significantly, differences occur in the neural formula of the Paleocene material, but, as Hutchison and Bramble (1981) and Hutchison (1991) noted and our own observations confirm, the neural formula of many extant kinosternoid species is highly variable as well. As a result, we thus dismiss this variation as a source of meaningful diagnostic characters. We therefore go beyond Hutchison and Holroyd (2003) and not only synonymize *H. crassa* with *H. bicarinata* and *H. laqueata*, but *H. saliens*, *H. paludosa*, and *H. elongata* as well. On the other hand, all Paleocene *Hoplochelys* specimens can be morphologically diagnosed relative to all other kinosternoids by the presence of three uninterrupted keels (a potential synapomorphy with more derived representatives of the *D. mawii* lineage) and the placement of the humeral/femoral sulcus along the hyo/hypoplastral suture (an autapomorphy). Thus, for our second phylogenetic analysis we a priori recognize two *Hoplochelys* spp. as distinct OTUs: a unified *H. crassa* and *Hoplochelys clark* n.

sp. This analysis places these two *Hoplochelys* spp. OTUs as sister taxa.

Unlike the Paleocene *Hoplochelys* spp. we synonymized, the new taxon described herein, *H. clark*, possesses taxonomically diagnosable characters. Thus, we are justified in recognizing it as a distinct species according to the morphologic diagnosable species concept. Unlike, *H. crassa*, *H. clark* possesses an interrupted neural keel (an autapomorphy) and the humeral/femoral sulcus is placed posterior to the hyo/hypoplastral suture (a plesiomorphy). More significantly, fragmentary material collected from the early Maastrichtian Ojo Alamo Formation of New Mexico (SMP VP 1650, partial left hypoplastron; SMP VP 2109, isolated peripheral II) overlaps with the characters seen in *H. clark*. We thus are confident that this character combination is not unique to the holotype and referred material but was significantly more widespread in the Maastrichtian throughout North America. Although we speculate that both characters diagnostic of *H. clark* may be revealed by future analyses to be plesiomorphies for Pan-Dermatemys, the currently supported sister group relationship with *H. crassa* prevents us from naming a new genus and we place *clark* within *Hoplochelys*.

Finally, while we feel justified in naming *H. clark* as a distinct species we feel it is important to recognize the possibility that *H. clark* may be an ancestral species of *H. crassa*, because, although some ancestors must occur within the fossil record, phylogenetic software produces cladograms, not phylograms. So while the cladogram indicates a sister group relationship, we feel it is entirely possible that this relationship may be an anagenetic event, rather than a cladogenetic event, or, to phrase more carefully, that *H. clark* represents the ancestral morphology that gave rise to *H. crassa*. However, *H. clark* and *H. crassa* are morphologically diagnosable, and we are therefore justified in recognizing them as distinct OTUs.

Phylogeny of Kinosternoidea

An interesting aspect of our phylogenetic analysis is the placement of the taxon *Agomphus pectoralis* and *Hoplochelys* spp. along the phylogenetic stem of *Dermatemys mawii*. This phylogenetic placement breaks with the tradition started by Hutchison and Bramble (1981), which suggest that *Agomphus* spp. is a stem-kinosternoid and *Hoplochelys* spp. is a representative of the kinosternid stem (Hutchison 1991; Meylan and Gaffney 1989; Joyce 2007). The placement of these taxa along the phylogenetic stem of *Dermatemys mawii* is supported by the following list of synapomorphies: anterior contact of neural III with costals II and III (character 13), vertebrals more or less rectangular in adults (character 18), and presence of an elongate hypoplastral buttress that terminates on peripheral VIII

(character 23, state 2). Although the reduction of the number of the inframarginal series to three elements (character 26, state 1) is unique to this clade within Kinosternoidea, ordering this character renders this distribution a symplesiomorphy for Kinosternoidea. The alternative placement of *Hoplochelys* spp. along the phylogenetic stem of Kinosternidae (Hutchison and Bramble 1981; Hutchison 1991; Joyce 2007) or Kinosternoidea is one step longer. Nonmonophyly of *Hoplochelys* is at least three steps longer.

