NEW CRANIAL MATERIAL OF *GILMOREMYS LANCENSIS* (TESTUDINES, TRIONYCHIDAE) FROM THE HELL CREEK FORMATION OF SOUTHEASTERN MONTANA, U.S.A.

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ABSTRACT—Plastomenidae is a speciose clade of soft-shelled turtles (Trionychidae) known from Campanian to Eocene deposits throughout western North America. We here describe two large skulls from the Upper Cretaceous (Maastrichtian) Hell Creek Formation of Carter County, Montana, that document the adult morphology of the plastomenid *Gilmoremys lancensis*. Whereas juveniles of this species, as previously documented by five subadult skulls, have narrow skulls, a narrow processus trochlearis oticum, a deep and narrow median palatal groove, low accessory ridges, and a secondary palate fully formed by the maxilla, skeletally mature individuals have notably broad skulls, a broad processus trochlearis oticum, a shallow but broad median palatal groove, high accessory ridges, and a substantial contribution of the vomer to the secondary palate. An expanded phylogenetic analysis reveals that the Campanian *Aspideretoides foveatus* and the Paleocene *Aspideretoides superstes*, nov. comb., are situated within Plastomenidae as sister to all previously identified plastomenid turtles, despite their general resemblance to trionychine soft-shelled turtles. The name *Aspideretoides* should therefore not be used as a taxonomic wastebasket for fossil trionychids with unclear phylogenetic relationships.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Soft-shelled turtles (Trionychidae) are a clade of cryptodiran turtles with a particularly rich Late Cretaceous to Paleogene fossil record throughout North America (Hay, 1908; Vitek and Joyce, 2015). Despite the abundance of fossil material available for study, the evolutionary history of the group is still poorly understood because undiagnostic types (Vitek and Joyce, 2015), high levels of homoplasy (Meylan, 1987; Gardner et al., 1995), and a lack of attention plague the alpha taxonomy of the group. A recent review of North American fossil trionychids (Vitek and Joyce, 2015), the first such review since the classic study of Hay (1908), concludes that of 101 named North American fossil trionychids, only 31 can be considered valid and that even their generic attributions are mostly uncertain.

The Late Cretaceous (Maastrichtian) Turtle Graveyard locality in Slope County, North Dakota (Fig. 1), has yielded a rich fauna dominated by baenid turtles (Lyson and Joyce, 2009a, 2009b; Joyce and Lyson, 2011). Sedimentological data indicate a ponded water environment within the lower portions of the Hell Creek Formation (Lyson and Joyce, 2009a). The quarry also yielded five well-preserved trionychid skulls and rich shell material (Joyce and Lyson, 2011) referable to *Gilmoremys lancensis* (Gilmore, 1916), a taxon that had previously been known from a single carapace only from the Maastrichtian Lance Formation of Niobrara County, Wyoming (Fig. 1). Morphological analysis of the unusual cranial anatomy of *G. lancensis* revealed that this taxon is not a classic trionychine soft shell turtle, but rather a

representative of Plastomenidae (Joyce and Lyson, 2011), a group of North America trionychids that usually possess extensively ossified shells (Hay, 1908). The cranial anatomy of *G. lancensis* is therefore the best understood of all plastomenid turtles.

Two large trionychid skulls and isolated shell pieces were recently discovered, once again in association with a large number of baenids, at the Ninja Turtle locality, which is located in deposits of the Hell Creek Formation exposed in Carter County, southeastern Montana (Fig. 1). The skulls are noticeably larger than those previously known from *G. lancensis* and differ in their overall form by being significantly broader, but detailed analysis reveals that the new skulls and shell fragments completely correspond with those previously described for *G. lancensis* and that the changes in overall form represent an ontogenetic shift towards the adult morphology of this species. The five skulls from the Turtle Graveyard locality therefore coincidentally sample only juvenile and subadult morphotypes and those from the Ninja Turtle locality only adult morphotypes. Given the importance of *G. lancensis* as a basis for the comparative osteology of fossil trionychids (e.g., Danilov et al., 2011, 2014, 2015; Vitek, 2012; Danilov and Vitek, 2013; Vitek and Danilov, 2014, 2015; Li et al., 2015), we here figure and describe the new material, highlight notable similarities and differences with the previously described material, investigate ontogenetic changes, and provide an updated and expanded analysis of plastomenid relationships.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **BMRP**, Burpee Museum of Natural History, Rockford, Illinois, U.S.A.; **MRF**, Marmarth Research Foundation, Marmarth, North Dakota, U.S.A.; **NHMUK** (formerly **BMNH**), Natural History Museum, London, U.K.; **TMP**, Royal Tyrrell Museum of
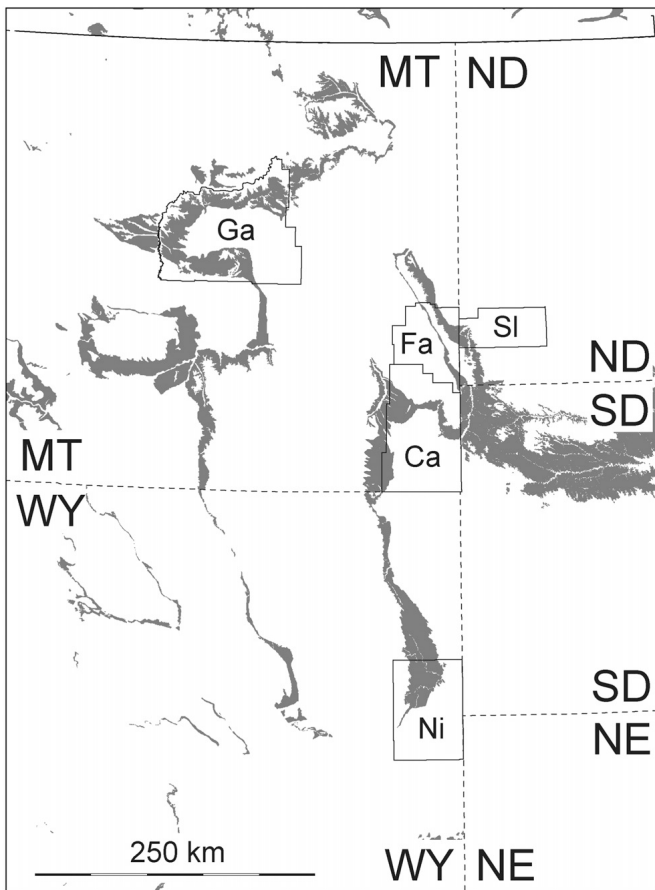
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FIGURE 1. A simplified map of the Western Interior, U.S.A., highlighting the known distribution of *Gilmoremys lancensis* at the county level. Outcrops exposing Maastrichtian sediments (i.e., Hell Creek and Lance formations) are highlighted in gray. **Abbreviations**: **Ca**, Carter County; **Fa**, Fallon County; **Ga**, Garfield County; **MT**, Montana; **ND**, North Dakota; **NE**, Nebraska; **Ni**, Niobrara County; **SD**, South Dakota; **Sl**, Slope County; **WY**, Wyoming.

