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Variation in the shell elements of *Chrysemys picta bellii* (Gray, 1831)

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Abstract: Assignment of fossil turtle shell elements to a specific taxon is often difficult because the range of variation within the population is usually not well characterized. In addition, it is sometimes not clear whether the fossil forms actually differ from their extant counterparts because often the range of shell element variation in modern species has not been determined. The emydid turtles are no exception, with confusion often arising in the identification of isolated fossil elements and sometimes intact shells representing *Emys, Pseudemys, Malaclemys,* and *Graptemys*, as well as the deirochelyids *Chrysemys, Clemmys, Deirochelys*, and *Trachemys*. In order to begin providing a database with modern counterparts of the deirochelyid turtles, I have photographed and illustrated seven extant *Chrysemys picta bellii* shells, six of which were collected at a single pond in Nebraska and one from Ladd Marsh in Union County, Oregon. Photographs and detailed illustrations indicate a broad range in the shapes of many characters. Side by side comparisons of some key elements show that there is significant variation in several important characters (nuchal shape/sulci, entoplastron shape/sulci, and pygal shape/sulci). I also conducted a limited morphometric analysis of several sulcus/suture distance ratios, showing substantial variation between individuals in some cases. Covariance and correlation analysis of this variation suggests that allometry is not involved in most cases. In summary, this work provides a visual and morphometric dataset for aid in identifying and assigning shell elements of fossil emydid turtles.

INTRODUCTION

Because turtle shell bones are very stable, they survive well in disarticulated state as isolated elements, and fossil remains of chelonians are frequently reported as part of larger assemblages. The within-species character variations in isolated elements from disarticulated specimens are usually uncharacterized, and it is often difficult to determine whether shell characters of fossil specimens actually fall within the range of variation observed in extant relatives. The fossil remains of emydid turtles have been discovered in many locales and species-level diagnoses based upon subtle differences have created taxonomic confusion, with, at times, multiple generic and specific names assigned to specimens that are either identical or morphologically very similar (McDowel 1964: Jackson 1976; Preston 1979; Holman 1984; Seidel and Smith 1986; Jackso, 1988; Seidel and Ernst 1996; Parmley et al. 2006; Jasinski, 2018; Parmley et al. 2019). The taxonomic confusion, perhaps better referred to as uncertainty, is typified by the in-depth studies of McDowel (1964), who concluded, based upon skull morphology, that *Trachemys*, *Pseudemys*, and *Chrysemys* were all one genus, and so assigned subgenus status to the three groups. This uncertainty was also exhibited by Preston (1979), who considered *Chrysemys* (*?Pseudemys*) *hibbardi* sp.nov, *Chrysemys* (*Pseudemys*) *concinna*, *Chrysemys* (*Trachemys*) *scripta*, and *Chrysemys* (*Chrysemys*) *picta* all to be sub-genera of *Chrysemys* (senso lato) rather than as individual species within the genus. In this work he also discussed and generally agreed with the sub-species designations of *Chrysemys* (*Trachemys*) *scripta*. Seidel and Smith (1986) then attempted to mitigate the confusion by re-elevating the three groups to generic status. Soon after, Jackson (1988) pointed out the difficulties of assigning fossil *Trachemys* material to even the species level and cautioned against assignments to the sub-species level. He also noted that there is significant intraspecific variation and character (both skull and shell) overlap in extant and fossil *Trachemys*. He also discussed what he considered to be an incorrect reassignment of fossil *Trachemys* to

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Chrysemys Gray 1831 and *Pseudemys*. In another study, Parmley et al. (2006) collected fragmentary material from Eocene deposits in Georgia, and discussed the difficulty in assigning those isolated shell elements to the even the broad emydid or batagurid lineages. These ambiguities and difficulties noted in those reports highlight the morphological similarities in the shells of the deirocheylid turtles.

Rigorous characterization of morphological variation in the shell elements of extant chelonians is not common, but has in some cases been reported. For example, in order to test hypotheses about the relationship between morphology and phylogeny, Germano (1993) conducted an extensive morphometric study of the *Gopherus* tortoises. In that work, a number of characters were measured in one dimension and grouped with principal components approaches; however, visual information about variation of individual elements was not presented. In another study, Delfino et al. (2009) analyzed variability in morphological characteristics of shell elements in a collection of the diminutive Egyptian tortoise, *Testudo kleinmanni*. Carapacial variation amongst extant soft-shelled turtles (Trionychidae) was characterized and related to fossil trionychid taxa by Gardener and Russell (1994), and morphological variation in the shell of Pancake tortoise, *Malachochersus tornieri*, has also been well characterized (Mautner et al. 2017). Vitek (2018) has conducted a thorough morphometric analysis of shell variation in 200 modern *Terrapene carolina* individuals, and concluded that a significant amount, but not all, of the variation in over 50 fossil *Terrapene carolina* falls within the modern range of variation. For many turtle genera, however, the lack of published shell osteological studies that include multiple individuals has made it difficult to assess whether or not fossil remains fall within the normal range of variation seen in extant populations of a given species.

In order to better characterize the variation in shell characters amongst extant emydids, I have collected, photographed, and illustrated seven western painted turtle shells (*Chrysemys picta bellii* Gray 1831). Six of these were collected from a single pond in northwestern Nebraska and one from Ladd Marsh in northeastern Oregon. *Chrysemys picta* is an extant emydid turtle with widespread distribution in the United States, southern Canada, and northern Mexico. The species contains four subspecies (Gray 1856; Bishop and Schmidt 1931; Ernst 1971; Starkey et al. 2003) and the fossil record of *Chrysemys* extends back to the late Eocene (Hutchison 1996). Hay (1908) described and illustrated one of the first fossil *Chrysemys* (which he named *Chrysemys timida*) that was collected from the Pleistocene *Equus* beds in Sheridan County, NE. Hutchison (1996) describes a number of Eocene and Oligocene emydid turtles that he assigned to *Chrysemys antiqua*, the oldest known *Chrysemys* (Clark 1937).

MATERIALS AND METHODS

In previous work, six of the specimens were collected from a pond in Nebraska (Corsini and Chamberlain 2009). One additional specimen (EOUVM R-unk-1 ODFW 1) was collected from Ladd Marsh in Eastern Oregon. All of these specimens ((EOUVM R-2004-1 Neb 3, EOUVM R-2004-2 Neb 4, EOUVM R-2004-3 Neb 5, EOUVM R-2004-4 Neb 12, EOUVM R-2004-5 Neb 13, EOUVM R-2004-6 Neb 14, EOUVM R-unk-1 ODFW 1) are accessioned in the Eastern Oregon University Vertebrate Museum (EOUVM). Scutes were detached from the bone by soaking the entire shell in water for two weeks followed by removal with forceps. Scute and shell element nomenclature follows Zangerl (1969). All specimens, including the Oregon specimen, displayed the elaborate plastral pattern covering more than half of the carapace that is characteristic of *C. picta. bellii* (Weller et al. 2010); this pattern is reduced to a small central pattern (*C. picta marginata*) or absent (*C. picta dorsalis*, *C. picta picta*) in the other subspecies.

