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Cover Photograph. Snake fossils from Clark Quarry, Glynn Co., GA. *Thamnophis* sp. indet. trunk vertebra (GCVP 17714) in dorsal (top left) and lateral (bottom left) view. On the right is a *Nerodia* (Group 3) trunk vertebra (GCVP 11706) in lateral view. Photograph © Heidi Mead, Georgia College.

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Amphibians and Squamates from the Late Pleistocene (Rancholabrean) Clark Quarry, Coastal Georgia

Dennis Parmley^{1,*}, Joshua L. Clark², and Alfred J. Mead³

Abstract - Pleistocene amphibians and squamates are reported from a coastal Georgia site known as the Clark Quarry, located in Glynn County. Although dominated by skeletal remains of giant bison and Columbian mammoths, the site has yielded a relatively diverse microfossil collection of amphibians and squamates to include two species of frogs, two salamanders, one lizard, and at least (conservatively) 10 snake species, for a total of 15 genera. Collectively, these microfossils provide noteworthy information about the taxonomic diversity and paleoecology of the Late Pleistocene paleoherpetofauna of southeast Georgia. The paleofauna suggests the presence of an aquatic habitat in a parkland during the time of deposition.

Introduction

Amphibians and reptiles are well documented from the North American Pleistocene, especially the Late Pleistocene (e.g., Holman 1995, 2000, 2003, 2006), but Pleistocene amphibians and reptiles from Georgia are poorly represented in the literature. Previously reported Pleistocene sites from Georgia that have yielded important collections of amphibians and reptiles include Ladds Quarry in Bartow Co. (northwest Georgia; Holman 1967, 1985a, b; Wilson 1975), Kingston Saltpeter Cave in Bartow Co. (northwest Georgia, Fay 1988) and Ile of Hope and Mayfair sites of Chatham Co. (coastal southeast Georgia, Hulbert and Pratt 1998). Additionally, a Late Pleistocene coastal site known as the Clark Quarry in Glynn Co. (southeast Georgia) was discovered in 2001 on private land near Brunswick (Mead and Spell 2002; also see Mead et al. 2006). Patterson et al. (2012) provide the most recent and most detailed information of the history and geology of the Clark Quarry fossil site. Clark et al. (2005) and Parmley et al. (2007) discussed some of the amphibians and reptiles known from the Clark Quarry local fauna (l.f.) and Clark (2009) provided a more detailed report of the paleoherpetofauna as it was known then. Here we provide for the first time an updated and detailed report of the Clark Quarry (hereafter CQ) paleoherpetofauna exclusive of the chelonians (the subject of an ongoing independent study). We offer a noteworthy picture of the herpetological life of southeastern North America approximately 21,000 radiocarbon years before the present; the CQ fossils offer insights of the taxonomic diversity and paleoecology of amphibians and reptiles from this region during the Late Pleistocene.

Geological Setting and Age

The CQ is a coastal site located near Brunswick parallel to the Brunswick Canal (see fig. 1 of Patterson et al. 2012). From a depositional standpoint, it is a fluvial deposit that formed

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as a cut-and-fill (probably) within older Satilla Formation sediments just prior to the Last Glacial Maximum. Radiocarbon dating of CQ mammoth and bison fossils place it as a Late Pleistocene site (Rancholabrean NALMA = North American Land Mammal Age) between 19,840 and 22,240 radiocarbon years before the present (rcybp; see table 1 of Patterson et al. 2012). Patterson et al. (2012:166) speculated that at about 20,000 rcybp sea level along the Georgia coast may have been about 80 m lower than today, “placing the CQ approximately 100 km inland”.

Materials and Methods

Clark Quarry Fossil Locality

Between the years 2001 and 2009, parties from Georgia College led by A.J. Mead made numerous excavation trips to the CQ. These excavations resulted in the collection of a moderately diverse but important paleofauna of fish, amphibians, reptiles, birds, and mammals dominated by *Mammuthus columbi* Falconer (Columbian Mammoth) and *Bison latifrons* Harlan (Long-horn Bison). Patterson et al. (2012) provide more detailed locality information (including a map) and information on the geology and vertebrate fauna of the CQ known at that time. Other references pertaining to the CQ include Bahn 2006; Bahn and Mead 2004, 2005; Clark et al. 2005; Clark et al. 2006; Mead and Spell 2002; Mead et al. 2006; Parmley et al. 2007; and references within.

Following the methods of Hibbard (1949), microfossils were collected from the CQ by traditional screen washing, drying, and sorting of excavated fossiliferous matrix. Unless noted, all of the CQ amphibian and reptile fossils discussed here are cataloged in the vertebrate paleontological collection of Georgia College (GCVP). Identification of the CQ amphibians and reptiles are to the lowest practical taxon based on (1) comparisons to modern comparative specimens in the comprehensive Georgia College herpetological skeletal collection and (2) pertinent information in the literature.

All fossil photographs were taken by GCSU employee Heidi Mead (Fossil Preparation Technician, Biological and Environmental Sciences) using a Cannon EOS D5SR, Lens MP-65mm and are used with her permission. The scale bar of all fossils figured = 2 mm.

Terminology

Terminology of anuran bones follows Parmley et al. (2010) and Parmley et al. (2015) and mainly Gardner (2003a, b) for salamanders of the families Amphiumidae and Sirenidae. Lizard and snake bone terminology follows Chovanec (2014) and Holman (1995, 2000), but also see Rage et al. (2008). Anatomical abbreviations and ratios of vertebral structures used within this paper include: CL, centrum length; ZW, zygosphenes greatest width; NSL, neural spine length (length along the top of the neural spine); NSH, greatest neural spine height; MNW, mid-neural arch width; CL/NAW, centrum length/mid-neural arch width ratio (see Parmley 1986a); NSL/ZW, neural spine length/zygosphenes width ratio. Additionally, SV is used to denote a standard snout to vent length of a given taxon and TL denotes a standard length from the tip of the snout to the end of the tail.

Taxonomic Note

Generic and common names follow Crother (2008) noting, however, that relatively recently suggested changes of long-standing generic names (e.g., Collins and Taggard 2009) are considered here as subgenera (Smith and Chiszar 2006).

Systematic Paleontology

Class Amphibia Gray
Subclass Lissamphibia Haeckel
Order Anura Fischer von Waldheim
Family Ranidae Batsch
Genus *Rana* (s.l. *Lithobates* and *Rana*) Linnaeus
Rana sp. indet. (Fig. 1A)

Material—110 ilia (GCVP 11802; 11846–11849; 11851–11885; 17755–17833; 17835–17843; 19828; 19858); 1 left scapula (GCVP 17762).

