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BASILEMYS MORRINENSIS, A NEW SPECIES OF NANHSIUNGCHELYID TURTLE FROM THE HORSESHOE CANYON FORMATION (UPPER CRETACEOUS) OF ALBERTA, CANADA

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ABSTRACT—We describe a new species of nanhsiungchelyid turtle, *Basilemys morrinensis*, based on a nearly complete shell from the Horsethief Member (lower Maastrichtian) of the Horseshoe Canyon Formation of Alberta. The species is intermediate in age between the Campanian forms *B. variolosa* and *B. gaffneyi* and the upper Maastrichtian forms *B. sinuosa* and *B. praeclara*. It is also intermediate in its morphology, possessing a unique suite of both plesiomorphic (e.g., divided extragulars) and derived (e.g., square epiplastral beak, pygal wider than long) traits. It is further characterized by an autapomorphic square cervical scale. Phylogenetic analysis assuming parsimony recovers *B. morrinensis* in a polytomy with *B. variolosa* and *B. gaffneyi*, outside the clade formed by the upper Maastrichtian forms *B. sinuosa* and *B. praeclara*. The holotype of *Basilemys morrinensis* provides the first evidence that this genus reached large size (~1 m long) in the Horseshoe Canyon Formation and was not diminutive as previously thought based on less complete shell material. Although *Basilemys* is usually regarded as terrestrial in habit based on its skull and limb morphology, we note that the low profile of its shell is a derived feature usually indicative of an aquatic mode of life. This suggests that there is yet much to learn about the life habits of this interesting turtle.

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

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INTRODUCTION

Basilemys is a genus of large (~1 m long) nanhsiungchelyid turtles found in Upper Cretaceous coastal plain deposits throughout North America (Fig. 1). Its members possess a thick shell with ornate sculpturing of rows of triangular tubercles separated by pits, and reduced inframarginal scales (Brinkman and Nicholls, 1993). The lifestyle of *Basilemys* is often likened to that of a tortoise, interpreted as living in terrestrial habitats and eating tough plants (Hutchison and Archibald, 1986; Hutchison, 2000; Brinkman, 2005), although some disagree (Nessov, 1981; Sukhanov, 2000).

The earliest definite record of *Basilemys* is from the upper Santonian Milk River Formation of Alberta (Brinkman, 2003). These remains are fragmentary and cannot be identified to the species level. The earliest known diagnostic species is *Basilemys variolosa*, originally described on the basis of a partial shell from the Judith River Formation (Campanian) of Montana (Cope, 1876; Hay, 1908). More complete specimens are

known from the time-equivalent Dinosaur Park Formation in Alberta (Lambe, 1902; Parks, 1933; Langston, 1956). '*Basilemys nobilis*' was originally named for scattered shell fragments from the Ojo Alamo Formation (lower Maastrichtian) of New Mexico (Hay, 1911), but Sullivan et al. (2013) recently determined this material to be undiagnostic. They instead erected a new species, *B. gaffneyi*, and attributed to it several specimens previously assigned to '*B. nobilis*,' including complete shells (e.g., Wiman, 1933; Gilmore, 1935), from the upper Fruitland and lower Kirtland formations (upper Campanian) of New Mexico. *Basilemys gaffneyi* (= '*B. nobilis*') also has been recently reported from the upper Campanian Kaiparowits Formation of Utah (Hutchison et al., 2013). *Basilemys sinuosus* was erected on the basis of material from the Hell Creek Formation (upper Maastrichtian) of Montana (Riggs, 1906). It also occurs in the Hell Creek Formation of North and South Dakota (Pearson et al., 2002), the Ferris Formation of Wyoming (Lillegraven and Eberle, 1999), and possibly the Laramie and Denver formations of Colorado (Hutchison and Holroyd, 2003). A second upper Maastrichtian form, *B. praeclara*, is originally known from the Hell Creek (= Lance) Formation of South Dakota (Hay, 1911), but more complete material has been described from the Frenchman Formation of Saskatchewan (Brinkman and Nicholls, 1993). These four currently recognized species are traditionally distinguished by features of the shell, including the development of the epiplastral beak, the arrangement of scales about the shell, and the sinuosity of the midline plastral sulcus.

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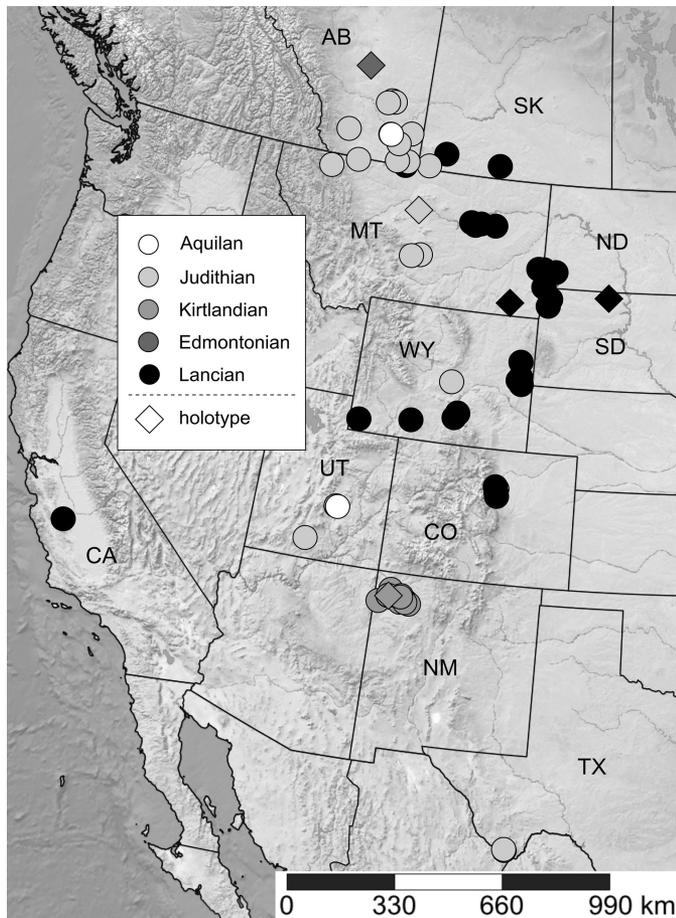


FIGURE 1. Map of western Canada and U.S.A. showing reported occurrences of *Basilemys*. Occurrence data derived from Paleobiology Database (<http://fossilworks.org/>). Map plotted using SimpleMappr (<http://www.simplemappr.net>). **Abbreviations:** AB, Alberta; CA, California; CO, Colorado; MT, Montana; ND, North Dakota; NM, New Mexico; SD, South Dakota; SK, Saskatchewan; TX, Texas; UT, Utah; WY, Wyoming.

The currently recognized *Basilemys* species are temporally restricted to middle/upper Campanian and uppermost Maastrichtian strata (Fig. 2). The genus is also known, mostly on the basis of fragmentary remains that cannot be identified to species (Brinkman, 2003), from intermediate uppermost Campanian/lower Maastrichtian strata of the Horseshoe Canyon Formation of Alberta. Brinkman (1998) also described a skull (CMN 8890) attributable to *Basilemys* sp. from the Horseshoe Canyon Formation, but the partial shell is taxonomically uninformative at the species level and was unavailable for study. The discovery of this specimen was mistakenly thought by Brinkman (1998) to have been made by Elmer Hiller near Morrin, Alberta, in 1924. However, CMN 8890 was instead found by T. P. Chamney in the Horseshoe Canyon Formation near Rumsey, Alberta, in 1947 and collected that year by Charles H. Sternberg. The specimen found by Hiller in 1924 (CMN 57059), also collected by Sternberg, was only recently prepared at the Canadian Museum of Nature. It is the first nearly complete shell of *Basilemys* from the Horseshoe Canyon Formation and is the holotype of a new species described here.

Institutional Abbreviations—CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.; PMU, Paleontological Collections, Museum of Evolution, Uppsala University, Uppsala,

Sweden; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

SYSTEMATIC PALEONTOLOGY

Order CRYPTODIRA Cope, 1868 (emended Gaffney, 1972)

Suborder EUCRYPTODIRA Gaffney, 1975

Family NANHSIUNGCHELYIDAE Yeh, 1966

Genus *BASILEMYS* Hay, 1902

BASILEMYS MORRINENSIS, sp. nov.