Plastron width was measured along the midline between the three-way junction of bridge sutures using a caliper. Plastron length was measured from center of epiplastron to the back of the anal notch on the xiphiplastron at the central suture along lateral and longitudinal center lines. Width of the carapace was measured at the center line of the bridge and length along the center line of the neural bones. The degree of posterior carapacial flaring was quantified by calculating the ratio of width at the margin where fourth and fifth marginal scutes join each other to the width between the centers of the left and right eight marginal scutes at the margin (Table 1). Variation in plastral scute position was assessed by calculating the ratio of the span between the hyo/hypoplastral suture at the center line to the span between the abdominal/femoral sulcus and the hyo/hypoplastral suture at the center line (Table 1). Variation in the pygal bone dimensions was quantified by calculating the ratio of pygal length to width at the longitudinal and lateral midlines (Table 1). Covariance and correlation between carapace length and indicated ratios were conducted in Microsoft Excel (Office 16) using the COVARIANCE.S and CORREL functions.

RESULTS

General Description

The shells are moderately domed with varying degrees of posterior carapacial flaring. The shell bones of all specimens are thin and lack the extensive ornamentation (sculpting) characteristic of *Trachemys*. They also exhibit weak to no peripheral notching and lack a keel. All but one (Neb 5) have a shallow anal notch on the plastron. Most specimens had some lateral growth ridges (wrinkling) on the costal bones. The suprapygal and neural formulae vary; four have two suprapygals (Neb 3, Neb 5, Neb 12, ODFW1), two have three suprapygals (Neb 4, Neb 13), and one has and odd round first suprapygal that is enclosed by the pygal and the second suprapygal (Neb 14). With one exception, the neural formulae vary from seven to eight (Neb 3 has a very small ninth neural bone). Two (Neb 3 and Neb 12) have an unusual ovoid bone between the between two of the terminal neural bones (Neb 3, Neb 12). All except one (Neb 3) have eight costal bones; neb 3 has nine.

Neb 3

Carapace is 13 cm wide and 16 cm long. Plastron is 10 cm wide, and 16.5 cm long. This individual has nine costal bones instead of the usual eight. The nuchal bone is very wide such that the marginal/pleural sulcus joins the first vertebral sulcus in an unusual four-way junction. The cervical scute (width/length is 0.6 cm x 1.0 cm) is cuneate in the dorsal view, though still longer than wide (Fig. 1). The cervical scute imprint on the distal nuchal bone is rounded with no toothed notch (Figs. 1, 8A). Peripheral margin of the cervical scute and underlying nuchal bone is recessed in the nuchal notch, rather than protruding. The proximal end of the entoplastron joins the humoral-pectoral sulcus at the midline. The anal-femoral sulcus joins the midline at the xiphi-hyoplastral suture. Some bone from the xiphiplastron of this animal was harvested for genetic analysis so xiphiplastral notch is no longer present. Scute growth rings appear as wrinkles in places on lower costals.

Neb 4

Carapace is 13 cm wide and 17 cm long. This individual exhibits a more pronounced carapacial doming than the others. Plastron is 10.5 cm wide and 16.5 long. Xiphiplastral notch is very shallow, nearly non-existent. The cervical scute (width/length is 0.6 cm x 1.6 cm) is slightly cuneate and the distal nuchal bone contains only one very shallow, nearly inapparent notch. The distance from the proximal end of the entoplastron to the humoral-pectoral sulcus at the midline is 4 mm. The anal-femoral sulcus joins the midline 4 mm below the xiphi-hyoplastral suture. There are eight neural and two suprapygal bones. Scute growth rings are present on lower posterior costals. The plastron of this individual has unusual sulci in several places (Fig. 2). In addition, the dorsal surface has many round excavations (1–3 mm in diameter) and grooves interpreted as gnaw marks.

Neb 5

Carapace is 10.4 cm wide and 12.6 cm long. Plastron is 8 cm wide and 11.5 cm long. This is a juvenile with partially fused costal-peripheral sutures. The cervical scute (width/length is 0.5 cm x 1.1 cm) is slightly cuneate. The distal nuchal bone underlying the cervical scute has a single distinct notch. This individual has a pronounced xiphiplastral notch. The distance from the proximal end of the entoplastron to the humoral-pectoral sulcus at the midline is 1 mm. The anal-femoral sulcus joins the midline 3 mm below the xiphi-hyoplastral suture. There are eight neural and two suprapygal bones. Faint growth rings are visible on the distal costal ends of middle and posterior costals (Fig. 3).

Neb 12

Carapace is 11.2 cm wide and 16.3 cm long. Plastron is 9.3 cm wide and 13.8 cm long. Scute growth rings present on lower costals. The cervical scute (width/length is 0.6 cm x 1.7 cm) is slightly cuneate and the distal nuchal bone underlying the cervical scute has three distinct notches. The distance from the proximal end of the entoplastron to the humoral-pectoral sulcus at the midline is 4 mm. The anal-femoral sulcus joins the midline 6 mm below the xiphi-hyoplastral suture. Growth rings are present on lower 3rd and 4th costals. There are 9 neural bones one of which is a tiny interloper between neurals 7 and 8 (Fig. 4).

Neb 13

Carapace is 13.2 cm wide and 17.5 cm long. Plastron is 11.3 cm wide and 17 cm long. The cervical scute (width/length is 0.7 cm x 1.6 cm) is slightly cuneate and the distal nuchal bone underlying the cervical scute is blunt and has no distinct notches (teeth). The distance from the proximal end of the entoplastron to the humoral-pectoral sulcus at the midline is 5 mm. The anal-femoral sulcus joins the midline 9 mm below the xiphi-hyoplastral suture. This individual has eight neural bones and 3 suprapygals (Fig. 5). Some growth rings apparent on the posterior costals.

Neb 14

Carapace is 11.2 cm wide and 16 cm long. Plastron is 9.1 cm wide and 14.9 cm long. The cervical scute (width/length is 0.5 cm x 1.5 cm) is slightly cuneate and curved laterally. The distal nuchal bone underlying the cervical scute is slightly rounded to blunt and has no distinct notches. Some shallow rugosity (sculpture) is present on the nuchal bone. The distance from the proximal end of the entoplastron to the humoral-pectoral sulcus at the midline is 3 mm. The anal-femoral sulcus joins the midline 9 mm below the xiphi-hyoplastral suture. This individual has 8 neural bones, a small round suprapygal 1 and an elongated suprapygal 2 (Fig. 6).

ODFW 1

This turtle was found with an arrow through its shell (Fig. 7). Carapace is 15.3 cm wide and 20.7 cm long. Pronounced growth rings (wrinkles) are visible on the lower costals, and some rugosity (sculpture) is present on the nuchal bone. This individual has a small inframarginal scute on the bridge bordering the right pectoral and abdominal scutes. Plastron is 13.2 cm wide and 19.8 cm long. The cervical scute (width/length is 0.5 cm x 2.0 cm) is slightly cuneate and the distal nuchal bone underlying the cervical scute has two distinct notches. The distance from the proximal end of the entoplastron to the humoral-pectoral sulcus at the midline is 4 mm. The anal-femoral sulcus joins the midline 3 mm below the xiphi-hyoplastral suture. This individual has eight neural and two suprapygal bones.

