ARTICLE

A NEW DERMATEMYDID (TESTUDINES, KINOSTERNOIDEA) FROM THE PALEOCENE-EOCENE THERMAL MAXIMUM, WILLWOOD FORMATION, SOUTHEASTERN BIGHORN BASIN, WYOMING

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ABSTRACT—*Gomphochelys nanus*, new genus and species, is described from the earliest Wasatchian (biohorizon Wa 0; ~55.8 Ma) of the southeastern Bighorn Basin, Washakie County, Wyoming. The new taxon represents the only known dermatemydid from the Paleocene–Eocene Thermal Maximum (PETM) interval and extends the lineage back from previous records by approximately 2 million years. *Gomphochelys nanus* has a thick tricarinate carapace and differs from other dermatemydids in attaining a smaller adult body size, having reduced plastral features, a posteriorly situated gular–humeral sulcus, an acarinate pygal, and thick shortened peripherals. Reexamination of previously described fossil dermatemydids suggests that the taxa *Baptemys tricarinata* and *Kallistira costilata* are junior synonyms of the middle–late Wasatchian *Notomorpha garmanii*, and *Baptemys fluviatilis* is likely a junior synonym of *Baptemys wyomingensis*. *Gomphochelys nanus* is a stem dermatemydid that is similar to *N. garmanii* but differs in possessing symplesiomorphies with the Late Cretaceous–Paleocene genera *Agomphus* and *Hoplochelys*. Aspects of shell morphology suggest that *G. nanus* was a commensurate swimmer and bottom-walker like extant *Dermatemys* and *Staurotypus*. The presence of a dermatemydid (a tropically distributed clade) in the southeastern Bighorn Basin during the PETM (when global temperatures increased by 5°C–10°C over a period of ~60 ky) further supports the hypothesis that climate was megathermal in the region during this interval and is consistent with previously documented geographic range changes in both plants and animals. Dermatemydids disappear from the fossil record at the end of the PETM and don't reemerge until the next warming event, Eocene Thermal Maximum 2.

http://zoobank.org/urn:lsid:zoobank.org:pub:19A98079-5CAD-4BC5-8C21-2810AA576D98

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

INTRODUCTION

Turtles of the epifamily Kinosternoidea are a clade comprising fossil and extant members of the families Dermatemydidae and Kinosternidae + *Hoplochelys* (Kinosternia) (Hutchison and Bramble, 1981; Gaffney and Meylan, 1988; Joyce et al., 2004). Extant members are exclusively inhabitants of the New World (North, Central, and South America), and the earliest fossil stem kinosternoids from the Late Cretaceous provide evidence for a North American origin of the group (Hutchison and Archibald, 1986). The Dermatemydidae Gray, 1870, comprises the living Central American river turtle *Dermatemys mawii* Gray, 1847, and species of the extinct genera *Baptemys* Leidy, 1870, and *Notomorpha* Cope, 1872, and form the less diverse part of an almost exclusively North American clade within Kinosternoidea (Gaffney and Meylan, 1988). A recent analysis concerning kinosternoids proposed that the genera *Hoplochelys* and *Agomphus* are stem dermatemydids and that dermatemydids split from the sister taxon Kinosternidae prior to the late Campanian (Knauss et al., 2010). The extant kinosternoids *Staurotypus* and *Claudius* were recently classified in the family Staurotypidae based on molecular evidence (Iverson et al., 2013); however, for the present study, these two genera are retained within the concept of Kinosternidae because we regard their phylogeny as unresolved (Hutchison and Bramble, 1981; Iverson, 1991; Bourque, 2012; see results of the cladistic analysis presented below).

Although living *Dermatemys* is restricted to southern Mexico, Belize, and Guatemala, fossil dermatemydids are reported from more northern latitudes during the Eocene and Miocene (Fig. 1). Fossils identified as *Dermatemys* are reported from the early Miocene Toledo Bend Local Fauna of Newton County, Texas (Albright, 1994). Species of *Notomorpha* and *Baptemys* are known from the latter part of the early Eocene (Wasatchian NALMA, Wa 5–Wa 7) of North Dakota, Wyoming, and New Mexico; Wasatchian–Bridgerian boundary of New Mexico (Cub Mountain Formation); middle Eocene (Bridgerian NALMA) of southwestern Wyoming; Bridgerian–Uintan of northern Colorado (Washakie Formation); late Uintan–Duchesnean of Texas; and Duchesnean of Utah (Lucas et al., 1989; Westgate, 1989, 2012; Eaton et al., 1999; Holroyd et al., 2001; Holroyd, 2002). Hutchison (1998) noted the presence of a form that might be ancestral to *Baptemys* from the Tiffanian and Clarkforkian of the Big Bend region of Texas. To date, no Oligocene dermatemydids have been reported.

Here we describe the oldest dermatemydid from the earliest Eocene of Wyoming and discuss its relationship to *Notomorpha*, *Baptemys*, and the extant *Dermatemys mawii*, and implications of its morphology for the divergence of dermatemydids. We also discuss the significance of its appearance within the Paleocene–Eocene Thermal Maximum (PETM), a period of abrupt climatic warming, and why the occurrence of a tropically distributed exotherm during this brief climatic event is important for understanding the mechanisms underlying faunal turnover at the PETM.

All specimens yet known for *Gomphochelys*, gen. nov., were recovered from localities within a ~35 m-thick sequence of

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1

A

B

C
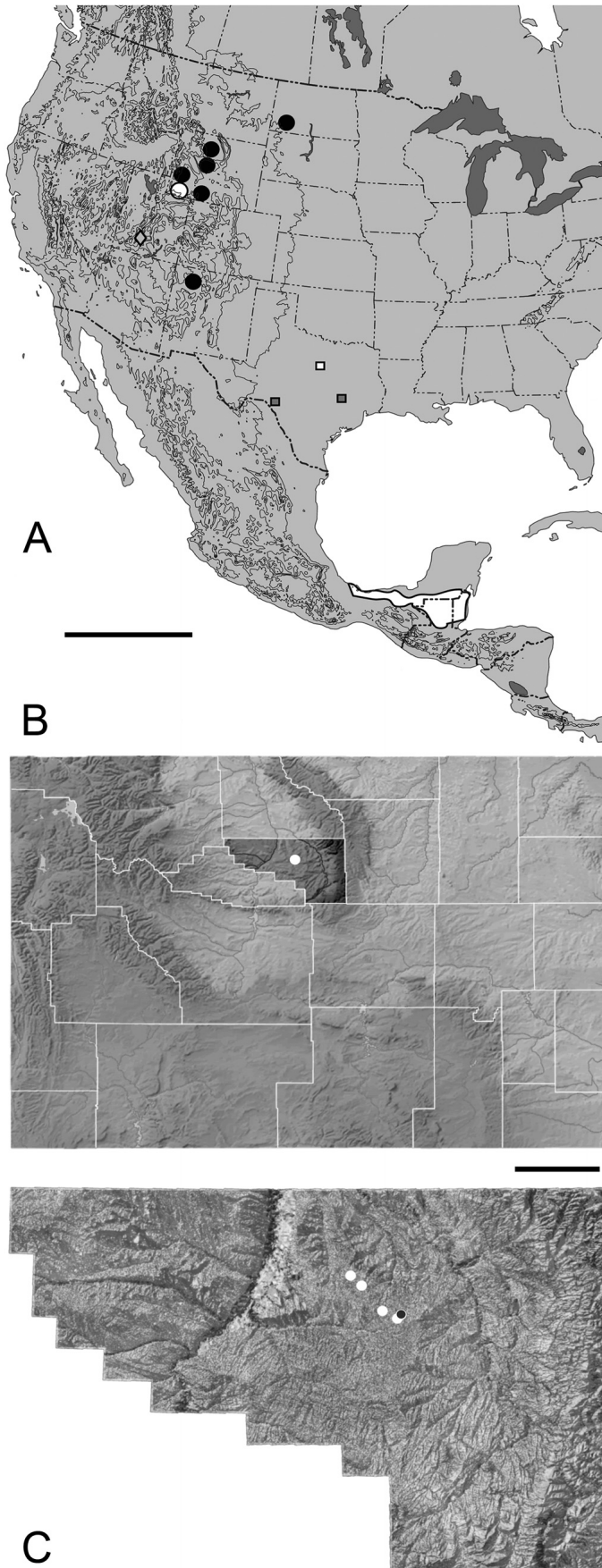
fluvial mudstones, floodplain soils (paleosols), and fluvial sandstones representing the basal-most part of the Willwood Formation in the southeastern Bighorn Basin, Wyoming (Figs. 1, 2). This sequence is recognized as spanning the PETM based on well-constrained chemostratigraphic (Wing et al., 2005; Smith et al., 2007; Secord et al., 2012; Baczynski et al., 2013; Kraus et al., 2013) and biostratigraphic (Chester et al., 2010; Rose et al., 2011; Secord et al., 2012) frameworks.

Institutional Abbreviations—**AMNH**, Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York; **ANSP**, Academy of Natural Sciences at Philadelphia, Drexel University, Philadelphia, Pennsylvania; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **FLMNH**, Florida Museum of Natural History, University of Florida, Gainesville, Florida; **UCMP**, University of California Museum of Paleontology, University of California, Berkeley, California; **UF**, Division of Vertebrate Paleontology, Florida Museum of Natural History, University of Florida, Gainesville, Florida; **UF/H**, Division of Herpetology, Florida Museum of Natural History, University of Florida, Gainesville, Florida; **USNM**, United States National Museum, Washington, D.C.; **YPM VP**, Division of Vertebrate Paleontology, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut; **YPM VPPU**, formerly part of the Princeton University Collection, now housed in the Division of Vertebrate Paleontology, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Stratigraphic Abbreviations—Terminology follows Woodburne (2004). **CIE**, Carbon Isotope Excursion; **NALMA**, North American Land Mammal Age; **PETM**, Paleocene–Eocene Thermal Maximum.

Anatomical Abbreviations—The terminology of the shell follows that of Zangerl (1969) except for plastral scales, which follows that of Hutchison and Bramble (1981): **C**, costal (e.g., C1 = first costal); **N**, neural; **P**, peripheral; scutes: **M**, marginal; **PL**, pleural; **V**, vertebral.

TAXONOMIC HISTORY OF DERMATEMYDIDAE

There has been no formal treatment of Eocene fossil dermatemydids since Hay (1908), so we take this opportunity to review and clarify the convoluted taxonomic history of the type specimens of some of the nominal species prior to description of the new form.

Notomorpha garmanii

Specimens that we now recognize as Eocene dermatemydids were first described in the equivocal genus *Notomorpha* Cope, 1872. Cope (1872) erected the genus and the three included species. All of the species came from the 'Wasatch Group' (now Wasatch Formation), a few miles east of 'Evanstown' (Evanston), Uinta County, Wyoming. He designated no type species

←FIGURE 1. Maps of dermatemydid fossil localities in North America. **A**, map of North America: gray squares, late Paleocene Dermatemydidae indet.; black dots, late Wasatchian *Notomorpha garmanii*; white dot, Bridgerian *Baptemys*; gray diamond, Duchesnean *Baptemys*; white square, Arikareean '*Dermatemys*'; highlighted area at the base of the Yucatan Peninsula (Mexico, Guatemala, and Belize) represents known range of the only extant dermatemydid, *Dermatemys mawii*. Scale bar equals 500 miles; **B**, map of Wyoming with Washakie County darkened; white dot encompasses portion of the study area where *Gomphochelys nanus* was collected. Scale bar equals 50 miles; **C**, Washakie County, Wyoming; white dots indicate localities in the southern Bighorn Basin where referred specimens of *G. nanus* were collected (diagonally from top to bottom): WY08025; WY08192, WY09029, and WY09031; WY04152; and WY07040. Black dot indicates type locality WY06111 and adjacent WY13064.

for the genus. The type of the first species, *Notomorpha testudinea*, was later transferred to the genus *Emys* by Cope (1873, 1884) and finally placed within the geoemydid (= batagurid) genus *Echmatemys* by Hay (1908) where it has since remained.

The type of the second species, *Notomorpha gravis*, consisted of "portions of one, and probably of other specimens" (Cope, 1872:476) and was represented by a hyoplastron and part of a costal. These bones were never figured and were apparently lost before 1908 (Hay, 1908).