Remarks—Ranid ilia are common elements in the CQ l.f. These fossils are unambiguously assigned to *Rana* based on the presence (or evidence) of the following features

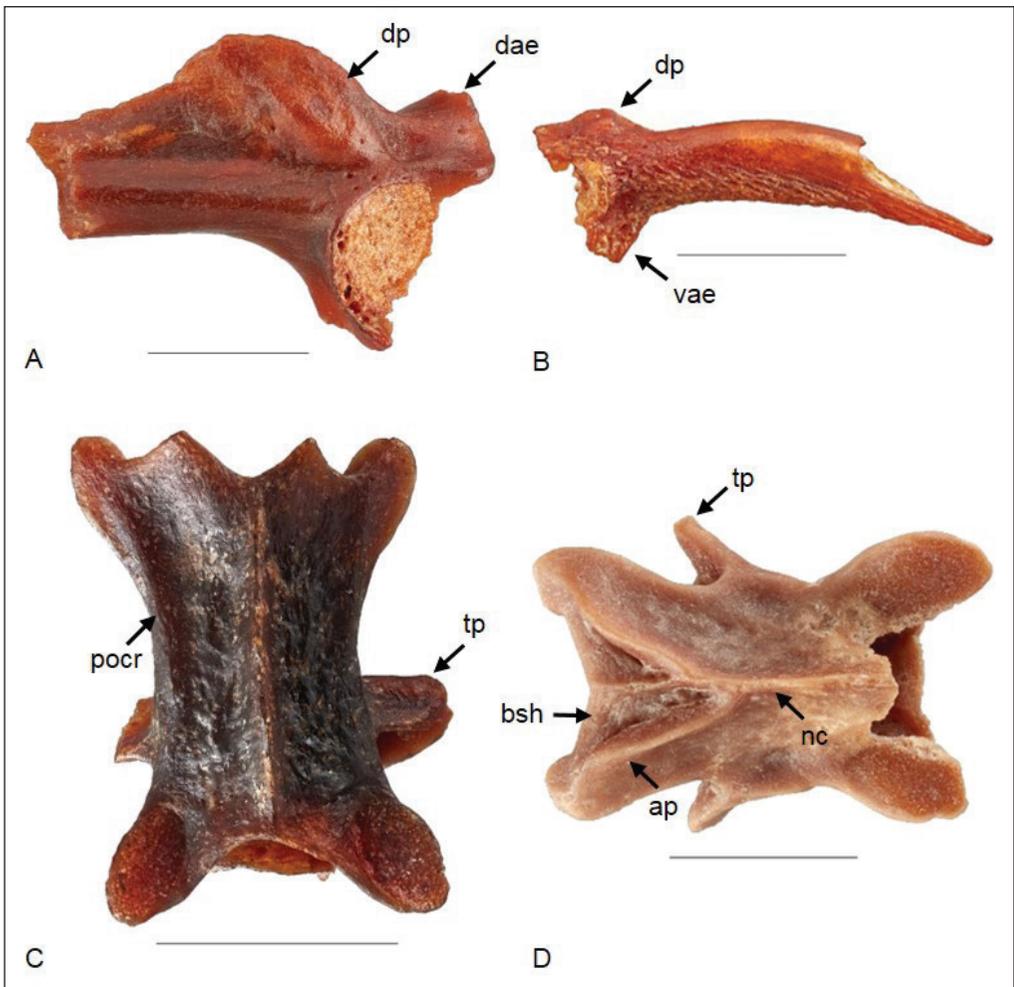


Figure 1. Anuran and salamander fossils from Clark Quarry, Glynn Co., GA. (A) *Rana* sp. indet. ilium (GCVP 11802) in lateral view; dp = dorsal prominence, dae = dorsal acetabular expansion. (B) *Bufo* sp. indet. ilium (GCVP 17772) in lateral view; dp = dorsal prominence, vae = ventral acetabular expansion. (C) *Amphiuma* sp. indet. trunk vertebra (GCVP 8310) in dorsal view; pocr = postzygapophyseal crest, tp = transverse process. (D) *Siren* sp. indet. trunk vertebra (GCVP 17704) in dorsal view; nc = neural crest, bsh = bone sheet, ap = aliform process, tp = transverse process.

or structures: (1) well-developed dorsal ilial crest (often damaged); (2) smooth dorsal prominence that may be slightly laterally deflected, but usually straight (Parmley et al. 2010); (3) dorsal acetabular expansion angled anteriorly (Holman 1962, 2003; Parmley 1992, Parmley and Peck 2002, Parmley et al. 2010, Parmley et al. 2015) and in-line with the ilial crest; and (4) a preacetabular fossa often present. Although the polarities of these characteristics are not yet clearly understood, collectively they make *Rana* ilia (at least North American taxa) easily identified at the generic level. Species level identification of *Rana* ilia, however, is controversial and certainly not possible in most cases. This issue has been discussed many times (e.g., Chantell 1971, Holman 2003, Parmley 1988a, Parmley et al. 2010). For example, Chantell (1971) commented on this very problem over 48 years ago, noting that the lack of fossil *Rana* ilia to study was not the problem, but rather their homogenous morphology makes them non-identifiable at the specific level. After examining hundreds of Miocene to Holocene ranid ilia and studying a large (1000+) taxonomically and geographically diverse collection of modern ranid ilia, we concur that North American members of this taxon cannot be differentiated at the specific level on the basis of ilial differences. The single scapula (GCVF 17762) is characteristic of this genus on the basis that the coracoid articular process lies near the clavicular articular forming a narrow glenoid opening (Parmley 1989).

It is interesting to note that the collection of CQ ranid ilia represents predominantly small frogs (approximately 85% in the 38 to 58 mm SV range). They appear to represent either a small species of *Rana*, certainly smaller than adult *R. catesbeiana* Boulenger (American Bullfrog) or other species of similar size, or perhaps young frogs of a larger species. It is not unusual to find “swarms” of post-metamorphic juvenile ranids inhabiting the shoreline of a pond or marsh (Parmley, pers. observ.). On the basis of right and left ilia, at least 58 individuals are represented in the paleofauna.

Ranid fossils first appear in North America during the Barstovian NALMA (Middle Miocene ca. 14 Ma; Woodburne 2004) and are common elements of Late Miocene to Holocene North American paleoherpetofaunas. As Parmley et al. (2010) previously noted, given that ranid frogs have been in North America at least 14 Ma (likely longer), and given the relatively diverse number of Recent North American and world-wide species (at least 28 North American species, s.l., Collins and Taggart 2009; ca. 380 world-wide, Frost 2017), it is likely that over this time period new species evolved and became extinct, all undetected by fossil remains.

Family Bufonidae Gray
Genus *Bufo* (s.l. *Anaxyrus*, *Ollotis*, *Rhinella*) Laurenti
Bufo sp. indet. (Fig. 1B)

Material—One right ilium (GCVF 1777).