The nuchal, the pygal, and the entoplastron bones are distinct and commonly recovered in fossil assemblages. Morphological variation of these elements in my collection of *C. picta bellii* is illustrated in Figures 8–10. Significant variation also occurs in a number of other characters, including the shape of the first peripheral bone, the shape of the first vertebral scute, and the distance between the anal/femoral sulcus and the hypo/xiphiplastral suture at the midline (Figs. 1–7). Variation in the suprapygal number and shape was also observed (Figs. 1–7). In order to better understand morphological variation amongst this population, a number of basic morphological ratios were calculated (Table 1). Because morphological characters can vary with age, it was of interest to determine whether any of the observed variation in pygal bone, first vertebral scute, the position of humeral, abdominal, and femoral scutes, and flaring of carapace could have an allometric origin. As such, covariance and correlation analyses were conducted (Table 2). Results show that only the pygal length to width ratio shows significant correlation with carapace length.

DISCUSSION

To my knowledge, there is no detailed shell osteology that includes multiple individuals for any extant emydid turtle in the published literature (Tucker et al. 1998 published measurements of *Trachemys scripta elegans*, but their analysis was limited to shell length, width, and height). In order to begin characterizing shell element variation in extant *Chrysemys*, I have illustrated a range of shell characters in a collection of *Chrysemys picta bellii*. In many cases, substantial variation in shell bone shape and location of sulci was observed, with some exhibiting major differences in shape and sulcus position. For example, significant variation was observed in the position of sulci on the nuchal bone; in particular, the position of the junction between the first vertebral and the first marginal/first pleural sulcus varies dramatically, and the nuchal of one individual (Neb 3) also contains the junction with the second marginal scute (Fig. 8). The entoplastron showed a range of minor variations in overall shape, with the gular sulci meeting the midline between one third to one half way down the longitudinal axis of the entoplastron (Fig. 9). The distance from the proximal end of the entoplastron to the humoral-pectoral sulcus at the midline varies somewhat, ranging from direct contact (Neb 3), to near contact for ODFW 1 and Neb 5 (within 2 mm), to 4–6 mm for the remainder of the specimens. Another shell element commonly identified in fossil assemblages is the pygal bone. We observed a range of subtle variation in that character, with one major deviation (due to presence of a round first suprapygal) seen in Neb 14 (Fig. 10). Note that the suprapygal formula varies (there are usually two, but Neb 13 has three), with interesting variations observed in the shape and relative size of those bones in Neb 3, Neb 5, Neb 13, and Neb 14. The anal-femoral sulcus joins the midline at the xiphi-hyoplastral suture in Neb 4, 1–2 mm below for ODFW 1 and Neb 13, and 5–10 mm below for the remaining specimens. There is also variation in the dimensions of the first vertebral scute; in some animals (Neb 5, Neb 12, and Neb 14) this scute is as long as it is wide, while in the remaining specimens that scute is longer than it is wide. Also, Neb 3 differs from all other individuals in that it has a 1st vertebral whose distal junction with the cervical and first marginal scutes is significantly narrower than the proximal junction with the second vertebral scute (Fig.1).

As with most of the chelonians, fossil forms of the deirochelyid turtles can be difficult to diagnose to the species level from isolated shell elements (Adler 1968; Jackson 1988; Vitek 2018), and even well-articulated shells are often assigned to a new species within the genus based upon subtle variations in shell characters. For example, the nuchal bone shapes and sulci of four different fossil *Trachemys* species illustrated in Jasinski (2018) all fall within the morphological range of the extant *Chrysemys* that we report in this manuscript. Similarly, apart from the extensive sculpture on the *Trachemys* specimen, the *Trachemys* and *Chrysemys* nuchal bones illustrated in Holman and Richards (1993) fall within the range of variation observed in our extant population of *Chrysemys*. In Preston (1979), the nuchal bones that he assigns to *Chrysemys* (*Trachemys*) *scripta* and *Chrysemys* (*Chrysemys*) *picta* also fall within the observed range in our small collection of extant *C. picta bellii*. Nuchal bones of early Pleistocene *Trachemys* depicted in Parmley et al. (2019) appear to have some sculpting, though in other ways would be fall within the range of modern *Chrysemys*. Nuchals of the *Pseudemys* species described in their work also appear to fall within the range of variation observed in our collection of *C. picta bellii*. Comparisons of the first vertebral scute in extant *Chrysemys* with *Chrysemys antiqua* and *Pseudograptemys inornata* figured in Hutchison (1996) as well as *Chrysemys timida* in Hay (1908, p. 347) show that the first vertebral scute of modern *Chrysemys* specimens is shaped differently