The type of the third species, *Notomorpha garmanii*, consists of mostly carapace fragments and is now conserved in the USNM under the number USNM 4129. Between Cope's (1872) original description of *N. garmanii* and Hay's (1908) review, Cope (1873) synonymized *N. gravis* and *N. garmanii* and in 1884 figured the bones (none of them plastral bones) of *N. garmanii* under the name *N. gravis*. In his review, Hay (1908:269) summarized the status of the two species as follows:

"As stated above, Cope made his *N. garmanii* a synonym of *N. gravis*, a proper course in case there is only a single species involved; but of this there may be grave doubts. Of his *gravis* he described a hyoplastron and an epiplastral of one individual and a costal of what was doubtfully another. The costal had a width of 58 mm, which indicated a very large turtle. Cope at first recognized important differences between the epiplastrals; but later he considered these of less importance. We may, then, have doubts regarding the specific identity of the two lots of bones. Besides this, the materials figured all belong to his *N. garmanii*. Notwithstanding all this, until future discoveries shall have thrown additional light on *Notomorpha*, it will be best to place the few known remains under the specific name *gravis*."

However, it seems clear from Cope's (1872, 1873) description of *N. gravis* that the plastral bones belong to a testudinoid (wide hyoplastral lip) and do not belong to the same species as *N. garmanii*, which is a dermatemydid (see below). It seems likely, but unproven in the absence of the type, that *N. gravis* is referable to *Echmatemys*, possibly *E. testudinea* (= *Notomorpha testudinea* Cope, 1872). The name *N. gravis* is hereby restricted to the type specimen, now lost, and is best considered a nomen dubium.

Notomorpha garmanii was described based on a number of isolated bones, mostly fragmentary, found together and thought by Cope (1884) to belong to the same individual. Hay (1908:269) states that "those (bones) which Cope described as *N. garmanii* are now in the U. S. National Museum, some of these bearing the number 4103; others, belonging to the same individual, have the number 4129." As it now stands, all of the figured bones from this lot are cataloged under USNM 4129 and labeled as *Notomorpha gravis*. USNM 4103 now encompasses the types of *Echmatemys testudinea*. We agree with Cope and Hay that only one individual seems to be represented (USNM 4129). The type of *N. garmanii* is the basis of Hay's maintenance of the genus *Notomorpha* and is hereby considered as the genotypic species, despite the fact that Hay considered these same specimens as the type of *N. gravis* while simultaneously acknowledging them as the original type of Cope's *N. garmanii*.

As noted by Hay (1908), the basis for the genus and species rests almost entirely on the peculiar nature of the epiplastron. Hay (1908:269) was "unable to convince himself that this is the epiplastron, altho [sic] it may be such. It may be a first peripheral." Hay was nearly correct in that the bone in question is a nuchal lacking the dorsal part and most of the left side.

Baptemys tricarinata

Although the other bones in the sample have poorly preserved surficial features, some costal fragments show the presence of a dorsal carina but are not otherwise thickened dorsally. They and the associated peripherals are in complete morphological agreement with *Baptemys tricarinata* of Hay (1908). *Baptemys tricarinata* was the last Wasatchian dermatemydid to be described. It was based upon good material from the Wind River Formation of Wyoming and includes a complete plastron and the central portion of the carapace (Hay, 1908:figs. 346–349). Although the types of *Notomorpha garmanii* and *B. tricarinata* are not completely comparable because of their fragmentary nature, they are in agreement with referred material from the type area of *B. tricarinata* in the University of California Museum of Paleontology Collections (see below). There is no morphological or stratigraphic reason to maintain both *N. garmanii* and *B. tricarinata* as separate species. *Notomorpha garmanii* Cope, 1872, thus becomes the senior synonym of *B. tricarinata* (Hay, 1908). *Baptemys tricarinata* is a subjective junior synonym of *N. garmanii* based upon the above comparisons.

Kallistira costilata

Dermatemys? *costilatus* was named by Cope (1875a:36) on the basis of fragments from six individuals from the 'Wasatch beds' (now San Jose Formation) of northwestern New Mexico. At first, Cope questionably referred them to the extant genus *Dermatemys* Gray. Cope (1875b, 1877) later removed the question mark; however, he noted that the reference to the genus was based on resemblances to *Dermatemys wyomingensis* (Leidy, 1870) from the Bridger Formation of Wyoming. He considered *Baptemys* Leidy (type, *B. wyomingensis* Leidy, 1870) as a synonym of *Dermatemys*. Hay (1908:267) later noted that some of Cope's original specimens of *Dermatemys costilatus* had been lost but considered the combination of a thick and solid shell with three carinae and high extension of the inguinal buttress as the basis for erecting a new genus, *Kallistira*, using Cope's remaining specimens. Hay did not designate a type specimen for *Kallistira costilata* (Cope) and stated that "there appears to be no reason for doubting that all of these individuals belonged to the same genus." Examination of the material studied by Hay reveals that this statement is incorrect. At least two genera are represented in the syntype sample, *Echmatemys* (a geoemydid) and a dermatemydid. Thus, the designation of a lectotype is critical to the disposition of the genus. All of Cope's extant syntypes in the USNM are conserved under a single museum number, USNM 1152. There is no basis now (other than Cope's and Hay's statements that there were six and four individuals represented, respectively) for assuming that any of the isolated bones belong to the same individual. Numbered paper labels glued on the specimens refer to the figure numbers in Cope (1877:pl. 24). Of those that J.H.H. has examined, Cope's numbers 21–21a (Hay, 1908:fig. 330), 18 (Hay, 1908:fig. 332), 25 (Hay, 1908:fig. 332a), and 22 (Hay, 1908:fig. 333), and three unfigured fragments, are referable to *Notomorpha*, as are (judging from Cope's figures) the missing specimens numbered 17 and 20. Specimens 19, 29–29a (Hay, 1908:figs. 334–334a), 30–30a (Hay, 1908:fig. 331), and 27–28 (Hay, 1908:fig. 329) are referable to *Echmatemys*.

Reference of some of the specimens to *Echmatemys* is based upon essential identity in morphology and shell texture with comparable elements of the *Echmatemys testudinea–Echmatemys megaulax* (Cope, 1872) complex. The remains referred to *Notomorpha* are all smooth and identical to comparable elements of *Baptemys tricarinata* (= *Notomorpha garmanii*). The costal fragment showing a carina in Cope (1877:figs. 21–21a) and Hay (1908:fig. 330) is hereby selected as the lectotype of *Dermatemys*? *costilatus* Cope, 1875a (= *Kallistria costilata* Hay, 1908). There are no morphological criteria upon which *K. costilata* can be distinguished from *N. garmanii* (including *B. tricarinata*) at present. Therefore, *K. costilata* is here considered a junior synonym of *N. garmanii* Cope, 1872.

Baptemys fluviatilis

Hay (1908) named *Baptemys fluviatilis* based on a shell that lacked most of the plastron, which was represented, in part, by the impression of the internal mold. The specimen lacked reliable locality data, but Hay thought (and we concur) that it probably came from the Bridger Formation. As noted by Hay, the specimen agrees well with typical *Baptemys wyomingensis* in size and morphology. Hay distinguished the two taxa by differences in the suprapygal region and shape of the plastral hindlobe. Hay (1908:268) stated that *B. fluviatilis* has only two suprapygals and *B. wyomingensis* has three; however, his figures of *B. wyomingensis* (Hay, 1908:text-fig. 337; pl. 40, fig. 1; pl. 41, fig. 1) clearly indicate the presence of only two suprapygals. Because the plastral hindlobe is represented by only an impression of the dorsal surface, the actual shape of its margins are in doubt. Moreover, the specimen has been weathered (Hay, 1908:pl. 42, fig. 1) such that the margins have been planed off, thus reducing and narrowing its outline. Therefore, we suggest that *B. fluviatilis* be placed in synonymy with *B. wyomingensis*.

MATERIALS AND METHODS

Specimens Examined

The following specimens were utilized for comparison with the new dermatemydid fossils. *Agomphus pectoralis*: AMNH 1478, AMNH 1481, AMNH 1482 (*Adocus petrosus*, holotype), YPM VP .000671, YPM VP .000774 –.000776, YPM VP .000900; *Baltemys staurogastros*: UCMP 127200 (holotype), *Baptemys fluviatilis*: AMNH 4913 (holotype); *Notomorpha garmanii*: AMNH 6109 (*Baptemys tricarinata*, holotype), AMNH 6110, CM 26282, YPM VPPU 17402, UCMP 95902, UCMP 110601, UCMP 110605, UCMP 132074, UCMP 151754–151756, UCMP 151772, UCMP 152584, UCMP 152683, UCMP 152693, UCMP 152696–152699, UCMP 152703–152707, UCMP 152714–152722, UCMP 152727, UCMP 152732–152742, UCMP 152749–152766, UCMP 152770, UCMP 152772, UCMP 152774, UCMP 152776, UCMP 152779, UCMP 152782, UCMP 152783, UCMP 152788, UCMP 152802–152806, UCMP 152809–152812, UCMP 152814, UCMP 152820, UCMP 152824, UCMP 152825, UCMP 152828, UCMP 152829, UCMP 152837–152839, UCMP 152841, UCMP 152849, UCMP 152850, UCMP 152855–152858, UCMP 152874, UCMP 152882–152888, UCMP 152899–152904, UCMP 152910, UCMP 158652, UCMP 168857, UCMP 170982, UCMP 171792, UCMP 171887, UCMP 173811, UCMP 189118, UCMP 399806, UCMP 399808, UCMP 399821, UCMP 399824, UCMP 399831–399833, UCMP 399837–399839, UCMP 399845, UCMP 399849, UCMP 399859, UCMP 399860, UCMP 399866–399869, UCMP 399881–399886, UCMP 399894, USNM 1152 (*Kallistira costilata*, syntype), USNM 4129 (holotype); *Baptemys wyomingensis*: AMNH 6004, AMNH 1107, AMNH 25564, UCMP 125353, UCMP 125354, YPM VP .000136; *Dermatemys mawii*: UF/H 29168, UF/H 47723, UF/H 80653, UF/H 10186; *Hoplochelys*: AMNH 1064, AMNH 1200 (*Hoplochelys saliens*, holotype), AMNH 6079 (*Hoplochelys paludosa*, holotype), AMNH 6091 (*Hoplochelys crassa*, holotype), UCMP 93116; *Staurotypus salvinii*: UF/H 165992; *Staurotypus triporcatus*: UF/H 13482, UF/H 13484; *Xenochelys formosa*: AMNH 1097 (holotype); *Xenochelys bridgerensis*: UCMP 121734 (holotype); *Xenochelys lostcabinensis*: UCMP 112341 (holotype).

SYSTEMATIC PALEONTOLOGY

Order TESTUDINES Linnaeus, 1758
Suborder CRYPTODIRA Cope, 1868
Superfamily TRIONYCHOIDEA Gaffney, 1975
Epifamily KINOSTERNOIDEA Agassiz, 1857

Cinosternoidae Agassiz, 1857.
Kinosternoidae Agassiz, 1857: Gaffney and Meylan, 1988 (emended spelling).
Kinosternoidea Agassiz, 1857: Hutchison et al., 1997:p. 394 (emended spelling).
Kinosternoidea Agassiz, 1857: Joyce et al., 2004.

Family DERMATEMYDIDAE Gray, 1870
Dermatemydae Gray, 1870.
Dermatemydidae Gray, 1870: Baur, 1888 (emended spelling).

Included Genera—*Dermatemys* Gray, 1847, *Baptemys* Leidy, 1870, *Notomorpha* Cope, 1872, and *Gomphochelys* new genus (described below).