Prior to this study, the oldest described stem representative of the *Dermatemys mawii* stem lineage was known from the early Eocene (late Wasatchian; Hay 1908a), although even older material attributable to this lineage is mentioned in the literature from the Paleocene/Eocene boundary (latest Clarkforkian to earliest Wasatchian; Bourque et al. 2008) and early late Paleocene (Tiffanian; Hutchison 1998). The oldest confirmed stem-kinosternid is known from the late Campanian (Brinkman and de la Rosa 2006). This distribution implied a ghost range for the *D. mawii* lineage of approximately 25 Ma. Addition of the late Maastrichtian taxa *A. pectoralis* and *H. clark* to the phylogenetic stem of *D. mawii* shortens the ghost range to approximately 5 Ma.

Appendix 1: Materials

Extant turtles

Chelydra serpentina; YPM R 16622, YPM R 17755, YPM R 10821, YPM R 10835, YPM R 15180.

Claudius angustatus; FMNH 4165, AMNH 119937, AMNH 65865, USNM 7072.

Dermatemys mawii; FMNH 4163; FMNH 98950, USNM 66669.

Kinosternon flavescens; FMNH 6849, YPM R 11305.

Macrochelys temminckii; YPM R 13495.

Sternotherus carinatus; YPM R 11301.

Staurotypus triporcatus; AMNH 108906, USNM 40045, USMN 524353.

Fossil turtles

Agomphus pectoralis Cope, 1868; ANSP 15359, YPM 774, YPM 671.

Baltemys staurogastros Hutchison, 1991; UCMP 12700 (holotype).

Baptemys garmanii Cope, 1872; YPM PU17402, AMNH 6109, AMNH 6110, UCMP 132074.

Baptemys wyomingensis Leidy, 1870; ANSP 10074 (holotype), AMNH 1494, AMNH 4913, AMNH 5934, AMNH 5967, YPM 3754, USNM 13437, UCMP 45477, UCMP 158845.

Hoplochelys crassa Cope, 1888; AMNH 6091 (lectotype, scored from Hay, 1908a).

Hoplochelys crassa; USNM 8525, USNM 8252.

Hoplochelys bicarinata Hay, 1910; USNM 8524.

Hoplochelys laqueata Gilmore, 1919; USNM 8527 (holotype).

Hoplochelys elongata Gilmore, 1919; USNM 8553 (holotype).

Hoplochelys saliens Hay, 1908a; AMNH 1200 (holotype).

Hoplochelys clark n. sp.; PTRM 16173 (holotype), PTRM 10015, PTRM 6794, PTRM 8558, PTRM 2953, PTRM 2961, PTRM 10009, PTRM 9475, PTRM 2949, PTRM 2920, YPM 57288, YPM 57648, YPM 57706SMP 1578, SMP VP 1650, SMP VP-2109, SMP VP 2514.

Xenochelys lostcabinensis Hutchison, 1991; UCMP 1122341 (holotype).

Xenochelys formosa Hay, 1906; AMNH 1097 (holotype); SDSM 08662.

Appendix 2: Characters

(All characters highlighted with an asterisk are multistate characters that were run ordered.)

(1) Presence and development of projecting costal keel or tenting in adults (modified from Hutchison and Bramble 1981, 11; Hutchison 1991, 13): 0 = absent; 1 = present, spans majority of shell as "tenting"; 2 = present, spans majority of shell as a low, rounded, but projecting keel; 3 = present, spans majority of shell as sharp, distinct, projecting keel.

Comments: We score chelydrids as not having keels per se because these forms typically have pleural prominences that are not connected with one another. We furthermore distinguish between projecting keels and "tenting." Projecting keels are longitudinal structures that are formed by a buildup of bony material. In contrast, tenting is the result of a sharp bend in the shell without significant buildup of material, which produces a longitudinal structure as well. The four character states developed herein do not form a logical morphocline and we thus run this character unordered.

(2) Presence and extent of median keel: 0 = absent; 1 = present, only developed along the posterior half of shell; 2 = present, developed along majority of shell, even if faint on the anterior half of the shell.

Comments: This character only refers to true keels that consist of a buildup of bony material. Keels that are the result of "tenting" (i.e., a sharp bend in the shell) are not included in this character definition. Although this character can be ordered into a morphocline, we do not feel that character state 2 must evolve via character state 1 and thus leave this character unordered.

