

2019

Turtles of the Early Pleistocene Santa Fe River 1B Locality

Dennis Parmley

Department of Biological and Environmental Sciences, Georgia College and State University, dennis.parmley@gcsu.edu

Robert Chandler

Department of Biological and Environmental Sciences, Georgia College and State University

Linda Chandler

Department of Biological and Environmental Sciences, Georgia College and State University

Follow this and additional works at: <https://digitalcommons.gaacademy.org/gjs>

 Part of the [Evolution Commons](#)

Recommended Citation

Parmley, Dennis; Chandler, Robert; and Chandler, Linda (2019) "Turtles of the Early Pleistocene Santa Fe River 1B Locality," *Georgia Journal of Science*, Vol. 77, No. 2, Article 9.

Available at: <https://digitalcommons.gaacademy.org/gjs/vol77/iss2/9>

This Research Article is brought to you for free and open access by Digital Commons @ the Georgia Academy of Science. It has been accepted for inclusion in Georgia Journal of Science by an authorized editor of Digital Commons @ the Georgia Academy of Science.

Turtles of the Early Pleistocene Santa Fe River 1B Locality

Acknowledgements

This work could not have been completed without the loan of modern turtle comparative material from the following collections managers, for which we are very grateful: L. Abraczinskas (Michigan State University Museum); K. Krysko (Florida Museum of Natural History); G. Schneider (Museum of Zoology, University of Michigan). We also thank M. Welker of Ocotillo Herps and Inverts (Texas) for providing important comparative specimens during the course of this study. Illustrations are by GCSU biology students H. Davis and C. Poore. We especially thank J. Bourque (UF) for bringing the possible molluscivorous *Trachemys* to our attention and greatly improving an earlier draft of this manuscript. We thank R. Franz for sharing his knowledge of fossil *Gopherus*. Lastly, we thank A. Mead of GCSU for improving an early draft of this manuscript.

TURTLES OF THE EARLY PLEISTOCENE SANTA FE RIVER 1B LOCALITY

Dennis Parmley*, Robert Chandler, and Linda Chandler
Department of Biological and Environmental Sciences
Georgia College & State University
Milledgeville, Georgia, 31061
*corresponding author
dennis.parmley@gcsu.edu

ABSTRACT

The early Pleistocene (ca. 2.588–1.806 Ma) Santa Fe River 1B fossil site (SF1B) of Gilchrist County, Florida has yielded turtle fossils representing nine genera and at least 10 species. Of these, at least six genera are aquatic turtles (*Macrochelys* and/or *Chelydra*, *Apalone*, *Trachemys*, *Pseudemys*, *Sternotherus*, and *Kinosternon*) and three are terrestrial (*Hesperotestudo*, *Gopherus*, and *Terrapene*). *Hesperotestudo* and an undescribed cf. *Trachemys* are the only extinct turtles identified in the paleoherpetofauna. Overall, the generic composition of the turtle fauna is predominantly modern and indicative of the southeastern United States today.

Keywords: Early Pleistocene turtles, Santa Fe River, Florida

INTRODUCTION

Fragmentary turtle remains (especially shell elements) often are common components of North American late Cenozoic (Oligocene to Holocene) fossil deposits (e.g., Ehret and Bourque 2011; Holman 1996; Meylan 1995; Moodie and Van Devender 1978; Morgan and Ridgway 1987; Parmley 1992; Parris and Deschler 1995; Preston 1979). Overall, fossil turtles can be good indicators of ancient environmental conditions and habitat types present in an area during the time of deposition. Here we report an important collection of turtle fossils from an early Pleistocene (2.588–1.806 Ma; see time scale of Gibbard et al. 2009) fossil site in Gilchrist County, Florida, known as the Santa Fe River 1B fossil site (hereafter SF1B). The SF1B fossils provide new and noteworthy information that improve our understanding of the taxonomic diversity and distribution of early Pleistocene turtles from this region of North America.

SF1B fossil site.— Santa Fe River fossil sites of Florida are well known from an approximately 10 km section of the river within Columbia and Gilchrist counties (e.g., Kurten and Anderson 1980; MacFadden and Hulbert 2009; Morgan and Ridgway 1987; Webb 1974). While there are many known fossil localities along this stretch of the river, the most diverse thus far known is the Santa Fe River 1 locality, which includes two sites: 1A and 1B (SF1A and SF1B; High Springs quadrangle map T7S, R16E, SEC 34, NW1/4; see Figure 1B of MacFadden and Hulbert 2009). This Santa Fe River locality has yielded late Pliocene and early Pleistocene vertebrates (previously considered late Blancan, see Brodkorb 1963; Chandler 1994; Weaver and Robertson 1967) such as the extinct bird *Titanis walleri* (Brodkorb 1963; Chandler 1994) and the presence of a plethora of mammals to include xenarthrans, rodents, carnivores, a proboscidean, perissodactyls,

and artiodactyls (see table 2 of Morgan and Ridgway 1987). Although no radiometric dates (numerical dates) are available for SF1A or SF1B, biochronological evidence and a relatively recent time reorganization of the Pleistocene Epoch (Gibbard et al. 2009) support a predominantly mixed fauna of mainly late Pliocene and early Pleistocene vertebrates for SF1A and an early Pleistocene fauna for SF1B (see Chandler 1994; Kurten and Anderson 1980; Morgan and Ridgway [and references within] 1987; Webb 1974; Woodburne 2004). SF1B is a near shore, in-place, early Pleistocene site adjacent to 1A (as noted by Chandler 1994; Morgan and Ridgway 1987; Webb 1974 [also personal observations by Chandler and Parmley]). The early Pleistocene age of the SF1B site is biochronologically supported by mammalian material (some considered Pliocene-early Pleistocene in age) in addition to unreported fossils in the GCVP (Georgia College vertebrate paleontology) collections such as *Glossotherium chapadmalense* (Pilosa), *Nannippus (Dolichohippus) simplicidens*, *Tapirus* sp. (both Perissodactyla), and *Hemiauchenia blancoensis* (Artiodactyla). Thus, we contend that at this time biochronological evidence and time scale evidence presented by Gibbard et al. (2009) accurately gives an early Pleistocene age of ca. 2.588–1.806 Ma for the SF1B fauna.

From 1996 to 2003, field crews from Georgia College and State University periodically collected SF1B macro- and microfossils from in situ sediments in a vertical cut bank face. Thousands of SF1B early Pleistocene fossils were collected including plants (seeds), fish, amphibians, alligators, turtles, many squamates (the amphisbaenid *Rhineura*, lizards, and snakes), some birds, and many mammals. Here we describe turtle fossils collected from in situ early Pleistocene SF1B sediments.

MATERIALS AND METHODS

Unless noted, the SF1B turtle fossils reported here are cataloged in the vertebrate paleontological collections of Georgia College and State University. Taxonomic classification and shell terminology (carapace, plastron, bone, and scute) mainly follow Ernst and Lovich (2009). Reference material in the modern comparative skeletal collections of the Georgia College and State University herpetological collection, Florida Museum of Natural History (University of Florida), University of Michigan Museum of Zoology, and Michigan State University Museum, as well as pertinent information in the literature, was used to identify the SF1B fossils to the lowest practical taxon. More specifically, identifications of carapacial and plastral elements were based mainly on the characteristics of surface ornamentation (if applicable), shape, degree of development and location of dermal bones, and the relative position and shape of epidermal scute impressions and sulci of the most complete or diagnostic elements.

SYSTEMATIC PALEONTOLOGY

Class Reptilia Laurenti, 1768
 Order Testudines Batsch, 1788
 Family Testudinidae Gray, 1825
 Genus *Gopherus* Rafinesque, 1832
Gopherus aff. *G. polyphemus* (Daudin, 1802)
 (Figure 1A)

Material.— GCVP 12855, 12856, two partial nuchal bones.