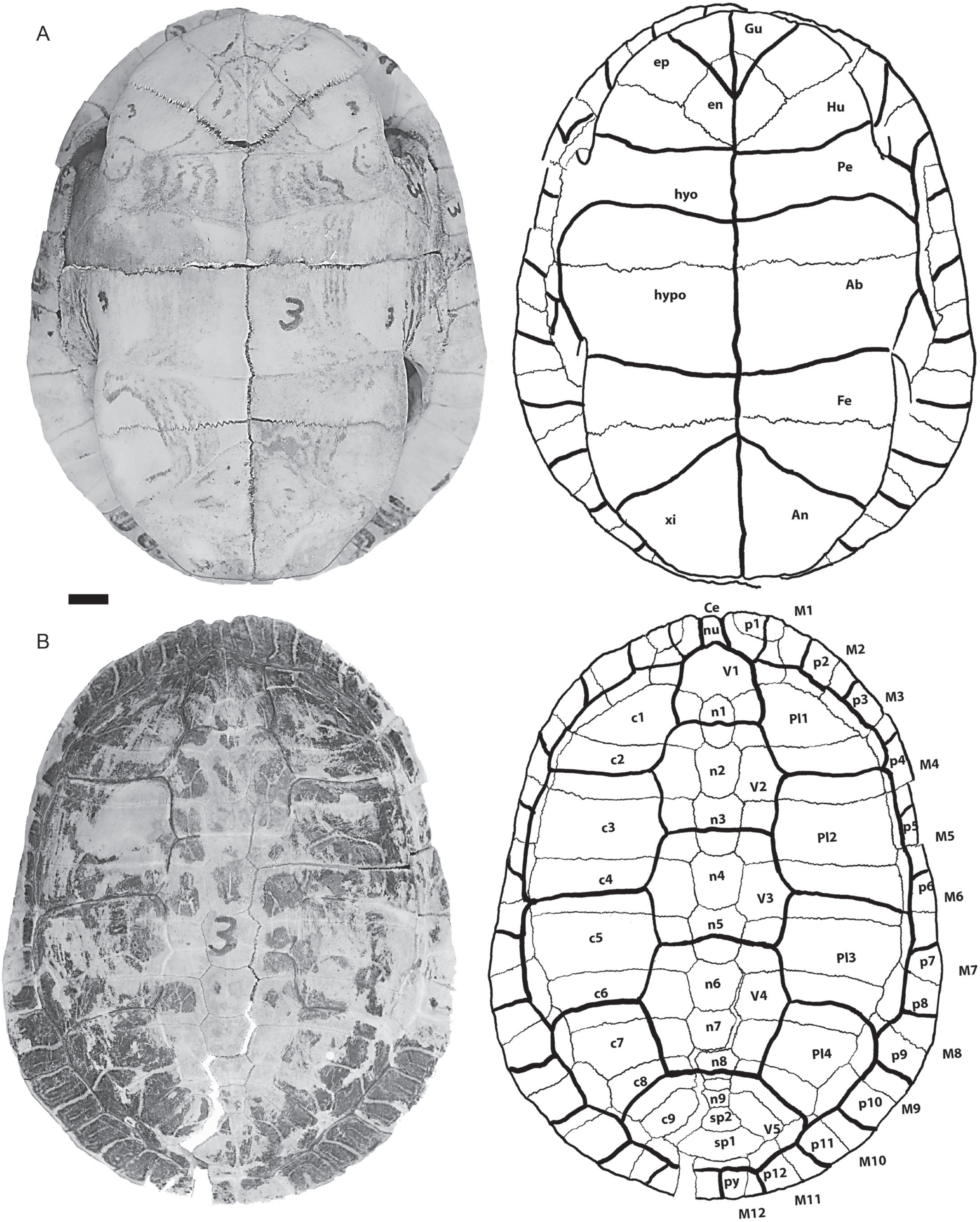

Figure 1. *Chrysemys picta bellii,* Neb 3. A, plastron and B, carapace. Abbreviations: Ab, abdominal scute; An, anal scute; c, costal; en, entoplastron; ep, epiplastron; Fe, femoral scute; Gu, gular scute; Hu, humeral scute; hyo, hyoplastron; hypo, hypoplastron; n, neural; nu, nuchal; Pe, pectoral scute; py, pygal; sp, suprapygal; xi, xiphiplastron. Scale bar = 1 cm.

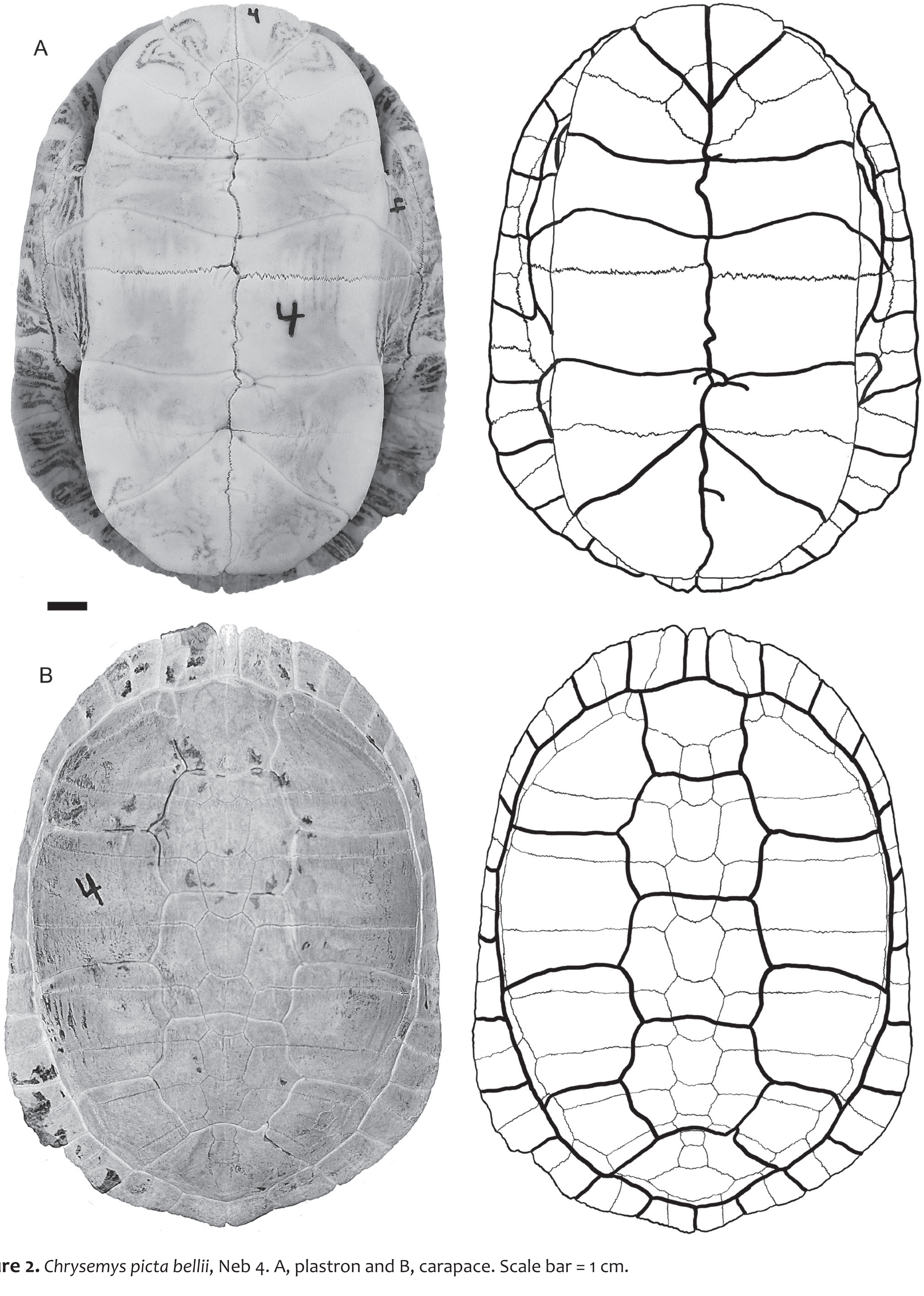

Figure 2. *Chrysemys picta bellii*, Neb 4. A, plastron and B, carapace. Scale bar = 1 cm.