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GEOLOGICAL SETTINGS

The Ninja Turtle locality is located in T1N, R55E near the town of Ekalaka, Carter County, southeastern Montana (Fig. 1). More detailed locality information is available from the BMRP to qualified persons upon request. The locality is situated in the Hell Creek Formation and is therefore Late Cretaceous (latest Maastrichtian) in age. The overlying contact with the Paleocene (Danian) Fort Union Formation is not exposed in the vicinity, making it difficult to assess the precise stratigraphic position of the locality. However, leaves collected at the quarry, including *Leepierceia preartocarpoides* and *Dryophyllum subfalcatum*, are typical for the Hell Creek 1a biozone floral assemblage (Johnson, 2002) and indicate that the locality is situated within the lower third of the Hell Creek Formation.

The locality is dominated by baenid turtle material, including 14 shells, several lower jaws, and numerous appendicular elements. The shells and lower jaws indicate the presence of at least four species of baenids, in particular *Eubaena cephalica* (Hay, 1904), *Neurankylus* sp., *Palatobaena cohen* Lyson and Joyce, 2009a, and an as-of-yet unidentified baenid. The assemblage

consists of juvenile to adult individuals and preservation ranges from completely articulated skeletons to disarticulated elements. The site furthermore produced shell fragments of a chelydroid, *Basilemys* sp., *Compsemys victa* Leidy, 1857b, and the trionychines *Axestemys* sp. and '*Trionyx*' *beecheri* Hay, 1908. The Ninja Turtle locality also yielded isolated elements of a number of dinosaurs, including the horn corn of a juvenile *Triceratops* sp., the teeth and pedal phalanx of juvenile *Tyrannosaurus* sp., a complete humerus of an undetermined theropod, cranial and postcranial material belonging to at least three individuals of *Thescelosaurus* sp., and the manual claw of *Anzu* sp. Finally, the locality also produced isolated elements of crocodylians and champsosaurs, teeth of the elasmobranch *Myledaphus bipartitus*, and scales of *Lepisosteus* spp.

The fossil-bearing layer is a lag deposit at the base of a point bar. The layer is wedge-shaped, pinches out towards the south, and rests upon a weakly rooted mudstone paleosol. The fossil layer is composed of a sandstone unit that coarsens upwards from a medium to medium/coarse sandstone and contains numerous small (<1 cm) clay rip-up clasts. In addition to the large diversity of vertebrates preserved, the unit contains numerous lignified logs, which commonly occur at other turtle localities (Lyson and Joyce, 2009a). The fossils appear to not have been transported great distances post mortem in a fluvial setting, because the material shows little to no abrasion, some of the material is completely articulated, and the vast majority of carapaces are oriented upwards. Combined, these indicate that the specimens were deposited in a low-energy, fluvial system.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788, sensu Joyce et al., 2004
CRYPTODIRA Cope, 1868, sensu Joyce et al., 2004
TRIONYCHIDAE Gray, 1825, sensu Joyce et al., 2004
GILMOREMYS LANCENSIS (Gilmore, 1916)
(Figs. 2–5)

Type Specimen—USNM 6727, a nearly complete carapace and an isolated hyoplastral fragment (Gilmore, 1916).

Type Locality and Horizon—Niobrara County, Wyoming, U.S.A. (Fig. 1); Lance Formation (Lancian), Late Cretaceous (Maastrichtian).

Distribution—Upper Cretaceous (Maastrichtian) of Fallon and Garfield counties, Montana, and Slope County, North Dakota (material previously referred by Joyce and Lyson, 2011); Upper Cretaceous (Maastrichtian) of Carter County, Montana: BMRP 2013.4.214 (a skull; Fig. 2), BMRP 2012.4.336 (a skull; Fig. 3), BMRP 2013.4.240 (a nuchal; Fig. 4A), BMRP 2013.4.241 (a partial right hypoplastron; Fig. 4B), and a right xiphiplastron (BMRP 2013.4.239; Fig. 4C).

Diagnosis—*Gilmoremys lancensis* is diagnosed as a representative of Pan-Trionychidae by the absence of carapacial and plastral scutes, the absence of peripherals and pygal bones, and sculpturing that covers all metaplastic portions of the shell bones. *Gilmoremys lancensis* is diagnosed as a representative of Plastomenidae by an extensive secondary palate that is mostly formed by the maxillae, an anteroposteriorly elongate mandible, and a contribution of the parietal to the wall of the orbit. The following combination of characters is unique to *Gilmoremys lancensis*: carapace covered by elongate sinusoidal sulci; preneural present; costal II expands distally at the expense of costal I; neural column lacks reversal; anterior hyoplastra lappet forms minor plastomenid 'shoulder;' xiphiplastra contact one another along their entire midline length; frontals fuse with one another ventromedially; sulcus olfactorius absent; posterior portion of narial canal defined by bone; anterior portion of maxillary triturating surface with accessory ridges; and skulls relatively narrow in
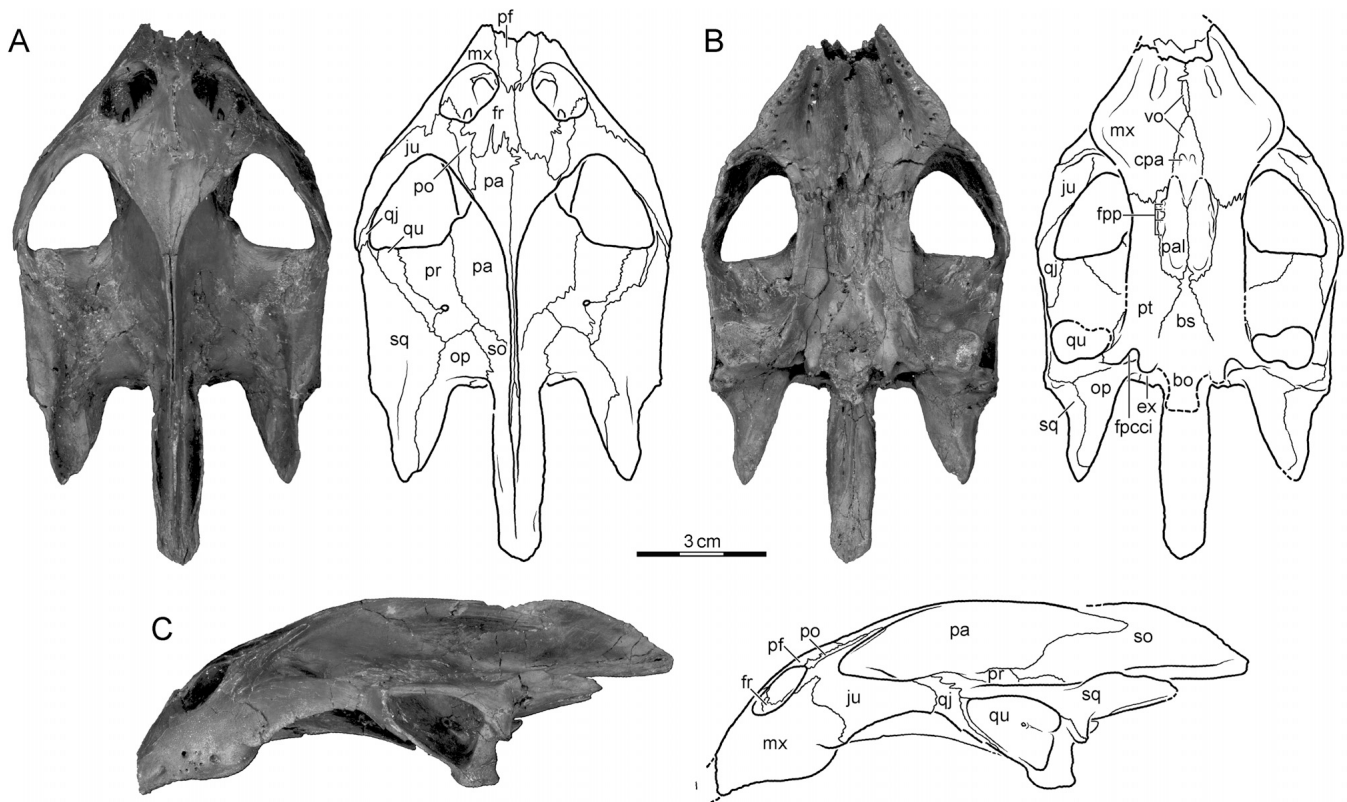
FIGURE 2. BMRP 2013.4.214, *Gilmoremys lancensis* skull, Upper Cretaceous (Maastrichtian) of Montana. Photographs and illustrations in **A**, dorsal, **B**, ventral, and **C**, left lateral views. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **cpa**, canal of the pseudopalatine artery; **ex**, exoccipital; **fpcci**, foramen posterius canalis carotici interni; **fpp**, foramen palatinum posterius; **fr**, frontal; **ju**, jugal; **mx**, maxilla; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pf**, prefrontal; **po**, postorbital; **pr**, prootic; **pt**, pterygoid; **qj**, quadratojugal; **qu**, quadrate; **so**, supraoccipital; **sq**, squamosal; **vo**, vomer.