Remarks—This ilium is unambiguously a *Bufo* species based mainly on its overall robust build (unlike North American ascaphids, hylids, microhylids, pelobatids, and ranids), lack of any evidence of a true ilial crest, and in having a well-defined, low and domed dorsal prominence (Tuber Superior of some). Moreover, there is evidence of a well-developed, but low, dorsal protuberance. The dorsal acetabular expansion is missing, but the ventral acetabular expansion is complete enough to determine it was relatively wide and short. While a well-defined and deep preacetabular fossa exists, there is no evidence of a preacetabular foramen.

The difficulty of the specific identification of isolated *Bufo* ilia (fossil and Recent) has been well articulated by Bever (2005), although there are species that clearly are iden-

tifiable to the specific level on the basis of ilial morphology (e.g., *B. holmani*, Parmley 1992). Nonetheless, the CQ ilium is somewhat of an enigma. The overall size of the ilium is equivalent to a large adult *B. quercicus*, Holbrook (Oak Toad), a small toad (SV = 35 mm) endemic to the coastal regions of southeastern United States (Jensen et al. 2008), which includes the area of the present-day fossil site. Despite the fact the fossil is badly eroded, it is not like *B. quercicus* in being distinctly more robust. It is possible that the ilium is of an immature individual of a much larger species. After comparing the fossil to ilia of every modern species currently living in the southeastern United States, as well as most western US species, and equivalent-sized extinct species (via comparative specimens and literature descriptions with illustrations), we believe the prudent identification of the ilium should be to genus only. Unfortunately, this is the only CQ bufonid element thus far available for study.

Order Caudata Scopoli
Family Amphiumidae Gray
Genus *Amphiuma* Garden
Amphiuma sp. indet. (Fig. 1C)

Material—Four trunk vertebrae (GCVP 8310; 8311; 11910; 19812).

Remarks—Parmley et al. (2007, fig. 1) previously reported in detail on two vertebrae of this endemic paedomorphic, aquatic North American salamander genus from the CQ (GCVP 8310, 8311). *Amphiuma* vertebrae are distinctive and easily identified using criteria given by Gardner (2003a) and Parmley et al. (2007). This salamander occurs today in the southeastern US sympatrically with the other North American eel-like obligate aquatic salamander *Siren* (including Glynn Co.; Jensen et al. 2008). The vertebrae of *Amphiuma* and the CQ fossils distinctly differ from those of *Siren* in several ways: (1) the presence of a pair of postzygapophyseal crests (an autapomorphic structure in amphiumids; Estes 1969, 1981; Gardner 2003a, fig. 1; Naylor 1978), and (2) the lack of a thin sheet of bone between aliform processes (well-developed in *Siren*; Parmley et al. 2007; Fig. 1D). Moreover, the angle of the transverse processes of *Amphiuma* are perpendicular (or nearly so) to the long axis of the centrum, but strongly angled in *Siren* (Parmley et al. 2007, fig. 1; compare Fig. 1C and D).

Other than the diminutive species *A. pholeter* Neil (One-toed Amphiuma; discussed below), *A. means* Garden in Smith (Two-toed Amphiuma) is the only large-sized *Amphiuma* (adult size 460–1160 mm TL; Petranka 1998) occurring in Georgia today. The only other large amphiuma is *A. tridactylum* Cuvier (Three-toed Amphiuma; 460–1060 mm TL); a species that occurs no closer to Glynn Co. than about east-central Alabama (Petranka 1998). As previously mentioned *A. pholeter* occurs in Georgia but it is not represented in the CQ fauna for the following reasons: (1) it occurs today only in a small section of the southwest corner of the state; and (2) most importantly, however, the CQ vertebrae are clearly larger than those of this species; a species that reaches a TL of only about 240–280 mm (Jensen et al. 2008, Parmley et al. 2007; Parmley, pers. observ.). Because the CQ vertebrae are identical to *A. means* and *A. tridactylum* in all discernible ways to include size, we suggest that only a generic identification of the fossils is reasonable. Moreover, it is possible the fossils represent an extinct amphiumid species.

Amphiumid salamanders date back to the Late Paleocene (ca. 55–56 Ma) of the western United States and Canada, and they may have been present in the Middle Miocene of Texas (Estes 1981, Gardner 2003a, Salthé 1973). Reports of *Amphiuma* as a fossil are, however,

well known from the Pleistocene of Texas, Florida, Georgia and South Carolina (e.g., Holman 2006, Hulbert 2001, Hulbert and Pratt 1998, Knight and Cicimurri 2010, Parmley et al. 2007).

Family Sirenidae Gray
Genus *Siren* Linnaeus
Siren sp. indet. (Fig. 1D)

Material—Two vertebrae (GCVP 17704; 17705).

Remarks—These vertebrae are well preserved and based on differences in anatomy with the amphiumid vertebrae discussed above, belong to a sirenid salamander, a unique group of paedomorphic aquatic North American salamanders. Gardner (2003b) was not able to identify autapomorphies for the family Sirenidae (at least not using vertebrae), but suggested a suite of characters that are collectively unique to the two living genera of the family (*Siren* and *Pseudobranchius* Gray, Dwarf sirens). The following vertebral characters confidently identify the CQ vertebrae as a sirenid: (1) elongate morphology; (2) presence of well-developed alar processes (smaller in amphiumid salamanders), but not always discernable on damaged or eroded fossils; (3) transverse processes angled posteriorly; and (4) dorsal face of neural arch with a Y-shaped arrangement of crests composed of a median neural crest (“leg” of the Y) that diverges posteriorly as two anterior aliform crest processes (“arms” of the Y) onto the postzygapophyseal processes. An additional character we found useful in identifying sirenid vertebrae is the presence of a flat sheet of bone that lies between the aliform processes (easily seen in dorsal view; Parmley et al. 2007; Fig. 1D). This sheet of bone appears to be part of the roof of the posterior extent of the neural arch and we believe it is unique (an autapomorphy) to sirenid salamanders as we found no evidence of it occurring in the North American salamander families Ambystomatidae, Amphiumidae, Cryptobranchidae, Dicamptodontidae, Plethodontidae, Proteidae, Rhyacotritonidae, and Salamandridae. We excluded *Habrosaurus* on the basis of geographic and temporal considerations, as this taxon is known only from the Late Cretaceous to Middle Paleocene of the North American Western Interior (Gardner 2003b). Of the two modern genera, the vertebrae of *Siren* (and the fossils) differ from those of the diminutive genus *Pseudobranchius* in being distinctly larger with the lower margin of the centrum straight (or nearly so) viewed laterally, rather than concave (often distinctly so) as in *Pseudobranchius* (Goin and Auffenberg 1955, Holman 1977). Both of the living species *S. intermedia* Barnes (Lesser Siren) and *S. lacertina* Osterdam (Greater Siren) presently occur at, or near, the fossil site area (Jensen et al. 2008, Petraska 1998). *Siren lacertina* is the larger of the two species reaching TL of 915 mm, versus 380 mm for *S. intermedia*. Nonetheless, only a generic assignment of the fossils is possible given that (1) the CQ vertebrae fall well within the size-range of both species (adult *S. intermedia* and smaller individuals of *S. lacertina*) and (2) we could not identify vertebral characters or features that confidently differentiate these sister species. Hulbert and Pratt (1998) tentatively identified *Siren* vertebrae from the coastal Pleistocene Isle of Hope l.f. to the smaller species *S. intermedia* on the basis of vertebral size.