(3) Development of median keel (new character): 0 = consisting of multiple posteriorly fading subkeels that abut at intervertebral sulcus; 1 = consisting of a single, more or less uninterrupted keel.

Comments: Even though the median keel is incomplete in *Baptemys wyomingensis*, we nevertheless score this taxon as having a continuous keel because the keel spans two vertebral scales without interruption.

*(4) Costiform processes (modified from Hutchison and Bramble 1981, 12; Joyce 2007, 63): 0 = costiform processes rib-like, span two peripherals to insert in peripheral III; 1 = costiform processes tapered, span peripheral I to insert into peripheral II; 2 = costiform processes short, but tapered, inserts into peripheral I; 3 = costiform processes absent.

Comments: Joyce (2007) scored *Dermatemys mawii* as sometimes lacking a costiform process, but observations of FMNH 98950 reveal that the process is developed, but hidden in bone. Our scorings for *Baltemys staurogastros* and *Xenochelys lostcabinensis* follow the description of Hutchison (1991). All four character states form a logical morphocline, and we thus run this character ordered.

(5) Relative position of costal I/II suture relative to peripheral series (modified from Hutchison 1991, 17): 0 = contacts peripheral III; 1 = contacts peripheral IV.

(6) Relative position of costal II/III suture relative to peripheral series (modified from Hutchison and

Bramble 1981, 14; Hutchison 1991, 34): 0 = contacts peripheral IV; 1 = contacts peripheral V.

(7) Relative position of costal III/IV suture relative to peripheral series (modified from Hutchison and Bramble 1981, 34; Hutchison 1991, 35): 0 = contacts peripheral VI; 1 = contacts peripheral V.

(8) Termination of costal I rib (modified from Hutchison 1991, 32): 0 = costal rib I terminates within peripheral III; 1 = costal rib I may enter peripheral III, but terminates within peripheral IV.

(9) Costal rib VIII (reworded from Hutchison 1991, 7): 0 = medially contacts vertebral column; 1 = medial portion of rib not developed.

*(10) Reduction of neural column (Hutchison and Bramble 1981, 9, 25, 48; Hutchison 1991, 3): 0 = eight neurals present; 1 = seven neurals present; 2 = six neurals present.

Comment: Our three character states form a morphocline, and we consequently run this character ordered. The best-preserved specimens of *Agomphus pectoralis* unfortunately only preserve seven neurals, but more may have been there. We thus score it as 0/1, because we are confident that it has more than six neurals.

(11) Number of suprapygals (Hutchison and Bramble 1981, 44; Hutchison 1991, 12): 0 = two present; 1 = one present.

(12) Anterior contacts of neural II (reworded from Hutchison 1991, 14): 0 = costal I and II; 1 = costal II only.

(13) Anterior contacts of neural III (reworded from Hutchison 1991, 9): 0 = costal III only; 1 = costal II and III.

(14) Anterior contacts of neural IV (reworded from Hutchison 1991, 25): 0 = costal III and IV; 1 = costal IV only.

(15) Anterior contacts of neural V (reworded from Hutchison 1991, 28): 0 = costal V only; 1 = costal IV and V.

(16) Presence and development of musk duct groove (modified from Hutchison and Bramble 1981, 26, 45, 49; Hutchison 1991, 11, 18): 0 = musk duct groove absent; 1 = musk duct groove present and terminates on peripheral II; 2 = groove present and terminates on peripheral I.

Comment: The characters in Hutchison and Bramble (1981) and Hutchison (1991) address how deep the musk duct grooves are developed, yet, we omit this set of characters because it is difficult to replicate the results, especially with fossil taxa. Our three character states can be arranged in a morphocline; however, given that we do not feel that character state 2 necessary derived from character 0 via character state 1, we do not order this character.

(17) Number of peripherals (Hutchison and Bramble 1981, 27; Hutchison 1991, 1): 0 = 11 pairs of peripherals present; 1 = 10 pairs of peripherals present.

