A NEW SOFT-SHELLED TURTLE (TRIONYCHIDAE, *APALONE*) FROM THE LATE MIOCENE OF NORTH-CENTRAL FLORIDA

Natalí Valdes[1], Jason R. Bourque[1,2], and Natasha S. Vitek[1,3]

ABSTRACT

Trionychid fossils from the late Miocene (late Clarendonian) Love Bone Bed in Alachua County, Florida, are described as a single taxon that represents a new species, ***Apalone amorense* sp. nov.** A phylogenetic analysis recovers *A. amorense* as sister to all extant representatives of *Apalone*. The new species is relatively small at adult size compared to other species of *Apalone* and exhibits a mosaic of similarities with extant species of *Apalone*. It shares the presence of four plastral callosities, lack of surface contact between the jugal and parietal, and a mid-sized postorbital bar with *A. ferox*, and unfused hyo-hypoplastra (except in some older individuals where these fuse), variably open suprascapular fontanelles in all but the largest individuals, and dermal sculpturing similar to *A. mutica* and *A. spinifera*. The age and proposed phylogenetic position of *A. amorense* are consistent with previously published estimated divergence dates for the clade.

Key words: Testudines; Trionychidae; *Apalone*; Clarendonian; Florida; Love Bone Bed; new species.

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank Publication number for this issue is 625F2C6D-5FA6-426B-BCA3-F3CC1725DFD6.

ISSN 2373-9991

[1] Division of Vertebrate Paleontology, Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611-7800 USA
[2] Corresponding author: <jbourque @flmnh.ufl.edu>
[3] Corresponding author: <nvitek@ufl.edu>

Valdes, N., J. R. Bourque, and Natasha S. Vitek. 2017. A new soft-shelled turtle (Trionychidae, *Apalone*) from the Late Miocene of north-central Florida. Bulletin of the Florida Museum of Natural History 55(6):117–138.

INTRODUCTION

Soft-shelled turtles (Trionychidae) are a fully aquatic clade of turtles commonly characterized by the presence of rubbery skin covering their bony shell. Representatives lack certain features ubiquitous in other turtle groups, such as keratinous scutes, pygals , and an ossified bridge that suturally connects the carapace and plastron (Ernst and Barbour, 1989). All but one clade of trionychids, *Lissemys* spp., also lack peripherals, and those bones in *Lissemys* spp. may be neomorphic (Delfino et al., 2010). Trionychids have a global distribution and are found in Africa, Asia, Oceania, Europe, and North America (Meylan, 1987; Ernst and Barbour, 1989; Engstrom et al., 2004; Turtle Taxonomy Working Group, 2014).

In the New World, extant trionychids are distributed throughout North America. Their distribution includes regions east of the Rocky Mountains, south of the 49th parallel, and as far south as central Mexico (Turtle Taxonomy Working Group, 2014). The distribution of New World trionychids was even greater in the Neogene (Hay, 1908), including the Miocene of Venezuela (Wood and Patterson, 1973; Sanchez-Villagra et al., 2004; Head et al., 2006; Sanchez-Villagra and Aguilera, 2006), and Panama (Cadena et al., 2012). These findings suggest that trionychids once inhabited parts of Central and northern South America, in addition to their current North American range, in near-shore marine environments (Sanchez-Villagra and Aguilera, 2006).

Extant New World trionychid diversity consists of a single clade of three species: *Apalone ferox, A. spinifera,* and *A. mutica* (Turtle Taxonomy Working Group, 2014). The relationship of extant *Apalone* spp. to extinct New World trionychid diversity is unclear (Vitek and Joyce, 2015). Preliminary divergence date estimates based on molecular data place the origin of crown group *Apalone* in the Miocene (Le et al., 2014). Multiple Neogene specimens were referred to *Apalone*. In addition, "*Trionyx*" *leucopotamicus* from the late Eocene of western North America was referred to *Apalone* on the basis of neural reversal position and the reduction or loss of the eighth costal pair (Hutchison, 1996). More surprisingly, one Late Cretaceous taxon, "*Trionyx*" *latus*, known only from carapacial material, was recovered as a member of crown-*Apalone* (Gardner et al., 1995). However, those results have not yet found rigorous support. Some of the morphology-based hypotheses are incongruent with results from molecular data. None of the Paleogene or Neogene specimens proposed to be members of *Apalone* have been included in published phylogenetic analyses. Furthermore, homoplasy may contribute to the placement of Mesozoic fossils in extant genera (Gardner et al., 1995; Li et al., 2015; Vitek et al., 2017).

The incomplete nature of the fossil record has long impeded an understanding of relationships within Trionychidae, complicating interpretations of the phylogenetic position of extinct taxa (Gaffney, 1979; Meylan, 1987). Since Meylan's (1987) monograph presenting a morphology-based phylogeny of Trionychidae, soft-shelled turtle relationships have received more attention, both morphologically and genetically (e.g., Gardner et al., 1995; Engstrom et al., 2004; Joyce et al., 2009; Joyce and Lyson, 2011; Vitek, 2011, 2012; Le et al., 2014). The inclusion of more complete Miocene material in phylogenetic analyses may help obviate problems of homoplasy in resolving relationships between extant *Apalone* spp. and extinct taxa.

The Love Bone Bed, or Love Site (Fig. 1), represents a late Miocene (late Clarendonian) environment that preserves estuarine, freshwater, and terrestrial vertebrates (Webb et al., 1981). Trionychid fossils, including skull, shell, and postcranial material, were collected along with tens of thousands of other vertebrate fossils between 1974 and 1981 after the site's discovery (Webb et al., 1981). The trionychids were initially identified as *Trionyx* (= *Apalone*) cf. *ferox* (Webb et al., 1981) or as *Trionyx* spp., but were not described or analyzed in detail. Later, Bourque (2013) questioned the species identification and suggested that the fossils did not represent *Apalone ferox* by noting that the Love species was more gracile than *A. ferox* with dissimilar dermal pit sculpturing. In order to understand the trionychid material from the Love Bone Bed in

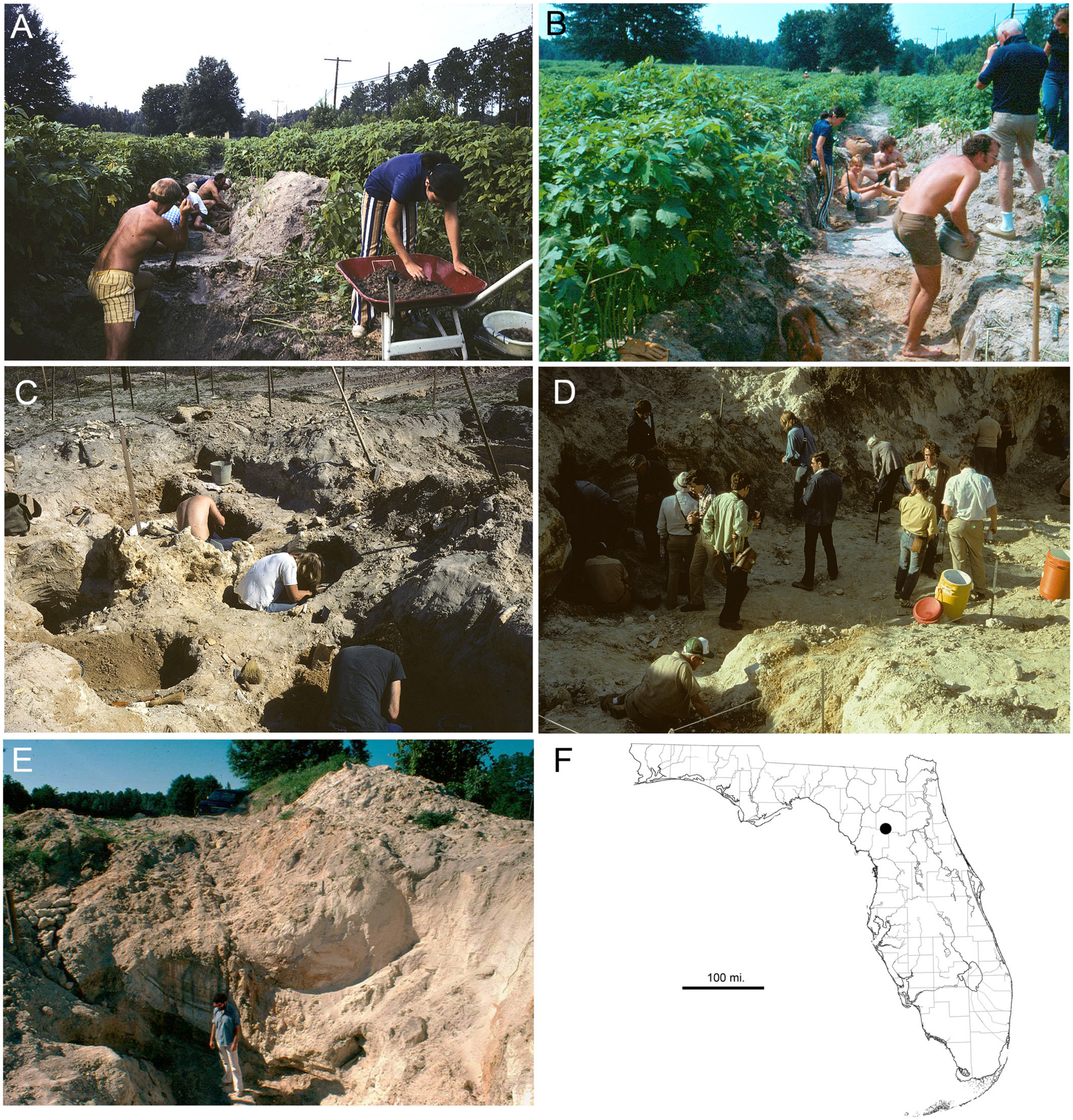

Figure 1. The Love Bone Bed. **A**–**E**, Photographs of field excavations from the 1970s to 1981. **A**–**B**, Field crew removing surface sediments in the original okra fields at the Love Bone Bed during the initial stages of excavation in 1974 (Photograph by David Webb). **C**, Graduate students digging at the site in 1975 (Photograph by David Webb). **D**, Field trip at the Love Bone Bed during the 1980 Society of Vertebrate Paleontology annual meeting. **E**, Richard C. Hulbert, Jr. as a beginning Ph. D. student standing in the excavated pit early in 1981 during the final stages of excavation. All photographs courtesy of the Florida Museum of Natural History and background information provided by Richard Hulbert (pers. comm.). **F**, Map of Florida. Black dot in southwestern Alachua County indicates location of the Love Bone Bed.

an evolutionary context, we describe the material and explore its phylogenetic relationships with respect to extant species and putative extinct species of *Apalone*.

MATERIAL AND METHODS

A morphological dataset based on the matrix published in Vitek (2012) was used to conduct a phylogenetic analysis. The matrix builds on additions and revisions to Meylan's (1987) original character matrix (Joyce et al., 2009; Joyce and Lyson, 2011; Vitek, 2011; Joyce et al., 2016). Character 85 of Vitek (2012), which delimits giant trionychids, was deleted. Gigantism (straight line, bony carapace length greater than 600 mm) was instead included as an additional state of character 20 (carapace straight line length).