juveniles and subadults but increasingly broad in adult individuals (modified from Joyce and Lyson, 2011).

Comments—Gilmore (1916) originally described *Gilmoremys lancensis* under the name *Aspideretes lancensis*, but this species was virtually ignored by paleontologists for most of the following century. Based on insights gained from new material, Joyce and Lyson (2011) transferred this species to *Gilmoremys*, which is typified by *Gilmoremys lancensis*.

DESCRIPTION

A detailed description was previously provided for the five subadult skulls found in Slope County, North Dakota (Joyce and Lyson, 2011). Given how closely the new material corresponds to these specimens, we here refer the reader to this contribution and only highlight significant differences.

Skull—The smaller of the two new skulls, BMRP 2013.4.214, has a length of approximately 120 mm from the tip of the left maxilla to the end of the supraoccipital crest (Fig. 2), whereas the larger one, BMRP 2012.4.336, has a preserved length of approximately 136 mm (Fig. 3). The supraoccipital crests of both specimens are intact, but their anterior margins are damaged. Specimen BMRP 2013.4.214 shows only minor signs of crushing and only lacks the most anterior portions of the snout, portions of the basioccipital, and minor fragments of the remaining bones. Specimen BMRP 2012.4.336, by contrast, is heavily fragmented in areas and lacks the anterior portions of the snout in addition to the left quadratojugal and squamosal.

Prefrontal—The prefrontals of the new material generally resemble those of the previously described subadult skulls. The only variation of note is the exclusion of the right prefrontal from the orbit in BMRP 2013.4.214 through a small contact of the frontal with the maxilla (Fig. 2). The prefrontals are clearly excluded from the orbits on both sides of the skull in the only available skull of *Plastomenus thomasii* (Gaffney, 1979).

Frontal—The new material adds significantly to the previously described variation apparent to the frontal/parietal suture. This suture is heavily interdigitated on the left side of the skull of BMRP 2013.4.214 (Fig. 2) and heavily interdigitated on both sides of BMRP 2012.4.336 (Fig. 3). In contrast to all other specimens, the frontal of BMRP 2013.4.214 exhibits a minor contact with the maxilla along the margin of the right orbit and a relatively extensive posterolateral contact with the postorbital. These enlarged contacts are in part due to the unusually long anteroposterior development of the postorbital in this region and the truncated anterolateral extension of the parietal in this specimen.

Parietal—The previously described skulls display a number of unusual characters in the parietal, such as the contribution of the parietal to the posteromedial wall of the orbit, including an anterior contact with the frontal, a dorsal contact with the postorbital, and a lateral contact with the jugal via the formation of a broad, anterior process that underlies the posterior process of the jugal. There is a clear exclusion of the parietal from the trigeminal foramen. The new material corresponds in all regards to these descriptions (Figs. 2, 3).

Postorbital—The postorbitals of the new material closely correspond to those of the previously described specimens. Among
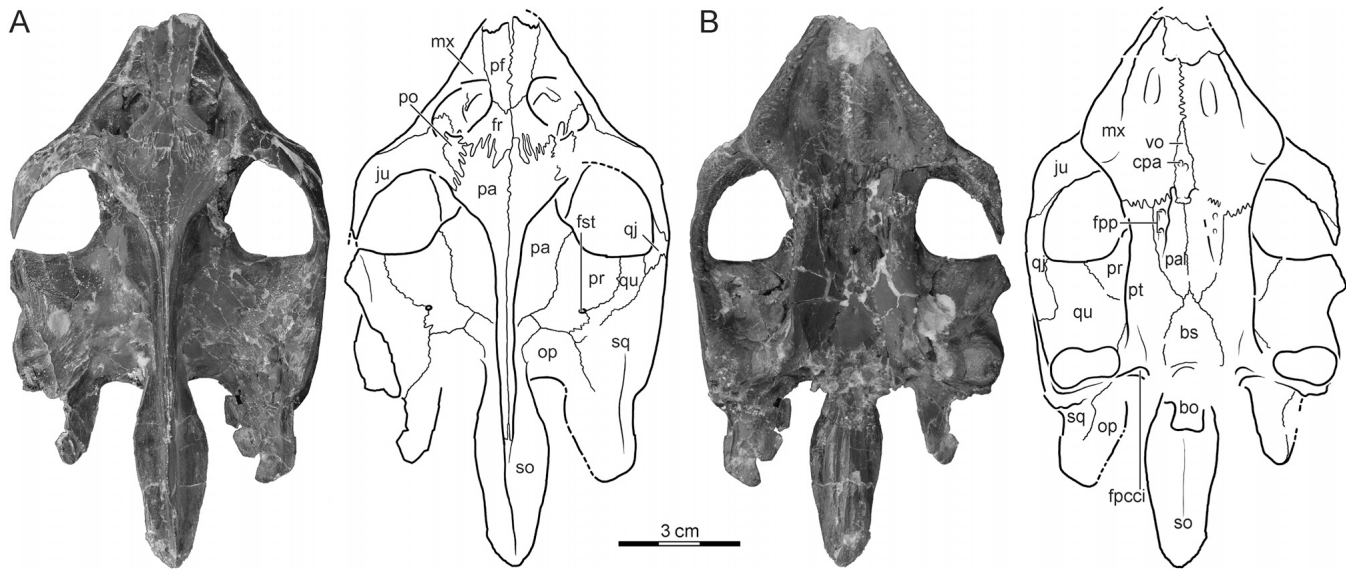
FIGURE 3. BMRP 2012.4.336, *Gilmoremys lancensis* skull, Late Cretaceous (Maastrichtian) of Montana. Photographs and illustrations in **A**, dorsal and **B**, ventral views. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **cpa**, canal of the pseudopalatine artery; **fpcci**, foramen posterius canalis carotici interni; **fpp**, foramen palatinum posterius; **fr**, frontal; **fst**, foramen stapedio-temporale; **ju**, jugal; **mx**, maxilla; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pf**, prefrontal; **po**, postorbital; **pr**, prootic; **pt**, pterygoid; **qj**, quadratojugal; **qu**, quadrate; **so**, supraoccipital; **sq**, squamosal; **vo**, vomer.