(Figs. 4–6)

Holotype—CMN 57059, a mostly complete shell.

Locality, Horizon, and Age—The original quarry coordinates of CMN 57059 provided by C. M. Sternberg (1924 field notes, CMN) are Sec. 4, Twp. 32, R. 21, W. of 4, 50' [15.2 m] above river. A labeled map at the CMN further locates the site in the lower southwest quadrant of Sec. 4. One of us (D.B.B.) was able to relocate the site with E. Hiller in 1992 and can confirm that it is located within the lower Maastrichtian Horseshoe Member of the Horseshoe Canyon Formation. This member is characterized by organic-rich shales and coals, lenticular paleochannel sandstones, and a limited variety of interfluvial mudstones. The presence of abundant coals in the unit suggests saturated landscapes and relatively high water tables. These and other fossil indicators suggest that relatively warm, wet conditions were prevalent ~71 Ma (Eberth and Braman, 2012).

Diagnosis—Turtle of the genus *Basilemys* having a single autapomorphy: cervical scale rectangular. Differs from *B. variolosa* and *B. gaffneyi* as follows: pygal wider than long, epiplastral beak elongate and square. Differs from *B. sinuosa* as follows: only two suprapygal present, vertebral scutes narrow. Differs from *B. sinuosa* and *B. praeclara* in that the extragulars are divided by the gulars. Further differs from *B. praeclara* as follows: midline epiplastral notch present, entoplastron large and hexagonal.

Etymology—Species epithet after the village of Morrin, Alberta, near where the shell was found by Elmer Hiller as a boy in 1924.

Comments on Preservation of CMN 57059

The specimen was found in a sandy clay and clay ironstone (C. M. Sternberg, 1924 field notes, CMN archives). It is associated with abundant comminuted plant debris, some of which can be identified as the segmented stalks of *Equisetum* cf. *E. perlaevigatum* (Bell, 1949), approximately 20 mm in diameter (Fig. 3A). These few details are consistent with an overbank depositional setting (Dodson, 1971).

A field photo of the specimen in situ (Fig. 3B) shows that it was found dorsal side up. The carapace is mostly complete, save for a central portion of the left side and various portions about the margin. Modest compression of the shell has caused some flattening of the left posterolateral margin of the carapace, exaggerating the lateral flare of the shell margin in this area. The plastron is mostly complete except for small portions of the hyoplastra, bridge, and xiphoplastra. The surface of the shell is poorly preserved in many places, riddled by many fine cracks (possibly the result of predepositional surface weathering), infilled by calcite.

DESCRIPTION

The following description adheres to the terminology of Zangerl (1969) with plastral scale terminology after Hutchison and Bramble (1981). A three-dimensional surface model of the shell (.stl format; doi: 10.17602/M2/M31637) is available at MorphoSource (https://www.morphosource.org/index.php/Detail/MediaDetail/Show/media_file_id/31637).

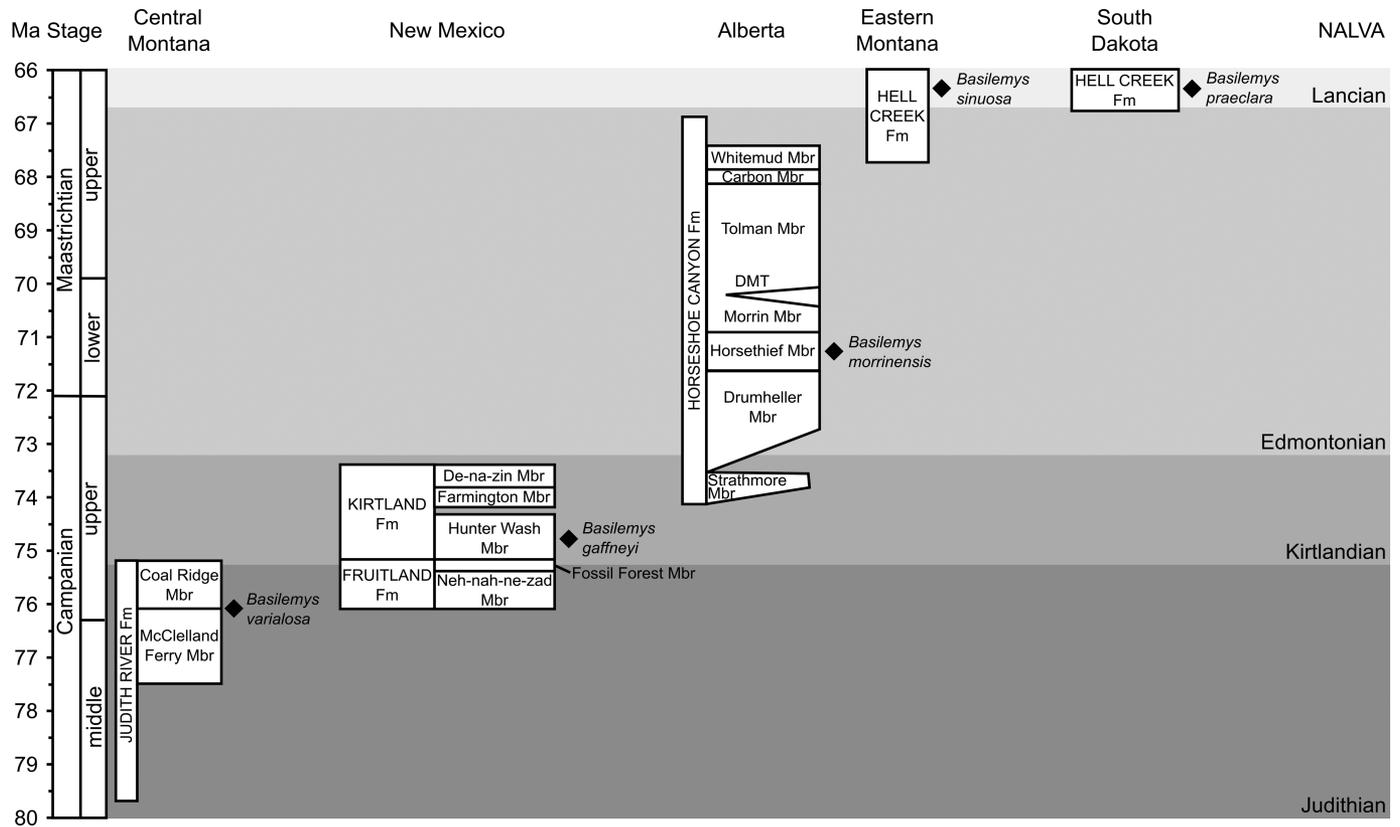


FIGURE 2. Stratigraphic distribution of currently recognized *Basilemys* holotypes. *Basilemys morrinensis* fills the temporal gap between the middle/upper Campanian forms and the uppermost Maastrichtian forms. Stratigraphic framework after Fowler (2017). **Abbreviations:** DMT, Drumheller Marine Tongue; **Fm**, Formation; **Ma**, mega-annum; **Mbr**, Member; **NALVA**, North American Land Vertebrate Age.

The carapace (Figs. 4, 5) is slightly longer than wide, with the maximum preserved width occurring at the level of costal 3 (Table 1). However, plastic deformation has pushed the right posterior peripherals ventromedially, reducing the outward flare that they would have exhibited in life. Therefore, it seems likely that the shell would have been widest near the level of costal 5, as shown in our reconstruction (Fig. 6). In *Basilemys variolosa*, the carapace is purportedly widest at the level of costal 8 (Langston, 1956), but the specimen on which this judgment was based (CMN 8516) is heavily reconstructed with plaster in this region, so it is unclear whether the reconstructed morphology is accurate. Other complete specimens (e.g., ROM 853; Parks, 1933) suggest that the shell of *B. variolosa* is widest at the level of costal 3 or 4. The carapace of CMN 57059 forms a low dome in profile, in agreement with other *Basilemys* (e.g., Langston, 1956:pl. II), and contrasting with the more domed carapace seen in many of the Asian nanhsiungchelyids (e.g., Sukhanov et al., 2008:fig. 4; Tong and Mo, 2010:fig. 2; Danilov et al., 2013:figs. 22.2, 22.5; Brinkman et al., 2015:figs. 1, 2). The quotient of mid-length shell depth to midline carapace length is 0.315 (Table 1). Although postmortem compaction may have slightly exaggerated the flattened appearance of the shell, the similar low profile of relatively uncrushed *Basilemys* shells (e.g., CMN 8516, ROM 853) suggests that the above value approximates the uncrushed condition. The nuchal emargination, spanning the nuchal and first peripherals, is only weakly developed as in other *Basilemys* (Langston, 1956), and again in contrast to the condition seen in many of the Asian nanhsiungchelyids where the emargination is strongly developed and the free edge of the first peripherals is angular (see Sukhanov, 2000). The postneural part of the carapace is shallowly deflected (16°), and the posterior peripherals

flare externally, creating a broad, low shelf (lip) on the posterior part of the carapace.