Specimens from the Love Bone Bed were scored independently by two of the authors (NV and NSV) and scores were compared before analysis to minimize observer error (see Systematic Paleontology section for specimen numbers). Individually scored specimens were then compared to each other to determine whether they represented the same taxon. All specimens were combined into a single operational taxonomic unit (OTU) because all character differences were within the range of previously documented intraspecific variation (Gardner and Russell, 1994).

Two additional taxa were scored and added to the matrix: "*Trionyx*" *leucopotamicus* (AMNH 6045) was previously hypothesized to belong to *Apalone* and "*Trionyx*" *miocaenus* (AMNH 6298) is the only currently recognized valid species of trionychid from the Miocene of North America (Matthew, 1924; Hutchison, 1996; Vitek and Joyce 2015). These species are known only from carapacial material. Within the matrix, "*T.*" *miocaenus* and "*T.*" *latus* were taxonomic equivalents of "*T.*" *leucopotamicus* (Kearney and Clark, 2003). Because taxonomic equivalence along with high amounts of missing data can cause some taxa to act as wildcards and decrease resolution in consensus trees, "*T.*" *miocaenus*, and "*T.*" *latus* were excluded from further analyses (Kearney, 2002; Vitek, 2012). Appendix I contains the character/taxon matrix for all taxa considered in the analysis.

The matrix of 87 characters and 39 taxa was analyzed in a parsimony framework. Parsimony analyses were conducted in PAUP* 4.0b10 using TBR branch swapping and all characters run unweighted over 1,000 replicates and 100 random sequence additions. Each replicate was limited to saving only the 100,000 most parsimonious trees. Characters were ordered and a molecular scaffold was imposed following Joyce et al. (2016). Zero-length branches were set to collapse. Support for nodes was calculated using a bootstrap analysis with 100 replicates.

Measurements were taken of the interorbital width and prefrontal length of the Love specimen and extant *Apalone* to determine the potential usefulness of the interorbital width as a diagnostic character for the specimens from Love Bone Bed (*Apalone ferox*, n=14; *A. spinifera*, n=9; *A. mutica*, n=7; and *A. amorense*, n=1). Measurements were log-transformed and a Spearman's correlation was performed using R (R Core Team, 2014). Standard deviations of the residuals of extant skull measurements were used in a linear model to compare the proportions of the Love skull to those of extant *Apalone*.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, New York; **UF**, Division of Vertebrate Paleontology, Florida Museum of Natural History, Gainesville, Florida; **UF/H**, Division of Herpetology, Florida Museum of Natural History, Gainesville, Florida.

ANATOMICAL ABBREVIATIONS

C, costal; **N**, neural.

MATERIALS EXAMINED

Fossils: UF 19417, UF 43033, UF 43067–43074, UF 244956–244987, UF 246380–246384, UF 278205, UF 314932–314998. Modern specimens: *Apalone ferox*: UF/H 10963, UF/H 14114, UF/H 19104, UF/H 32999–32300, UF/H 33431, UF/H 54547, UF/H 150414, UF/H 150422, UF/H 150425, UF/H 150609, UF/H 178778–178780; *Apalone mutica*: UF/H 57724–57725, UF/H 59695–59696, UF/H 155062-10, UF/H 155062-70, UF/H 155062-71; *Apalone spinifera*: UF/H 45182, UF/H 45356, UF/H 48257, UF/H 51993, UF/H 102169, UF/H 150360, UF/H 150363–150364, UF/H 178777.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788
TRIONYCHIDAE Gray, 1825
TRIONYCHINAE Gray, 1825
APALONE Rafinesque, 1832
APALONE AMORENSE sp. nov.

Figures 2–7

Trionyx cf. *ferox* Webb et al., 1981:5, Table 1
Apalone cf. *ferox* Bourque, 2013:462 (updating generic designation of Webb et al. 1981)
Trionychidae Bourque, 2013:462 (stating 'does not appear to be *A. ferox*')
Trionychidae Bourque, 2016:823

Holotype.—UF 43069, nearly complete carapace. A right hyoplastron (UF 246380) may represent part of the same individual (see Remarks).

Zoobank Nomenclatural Act.—E859DDFA-0602-4176-8C6B-198918E60F50.

Remarks.—Two right hyoplastra of different sized individuals (UF 246380 and UF 246381), a right hypoplastron (UF 246382), and right xiphiplastron (UF 246383) were originally included in UF 43069 along with some trionychid cranial fragments, emydid turtle, and fish material (now included under the batch catalogue number UF 246384). No notes from the original recovery were made or found during this study, making it unclear which hyoplastron (UF 246380 or UF 246381) might belong to the carapace UF 43069. Ratios of carapace length and hyoplastral width were collected from specimens of *Apalone ferox* and plotted to determine which hyoplastron, if any, might belong with UF 43069. The smaller of the two, UF 246380, plotted along the regression line as expected for two elements from the same individual while the larger hyoplastron, UF 246381, plotted above the regression line. Furthermore, the deep dermal processes of the smaller hyoplastron are long and exposed to a similar degree as the rib ends of the carapace UF 43069, whereas the larger hyoplastron exhibits greater callosity growth, suggesting it likely belonged to a specimen of older age than UF 43069.

Etymology.—The species epithet refers to the Love Bone Bed where the type specimens of the new species were collected, and is derived from the Latin *amor* for 'love', and *-ense*, the suffix meaning 'of or from a place'. The Love Bone Bed was named in reference to the surname of Ron Love, the property owner (Webb et al., 1981).

Type Locality and Horizon.—Love Bone Bed, Clarendonian NALMA (~10–9 Ma), Alachua Formation, Alachua County, Florida, USA (Webb et al., 1981; Hulbert, 2001; Tedford et al., 2004).

Referred Material.—UF 19417, partial carapace; UF 43033, partial skull; UF 43066–UF 43070, partial carapaces; UF 43071, partial carapace and right hyo-hypoplastron; UF 43072, partial fused left hyo-hypoplastron; UF 43073, left hyo-hypoplastron and right hyoplastron; UF 43074, partial carapace; UF 244956–244987, nuchals; UF 246380–246381, right hyoplastra; UF 246382, right hypoplastron (possibly associated with UF 246381); UF 246383, right xiphiplastron; UF 278205, left xiphiplastron; UF 314932–314937, left xiphiplastra; UF 314938, right xiphiplastron; UF 314939–314951, left xiphiplastra; UF 314952, right xiphiplastron; UF 314953–314962, left xiphiplastra; UF 314963–314995, right xiphiplastra; UF 314996–314997, right epiplastra; UF 314998, left epiplastron; UF 410238–UF 410251, left humerus; UF 410252–UF 410258, right humerus; UF 410198–410201 left scapula; UF 410202–410203, right scapula; UF 410197, left ischium; UF 410196, right ischium; UF 410220–410237, left femur; UF 410204–410219, right femur. Additionally, numerous uncatalogued specimens from the Love Bone Bed housed in the UF collection likely represent *Apalone amorense*.

Diagnosis.—*Apalone amorense* is diagnosed as a member of Trionychini by the presence of eight or fewer neurals (N1–8) and strong emargination of the dorsal margin of the apertura narium aexterna. It is diagnosed as a member of Apalonina by the frequent absence of the eighth costal pair (C8). *Apalone amorense* shares with other species of *Apalone* high variability in the location of the posteriormost neural reversal and the location of the reversal, which often occurs at N5 *Apalone amorense* is distinguished from other *Apalone* by costal contact at the midline posterior to N6, permanent loss of C8, and potentially greater interorbital width. It can be distinguished from "*Trionyx*" *miocaenus* by the permanent loss of the C8.

DESCRIPTION

Skull

UF 43033 (Figs. 2–3) is the only known skull. It is crushed with the occipital portion missing. UF 43033 preserves portions of the prefrontal, frontal, parietal, postorbital, maxilla, jugal, palatine, pterygoid, prootic, and supraoccipital. The snout is short and blunt like *Apalone ferox* but unlike *A. spinifera* and *A. mutica*.

The prefrontals contribute minimally to the orbit margin compared to the maxillae and frontals. They contact the anterodorsal processes of the maxillae and the frontals along the interorbital bar. The profrontals are short and wide compared to the prefrontals of extant *Apalone* spp., particularly on the interorbital bar. The prefrontals are not as narrow between the orbit as those of *A. spinifera* and *A. mutica*. The dorsal edge of the apertura narium externa is strongly emarginated laterally but not medially (Meylan, 1987). Like the prefrontals, the frontals are short and wide. The frontals make contact with the parietals and postorbitals and contribute to the orbital margins.

The parietals do not contribute to the orbital margins or orbit walls. They contact the postorbitals and preserved prootic, but no other contacts can