Emended Diagnosis—Plastron suturally united to the carapace; entoplastron present (Appendix S1:Ch. 28); plastral lobes reduced; nuchal with or without costiform processes; three to five pairs of inframarginal scutes present (Appendix S1:Ch. 30)

FIGURE 2. **A**, J.H.H. in July of 2007 prospecting the type locality (WY06111) of *Gomphochelys nanus*, UF 225761, where it was collected the previous year (area encircled in the right of the picture); **B**, UF 225761 in situ just prior to collection by J.R.B. in July of 2006. Two posterior peripherals with associated carapacial and plastral fragments from another individual of the same size (UF 249081) were recovered approximately 2 to 3 m from this specimen at the same stratigraphic level (in the area with the thickest vegetation in the center of picture **A**).
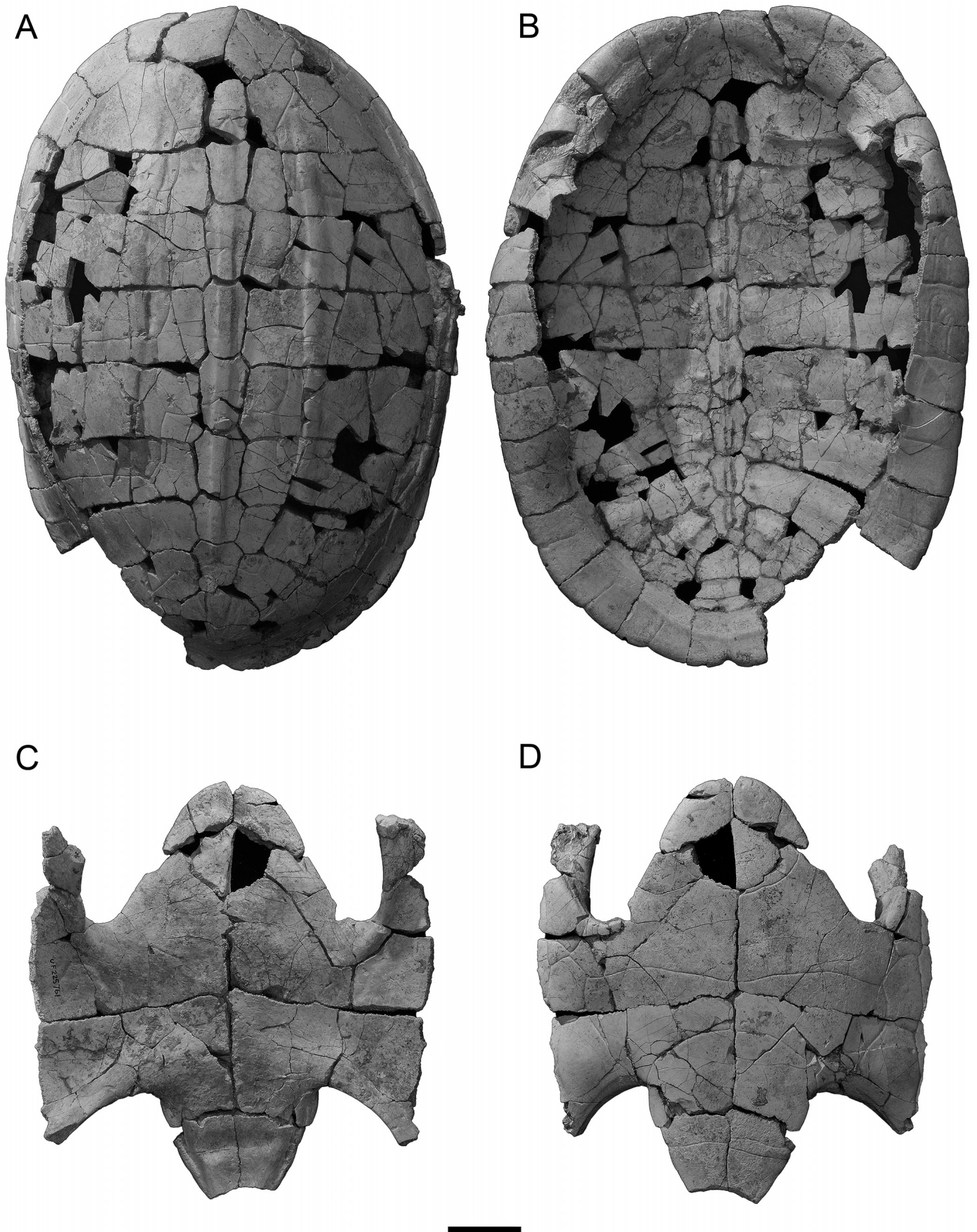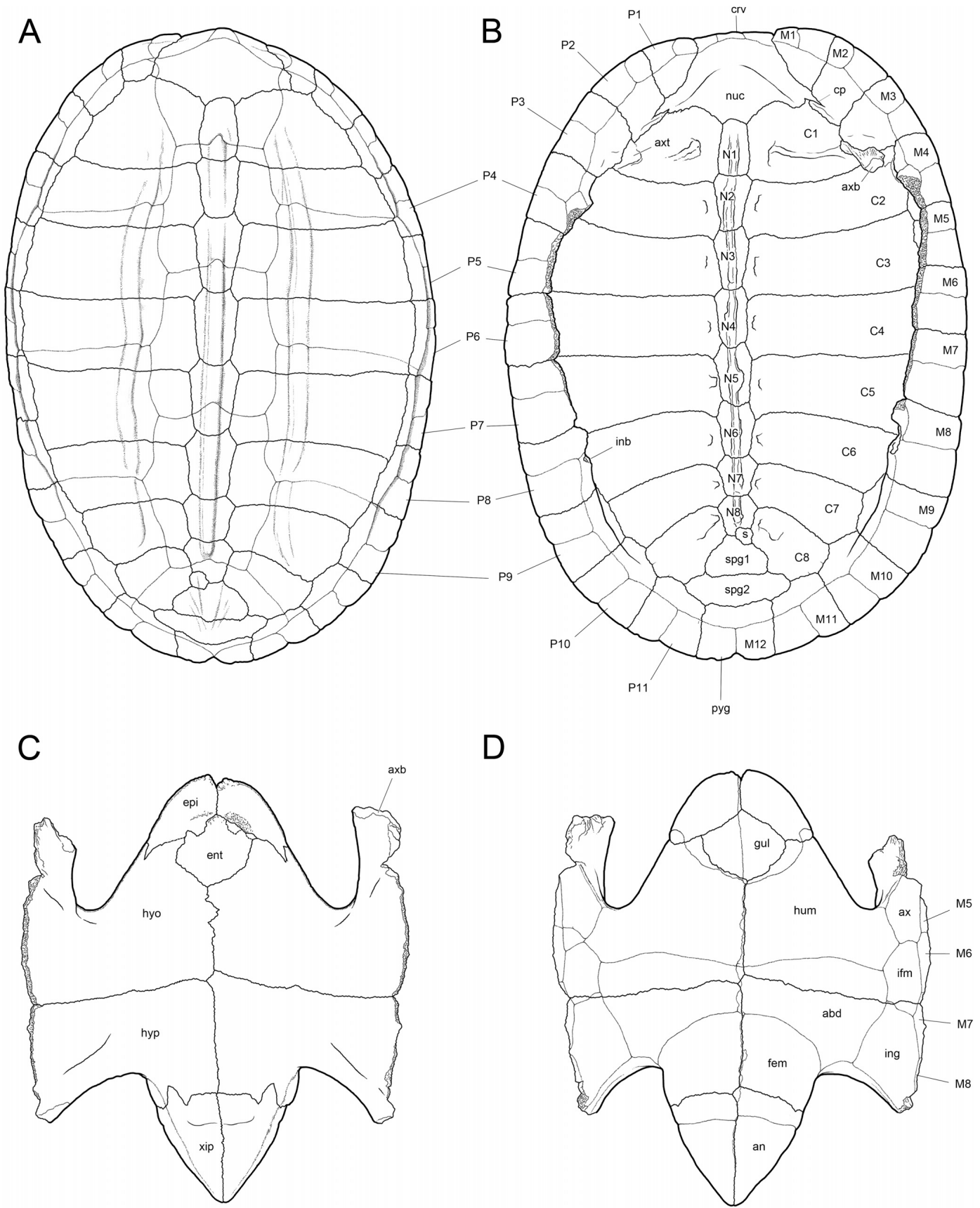
FIGURE 3.   Shell of *Gomphochelys nanus*, gen. et sp. nov., holotype, UF 225761. Carapace in **A**, dorsal and **B**, ventral views. Plastron in **C**, dorsal and **D**, ventral views. Scale bar equals 3 cm.

(Hay, 1908); temporal region emarginated from behind, separating squamosal from parietal and postorbital; frontals enter orbital margin; maxilla does not meet quadratojugal; quadrate does not surround stapes; no foramen present in prootic for temporal artery; dentary expanded posteriorly over much of external surface of jaw; only one biconvex centrum in cervical vertebrae; eighth centrum doubly concave anteriorly; caudal vertebrae procoelous; paired pubes and ischia meet ventrally, but pubic and ischiadic symphyses are widely separated; trochanteric fossa of femur widely open (Iverson and Mittermeier, 1980); axillary buttress contacts C1 (Appendix S1:Ch. 25) (Meylan and Gaffney, 1989); carapace smooth or with some crenulated sculpturing; club-shaped terminus of axillary buttress; C3 spans P5 dorsally (Hutchison and Bramble, 1981); distal C1 terminates in P3 (Appendix S1:Ch. 7); two suprapygals present (Appendix S1:Ch. 10); lack of distinct anterior musk duct groove (Appendix S1:Ch. 15); loss of extragular and pectoral scutes; marginals not encroaching upon suprapygals or costals; abdominals contribute to axillary notch (Appendix S1:Ch. 34); femoral–humeral sulcus arched anteriorly; reduction or loss of foramen stapedio-temporale; medial triturating ridge of dentary curving laterally anteriorly and contacting lateral ridge to form a pocket.

Genus *BAPTEMYS* Leidy, 1870

Type Species—*Baptemys wyomingensis* Leidy, 1870.

BAPTEMYS WYOMINGENSIS Leidy, 1870

Adocus wyomingensis Cope, 1869:233.
Dermatemys wyomingensis Cope, 1873:624.
Baena ponderosa Cope, 1873:624.
Dermatemys wyomingensis Cope, 1884:142.
Baena? ponderosa Hay, 1902:438.
Baptemys wyomingensis Hay, 1908:270.
Baptemys wyomingensis Hutchison and Bramble, 1981.
Baptemys wyomingensis West and Hutchison, 1981.
Baptemys wyomingensis Stucky et al., 1996.
Baptemys wyomingensis Zonneveld et al., 2000.
Baptemys wyomingensis Gunnell and Bartels, 2001.
Baptemys wyomingensis Knauss et al., 2010.

Holotype—ANSP 10074, partial carapace and plastron.
Type Locality and Formation—Near Fort Bridger, Wyoming.
Age of Type Locality—Bridgerian NALMA (early Eocene).
Emended Diagnosis—Carapace unicarinate; xiphiplastra curved convexly at outer margins; plastral forelobe broad; plastral hindlobe lobate and lacking caudal notch; entoplastron wider than long, with gular–humeral sulcus positioned halfway or on posterior two-thirds of element.

Genus *NOTOMORPHA* Cope, 1872

Type Species—*Notomorpha garmanii* Cope, 1872.

NOTOMORPHA GARMANII Cope, 1872

Notomorpha garmanii Cope, 1872:477.
Notomorpha gravis Cope, 1872:476.
Dermatemys? costilatus Cope, 1875a:36.
Dermatemys costilatus Cope, 1872; Cope, 1875b:96.
Dermatemys costilatus Cope: Cope, 1877:52–53, pl. 24, figs. 17–18.
Baptemys costilatus (Cope): Hay, 1902:445.

Kallistira costilata (Cope): Hay, 1908:267–269, figs. 329–334.
Baptemys gravis (Cope): Hay, 1908:269–270, figs. 335–336.
Baptemys tricarinata Hay, 1908:275, figs. 346–349.
Baptemys garmanii (Cope): Hutchison, 1980.
Baptemys tricarinata Hay: Hutchison, 1980:117.
Baptemys tricarinata Hay: Hutchison and Bramble, 1981:79, fig. 5D.
Kallistira costilata (Cope): Lucas et al., 1981:956.
Baptemys tricarinata Hay: Estes, 1988:547, fig. 3.
Kallistira costilata (Cope): Kues, 1993:255.
Baptemys garmani (Cope): McCord, 1996.
Baptemys garmanii (Cope): Hutchison, 1998:404, fig. 18.2E.
Baptemys garmanii (Cope): Hutchison and Frye, 2001:12, fig. 13.
Baptemys garmanii (Cope): Holroyd and Hutchison, 2000.
Baptemys garmanii (Cope): Knauss et al., 2010.

Holotype—USNM 4129, weathered fragments of carapace supposedly of one individual, including fragments of costals and nuchal, damaged right and left P3s, left P8, right and ?left P9s, and left P11.
Type Locality and Formation—"From a bluff, six miles north of the Bear River" (Cope, 1872:477). "From Green River strata, near Evanston, Wyoming" (Cope, 1873:627). "From the Wasatch beds of Wyoming, six miles north of Evanston, near Bear River" (Cope, 1884:144). Uinta County, Wyoming, Wasatch Formation.
Age of Type Locality—Wasatchian NALMA (early Eocene).
Diagnosis—Carapace tricarinate; xiphiplastra straight-sided, relatively long and narrow, and converging to a point (Hay, 1908); plastron with narrowed plastral lobes, entoplastron wider than long with gular–humeral sulcus positioned on posterior two-thirds of element.

GOMPHOCHELYS NANUS, gen. et sp. nov.
(Figs. 3–6, 8)
Baptemys, sp. nov., Bourque et al., 2008.