the available material, the postorbitals of BMRP 2013.4.214 (Fig. 2) are nevertheless unique by having particularly elongate posterior processes.

Jugal—The jugals of the new material are large elements that match the complex internal and external morphology previously described for *G. lancensis*. The only notable variation is the clear absence of a contact between the posterior processes of the jugal and the anterior process of the squamosal along the upper temporal emargination in BMRP 2013.4.214 (Fig. 2), although these two bones closely approximate each other. This region is not sufficiently preserved in BMRP 2012.4.336 (Fig. 3).

Quadratojugal—The quadratojugals of BMRP 2013.4.214 and 2012.4.336 again resemble those of the previously described specimens in all aspects, with the exception of the minor contribution of the quadratojugal to the upper temporal emargination already discussed above for BMRP 2013.4.214 (Fig. 2).

Squamosal—The squamosals are particularly well preserved in BMRP 2013.4.214 (Fig. 2), whereas BMRP 2012.4.336 (Fig. 3) has a crushed right squamosal and is completely lacking its left squamosal (Fig. 3). The squamosal forms a thin sheet of bone within the upper temporal fossa, which easily flakes off. The illustrated lines therefore highlight the former distribution of the bone as inferred from the attachment marks left behind on the bones below. In all respects the squamosals of the new material replicate those of previously described specimens, with the exception of the absence of an anterior contact with the jugal (see Jugal).

Premaxilla—The tip of the snout is not preserved in the two new specimens, and the premaxillae are therefore missing (Figs. 2, 3). The premaxillae are therefore not known from any specimen of *G. lancensis*.

Maxilla—The maxillae are well preserved in BMRP 2013.4.214 and 2012.4.336 (Figs. 2, 3) and display the most notable differences to previously described specimens. The anterior tips of the maxillae are damaged, and the likely midline contact of these elements anterior to the intermaxillary foramen or with the premaxillae is therefore not preserved. The main contacts of the maxillae replicate those of previously described specimens, with the notable exception of the minor contact with the frontals

along the anterior margin of the orbit apparent on both sides of BMRP 2013.4.214 (Fig. 2). Numerous complex structures apparent in the orbits are identical to those previously described for *G. lancensis*. Significant differences, however, are apparent in the palate. In the previously reported material from North Dakota, the maxillae expand posteriorly to form flat crushing surfaces and small accessory ridges are present along the anterior half of the triturating surfaces. The maxillae furthermore contact one another along much of their midline length to form an elongate secondary palate and a narrow median palatal groove that runs along the full length of the secondary palate. The new material is different by exhibiting triturating surfaces that are extremely broad, distinct accessory ridges, substantial broadened median palatal grooves, and a substantial contribution of the vomer to the midline of the secondary palate that greatly reduces the midline contact of the maxillae. The two specimens that most starkly embody these differences are MRF 277, which is the smallest, and BMRP 2012.4.336, which is the largest (Fig. 5). All remaining specimens fill intermediate morphologies between the two extremes that correlate with their size (i.e., from smallest to largest: MRF 277, 758, 759, 309, 275, BMRP 2013.4.214, and 2012.4.336). The disproportionate broadening of the posterior triturating surfaces correlates with a notable change in gestalt to the skull in dorsal view, because small individuals have a narrow, wedge-shaped skull, whereas large individuals exhibit box-like skulls with a notable constriction at the orbits (Fig. 5).

Vomer—The vomer of the new specimens from Montana is identical to those of the previously described specimens from North Dakota, including delicate structures related to the interorbital area. As noted above, however, the vomers of the new material have a greater exposure on the secondary palate in ventral view, which appears to correlate with size (see Maxilla above).

Palatine—The palatines of the new material resemble those of the previously available skulls, but notable differences are apparent in the formation of the posterior palatine foramina, a region already known to exhibit much variation among extant trionychid species (Meylan, 1987). In BMRP 2013.4.214 (Fig. 2), posterior palatine foramina are not formed. Instead, two open grooves

are apparent along the lateral margins of the palatines that converge to form a single opening near the dorsolateral margin of the internal choanae. Specimen BMRP 2012.4.336, by contrast, shows the more regular morphology consisting of two serially arranged foramina, a larger anterior one and a smaller posterior one, that are fully formed by the palatines and likely converged with one another within that bone (Fig. 3). The palatines contact the basisphenoid posteriorly in both specimens and therefore agree with the majority of previously reported skulls, only one of which lacks this contact.

Pterygoid—The pterygoid of the new specimens corresponds with the majority of previously described skulls by lacking a medial contact. The fenestra postotica is poorly preserved in BMRP 2012.4.336 (Fig. 3), and only few details can be gleaned. This area is better preserved in BMRP 2013.4.214 (Fig. 2), but the skull shows minor crushing in this region and various bony processes are damaged. Although it is clear that the pterygoid here too forms the ventrolateral aspects of the fenestra postotica, it is unclear if the fenestra was subdivided to form an enclosed posterior jugular foramen as in some of the previously described specimens (e.g., MRF 275).

Epipterygoid and Trigeminal Foramen—The trigeminal area is only well preserved in BMRP 2013.4.214 (not figured), but fully corresponds to the morphology previously reported for this taxon.

Quadrate—Even though the quadrates are complex bones that contribute to many structures, we find no significant differences between the new material and previously described specimens. The left side of BMRP 2012.4.336 (Fig. 3) is notable because the squamosal disarticulated prior to deposition, thereby fully exposing the intact quadrate in dorsal and lateral views and highlighting the articulation surfaces of the quadrate with the squamosal.