Remarks.— Two genera of tortoises are known to have lived during the North American Pliocene and early Pleistocene: the extinct genus *Hesperotestudo* (*Geochelone* in older literature, e.g., Auffenberg 1963; Parmley 1992) and the extant genus *Gopherus* (e.g., Franz and Quitmyer 2005; Morgan et al. 1998). The identification of primarily isolated shell elements of these genera has been discussed many times in the literature (e.g., Auffenberg 1963, 1976; Franz and Quitmyer 2005; Holman 1995; Meylan 1995; Parmley 1992). Fortunately, the nuchal bone is easily one of the most identifiable elements of both genera (e.g., Meylan 1995). Included in the SF1B collection are two *Gopherus* nuchals. The most complete nuchal (GCVP 12856, Figure 1A) retains the following characters that are distinctly *Gopherus* and distinguish it from *Hesperotestudo*: scute sulci wide and deep; cervical scute short, relatively large and square (or nearly so); and left marginal scute long, only slightly projected past the bone of the cervical scute. In ventral view, there is evidence that this fossil had a vertebral strut scar from the attachment of the first thoracic vertebra (a unique testudinoids character state of the burrowing clade of this genus [*G. polyphemus-flavomarginatus*]; Bramble 1971, 1982; Franz and Franz 2004; Franz and Quitmyer 2005; Meylan 1995). GCVP 12855 is not complete enough for us to detect a ventral vertebral scar, but otherwise it is like *Gopherus*. Judging from nuchals of living *G. polyphemus*, GCVP 12856 is from a moderately small tortoise while GCVP 12855 is from a very small individual. Although the fossils seem unquestionably assignable to *Gopherus*, we are more guarded about their specific identifications because of the possible existence of an undescribed small extinct burrowing species of *Gopherus* from the late Pliocene-early Pleistocene of Florida (e.g., Franz and Quitmyer 2005).

Genus *Hesperotestudo* Williams, 1950
Hesperotestudo sp. indet.
 (Figure 1B)

Material.— GCVP 12814, 12956, two nuchals; GCVP 12809, one entoplastron; GCVP 12810, one peripheral; GCVP 9950, 9962, 9965, three carapacial fragments; GCVP 9947, 9963, 12811, 12812, four plastral fragments.

Remarks.— This extinct genus of tortoise is well documented from Pliocene and Pleistocene North American sites. It is known from the Pleistocene of southeast Georgia, where it occurred sympatrically with *Gopherus* (Clark 2009; Hulbert and Pratt 1998). *Hesperotestudo* is represented in the SF1B fauna by numerous carapacial and plastral fragments (some of which are quite large and thick), osteoderms, spurs (many of which are not yet accessioned), and two relatively well-preserved nuchals. The nuchal bones are typical of *Hesperotestudo* in exhibiting growth rings and scute sulci that are distinct but not as wide or as deep as in *Gopherus*, and in having somewhat rectangular cervical scutes and anteriorly pointed first marginal scutes that are relatively short (compared with *Gopherus*), taller than wide, and projecting past the bone of the cervical scute (marginals of *Gopherus* equal or nearly equal with the cervical). They are about the same size and represent relatively thin-shelled small tortoises, perhaps juveniles or adults of a small *Hesperotestudo* (subgenus *Hesperotestudo*). In contrast, some of the SF1B tortoise shell fragments are indicative of much larger individuals (e.g., GCVP 9965 is 30 mm thick),

perhaps a large species of the subgenus *Caudochelys*. The fragmented condition of the fossils and nonspecific nature of some of the bones in general, however, prevent identification of this material to a species or species group level.

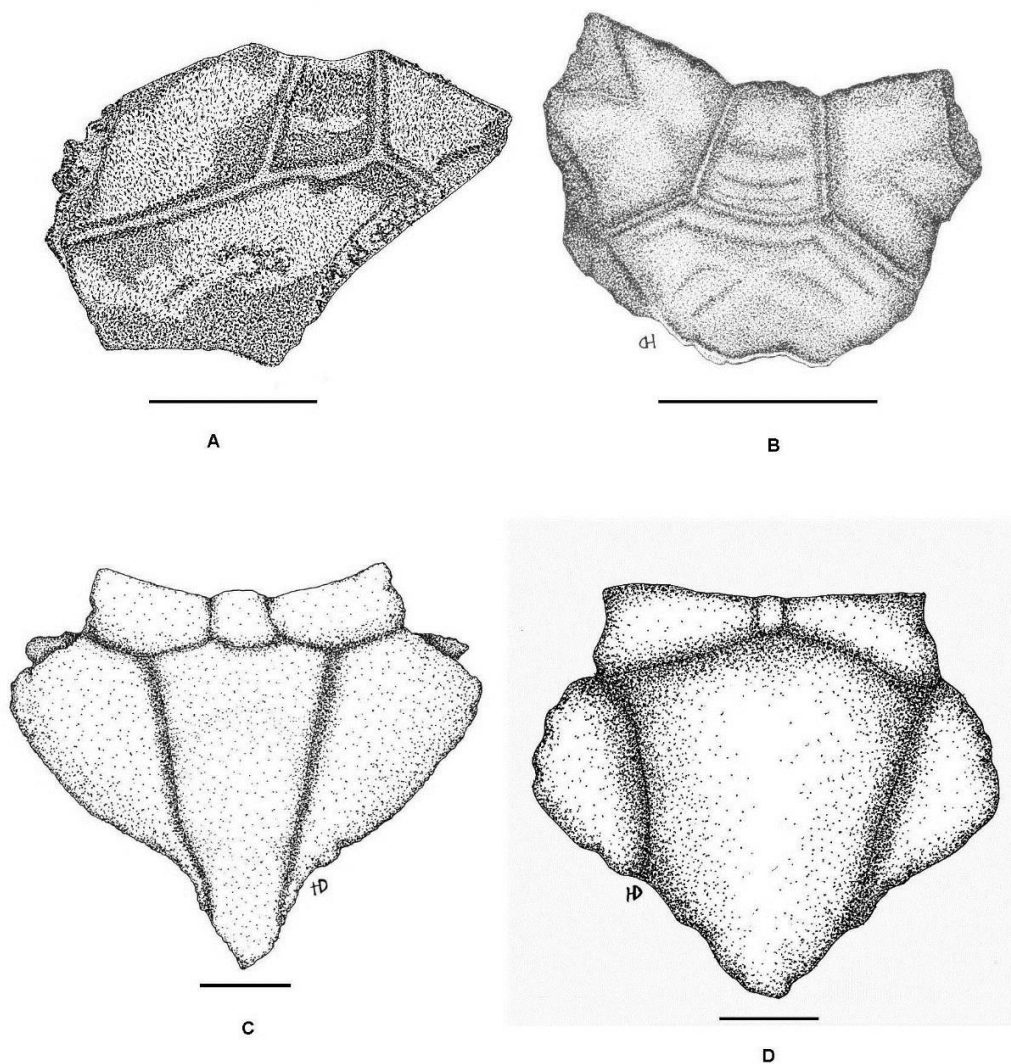


Figure 1. SF1B nuchal bones in dorsal view identified as A) *Gopherus* aff. *G. polyphemus*, GCVP 12856, scale bar = 20 mm; B) *Hesperotestudo* sp. indet., GCVP 12956, scale bar = 20 mm; C) *Sternotherus* sp. indet., GCVP 12853, scale bar = 5 mm; D) *Kinosternon* sp. indet., GCVP 12854, scale bar = 5 mm.

Family Kinosternidae Agassiz, 1857

Living North American genera of this highly aquatic family date back to at least the Hemingfordian North American Land Mammal Age (NALMA; Miocene, 16–17 Ma; see Bourque 2015). Kinosternid nuchal bones are common elements in the SF1B turtle material, representing at least 46 individuals. They are easily recognized at the family level by their small size, domed shape, smooth (unsculptured) dorsal bone surfaces, and small cervical scutes flanked by relatively long and narrow marginal scutes. Because of

intergeneric overlapping features of some bones or scute patterns, the identification of at least some isolated bones of the two North American genera, *Sternotherus* and *Kinosternon*, can be problematic. With some degree of caution, we report the presence of both genera in the Pleistocene SF1B turtle fauna on the basis of nuchal bones (see below) noting, however, that Bourque (2012) and Bourque and Schubert (2015) noted that there can be overlapping nuchal characteristics between these genera in some cases and that shell elements can be very useful in differentiating between the genera. While we feel confident that *Sternotherus* and *Kinosternon* are represented in the paleofauna, carapace and plastron bones recovered from the site are currently under study, and will be reported on at a later date. These elements will likely yield specific evidence of at least some of the CQ kinosternids. Nonetheless, this project is a year (at least) away from completion.