Where preservation permits, the surface texture of the carapace appears characteristic of *Basilemys*, consisting of many small, shallow pits, arranged in a chain-link pattern, bordered by low, tetrahedral prominences. The pits tend to be lenticular and shallowest near the center of the carapace, becoming deeper and more circular in outline towards the margins, particularly along the posterior shelf. In *Nanhsiungchelys*, the pits are arranged in tightly spaced, transverse rows over the costals (Yeh, 1966), but this is not the case in *Basilemys* where the pattern is nearly isotropic.

The lateral margins of the large, hexagonal nuchal are convex, as in *B. sinuosa* and *B. gaffneyi* (Riggs, 1906; Sullivan et al., 2013); in *B. variolosa*, the lateral margins are concave (Langston, 1956). The nuchal is 7–12 mm thick along the free margin. Further posteriorly, the neural series cannot be distinguished, owing to a combination of sutural fusion and poor surface preservation. There is no reason to suppose that CMN 57059 did not have eight neurals, as in other *Basilemys*. Suprapygals 1, assuming it is present, is similarly indistinguishable from the neural series, but the partially preserved suprapygals 2 appears large and octagonal, spanning the junction of the last vertebral and marginal scales, as in *B. variolosa* and *B. gaffneyi* (Langston, 1956). There is no indication of a third suprapygals, which otherwise has only been reported in *B. sinuosa* (Riggs, 1906), although it should be noted that supernumerary neurals and suprapygals are common among turtles (Webb, 1962; McEwan, 1982; Gardner and Russell, 1994; Cherepanov, 2016). The large, rectangular pygal is wider than long, a condition shared with *B. praeclara* and *B. sinuosa* (Riggs, 1906; Brinkman and Nicholls, 1993).

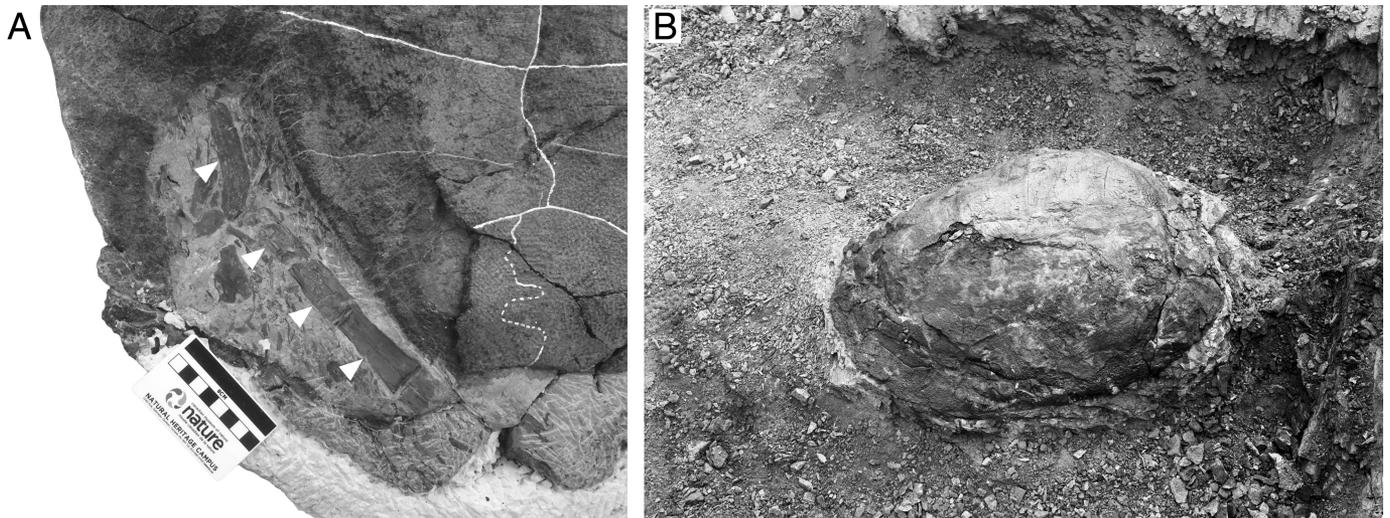


FIGURE 3. Depositional context of CMN 57059. **A**, segmented stalks of *Equisetum* cf. *E. perlaevigatum* (marked by arrowheads) found associated with shell. **B**, CMN 57059 as it was originally uncovered in the field (CMN negative #61554). Scale bar equals 8 cm (**A**).

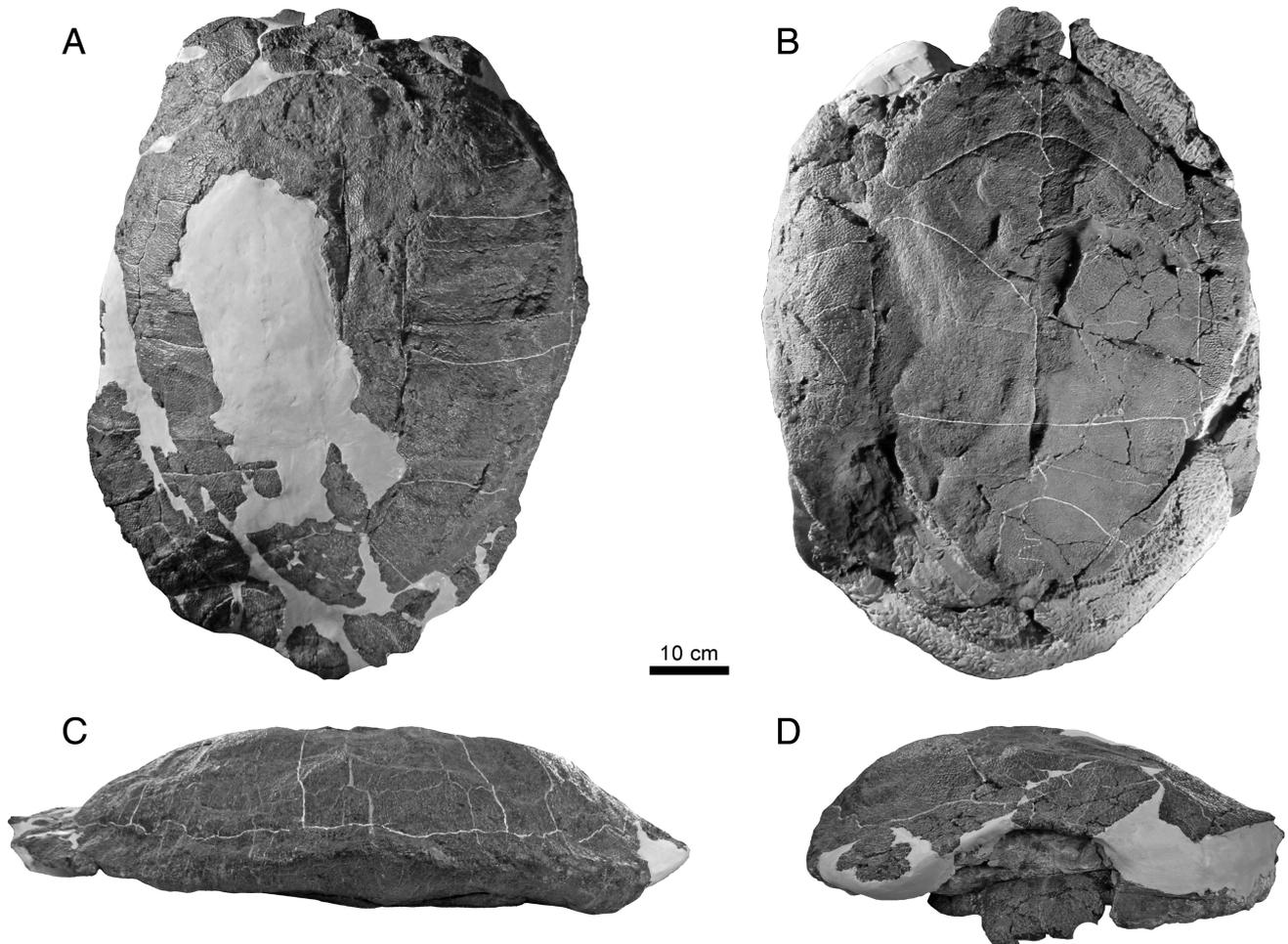


FIGURE 4. *Basilemys morrinensis*, CMN 57059, shell, in **A**, dorsal, **B**, ventral, **C**, right lateral, and **D**, anterior views.