Holotype—UF 225761 (Figs. 3–5), nearly complete associated carapace and plastron, missing left P10–11, most of right P4–5, most of distal C6, right half of the entoplastron, as well as the posterior-most ends of the nuchal and xiphiplastra. The holotype was first discovered by Scott Wing, Doug Boyer, and Aaron Diefendorf while they were bed tracing in July of 2006. UF 225761 was partially weathered out near the top of a ridge as disarticulated fragments (Fig. 2). It was collected and reassembled by the first author.
**Type Locality**—UF locality WY06111, meter level 24.85 (refer to Secord et al. [2012] for meter level context), Cabin Fork area, southeastern Bighorn Basin, Washakie County, Wyoming, U.S.A. More specific locality data are available on file in the Division of Vertebrate Paleontology, Florida Museum of Natural History. Pieces of a second *Gomphochelys nanus* specimen, UF 249081, as well as a large trionychid were also collected from this locality.
Age and Formation—Earliest Wasatchian NALMA (latest Paleocene–earliest Eocene), Willwood Formation, mammalian biohorizon Wa 0 (~55.8 Ma).
Etymology—Generic epithet is a combination of Greek 'gomphos' for 'nail, peg, or bolt' (in reference to the developed club-like axillary buttresses) and 'chelys' for 'turtle.' Specific epithet 'nanus' is Latin for 'small' or 'dwarf.'
Referred Specimens—(Listed by locality, meter level, specimen number, and nature of specimen.) WY04152 (out of place):

←FIGURE 4. Illustration of *Gomphochelys nanus*, gen. et sp. nov., holotype, UF 225761. Carapace in **A**, dorsal and **B**, ventral views. Plastron in **C**, dorsal and **D**, ventral views. **Abbreviations**: **abd**, abdominal scute; **an**, anal scute; **ax**, axillary scute; **axb**, axillary bridge buttress; **axt**, terminus for the axillary buttress; **C1–8**, costals 1–8; **cp**, costiform process of the nuchal; **crv**, cervical scute; **ent**, entoplastron; **epi**, epiplastron; **fem**, femoral scute; **gul**, gular scute; **hum**, humeral scute; **hyo**, hyoplastron; **hyp**, hypoplastron; **ifm**, inframarginal scute; **inb**, terminus for the inguinal buttress; **ing**, inguinal scute; **M1–12**, marginals 1–12; **N1–8**, neurals 1–8; **nuc**, nuchal; **P1–11**, peripherals 1–11; **pyg**, pygal; **s**, supernumerary suprapygal; **spg1–2**, suprapygals 1–2; **xip**, xiphiplastron. Scale bar equals 3 cm.
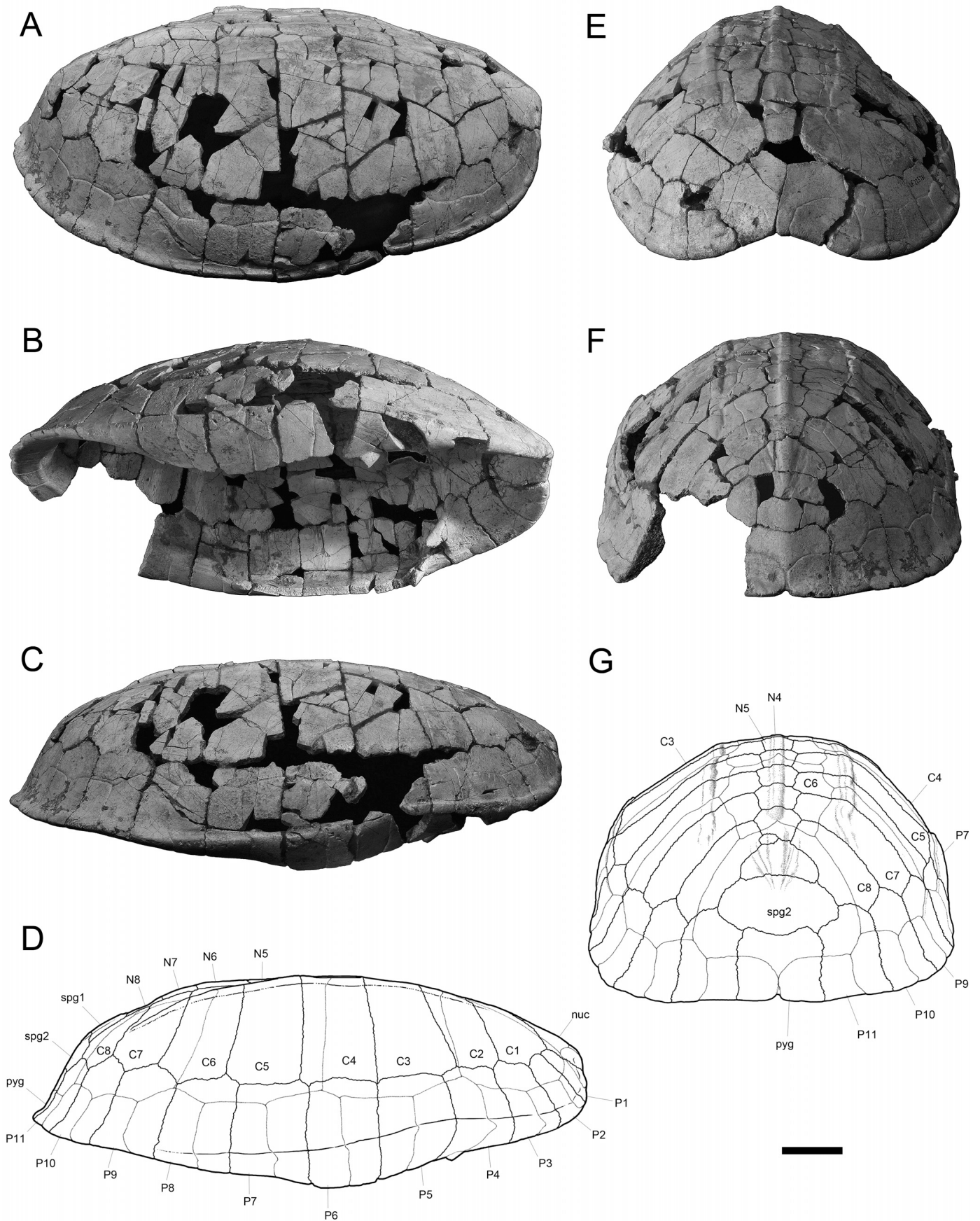
UF 249082, partial peripheral; UF 249083, left P2; UF 249084, left partial xiphiplastron; WY06111 (24.85 m): UF 249081, left and right P9s with isolated carapace and plastral fragments; WY07040 (46.5 m): UF 249086, left P2; V08025 (40.9 m): UF 249085, partial carapace and plastron; WY08192 (46.5 m): UF 249075, partial neural; UF 249076, partial right half of nuchal; UF 249077, entoplastron; UF 249078, N3; UF 249079, posterior N6; UF 249080, N4; V09001 (45.62 m): UF 249055, N4; UF 249056, posterior N5; UF 249057, N6; UF 249058, N7; UF 249059, partial nuchal; UF 249060, left partial xiphiplastron; WY09029 (39.9 m): UF 249061, left partial xiphiplastron; UF 249062, right partial xiphiplastron; UF 249063, right P2; UF 249064, right P9; UF 249065, left P1; UF 249066, N4; UF 249067, N6; UF 249068, right partial P2, UF 249069, left partial xiphiplastron; UF 249070, left partial hypoplastron; UF 249071–249073, neurals; UF 270845, distal fragment of right C1; WY09031 (41.76 m): UF 271117, posterior peripheral; WY13064 (~24.85 m): UF 293396, partial carapace.

Diagnosis—*Gomphochelys nanus* differs from other dermatemydids by the following: relatively small adult size for the family Dermatemydidae (carapace ~32 cm long for UF 225761); bones of the shell robust with thickened peripherals and pygal (shared with *Agomphus pectoralis*); pygal lacks keel or crest (shared with *Agomphus* and *Dermatemys mawii*); posterior peripherals relatively straight and shortened (shared with *A. pectoralis*); marginal scutes short in dorsal aspect with narrow underlap ventrally (shared with *A. pectoralis*); plastral forelobes and hindlobes reduced; entoplastron reduced, about as wide as long or only slightly wider than long (shared with *A. pectoralis*); and gular–humeral sulcus positioned either along, just anterior to, or just posterior to the ento–hyoplastral suture. The following are synapomorphies of *G. nanus* and other dermatemydids: costiform processes extend across P1 and terminate in the anterior third of P2 (shared with some *Notomorpha garmanii*, *Staurotypus*, *Claudius*, and *Hoplochelys*); three pronounced longitudinal carinae on the dorsum of the carapace (shared with *N. garmanii*, *Hoplochelys*, and *Agomphus alabamensis*) composed of a set of rounded lateral carinae that extend from the posterior half of C1 to posterior-most C7, as well as a pronounced dorsally flattened medial keel that extends from the posterior N1 (at the intervertebral sulcus for V1–2), is interrupted at the V4–5 sulcus on N8, and terminates on the suprapygals (terminates on N8 in referred specimen UF 249085); pygal wider than long (it is longer than wide in most *N. garmanii* and in all *Baptemys wyomingensis* and *Dermatemys* examined); and xiphiplastron pointed and lacks caudal notch (shared with *A. pectoralis*, *Hoplochelys*, and *N. garmanii*).

Comments—Fossils of *G. nanus* older than Wa 0 were mentioned by Bourque et al. (2008) and subsequently cited by Knauss et al. (2010). These specimens comprise a few fragmentary, probably associated shell pieces (UF 249082–249084) that were collected from a late Clarkforkian (Cf 3) area in the southern Bighorn Basin and most likely represent temporally younger fossils from the PETM that eroded into Cf 3, because they were collected near a wash and are highly weathered in appearance. Likewise, Chester et al. (2010) report Wa 0 contaminants within a Cf 3 mammalian assemblage from the southern Bighorn Basin.

DESCRIPTION AND COMPARISONS

The shell of *Gomphochelys nanus* is overall smaller, thicker, and more robust than similarly sized individuals of other dermatemydid taxa. In UF 225761, the sutures of the individual bony elements are well formed throughout the shell and all of the distal costals completely contact their corresponding peripheral sets (where preserved). This level of ossification indicates that *G. nanus* reached maturity at a relatively small size. All other species of dermatemydid examined, such as *Notomorpha garmanii* (including the holotype of *Baptemys tricarinata*), *Baptemys wyomingensis*, and the Central American river turtle *Dermatemys mawii*, reach a much larger adult size (to 65 cm for the latter sensu Ernst and Barbour [1989]). When compared with the holotype of *G. nanus*, similarly sized *N. garmanii* from the UCMP were clearly subadults (e.g., UCMP 152739) because they exhibited excessively thin shell bones, porous bone at unformed sutures along the distal costal ends and proximal peripheral ends, and the costals and periperals were not in complete sutural contact. The shell of *G. nanus* is comparable in overall size to *Agomphus pectoralis*, *Hoplochelys crassa*, and *Staurotypus*.

Carapace

The carapace of UF 225761 is preserved almost in its entirety, with some minor distortion due to crushing and carbonate-filled fractures. It is 31.8 cm in length (Table S1) and is composed of a nuchal, eight neurals, two fully formed suprapygals, a diminutive supernumerary suprapygal, eight sets of costals, a pygal, and presumably 11 sets of peripherals despite two posterior peripherals not preserved (left P10–11). The costiform processes of UF 225761 extend through P1 and terminate in the anterior third of P2. The extent of the costiform process can also be seen in the left P2 specimens, UF 249083 and UF 249086, and right P2, UF 249063, in which the cavity that receives the costiform process is preserved. In the partial shell, UF 249085, the right P1 exhibits a deep sutural cavity that would have housed the costiform process. The sutural cavity is expansive and extends across the visceral face, suggesting that the costiform process would have terminated well into P2. The costiform process is more extensive in *G. nanus* than in examined *N. garmanii*, and compares well to that of *Hoplochelys clark* Knauss, Joyce, Lyson, and Pearson, 2010. Peripherals of the anterior (P1–4) and posterior (P8–11) margins of the shell are short in height and thickened (Fig. 6), almost to the degree seen in *Agomphus pectoralis* (e.g., YPM VP .000900). The posterior peripherals are straighter, and overall the posterior margin of the carapace is straighter and less flared than that of other dematemydids. The pygal of *G. nanus* is wider than long, with a length of 8–9% CL. This is in contrast to *D. mawii*, which has a thin elongated pygal ~16% CL (e.g., UF/H 29168). P11 is likewise long and narrow in *D. mawii*, with very narrow sutural contact with the suprapygal. Conversely, P11 broadly contacts the suprapygal in *G. nanus*.