Genus *Sternotherus* Gray, 1825
Sternotherus sp. indet. (Figure 1C)

Material.— GVCP 9985, 9986, 10101, 10102, 10247, 10249-10258, 11587, 12421, 12449, 12834-12853, forty-one nuchals.

Remarks.— At the generic level, differences in nuchal characters that separate *Sternotherus* from *Kinosternon* include (noting the caution given below) the following. In *Sternotherus* (and the SF1B fossils) there is broad coverage by the pleural scutes (on either side of the vertebral scute) that produces a narrow and strongly tapered first vertebral scute whereas, in *Kinosternon*, the pleural overlap is much less invasive resulting in a wider, less tapered (narrower) first vertebral scute (compare Figure 1C,D; Holman and Winkler 1987; Preston 1979;). Bourque and Schubert (2015), however, noted that some *Sternotherus* nuchals can have a rather wide vertebral I scute.

Although we believe at least most of the SF1B nuchal elements represent *Sternotherus*, the specific identification of the fossils is more problematic. Bourque (2012) and Bourque and Schubert (2015) discussed nuchal characters that can be used to differentiate among some living and extinct kinosternid turtles. However, because of our lack of a taxonomically (at the specific level) and geographically diverse comparative collection of Recent and fossil kinosternid material, and given the overall lack of literature dealing with specific differentiation of these taxa, only a generic identification of the SF1B material seems prudent at this time.

Genus *Kinosternon* Spix, 1824
Kinosternon sp. indet.
(Figure 1D)

Material.— GCVP 8834, 9987, 10248, 12813, 12854, five nuchals.

Remarks.— *Kinosternon* is represented in the SF1B fossil assemblage by five nuchals that are well preserved and characteristic of this genus mainly in having wide vertebral scutes. For the same reasons given under the *Sternotherus* account, we offer only a generic level identification of the fossils.

Family Chelydridae Swainson, 1839
Macrochelys sp. indet.
or *Chelydra* sp. indet.
(Figure 2A–C)

Material.— GCVP 12495, one right humerus; GCVP 13115, one right hyoplastron; GCVP 16010, one right scapula; GCVP 9966, 9968, 9969, 9981, 12494, five peripherals.

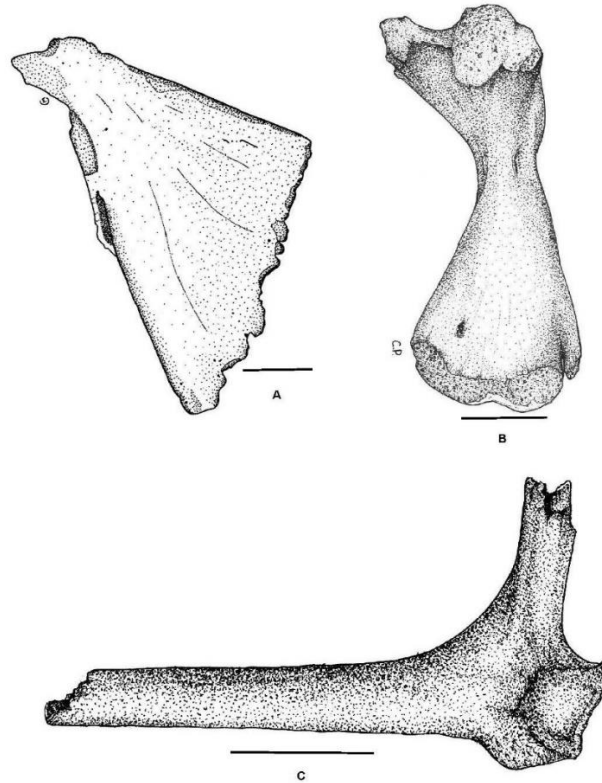


Figure 2. SF1B *Macrochelys* sp. indet. or *Chelydra* sp. indet. bones : A) hyoplastron, GCVP 13115; B) right humerus in anterior view, GCVP 12495; C) right scapula, GCVP 16010. Scale bar = 20 mm for A, B, and C.

Remarks.— Included in the SF1B collection of turtle fossils are elements of chelydrid turtles that collectively may represent two genera: *Macrochelys* and *Chelydra*. These genera commonly co-occur in late Blancan through Irvingtonian NALMA deposits in Florida (Thomas et al. 2014). All of the SF1B chelydrid bones are large, chelydrid-like in their features, and at least recently they likely would have been identified as *Macrochelys* rather than *Chelydra* based on their large size. Now, however, Thomas et al. (2014) convincingly argued that the extinct taxon *M. floridana* Hay 1907, 1908 first described from the Pleistocene of Florida is actually a large *Chelydra*, one that obtained the size of *Macrochelys*. Moreover, this giant *Chelydra* co-occurred with *Macrochelys* during the late Pliocene to Pleistocene of Florida (Thomas et al. 2014). Subtle differences in characteristics and features of some of the SF1B chelydrid fossils described below suggest *C. floridana* and a large *Macrochelys* likely were present in the SF1B paleoherpetofauna, noting, however, we cannot differentiate between the genera with absolute confidence.

The SF1B humerus (GCVP 12495) easily is identified as that of an adult chelydrid turtle mainly on the basis of its large size, strongly flared lateral tubercle (greater tuberosity), well-developed ectepicondylar groove, and slit-shaped ectepicondylar foramen. The scapula (GCVP 16010) is, overall, identical to a Recent *Macrochelys* in the GC collection of comparative specimens in being large, robust, with a gently curved anterodorsally margin, and an approximately 90° angle between the scapular prong and acromial process (shoulder girdle terminology after Depecker et al. 2006). The hyoplastron (GCVP 13115) is short and retains a distinct insertion channel for the epiplastron. The peripherals (GCVP 9966, 9968, 9969, 9981, 12494) appear to be from the posterior rim of the carapace of a large chelydrid. They differ from those of *Macrochelys* in being more inflated with more narrowly notched posterior serrations. To us, this suggests that most likely several of the peripherals represent a giant *Chelydra*, but a detailed study of the osteology and taxonomic status of this large, extinct chelydrid is beyond the scope of this paper.

Family Trionychidae Bell, 1825
Genus *Apalone* Rafinesque, 1832

Most workers over the past few years have relegated the trionychid genus *Trionyx* to *Apalone* based on Meylan's (1987) extensive study of the taxonomic and systematic arrangement of this group of turtles. Based on our study of numerous trionychid skeletons, we feel the assignment of *Trionyx* to *Apalone* may not be resolved and is in need of further study. These issues, however, are beyond the scope of this report (also see Ernst et al. 1994, p.103; Webb 1998) and to remain in compliance with most other workers we use *Apalone* here.

Apalone sp. indet.
(Figure 3A,B)

Material.— GCVP 9993, one partial right hypoplastron; GCVP 7380, 9991, 9997, 10226, 12819-12823, nine costals; GCVP 9992, one neural; GCVP 12815-12818, four plastral fragments; 40 shell fragments; GCVP 5967, 7368-7379, 7381-7384, 9994-9996, 9998, 10217, 10225, 10227-10233, 12824-12833; GCVP 16011, one left scapula.

Remarks.— Partial trionychid carapacial and plastral elements are numerous in the collection of SF1B turtle fossils. Although most of the elements are fragmentary, they bear the rugosity and pitted sculpturing characteristic of North American *Apalone* turtles (e.g., Parmley 1992; Parmley et al. 2006). Unfortunately, most of the fossils are too incomplete for specific identification and the only complete bone, a neural (GCVP 9992), is undiagnostic to species. The scapular prong of the relatively short scapula makes an approximately acute angle with the acromial process, which is typical of trionychids (Depecker et al. 2006; Sobolik and Steele 1996). Trionychid fossils are common elements in many late Eocene to Pleistocene fossil sites in the southeastern United States (e.g., Hulbert 2001; Parmley et al. 2006).