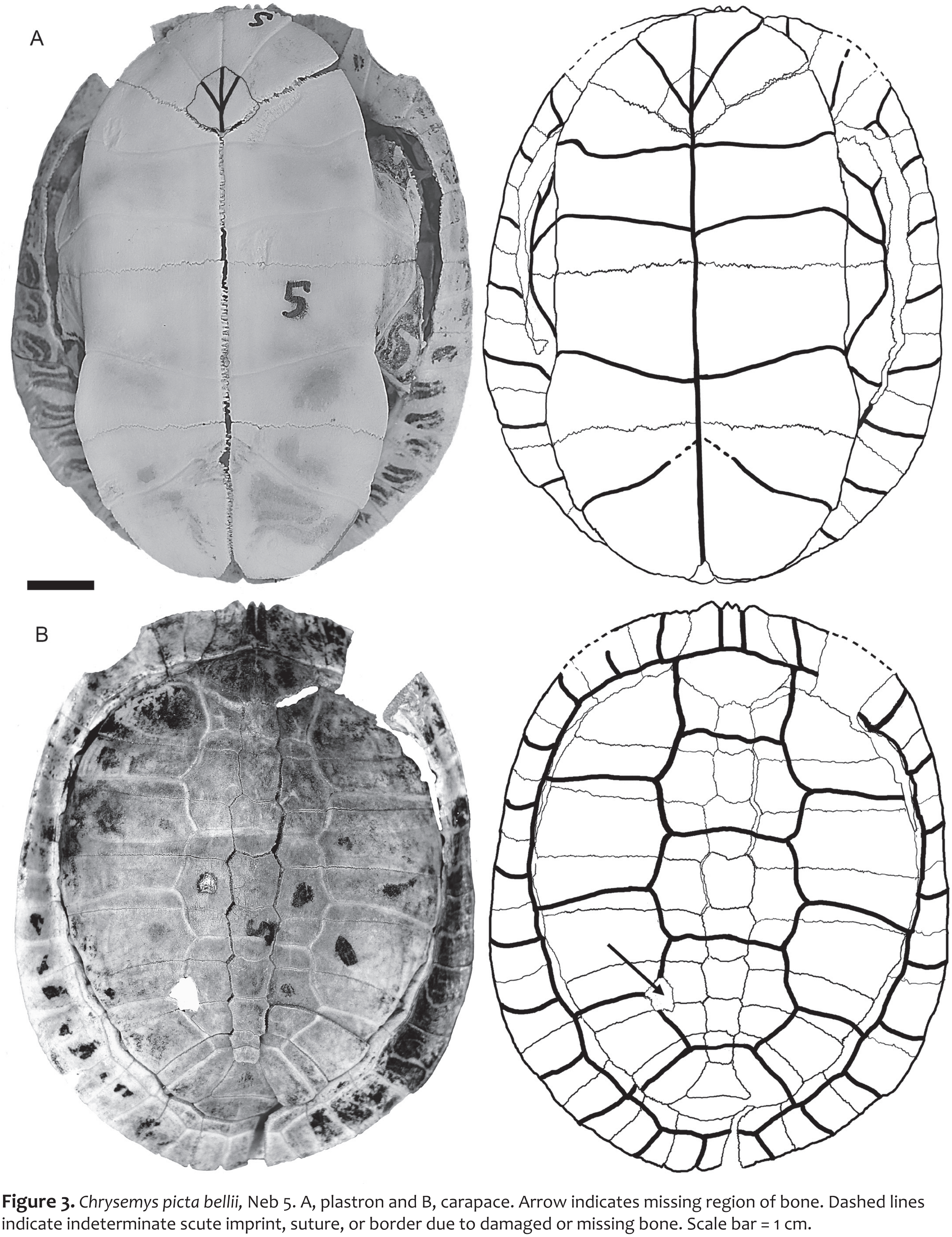

Figure 3. *Chrysemys picta bellii*, Neb 5. A, plastron and B, carapace. Arrow indicates missing region of bone. Dashed lines indicate indeterminate scute imprint, suture, or border due to damaged or missing bone. Scale bar = 1 cm.

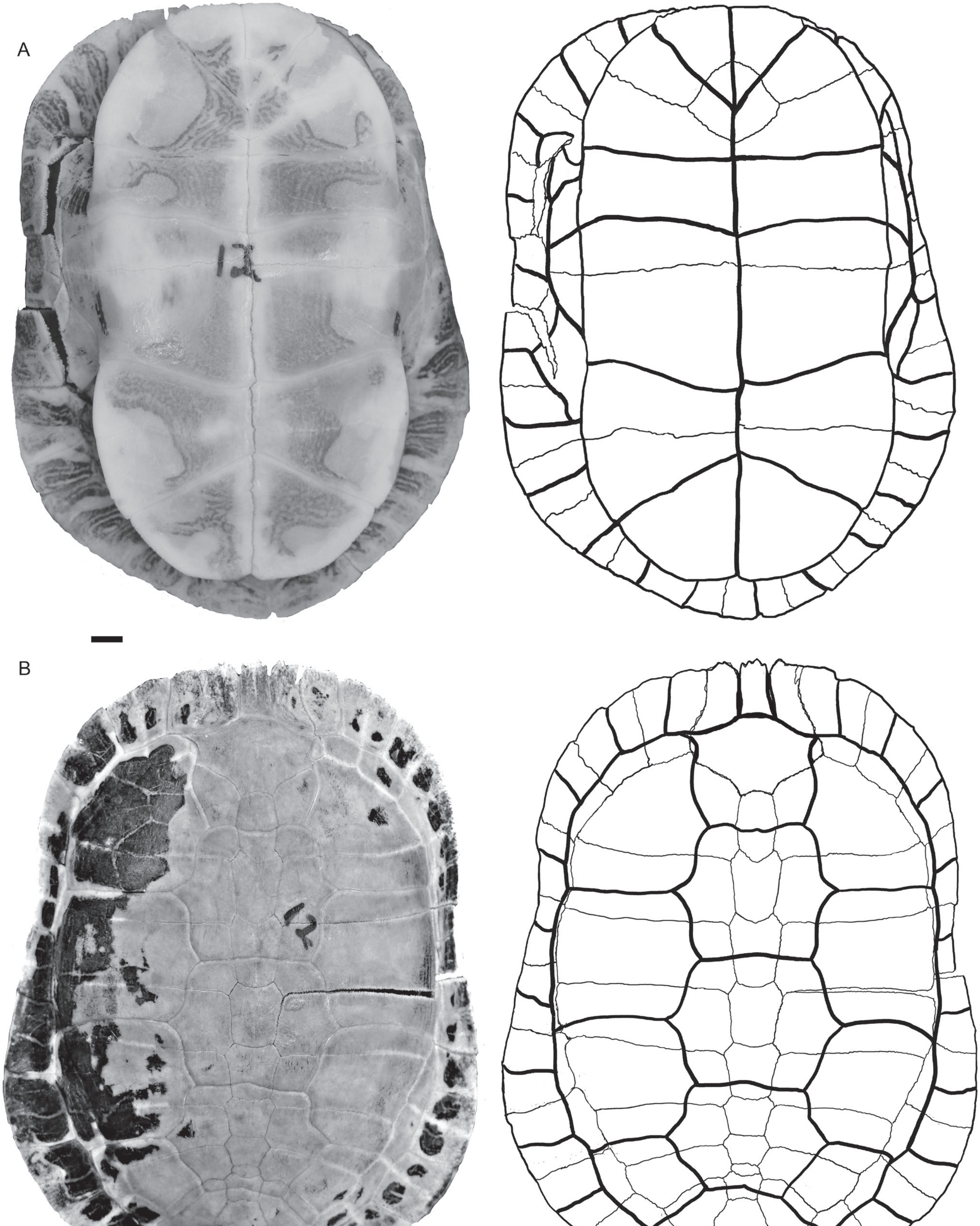

Figure 4. *Chrysemys picta bellii,* Neb 12. A, plastron and B, carapace. Arrow indicates missing bone. Dashed lines indicates indeterminate scute imprint, suture, or border due to damaged or missing bone. Scale bar = 1 cm.