Prootic, Opisthotic, and Supraoccipital—The three bones that form the otic capsule correspond closely to those of the previously described specimens in all respects (Figs. 2, 3). Two notable differences, however, are apparent. First, the anterior margin of the otic capsule is relatively narrow in the smallest of the previously available specimens and the processus trochlearis oticum exhibits a clear depression formed by the prootic for the adductor musculature. In the largest specimen, by contrast, the anterior margin of the otic capsule is greatly broadened and a clear trochlear process is not apparent (Fig. 5). As with the palate (see Maxilla above), the full set of skulls documents all intermediate morphologies correlated with size. Second, the supraoccipital crests are particularly well preserved in both new specimens and confirm that the horizontal plates that help form the 'T'-shaped supraoccipital crest can broaden half way along the length of the crests, such as in BMRP 2012.4.336, or the lateral margins of the horizontal crests can be partially upturned, likely a response to the increasing size of the adductor musculature attaching in larger specimens.

Exoccipital and Basioccipital—The exoccipitals and basioccipitals are present in both new specimens, but many of their surfaces and processes are damaged (Figs. 2, 3). Although it is apparent that the basic contacts correspond to those observed in the previously described specimens, it is unclear how many hypoglossal foramina are present or whether the fenestra postotica was subdivided.

Basisphenoid—The basisphenoid of the new specimens corresponds to most previously described specimens by being triangular and by contacting the palatines anteriorly.

Shell—In addition to the two skulls, the Ninja Turtle Quarry has yielded at least three shell fragments referable to *Gilmoremys lancensis*: a nuchal (BMRP 2013.4.240; Fig. 4A), a partial right hypoplastron (BMRP 2013.4.241; Fig. 4B), and a right xiphiplastron (BMRP 2013.4.239; Fig. 4C). All shell material resembles previously referred specimens in being relatively thin (ca. 4 mm) and by being covered by an even, shiny, dense shell

texture consisting of fine reticulations. The small pits so typical of trionychid shell sculpturing are 1–2 mm in diameter.

The nuchal is approximately 30% smaller than the previously reported nuchals from the Turtle Graveyard locality (Joyce and Lyson, 2011), but corresponds fully in its morphology by having a posterior attachment site for a broad preneural and short lateral processes that are fully covered by metaplastic bone (Fig. 4A).

The distal hypoplastron is also approximately 30% smaller that previously described specimens (Joyce and Lyson, 2011), but, once again, fully conforms morphologically by having two slightly anteroposteriorly flattened distal processes, lateral metaplastic ossification that does not fully cover the distal processes, and a narrow bridge (Fig. 4B).

The xiphiplastron lacks its posterior tip, but is equivalent in size to previously reported material (Joyce and Lyson, 2011). This element largely corresponds with previously reported material by exhibiting a straight medial margin for articulation with its counterpart, a slightly rounded peripheral margin, and by having two proximal processes and one distal process (Fig. 4C).

PHYLOGENETIC ANALYSIS

To explore the phylogenetic relationships of plastomenid turtles, we here modify and expand the phylogenetic analyses of Joyce et al. (2009) and Joyce and Lyson (2010, 2011), which are based on the phylogenetic analysis of extant trionychids of Meylan (1987). This matrix has been utilized in a series of studies exploring the phylogenetic relationships of North American and
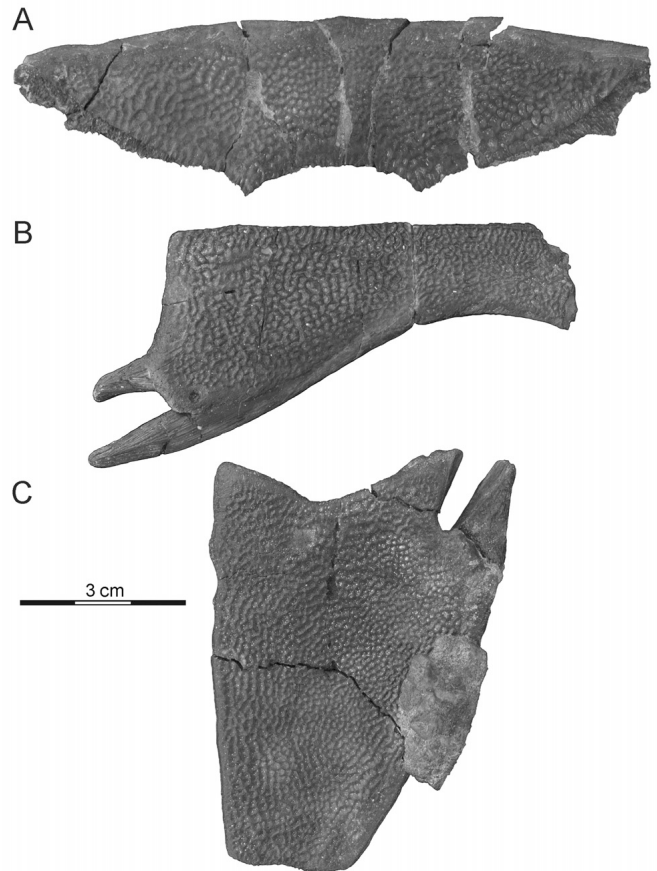

FIGURE 4. *Gilmoremys lancensis*, isolated shell pieces, Late Cretaceous (Maastrichtian) of Montana. **A**, BRMP 2013.4.240, a nuchal in dorsal view; **B**, BRMP 2013.4.241, a partial right hypoplastron in ventral view; **C**, BMRP 2013.4.239, a partial left xiphiplastron in ventral view.

Asian trionychids (e.g., Vitek, 2011, 2012; Danilov et al., 2014; Li et al., 2015). These data sets, however, typically resolve the included fossil taxa as pan-trionychines or cannot resolve their placement at all. These expanded data sets are therefore not utilized in this study.

The original matrix of Meylan (1987) included a number of characters that utilize polymorphism as a character state. Following the protocols first implemented by Vitek (2011), we converted characters 5 (Meylan, 1987:5), 12 (Meylan, 1987:14), 15 (Meylan, 1987:17), 25 (Meylan, 1987:34), 40 (Meylan, 1987:64), 44 (Meylan, 1987:68), and 47 (Meylan, 1987:71) into characters with discrete character states, and we scored taxa that exhibit two of the newly established character states as polymorphic. The contents of characters 35 and 36 (Meylan, 1987:58, 59) were reorganized into two characters: presence of an enclosed foramen jugulare posterius and the contribution of the pterygoid or opisthotic to this closure. Here and elsewhere we count our characters starting at 1.

For this study, the matrix was expanded through the addition of *Aspideretoides foveatus* (Leidy, 1857a; based on specimens TMP 1981.24.7, 1998.12.24, 1994.12.873, 2006.12.224, and P85.35.87 from the Campanian Dinosaur Park Formation of Alberta) and *Atoposemys superstes* (Russell, 1930; based on the description of Hutchison, 2013), two taxa with untested plastomenid affinities. The following modifications were made to the scoring of previously included plastomenids: *Plastomenus thomasii* was rescored as possessing five, not seven, plastral callosities (see Hutchison, 2009), whereas *Gilmoremys lancensis* and *Hutchemys tetanetron* were scored as having at least four plastral callosities (see Hutchison, 2009; Joyce and Lyson, 2011). With the exception of *P. thomasii*, all plastomenids with epiplastra preserved were rescored as having 'J'-shaped, not 'I'-shaped, epiplastra (see Hutchison, 2009, 2013). Finally, instead of scoring *P. thomasii* as having a parietal contribution to the orbit, Joyce and Lyson (2011) accidentally scored *T. triunguis* as having such a contribution. We corrected this mistake. No characters needed to be rescored for *G. lancensis*. The final character list is provided in Appendix 1, whereas the updated character-taxon matrix is provided in Appendix 2 and Supplementary Data 1.