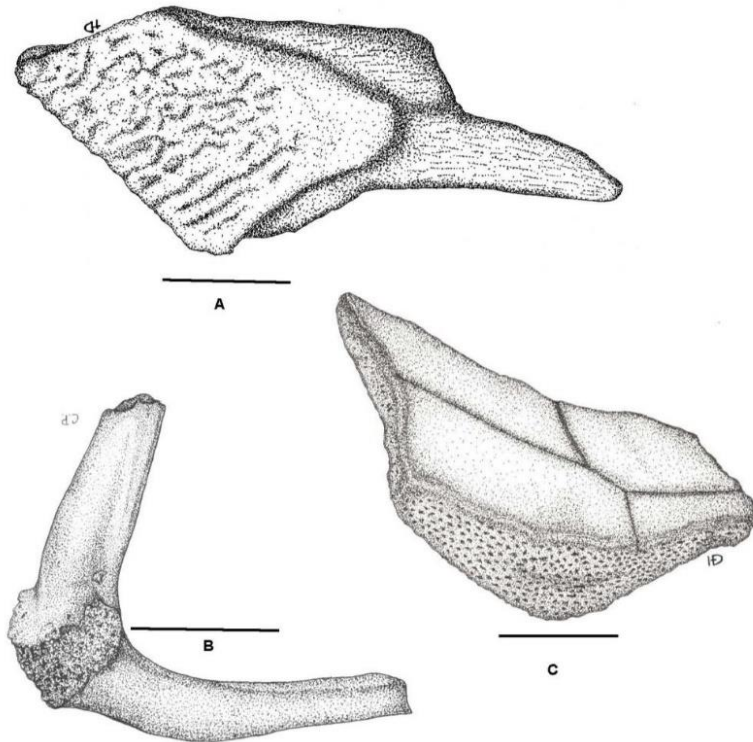


Figure 3. SF1B turtle bones: A) *Apalone* sp. indet. hypoplastron, GCV 9993, scale bar = 15 mm and B) left scapula, GCV 16011, scale bar = 10 mm; C) *Terrapene carolina* carapace fragment, GCV 13116, scale bar = 10 mm.

Family Emydidae Gray, 1825
Genus *Terrapene* Merrem, 1820
Terrapene carolina (Linnaeus, 1758)
(Figure 3C)

Material.— GCV 13116, carapace fragment.

Remarks.— GCV 13116 consists of a fused anterior carapace section with no evidence of sutures, which is typical of adult *Terrapene* (Hulbert 2001), especially *T. carolina* (Parmley personal observ.). The fossil comes from the left side of the nuchal area and retains (at least in part) the first two marginals, first vertebral, and first pleural scute areas. Overall it compares closely with Recent *T. carolina* in shape, degree of flaring, and in sulci pattern, especially for the first marginal sulcus. The fossil represents a relatively large, thick-shelled, box turtle similar to the extinct subspecies *T. c. putnami* Hay, 1908. *Terrapene* dates back to the Miocene (ca. 14.5–13.0 Ma; Holman and Fritz 2005), and records from the Pliocene and Pleistocene are common (Holman 1995).

Genus *Trachemys* Agassiz, 1857

Shell fragments of *Trachemys* are exceptionally common in the SF1B collection of turtle fossils. In fact, fossils of turtles in the *Trachemys* clade often are common in North American Pliocene and Pleistocene fossil sites. The history of *Trachemys*'s classification is long and complex, especially at the species level. Since Hay's early 20th century (1908) treatment of *Trachemys*, the *Trachemys scripta* complex has been taxonomically unstable and sometimes confusing (e.g., Jackson 1988; McDowell 1964; Parmalee et al. 2002; Weaver and Robertson 1967). We believe that at least three species of *Trachemys* likely are present in the SF1B turtle fauna. Because of the damaged condition of much of the SF1B *Trachemys* material, in addition to the poorly understood variability of carapacial and plastral characters of Miocene to Recent species of this genus (e.g., Parmalee et al. 2002) and poorly represented modern skeletal holdings, we offer only comparative (*conferre*) identifications of the best preserved and most diagnostic SF1B material which are presented below as Types A–D.

Type A: *Trachemys scripta* complex cf. *T. platymarginata*
(Weaver and Robertson 1967)
(Figure 4A)

Material.— GCVF 12776, one nuchal bone.

Remarks.— This SF1B nuchal exhibits several features characteristic of the extinct *T. scripta* complex species *T. platymarginata*, at least enough to suggest a strong affiliation with this taxon (discussed below). This emydid originally was described as *Chrysemys platymarginata* by Weaver and Robertson (1967) and as “a member of the *scripta* complex” (p. 58) on the basis of a nearly complete Pleistocene carapace and plastron of an adult specimen from Alachua Co. Florida. Jackson (1988) later assigned this taxon to the genus *Trachemys* on the basis of mainly skull elements. According to Jasinski (2018; p. 69) the nuchal of *T. platymarginata* differs from the nuchal of *T. inflata* (a common *Trachemys* of earlier Blancan NALMA times) by a smooth marginal scute (nuchal of some) area, rugose vertebral 1, an absence of notches between the cervical scute and first marginals, a longer first marginal, and a more elongated cervical scute (also, see fig. 1 of Jasinski 2018). Additionally and mainly on observations given by others (e.g., Jackson 1988; Weaver and Robertson 1967) the nuchal of *T. platymarginata* is characterized by the following: 1) marginal scute area smooth (no diagonal rugose lines for the most part) but strong rugosity on costal scute areas; 2) anterior notch (between nuchal and marginal scutes) present but not strongly V-shaped as in *T. inflata*; 3) and a well-developed median keel on the carapace, which appears to be true for the SF1B specimen based on the evidence of a keel on the 1st vertebral scute area. Overall, GCVF 12776 possesses these characteristics with one noted exception—the marginal scute exhibits some degree of rugosity. Given this feature and the limited SF1B fossil nuchals available for study, we suggest only a tentative species identification of the fossil at this time.

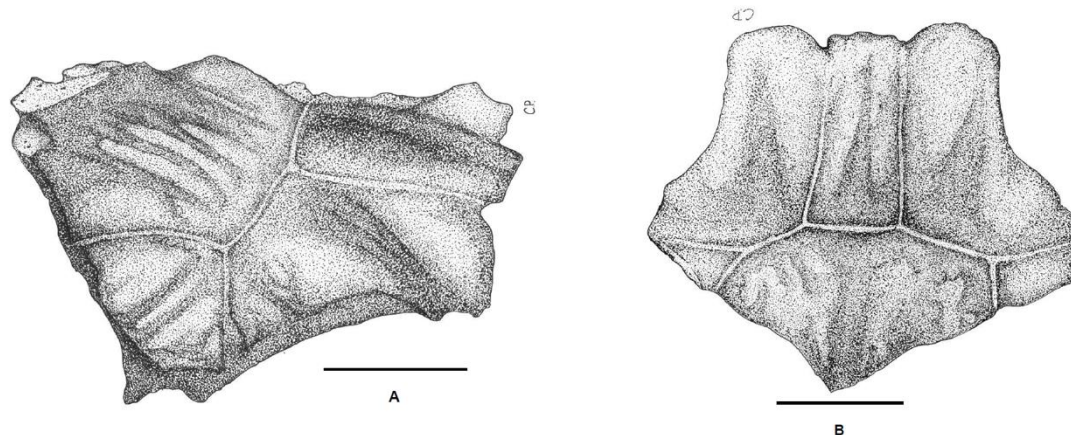


Figure 4. SF1B *Trachemys* nuchal bones: A) *T. scripta* complex cf. *T. platymarginata* nuchal, GCVF 12776, and B) *T. scripta* complex cf. *T. scripta* nuchal, GCVF 12957. Scale bar = 15 mm for A and B.

Type B: *Trachemys scripta* complex cf. *T. scripta* (Schoepff 1792)
(Figure 4B)

Material.— GCVF 12957, 12777-12780, five nuchals.

Remarks.— These nuchals are very similar to, if not indistinguishable from *T. scripta* in overall shape, upraised topography, and sculpturing. Two size classes are represented in the collection of nuchals, suggesting the presence of male (small) and female (large) individuals.

Type C: cf. *Trachemys* complex undescribed durophagous species
(Figure 5)

Material.— GCVF 12783, one dentary; GCVF 12781, 12782, two nuchals.