Neural 1 is ovoid and four-sided and broadly contacts the nuchal. Neurals 2–8 are hexagonal and anteriorly symmetrically short-sided. The lateral sutures of N1 and N4 are nearly parallel-sided. There are two fully formed suprapygals in both UF 225761 and UF 249085, but in the former there is an extra diminutive round suprapygal between the sutural contact of the left C8, N8, and suprapygal 1.

The carapace possesses three well-developed longitudinal keels, almost intermediate in relief between *Hoplochelys* and *Notomorpha garmanii*. The medial keel extends across the entire neural series. It begins on N1 at the V1–2 intervertebral sulcus, abruptly becomes faint on N2, grows prominent on the anterior of N3, becomes most prominent on N6–7, ceases (or becomes

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←FIGURE 5. Carapace of *Gomphochelys nanus*, gen. et sp. nov., holotype. UF 225761. **A**, right dorsolateral view; **B**, right ventrolateral view; **C**, right lateral view; **D**, illustration in right lateral view; **E**, anterodorsal view; **F**, posterodorsal view; **G**, illustration in posterodorsal view. **Abbreviations**: **C1–8**, costals 1–8; **N4–8**, neurals 4–8; **nuc**, nuchal; **P1–11**, peripherals 1–11; **pyg**, pygal; **spg1–2**, suprapygals 1–2. Scale bar equals 3 cm.
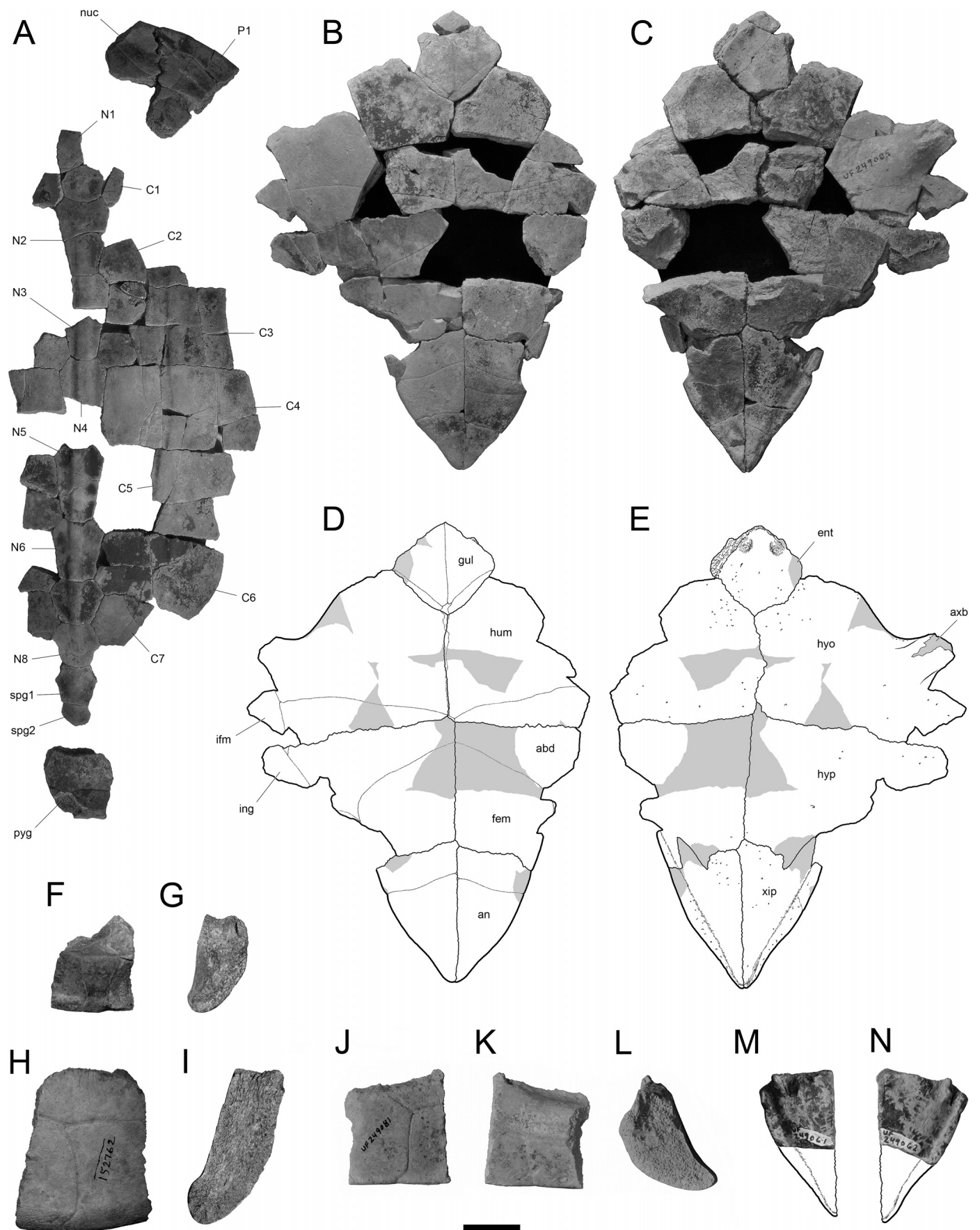
interrupted) at the V4–5 intervertebral sulcus on N8, reemerges on suprapygal 1, and terminates on suprapygal 2. The medial keel does not extend onto the pygal in either the holotype of *Gomphochelys nanus*, UF 225761, or referred specimen UF 249085, which is probably plesiomorphic for dermatemydids. *Dermatemys mawii* also lacks a keeled pygal, but it is probably secondarily lost in that species. In UF 225761 and UF 249085, the pygal is smooth dorsally and lacks any discernible keel, although it is slightly humped medially. The medial keel is crenulated on suprapygal 1 and at its posterior terminus on the anterior-most suprapygal 2 (Figs. 4, 5). In the referred specimen, UF 249085, the medial keel terminates at the V4–5 intervertebral sulcus more anteriorly than in the holotype and lacks crenulations. The location of the posterior terminus for the medial keel in *G. nanus* is similar to the medial keel terminus in juvenile *D. mawii*, i.e., around the anterior of V5. The medial carapacial keel is most pronounced and dorsally squared along the edges on N3–7. The costal keels are more rounded along the edges and extend from the middle of C1 to the posterior-most C7. On C7, the keel curves distally and terminates. These carinae are most pronounced along sets C3–6. Characteristics seen in *G. nanus*, such as a thickened tricarinate carapace with some narrow and nearly parallel-sided neurals (N1 and N4), are mildly similar to features in the taxon *Agomphus alabamensis* Gilmore, 1919, from the Paleocene Midway Formation (Garrote et al., 2006) of Alabama. That species possesses three dorsal carapacial carinae, which are autapomorphic for the genus *Agomphus*. Hutchison and Weems (1998) report a taxon similar to *A. alabamensis* from the Paleocene Williamsburg Formation of South Carolina and question the generic designation of *Agomphus* for that taxon.

In *Gomphochelys nanus*, the axillary plastral buttress terminates in the posterior third of C1. The axillary buttress contacts C1 more anteriorly in *Dermatemys*. The terminus for the axillary buttress is an ovate sutural pocket that lies just proximal to the C1–P3 suture. This pocket is seen clearly in the C1 fragment UF 270845, which is very thick for its small size, particularly at the peripheral–costal suture. C1 is more strongly buttressed viscerally in *Dermatemys* than in *G. nanus*. In the holotype of *G. nanus*, the right axillary buttress extends through P4, well into P3, and just contacts P2 along the inner C1–P2–P3 suture. Slight contact with P2 is also clear in UF 249063, UF 249083, and UF 249086 by a pit exhibited on each of these elements. The left axillary buttress terminates on C1 in the holotype, similar to that seen in the C1 fragment UF 270845. In *Dermatemys*, the axillary buttress substantially contacts the posterior of P2. In *G. nanus*, the inguinal buttress does not extend onto the costals but extensively contacts the anterior two-thirds of P8, whereas in *Dermatemys* it contacts the anterior third of P8.

Gomphochelys nanus possesses five vertebral scutes and four pairs of pleural scutes. In UF 225761, the V1–PL1 sulci extend across costal set 1 and onto the nuchal, forming an hourglass-shaped V1. V1 is typically more straight-sided or with rounded convex lateral borders in other dermatemydids. The V1–PL1 sulcus just contacts P1 in UF 225761, but there is more significant contact in UF 249065, a left P1. Vertebrals 2–4 are elongate in shape, being much longer than wide. Vertebral 5 is roughly triangular or 'teardrop-shaped.' The vertebral and pleural sulci jut

anteriorly where they overlap the three carapacial keels: on the neurals where crossed by the vertebral scutes and on the proximal costals where crossed by the pleural scutes.

In *Gomphochelys nanus*, the cervical scale is thick and triangular or trapezoidal (UF 225761) to square (UF 249059) in shape. There are 12 pairs of marginal scutes. M3–9 are raised on the surface of the peripherals along the dorsal sulci (i.e., the marginals are stepped above the plane of the pleurals), similar to but not as pronounced or anteroposteriorly extensive as seen in *Hoplochelys* and adult *Staurotypus triporcatus*. None of the marginals in UF 225761 contact the costals. In *Dermatemys*, M5 contacts or nearly contacts C2, and M7 typically contacts C4 (e.g., UF/H 29168). M9 is elevated in height from M8 and M10, similar to but convergent with the conditions seen in the kinosternine *Kinosternon flavescens* and geoemydid *Rhinoclemmys*. M9 and M11 are nearly equally elevated, and M11 is more elevated than M12. The underlap of the posterior marginals is narrow, particularly for M12 on the pygal.

Plastron

The plastron of *Gomphochelys nanus* is composed of an entoplastron and paired epiplastra, hyoplastra, hypoplastra, and xiphiplastra. The forelobe (i.e., the portion of the plastron comprising the epiplastra, entoplastron, and associated dermal scutes) is short, and the epiplastra and entoplastron are more reduced than other dermatemydids, similar to *Agomphus pectoralis* (Fig. 7). The gular–humeral sulcus of *G. nanus* is posteriorly situated on the forelobe (Fig. 8). In the holotype UF 225761, the sulcus extends along and just posterior to the ento–hyoplastral suture (Fig. 8A), convergent with *Staurotypus* (Hutchison and Bramble, 1981). *Staurotypus* possesses a kinetic forelobe accompanied by pliable connective tissue and only slight sutural contact between the hyoplastra and the forelobe (Bramble et al., 1984), which is not the case for *G. nanus*. Instead, there is rigid sutural contact between the epi-, ento-, and hyoplastra in *G. nanus*. In the referred specimen UF 249077 (an isolated entoplastron), the gular–humeral sulcus is situated along the ento–hyoplastral suture (Fig. 8B). In the partial shell UF 249085, the gular–humeral sulcus is situated along but just anterior to the ento–hyoplastral suture (Fig. 8C), but it is still more posteriorly positioned than what is typical for *Hoplochelys*, *Notomorpha garmanii*, *Baptemys wyomingensis*, and *Dermatemys mawii*. A notable condition is present in *Agomphus pectoralis*, YPM VP .000776 (Fig. 7E), where the gular–humeral sulcus was probably situated posteriorly on the entoplastron (which is not preserved), more so than in other *A. pectoralis* specimens examined. In that specimen, the gular–humeral sulci abruptly curve posteriorly on the hyoplastra from the ento–hyoplastral suture, well posterior to the ento–hyoplastron sutural plane. The gular–humeral sulci abruptly recurve anteriorly to the outer margins of the epiplastra. The condition in *G. nanus* is somewhat intermediate between YPM VP .000776 and *N. garmanii* (Fig. 7). There is a morphocline within the dermatemydid lineage involving the position of the gular–humeral sulcus, where it migrates progressively anteriorly on the entoplastron through time, eventually being situated either midway or on the anterior half of the