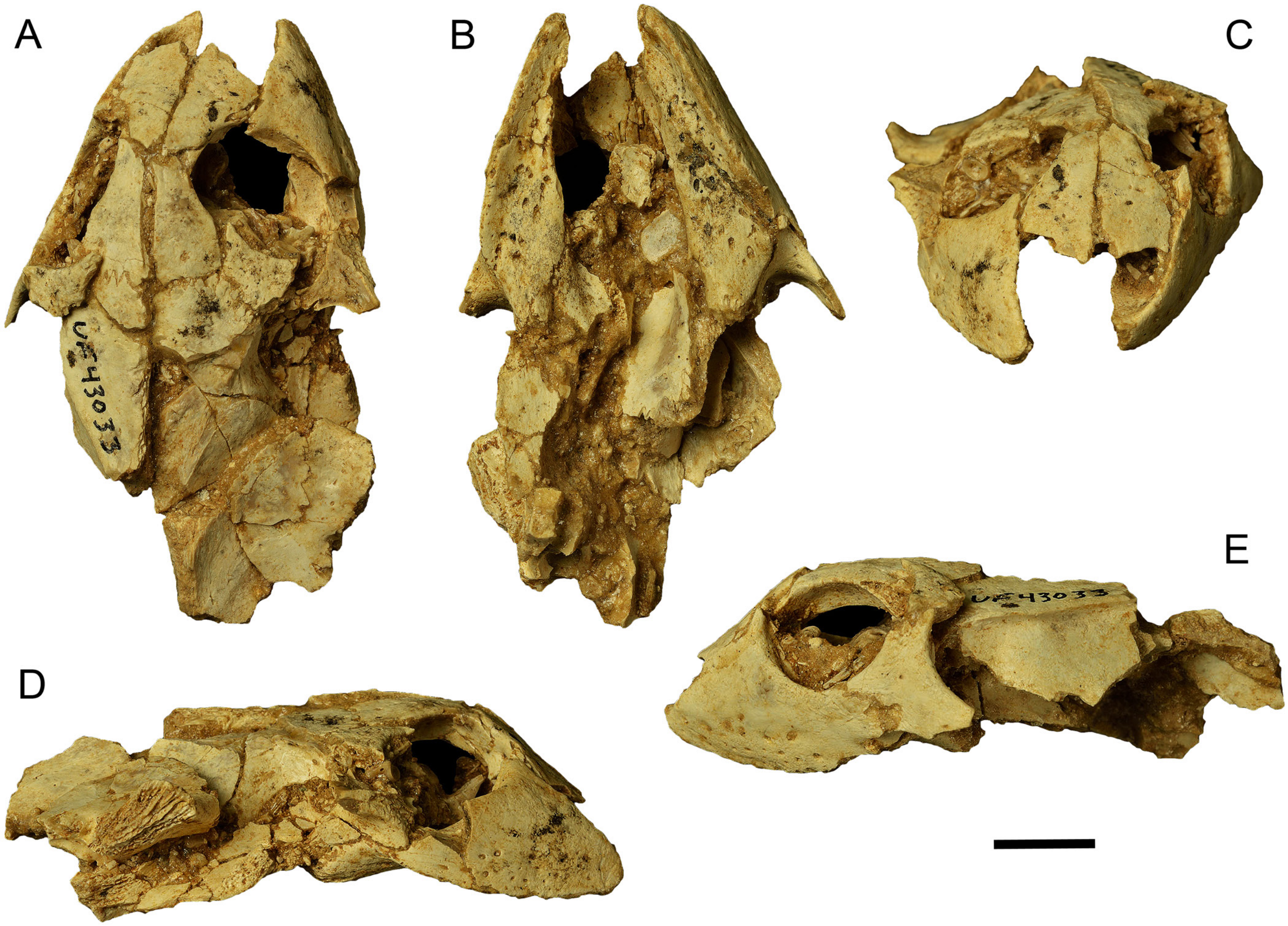

Figure 2. Skull of *Apalone amorense*, referred specimen UF 43033 from the Love Bone Bed, in **A**, dorsal; **B**, ventral; **C**, anterior; **D**, right lateral; and **E**, left lateral aspects. Scale bar equals 1 cm.

be determined. The length of the postorbital bar is approximately equal to the diameter of the orbit. The postorbitals contact the jugals, frontals, and parietals. We cannot determine if the postorbitals contributed to the upper temporal emargination, although it is likely that they did. Like other trionychids, the maxillae contacts the prefrontals anteromedially and the jugals posteriorly on the skull surface. They form approximately one quarter of each orbit margin. In palatal view, the triturating surface of the maxillae are not expanded. Midline contacts between the maxillae and vomer are unclear.

The jugals contact the postorbitals and do not appear to contact the parietals on the skull surface. They form a small component of the posterior of the orbital margin. The palatines are relatively large bones that contact the maxillae anterolaterally, each other along the midline, and the pterygoid posteriorly. A fragment of the right external pterygoid process and the pterygoid crest is preserved, contacting the maxilla and palatine anteriorly and the prootic dorsally. The right prootic is long and narrow dorsally. It contacts the parietal medially, the supraoccipital posteriorly, and forms part of the processus trochlearis oticum along its entire anterior margin. Ventrally, it contacts the pterygoid. Much of the supraoccipital is left exposed by taphonomic loss of the posterior part of the right

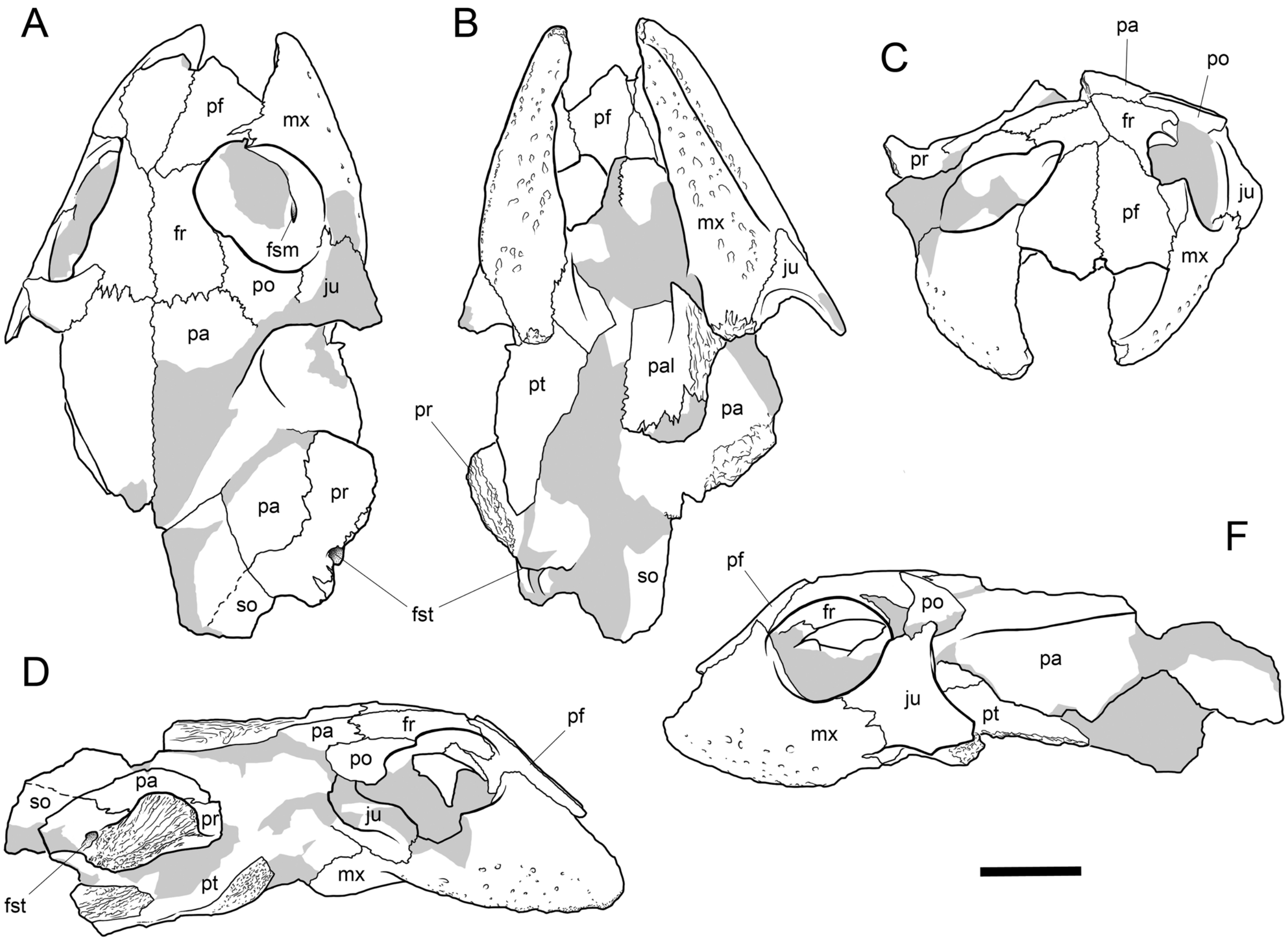

Figure 3. Skull reconstruction of *Apalone amorense*, referred specimen UF 43033, in **A**, dorsal; **B**, ventral; **C**, anterior; **D**, right lateral; and **E**, left lateral aspects. Abbreviations: fr, frontal; fsm, foramen supramaxiliare; fst, foramen stapedio–temporalis; ju, jugal; mx, maxilla; pa, parietal; pal, palatine; pf, prefrontal; po, postorbital; pr, prootic; pt, pterygoid ; so, supraoccipital. Scale bar equals 1 cm.

parietal. It contacts the prootic anterolaterally.

CARAPACE

UF 43069 (Fig. 4) is approximately 203 mm when measured at the midline with the nuchal and 175 mm without the nuchal. The other referred carapaces lack preserved nuchals but were measured at the midline (UF 43066 [Fig. 5] =188 mm, UF 43070 = 191 mm, UF 43071 = 177 mm; mean = 181 mm). Overall, carapacial shape varies from ovate to circular across specimens (sensu Gardner and Russell, 1994:fig. 2A). All specimens exhibit a sub-scalloped costal margin outline (sensu Gardner and Russell, 1994:fig. 2E). There is continuous pitted sculpturing over the neurals and costals with a narrow unsculptured outline of immature bone surrounding the costal callosities of the carapace. Specimens exhibit convex transverse distal costal margins (type "A" or "B" of Gardner and Russell 1994:fig. 2F). Bourque (2013) noted that specimens of *Apalone amorense* possess finer dermal pitting than *A. ferox*. *Apalone spinifera* and *A. amorense* exhibit a finely pitted shell, while *A. ferox* has a more broadly pitted shell. The nature of the sculpturing is consistent between all of Love Site shells.

Nuchal.—A survey of isolated nuchals (Fig. 6) from the site documents the range of variation of nuchal morphology. That variation is consistent with ontogenetic variation in extant trionychids. The nuchal of the holotype, UF 43069 (Figs. 2–3), is nearly complete, but damaged. It is approximately three times wider than long. The posterior and anterior costiform processes are united, forming a comb (Meylan, 1987). Indentations indicating contact with the first body vertebra are present in the middle of the visceral surface of the nuchal. The posterior margin of the nuchal is not preserved, but other isolated nuchals contain suprascapular fontanelles (Fig. 6A-C). The largest isolated nuchals lack suprascapular fontanelles as evidenced by the continuous posterior sutures (Fig. 6D-E).

Neurals.—Four of five carapaces have fully-preserved neural sets. None of these carapaces exhibit a preneural. One specimen contains five neurals (UF 43066). Its last neural does not exhibit a reduction in size like that of the other specimens. Two of the four carapaces with preserved neurals have six neurals (UF 43069 and UF 43071). UF 43070 has seven neurals, the last of which is highly reduced compared to the N6 observed in the other specimens. The N6 of all specimens with six neurals is reduced. The shape and costal contacts of N1–2 vary. The N1 of two specimens (UF 43071 and UF 43066) exhibit a similar left-right symmetrical shape anteriorly and contribute to the suprascapular fontanelles. UF 43071 exhibits a symmetrical contact between N1 and C2 (posterior neural symmetry), while UF 43066 and UF 43069 have asymmetrical contacts between N1 and C2 (posterior neural asymmetry). The N1 of the other two specimens (UF 43070 and UF 43069) is too damaged to determine their shape anteriorly, but UF 43070 has symmetrical contacts between N1 and C2. Posterior symmetrical contacts between N2 and C3 occur in all four specimens, similar to extant specimens of *Apalone*. There is additional variation with respect to where the degree of symmetry between contacts (whether anterior or posterior on a neural) throughout the rest of the neural set in all specimens. Reversal in neural orientation occurs at N5 in three of the four specimens in which the character can be observed. The fourth specimen, UF 43066, has only five neurals and no reversal in the column.