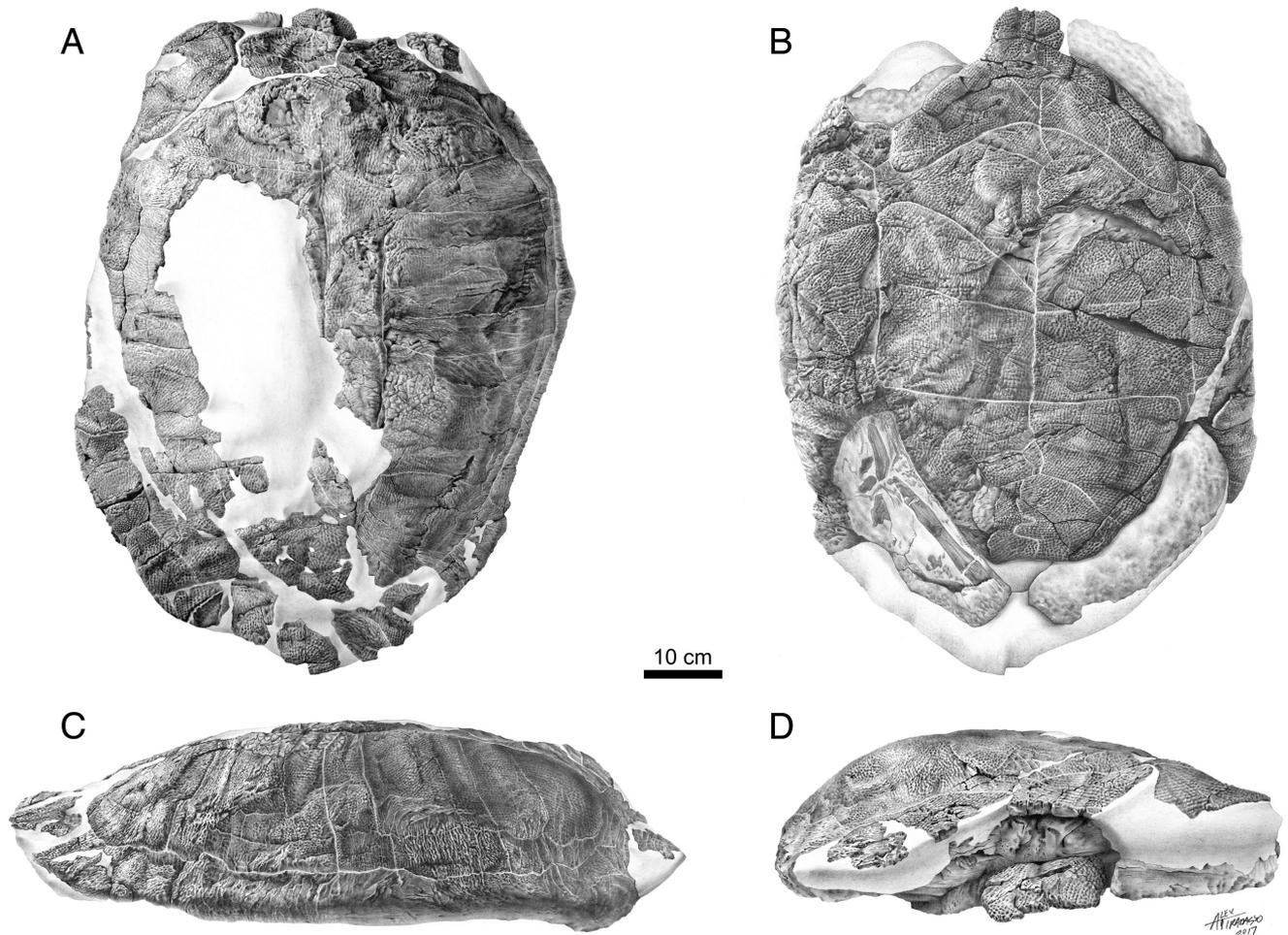


FIGURE 5. *Basilemys morrinensis*, CMN 57059, interpretive drawing of shell, in **A**, dorsal, **B**, ventral, **C**, right lateral, and **D**, anterior views.

The costals total eight in number, and the sutures between them are well delineated although they cannot be traced medially beyond the vertebral scute margins. They are broadly arched to form the low dome of the carapace. Costal 1, shaped like a quadrant, is anteroposteriorly the longest in the series. The remaining costals are subrectangular and generally expand slightly towards their peripheral margins (Table 1). The transversely widest costals occur near the middle of the carapace, decreasing in width towards each end. The two posterior-most costals arch posterolaterally along their lengths, away from the sagittal plane. There is no evidence that they met along the midline as they do in *B. gaffneyi* (Langston, 1956), but sutures in this region are indistinguishable in any case.

The peripherals are easily distinguished about the shell margins, particularly on the dorsal side. There are 11 peripherals in total. Peripheral 1 is approximately wedge-shaped in dorsal outline, but the remainder are subrectangular. Peripherals 4–7 are broadly arched laterally to anchor the extensive bridge, although it is difficult to trace their sutures onto the ventral surface of the shell. The posterior peripherals that form the low, broad shelf vary between 10 and 15 mm thick.

The cervical scale is contained completely within the margins of the underlying nuchal and is square in outline, with parallel contacts for the marginals. By comparison, the scale is narrower and centrally waisted in cf. *B. variolosa* (maximal transverse width is 35% sagittal length in TMP 1994.666.0028), and the

marginal contacts converge anteriorly. Langston (1956:fig. 2) reconstructed the cervical scale of *B. variolosa* as more nearly square, but the specimen on which his restoration was based (CMN 8516) is heavily reconstructed with plaster in this area so that its original morphology cannot be discerned. The scale is narrow and anteriorly constricted in other *Basilemys* as well (e.g., PMU.R29 and USNM 11084, *B. gaffneyi*; FMNH P12008, *B. sinuosa*). The lateral margins of the vertebral scale series of CMN 57059 are deeply engraved into the underlying nuchal and costals, more so than sulci elsewhere on the carapace, but the sulci dividing these scales are much less distinct, visible only anteriorly. Pinching of the lateral margins of these scales between the alternately arrayed pleurals is absent. Vertebral scale 1 is strongly cinched in its anterior third, giving it a keyhole shape. This condition is not typically seen in other nanhsiungchelyids although a similar degree of cinching is seen in *B. variolosa* (Langston, 1956:fig. 2; ROM 853; TMP 1996.145.0001), *Zangerlia neimongoliensis* (Brinkman et al., 2015:fig. 1), and *Jiangxichelys ganzhouensis* (Tong and Mo, 2010:figs. 2, 3). Vertebral 2 is 1.57 times longer than vertebral 1. Vertebrales 2–4 are mediolaterally narrow (~65 mm wide) compared with their lengths (ratio ≈ 0.39), which contrasts with the condition seen in *B. sinuosa*, where the scales are relatively wide (Riggs, 1906). Vertebral 5 is wide and resembles an isosceles trapezoid with a wavy posterior margin. The anterolateral margins of vertebral 5 are straight compared with the slightly convex condition seen in