The matrix was analyzed by parsimony analysis using the software program TNT (Goloboff et al., 2008). Characters 1, 3, 8, 12, 14, 15, 16, 18, 75, and 77 form morphoclines and were therefore ordered. We performed 1000 replicates of random addition sequences followed by a second round of tree bisection-reconnection. Given that no meaningful outgroup is available to explore trionychid relationships (see Joyce and Lyson, 2010), we did not root the trees while assuming the monophyly of Cyclanorbinae, Trionychinae, and Plastomenidae. The analysis retrieved six most parsimonious trees with 227 steps (consistency index = 0.471; retention index = 0.655). An abbreviated strict consensus tree is provided in Figure 6. The full strict consensus tree, common synapomorphies, and Bremer support values are provided in Supplementary Data 2.

DISCUSSION

Alpha Taxonomy and Ontogeny

Gilmoremys lancensis was originally described based on a nearly complete carapace from the Upper Cretaceous (Maastrichtian) Lance Formation of Wyoming as *Aspideretes lancensis* (Gilmore, 1916). Although two additional carapaces and numerous carapacial fragments have since been recovered, particularly at the Turtle Graveyard site in North Dakota, no single carapace has been found in direct association with plastral or skull material (Joyce and Lyson, 2011). Joyce and Lyson (2011) previously assigned the skulls and plastral elements found at the Turtle Graveyard site to the carapacial material found at the same quarry based on similarities in surface texture, equivalent size,

and frequency. Although this referral is reasonable and remains unchallenged to date (e.g., Holroyd et al., 2014), it is important to recollect that it only serves as a testable hypothesis until articulated material is found.

In terms of gross morphology, the two new skulls from Montana correspond almost entirely to the five skulls previously reported from North Dakota. A few differences are apparent in the topological arrangements of the bones, in particular the small contact of the maxilla and frontal that excludes the prefrontal from the orbit, the presence of particularly elongate postorbitals, the reduced anterior extent of the right parietal, and a lack of a jugal-squamosal contact and the associated minor contribution of the quadratojugal to the rim of the upper temporal emargination, all of which are apparent in BMRP 2013.4.214 (Fig. 2). Although most of these differences would score differently in a character matrix, the actual differences are minor and we therefore attribute all to intraspecific variation.

A number of significant changes are apparent on the palate that are best illustrated with reference to MRF 277, the smallest available skull from North Dakota, and BMRP 2012.4.336, the largest available skull from Montana. In dorsal view, MRF 277 is elongate, the anterior half is gently tapered, and the trochlear surface is narrow and shows a groove for the jaw adductor musculature. In palatal view, the triturating surfaces only expand slightly towards the posterior, the maxillae form the elongate secondary palate, and low accessory ridges that form a deep, but narrow median palatal groove decorate the triturating surfaces. By contrast, BMRP 2012.4.336 is extremely broad in dorsal view, its snout tapers abruptly, and the trochlear surfaces are broadened and flat. In ventral view, the maxillae expand strongly towards the posterior, the vomer contributes substantially to the secondary palate, and the triturating surfaces exhibit pronounced accessory ridges and a notably broad and shallow median palatal groove. Interestingly, the five remaining skulls are not identical to the two available morphotypes, but rather fill the full spectrum in between. The seven available skulls therefore form an even morphocline that correlates with size (Fig. 5).

Dalrymple (1977) documented ontogenetic changes to the skull of the extant soft-shelled turtle *Apalone ferox*. In addition to observing large amounts of intraspecific variation, Dalrymple (1977) also noted that *A. ferox* can form broadened triturating surfaces relatively late in ontogeny. We are not aware of this pattern having been formally documented for any other group of soft-shelled turtle, but have casually observed similar trends among the extant *Amyda cartilaginea* (USNM 72728, 222522, 82273) and *Trionyx triunguis* (AMNH 36599, 80026; NHMUK 1947.3.6.12). It is therefore consistent with observations from extant trionychids to interpret the seven skulls from the Hell Creek Formation of Montana and North Dakota as an ontogenetic series, with the adult skulls becoming increasingly macrocephalic. Dalrymple (1977) attributed these changes in skull morphology in *A. ferox* to a shift in dietary preference towards a more durophagous diet in adult individuals, and we think this to be plausible for *G. lancensis* as well.