Remarks.— Paleontologists of the University of Florida (Gainesville) currently are studying numerous fossils of an early Blancan emydid from the Suwannee River of Florida that may be from an enigmatic and undescribed species of molluscivorous *Trachemys* (Jason Bourque, personal comm.). We were made aware of this when an unusually wide and robust turtle dentary discovered in the collection of SF1B fossils clearly matched their material (via exchange of digital images). The presumed molluscivorous dietary habits of this undescribed cf. *Trachemys* are reflected clearly in the size and robust nature of its dentary bone. When the SF1B dentary was first discovered, we believed that it likely was from a large female *Graptemys*, given that adults of the molluscivorous clade of this genus (especially females) are known to have broad dentaries to facilitate feeding mainly on hard-shelled prey, such as snails and clams (even the dense-shelled invasive species *Corbicula maniliensis*; Ernst and Lovich 2009). The SF1B dentary differs from *Graptemys* in many ways. For example, in dorsal view, the SF1B mandible is domed to form an inverted U-shape, even more so than the extinct *Graptemys kernerii* Ehret and Bourque from the Late Pleistocene of Florida (Ehret and Bourque 2011). In *Graptemys*,

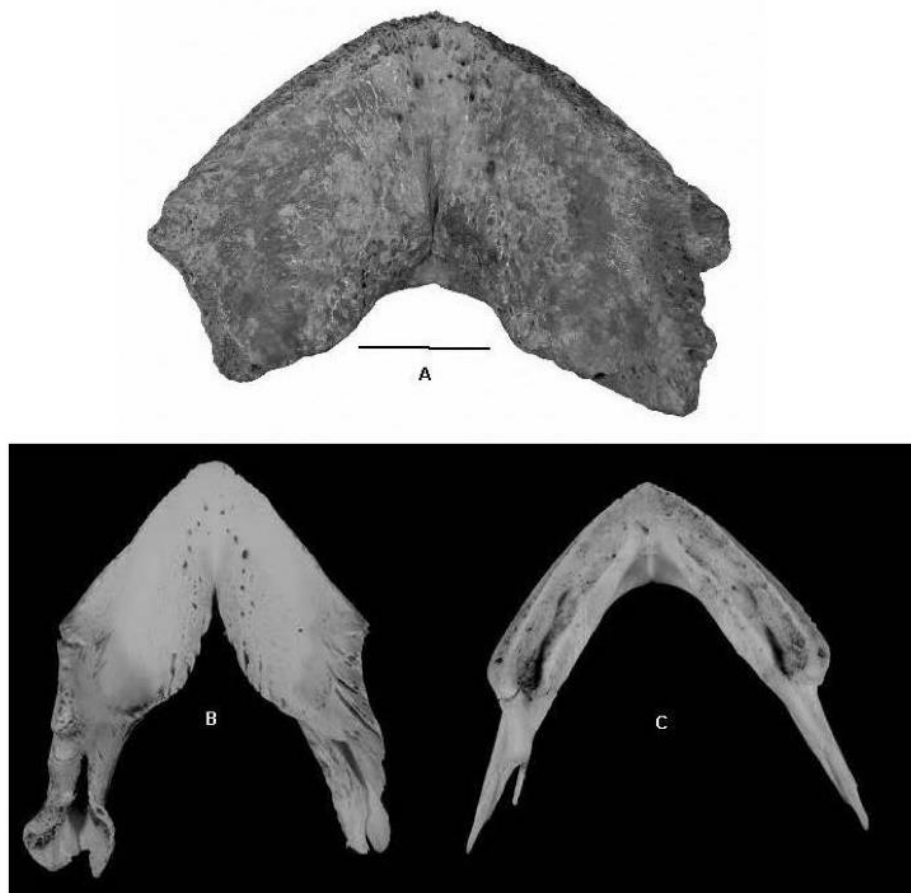


Figure 5. SF1B cf. *Trachemys dentary*: A) durophagous cf. *Trachemys sp. indet.* GCVP 12783, Scale bar = 10 mm; modern dentaries of B) *Graptemys barbouri*, UF 6155, and C) *Trachemys scripta*, UF 87983.

the dentaries meet to form a more acute angle giving an inverted V-shape. The SF1B fossil is somewhat eroded, but discernible features include the following: labial ridge low and relatively thin; lingual ridge wide and robust; a distinct sulcus running medially between the triturating surfaces; triturating surfaces greatly expanded laterally resulting in very broad crushing surfaces, each with a shallow trough; and no evidence of a terminal hook, although a small one may have been present. To give a sense of the overall morphology and robust build of this dentary, we depict it with the dentary of an adult *Trachemys scripta* and an adult female *Graptemys barbouri* (see Figure 5).

With reservations, we also tentatively associate two partial nuchals with this undescribed species. The fossils consist of anterior sections of nuchal bones that include cervical and lateral marginal scute areas only. While the scute areas in both specimens, are inflated in the typical fashion of a *T. scripta*-like turtle, they also are quite smooth which is unlike members of this complex. A digital image of one of the University of Florida Suwannee River nuchals shows it to be smooth as well, although the cervical scute is shaped differently than in the SF1B specimens (wide and flat-ended in the UF specimen; narrow and pointed in the SF1B specimens).

Type D: *Trachemys* sp. indet.

Material.— GCVP 12797-12800, four costals; GCVP 12801-12804, four posterior peripherals; GCVP 12796, bridge area peripheral; GCVP 12784, one pygal; GCVP 2786-12795, 10 neurals; GCVP 12785, one epiplastron.

Remarks.— These fossils appear to represent *Trachemys* (e.g., highly sculptured costals [grooves and ridges], notched peripherals, neurals with medial keels, and strong gular scute overlap of epiplastra [Seidel and Jackson 1990; Weaver and Robertson 1967]), and likely more than one species is present. For example, some of the fossils are closest in features to *T. scripta*, while others differ in various details and may represent *T. platymarginata* or the previously mentioned undescribed molluscivorous species.

Genus *Pseudemys* Gray, 1855
Pseudemys nelsoni Carr, 1938
(Figure 6A)

Material.— GCVP 9990, 12805, two nuchal bones.

Remarks.— These fossil nuchals compare well with *Pseudemys* and lack the upraised cervical scutes and overall dorsal rugosity and inflation typical of *Trachemys*. They exhibit the following features characteristic of large adult individuals of *P. nelsoni*: overall very thick and robust; cervical scute flat and long; and dorsal surface ornamented with narrow parallel striations, especially on the marginals and first vertebral scute surfaces (Dobie and Jackson 1979; Holman 1985). The anterior edge of one of the marginal scutes on GCVP 12805 is complete enough to determine that they were indented (angled), but less so than typically is seen in *T. scripta* and more so than in *P. floridana*. *Pseudemys floridana* normally has the anterior outline of its nuchal straight or only slight notched. The other fossil (GCVP 9990) is too damaged for us to evaluate this feature, but it clearly retains the dorsal striations indicative of *P. nelsoni*.

Pseudemys concinna (LeConte, 1830)
(Figure 6B)

Material.— GCVP 5187, one complete nuchal; GCVP 12806-12808, three partial nuchals.