Costals.—The anterior margin of the holotype C1 are complete. They lack toothed sutures and exhibit slight concavities indicating the presence of suprascapular fontanelles. Four of the five carapaces have a complete margin of the C1, as well, and all four exhibit the presence of suprascapular fontanelles, including a pair of indentations at the anterior margin of the C1. All five carapaces have seven pairs of costals. There is contact at the midline at C6 in all carapaces except for the carapace with seven neurals (UF 43070).

PLASTRON

The sampled plastral elements contain at least four sculptured callosities: one on each hyo-hypoplastron and xiphiplastron. The epiplastra do not have callosities. The entoplastron of *Apalone amorense* is currently unknown.

Epiplastron.—The epiplastra are j-shaped (Meylan, 1987). The three available elements (UF

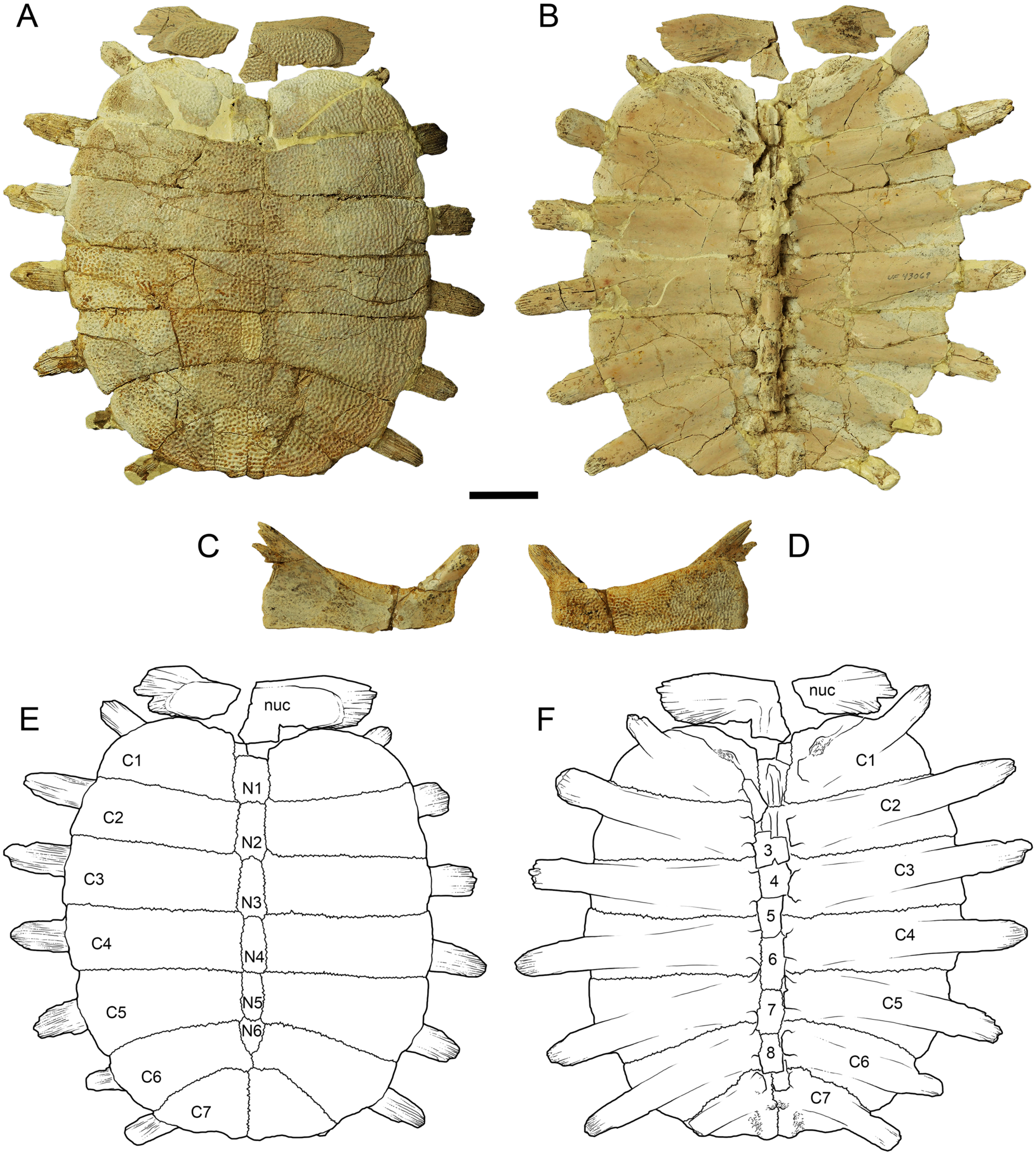

Figure 4. *Apalone amorense* holotype, UF 43069. **A**–**B**, Carapace in dorsal and ventral views respectively. **C**–**D**, UF 246380, right hyoplastron in dorsal and ventral views respectively. **E**–**F**, Reconstructions of carapace in dorsal and ventral views respectively. Abbreviations: C1–C7, costals 1–7; N1–N6, neurals 1–6; nuc, nuchal. Numbers 1–8 in F refer to vertebral centra. Scale bar equals 3 cm.

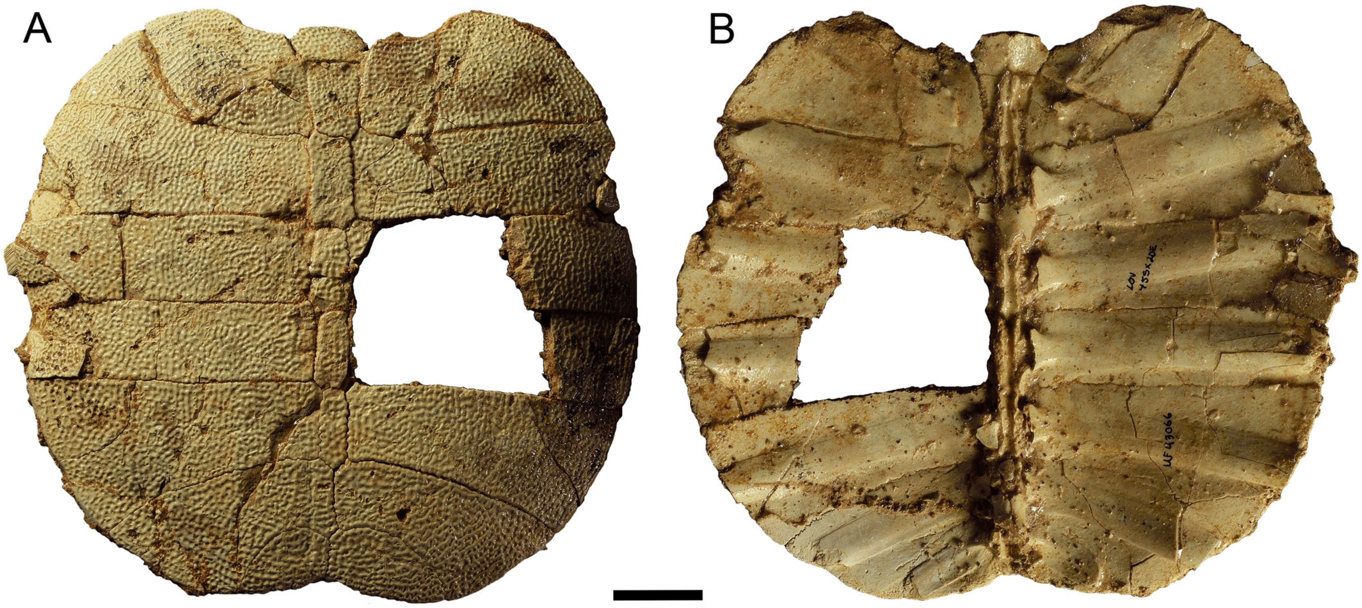

Figure 5. Referred carapace of *Apalone amorense*, UF 43066, in **A**, dorsal, and **B**, ventral aspects. Scale bar equals 3 cm.

314996–314998) lack callosities. Although they are unassociated with other material and cannot be measured relative to hypoplastron width, the anterior epiplastral extensions are relatively shorter but qualitatively similar to those in other species of *Apalone* (Fig. 7A–F).

Hyo-Hypoplastron.—(Figs. 4C–D and 7G–H) Midline contact between the hyo-hypoplastra is not observed in any of the referred specimens. There is one lateral process in the hyoplastron and at least three smaller ones anteromedially. There are two lateral processes in the hypoplastron as well as one medial process and two sets of "fanned" processes posteromedially that contact the xiphiplastron. Of the 31 specimens for which the condition can be assessed, only seven hyo-hypoplastra are fused. Those seven specimens are no larger or smaller than the unfused specimens. The callosity overlaps the medial processes completely in large, presumably adult, specimens but does not extend beyond them in the sampled hyo-hypoplastra. The medial processes in UF 43069 and UF 43073 remain partially exposed, suggesting these specimens are not fully grown adults. The callosities only partially overlap the lateral processes.

Xiphiplastron.—The xiphiplastron (Fig. 7I–O) is broad, similar to some *Apalone ferox* and *A. spinifera,* but unlike *A. mutica*. Two anterolateral process contact the posteromedial processes of the hypoplastron laterally. They form a deep indentations in the callosities where they articulate with the hypoplastral processes. Two medial processes of each xiphiplastron contact at the midline. The callosity on the xiphiplastron extends anteriorly and posteriorly beyond the deep tissue of the bone. In larger specimens (e.g., UF 314949), the callosity overlaps much of the medial and lateral processes but does not extend beyond them. Some xiphiplastra exhibit a subtle medial concavity in the callosity while others show a marked medial notch where the processes touch at the midline. In some specimens the callosities of opposing xiphiplastral contact at the midline posterior to the anteromedial process. The callosity on the largest xiphiplastra have a prominent, anteromedial bulge (e.g., UF 314946, UF 314947, and UF 314949; Fig. 7M–O).