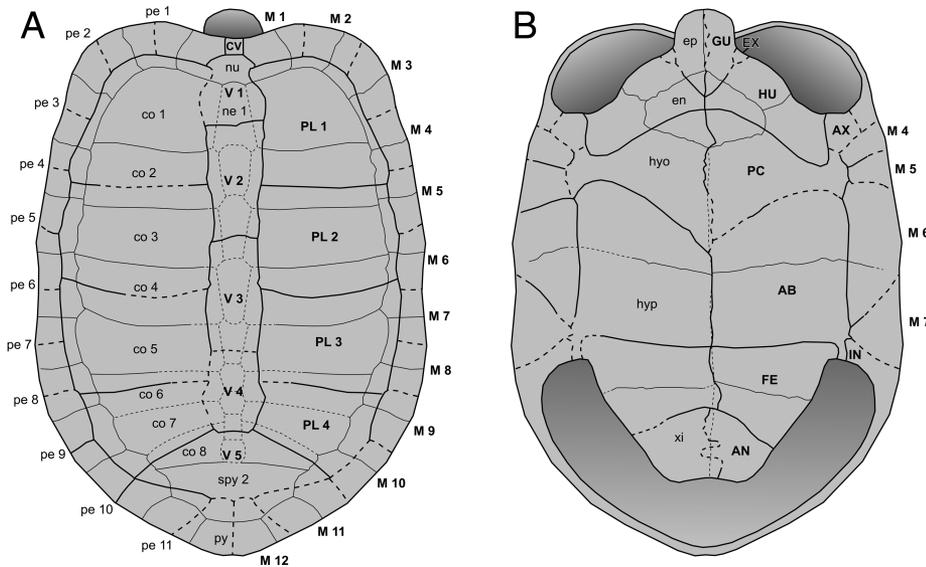


FIGURE 6. *Basilemys morrinensis*, CMN 57059, reconstructed shell. **A**, carapace in dorsal view; **B**, plastron in ventral view. Thin and thick lines delineate bone margins and scale margins, respectively. Dashed lines indicate reconstructed suture or sulcus margins. **Abbreviations:** **AB**, abdominal scale; **AN**, anal scale; **AX**, axillary scale; **co 1–8**, costals 1–8; **CV**, cervical scale; **en**, entoplastron; **ep**, epiplastron; **EX**, extragular scale; **FE**, femoral scale; **GU**, gular scale; **HU**, humeral scale; **hyo**, hyoplastron; **hyp**, hypoplastron; **IN**, inguinal scale; **M 1–12**, marginal scales 1–12; **ne 1**, neural 1; **nu**, nuchal; **PC**, pectoral scale; **PL 1–4**, pleural scales 1–4; **pe 1–11**, peripherals 1–11; **py**, pygal; **spy 2**, suprapygals 2; **V 1–5**, vertebral scales 1–5; **xi**, xiphial scale.

B. variolosa (Langston, 1956). The scale margins presumably envelop suprapygals 1 and overlap costal 8, suprapygals 2, and peripheral 10.

The pleural scale margins are well delineated. Pleural 1 is shaped like a quadrant, much like the underlying costal, only larger. Its margins overlap the nuchal, costals 1 and 2, and peripherals 1–4. The remaining three pleurals are more nearly rectangular in outline. They are variably pinched laterally between the alternating marginal scales. Pleural 2 overlaps costals 2–4 and peripherals 4–6. Pleural 3 overlaps costals 4–6 and peripherals 6–8. Pleural 4 is the smallest in the series and has a high aspect ratio compared with its equivalent in *B. sinuosa* (Riggs, 1906:pl. LXXVI), likely due to the increased width of the vertebral scales in the latter taxon. Pleural 4 overlaps costals 6–8 and peripherals 8–10.

The borders of the marginal scale sulci are ill-defined, visible only sporadically over the shell. Where visible, they overlap two peripherals, which is typically the case among turtles (Zangerl, 1969; Pritchard, 2008). Marginal 1 covers the upper quadrant of the underlying nuchal. There is no medial process on marginal 2, which is otherwise seen in *Zangerlia neimongoliensis* and *Jiangxichelys ganzhouensis*. Marginals 4–7 appear to cover the shell bridge, as in *B. sinuosa* (Riggs, 1906:pl. LXXVII). Marginal 6 is expanded along its contact with the abdominal scales, which is seen in all nanhsiungchelyids except *Zangerlia ukhaachelys* (Joyce and Norrell, 2005). The posterior marginals are larger than those of *B. sinuosa* and do not appear to differ appreciably from those seen in other *Basilemys*. There is no reason to suspect there were not 12 marginals in total, as in other members of the genus.

Typical of other *Basilemys*, the octagonal plastron (Figs. 4, 5) is elongate (89% of the midline length of the carapace) compared with *Jiangxichelys* (Tong and Mo, 2010), *Kharakhutulia* (Sukhanov et al., 2008), or any of the various species assigned to *Zangerlia* (Mlynarski, 1972; Joyce and Norrell, 2005; Danilov et al., 2013; Brinkman et al., 2015). The long epiplastral beak, distinguished by its angular discontinuity with the anterior plastral lobe, projects anteriorly beyond the margin of the carapace by approximately 40 mm. The square shape of the beak is reminiscent of that seen in *B. sinuosa* (Riggs, 1906:pl. LXXVII) and especially *B. praeclara* (Brinkman and Nicholls, 1993:fig. 1). In *B. variolosa* and *B. gaffneyi*, the beak is short, anteriorly rounded, and its lateral margins are directed posterolaterally, more nearly confluent with the remainder of the anterior plastral

lobe (Lambe, 1902:fig. 6; Hay, 1908:fig. 287; Parks, 1933:pl. X; Langston, 1956:fig. 2; Sullivan et al., 2013:fig. 20.12). In several specimens of *B. variolosa* (ROM 853, TMP 1979.008.0230, TMP 2000.052.0001, TMP 2009.082.001), the beak is indistinguishable, indicating some intraspecific variability in the development of this feature (cf. *Terrapene coahuila*; Burroughs et al., 2013). The beak of CMN 57059 is subtly concave ventrally and bears a small medial notch anteriorly, as in other *Basilemys* except *B. praeclara* (Hay, 1911; Brinkman and Nicholls, 1993). The beak is thickest along its lateral margins (24 mm), thinning to 17 mm anteriorly. Sculpturing extends onto the dorsal surface of the beak to cover its entirety. The posterior lobe of the plastron is subequal in size to the anterior lobe. The ventral surface of the lobe is concave near the junction of the abdominal and femoral scales. This concavity is common in the males of living turtles (Pritchard, 2008), but the condition in the fossil might equally be attributed to localized crushing. The squared posterior end of the posterior lobe bears a modest emargination, less developed than in *Kharakhutulia* (Sukhanov et al., 2008).

Sculpturing of the plastron matches that seen on the carapace, with variably lenticular or circular pitting, although it is not as pronounced as on some parts of the carapace. Infilled matrix and plaster prevent observation of how far the sculpturing extends onto the dorsal surface of the plastron; however, the sculpturing does cover the entire dorsal surface of the epiplastral beak.

The epiplastron, which contribute to most of the free margin of the plastral lobe, are obtusely 'L'-shaped, as in trionychids. The lateral ramus of each epiplastron overlies the entoplastron and hyoplastron, and the anterior ramus meets its opposite about an elongate contact along the midline. The hexagonal entoplastron straddles the midline. It is mediolaterally broad, bounded anteriorly by the epiplastron (where the sutures are obscured by coossification) and posteriorly by the hyoplastron. This condition agrees with that seen in other *Basilemys* except *B. praeclara*, where the entoplastron is mediolaterally narrower and possibly pentagonal (Brinkman and Nicholls, 1993:fig. 1). The hyoplastron is large and square, with a short projection at the anterolateral edge that contributes to the margin of the anterior plastral lobe. The posterior edge shallowly slopes posteriorly where it meets its opposite at the midline. Local breakage reveals that the hyoplastron is 6–7 mm thick centrally. The square hypoplastron is subequal in size to the hyoplastron. It contributes to the anterior-most margin of the posterior plastral lobe. The trapezoidal xiphial scales

TABLE 1. Rectilinear measurements (in mm) for CMN 57059, the holotype of *Basilemys morrinensis*.