Remarks.— These nuchal bones compare best with *Pseudemys concinna*. The most complete nuchal (GCVP 5187) is assigned to this species on the basis of the following features: dorsal surface weakly wrinkled (striated in *P. nelsoni*; rugose to nearly smooth in *Trachemys*); cervical scute long and moderately wide; cervical and first marginal scutes flat (upraised to inflated in *Trachemys*); and anterior edge of marginal scute bone only moderately indented and projected anteriorly (but more indented than in *P. nelsoni*, straight in *P. floridana*, and often strongly indented in *Trachemys*; in part, Holman

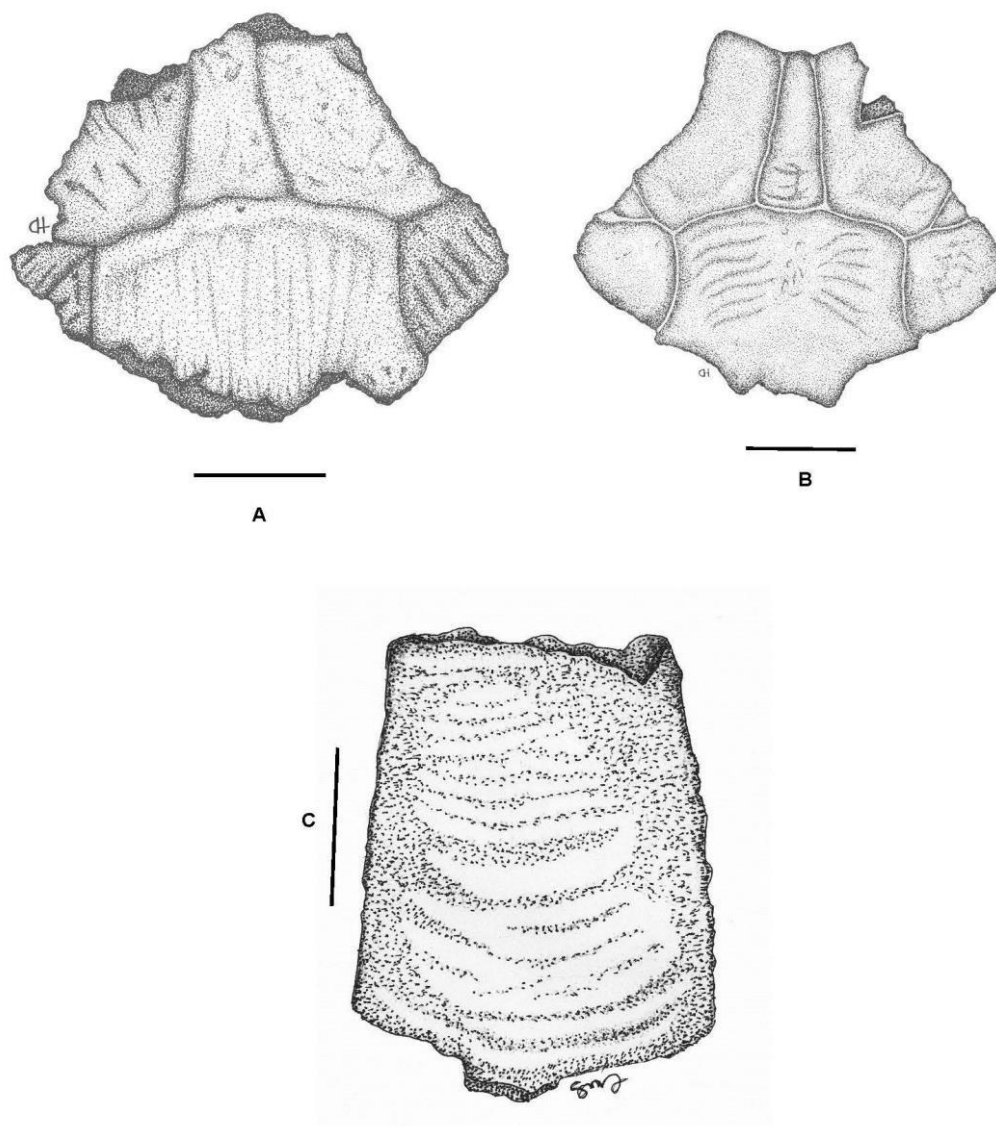


Figure 6. SF1B nuchals of A) *Pseudemys nelsoni*, GCVF 12805, Scale bar = 15 mm and B) *Pseudemys concinna*, GCVF 5817, Scale bar = 20 mm; C) *Pseudemys* sp. indet. partial costal, GCVF 13114, Scale bar = 20 mm

1985). Based on comparative specimens available to us, GCVF 5817 is nearly identical in its features to nuchal bones of large female individuals of this species. The partial nuchals are more questionable in their assignment to *P. concinna*, but they all have the flat and weakly wrinkled dorsal surfaces and marginal and cervical scute characteristics of this species.

Pseudemys sp. indet. (Figure 6C)

Material.— GCVP 13114, one costal.

Remarks.— The horizontal rippling of many of the SF1B costal bones is more characteristic of *Pseudemys* than it is of *Trachemys*. Very few of the bones are accessioned into the GC collections, but GCVP 13114 depicts a typical example.

DISCUSSION

The SF1B turtle fauna is diverse and is represented by at least nine genera and 10 species (e.g., if *Trachemys* does represent three species). From a temporal view, the fauna is mostly modern; the only members identified with confidence as being extinct are the land tortoise *Hesperotestudo* and the enigmatic durophagous emydid, but likely other extinct taxa are present (e.g., cf. *T. platyspondyla* and a small species of *Gopherus*). Furthermore, all of the modern SF1B turtle genera occur today in the southeastern United States (Ernst and Lovich 2009). Two especially southeastern components of the SF1B turtle fauna include *Gopherus* (possibly *G. polyphemus*) and *Pseudemys nelson* (Ernst and Lovich 2009). Unlike the mammalian fauna, overall, the SF1B turtle assemblage supports previous findings that the North American late Pliocene to early Pleistocene herpetofauna was very modern, especially at the family and generic level (e.g., Estes and Baez 1985; Holman 2000, 2006; Mead and Bell 2001; Parmley and Walker 2003; Rogers 1976).

Paleoecological considerations.— The SF1B turtles mostly are characteristic of an aquatic community as evidenced by the fact that 67% of the genera and 60% of the SF1B species are aquatic taxa. The aquatic makeup of the SF1B turtles include the genera *Macrochelys* and/or *Chelydra*, *Apalone*, *Trachemys*, *Pseudemys*, *Sternotherus*, and *Kinosternon*, all of which suggest the primary habitat may have been a stream with some deep water, but also shallow vegetated areas (perhaps backwaters) with sandy or gravel areas or tree deadfalls for basking. Based on the known ecological preferences of the living counterparts of these aquatic turtles (Ernst and Lovich 2009; Jensen et al. 2008; Powell et al. 2016; Parmley personal field experience), the SF1B aquatic turtles may have inhabited the stream as follows. The deeper, probably quieter cove waters likely would have been inhabited by *Macrochelys* and *Chelydra*. Of these two aquatic taxa, *Chelydra* will bask and often wander from its water habitat (Parmley, personal observ., also see Jensen et al. 2008, p. 457) while *Macrochelys* “is the most aquatic nonmarine turtle in the country, almost never leaving the water” (Jensen et al. 2008, p. 461). *Apalone*, another highly aquatic turtle, would have preferred littoral sandy or mud-bottomed areas for hiding and exposed sand or gravel bars for basking. *Trachemys* and *Pseudemys* would have been more generalists, but probably would have congregated at basking sites. It is likely that nearby smaller wetlands were present such as ponds, creeks, marshes, or cypress-type swamps (also evidenced by *Amphiuma*, *Siren*, and *Pseudobranchius* in the fauna [unreported fossils in GCVP collections]). The kinosternids, *Chelydra*, small (especially hatchling) trionychids, and sliders may have occurred in the quiet, calmer areas of the stream or in nearby ponds or creeks.