Postcrania

Scapula.—Partial scapulae are preserved, though no coracoids were identified. In one complete scapula, the length of the acromion process is shorter than the length of the body of the scapula (Fig. 8A). The angle between these two features

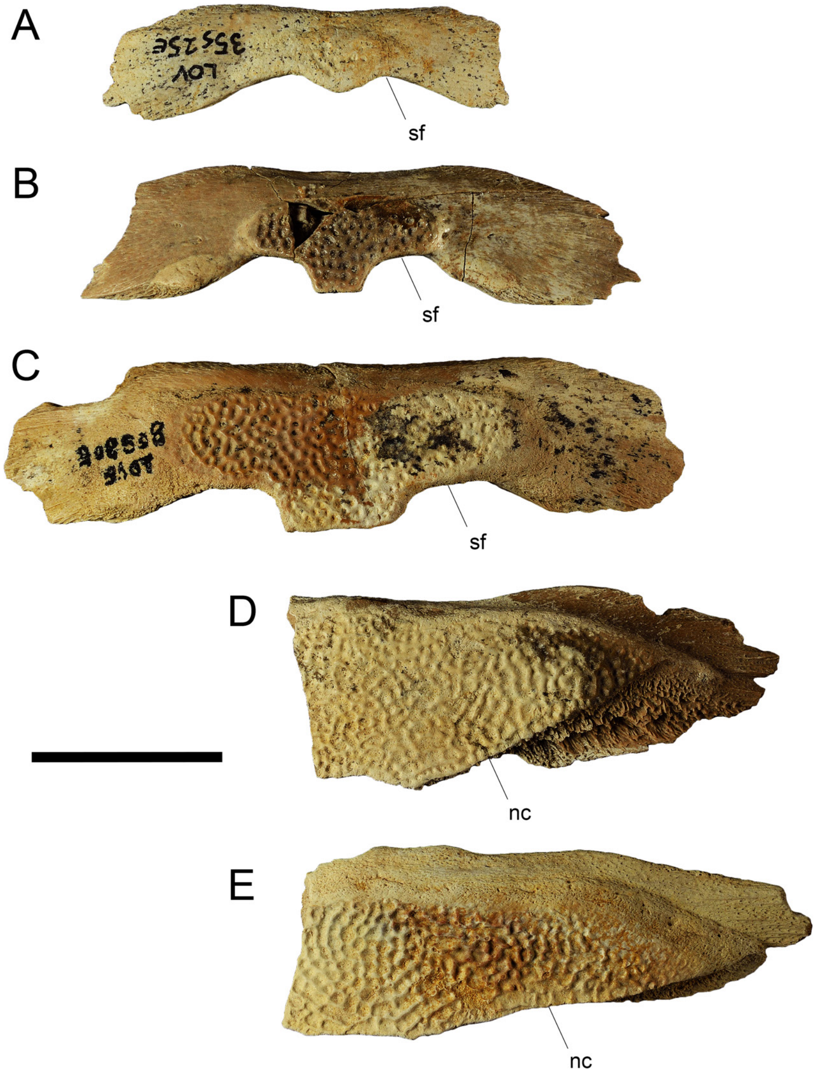

Figure 6. Ontogenetic series of nuchals of *Apalone amorense* in dorsal view, illustrating closure of the suprascapular fontanelles in larger individuals. **A**, UF 244958; **B**, UF 244957; **C**, UF 244956; **D**, UF 244960; **E**, UF 244962. Abbreviations: nc, nuchal–costal 1 suture; sf, suprascapular fontanelle. Scale bar equals 3 cm.

among the four specimens that could be measured is 67–77° (Meylan, 1987).

Humerus.—Humeri of *A. amorense* are recognized by an open entepicondylar foramen and a lesser trochanter on the same plane as the s-shaped main axis of the bone (Meylan, 1987). Extant *Apalone* spp. vary in the degree of separation between the humeral head and the greater trochanter and the development of a ridge in the intertubercular fossa (Fig. 8B–C). That range of variation is encompassed within the sample from Love Bone Bed (Fig. 8D–F).

Ischium.—One ischium has a complete medial margin (Fig. 8G). A small, metischial process is present, and is less than half the length of the medial margin of the ischium (5.1 mm and 13.8 mm, respectively). The point of the process is directed medially. That process is absent in *A. ferox* (Fig. 8H) but present in *A. spinifera* (Fig. 8I; Meylan, 1987).

Femur.—Femora can be differentiated from humeri by the lack of an open entepicondylar foramen, a less strongly curved shaft, and a narrower greater trochanter (Fig. 8J–N). Based on their size, degree of curvature, and angle of both trochanters relative to the primary axis of the bone, we identify them as trionychid femora (Meylan, 1987). A majority of femora have a narrow greater trochanter separated from the femoral head by a deep notch (Fig. 8J, K, N), more similar to *A. ferox* (Fig. 8L) than *A. spinifera* or *A. mutica* (Fig. 8M).

RESULTS

PHYLOGENETIC ANALYSIS

A parsimony analysis produced 294 most parsimonious trees. The strict consensus (Fig. 9)

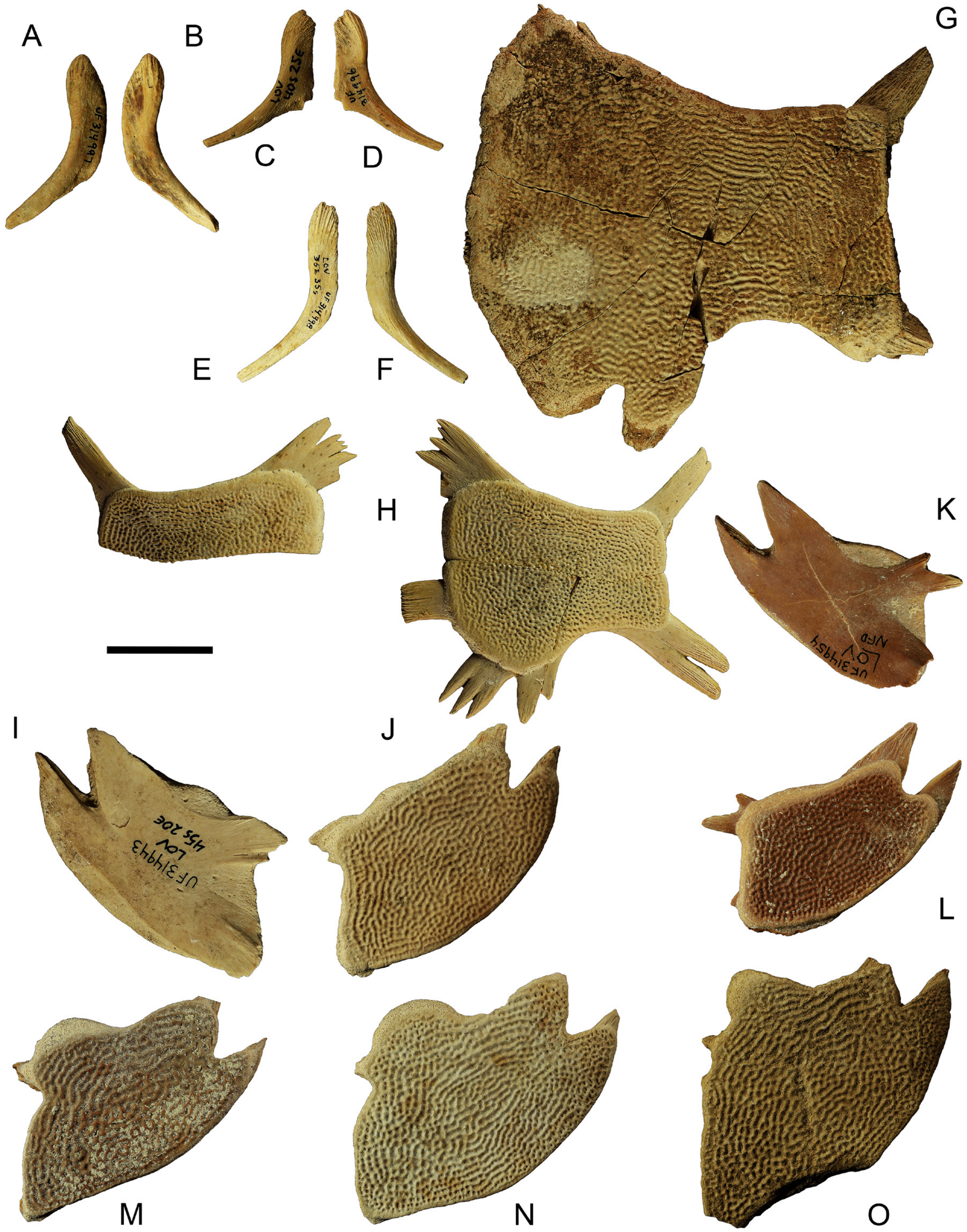

Figure 7. Plastral bones of *Apalone amorense*. **A–B**, right epiplastron, UF 314997, in **A**, ventral and **B**, dorsal aspects. **C–D**, right epiplastron, UF 314996, in **C**, ventral and **D**, dorsal aspects. **E–F**, left epiplastron, UF 314998, in **E**, dorsal and **F**, ventral aspects. **G**, Fused left hyo-hypoplastron of an adult, UF 43027, in ventral aspect. **H**, Right hyoplastron and associated left unfused hyoplastron and hypoplastron of a subadult, UF 43073, in ventral aspect. **I–J**, Left xiphiplastron of an adult, UF 314943, in **I**, dorsal and **J**, ventral aspects. **K–L**, Left xiphiplastron, UF 314954, in **K**, dorsal and **L**, ventral aspects. **M–O**, Left xiphiplastra of adults in ventral aspect. **M**, UF 314946; **N**, UF 314949; **O**, UF 314947. Scale bar equals 3 cm.