| Element | Dimension | Value |
|------------------|--|---------------|
| Carapace | Midline length | 798 |
| Nuchal | Free margin | 98 |
| | Contact with peripheral 1 | 83(L)/88(R) |
| | Distance between junction of peripheral 1 and costal 1 | 143 |
| | Contact with neural 1 | 26 |
| Pygal | Contact with suprapygal 2 | 63 |
| | Contact with peripheral 11 | 57(R) |
| Suprapygal 2 | Free margin | 103 |
| Peripheral 1 | Contact with peripheral 11 and pygal | 152 |
| | Free margin | 111(L) |
| Peripheral 2 | Contact with peripheral 2 | 101(L) |
| | Contact with costal 1 | 48(L) |
| | Free margin | 102(L) |
| Peripheral 3 | Contact with peripheral 3 | 106(L) |
| | Contact with costal 1 | 62(L) |
| | Free margin | 109(L)/99(R) |
| Peripheral 4 | Contact with peripheral 4 | 135(L)/62(R) |
| | Contact with costal 1 | 82(L)/64(R) |
| | Free margin | 87(R) |
| Peripheral 5 | Contact with peripheral 5 | 74(R) |
| | Contact with costals 1 and 2 | 73(L)/77(R) |
| | Free margin | 84(R) |
| Peripheral 6 | Contact with peripheral 6 | 68(R) |
| | Contact with costals 2 and 3 | 84(L)/82(R) |
| | Free margin | 104(R) |
| Peripheral 7 | Contact with peripheral 7 | 106(L) |
| | Contact with costals 3, 4, and 5 | 89(L)/109(R) |
| | Free margin | 90(R) |
| Peripheral 8 | Contact with peripheral 8 | 80(R) |
| | Contact with costals | 86(R) |
| | Free margin | 103(L)/105(R) |
| Peripheral 9 | Contact with peripheral 9 | 102(L)/90(R) |
| | Contact with costals | 62(R) |
| | Free margin | 99(L)/116(R) |
| Peripheral 10 | Contact with peripheral 10 | 102(L)/94(R) |
| | Contact with costals | 81(L)/90(R) |
| | Free margin | 97(L)/110(R) |
| Peripheral 11 | Contact with peripheral 11 | 73(L)/73(R) |
| | Contact with costals | 72(L) |
| | Contact with suprapygal 2 | 35(L) |
| Costal 1 | Free margin | 78(L)/96(R) |
| | Contact with pygal | 57(R) |
| | Contact with suprapygal 2 | 56(L)/61(R) |
| Costal 2 | Contact with vertebrals 1 and 2 | 104(L)/107(R) |
| | Contact with costal 2 up to vertebral scale junction | 183(L)/171(R) |
| | Contact with vertebral scale 2 | 87(L)/85(R) |
| Costal 3 | Contact with peripherals 4 and 5 | 78(L)/88(R) |
| | Contact with costal 3 up to vertebral scale junction | 209(L)/200(R) |
| | Contact with vertebral scales 2 and 3 | 81(R) |
| Costal 4 | Contact with peripherals 5 and 6 | 103(L)/81(R) |
| | Contact with costal 4 up to vertebral scale junction | 194(R) |
| | Contact with vertebral scale 3 | 76(R) |
| Costal 5 | Contact with peripheral 6 | 89(L)/83(R) |
| | Contact with costal 5 up to vertebral scale junction | 194(R) |
| | Contact with peripherals 6 and 7 | 90(L)/106(R) |
| Costal 6 | Contact with costal 6 up to vertebral scale junction | 159(R) |
| | Contact with peripherals 7 and 8 | 78(L) |
| | Contact with peripherals 9 and 10 | 71(L) |
| Costal 7 | Contact with peripheral 10 | 50(L) |
| | Free margin | 23 |
| | Contact with marginal scale 1 | 32(L) |
| Costal 8 | Contact with vertebral scale 1 | 24 |
| | Midline length of vertebrals 1 to 4 | 574 |
| | Contact with vertebral scale 1 | 24 |
| Cervical scale | Free margin | 23 |
| | Contact with marginal scale 1 | 32(L) |
| Vertebral series | Contact with vertebral scale 1 | 24 |
| | Midline length of vertebrals 1 to 4 | 574 |
| Vertebral 1 | Contact with pleural 1 | 110(L)/104(R) |

(continued on next column)

TABLE 1. (Continued). Rectilinear measurements (in mm) for CMN 57059, the holotype of *Basilemys morrinensis*.

| Element | Dimension | Value |
|-----------------|--|---------------|
| Vertebral 2 | Contact with vertebral 2 | 83 |
| | Contact with pleurals 1 and 2 | 173(L)/163(R) |
| Vertebral 5 | Contact with vertebral 3 | 65 |
| | Midline length between vertebral 4 and marginal 12 | 142 |
| Pleural 1 | Contact with pleural 4 | 171(L)/127(R) |
| | Contact with marginals 11 and 12 | 254 |
| | Contact with vertebrals 1 and 2 | 189(L)/190(R) |
| Pleural 2 | Contact with pleural 2 | 229(L)/227(R) |
| | Contact with marginals 5–7 | 169(L)/164(R) |
| Pleural 3 | Contact with vertebrals 2 and 3 | 144(R) |
| | Contact with pleural 3 | 232(R) |
| | Contact with marginal 7–9 | 170(L)/194(R) |
| Pleural 4 | Contact with vertebrals 3 and 4 | 145(R) |
| | Contact with pleural 4 | 185(R) |
| | Contact with marginals 9–11 | 139(L) |
| Marginal 1 | Contact with vertebral 4 | 88(L)/79(R) |
| | Contact with vertebral 5 | 171(L)/127(R) |
| Marginal 2 | Contact with vertebral 1 and pleural 1 | 91(L)/93(L) |
| | Contact with pleural 1 | 70(L)/63(R) |
| Marginal 9 | Free margin | 101(L) |
| | Contact with marginal 10 | 64(L) |
| Marginal 10 | Free margin | 101(L) |
| | Contact with marginal 11 | 64(L) |
| Plastron | Midline length | 705 |
| | Axial notch to inguinal notch | 326(L)/362(R) |
| Gulars | Width of epiplastral beak | 92 |
| | Midline contact | 91 |
| | Free margin | 175(L)/181(R) |
| Entoplastron | Contact with entoplastron | 101(L)/101(R) |
| | Midline length | 112 |
| Hyoplastral | Ventral contact with hyoplastron | 170 |
| | Midline contact | 187 |
| Hypoplastron | Contact with hypoplastron | 313(L) |
| | Midline contact | 175 |
| Xiphiplastron | Lateral contact with hyoplastron to lateral contact with xiphiplastron | 266(L) |
| | Midline contact | 139 |
| | Minimum width of posterior plastral lobe | 177 |
| Humeral scale | Midline contact | 24 |
| | Contact with pectoral scale | 192(L)/204(R) |
| Pectoral scale | Midline contact | 207 |
| | Contact with marginals | 76(L)/61(R) |
| | Contact with abdominal scale | 212(L) |
| Abdominal scale | Midline contact | 147 |
| | Contact with marginals | 250(L)/234(R) |
| Femoral scale | Contact with femoral scale | 195(R) |
| | Midline contact | 192 |
| Anal scale | Contact with anal scale | 124(R) |
| | Midline contact | 107 |
| Shell | Depth at midlength | 251 |

Abbreviations: L, left; R, right.

constrict posteriorly and form most of the posterior lobe. They are coossified, so it is not possible to trace their adjoining suture about the midline. The sutures between the plastral bones and bridging peripherals are likewise difficult to distinguish. The minimum length of the bridge between the axillary and inguinal notches is 51% the midline length of the plastron.

Owing to poor surface preservation, it is difficult to discern the scale sulci on the anterior plastral lobe. However, a faint 'V'-shaped sulcus can be seen on the anterior portion of the entoplastron about the midline. Its location likely marks the posterior extent of the gular scales, as in all *Basilemys* species except *B. praeclara*, where the gulars are restricted to the epiplastra alone. If the sulcus marked

the posterior extent of the conjoined extragulars, as in *B. sinuosa* and *B. praeclara*, it would be expected to nearly divide the humeral scales, which is not the case. For this reason, we suspect that the extragular scales were small and triangular, as in *B. variolosa* and *B. gaffneyi*, but more material is necessary to verify this. The midline plastral sulcus visibly extends to the dorsal apex of the entoplastron (beyond this, surface preservation diminishes), suggesting that the gular scales were divided. This is opposite to the condition of *B. gaffneyi* and at least some specimens of *B. variolosa* (e.g., CMN 376, TMP 1997.008.0230), where there is no unambiguous evidence for divided gular scales, despite previous interpretations to the contrary (Lambe, 1902).