(18) Shape of vertebrals II–IV in adult specimens (modified from Hutchison and Bramble 1981, 29; Hutchison 1991, 5): 0 = more or less square; 1 = more or less rectangular, at least one and a half times longer than wide; 2 = distinctly hexagonal.

Comment: We run this character unordered because the three character states do not form a logical morphocline.

(19) Elevation of marginal X relative to marginal IX (modified from Hutchison 1991, 6): 0 = even or only slightly elevated; 1 = distinctly elevated.

(20) Posterior plastral lobe shape (modified from Hutchison and Bramble 1981, 20; Hutchison 1991, 20): 0 = posterior lobe tapers to a distinct point; 1 = posterior lobe rounded, anal notch absent; 2 = posterior lobe rounded, distinct anal notch present.

(21) Hyoplastral buttress (modified from Hutchison and Bramble 1981, 15): 0 = elongate hyoplastral buttress absent; 1 = hyoplastron forms long buttress that runs along the visceral surface of peripherals and terminates on peripherals; 2 = hyoplastron forms buttress that runs along the visceral side of the peripherals and terminates on costals.

(22) Anterior extent of surficial ossified hyoplastral bridge (modified from Hutchison and Bramble 1981, 13, 37; Hutchison 1991, 29): 0 = hyoplastron contacts peripheral IV on the shell surface; 1 = hyoplastron contacts peripheral V on the shell surface.

Comment: This character does not refer to contacts formed by a hyoplastral buttress that runs along the visceral side of the peripherals, but rather only those portions of the bridge that are surficial and covered by scales. All taxa with ligamentous bridges are scored as inapplicable.

*(23) Hypoplastral buttress (modified from Hutchison and Bramble 1981, 13, 37; Hutchison 1991, 8): 0 = elongate hypoplastral buttress absent; 1 = hypoplastron forms buttress that runs along the visceral surface of peripherals and terminates on peripheral VII; 2 = hypoplastron forms long buttress that runs along the visceral surface of peripherals and terminates on peripheral VIII; 3 = hypoplastron forms long buttress that runs along the visceral surface of peripherals and terminates on peripheral IX.

Comment: The four character states of this character form a logical morphocline, and we thus run it ordered.

(24) Posterior extent of surficial ossified hypoplastral bridge (modified from Hutchison and Bramble 1981, 13, 37; Hutchison 1991, 8): 0 = hypoplastron contacts peripheral VI on the surface; 1 = hypoplastron contacts peripheral VII on the surface; 2 = hypoplastron contacts peripheral VIII on the surface.

Comment: Similar to character 22, this character is only intended to reveal the extent of those portions of the bridge that are covered by scales. All taxa with unossified bridges are scored as inapplicable.

(25) Entoplastron (Hutchison and Bramble 1981, 52 in part; Hutchison 1991, 31): 0 = present; 1 = absent.

(26) Number of inframarginals (modified from Hutchison and Bramble 1981, 5, 10, 19; Hutchison 1991, 4): 0 = four or more; 1 = three; 2 = two.

(27) Overlap of hyo/hypoplastral suture by inframarginal series (modified from Hutchison and Bramble 1981, 6): 0 = axillary overlaps hyo/hypoplastral suture; 1 = inframarginal II or III overlap hyo/hypoplastral suture; 2 = inguinal overlaps hyo/hypoplastral suture.

(28) Intergular (Hutchison and Bramble 1981, 22; Hutchison 1991, 19): 0 = absent; 1 = large intergular present.

(29) Pectorals (Hutchison and Bramble 1981, 2): 0 = present; 1 = absent.

*(30) Abdominals (Hutchison and Bramble 1981, 23, 28; Hutchison 1991, 2): 0 = absent; 1 = present, but medial contact absent; 2 = present, partial medial contact present; 3 = present, medial contact along almost the entire anteroposterior length (i.e., the abdominal medial length is nearly equal to or possibly greater than its lateral length).

Comment: The character states of this character form a morphocline, and we thus run this character ordered.

(31) Contribution of the abdominal to the axillary notch (new character): 0 = present, pectorals or humerals do not contact inframarginals; 1 = absent, pectorals or humerals contacts inframarginals.

(32) Anal scales (Hutchison and Bramble 1981, 33): 0 = paired; 1 = fused.