The extensive secondary palate apparent in *G. lancensis* is unique among Cretaceous trionychids, but also occurs in the small-bodied Eocene species *Plastomenus thomasii* (Hay, 1908). The presence of a secondary palate therefore serves as a synapomorphy for the clade Plastomenidae (Joyce and Lyson, 2011) and should be inferred to have been present in other plastomenids. Although the phylogenetic relationships are not fully resolved among Cretaceous trionychids (Vitek and Joyce, 2015), at least four plastomenids have been reported from the Hell Creek Formation and several more can be inferred to have been present using phylogenetic arguments (see below). However, in addition to *G. lancensis*, only *Helopanoplia distincta* Hay, 1908, is known to have a carapace length greater than 30 cm, and it is therefore possible that the large skulls here reported from
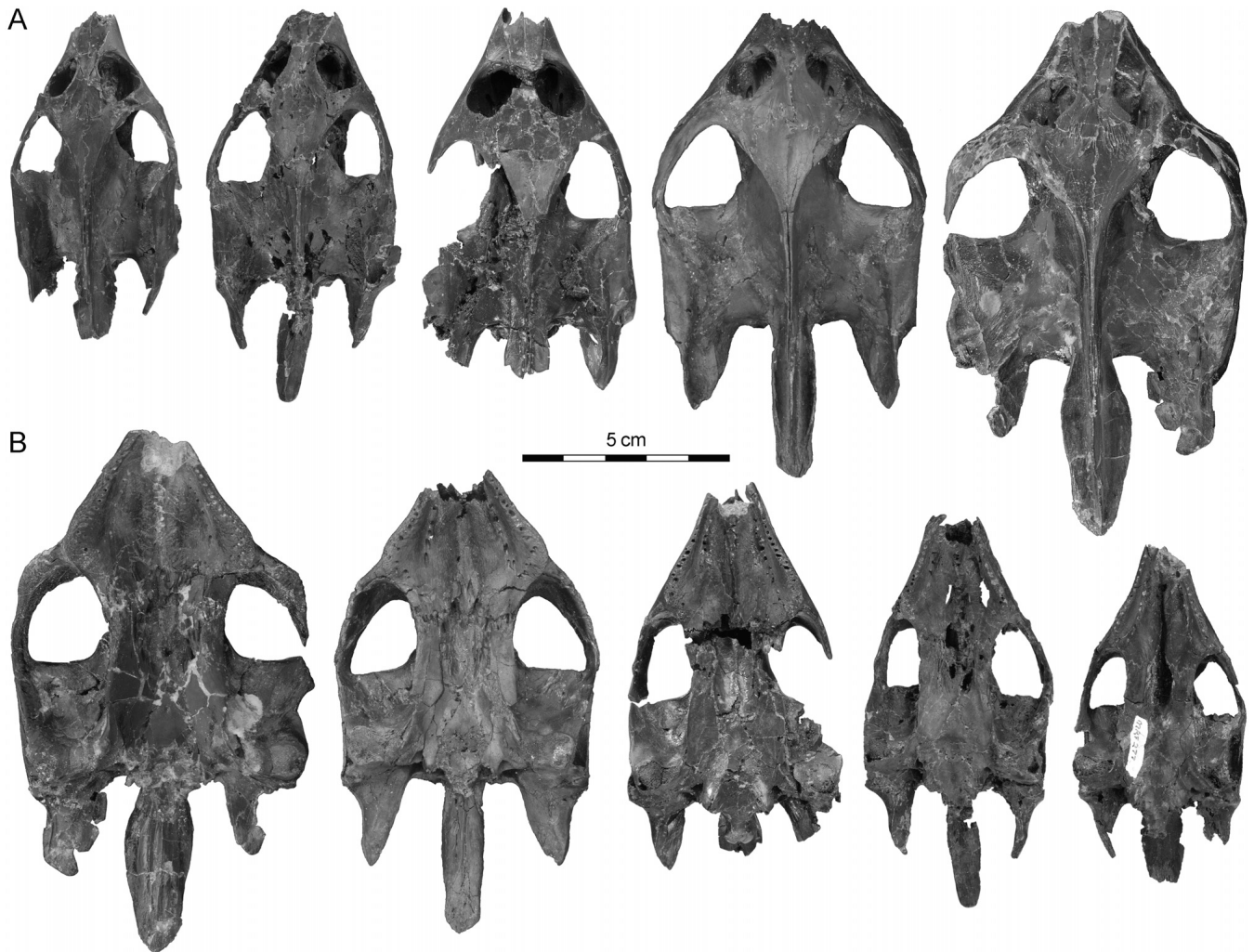
FIGURE 5. Cranial ontogeny of *Gilmoremys lancensis*, Upper Cretaceous (Maastrichtian) of Montana and North Dakota. **A**, dorsal view, specimens arranged by increasing size, from right to left: MRF 277, MRF 758, MRF 275, BMRP 2013.4.214, and BMRP 2012.4.336; **B**, ventral view, the same specimens arranged by decreasing size.

Montana belong to that taxon. Although we cannot rule out this possibility because many trionychids have skulls that greatly resemble one another, we here note the extreme consistency of the morphology of the new skulls with the previously reported ones, the presence of associated shell fragments diagnosable as *G. lancensis*, and the complete lack of the highly diagnostic shell fragments so typical of *H. distincta* at the Ninja Turtle locality. We therefore refer the two new skulls to *Gilmoremys lancensis* but await the discovery of articulated specimens for either taxon.

Phylogenetic Relationships and the Taxonomy of *Aspideretoides*

Trionychids have remained remarkably conservative in their morphology ever since they first appeared in the Early Cretaceous, and it is therefore difficult to classify fossil and recent trionychids (Meylan, 1987; Li et al., 2015). Among North American fossil trionychids, a notable exception has been plastomenid trionychids, which can readily be diagnosed by their highly apomorphic shell morphology (Hay, 1908). However, the remaining fossil trionychids of North America have been more difficult to classify. Hay (1908) provided a simple classificatory system using three shell characters that he thought to be of relevance: the lack of a well-developed surface sculpturing (= *Axetemys*), and

among those trionychids with surface sculpturing, the lack of costals VIII (= *Platypeltis*) and the absence (= *Amyda*) or presence (= *Aspideretes*) of a preneural.

Although the phylogenetic analysis of Gardner et al. (1995) only sampled the four valid fossil trionychids they recognized in Campanian rocks in Canada, none were retrieved in the broad vicinity of the Asiatic soft-shelled turtles *Aspideretes gangeticus* (currently *Nilssonia gangetica*), the type species of *Aspideretes*, even though they possess preneural bones and had previously been placed within *Aspideretes*. Gardner et al. (1995) therefore proposed a replacement name, *Aspideretoides*, for which designated the relatively small-bodied Campanian soft-shelled turtle *Trionyx foveatus* Leidy, 1857a, as the type species.

Our expanded phylogenetic analysis of trionychid turtles places *Aspideretoides foveatus* and *Atoposemys superstes* in a polytomy with the clade containing all previously recognized plastomenid turtles (Fig. 6). This conclusion is somewhat surprising, because plastomenids were historically recognized by their heavily ossified shell, especially a full midline contact of all elements in the plastron, a characteristic not apparent in *Aspideretoides foveatus* or *Atoposemys superstes*. The historical diagnosis of Plastomenidae was initially challenged by the analysis of Joyce and Lyson (2011), which identified *Gilmoremys lancensis*
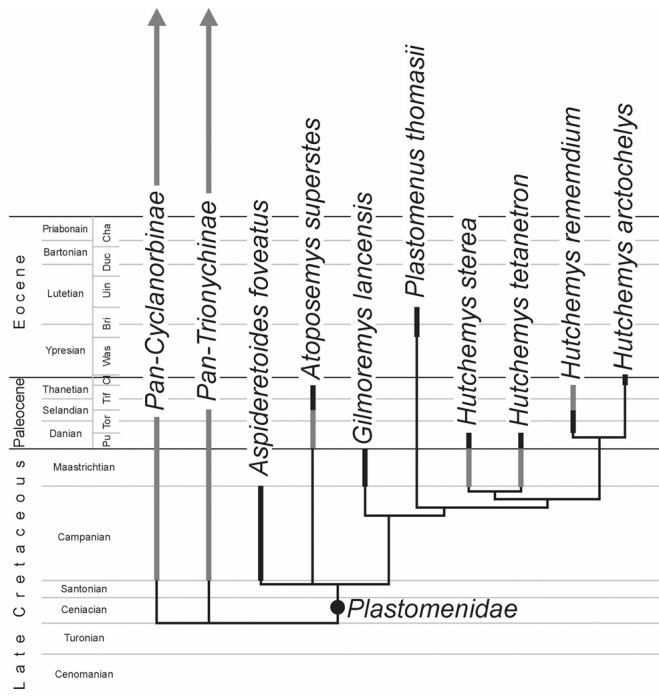
FIGURE 6. A simplified, time-calibrated cladogram depicting the strict consensus topology of six equally parsimonious trees retrieved from the phylogenetic analysis. Note that the cladogram is not polarized and that the monophyly of Trionychinae and Cyclanorbinae was assumed a priori. Thick dark bars denote the type range of a particular species, and gray bars connote the range of referred material.