Siren has a relatively long and geographically diverse fossil record dating back to the Middle Eocene (ca. 42 Ma) of Wyoming (Gardner 2003b), Miocene of Florida, Nebraska, and Texas (Holman 2006), Pliocene of Florida (Morgan and Hulbert 1995), and Pleistocene of Florida (Holman 2006, Hulbert 2001) and Georgia (Hulbert and Pratt 1998).

Class Reptilia Laurenti
Order Squamata Opperl
Suborder Sauria McCartney
Family Polychridae Fitzinger
Genus *Anolis* Daudin
Anolis sp. indet. (Fig. 2A, B)

Material—Two left dentaries (GCVF 17711; 17712).

Remarks—Dentaries of *Anolis* are distinct among North American lizards on the basis of their: (1) delicate build; (2) low, slender and straight (viewed laterally) profile; (3) fused Meckelian Groove with the possible exception of a tiny foramen at the symphysis (not always present); and (4) having the first 5–6 anterior teeth unicuspid, to weakly tricuspid, and most of the posterior teeth transversely wide and distinctly tricuspid with unstriated crowns (the last 3–4 teeth are especially wide and robust). Other North American lizards have anterior unicuspid and posterior tricuspid teeth (Holman 1995), but unlike *Anolis*, the Meckelian Groove is open to some degree, often widely. Chovanec (2014) noted the presence of a slit-shaped opening at the posterior end of the dentary (best seen in lingual view) that extends to near the last tooth in the dentary in *Anolis*. He suggested this opening “represents the combined alveolar-mylohyoid foramen” (CAMF). We examined 60 dentaries of Recent *Anolis* and found the CAMF present in all specimens to some degree. In a few specimens it reached the base of the last tooth. One of the CQ fossils (GCVF 17711) is complete enough to determine the presence of this opening, the other (GCVF 17712) is missing too much of the posterior end to detect a CAMF. *Anolis carolensis* Voigt in Cuvier and Voigt (Green Anole) is the only native anole in the United States and may have been present in the CQ paleofauna. However, given the fact that there are at least 400 species of anole (Castaenda

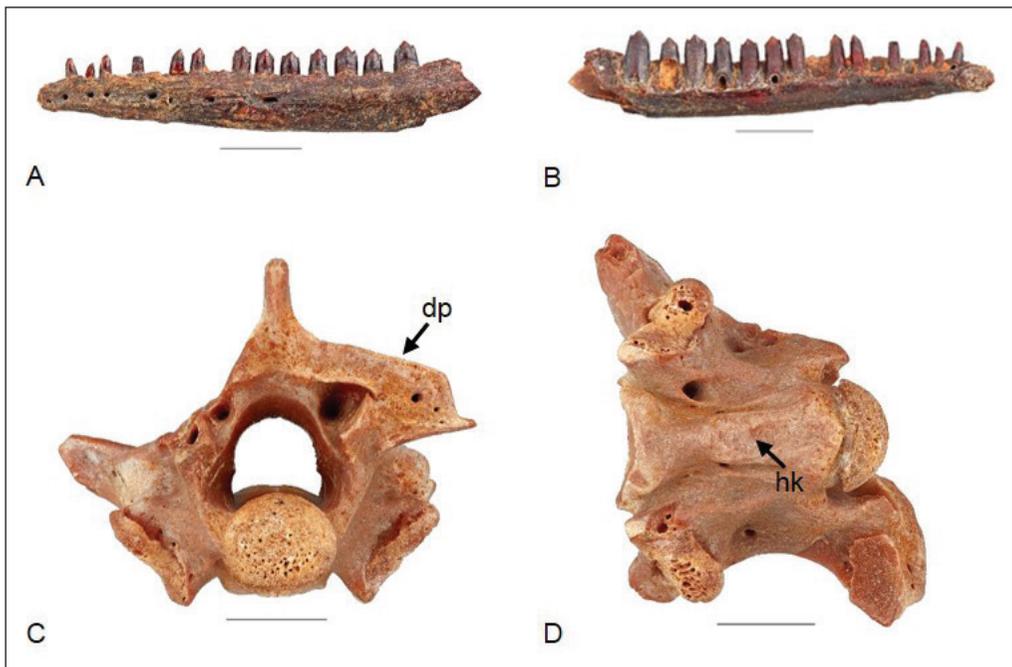


Figure 2. Lizard and snake fossils from Clark Quarry, Glynn Co., GA. *Anolis* sp. indet. dentary (GCVF 17712) in labial (A) and lingual (B) view. *Heterodon* sp. indet. trunk vertebra (GCVF 19802) in posterior (C) and ventral (D) view; dp = depressed neural arch, hk = hemal keel in ventral view.

and de Queiroz 2013, Losos and Thorp 2004) and little is published about the osteological features of many species, a tentative generic assignment of the CQ fossils is best at this time.

Hulbert (2001) mentioned that *Anolis* may have been present in the Late Miocene of Florida, but suggests the earliest known confirmed appearance is Middle Pleistocene. Chovanec (2014), however, identified the genus from the Arikarean NALMA of Florida (Brookeville 2 l.f.; Late Oligocene, ca. 26-28 Ma; also see Morgan and Czaplewski 2012). Holman (1995) reported several Pleistocene records of this genus in Georgia.

Suborder Serpentes Linnaeus

(In Holman 2000: suborders Scolecophidia Dmeril and Bibron; Alethinophidia Nopcsa)

Underwood (1967) subdivided this suborder into three infraorders: (1) Scolecophidia (blind snakes), basal lineage (see Heise et al. 1995); (2) Henodphidia (boas, pythons, and relatives), sometimes referred to as the “primitive” snakes; and (3) Caenophidia (Superfamily Colubroidea in Holman 2000), advanced snakes and the dominant clade today that includes mainly the subclades Viperidae, Elapidae, and particularly Colubridae in North America. Among the CQ snakes, other than one viperid, only members of the advanced family Colubridae are represented. This large and diverse family has been divided into subfamilies by some workers: Colubrinae, Xenodontinae (primitive and likely polyphyletic), and Natricinae, all of which are present in the CQ snake fauna. Additional details and discussion of these subfamilies can be found in Holman (2000), Lawson et al. (2005) and Smith et al. (1977).