←FIGURE 6.   Referred specimens of *Gomphochelys nanus* (**A**–**G**, **J**–**N**). **A**, partial carapace of UF 249085 in dorsal view. Partial plastron of UF 249085 in **B**, ventral and **C**, dorsal views. Illustrations of plastron of UF 249085 in **D**, ventral and **E**, dorsal views. Left P2 of adult *G. nanus* (UF 249086) in **F**, dorsal and **G**, posterior views. Left P2 of adult *Notomorpha garmanii* (UCMP 152762) in **H**, dorsal and **I**, posterior views for comparison. The peripherals of *G. nanus* are relatively thick for their small size, similar to the condition in *Agomphus*. The peripherals of *N. garmanii* are comparatively longer and thinner. Left P9 of *G. nanus*, UF 249081, in **J**, dorsal, **K**, ventral, and **L**, anterior views. This specimen was found at the same locality as the holotype UF 225761. **M**, partial left xiphiplastron, UF 249061, in dorsal view. **N**, partial right xiphiplastron, UF 249062, in dorsal view. **Abbreviations**: **abd**, abdominal scute; **an**, anal scute; **axb**, axillary bridge buttress; **C1–7**, costals 1–7; **ent**, entoplastron; **fem**, femoral scute; **gul**, gular scute; **hum**, humeral scute; **hyo**, hyoplastron; **hyp**, hypoplastron; **ifm**, inframarginal scute; **ing**, inguinal scute; **N1–8**, neurals 1–8; **nuc**, nuchal; **P1**, peripheral 1; **pyg**, pygal; **spg1–2**, suprapygals 1–2; **xip**, xiphiplastron. Scale bar equals 2 cm.
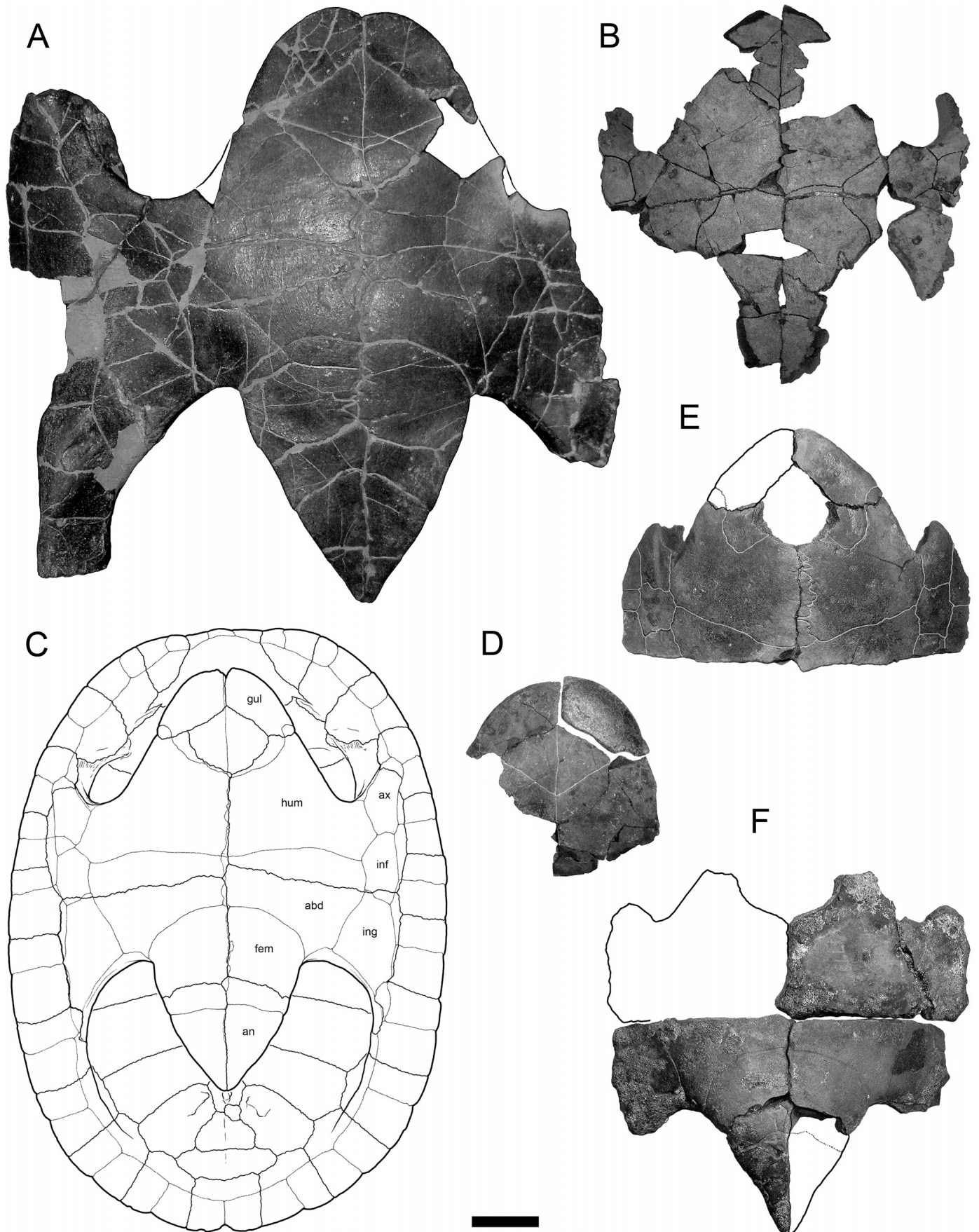
element. This morphocline, coupled with an increase in size over time, is expressed in succession across the taxa *G. nanus*, *N. garmanii*, *B. wyomingensis*, and *D. mawii* (see also Discussion).

In UF 225761, there is a set of gulars (scale set 1 of Hutchison and Bramble, 1981), of which only the medial sulcus crosses the entoplastron. Paired humerals (scale set 3 of Hutchison and Bramble, 1981) are contained almost wholly on the hyoplastra except for the anterodistal-most extensions, which overlap onto the posterior-most ends of the epiplastra. There are paired abdominals (scale set 5 of Hutchison and Bramble, 1981), femorals (scale set 6 of Hutchison and Bramble, 1981), and anals (scale set 7 of Hutchison and Bramble, 1981), the latter contained entirely on the xiphiplastra. The forelobe lacks the intergular (scale 8 of Hutchison and Bramble, 1981), which is lacking in other dermatemydids with the exception of *Dermatemys*. The anterior-most portions of the epiplastra are preserved intact but do not contact one another well at the midline along the inter-epiplastral suture. This gives the appearance of a slightly notched anterior forelobe and could be an indication that medial skin or connective tissue was present at least anteriorly between the epiplastra. A similar condition was observed in some *Staurotypus*, which had medial skin overlapping onto the ventral face of anterior-most forelobe. The lack of a strong inter-epiplastral sutural connection in *G. nanus* could indicate very slight (probably passive) medial kinesis in the forelobe, or perhaps just poor preservation along the medial suture.

The posterior tip of the hindlobe is missing in the holotype UF 225761, but it is complete in UF 249085 (Fig. 6). The posterior tip (composed of the xiphiplastral set) is pointed, which is a primitive kinosternoid feature seen in *Agomphus*, *Hoplochelys*, and *Staurotypus* (Hutchison and Bramble, 1981). Within Dermatemydidae, a pointed hindlobe is shared with *N. garmanii*. Although missing, the weathered impression of the hindlobe for the holotype of *B. fluviatilis* Hay, 1908 (= *B. wyomingensis* here; see Taxonomic History of Dermatemydidae, above), could be perceived as pointed. *Baptemys wyomingensis* has a broader more lobate hindlobe. Conversely, an undescribed species of *Baptemys* from the late middle Eocene (Duchesnean) of south-central Utah (Eaton et al., 1999) and *Dermatemys mawii* have medially notched hindlobes. In *G. nanus*, the hindlobe is most similar to, but more blunt and shorter than, *Agomphus*, *Hoplochelys*, and *N. garmanii*. In UF 225761, there is a transverse trench–like concavity just posterior to the hypo–xiphiplastral suture in visceral aspect that likely accommodated the pubis. This concavity was either not present or not as pronounced in other xiphiplastral specimens of *G. nanus* (e.g., UF 249061 and UF 249062) or in *Notomorpha* and *Baptemys* specimens examined. A similar concavity was observed in *D. mawii*, being distinct in UF/H 29168 and more subtly expressed in UF/H 47723.

In the holotype of *Gomphochelys nanus*, there are four inframarginals on the right side of the plastron and three on the left. The right inframarginal series is composed of three large and a single reduced scute, which is typical for *Notomorpha* and *Baptemys* (Hutchison and Bramble, 1981). These represent (from anterior to posterior) the axillary, inframarginal 1, inframarginal 2, and inguinal scutes. The inframarginals are contained almost entirely on the plastron, with the exception of the anterior-most axillary, which extends onto the middle of P4, and the posterior-most inguinal, which just overlaps the anterior quarter of P8. The posterior of inframarginal 2 (on the right) and inframarginal 1 (on the left side), as well as the anterior-most inguinals, overlap the hyo–hypoplastral sutures.

PHYLOGENETIC ANALYSIS

Characters scored in the current analysis are from Hutchison and Bramble (1981), Hutchison (1991), Iverson (1991), and Knauss et al. (2010), with the addition of six new characters (Appendix S1). The analysis comprised 38 morphological characters among 14 kinosternoid taxa (13 ingroup, one outgroup), and the character-taxon matrix was developed in the program Mesquite 2.5 (Maddison and Maddison, 2008) (Appendix S2). Taxa utilized reflect those of Knauss et al. (2010), including synonymies within the *Agomphus* and *Hoplochelys* lineages (Hutchison and Weems, 1998; Knauss et al., 2010); however, the chelydrids *Macrochelys temminckii* and *Chelydra serpentina* were not incorporated into this analysis. Two different analyses were run: one using the taxon *Agomphus pectoralis* as the outgroup and one using *Hoplochelys clark* as the outgroup, both taxa being Late Cretaceous (Maastrichtian) in age (Knauss et al., 2010). Characters 3, 22, and 29 of Knauss et al. (2010) were omitted because the former two are regarded as autapomorphic for the taxa *Hoplochelys clark* and *Claudius angustatus*, and the latter is a chelydrid synapomorphy. Skull characters were not utilized because skulls for many of the fossil taxa including *Gomphochelys nanus* are unknown. A parsimony analysis was conducted in PAUP* 4.0-b10 (Swofford, 2003) using 1000 branch-and-bound search replicates with furthest addition sequence, and 1000 bootstrap replicates were performed to assess support for the topologies. Character states were unordered and equally weighted, multistate characters were regarded as polymorphisms, and the maximum number of trees was set to 100,000.

Results

A single most parsimonious tree was recovered (tree length = 111; consistency index = 0.703; retention index = 0.750; rescaled consistency index = 0.527; homoplasy index = 0.514) regardless of whether *Agomphus pectoralis* or *Hoplochelys clark* was used as the outgroup taxon (Fig. 9). *Gomphochelys nanus* was recovered as the most basal member of the dermatemydid lineage. In Figure 9A, the Dermatemydidae and *Hoplochelys* are sister taxa, which in turn are sister to the Kinosternidae. In Figure 9B, *Agomphus* is directly ancestral to the Dermatemydidae. *Staurotypus triporcatus* and *Claudius angustatus* do not form a monophyletic group in either result. In both cladograms, *Xenochelys* is recovered as paraphyletic with regard to the early Eocene species *Xenochelys lostcabinensis* Hutchison, 1991, and late Eocene *Xenochelys formosa* Hay, 1906. Results of Knauss et al. (2010) and Bourque (2013) also suggest this hypothesis.


←FIGURE 7. Plastron comparison of some fossil kinosternoids. **A**, holotype of *Baptemys tricarinata* (= *Notomorpha garmanii*), AMNH 6109, from the Wasatchian (Lostcabinian) Wind River Formation, Fremont County, Wyoming; **B**, *Hoplochelys* sp., UCMP 93116, from the Puercan Nacimiento Formation of San Juan County, New Mexico; **C**, illustration of articulated carapace and plastron of *Gomphochelys nanus* holotype, UF 225761, from the earliest Wasatchian (Wa 0) of Washakie County, Wyoming (with some restoration); **D**, partial forelobe of *Notomorpha garmanii*, UCMP 132074, from the Wasatchian (Lysitean or Lostcabinean) Luman Tongue of the Green River Formation, Sweetwater County, Wyoming; **E**, anterior plastron of *Agomphus pectoralis*, YPM VP .000776. **F**, Partial plastron of *Agomphus pectoralis*, YPM VP .000775, from the Late Cretaceous of Monmouth County, New Jersey. **Abbreviations**: **abd**, abdominal scute; **an**, anal scute; **ax**, axillary scute; **fem**, femoral scute; **gul**, gular scute; **hum**, humeral scute; **ifm**, inframarginal scute; **ing**, inguinal scute. Images of YPM VP .000775 and .000776 courtesy of the Division of Vertebrate Paleontology, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A. Photography by J.R.B. All specimens in ventral view. Scale bar equals 3 cm.