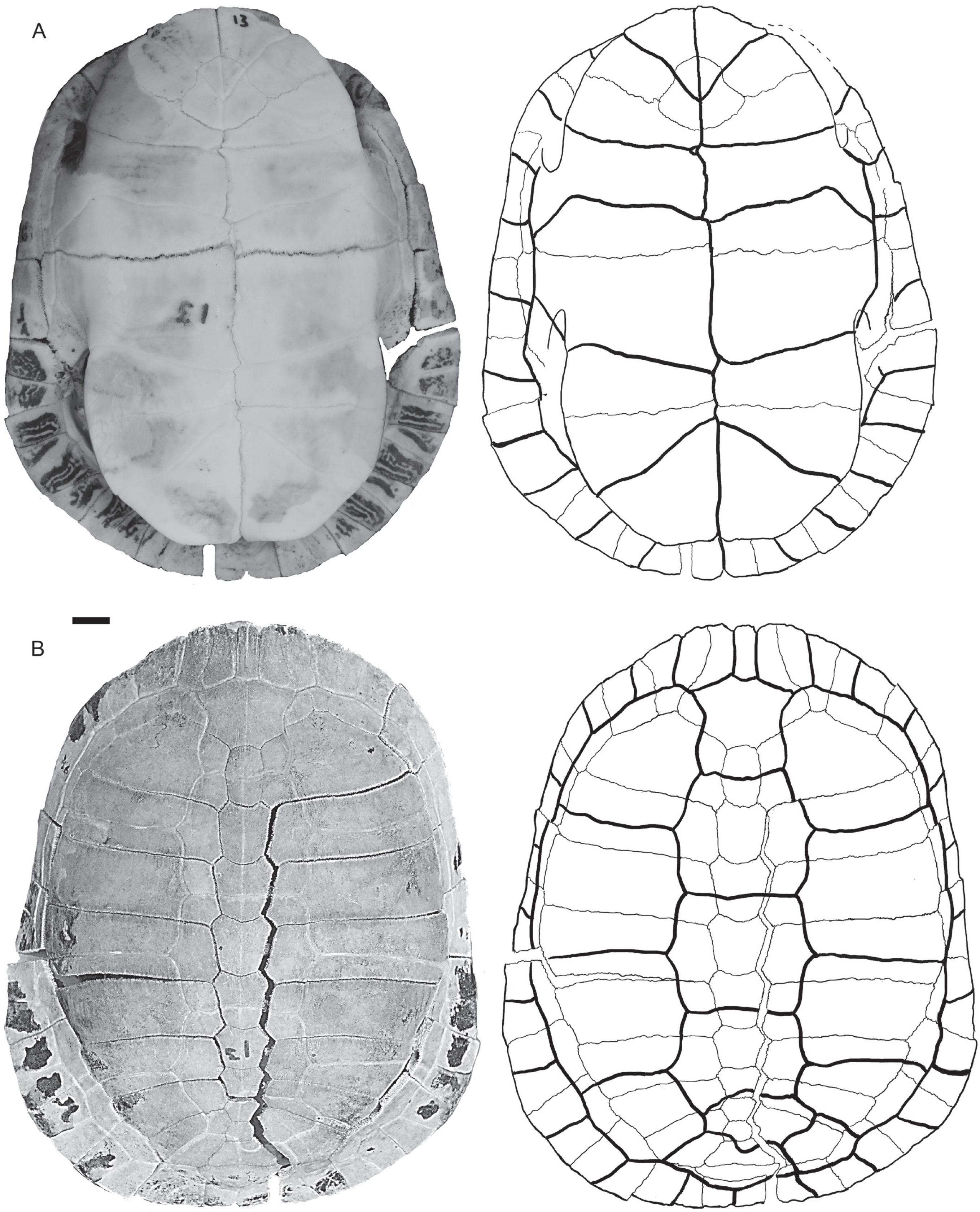

Figure 5. *Chrysemys picta bellii,* Neb 13. A, plastron and B, carapace. Scale bar = 1 cm.

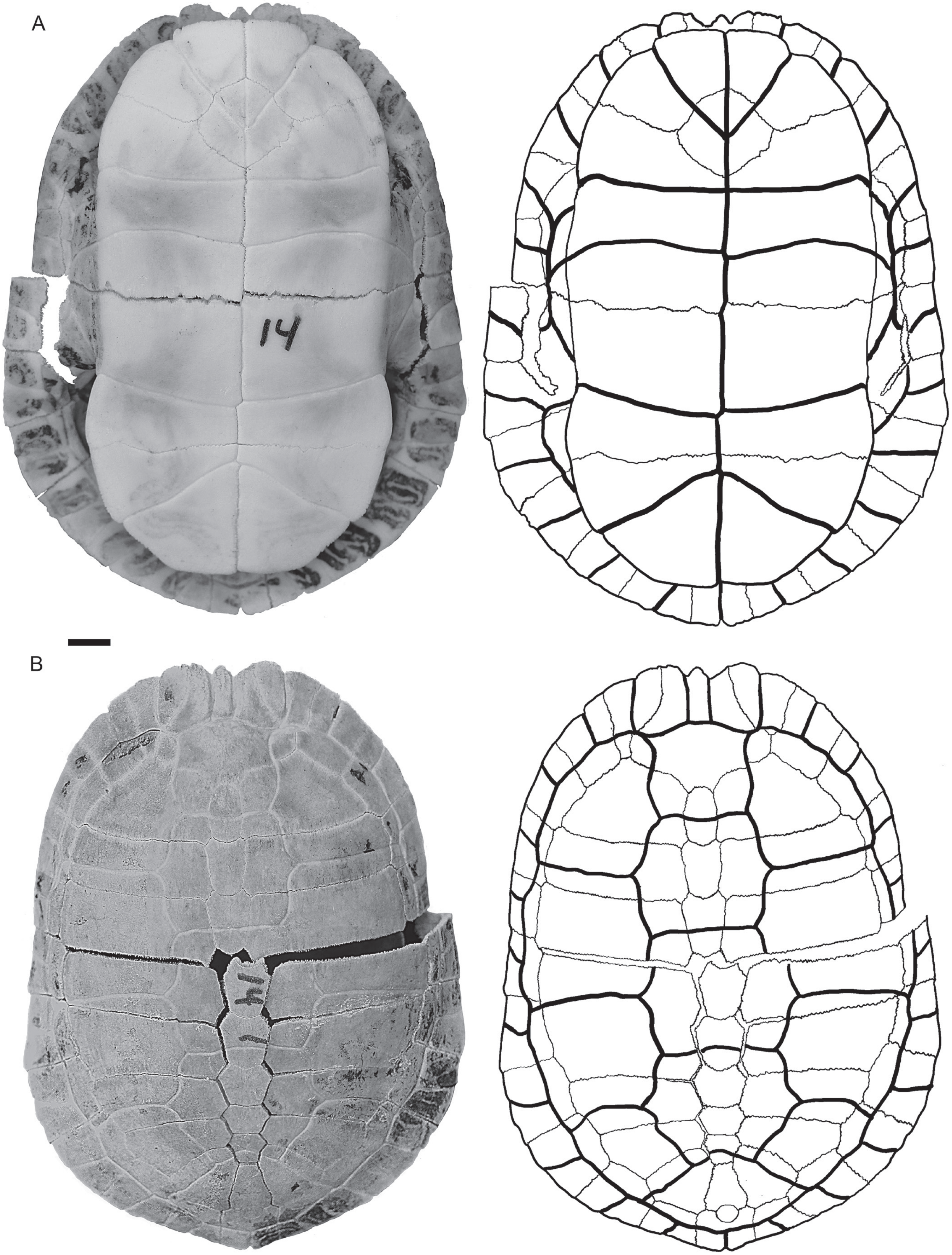

Figure 6. *Chrysemys picta bellii,* Neb 14. A, plastron and B, carapace. Scale bar = 1 cm.