Family Colubridae Oppel

Colubridae is the largest snake family in terms of numbers and taxonomic diversity. The family consists of at least 1,800 species world-wide, with species occurring on all continents except Antarctica. A detailed discussion of this family is beyond the scope of this paper, but phylogenetic systematics and improved molecular techniques are proving that this is a complex, and certainly polyphyletic, clade of snakes. In North America, the earliest species of colubrid is known from the Late Eocene (36.0–34.2 Ma) of central Georgia (Parmley and Holman 2003). For further discussion of this family see Parmley and Hunter (2010:529).

gen. et sp. indet.

Material—Five vertebrae (GCVF 19691–19693; 19825; 19827).

Remarks—Although variation occurs in Colubridae vertebrae, the most consistent characteristics are: (1) lightly built; (2) neural spines long, often thin and extend to the roof of the zygosphenes; (3) prezygapophyseal accessory processes well developed; (4) zygosphenes wide and thin anteriorly; (5) paradiapophyses distinctly divided into diapophyseal and parapophyseal units; (6) neural arches not distinctly posteriorly upswept; (7) paracotylar foramina present; (8) hemal keels distinct; and (9) subcentral ridges present (Holman 1981, 1984, 2000; Rage et al. 1992). GCVF 19691–19693, 19825, and 19827 are damaged, yet retain characteristics diagnostic to Colubridae.

Subfamily Xenodontinae Cope

Xenodontinae is a large complex clade of predominantly neotropical snakes, many of which are poorly studied. North American taxa (considered to be relics, Holman 2000) include at least 11 genera, but only two are of morphological concern in the CQ paleoherpetofauna: *Heterodon* and *Farancia*.

Genus *Heterodon* Latreille in Sonnini and Latreille
Heterodon sp. indet. (Fig. 2C, D)

Material—One trunk vertebra (GCVP 19802).

Remarks—Overall, GCVP 19802 is well-preserved and characterized by: (1) a CL/NAW ratio of 1.13 indicating a vertebral shape that is short and wide (Parmley 1986a) when viewed dorsally; (2) a depressed neural arch; and (3) a hemal keel that is broad and flat. This combination of characteristics of the CQ vertebra (CL=5.21 mm) is typical of two North American xenodontine snakes, *Heterodon* and *Farancia* (see Holman 2000, Meylan 1982, and Parmley and Hunter 2010). Holman (2000) commented on the differentiation of these genera, noting that *Heterodon* usually has a more depressed neural arch than *Farancia*. On the basis of numerous modern comparative specimens with vertebrae in the size range of the CQ fossil, we found an additional character that differentiates the genera. The hemal keel of *Heterodon* and GCVP 19802 (slightly damaged) is broad, low and flat to slightly domed; whereas those of *Farancia* are more variable in shape, but not as broad as in *Heterodon*, and often constricted medially or anteriorly (rarely seen in *Heterodon*). Thus, we suggest GCVP 19802 represents *Heterodon* rather than *Farancia*.

All three of the living species of *Heterodon* have been reported from the North American Pleistocene (Holman 2000, Parmley and Hunter 2010): *H. simus* (Southern Hognose); *H. platirhinos* (Eastern Hognose); and *H. nasicus* (Western Hognose). Auffenberg (1963) arranged the living species into two groups on the basis of vertebral characteristics (*H. platirhinos* and *H. simus/nasicus*; also see Holman 2000 and literature within). Today two species of *Heterodon* occur in Glynn Co. (*H. simus* and *H. platirhinos*; Jensen et al. 2008) and both species have been reported on the basis of vertebral remains from Early and Late Pleistocene sites in Florida (Holman 2000, Hulbert 2001). Of these, only *H. platirhinos*, the largest of the three species, has been reported from the Late Pleistocene of Georgia (Fay 1988).

After careful and critical examination of numerous skeletons of all three species of living *Heterodon* from a wide geographical distribution, we are of the opinion that the species cannot reliably be differentiated on the basis of vertebral characters and features. We do contend that *H. platirhinos* is the largest species and bears the largest vertebrae. Nonetheless, if a fossil *Heterodon* vertebra is within the size range of all three species, as is the case with the CQ specimen, then vertebral size is of no diagnostic value. Thus, we offer only a generic identification of GCVP 19802.

The fossil history of *Heterodon* is still in question (Parmley and Hunter 2010). For example, Head et al. (2016) reported the extinct *H. plionasicus* from the Middle Pliocene of Kansas to be the oldest unambiguous record of *Heterodon*. We consider Late Miocene records from the Great Plains to represent the earliest records (Parmley and Hunter 2010 and references within). Pleistocene records of this genus are, however, common (Holman 1995, 2000).

Subfamily Natricinae Bonaparte

The separation of isolated natricine vertebrae from other snake subfamilies or clades within the Colubridae has been a topic of debate and overall discussion for several years now (e.g., Fay 1988, Meylan 1982, Parmley 1988b, Parmley and Holman 1995, Parmley and Hunter 2010; among others). The Caenophidia clade of snakes (a diverse, advanced group) share similar vertebral features. Here we briefly discuss how we separated the natricine snakes discussed in this study from other caenophidians.

Notably among these cenophidian clades, colubrine snakes bear hypapophyses only along the anterior section of their vertebral column. They are (mostly) posteriorly directed and flat along the ventral surface (often quite more so than in the other subfamilies of this clade). In contrast, natricines, viperids, and elapids bear vertebral hypapophyses along the entire pre-caudal vertebral column. Natricine vertebrae, however, differ from those of the colubrine in having relatively wider, and more laterally compressed, hypapophyses. In viperids and elapids the hypapophyses are more spine-like. Moreover, North American elapid hypapophyses are shorter and noticeably more posteriorly directed than those of medium to large sized natricines and viperids.

Genus *Seminatrix* Cope
Seminatrix sp. indet.

Material—Two vertebrae (GCVP 17701; 17719).

Remarks—Neither Auffenberg (1963), Holman (1995, 2000) nor Meylan (1982) reported fossil remains of *Seminatrix* in their extensive works on fossil snakes of North America (Auffenberg and Meylan's works were often limited to taxa of the southeastern region of the US). Moreover, Hulbert's (2001) review of the fossil vertebrates of Florida did not mention *Seminatrix* from the Miocene or Pleistocene of this southern neighboring state. Here we report one relatively well-preserved pre-caudal trunk vertebra (GCVP 17719), and one damaged pre-caudal vertebra (GCVP 17701), of *Seminatrix*. This natricine can be generically distinguished from all other small natricine snakes of the eastern United States (*Storeria*, *Virginia*, *Regina*, small individuals of *Thamnophis*) based on a combination of characters and features. In overall shape, *Seminatrix* vertebrae are wider, in addition to being more robust with shorter (in length) but higher neural spines, than seen in *Virginia*, *Storeria* and similar-sized *Thamnophis*. *Seminatrix* vertebrae and the CQ fossils are most easily confused with the trunk vertebrae of small individuals of *Regina* Baird and Girard, especially *R. rigida* Say (Glossy Crayfish Snake). When compared side-by-side, however, *Seminatrix* (and the CQ fossils) consistently have: (1) lower, thicker neural spines; (2) higher neural arches; (3) shorter accessory processes that are often positioned more perpendicular to the long axis of the centrum than in *Regina*; (4) smaller condyles; and (5) longer, less truncated hypapophyses although, this characteristic does exhibit some degree of interspecific variation. Nonetheless, collectively these differences separate *Seminatrix* from equal-sized *Regina* vertebrae.