DISCUSSION

Paleoclimate

Dermatemydids are reliable indicators of a warm, relatively wet climate. The sole living survivor of this family, *Dermatemys mawii*, inhabits numerous aquatic habitats in the neotropics of Central America from Tabasco, northern Chiapas, southern Campeche, southern Quintana Roo, and Veracruz, Mexico; northern Guatemala; Belize; and possibly northwestern Honduras (Fig. 1A) (Ernst and Barbour, 1989). The mean annual temperature (MAT) in this part of Central America ranges from 20°C to more than 25°C (68°F to more than 79°F) (Legates and Willmot, 1990a), with mean annual precipitation (MAP) of 2000–4000 mm (Legates and Willmot, 1990b). More specifically, seasonal MATs during a 2-year study on *Dermatemys* in Belize were 16°C–17°C (61°F–63°F) in winter and 32°C–33°C (90°F–91°F) in summer (Polisar, 1996). Campbell (1972) reported that *D. mawii* requires warm water temperatures of 28°C–30°C (82°F–86°F) in order to be kept successfully in zoos. MATs in the Bighorn Basin during the Wasatchian have been proposed as subtropical, in the range of 12°C–18°C (54°F–65°F) (Gunnell, 1997). However, temperatures spiked during the Carbon Isotope Excursion (CIE) at the PETM, with MATs hypothesized to have been 20°C–27°C (68°F–81°F) and MAP of approximately 1150–1200 mm (Wolfe and Dilcher, 2000; Zachos et al., 2001; Fricke and Wing, 2004; Wing et al., 2005; Woodburne et al., 2009; Secord et al., 2012). Kraus et al. (2013) document major drying of paleosols, with MAP estimates between 900 and 1200 mm during the main body of the PETM.

The first and last known occurrences of *Gomphochelys nanus* in the Bighorn Basin are coincident with the span of the CIE (Fig. 10); thus, its presence in the southeastern Bighorn Basin can be attributed to increased temperatures in the region at that time. *Gomphochelys nanus* first occurs shortly after the onset of the CIE, during either the wettest portion (Bowen et al., 2004; Secord et al., 2012) or initial dry portion (Kraus et al., 2013) of that interval. It seems to disappear from the southern Bighorn Basin at the end of the CIE, which was marked by decreased temperatures and either increased (Secord et al., 2012) or decreased (Kraus et al., 2013) aridity. After its disappearance at the end of the PETM, dermatemydids are missing from the fossil record in the Bighorn Basin until the late Wasatchian (Wa 5 or Biohorizon B), when they reappear with the first occurrence of *Notomorpha garmanii*, concurrently with the first records of the large land tortoise *Hadrianus* (Hutchison, 1980; Holroyd and Hutchison, 2000; Holroyd et al., 2001) and during an interval of mammalian turnover (Chew, 2009). The reemergence of dermatemydids in the central Bighorn Basin stratigraphic section is coincident with Eocene Thermal Maximum 2 (Abels et al., 2012; Chew and Oheim, 2013) and represents the beginning of the second early Eocene interval of climatic warming, with greatly increased MATs (23°C, 73°F) and increased MAP of 1400 mm (Woodburne et al., 2009). Decreased $\delta^{18}O$ and $\delta^{13}C$ values and leaf margin analyses during Wa 5 suggest that MATs approached or nearly approached those experienced at the PETM (Zachos et al., 2001; Woodburne et al., 2009).
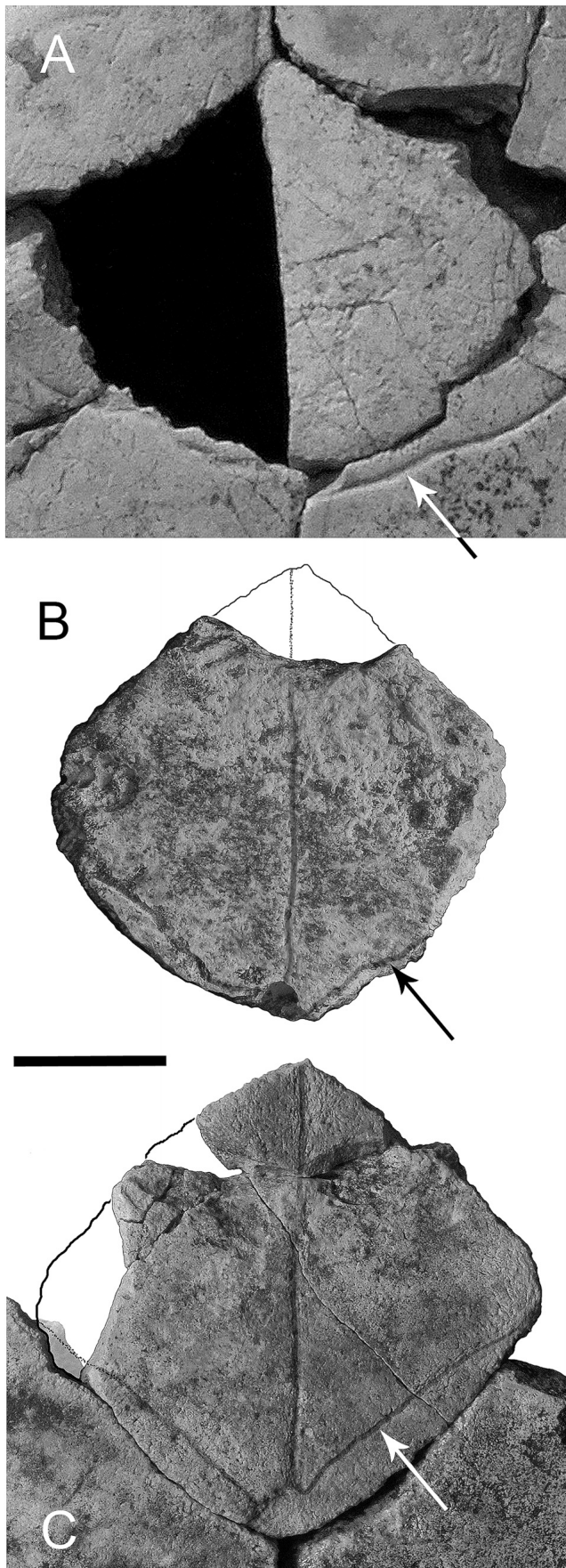
←FIGURE 8. Entoplastra of *Gomphochelys nanus* illustrating variability in the position of the gular–humeral sulcus (indicated by arrows). This sulcus is situated more posteriorly in *G. nanus* than in other dermatemydids. **A**, UF 225761 with sulci situated along and just posterior to the ento–hyoplastral suture; **B**, UF 249077 with sulci along and just anterior to the ento–hyoplastral suture; **C**, UF 249085 with sulci well anterior to the ento–hyoplastral suture. Both UF 249085 and UF 249077 possess an almost identical round pock or depression at the medial junction of the gular and humeral scutes, which could indicate pathology or perhaps a trace of medial skin. Scale bar equals 1 cm.
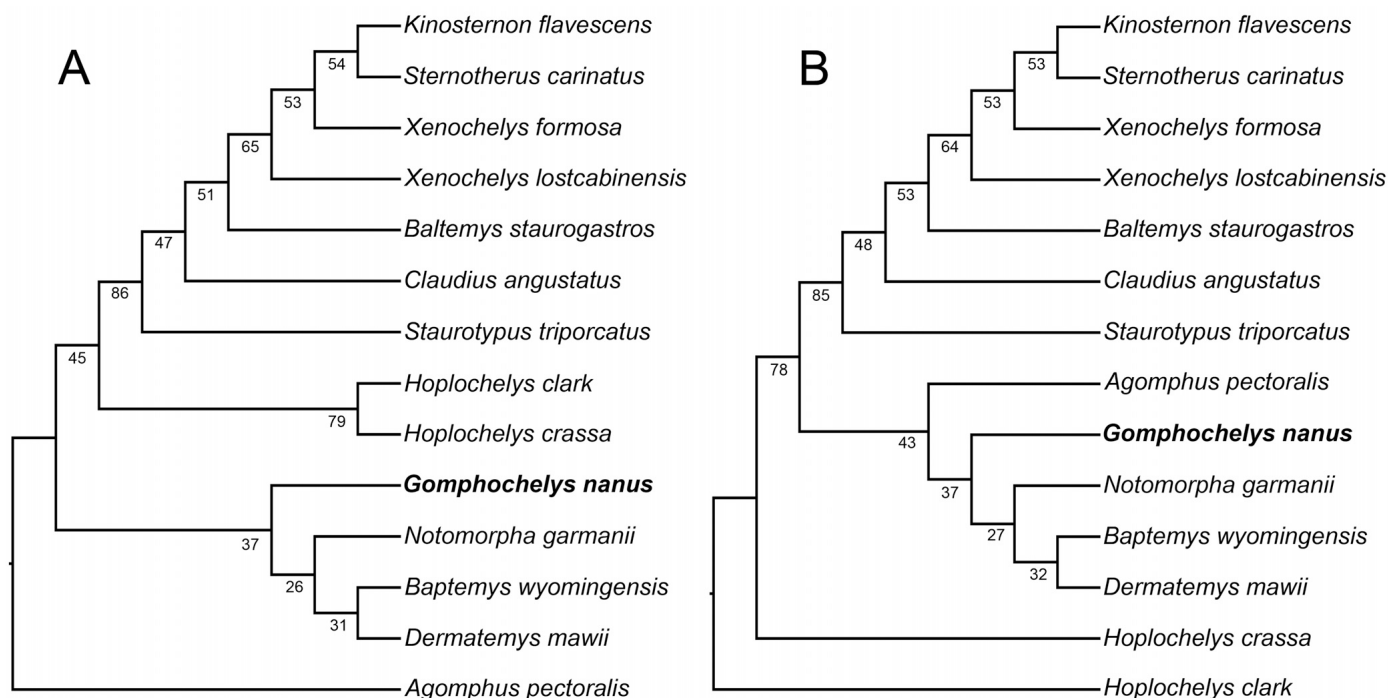
FIGURE 9. Phylogenetic hypotheses for relationships of *Gomphochelys nanus* and other Kinosternoidea based on morphological evidence. **A**, single most parsimonious cladogram with *Agomphus pectoralis* used as the outgroup; **B**, single most parsimonious cladogram with *Hoplochelys clark* used as the outgroup. Numbers indicate bootstrap support values.

A taxon ancestral to *Baptemys* has been mentioned anecdotally from the Tiffanian of Texas (Hutchison, 1998). Other Paleocene kinosternoid records include *Agomphus* cf. *Agomphus pectoralis* and *Agomphus* aff. *Agomphus alabamensis* from the late Paleocene of South Carolina (Hutchison and Weems, 1998) and *A. alabamensis* from the Paleocene Midway Formation of Alabama (Gilmore, 1919). These reports of kinosternoids that are more closely related to dermatemydids than the more pan-continental Cretaceous to Paleocene *Hoplochelys* (Knauss et al., 2010) in the southern part of the United States, and the absence of kinosternoids outside of North America, suggest that dermatemydids immigrated into the Bighorn Basin from the south and/or southeastern United States coincident with climate warming. Whereas much of the literature discussing dispersal during the PETM has focused on the importance of high-latitude dispersal to the reorganization of the fauna (Koch et al., 1992; Clyde and Gingerich, 1998; Bowen et al., 2002; Gingerich, 2003; Smith et al., 2006; Beard, 2008; Beard and Dawson, 2009), there is increasing evidence that within-continent northward range expansion is also an important component in biotic turnover at the PETM.

Northward range expansion with PETM warming has been hypothesized for selected mammals: the primate *Teilhardina*, the phenacodontid condylarth *Ectocion parvus*, and possibly the condylarth *Meniscotherium* (Gingerich and Smith, 2006; Beard, 2008; Burger, 2012). Several fossil plants ('*Artocarpus*' *lessigiana*, *Brosipollis*, ?*Lanagiopollis*, cf. *Tricolpites hians*, and *Platycarya swasticoides*) also have earlier occurrences or close relatives present in the Gulf Coastal Plain (e.g., Wing et al., 2005). However, the most significant and clearest evidence for intracontinental dispersal in the PETM comes from the herpetological record, in which North American endemic lineages make their first appearance within the rocks of the PETM and persist today in the North American neotropics. Smith (2009) documented a minimum of six lineages appearing within the PETM of the Bighorn Basin: three iguanid lizards, stem representatives of the

xantusiid *Lepidophyma* (extant tropical night lizards), the extant *Anniella* (California legless lizard), and diploglossine anguid lizards (galliwasps). Today, representatives of these lineages are exclusively or almost exclusively found in warm and frost-free (megathermal) parts of the New World. To this list of tropical herpetofauna dispersing north at the PETM, we can now add dermatemydids. Moreover, the sole extant dermatemydid *Dermatemys* shares a sympatric distribution with extant representatives of PETM-associated lizard groups (e.g., numerous iguanids, *Lepidophyma*, and diploglossine *Celestus*) at the base of the Yucatán Peninsula today (Lee, 2000).