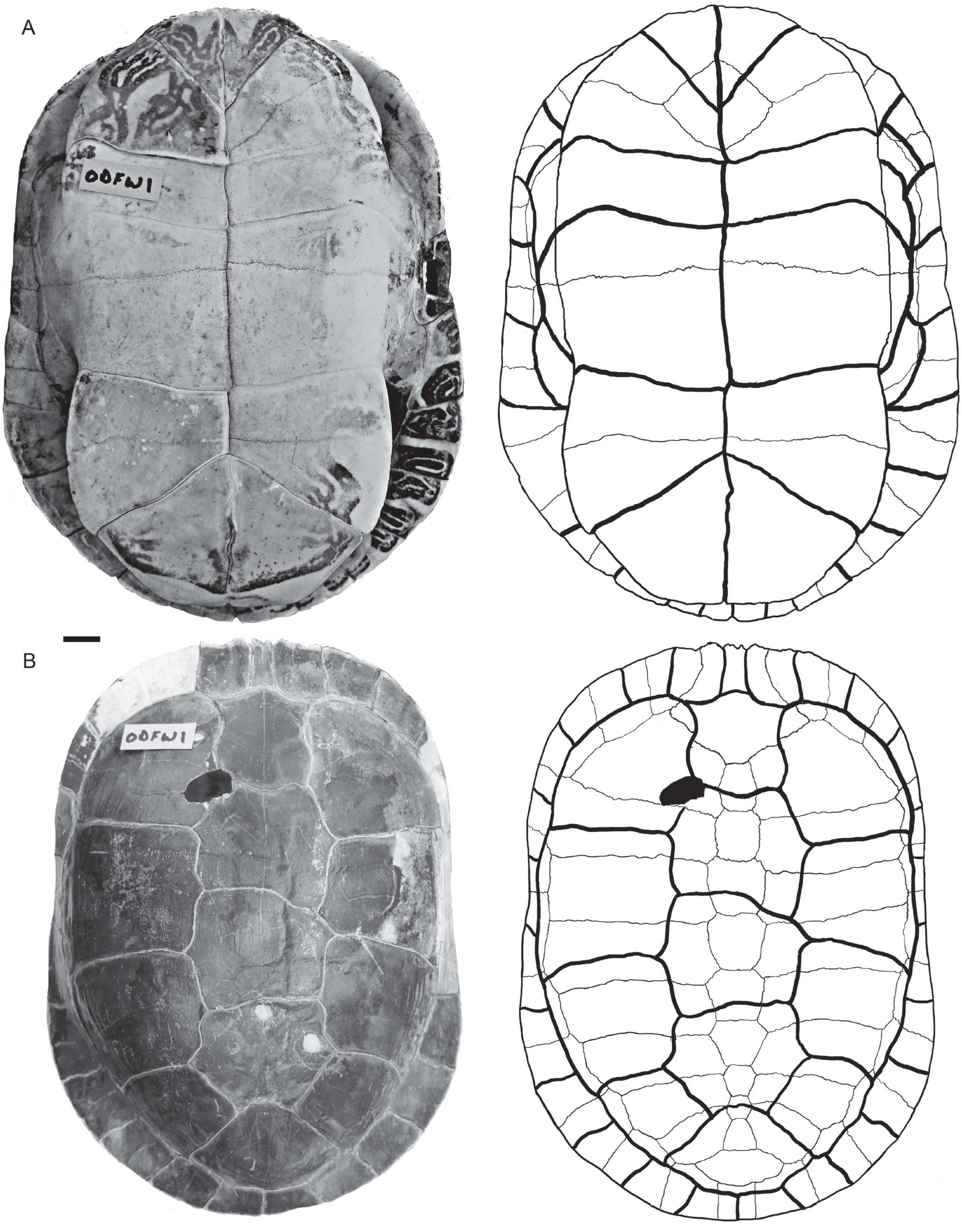

Figure 7. *Chrysemys picta bellii,* ODFW 1. A, plastron and B, carapace. The black region on the first left costal is an arrow hole. Scale bar = 1 cm.

Table 1. Morphometric variation of shell characters. Abbreviations: L, length of carapace in centimeters; WFF, carapace width at margin where the fourth and fifth marginal scutes meet; WCE, carapace width at midpoint of the eighth marginal scute; D FV, distal width of first vertebral scute; P FV, proximal width of first vertebral scute; HA, distance between humeral/abdominal sulcus and the hyo/hypoplastral suture at the midline; AF, distance between the abdominal/femoral sulcus and the hyo/hypoplastral suture at the midline; PL, pygal length at the midpoint; PW, pygal width at the midpoint.

Specimen	Carapace L	WFF/WCE	D/P FV	HA/AF	PL/PW
Neb 3	16.3 cm	0.91	0.75	0.78	0.87
Neb 4	17.4 cm	0.90	1.27	0.63	0.97
Neb 5	11.5 cm	0.97	1.15	0.32	1.15
Neb 12	16.2 cm	0.95	1.50	0.26	1.03
Neb 13	17.9 cm	0.88	1.17	0.29	0.92
Neb 14	15.5 cm	0.85	1.05	0.43	1.16
ODFW1	20.9 cm	0.94	1.03	0.33	0.92