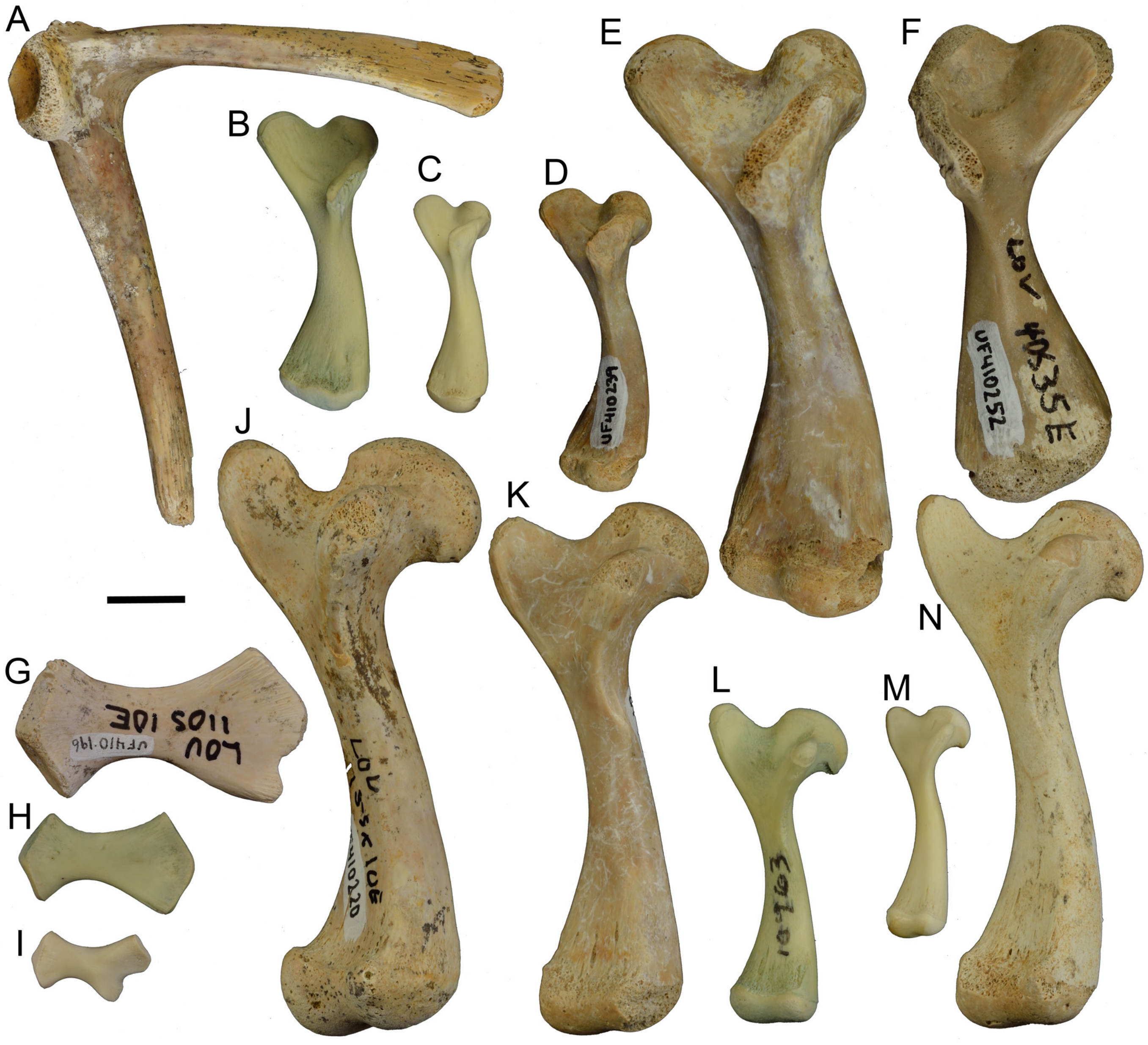

Figure 8. Postcrania of *Apalone amorense* and Recent comparative material. **A,** UF 410200, left scapula. **B,** UF/H 10963, left humerus of *Apalone ferox.* **C,** UF/H 51093, left humerus of *Apalone spinifera.* **D,** UF 410238, **E,** UF 410239, left humeri. **F,** UF 410252, right humerus. **G,** UF 410196, right ischium. **H,** UF/H 10963, right ischium of *Apalone ferox.* **I,** UF/H 51093, right ischium of *Apalone spinifera.* **J,** UF 410220, **K,** UF 410204, left femora. **L,** UF/H 10963, left femur of *Apalone ferox.* **M,** UF/H 51093, left femur of *Apalone spinifera.* **N,** UF 410221, left femur. Scale bar equals 1 cm.

recovered Plastomenidae as fully resolved. A clade containing *Apalone*, including *Apalone amorense* and '*Trionyx*' *leucopotamicus*, was also recovered in the strict consensus tree. Pelodiscini, *Nilssonia* + *Amyda*, and a derived subset of *Axestemys* were also each recovered as monophyetic groups. Outside of the relationships described above, the tree was generally poorly resolved beyond the relationships constrained by the molecular scaffold. Bootstrap values were generally low across the tree.

Interorbital Width

Interorbital width and prefrontal length are correlated across species ($r = 0.843$, $p = 1.34 \times 10^{-6}$). The skull of *Apalone amorense* (UF 43033) was outside of the expected range of variation when plotted on a linear model (Fig. 10). All specimens of the three species of extant *Apalone* plotted within two standard deviations of the model.

DISCUSSION

Because skull and shell material from the Love Site was found dissociated, we considered whether multiple trionychid species could be represented in the Love Bone Bed collection. Closely related spe-

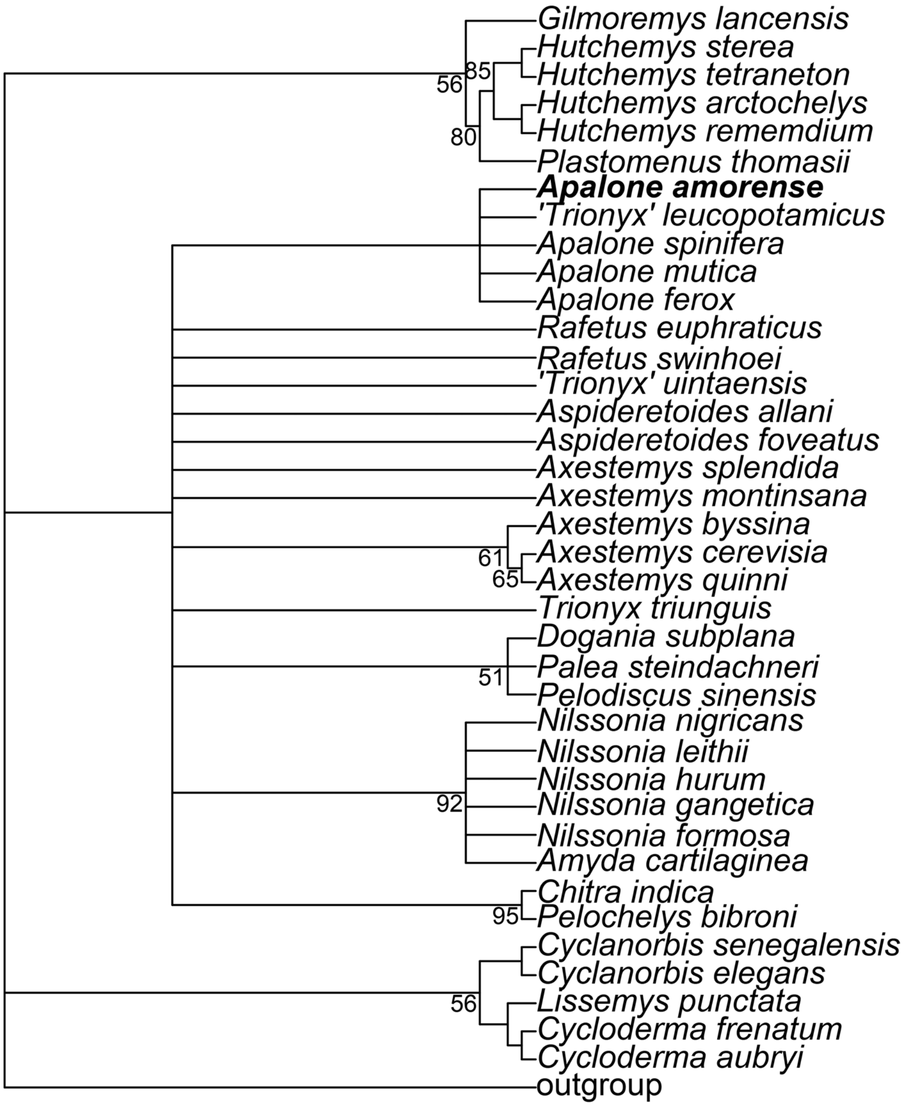

Figure 9. Strict consenus tree resulting from a parsimony analysis of morphological characters of extinct and extant Trionychidae. Consensus trees derived from 294 most parsimonious trees of 305 steps, CI = 0.386, RI = 0.6131. Numbers at nodes indicate bootstrap values.

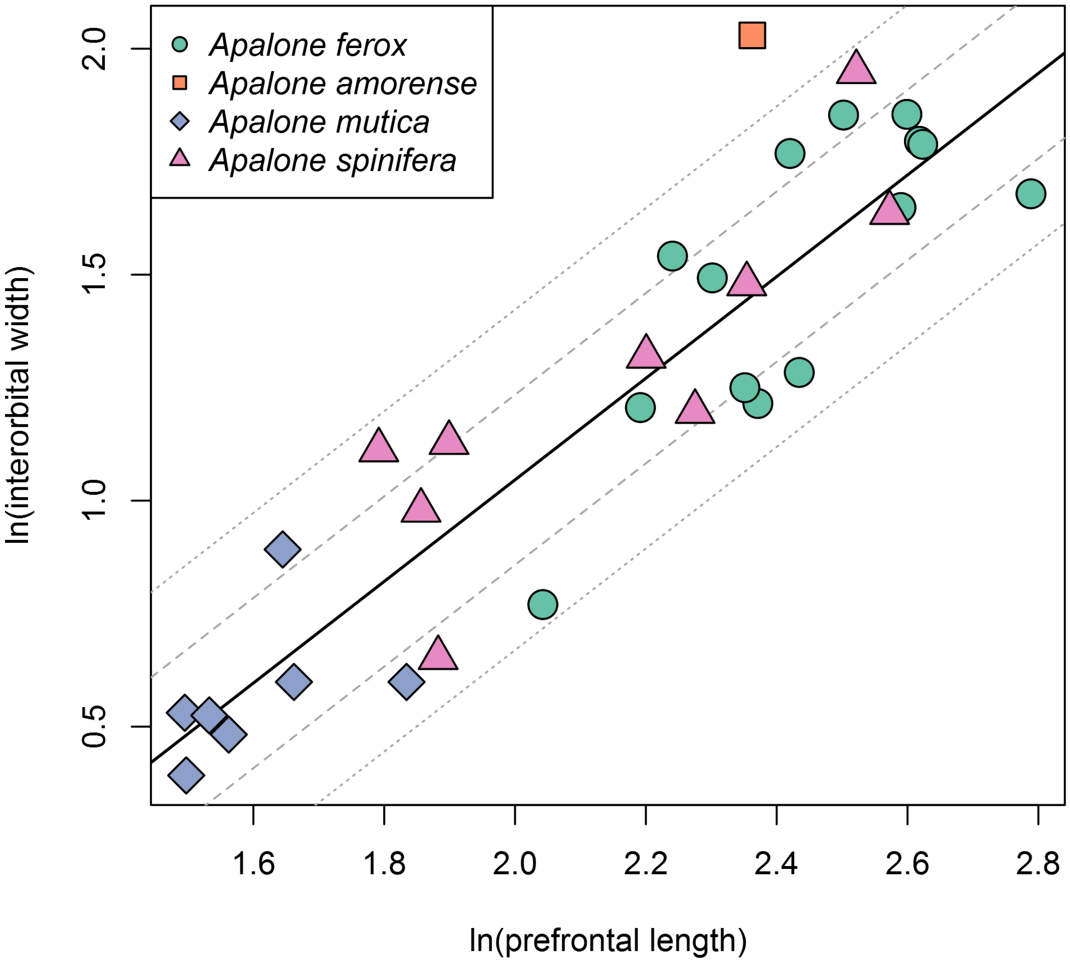

Figure 10. Log-transformed measurements for interorbital width and prefrontal length for species of extant *Apalone* and *A. amorense* (*Apalone ferox*, n=11; *A. spinifera*, n=5; *A. mutica*, n=6; and *A. amorense*, n=1). Dotted and dashed lines are ±1 and ±2 standard deviations, respectively. Results are considered preliminary.

cies often have overlapping ranges, as seen with *Apalone spinifera, A. mutica,* and *A. ferox* (Weisrock and Janzen, 2000; Turtle Taxonomy Working Group, 2014). However, the carapaces scored in this study (Appendix 1) fell within the expected range of intraspecific variation characteristic of any given species of Trionychidae (Meylan, 1987).