The humeral scales are large and rectangular, overlapping the epiplastra anteromedially, the entoplastron posteromedially, and the hyoplastra posterolaterally. The adjacent pectoral scales are pisciform; they are longest medially and constrict laterally before slightly expanding again below the axillary notch. The pectoral scales are relatively much shorter medially in *Nanhsiungchelys*, *Kharakhutulia*, and *Zangerlia* sensu lato (Mlynarski, 1972; Joyce and Norell, 2005; Danilov et al., 2013; Brinkman et al., 2015). The midline sulcus between the pectoral scales of CMN 57059 is slightly sinuous, but nowhere near the same degree seen in *B. sinuosa*, *B. gaffneyi*, or even some specimens of *B. variolosa* (Lambe, 1902). Except for between the anal scales (see below), the midline plastral sulcus is relatively straight where visible. The pectoral scales overlap the entoplastron anteromedially, but otherwise lie entirely within the margins of the hyoplastron. The abdominal scales resemble right trapezoids, increasing in length laterally. They overlap the hyoplastron anteriorly and hypoplastron posteriorly. Each abdominal scale gives rise to a small projection of the posterolateral corner, inserting between the femoral and inguinal scales to reach the inguinal notch. The femoral scales also resemble inverted right trapezoids, although they are smaller than the abdominal scales and bow laterally where they contribute to the margin of the posterior plastral lobe. They evenly overlie the hypoplastron anteriorly and xiphiplastron posteriorly. The quadrilateral anal scales are divided by an apparently sinuous suture, although it is difficult to trace over much of its course (the reconstruction in Fig. 6 is a best approximation). This suture is often interpreted or figured as being highly sinuous in *B. sinuosa* and *B. praeclara* (Riggs, 1906; Wiman, 1933; Gilmore, 1935; Brinkman and Nicholls, 1993), and less so in *B. variolosa* and *B. gaffneyi* (Langston, 1956; Sullivan et al., 2013). However, it is evident from looking at the range of variation seen in *B. variolosa* that the suture between the anal scales may also be highly sinuous (e.g., TMP 2000.052.0001, TMP 2014.028.0004) or absent entirely (TMP 1964.004.082). The anal scales cover only the posterior ends of the xiphiplastra.

Specimen CMN 57059 is like other *Basilemys* in lacking a complete set of inframarginal scales, but axillary and inguinal scales can be discerned. The margins of the axillary scales are not easily distinguished; however, the scale obviously contributes to the axillary notch and otherwise appears to be bordered by the humeral scale medially, the pectoral scale posteriorly, and marginal 4 posterolaterally (it may or may not abut marginal 3 anterolaterally). The medial sulcus for the inguinal scale is barely visible, but the scale evidently inserted between the abdominal scale medially and marginal 7 anterolaterally. There is no infra-marginal intercalated between marginals 6 and 7, otherwise seen in *B. gaffneyi* (Wiman, 1933; Sullivan et al., 2013), although this feature is evidently variable (Gilmore, 1935).

PHYLOGENETIC ANALYSIS

To determine the phylogenetic position of *Basilemys morrinensis* within Nanhsiungchelyidae, we conducted a cladistic analysis assuming parsimony. We added *B. morrinensis* to the character matrix of Brinkman et al. (2015), which we further

modified as follows (see Description, above, for reasoning): (1) character 36 (fusion of gulars) was coded as polymorphic for *B. variolosa*; (2) character 41 (number of inframarginals) was coded as polymorphic for *B. gaffneyi*; and (3) character 42 (expansion of the ventromedial edge of marginal 6) was likewise coded as polymorphic for *B. gaffneyi*. Two new characters were also added to better describe the morphology of the anterior plastral lobe and epiplastral beak: (4) ratio of midline epiplastral suture length to total midline plastral length (0 = 0.10 or less; 1 = greater than 0.10); and (5) epiplastral beak distinct from anterior plastral lobe (0 = absent; 1 = present). *Basilemys variolosa* was coded as polymorphic for the last character because some specimens have it and others do not (see above). This may represent a sexually dimorphic character, as in some Testudinidae (Pritchard, 2008), but in the absence of convincing support for such an interpretation, and to facilitate comparison with previous analyses that used this character, we retain it here. The matrix (Supplemental Data 1) included 47 characters (21 of which were parsimony-uninformative) and 15 taxa, and was 62% complete. *Adocus* sp. was designated as the outgroup. All characters were unordered and equally weighted. We used TNT 1.1 (Goloboff et al., 2003) to conduct an implicit enumeration search. The analysis recovered eight most parsimonious trees, each with a length of 70 steps, a consistency index (CI) of 0.729, and a retention index (RI) of 0.694. Using the iterative restricted positional congruence (PCR) method of Pol and Escapa (2009), we determined that the position of '*Zangerlia*' *ukhaachelys* was unstable, so it was excluded from reconstruction of the reduced strict consensus tree, which is given in Figure 7. Standard bootstrapping, using implicit enumeration search and 1000 replicates, and Bremer support values were likewise calculated in TNT.

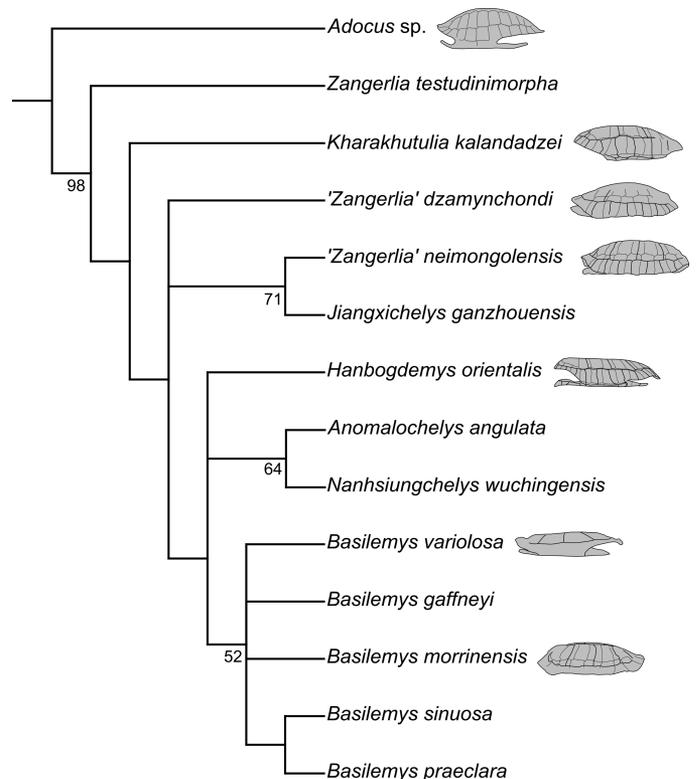


FIGURE 7. Reduced strict consensus tree derived from initial cladistic analysis showing interrelationships within Nanhsiungchelyidae. Shell outlines illustrate that the low profile shell of *Basilemys* is a derived condition, not a primitive one (see Discussion). Bootstrap values >50% are depicted below the nodes; Bremer support values were universally low (= 1) and are not shown here.

The reduced strict consensus tree (tree length = 73 steps, CI = 0.699, RI = 0.645; Fig. 7) is more poorly resolved than that of Brinkman et al. (2015), on which the analysis is based, likely due largely to the numerous polymorphisms included here. Nanhsiungchelyidae garners strong bootstrap support (98%) and is diagnosed by a medioventrally expanded marginal 6. In agreement with Brinkman et al. (2015), *Zangerlia testudinimorpha* is recovered as the basal-most nanhsiungchelyid, even more basal than *Kharahhutulia*, which is often not the case (e.g., Sukhanov et al., 2008; Danilov et al., 2013; Sullivan et al., 2013). The informal ‘*Zangerlia*’ clade (sensu lato), including *Jiangxichelys*, collapses partly to a polytomy, although the relationship between ‘*Z.*’ *neimongoliensis* and *Jiangxichelys* is retained and garners modest (71%) bootstrap support. The last two taxa are united by the presence of a steep deflection of the postneural part of the carapace, and by the presence of a medial process of marginal 2. *Nanhsiungchelys* and *Anomalochelys* are closely related (bootstrap support = 64%), united by an anteriorly constricted vertebral 1, which is in contact with the cervical scale only, by the presence of a first vertebral scale with lateral margins converging anteriorly, and by vertebral scales 2–4 having widths greater than half their lengths. The relationships of these two taxa with *Hanbogdemys* and *Basilemys* are unresolved, as is often the case (e.g., Sukhanov et al., 2008; Danilov et al., 2013; Sullivan et al., 2013). *Basilemys* is recovered as monophyletic (52% bootstrap support), diagnosed by a shallow nuchal notch, vertebral scale 5 that contacts marginals 10 and 11, vertebral scale 5 that covers part of peripheral 10, two pairs of inframarginals, and a well-developed epiplastral beak. Species belonging to the genus are poorly resolved, with the exception of the Lancian forms *B. sinuosa* and *B. praeclara*, which form a sister pair, in agreement with most recent studies (e.g., Sukhanov et al., 2008; Danilov et al., 2013; Sullivan et al., 2013; Brinkman et al., 2015).