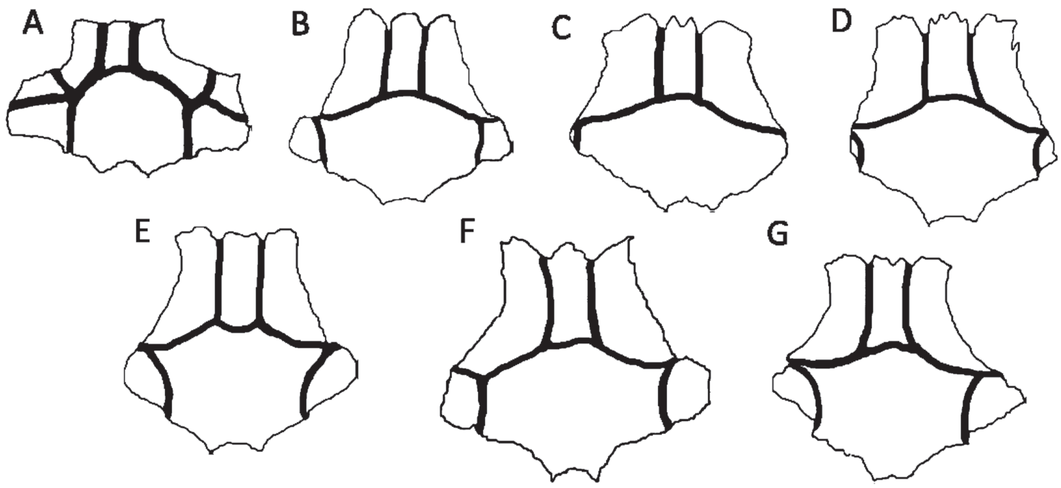

Figure 8. Nuchal bones of *Chrysemys picta bellii.* A, Neb 3; B, Neb 4; C, Neb 5; D, Neb 12; E, Neb 13; F, Neb 14; and G, ODFW 1.

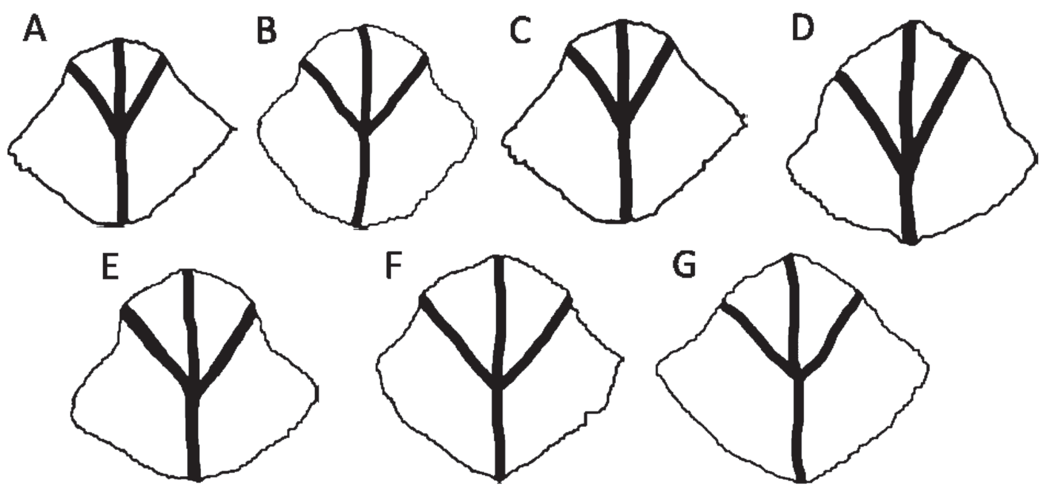

Figure 9. Entoplastron bones of *Chrysemys picta bellii.* A, Neb 3; B, Neb 4; C, Neb 5; D, Neb 12; E, Neb 13; F, Neb 14; and G, ODFW 1.

Table 2. Covariance and correlation of morphometric characters with carapace length. Abbreviations: WFF, carapace width at margin where the fourth and fifth marginal scutes meet; WCE, carapace width at midpoint of eight marginal scute; D FV, distal width of first vertebral scute; PFV, proximal width of first vertebral scute; HA, distance between humeral/abdominal sulcus and the hyo/hypoplastral suture at the midline; AF, distance between the abdominal/femoral sulcus and the hyo/hypoplastral suture at the midline; PL, pygal length at the midpoint; PW, pygal width at the midpoint.

	Covariance	Correlation
WFF/WCE	-0.029	-0.24
DFV/PFV	-0.053	-0.08
HA/AF	0.012	0.02
PL/W	-0.23	-0.71

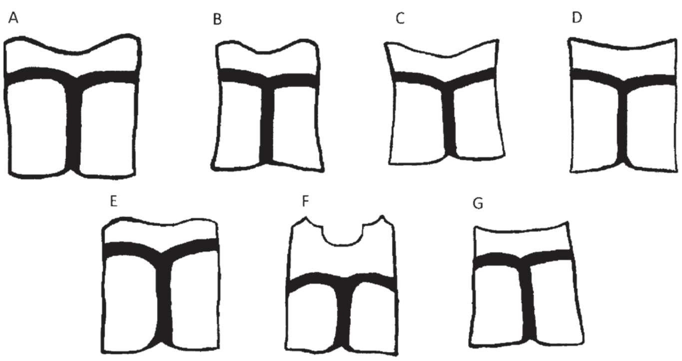

Figure 10. Pygal bones of *Chrysemys picta bellii*. A, Neb 3; B, Neb 4; C, Neb 5; D, Neb 12; E, Neb 13; F, Neb 14; and G, ODFW 1.

than *C. timida* and *C. antiqua*, and that the first vertebral of extant *C. picta* more closely resembles that of the fossil *Pseudograptemys inornata*.

Sculpture (rugosity) has been used as a diagnostic character because it is largely absent in the extant *Chrysemys picta*. Hutchison (1996) notes that sculpting is present in the late Eocene and early Oligocene specimens of *C. antiqua*, but is not present later in the early Oligocene. *Pseudograptemys inornata* is described as 'unsculptured', hence is very similar to extant *Chrysemys* in that regard (though presence of inguinal and axillary musk ducts, cervical scute nearly as wide as long, and posterior carapacial notching readily distinguish *P. inornata* from *Chrysemys*). Jackson (1976) describes a 'rugose' Pliocene *Chrysemys* (*C. caelata*) that exhibits extensive sculpting, and comments that there is a range of variation in that character (sculpture). More recently Jackson (1988) reevaluated fossil *Chrysemys platymarginata* and *Pseudemys idahoensis* (both Pliocene) using skull characters to reassign them to *Trachemys*. Thus, although sculpture is largely absent on extant *Chrysemys*, it does occur, and appears to be variable in fossil *Chrysemys*, bringing into question its value as a diagnostic character.

The fact that I have observed significant variation in many shell characters from six individuals that were living in the same pond suggests that there is significant variation even in local populations. Allometric contributions to individual turtle shell characters have not been well characterized, though some work has addressed this issue (Mosimann 1958; Vitek 2018). Since the collection of individuals in this study contains a variety of ages, the possibility of allometric contributions to the observed variation in four ratios was examined (Table 1). In my limited analysis using carapace length as an age proxy, it appears that only the ratio of length to width of the pygal bone has any significant allometric component to its variation (Table 2). It is not clear whether the non-allometric variation in a variety of characters relates to functional aspects of the shell that afford the species some selective advantage or whether they are simply ontogenetic variations that occur because of varying environmental conditions. In addressing this question of environmental influences on morphology, Fritz et al (2005) and Fritz et al. (2007) showed that observed phenotypic plasticity of *Testudo marginata* and of the *Testudo graeca* complex does not correlate well with genetic variability, suggesting that in other chelonians such as *Chrysemys* environmental factors could be responsible for the observed variation in these characters.

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