Costal contact at the midline posterior to N6 (Character 14; Table 1) represents the only autapomorphy identified using the character-taxon matrix in this study, but we identified other autapomorphic features of the material from the Love Site whose broader character state distribution across Trionychidae is unknown. C8 is absent in all examined carapaces, which is considered a derived feature within the Trionychidae (Meylan, 1985, 1987). Gardner and Russell (1994) noted intraspecific variation in the presence and absence of C8, suggesting it may not be a useful character to diagnose trionychids. Variation in costal pair count in *Apalone ferox* and *A. spinifera* (range: 7–8 pairs) was noted by Gardner and Russell (1994), while all *A. mutica* sampled in their study invariantly lacked C8. Four of the 34 *A. mutica* sampled in Webb (1962, table 5) exhibited C8. Variability in costal pair count was also observed in *Trionyx triunguis* and *Rafetus* spp. (Webb, 1962; Gardner and Russell, 1994). In contrast, *A. amorense* does

Table 1. Comparison of *Apalone amorense* to congeners.

Character	*A. spinifera*	*A. mutica*	*A. ferox*	*A. amorense*
costal contact at the midline	C7 and C8	C7 and C8	C7 and C8	C6 and C7
complete loss of the eighth costal pair	no	no	no	yes
six neurals or less	no	no	no	yes

not exhibit intraspecific variation in this feature. *Apalone amorense* is the only species of *Apalone* observed thus far that lacks the C8 in all known specimens. Therefore, we suggest that the loss of C8 is a potentially invariant and diagnostic feature of this taxon. However, further analysis with larger samples is necessary to confirm this hypothesis.

A majority of the carapaces of *Apalone amorense* have a reduced neural count beyond the reduction reported in other species of the genus. Extant species of *Apalone* and "*Trionyx*" *leucopotamicus* generally have seven neurals. Three of the four carapaces with preserved neural columns from Love Bone Bed have six or fewer neurals, while one carapace has an anomalous, highly reduced N7.

The ratio of interorbital width to prefrontal length in *Apalone amorense* may be a diagnostic character within *Apalone*. When compared to the sampled Recent specimens, the single skull of *A. amorense* (UF 43033) shows a relatively larger interorbital width, suggesting this feature may be diagnostic (Fig. 10). However, our sample size of Recent material is small and therefore our conclusion is preliminary. More specimens should be sampled to see if the range of ratios in extant species encompasses that seen in *A. amorense*.

The results of our phylogenetic analyses support our placement of this new species as a member of a monophyletic group including extant *Apalone*. *Apalone amorense* has strongly dorsally emarginated apertura naria externa, a highly variable neural reversal position, average position of neural reversal at the posterior margin of N5, and the presence of one lateral hyoplastral process, which are synapomorphies of *Apalone*. *A. amorense* also exhibits the presence of four plastral callosities, lack of surface contact between the jugal and parietal, and a mid-sized postorbital bar, similar to *A. ferox*. Open suprascapular fontanelles are found in *A. amorense*, *A. spinifera*, and *A. mutica*. *A. amorense* and *A. spinifera* also have a nuchal width:length ratio of at least 3. In short, it possesses a mosaic of features shared with the three extant species of *Apalone* as well as carapacial and plastral autapomorphies.

An additional hypothesis resulting from phylogenetic analysis is that "*Trionyx*" *leucopotamicus*, and by taxonomic equivalence "*T.*" *miocaenus*, and "*T.*" *latus* are all sister species or conspecific with the extant *A. spinifera* and *A. mutica* (Figure 8B). In contrast to *Apalone amorense*, "*Trionyx*" *leucopotamicus,* "*T.*" *miocaenus*, and "*T.*" *latus* are all carapace-only specimens that are 78–89% incomplete in the character–taxon matrix. The only derived character shared between *A. spinifera* and *A. mutica* and those three carapace-only species is the presence of open suprascapular fontanelles. The local synapomorphy uniting those three species to *Apalone* is neural reversal at the posterior edge of N5. Neither of these characters are global synapomorphies of *Apalone*, even among only North American taxa. Other character states that were proposed to identify *Apalone* or certain species therein, such as reduced C8, are more common features among Cretaceous species of trionychids in both Asia and North America (Gardner et al., 1995; Hutchison, 1996; Vitek and Danilov, 2014). The polarity of those features is likely to shift depending on which extinct taxa are included in the character-taxon matrix. The two synapomorphies for *Apalone* for which the three carapace-only taxa can be scored, the presence of suprascapular fontanelles and neural reversal at or before N5, appear multiple times as both intraspecifically and interspecifically variable characters within Trionychinae. Sparse temporal sampling of taxa with those characters in addition to the incompleteness of the carapace-only taxa may be supporting the relationship between "*T.*" *leucopotamicus*, "*T.*" *latus*, and "*T.*" *miocaenus* and *A. mutica* (Gardner et al., 1995).

Given the incompleteness of the carapace-only taxa and the high levels of homoplasy in their scoreable characters, we prefer to consider *Apalone amorense* the oldest described representative of *Apalone*. This is strongly supported by a wider suite of skull and plastral characters. Additionally, this hypothesis is more congruent with previously published diversification time estimates (Le et al., 2014) and with a widespread pattern of first appearances of extant genera of plants and birds by the Miocene (Behrensmeyer et al., 1992).

ACKNOWLEDGMENTS

We greatly thank R. Hulbert for curatorial and loan assistance, pertinent literature, and for providing photos of the Love Bone Bed used in this article. N. Valdes would like to thank her undergraduate honors thesis advisors, J.I. Bloch and J. Krigbaum, for making the initial research project possible. Thanks to W.J. Joyce and P.M. Meylan for comments and insight that greatly improved the manuscript. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1315138 to N. Vitek. This is University of Florida Contribution to Paleobiology 830.

LITERATURE CITED

Batsch, A. J. G. C. 1788. Versuch einer Anleitung, zur Kenntniss und Geschichte der Thiere und Mineralien. Akademische Buchhandlung, Jena, 528 p.

Behrensmeyer, A. K., J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing. 1992. Terrestrial Ecosystems Through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals. The University of Chicago Press, Chicago, 568 p.

Bell, C. J., J. A. Gauthier, and G. S. Bever. 2010. Covert biases, circularity, and apomorphies: A critical look at the North American Quaternary Herpetofaunal Stability Hypothesis. Quaternary International 217:30–36.

Bourque, J. R. 2013. Fossil Kinosternidae from the Oligocene and Miocene of Florida, USA. Pp. 459–475 *in* D. B. Brinkman, P. A. Holroyd, and J. D. Gardner, eds. Morphology and Evolution of Turtles. Springer, Dordrecht, Netherlands.

Bourque, J. R. 2016. New mud turtles (Kinosternidae, *Kinosternon*) from the middle–late Miocene of the United States. Journal of Paleontology DOI: 10.1017/jpa.2015.63.

Brinkman, D. B. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. Canadian Journal of Earth Science 40:557–572.

Cope, E. D. 1868. On the origin of genera. Proceedings of the Academy of Natural Sciences of Philadelphia 20:242–300.

Delfino, M., T. M. Scheyer, U. Fritz, and M. R. Sánchez-Villagra. 2010. An integrative approach to examining a homology question: shell structure in soft-shelled turtles. Biological Journal of the Linnean Society 99:462-476.

Engstrom, T. N., H. B. Shaffer, and W. P. McCord. 2004. Multiple data sets, high homoplasy, and the phylogeny of softshell turtles (Testudines: Trionychidae). Systematic Biology 53(5):693–710.

Ernst, C. H., and R. W. Barbour. 1989. Turtles of the World. Washington: Smithsonian Institution Press, 313 p.

Gaffney, E. S. 1979. Description of a large trionychid turtle shell from the Eocene Bridger Formation of Wyoming. Rocky Mountain Geology 17(1):53–57.

Gardner, J. D., and A. P. Russell. 1994. Carapacial variation among soft-shelled turtles (Testudines: Trionychidae), and its relevance to taxonomic and systematic studies of fossil taxa. Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen 193(2):209–244.

Gardner, J. D., A. P. Russell, and D. B. Brinkman. 1995. Systematics and taxonomy of soft-shelled turtles (Family Trionychidae) from the Judith River Group (mid-Campanian) of North America. Canadian Journal of Earth Sciences 32(5):631–643.

Gray, J. E. 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. Annals of Philosophy 10:193–217.

Hay, O. P. 1908. The fossil turtles of North America. Carnegie Institute of Washington Publications 75:1–568.

Hulbert Jr., R. C. 2001. The Fossil Vertebrates of Florida. University Press of Florida, Gainesville, Florida, 384 p.

Hutchison, J. H. 1996. Testudines; pp. 337–353 in D. R. Prothero and R. J. Emry (eds.), The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, New York, NY.

Joyce, W. G., and T. R. Lyson. 2011. New material of *Gilmoremys lancensis* nov. comb. (Testudines: Trionychidae) from the Hell Creek Formation and the diagnosis of plastomenid turtles. Journal of Palaeontology 85(3):442–459.

Joyce, W. G., A. Revan, T. R. Lyson, and I. G. Danilov. 2009. Two new plastomenine softshell turtles from the Paleocene of Montana and Wyoming. Bulletin of the Peabody Museum of Natural History 50(2):307–325.

Joyce, W. G., T. R. Lyson, and S. Williams. 2016. New cranial material of *Gilmoremys lancensis* (Testudines, Trionychidae) from the Hell Creek Formation of southeastern Montana, U.S.A. Journal of Vertebrate Paleontology e1225748.

Kearney, M. 2002. Fragmentary taxa, missing data, and ambiguity: mistaken assumptions and conclusions. Systematic Biology 51:369–381.

Kearney, M., and J. M. Clark. 2003. Problems due to missing data in phylogenetic analyses including fossils: a critical review. Journal of Vertebrate Paleontology 23:263–274.

Le, M., H. T. Duong, L. D. Dinh, T. Q. Nguyen, P. C. H. Pritchard, and T. McCormack. 2014. A phylogeny of softshell turtles (Testudines: Trionychidae) with reference to the taxonomic status of the critically endangered, giant softshell turtle, *Rafetus swinhoei.* Organisms Diversity & Evolution 14:279–293.

Li, L., W. G. Joyce, and J. Liu. 2015. The first soft-shelled turtle from the Jehol Biota of China. Journal of Vertebrate Paleontology 35:e909450: DOI:10.1080/02724634.2014.909450.

Matthew, W. D. 1924. Third contribution to the Snake Creek fauna. Bulletin of the American Museum of Natural History 50:59–210.

Meylan, P. A. 1985. Evolutionary relationships of recent trionychid turtles: evidence from shell morphology. Studia Geologica Salmanticensia 22(3–4):236–243.

Meylan, P. A. 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). Bulletin of the American Museum of Natural History 186:1–101.

R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rafinesque, C. S. 1832. Description of two new genera of soft shell turtles of North America. Atlantic Journal and Friend of Knowledge 1(2): 64–65.

Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Hohna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huelsenbeck. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61:539–542.