(33) Orientation of epi/hyoplastral suture (modified from Hutchison and Bramble 1981, 35, 40, 50; Hutchison 1991, 21): 0 = oriented sloping backwards; 1 = oriented transverse or rising towards the front.

(34) Direct overlap of gular/humeral sulcus with epi-ento/hyoplastral suture (modified from Hutchison 1991, 33): 0 = absent; 1 = present.

*(35) Placement of humeral/femoral sulcus (modified from Hutchison and Bramble 1981, 32, 53; Hutchison 1991, 26, 36): 0 = placed over hyo/hypoplastral suture; 1 = placed over hypoplastron; 2 = placed over hypo/xiphiplastral suture.

Comment: All three character states form a morphocline, and we thus run this character ordered. An overlap of the humeral/femoral sulcus with the hypo/xiphiplastral suture generally correlates with the presence of posterior lobe kinesis.

(36) Frontal contribution to orbit (Hutchison 1991, 38; Meylan and Gaffney 1989, 16): 0 = absent; 1 = present.

(37) Maxilla/quadratojugal contact (Hutchison 1991, 39; Meylan and Gaffney 1989, 17): 0 = absent; 1 = present.

(38) Lingual ridges (i.e., maxillary tooth of Meylan and Gaffney 1989) on the palate (Hutchison and Bramble 1981, 16; Hutchison 1991, 40; Meylan and Gaffney 1989, 5): 0 = absent; 1 = present.

(39) Enlarged nose scale (Hutchison 1991, 41): 0 = absent; 1 = present.

(40) Parietal contribution to processus trochlearis oticum (taken from Hutchison 1991, 42; Meylan and Gaffney 1989, 44): 0 = absent, or very slightly present; 1 = significant contribution present.

*(41) Foramen stapedio-temporale (Hutchison and Bramble 1981, 4; Meylan and Gaffney 1989, 1): 0 = large foramen for thick blood vessel present; 1 = stapedial foramen reduced to the size of a cranial nerve foramen; 2 = absent.

Comment: We run this character ordered because the character states can be arranged in a morphocline.

(42) Foramen posterius canalis carotici interni (modified from Gaffney and Meylan 1989, 3; Hutchison 1991, 43): 0 = not fully formed by bone; 1 = fully surrounded by pterygoid; 2 = fully surrounded by the pterygoid ventrally and the opisthotic dorsally.

Comment: The three character states of this character cannot be arranged in a logical morphocline, and we thus run this character unordered.

(43) Ventral process of cervical vertebra VIII (Hutchison and Bramble 1981, 31; Hutchison 1991, 44; Meylan and Gaffney 1989, 26): 0 = single; 1 = double, split lengthwise.

(44) Size of pectineal process (modified from Hutchison 1991, 47): 0 = short; 1 = long.

(45) Orientation of pectineal process (modified from Hutchison 1991, 47): 0 = anteriorly oriented; 1 = laterally oriented.

*(46) Thelial process (modified from Meylan and Gaffney 1989, 37; see Joyce 2007 for comment regarding primary homology): 0 = absent; 1 = low process developed; 2 = clear process developed.

Comment: We run this character ordered because the character states form a morphocline.

*(47) Iliac notch (modified from Meylan and Gaffney 1989, 36): 0 = absent; 1 = slight notch developed; 2 = deep notch developed.

Comment: We run this character ordered, because the character states form a morphocline.

(48) Medial pectoral processes and ridges (new character): 0 = absent; 1 = present.

Comments: In all living kinosternoids, a number of unique features can be found in the pectoral girdle. In particular, a distinct accessory ridge arises near the glenoid from the medial side of the acromial process of the scapula that appears to correlate with a small process that arises from the medial side of the scapula. These ridges are highly distinct in *Dermatemys mawii* and *Baptemys wyomingensis* but have previously not been noted for kinosternids. We are unaware of the function of these structures.