as a plastomenid, even though it only possesses a midline contact of the xiphiplastra. Instead, *G. lancensis* is diagnosed as a plastomenid by numerous cranial characters otherwise found in the Eocene plastomenid *Plastomenus thomasii* only. *Aspideretoides foveatus* and *Atoposemys superstes* once again lack the traditional characters used to diagnose Plastomenidae, but our phylogeny places these species within the plastomenid lineages based on the plesiomorphic presence of a preneural (character 4), small hyoplastral lappets that partially block the movement of the entoplastron (character 75), and the synapomorphic presence of an extremely broad nuchal that is more than four times wider than long (character 1), and a broadly rounded entoplastron (character 74). The novel placement of *Aspideretoides foveatus* outside of Pan-Trionychinae (e.g., Gardner et al., 1995; Vitek, 2011), incidentally, is not a result of the addition of *Aspideretoides superstes* to the matrix, but rather results from changes to the scoring of this taxon based on our personal observations of material. For instance, we score the placement of the first thoracic vertebra (character 3) as unknown, because we are unaware of any specimens preserving this part of the skeleton. Our observation of several specimens similarly allows us to conclude that the placement of the neural reversal is relatively stable (character 13) at neural VI (character 15), not highly variable and at neural VI or VII. We finally conclude that the suprascapular fontanelles are closed early in life (character 18), not late on ontogeny, and that *Aspideretoides foveatus* possesses a bow-shaped entoplastron (character 74) that is partially embraced by minor hyoplastral shoulders (character 75). These changes cumulatively impact the placement of this taxon.

The conclusion that *Aspideretoides foveatus* is a plastomenid is significant, because *Aspideretoides* has served as a taxonomic harbor for numerous Late Cretaceous and Paleogene trionychids with a trionychine morphotype (e.g., Gardner et al., 1995;

Hutchison and Holroyd, 2003; Vitek and Danilov, 2010; Hutchison et al., 2013; Sullivan et al., 2013; Holroyd et al., 2014; Weems, 2014). It is beyond the scope of this contribution to reassess the taxonomic placement of all affected material, but we nevertheless recommend caution when utilizing *Aspideretoides* in the future.

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APPENDIX 1. List of characters used in phylogenetic analysis. Changes are highlighted relative to the character list provided by Joyce and Lyson (2011). Characters 1–4, 6–11, 13, 14, 16–24, 26–34, 37–39, 41–43, 45, 46, and 48–83 are unmodified.

(5) Neomorphic peripherals: absent (0); present (1).

(12) Number of neurals: eight (1); seven (2); six or less (3).

(15) Point of neural reversal: neural VII (1); neural VI (2); neural V (3); neural IV (4).

(25) Jugal-parietal contact: absent (1); present (2).

(35) Foramen jugulare posterius: open (1); enclosed (2).

(36) Enclosed foramen jugulare posterius: enclosed by pterygoid (1); enclosed by opisthotic (2).

(40) Basisphenoid shape: not constricted (1); medially constricted (2).

(44) Epipterygoid-palatine contact: present (1); absent (2).

(47) Epipterygoid-prootic contact anterior to trigeminal foramen: absent (1); present (2).

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis. **Abbreviations**: **a**, 0/1; **b**, 1/2; **c**, 2/3; **d**, 1/2/3. Note that polymorphic scoring can represent true polymorphism (i.e., 0 and 1) or exclusion of other character state (i.e., 0 or 1).

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Taxon                    10          20          30          40          50
C. aubryi         2121011122  2212112111  1211222112  2142213111  112b2-1211
                  1111221121  2212110000  0000101000  000
P. bibroni        3222011311  1b11c21122  1111211111  12211-2111  311210b121
                  1112232211  1121220000  0000002000  000
A. cartilaginea   3222011211  1111221322  1111112112  21211-211b  111b10b131
                  1212132112  1121120000  0000002000  000
C. elegans        2221011421  2b12111122  1111211212  2132213111  11112-1221
                  1221121121  2122210000  0000101000  000
R. euphraticus    3222012411  1212c21122  1111112121  11211-311b  1111101132
                  1222133111  2122120000  0000002000  000
A. ferox          3222012311  1232321122  1121113111  11211-3111  1111101132
                  1221133111  1122120000  00a0a01000  000
N. formosa        2222011311  1111211122  1112212112  21211-3112  1111111131
                  111---2112  212---0000  000000?000  000
C. frenatum       2111011121  2b12212111  1211221112  2142213111  22122-1221
                  1211221121  2212110000  0000101000  000
N. gangetica      3221011211  1b22c11222  1111112112  21211-3112  1111111121
                  1211123112  1121120000  0000002000  000
N. hurum          3221011211  1122c11222  1111b13112  21211-3112  111111b131
                  1111131112  1121120000  0000002000  000
C. indica         3232011311  1111c11122  1121221111  11211-2111  2112102130
                  0112232211  2121220000  0000002000  000
A. mutica         4222012111  1b32331122  2122b13111  21211-3111  11112-1122
                  2221122111  1121220000  0000a01000  000
L. punctata       2111121122  2c12212111  1211b11112  1122213111  111b111111
                  1111121121  2112120000  0000111000  000
C. senegalensis   3221021021  23-4-11111  1111222111  1132213111  11122-1211
                  1111121121  2222210000  0000102000  000
P. sinensis       4222011111  1b32321322  2112b13112  2122223112  1111121131
                  1211122111  1121120000  0000002000  000
A. spinifera      3222012111  1232331122  2121113111  11211-311b  11112-1132
                  2221123111  1121220000  0000a01000  000
P. steindachneri  2222011311  1b12211322  2111213112  2121223112  11112-2131
                  211--22111  1-2---0000  000000?000  000
D. subplanus      4222011311  1120231322  2111b13112  212122321b  11111-1121
                  2211132112  1121120000  0000002000  000
T. triunguis      3222011311  1212c21122  1111113112  21211-3121  1111101121
                  ?221122111  1121120000  0000002000  000
G. lancensis      42?1011d12  12-2-1??22  11?22231b2  21322b3111  ?1112-2131
                  111??????? ?????? 0000  000?102111  110
P. thomasii       42?1011212  2c-c-12111  11?11???12  21222b3211  111??????-
                  211??????1  ?????? 0000  001110210?  111
H. rememdium      42?1011112  22122111?1  11????????  ??????????  ??????????
                  ??????????  ??21??1111  0011201???  ??a
H. arctochelys    42?1011112  221221??11  11????????  ??????????  ??????????
                  ??????????  ??????1011  1111211???  ??1
H. tetraneton     42?1011d11  221221???1  21????????  ??????????  ??????????
                  ??????????  ??????1101  001?20????  ??0
H. sterea         32?1011112  2212511111  21????????  ??????????  ??????????
                  ??????????  ??????1001  001120????  ??1
A. foveatus       42?1011311  1212211122  11????????  ??????????  ??????????
                  ??????????  ??????1000  0001101???  ??0
A. superstes      42?1011311  1c1221??22  21????????  ??????????  ??????????
                  ??????????  ??????0001  0001101???  ??0
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