Tedford, R. H., L. B. Albright III, A. D. Barnosky, I. Ferrusquia-Villafranca, R. M. Hunt Jr, J. E. Storer, C. C. Swisher III, M. R. Voorhies, S. D. Webb, and D. P. Whistler. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs). P.p. 169–231. *in* Woodburne, M.O. ed. Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York.

Turtle Taxonomy Working Group. 2014. Turtles of the World, 7th Edition: Annotated Checklist of Taxonomy, Synonymy, Distribution with Maps, and Conservation Status. Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs *5*(7):1–329.

Vitek, N. S. 2011. Insights into the taxonomy and systematics of North American Eocene soft-shelled turtles from a well-preserved specimen. Bulletin of the Peabody Museum of Natural History 52(2): 189–208.

Vitek, N. S. 2012. Giant fossil soft-shelled turtles of North America. Palaeontologia Electronica 15(1):1–43.

Vitek, N. S., and I. G. Danilov. 2014. Soft-shelled turtles (Trionychidae) from the Cenomanian of Uzbekistan. Cretaceous Research 49:1–12.

Vitek, N., and W. G. Joyce. 2015. A review of the fossil record of New World turtles of the clade Pan-Trionychidae. Bulletin of the Peabody Museum of Natural History 56(2): 185-244.

Vitek, N. S., I. G. Danilov, Y. Nakajima, and R. Hirayama. 2017. Redescription of the skull of '*Trionyx' kyrgyzensis* and improved phylogenetic taxon sampling of Cretaceous and Palaeogene soft-shelled turtles (Trionychidae) of Asia, including the oldest crown trionychids. Journal of Systematic Palaeontology 1–13. DOI:10.1080/14772019.2017.1283365.

Webb, R. G. 1962. North American recent soft-shelled turtles (Family Trionychidae). University of Kansas Publications Museum of Natural History 13(10):429–611.

Webb, S. D., B. J. MacFadden, and J. A. Baskin. 1981.Geology and paleontology of the Love Bone Bed from the Late Miocene of Florida. American Journal of Science 281(5):513–544.

Weisrock, D. W., and F. J. Janzen. 2000. Comparative molecular phylogeography of North American softshell turtles (*Apalone*): implications for regional and wide-scale historical evolutionary forces. Molecular Phylogenetics and Evolution 14(1):152–164.

Wiens, J. J. 2005. Can incomplete taxa rescue phylogenetic analyses from long–branch attraction? Systematic Biology 54:731–742.

Wright, A. M., and D. M. Hillis. 2014. Bayesian analysis using a simple likelihood model outperforms parsimony for estimation of phylogeny from discrete morphological data. PLoS One 9(10):e109210.

APPENDIX 1

Symbols: {} = polymorphism; ? = unknown; - = not applicable.

Character/Taxon Matrix

outgroup 00000 00100 00010 00001 00000 00000 00000 00000 00001 00011 00000 00000 00000 00000 00010 ?0000 00000 00

aubryi 10103 00111 1{0 1}0{1 2}0 10001 10021 10111 03110 20000 0111- 01011 00010 00101 10100 00000 00010 00000 00000 00

bibroni 21113 00300 0{0 1}011 00111 00020 00100 11000 10002 00200 10111 00111 11000 01011 00000 00000 10000 000{0 1}0 00

cartilaginea 21113 00200 00011 02111 00000 10111 01000 10010 00100 10211 10101 00010 01001 00000 00000 10000 00010 00

elegans 11103 00410 1{0 1}0{1 2}0 00111 00020 01111 02110 20000 0001- 01111 11000 00101 01110 00000 00010 00000 00000 00

formosa 11113 00300 00010 00111 00120 10111 01000 20020 00001 00211 00--1 00011 01--- 00000 000?? ?0000 00010 00

frenatum 10003 00110 1{0 1}0{1 2}0 10001 10021 00111 03110 20001 1021- 01111 10010 00101 10100 00000 00010 00000 00010 00

gangeticus 21103 00200 0{0 1}1{1 2}0 01111 00000 10111 01000 20020 00001 00111 10002 00010 01010 00000 00000 10000 00{0 1}10 00

hurum 21103 00200 0{0 1}1{1 2}0 01111 00010 20111 01000 20020 00001 10211 00000 00010 01011 00000 00000 10000 00{0 1}10 00

indica 21213 00300 00010 00112 01021 00100 01000 10001 00200 20200 00111 11001 01011 00000 00000 10000 00{0 1}10 00

leithii 21103 00200 0{0 1}010 01111 00110 10111 01000 20020 00000 00211 00001 00010 01010 ????? ????? ????? ??{0 1}10 00

nigricans 21103 00200 000{1 2}- 01111 00100 10111 01000 10020 00201 00211 01001 00010 01010 ????? ????? ????? ??{0 1}10 00

punctata 10002 10111 1{1 2}0{1 2}0 10001 10010 00110 01110 20000 00101 00011 00000 00101 00110 00000 00011 00000 00010 00

senegalensis 21103 10010 12-40 00001 00021 10100 02110 20000 0021- 01011 00000 00101 11100 00000 00010 10000 00--0 00

sinensis 31113 00100 0{1 2}2{1 2}1 02110 00110 20111 01101 20020 00002 00211 10001 00000 01010 00000 00000 10000 00110 00

steindachneri 11113 00300 0{0 1}0{1 2}0 02110 00020 20111 01001 20020 0001- 20212 00--1 00000 -1--0 00000 000?? ?0000 00010 00

subplana 31113 00300 00102 02110 00010 20111 01001 21010 0000- 00112 10001 00010 01011 00000 00000 10000 00010 00

triunguis 21113 00300 010{1 2}1 00111 00000 20011 01000 20100 00000 0011? 11001 00000 01010 00000 00000 10000 10{0 1}10 00

thomasii 31?03 00101 1{1 2}-{2 3}0 ??001 0?00? ??01- 01111 21000 00??? ???-2 00??? ???0? ????? 00000 01110 11001 ?1--0 00 *rememdium* 31?03 00101 110{1 2}0 1?101 0???? ????? ????? ????? ????? ????? ????? ????? ?10?? 11110 01120 0???? ?{0 1}010 00

Arctochelys 31?03 00101 110{1 2}0 1?001 0???? ????? ????? ????? ????? ????? ????? ????? ????? 10111 11121 0???? ?1010 00

tetraneton 31?03 00?00 11010 ???00 0???? ????? ????? ????? ????? ????? ????? ????? ????? 11010 01?20 ????? ??010 00

sterea 21?03 00101 11020 10000 0???? ????? ????? ????? ????? ????? ????? ????? ????? 10010 01120 ????? ?1110 00

lancensis 31?03 00?02 01020 ??111 0?121 20{0 1}11 02111 2000? 0001- 20211 00??? ????? ????? 00000 00?10 111?1 100{0 1}0 00

quinni 2??03 01??? ?1?22 ????2 0???? ????? ????? ????? ????? ????? ????? ????? ????? 00000 0???? ????? ?000? ?1

cerevisia 31?03 01300 00?12 00?12 0???? ????? ????? ????? ????? ????? ???0? ????? ???0? -0000 00000 0???? ?0001 -1

byssina 311?3 01{2 3}00 0??22 0?112 0???? ????? ????? ????? ????? ????? ???0? ????? 0???? -0?00 00000 0???? ?0??1 10

montinsana 31113 0?300 0???{0 1} 00?12 ???0? 101?? 0??00 ?0?0? 00??? ????1 ?1?1? ???0? 01001 -000? ?0000 000?0 0???1 00

splendida 31103 00300 011{1 2}1 00112 0?000 10110 00000 {1 2}0000 00??? ??211 11??? ????? ????? 000?0 00000 {0 1}00?0 ?0{0 1}{0 1}0 00

foveatus 31103 00300 011{1 2}1 00111 0?000 21110 ?1??0 10?00 00??1 ?2?12 1???? ????? ????? 000?0 00000 00??0 ?0{0 1}10 00

allani 31103 00{1 2 3}10 0{0 1}0{1 2}1 00111 0???? ????? ????? ????? ????? ????? ????? ????? ????? -00?0 ?0000 1???? ?0011 10

uintaensis 31113 01300 01?{2 3}{0 1} 00111 0?010 10100 00000 000?0 00{0 1}00 {0 1}0211 0110? ???0? 01000 -0000 00000 100?0 00{0 1}10 10

ferox 31113 01300 012{1 2}1 00111 01000 20100 01000 20000 00000 00221 11002 00000 01101 00000 0{0 1}0{0 1}0 00000 00110 00

mutica 31113 01100 0{0 1}2{1 2}2 00111 01110 20101 01000 20000 0001- 00122 11001 00000 01010 00000 000{0 1}0 00000 00110 00

spinifera 21113 01100 012{1 2}2 00111 01000 20100 01000 20010 0001- 00222 11002 00000 01010 00000 000{0 1}0 00000 00110 00

swinhoei ---13 01400 0---- 00112 00100 10100 01100 20000 00000 00221 11--- 00001 -1--1 ????? ????? ????? ??--0 00

euphraticus 21113 01400 010{1 2}1 00111 00000 10100 01000 20010 00000 00221 11102 00001 01101 00000 00000 10000 00{0 1}10 00

leucopotamicus 31113 01??? ?1?22 ??1?1 0???? ????? ????? ????? ????? ????? ????? ????? ????? ??000 0???? ????? ??11? ??

miocaenus ??13 01??? ?1?2{1 2} ??1?1 0???? ????? ????? ????? ????? ????? ????? ????? ????? ??000 0???? ????? ??11? ??

latus ??11? ?1??? ?{0 1}0{1 2}2 ????1 ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ??11? ??

UF 43069 21113 01{0 1 2 3}0? 02?3{1 2} ??1?{0 1} 0???? ????? ????? ????? ????? ????? ????? ????? ????? 00000 00?00 0???? ?-110 0?

UF 43066 ???13 ?1??? ?3?3{1 2} ??1?1 0???? ????? ????? ????? ????? ????? ????? ????? ????? 0?000 0???? ????? ?-0-? ??

UF 43071 ???13 ?1{1 2 3 4}0? 02?3{1 2} ??11{0 1} 0???? ????? ????? ????? ????? ????? ????? ????? ????? 0?000 00?00 0???? ?-110 ??

UF 43070 ???13 ?1??? ?1?2? ??1?1 0???? ????? ????? ????? ????? ????? ????? ????? ????? ??000 0???? ????? ?-11? ??

UF 43074 ????3 ????? ????? ????{0 1} 0???? ????? ????? ????? ????? ????? ????? ????? ????? ??000 ????? ????? ????? ??

UF 43033 ????? ????? ????? ????? ???0? 10??? ????? ?0??? ?0??? ????1? ????? ????? ????? ????? ????? 00?00 ???? ??

UF 43072 ????? ????? 0???? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? 0???? ?0??? 0???? ????0 ??

UF 43073 ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?0?00 0???? ????? ??

amorense 21113 01{2 3}00 0{1 2 3}2{2 3}{1 2} 00111 0??0? 20??? ????? ?0??? ?0??? ????1 ????? ????? ??00? 00000 00000 000?0 0-110 00