Taxonomy within Dermatemydidae

An extensive gap in the fossil record between the last occurrence of *Baptemys wyomingensis* and the extant taxon *Dermatemys mawii* has made taxonomy within the Dermatemydidae somewhat convoluted. The Eocene taxa that we attribute to the Dermatemydidae (*G. nanus*, *N. garmanii*, *B. wyomingensis*, and some still undescribed species) are genuinely similar to one another morphologically, occur over a relatively short period of time from one another, appear not to co-occur with one another temporally or geographically, and are all found from the same region of North America. As such, there is a high likelihood that these taxa formed a monophyletic group in the early Eocene. The incorporation of *G. nanus* and *N. garmanii* into the genus *Baptemys* would result in a paraphyletic *Baptemys* with regard to *Dermatemys mawii* based on our phylogenetic results, as well as those of Knauss et al. (2010). Alternatively, the incorporation of *G. nanus*, *N. garmanii*, and *B. wyomingensis* into the genus *Dermatemys* would suggest that the Dermatemydidae represents a 55.8-million-year-old anagenetic lineage. A number of autapomorphies exist for *Dermatemys* that best warrant generic distinction between it and early Eocene dermatemydids. Shell-based autapomorphies of *D. mawii* include the following: complete loss
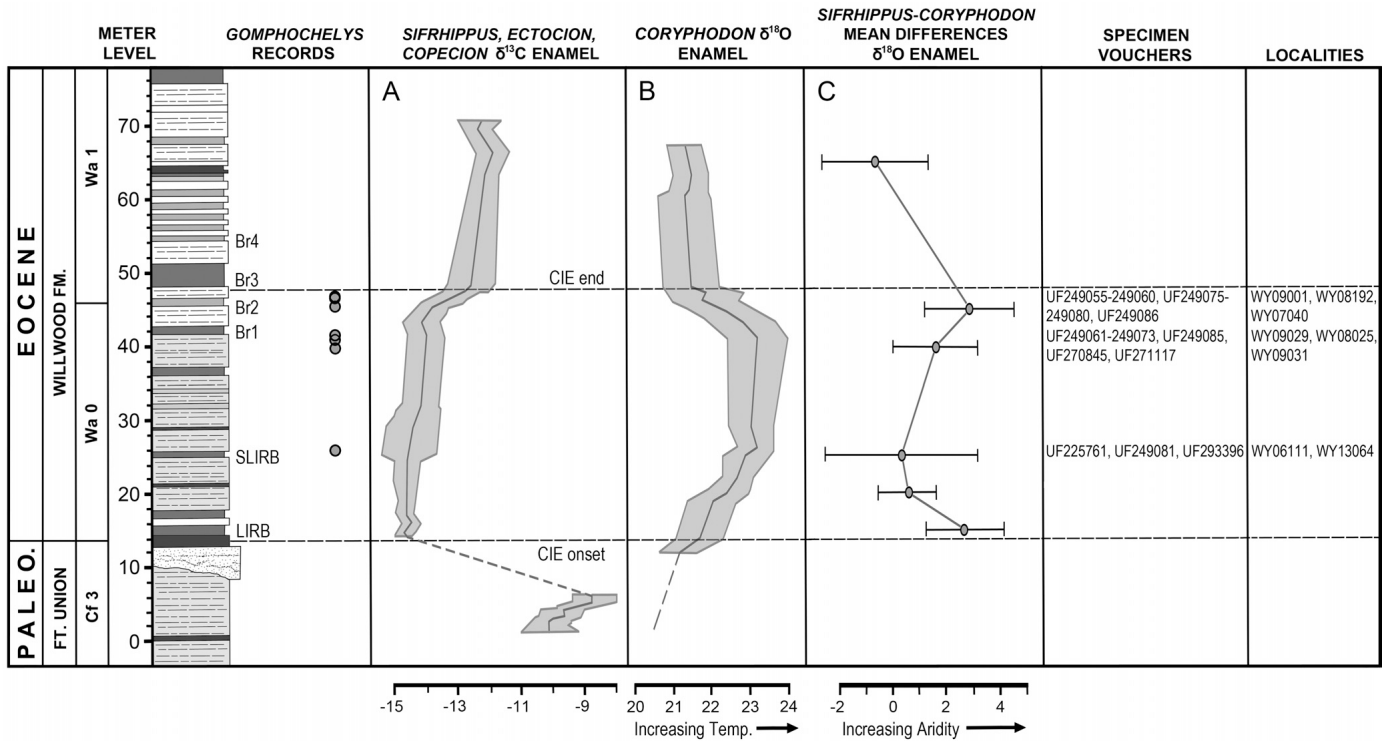
FIGURE 10. Correlation of *Gomphochelys nanus* occurrences within the Cabin Fork section of the southeastern Bighorn Basin with curves developed from **A**, δ^{13}C values for *Sifrhippus*, *Ectocion*, and *Copecion* tooth enamel; **B**, δ^{18}O values for *Coryphodon* tooth enamel; **C**, mean differences of δ^{18}O values for *Sifrhippus* and *Coryphodon* tooth enamel (modified from Secord et al., 2012). Scale bar values: **A**, δ^{13}C$_{Enamel}$ ($^0/_{00}$, vPDB), Vienna Pee Dee belemnite standard; **B**, δ^{18}O$_{Enamel}$ ($^0/_{00}$, vSMOW), Vienna standard mean ocean water standard; **C**, δ^{18}O$_{Sifrhippus-Coryphodon}$ ($^0/_{00}$, vSMOW). Gray areas for **A** and **B** represent 95% envelope of uncertainty, and error bars for **C** indicate 95% confidence of the mean (from Secord et al., 2012). All known records of *Gomphochelys nanus* occur within the Carbon Isotope Excursion. **Abbreviations: Br1–4**, Big Red Beds 1–4; **Cf**, Clarkforkian NALMA; **CIE**, Carbon Isotope Excursion; **Fm.**, Formation; **Ft. Union**, Fort Union Formation; **LIRB**, Lowest Intermittent Red Bed; **Paleo.**, Paleocene; **SLIRB**, Second Lowest Intermittent Red Bed; **Temp.**, Temperature; **Wa**, Wasatchian NALMA.

of carapacial carination (although juveniles retain a medial keel, such as UF/H 101861); presence of an intergular scute; increased number of inframarginals (typically five sets); an expansive caudal notch (Iverson and Mittermeier, 1980; Hutchison and Bramble, 1981); seven or fewer neurals; C7 and C8 pairs contact one another medially; very faintly incised scute sulci on the shell; upper borders of M4–9 do not protrude above the plane of the adjoining pleurals; larger plastron to carapace ratio; inguinal plastral buttress terminus in posterior-most P8 or anterior-most P9; free margins of posterior peripherals with sharp edge; hourglass-shaped to triangular pygal; narrow contact between P11 and suprapygal; M9 and M10 equal in height; M11 contacts pygal; and distal terminus of C8 situated in P10. Furthermore, Eocene dermatemydids can be recognized collectively by the following shell-based characters: plastral lobes short and narrow; hindlobe pointed to rounded and lacking a caudal notch; nuchal bone with short costiform processes that extend to P1 or P2; a full set of neurals (eight); marginal scutes not encroaching on the costal bones (Hay, 1908); three to four sets of inframarginals present; humeral scutes (sensu Hutchison and Bramble, 1981) extend forward and overlap epiplastra; close alignment of the epi–hyoplastral suture with the gular–humeral sulcus; anterior tips of hyoplastra curve medially around lateral wings of entoplastron; epiplastron with strong oblique suture with hyoplastron; free margins of anterior and posterior peripherals rounded; two suprapygals present; broad contact between P11 and suprapygal; pygal square to rectangular; well-incised scute sulci on the shell; upper borders of M4–9 protrude in relation to adjoining pleurals (forming a step); C7 pair with no medial contact; C8

pair with no medial contact; distal terminus of C8 situated between P10 and P11; M9 taller than M10; M11 does not contact pygal; mid-dorsal carina present at least posteriorly; and presence or absence of costal carinae. More refined character-taxon matrices combined with discoveries of dermatemydids from the late Paleogene and early Neogene, e.g., more complete dermatemydid specimens from the Duchesnean of Utah (Eaton et al., 1999) and Arikareean Toledo Bend locality (Albright, 1994), will perhaps better clarify the taxonomy and phylogeny of dermatemydids and elucidate the degree to which this group represents an anagenetic and/or cladogenetic lineage.

Dermatemydid Evolution

There are notable morphoclines with regard to size and shell thickness within the Dermatemydidae, exhibiting Cope's rule (increasing body size through time) from the Wasatchian through Uintan (Hutchison, 1980). Early Wasatchian *Gomphochelys nanus* fits serially into this morphocline. Both the size and relatively thickened shell of *G. nanus* are similar to the Cretaceous–Paleocene genus *Agomphus*, with which it shares a number of characters. These include shortened and thickened anterior and posterior peripherals and a completely acarinate pygal. A keeled or crested pygal develops later in the Eocene with the Wasatchian *Notomorpha garmanii*, becomes highly pronounced in the Bridgerian–Uintan *Baptemys wyomingensis*, but is probably secondarily lost in *Dermatemys mawii*. *Gomphochelys nanus* is relatively small and thick-shelled. The lineage becomes progressively larger and more thin-shelled (primarily

with regard to the carapacial margins and plastron) with the emergence of *N. garmanii* later in the Wasatchian (Wa 5–Wa 7), and continues with *B. wyomingensis* in the late early–middle Eocene. Other morphoclines within Dermatemydidae include the diminishment to loss of carapacial carination, forelobe expansion, and caudal notch development in the plastral hindlobe (Hutchison, 1980; Eaton et al., 1999). Wasatchian *G. nanus* and *N. garmanii* possess tricarinate carapaces, Bridgerian–Uintan *B. wyomingensis* are unicarinate, and modern *D. mawii* is acarinate; however, juvenile *D. mawii* (e.g., UF/H 101861) possess a unicarinate carapace (Iverson and Mittermeier, 1980). The forelobe in *G. nanus* is relatively reduced compared with confamilials and is comparable to *Agomphus*; this includes the small size of the entoplastron and epiplastra. The ento- and epiplastra become progressively wider and more expansive through time in dermatemydids, although the expansion in entoplastral width is most significant. In a similar morphocline, the hindlobe is acutely pointed in Wasatchian *G. nanus* and *N. garmanii* (similar to *Agomphus* and *Hoplochelys*); broadly lobate in Bridgerian–Uintan *B. wyomingensis*; with a weakly developed medial caudal notch in Duchesnean *Baptemys* sp. (sensu Eaton et al., 1999); and with a broad, well-developed caudal notch in extant *D. mawii*.

These morphological trends within the dermatemydid lineage suggest a shift towards becoming more adapted as open-water swimmers. The youngest and largest described dermatemydid species *Baptemys wyomingensis* and *Dermatemys mawii* convergently resemble extant riverine taxa, such as the geoemydids *Batagur* and *Orlitia* (see Moll and Moll, 2004, for overview of lotic-associated turtles), which have long, smooth, highly buttressed shells. This is most notable in *D. mawii*, which has evolved a smoother carapace and more expansive plastron than its predecessors (Hutchison and Bramble, 1981). Conversely, the small size, relatively flattened plastron with reduced plastral lobes, solid, well-ossified tricarinate carapace, and more straight-backed (less flared) posterior marginal rim of *G. nanus* somewhat resemble extant *Staurotypus* and provide evidence that *G. nanus* was at least in part a bottom-walking animal. However, although *Staurotypus* is primarily a bottom-walker, it does spend a great deal of time swimming freely as well, typically close to the substrate (J.R.B., pers. observ.). The plastron of *G. nanus* is not as reduced as those of more habitual bottom-walkers such as the chelydrids *Macrochelys* and *Chelydra*, which suggests that the new species was probably a commensurate active swimmer and bottom-walker. This is also seen in *D. mawii*, which despite its broadly developed plastron spends a great deal of time bottom-walking while foraging along the substrate (J.R.B., pers. observ.). The species *D. mawii*, *Staurotypus salvinii*, and *Staurotypus triporcatus* are probably good modern analogues for *G. nanus* with regard to locomotion, climatic requirements, and perhaps preference for lotic and associated lentic habitats.

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