Seminatrix appears to be relatively easily identified at the generic level, but we are more hesitant with a specific identification of the CQ fossils mainly because they exhibit some degree of damage. The vertebral size of the best-preserved fossil (GCVP 17701) indicates an adult snake with a TL of about 225 mm, which is well within the maximum 380 mm TL of the endemic Coastal Plain species *S. pygaea* Cope (Black Swamp Snake; Jensen et al. 2008). The more damaged vertebra (GCVP 17719) appears to be from a snake about 50 mm smaller. It is likely that *S. pygaea* is the species represented in the CQ paleoherpetofauna, but better preserved fossil material is needed to confirm this identification. As a taxonomic note, some workers consider *S. pygaea* to be in the genus *Liodytes* Cope (McVay and Carstens 2013).

Genus *Storeria* Baird and Girard
Storeria sp. indet. (Fig. 3A, B)

Material—10 trunk vertebrae (GCVP 11794; 11798–11801; 11715–11719).

Remarks—These vertebrae represent small but adult natricine snakes indicative of the genus *Storeria*. They clearly differ from *Thamnophis*, *Regina*, and *Seminatrix* in being smaller

overall, longer, and narrower in dorsal view (vs. square and wide in *Regina* and to a lesser degree, *Thamnophis* and *Seminatrix*). The differentiation of *Storeria* and the similar-sized natricine *Virginia* is, however, more problematic. Both genera have relatively long, narrow precaudal vertebrae, low and long neural spines, and short posteriorly directed hypapophyses. Nonetheless, the following differences taken collectively distinguish *Storeria* vertebrae from those of *Virginia*: (1) slightly wider MNW (mean 1.15 mm for 10 CQ *Storeria* fossils and 0.93 mm for three CQ *Virginia* fossils); (2) neural arches higher (especially viewed posteriorly); and (3) neural spines lower, usually thinner, with the posterior borders extending past the posterior borders of the neural arches (neural spine overhangs), but stop at, or extend only slightly past, the borders in *Virginia*. Moreover, according to Auffenberg (1963; also see Fay 1988), *Storeria* has greater NSL/ZW ratios than *Virginia*. We measured 15 Recent specimens (10 vertebrae per specimen) of each genus and found this to gener-

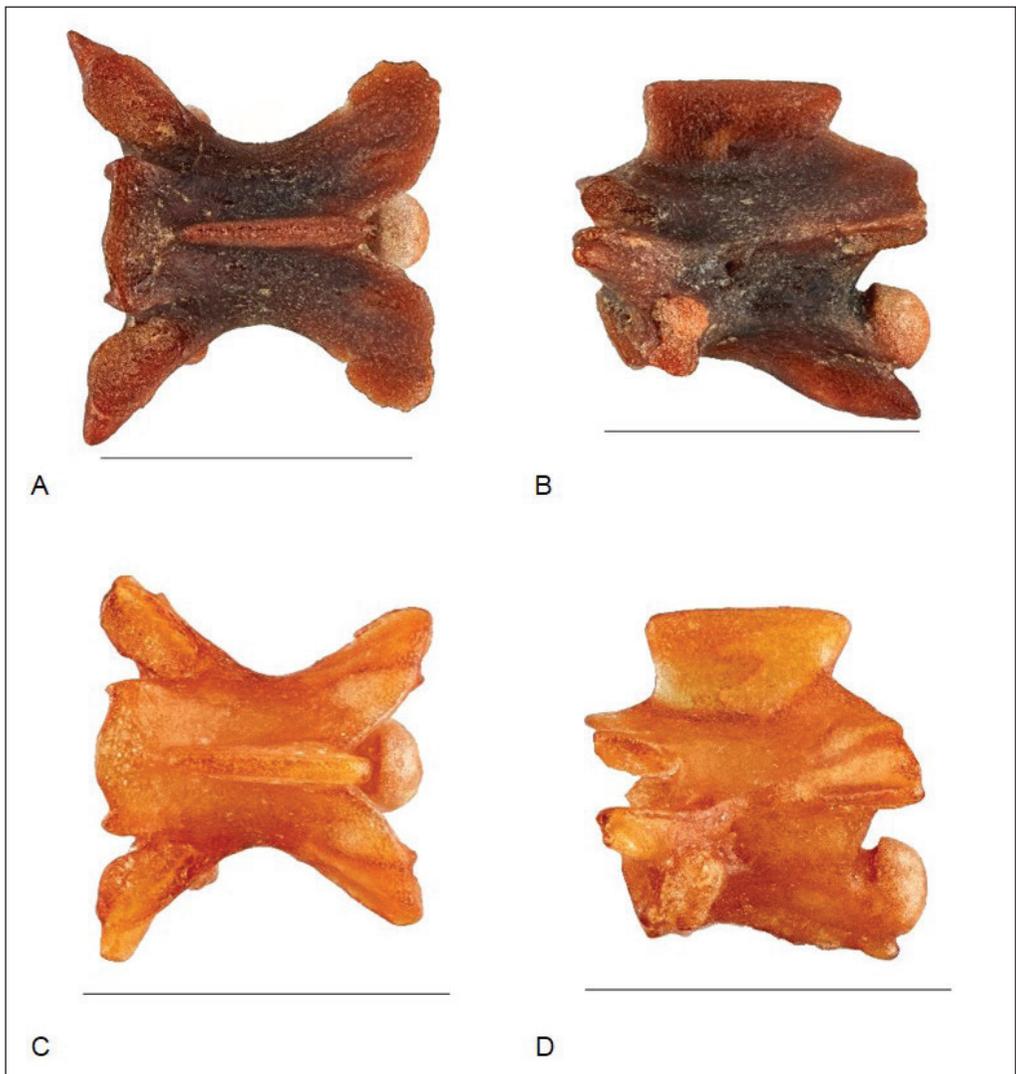


Figure 3. Snake fossils from Clark Quarry, Glynn Co., GA. *Storeria* sp. indet. trunk vertebra (GCVP 17718) in dorsal (A) and lateral (B) view. *Virginia* sp. indet. trunk vertebra (GCVP 17702) in dorsal (C) and lateral (D) view.