In addition to the above, we also ran a second analysis in much the same way, coding gular and extragular scale characters 36, 37, and 39 as ‘?’ in *B. morrinensis*, reflecting the uncertainty associated with our interpretation of these characters in the holotype. This resulted in 24 most parsimonious trees (MPTs; CI = 0.729, RI = 0.698) of 70 steps each. Post hoc removal of ‘*Zangerlia ukhaachelys*’ resulted in a reduced strict consensus tree (tree length = 74 steps, CI = 0.689, RI = 0.629) mirroring the first, but species composing *Basilemys* collapsed to a polytomy.

DISCUSSION

One might predict, based on the stratigraphically intermediate position of CMN 57059 between the middle/upper Campanian *Basilemys* and the uppermost Maastrichtian forms (Fig. 2), that it also should be morphologically intermediate. In many respects, this is the case. The specimen shares with the earlier Campanian forms, *B. variolosa* and *B. gaffneyi*, divided extragular scales; it shares with the later Maastrichtian forms, *B. sinuosa* and *B. praeclara*, a squared epiplastral beak and a pygal that is wider than long. It is partly this transitional morphology that influences the phylogenetic ambiguity concerning CMN 57059. However, this specimen is not intermediate in every respect: the square cervical scale is unique to the specimen. This autapomorphy, and the unique suite of shared character states, supports the recognition of the new species, *B. morrinensis*.

It became apparent over the course of this study that not all characters traditionally used to diagnose the different species of *Basilemys* are taxonomically informative. For example, *B. gaffneyi* is said to be diagnosed by an undivided gular scale (Langston, 1956; Sullivan et al., 2013); however, at least two specimens of *B. variolosa* (CMN 376, TMP 1979.008.0230) also have an undivided gular. Langston (1956) included the presence of an intermarginal scale between marginals 6 and 7 as a diagnostic feature of *B. gaffneyi* (= ‘*B. nobilis*’), but this, too, may be

absent in other specimens attributed to the species (Gilmore, 1935; Sullivan et al., 2013). Hay (1911) diagnosed *B. gaffneyi* (= ‘*B. nobilis*’) by the distinctive cross-sectional shape of the free xiphialastral margin. Sullivan et al. (2013) saw this as taxonomically insignificant and attributed the variation instead to individual differences, albeit without evidence. This character warrants further consideration, but this lies beyond the scope of the present paper. Presently, we note that there appear to be no unambiguous synapomorphies or suite of characters that can be used to uniquely diagnose *B. gaffneyi*. The variable development of the epiplastral beak is sexually dimorphic in modern Testudinidae (Pritchard, 2008) and therefore may not reliably differentiate species of *Basilemys*.

Similarly, *B. sinuosa* is diagnosed, in part, by a highly sinuous midline plastral sulcus, but the same state is seen in *B. praeclara*, where visible on the xiphialastral (Brinkman and Nicholls, 1993: fig. 1), and, variably, in *B. variolosa* (CMN 1145 [Lambe, 1902: fig. 6], TMP 2000.052.0001, TMP 2014.028.0004) and *B. gaffneyi* (Sullivan et al., 2013: fig. 20.12 d). The widespread polymorphic condition of this character renders its taxonomic utility questionable.

Basilemys morrinensis is from the uppermost Campanian/Maastrichtian Horseshoe Canyon Formation (HCF), which is characterized by low turtle diversity (~5 reported species) relative to both underlying Judithian and overlying Lancian strata (~10 reported species each). Brinkman (2003) and Brinkman and Eberth (2006) argued that this low turtle diversity reflects relatively low mean annual temperatures during this time interval and is not simply an reflection of taphonomic or collecting biases. The occurrence of *B. morrinensis* in the Horsethief Member is thus important from both a biostratigraphic and a paleobiological perspective. Brinkman (2003) wrote that all *Basilemys* specimens from the HCF are from individuals about half the size of typical specimens of *B. variolosa* from Campanian strata; however, the holotype of *B. morrinensis* is subequal in size to those reported elsewhere, nearing 1 m in total length (Langston, 1956). It is possible that the *Basilemys* sp. skull described by Brinkman (1998), also from the HCF, is attributable to *B. morrinensis*, but without more diagnostic shell material, it is impossible to be certain.

The paleoecology of *Basilemys*, and indeed that of Nanhsiungchelyidae as a whole, has been a matter of contention, with authors disagreeing over whether these were aquatic or terrestrial forms. Sukhanov and Narmandakh (1977) argued that the presence of powerful forelimbs, the construction of the humerus and its range of possible movements, and the construction of the pelvis and its position in relation to the carapace in *Hanbogdemys* were inconsistent with terrestrial habits. Nessov (1981) regarded these animals as specialized swimmers, using their powerful forelimbs to move along the riverbed against powerful currents. Sukhanov (2000) later pointed out that the considerably flattened shell of *Basilemys* is also consistent with an aqueous mode of life.

The majority of researchers, however, consider nanhsiungchelyids as terrestrial in habit, based on numerous lines of evidence. Yeh (1966) originally considered *Nanhsiungchelys* a terrestrial form, based on its short, stout limbs and broad, short phalanges. Mlynarski (1972) proposed a similar argument in favor of terrestriality in *Zangerlia testudinimorpha*. Hutchison and Archibald (1986) considered *Basilemys* a terrestrial form on account of its well-developed plastron and accordingly limited limb mobility, complex triturating surface of the jaws, robust limbs and elephantine feet, well-developed limb armor, and strong epiplastral projections. Danilov (1999) used depositional data to argue that *Zangerlia* lived in arid paleoenvironments. Based on the relationship between the length of the manus and the length of the forelimb in

aquatic versus terrestrial turtles documented by Joyce and Gauthier (2004), the presence of short digits provides strong evidence for a terrestrial mode of life, and currently the interpretation that nanhsiungchelyids were habitually terrestrial appears to be the consensus among researchers (Brinkman, 2005; Brinkman et al., 2015).

Hutchison (2000) thought that the features used to advocate for an aquatic mode of life in nanhsiungchelyids represent a retention of primitive aquatic ancestral features rather than specializations. However, this interpretation appears overly simplistic. For example, the low shell of *Basilemys*, otherwise characteristic of most aquatic forms (Claude et al., 2003; Benson et al., 2011; Stayton, 2011), is a derived feature. Progressive outgroups to *Basilemys*, including Asian nanhsiungchelyids and *Adocus* sp., have taller carapaces (Fig. 7). Some terrestrial turtles, including *Geoemyda* and *Malacochersus*, have unusually flattened shells that facilitate living under dead leaves or within rocky crevasses (Ernst and Barbour, 1989). However, the ability of the 1 m long *Basilemys* to practice this sort of crypsis is questionable. Lichtig and Lucas (2017) recovered *Basilemys* as terrestrial, not on account of its low shell, but because of its extensive plastron. Fossoriality, as practiced by *Gopherus*, may help to explain the low profile of the shell. Description of the (non-shell) postcranium would help provide a valuable test of this hypothesis (Bramble, 1982), but no such work has emerged. Therefore, if *Basilemys* was a terrestrial form, the adaptive significance of the flattened carapace remains elusive. Data pertaining to the usual depositional environment of the genus are ambiguous (Knell, 2012) and therefore do little to clarify the habits of *Basilemys*. These outstanding questions invite further inquiry into the life habits of this interesting turtle lineage.

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