Terrestrial turtles of the SF1B fauna include the extinct genus *Hesperotestudo* and the living genera *Gopherus* and *Terrapene*. The co-occurrence of a large nonburrowing

tortoise (*Hesperotestudo*) and a burrowing tortoise (*Gopherus*) is of interest. *Hesperotestudo* remains often are common components in North American Tertiary deposits. Hibbard (1960) suggested that the presence of large nonburrowing tortises is an indicator of mild winters. This idea has been carried forward by many post-Hibbard workers to include Auffenberg and Milstead (1965), Brattstrom (1961), Holman (1987, 1995), Moodie and Van Devender (1979), Morgan and Lucas (2005), Parmley (1988), and Webb and Barnosky (1989). If correct, then the occurrence of at least one large species of *Hesperotestudo* in the SF1B turtle fauna suggests that the area during the early Pleistocene likely experienced milder, more equable climatic conditions than today. It should be noted, however, in contrast to Hibbard (1960), others recently have challenged the idea that these giant fossil tortoises in themselves are good indicators of ancient, mild, warm, and more equable climatic conditions (e.g., see Brown et al. 2018; Esker et al. 2019). Several alternatives to Hibbard's (1960) hypothesis concerning fossil tortoises and climatic stability have been suggested. These include, for example (again, see Brown et al. 2018; Esker et al. 2019) "cold-adaptive morphology; behavioral thermoregulation; burrowing; use of caves as shelters; tolerance of prolonged cessation of food consumption; cryoprotection and supercooling; gigantothermy." Importantly, these giant *Hesperotestudo* may have evolved cold-tolerant adaptations, certainly more than previously believed. More detailed analyses of these ideas and hypotheses may reveal that ancient giant tortoises did have the ability to survive colder climatic conditions than previously believed, but it will take some time to carefully investigate if this is correct. On the basis of a vertebral strut scar on the SF1B *Gopherus* nuchal GCVP 12856 and inferring from known ecological requirements of modern *G. polyphemus* (Ernst and Lovich 2009), it seems likely that Pliocene-early Pleistocene SF1B *Gopherus* constructed burrows. These burrows may have been advantageous for living in dry, fire-prone habitats (e.g., Franz and Franz 2004; Franz and Quitmyer 2005). Overall, there probably was xeric habitat with friable sandy soil in the SF1B area based on the presence of *Gopherus*, but also supporting this is the presence of these burrowing taxa in the fauna (yet to be accessioned): *Pituophis melanoleucus* (probably *P. m. mugitus*); *Heterodon* (possibly *H. simus*; Bartlett and Bartlett 2003); and *Geomys* (probably *G. pinetis*). As for *Terrapene carolina*, it is likely that this turtle was common in mesic woodlands in the area, especially in riparian settings (Ernst and Lovich 2009; Jensen et al. 2008; Parmley personal observ.).

ACKNOWLEDGEMENTS

This work could not have been completed without the loan of modern turtle comparative material from the following collections managers, for which we are very grateful: L. Abraczinskas (Michigan State University Museum); K. Krysko (Florida Museum of Natural History); G. Schneider (Museum of Zoology, University of Michigan). We also thank M. Welker of Ocotillo Herps and Inverts (Texas) for providing important comparative specimens during the course of this study. Illustrations are by GCSU biology students H. Davis and C. Poore. We especially thank J. Bourque (University of Florida) for bringing the possible molluscivorous *Trachemys* to our attention and for greatly improving an earlier draft of this manuscript. We thank R. Franz for sharing his knowledge of fossil *Gopherus*. Lastly, we thank A. Mead of GCSU and J. Parmley for improving an early draft of this manuscript.

REFERENCES

- Auffenberg, W. 1963. Fossil testudinine turtles of Florida genera *Geochelone* and *Floridemys*. Bulletin of the Florida State Museum, 7, 5–7.
- Auffenberg, W. 1976. The genus *Gopherus* (Testudinidae): pt. 1. osteology and relationships of extant species. Bulletin of the Florida State Museum, 20, 47–110.
- Auffenberg, W. and W.W. Milstead. 1965. Reptiles in the Quaternary of North America. In *The Quaternary of the United States*, a review volume for the VII Congress of The International Association for Quaternary Research, H.E. Wright, Jr. and D. G. Frey. eds. 577–568. Princeton University Press.
- Bartlett, R.D. and P. Bartlett. 2003. Florida's Snakes: A Guide to their Identification and Habits. University Press of Florida. 256 pp.
- Bourque, J.R. 2012. A fossil mud turtle (Testudines, Kinosternidae) from the early Middle Miocene (Early Barstovian) of New Mexico. *Journal of Vertebrate Paleontology*, 32, 836–853.
- Bourque, J.R. 2015. New mud turtles from the middle-late Miocene of the United States. *Journal of Paleontology*, 89, 821–824.
- Bourque, J.R. and B.W. Schubert. 2015. Fossil musk turtles (Kinosternidae, Sternotherus) from the late Miocene-early Pliocene (Hemphillian) of Tennessee and Florida. *Journal of Vertebrate Paleontology*, 35, article e885441.
- Bramble, D. 1971. Functional morphology, evolution, and paleoecology of gopher tortoises. Ph.D. dissertation. University of California. 341 pp.
- Bramble, D. 1982. *Scaptochelys*: generic revision and evolution of gopher tortoises. *Copeia*, 198, 852–867.
- Brattstrom, B. 1961. Some new fossil tortoises from western North America with remarks on the zoogeography and paleoecology of tortoises. *Journal of Paleontology*, 35, 543–560.
- Brodkorb, P. 1963. A giant flightless bird from the Pleistocene of Florida. *Auk*, 80, 111–115.
- Brown, L.E., D. Moll, and E.S. Brown. 2018. Re-examination of the giant fossil tortoise *Hesperotestudo* from near the Illinois glacial-Sangamon interglacial boundary in North America with commentary on zoogeography. *Herpetological Journal*, 28, 73–86.
- Chandler, R. 1994. The wing of *Titanis walleri* (Aves: Phorusrhacidae) from the late Blancan of Florida. *Bulletin of the Florida Museum of Natural History*, 36, 175–180.
- Clark, J.L. 2009. A Late Pleistocene Herpetofauna from Clark Quarry, Glynn County, Georgia. Unpublished M.S. Thesis, Georgia College and State University.
- Depecker, M., C. Berge, X. Penin, and S. Renous. 2006. Geometric morphometrics of the shoulder girdle in extant turtles (Chelonii). *Journal of Anatomy*, 208, 35–45.
- Dobie, J.L. and D.R. Jackson. 1979. First fossil record for the diamondback terrapin, *Malaclemys terrapin* (Emydidae), and comments on the fossil record of *Chrysemys nelsoni* (Emydidae). *Herpetologica*, 35, 139–145.
- Ehret, D.J. and J.R. Bourque. 2011. An extinct map turtle *Graptemys* (Testudines: Emydidae) from the late Pleistocene of Florida. *Journal of Vertebrate Paleontology*, 31, 575–587.
- Ernst, C.H. and J.E. Lovich. 2009. *Turtles of the United States and Canada*. The Johns Hopkins University Press. 827 pp.
- Ernst, C.H., J.E. Lovich, R.W. Lovich, and R.W. Barbour. 1994. *Turtles of the United*

- States and Canada. Smithsonian Institution Press. 578 pp.
- Esker, D.A., S.L. Forman, and D.K. Butler. 2019. Reconstructing the mass and thermal ecology of North American Pleistocene tortoises. *Paleobiology*, 45, 363–377.
- Estes, R. and B.G. Baez. 1985. Herpetofaunas of North and South America during the Late Cretaceous: evidence for interchange? *In* The Great American Biotic Interchange, F.G. Stehi and S.D. Webb. eds. 139–197. Plenum Press.
- Franz, R. and S.E. Franz. 2004. Gopher tortoise evolution: east vs west. A possible paradigm shift. Twenty-ninth Annual Meeting and Symposium of the Desert Tortoise Council, February 20–23, abstract.
- Franz, R. and I.R. Quitmyer. 2005. A fossil and zooarchaeological history of the gopher tortoise (*Gopherus polyphemus*) in the southeastern United States. *Bulletin of the Florida Museum of Natural History*, 45, 179–199.
- Gibbard, P.L., M.J. Head, and M.C. Walker. 2009. Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. *Journal of Quaternary Science*, 25, 96–102.
- Hay, O.P. 1908. The fossil turtles of North America. Carnegie Institute, Washington. Publication, 75, 1–568.
- Hibbard, C.W. 1960. An interpretation of Pliocene and Pleistocene climates in North America. *Michigan Academy of Science, Arts and Letters*, 62, 5–30.
- Holman, J.A. 1985. Herpetofauna of Ladds Quarry. *National Geographic Research*, 1, 423–436.
- Holman, J.A. 1987. Herpetofauna of the Egelhoff site (Miocene: Barstovian) of north-central Nebraska. *Journal of Vertebrate Paleontology*, 7, 109–120.
- Holman, J.A. 1995. Pleistocene amphibians and reptiles in North America. Oxford University Press. 243 pp.
- Holman, J.A. 1996. The large Pleistocene (Sangmonian) herpetofauna of the Williston IIIA site, north-central Florida. *Herpetological Natural History*, 4, 35–47.
- Holman, J.A. 2000. The Fossil Snakes of North America. Indiana University Press. 357 pp.
- Holman, J.A. 2006. Fossil Salamanders of North America. Indiana University Press. 232 pp.
- Holman, J.A. and U. Fritz. 2005. The box turtle genus *Terrapene* (Testudines: Emydidae) in the Miocene of the USA. *Herpetological Journal*, 15, 81–90.
- Holman, J.A. and D. Parmley. 2005. Noteworthy turtle remains from the late Miocene (late Hemphillian) of northeastern Nebraska. *Texas Journal of Science*, 57, 1–9.
- Holman, J.A. and A.J. Winkler. 1987. A mid-Pleistocene (Irvingtonian) herpetofauna from a cave in southcentral Texas. *Pearce-Sellards Series*, Texas Memorial Museum, The University of Texas at Austin, 44, 1–17.
- Hulbert, R.C. 2001. The Fossil Vertebrates of Florida. University Press of Florida. 350 pp.
- Hulbert, R.C. and A.E. Pratt. 1998. New Pleistocene (Rancholabrean) vertebrate faunas from coastal Georgia. *Journal of Vertebrate Paleontology*, 18, 412–429.
- Jackson, D.R. 1988. A re-examination of fossil turtles of the genus *Trachemys* (Testudinidae: Emydidae). *Herpetologica*, 44, 317–325.
- Jasinski, S.E. 2018. A new slider turtle (Testudines: Emydidae: Deirochelyrinae: *Trachemys*) from the late Hemphillian (late Miocene/early Pliocene) of eastern Tennessee and the evolution of the deirochelyines. *PeerJ* 6:e4338; doi:[10.7717/peerj.4388](https://doi.org/10.7717/peerj.4388).