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ally be true. For Recent *Storeria* the mean NSL/ZW ratio was 1.07, and for Recent *Virginia* it was 0.99, although we found there was slight overlap in this measurement. Nonetheless the mean ratio of the CQ vertebrae was 1.05, thus supporting our identification to *Storeria*.

Two species of *Storeria* (*S. dekayi* Holbrook [Brown Snake]; *S. occipitamaculata* Storer [Red-bellied Snake]) presently occur sympatrically in North America over most of the eastern one-half of the United States, including the CQ fossil site area (Jensen et al. 2008). We examined numerous skeletal specimens of both species and could not determine reliable vertebral characteristics to separate the taxa with any degree of certainty. On this basis, we suggest only a generic identification of the CQ fossils.

Genus *Virginia* Baird and Girard
Virginia sp. indet. (Fig. 3C, D)

Material—Three trunk vertebrae (GCVP 17702; 19813; 19814).

Remarks—These vertebrae are well-preserved. They are differentiated from *Storeria* and assigned to *Virginia* on the basis of slightly wider MNW (see *Storeria* above) viewed dorsally and more importantly in having lower neural arches and noticeably higher and thicker neural spines. Dorsally the neural spine of one of the CQ specimens (GCVP 17702) does, however, extend slightly past the posterior edge of the neural arch, which is more characteristic of *Storeria*. Nonetheless, the other characteristics of GCSV 17702 and its relatively low NSL/ZW ratio (0.98) support our identification to *Virginia*.

Two species of *Virginia* presently occur in southeastern Georgia (Jensen et al. 2008): *V. striatula* Linnaeus (Rough Earthsnake) and *V. valeriae* Baird and Girard (Smooth Earthsnake). *Virginia striatula* occurs in Glynn Co. today, while *V. valeriae* occurs as close as Brantley and Wayne counties, approximately 85 km to the west. We suggest only a generic identification of the CQ fossils for two reasons: (1) after examining numerous skeletal specimens of both taxa, we cannot find any consistently reliable vertebral characters that separate the two species; and (2) it is possible they were sympatric in the CQ area during the Pleistocene given their close proximity today.

Genus *Thamnophis* Fitzinger
Thamnophis sp. indet. (Fig. 4A, B)

Material—Five trunk vertebrae (GCVP 17713; 17714; 17720; 19810; 19811).

Remarks—Included in the CQ collection of snake vertebrae are five relatively well preserved vertebrae of *Thamnophis* in the size range for *T. sauritus* Linnaeus (Eastern Ribbonsnake), *T. sirtalis* Linnaeus (Common Gartersnake) and/or *T. proximus* Say (Western Ribbonsnake). These fossils are larger than those of the small natricine genera *Virginia*, *Storeria*, and most *Regina*. Overall, they are differentiated from these other genera and are referred to *Thamnophis* on the basis of the following characteristics and features: (1) vertebral shape relatively long, medially constricted; (2) neural arch moderately low when viewed posteriorly, more so than in *Nerodia* and *Regina* (Brattstrom 1967); (3) neural spine long and relatively low (Holman 1971), certainly lower than *Regina* and most *Nerodia*; and (4) hypapophysis short and posteroventrally directed (longer and angled more downward in *Nerodia* and *Regina* [see Brattstrom 1967; Kasper and Parmley 1990; Parmley 1988b, 1990; Parmley and Holman 1995; Parmley and Hunter 2010]). Vertebral hypapophyses also occur on North American elapid and viperid trunk vertebrae. However, the hypapophyses of the CQ fossils are too large, too laterally compressed, and less anteriorly directed to represent a

New World elapid; and too short, more laterally compressed, and posteriorly directed than in North American viperids (even the diminutive genus *Sistrurus*).

The identification of isolated *Thamnophis* vertebrae to species has been a subject of controversy for many years. For example, some workers have argued that they can be identified at the specific level (e.g., Holman 1964, LaDuke 1991, Parmley 1990, Rogers 1976). However, after examining 1000's of vertebrae from a taxonomically diverse, and geographically wide collection of *Thamnophis*, it is our opinion that trunk vertebrae of this genus exhibit too many interspecific similarities to be reliably differentiated at the specific level (also see Parmley and Peck 2002, Parmley and Walker 2003). We do acknowledge, however, there may be exceptions. For example, we recently studied a small collection of *T. rufipunctatus* Cope (Narrowhead Gartersnake) skeletons; adults of this species have hypapophyses that are more ventrally truncated than any other *Thamnophis* species we examined from the continental United States. Nonetheless, the CQ vertebrae are not like *T. rufipunctatus* in hypapophyseal morphology (a species with a small continental United States range in western New Mexico into central Arizona; Ernst and Ernst 2003). Based on these facts, we maintain only a generic-level identification of the CQ vertebrae. *Thamnophis* has been in North America since at least the medial



Figure 4. Snake fossils from Clark Quarry, Glynn Co., GA. *Thamnophis* sp. indet. trunk vertebra (GCVP 17714) in dorsal (A) and lateral (B) view. (C) *Nerodia* (Group 3) trunk vertebra (GCVP 11706) in lateral view.

Barstovian NALMA (Middle Miocene, approximately 14 Ma; Holman 2000), and is also known from the Clarendonian NALMA (Parmley and Hunter 2010). Pleistocene records of *Thamnophis* are common (Holman 2000), thus its appearance in the CQ fauna is not unexpected.

Genus *Nerodia* Baird and Girard
Nerodia sp. indet. (Groups) (Fig. 4C)

Material—Eight trunk vertebrae (GCVP 11789; 11703; 11792; 11794; 11924; 11706; 11707; 11919).

Remarks—These vertebrae are relatively complete and well preserved, and are referred to the genus *Nerodia*, but separated from *Thamnophis*, Viperidae, and Elapidae, based on the following characteristics: (1) vertebral shape short and wide when viewed dorsally (more elongated and narrower in *Thamnophis*); (2) neural spine tall and relatively short in length (much more so than seen in *Thamnophis*); (3) hypapophysis broad, laterally compressed (more cylindrical in North American viperids and elapids) and ventrally directed (more posteriorly directed in *Thamnophis* and North American elapids); and (4) neural arch vaulted in posterior view (more depressed in *Thamnophis*; Meylan 1982, Parmley 1990, Parmley and Pfau 1997, Parmley and Hunter 2010). Additionally, the fossils have less truncated hypapophyses and larger condyles than seen in the natricine genus *Regina* (Holman 1972, Parmley and Pfau 1997).