Characters omitted from this study

Hutchison and Bramble (1981)

(3) Posterior lobe reduced in width: subjective and other less subjective characters appear to correlate with plastral size.
(7) Loss of sculpturing: uninformative, absent in outgroup and all ingroup taxa, an artifact from the use of trionychids as the outgroup.
(17) Femoral scale contacts inguinal: uninformative, autapomorphic for *Dermatemys mawii*.
(21) Increase in plastral size: see character #3.
(24) Megacephaly and probably increase in durophagy: not objective and largely uninformative as few fossil taxa have preserved skulls.
(30) Tendency to develop secondary palate: not discrete.
(36) Increased width of nuchal scale: character not discrete (must be measured to be objective).
(38) Scapular attachment transferred from entoplastron to epiplastra and marked by distinct pits: difficult to reproduce, as these are often not visible in fossils; in addition this character appears to correlate with the loss of the entoplastron.
(39) Usual loss of neural 7; anterior suprapygal elongated and often contacting neural 6 (or neural 7,

if present): uninformative, autapomorphic for *Staurotypus*.
(42) Fusion of hyoplastra with hypoplastra: uninformative, autapomorphic for *Claudius*.
(43) Great reduction in plastral size: see character #3.
(47) Distinct notch or step on margin of xiphiplastra at set 6–7 scale (anal-femoral) sulcus: subjective, not discrete.
(51) Upturned spurs developed on set 1 (gular) areas of epiplastra: uninformative, autapomorphic for *Xenochelys lostcabinensis*, contradictory information exists pertaining to *Baltemys staurogastros* (see Hutchison and Bramble 1981 versus Hutchison 1991).
(54) Head size decrease: see character #24.

Hutchison (1991)

(10) Relative height of M10 to M12: not discrete.
(15) Gular cusp present: see Bramble and Hutchison 1981 character #51.
(16) Femoral cusp present: see Bramble and Hutchison 1981 character #51.
(23) Width of anterior lobe: see Hutchison and Bramble 1981, character #3.
(24) Intergular (completely) separating gulars: uninformative, absent in all taxa used in analysis.
(30) Ventral scapular ligament attached to epiplastra only: see Hutchison and Bramble 1981, character #38.
(37) Foramen intermaxillaris: uninformative, feature was absent in all specimens viewed for this analysis.
(45) Ectepicondylar foramen open: uninformative, often varies with ontogeny.
(46) Pubis and ischium closely opposed or in contact: vague, and distribution was not confirmed as these elements are often connected by small pieces of calcified cartilage that may not be preserved in fossils.
(48) Ilia expanded at dorsal end: uninformative, expansion was not observed in any individual within the ingroup.

Appendix 3: Character matrix

See Table 1.

Table 1 Extant and fossil turtles studied and their characters

Species	Characters
Chelydra serpentina	00-00000000000a000000-1-0100010000-0000000000000
Macrochelys temminckii	00-000000001110000000-1-01?0010000-0000001100200

Table 1 continued

Species	Characters
Agomphus pectoralis	00-30001?a?0101?010000?10b20121000-?????????????
Dermatemys mawii	00-2000002a010100102203200111310a0-a010020011111
Baptemys garmanii	221?0a00?00010100100?02101201210a0-?????????????
Baptemys wyomingensis	011200a000001010010120320ab0121000-1010021010221
Staurotypus triporcatus	32110011110001212000001022010-10110101010110221
Claudius angustatus	00-100001110aaa2121001000–010-101-0101010110221
Baltemys staurogastros	10-1110112110012120000010220 10-0001??????????????
Xenochelys lostcabinensis	10-111011211001112120001022110-0101??????????????
Xenochelys formosa	00-11101?211010112120001022110-0101??????????????
Kinosternon flavescens	00-b010012110a1112ab0001122110-01020101112101221
Sternotherus carinatus	00-20100121a010112120001122010-01010101112101221
H. crassa	221???a????01???0100??????????????????????????
H. bicarinata	221?0????00?101?0100?02101201100000??????????????
H. laqueata	221?01a?0001101?0100?0?101201100000??????????????
H. elongata	221???a??0?0101?0100102101201100000??????????????
H. saliens	2211010?????111?0100???10??????????????????????
H. crassa (combined)	221101a?000a1a1?0100102101201100000??????????????
H. clark	2201aaa1?0?1101?0100102101201100001??????????????

a 0/1, *b* 1/2, *?* missing data, - not applicable

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