- Jensen, J.B., C.D. Camp, W. Gibbons, and M.J. Elliott. 2008. Amphibians and Reptiles of Georgia. University of Georgia Press. 575 pp.
- Kurten, B. and E. Anderson. 1980. Pleistocene Mammals of North America. Columbia University Press. 442 pp.
- MacFadden, B.J. and R.C. Hulbert, Jr. 2009. Calibrations of mammoth (*Mammuthus*) dispersal into North America using rare earth elements of Plio-Pleistocene mammals from Florida. *Quaternary Research*, 71, 41–48.
- McDowell, S.B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. *Proceedings of the Zoological Society of London*, 14, 239–279.
- Mead, J.I. and C.J. Bell. 2001. Pliocene amphibians and reptiles from Clark County, Nevada. *Bulletin of the Southern California Academy of Sciences*, 10, 1–11.
- Meylan, P.A. 1984. A history of fossil amphibians and reptiles in Florida. *Florida Paleontological Society, Plaster Jacket*, 44, 5–29.
- Meylan, P.A. 1987. The phylogenetic relationships of soft-shelled turtles (family Trionychidae). *Bulletin of the American Museum of Natural History*, 186, 1–101.
- Meylan, P.A. 1995. Pleistocene amphibians and reptiles from the Leisey Shell Pit, Hillsborough, Florida. *Bulletin of the Florida Museum of Natural History*, 37, 273–297.
- Moodie, K.B. and T.R. Van Devender. 1978. Fossil box turtles (genus *Terrapene*) from Southern Arizona. *Herpetologica*, 34, 172–174.
- Moodie, K.B. and T.R. Van Devender. 1979. Extinction and extirpation in the herpetofauna of the Southern High Plains with emphasis on *Geochelone wilsoni* (Testudinidae). *Herpetologica*, 35, 198–206.
- Morgan, G.S. and S.G. Lucas. 2005. Pleistocene vertebrate faunas in New Mexico from alluvial, fluvial, and lacustrine deposits. *In New Mexico's ice ages*. New Mexico Museum of Natural History and Science Bulletin no. 28, S. Lucas, S. Morgan, and K.E. Zeigler. eds. 185–248.
- Morgan, G.S. and R.B. Ridgway. 1987. Late Pliocene (late Blancan) vertebrates from The St. Petersburg Times site, Pinellas County, Florida, with a brief review of Florida Blancan faunas. *Papers in Florida Paleontology*, 1, 1–22.
- Morgan, G.S., S.G. Lucas, and J.W. Estep. 1998. Pliocene (Blancan) vertebrate fossils from Camp Rice Formation near Tonuco Mountain, Dona Ana County, southern New Mexico. *New Mexico Geological Society, Guidebook, 49th Field Conference*, pp. 237–250.
- Parmalee, P.W., W.E. Klippel, P.A. Meylan, and J.A. Holman. 2002. A late Miocene-early Pliocene population of *Trachemys* (Testudines: Emydidae) from east Tennessee. *Annals of Carnegie Museum*, 71, 233–239.
- Parmley, D. 1992. Turtles from the late Hemphillian (latest Miocene) of Knox County, northeastern Nebraska. *Texas Journal of Science*, 44, 339–348.
- Parmley, D. 1988. Additional Pleistocene amphibians and reptiles from the Seymour Formation, Texas. *Journal of Herpetology*, 22, 82–87.
- Parmley, D., J.H. Hutchison, and J.F. Parham. 2006. Diverse turtle fauna from the late Eocene of Georgia including the oldest records of aquatic testudinoids in southeastern North America. *Journal of Herpetology*, 40, 343–350.
- Parmley, D. and D. Walker. 2003. Snakes of the Pliocene Taunton local fauna of Adams County, Washington with the description of a new colubrid. *Journal of Herpetology*,

- 37, 235–244.
- Parris, D.C. and E. Deschler. 1995. Pleistocene turtles of Port Kennedy Cave (late Irvingtonian), Montgomery County, Pennsylvania. *Journal of Paleontology*, 69, 563–568.
- Powell, R., R. Conant, and J.T. Collins. 2016. *A Field Guide to Reptiles and Amphibians, Eastern and Central North America*. Houghton Mifflin Harcourt Company. 450 pp.
- Preston, R.E. 1979. Late Pleistocene cold-blooded vertebrate faunas from the mid-continental United States. I. Reptilia; Testudines, Crocodylian. *University of Michigan Museum of Paleontology, Papers on Paleontology*, 19, 1–53.
- Rogers, K.L. 1976. Herpetofauna of the Beck Ranch local fauna (upper Pliocene: Blancan) of Texas. *Publication of the Museum, Michigan State University, Paleontological Series*, 1, 163–200.
- Seidel, M.E. and D.R. Jackson. 1990. Evolution and fossil relationships of slider turtles. *In Life History and Ecology of the Slider Turtle*, J.W. Gibbons. ed. 68–73.
- Sobolik, K.D. and D.G. Steele. 1996. An atlas of turtles to facilitate archaeological identifications. The Mammoth Site, Inc., Hot Springs, South Dakota.
- Thomas, T.M., M.C. Grantosky, J.R. Bourque, K.L. Krysko, P.E. Moler, T. Gamble, E. Saurez, E. Leone, K.M. Enge, and J. Roman. 2014. Taxonomic assessment of alligator snapping turtles (Chelydridae: *Macrochelys*), with the description of two new species from the southeastern United States. *Zootaxa*, 3786, 141–165.
- Weaver, W.G. and J.S. Robertson. 1967. A re-evaluation of fossil turtles of the *Chrysemys scripta* group. *Tulane Studies in Geology*, 5, 53–66.
- Webb, R.G. 1975. *Reptiles of Oklahoma*. University of Oklahoma Press. 2nd printing 370 pp.
- Webb, R.G. 1998. *Apalone*. *Catalogue of American Amphibians and Reptiles*, 487:1–7.
- Webb, S.D. 1974. Chronology of Florida Pleistocene mammals. *In Pleistocene Mammals of Florida*, S.D. Webb. ed. 5–31. University of Florida Press.
- Webb, S.D. 1974. Chronology of Florida Pleistocene mammals. Pp. 5–31 *in* S.D. Webb (ed), *Pleistocene Mammals of Florida*. University of Florida Press.
- Webb, S.D. and A.D. Barnosky. 1989. Faunal dynamics of Pleistocene mammals. *Annual Review of Earth and Planetary Sciences*, 17, 413–438.
- Woodburne, M.O. (ed.). 2004. *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. Columbia University Press.