The specific identification of isolated *Nerodia* vertebrae is difficult, if not impossible, in many cases (Parmley and Pfau 1997). Some workers (Holman 1967, 1970, 1971; Meylan 1982) have suggested that certain species of this genus can be separated into broad groups based on differing neural spine height and length relationships, here designated as Group 1, Group 2, and Group 3. Group 1 includes those with the NSL longer than NSH: *N. sipedon* Linnaeus (Common Watersnake) and *N. fasciata* Linnaeus (Southern Watersnake). Group 2 includes those with the NSL approximately the same as the NSH: *N. erythrogaster* Forster (Plain-bellied Watersnake) and *N. clarki* Baird and Girard (Salt Marsh Snake). Group 3 includes those with the NSL less than NSH, these are taxa with the highest neural spines: *N. cyclopion* Duméril, Bibron and Duméril (Mississippi Green Watersnake); *N. taxispilota* Holbrook (Brown Watersnake); and *N. rhombifera* Hallowell (Diamond-backed Watersnake). The CQ *Nerodia* vertebrae with complete enough neural spines to evaluate this measurement suggest that all three groups are represented: Group 1: GCVP 1178, 17703; Group 2: GCVP 11924, 1179, 11794; Group 3: GCVP 11706, 17707, 11919. In fact, two of the fossil specimens in Group 3 (GCVP 11706 and 11919) are identical in neural spine features to *N. taxispilota*, a large species of *Nerodia* found in the CQ fossil site area today. Although this grouping is, admittedly, an artificial affiliation, and not taxonomically reliable for specific identification, it does suggest that more than one species (probably three) was present in the CQ paleoherpetofauna. Such diversity is not unreasonable given that three species occur in the CQ area today: *N. erythrogaster*; *N. fasciata*; and *N. taxispilota* (Jensen et al. 2008).

Nerodia no group affiliation

Material—Two vertebrae (GCVP 11790; 17708).

Remarks—These vertebrae are characteristically like *Nerodia*, but are missing their neural spines. Consequently, we cannot suggest a group affiliation for either specimen.

Natricinae gen. et sp. indet.

Material—46 non-caudal vertebrae (GCVP 11886–11907; 11793; 11795–11797; 17710; 17721–17723; 17725–17727; 17729–17742; 17744; 17746–17748).

Remarks—These vertebrae exhibit natricine features but are too damaged to be identified to the generic level. The specimens appear to represent small species of natricine snakes, mainly in the *Storeria-Virginia* size range, whereas others are large enough to represent small individuals of *Regina*, *Thamnophis* or *Nerodia*.

Subfamily Colubrinae Opper

In general, Colubrinae vertebrae differ from xenodontine and natricine snakes mostly by a process of elimination. Overall, their trunk vertebrae lack hypapophyses, have well-defined and often narrow hemal keels, especially when compared with North American xenodontine snakes (e.g., *Heterodon* Latreille; also see Parmley and Hunter 2010 and references within for further discussion). Many also have well-developed and relatively high neural spines.

Genus *Elaphe* (s.l. *Pantherophis*, *Scotophis*) Fitzinger in Wagler
Elaphe sp. indet. (Fig. 5A, B)

Material—One anterior trunk vertebra (GCVP 11788).

Remarks—Based on the large size of this vertebra (CL= 9.20 mm, ZW = 6.30 mm), when compared with other large North America colubrid snakes, GCVP 11788 represents a snake similar in size to adult *Drymarchon*, *Elaphe*, *Pituophis*, and to a lesser degree *Lampropeltis*. The vertebral details of *Elaphe* have been discussed in some detail by Parmley (1986a, b). The CQ vertebra clearly differs from *Drymarchon* in several ways (e.g., a thicker neural arch and neural spine base), so it likely does not represent this taxon. *Lampropeltis* and *Elaphe* vertebrae are more problematic, as the trunk vertebrae of large adults can be confused with one another (Parmley and Hunter 2010), thus it is not always possible to differentiate them. In fact, many of the characters provided by authors to differentiate these genera (Auffenberg 1963, Holman 1995, Meylan 1982, Parmley 1986a) need further study. Based on our examination of a large and geographically diverse sampling of adult skeletal specimens of *Elaphe* and *Lampropeltis*, we contend that anterior trunk vertebrae of these taxa can be differentiated at the generic level with a good degree of confidence (also see discussion about the separation of these genera in Parmley and Hunter 2010:531). In this case, we believe GCVP 11788 represents a large *Elaphe* and differs from large *Lampropeltis* based on the following: (1) large size; (2) overall robustness of the bone (more gracile in *Lampropeltis*); (3) neural arch highly vaulted when viewed posteriorly (lower in *Lampropeltis*); and (4) subcentral ridge canals relatively shallow (deeper in *Lampropeltis*). Lastly, large *Elaphe* vertebrae (including the CQ specimen) differ from those of adult *Pituophis* via a combination of characteristics including less vaulted neural arches, and wider hemal keels flanked by stronger, deeper, and better developed subcentral ridges. Unfortunately, the fossil is too damaged to suggest a specific allocation.

Elaphe first shows up in the Late Miocene (Holman 2000, Parmley and Holman 1995) of the Great Plains and its presence in the CQ fauna is not unexpected. Today it is a common diurnal predator with a large distribution that extends across much of the United States (Ernst and Ernst 2003).

Genera *Masticophis* Baird and Girard (Whipsnakes) and *Coluber* Linnaeus (Racers)
Masticophis sp. indet. or *Coluber* sp. indet. (Fig. 5C, D)

Material—One trunk vertebra (GCVP 17900).

Remarks—Although the vertebral morphology of *Masticophis* and *Coluber* is well documented, these “sister genera” cannot be differentiated on the basis of isolated trunk vertebrae (e.g., LaDuke 1991, Parmley 1986b, Parmley and Walker 2003), but are easily identified to the genus-complex. Diagnostic vertebral characters of *Masticophis-Coluber* include: (1) vertebral shape is longer than wide (or nearly so) and constricted through the mid-neural arch section; (2) neural spine long, moderately high and usually thin; (3) hemal keel well defined and uniformly narrow throughout its length (or nearly so) and flanked by well-developed subcentral ridges; (4) epizygapophyseal spines present and usually well



Figure 5. Snake fossils from Clark Quarry, Glynn Co., GA. *Elaphe* sp. indet. trunk vertebra (GCVP 11788) in dorsal (A) and posterior (B) view. *Masticophis/Coluber* sp. indet trunk vertebra (GCVP 17900) in dorsal (C) and lateral (D) view.

developed; and (5) neural arch moderately vaulted (Holman 2000, Parmley 1988b, Parmley and Holman 1995). The CQ fossil exhibits these characters and is definitively a member of the *Masticophis-Coluber* group of racer snakes. Both genera occur today in the CQ fossil site area (Jensen et al. 2008). The fossil history of *Masticophis-Coluber* snakes in North America dates back to the Late Clarendonian (Late Miocene) approximately 9.5 Ma. (Holman 2000, Parmley and Hunter 2010).

Family Viperidae Opper

The fossil record of North American viperid snakes is sparse compared to colubrids. Consequently, our understanding of the fossil history of North American pit vipers is poor (see discussion in Parmley and Hunter 2010). GCVP 17958 exhibits enough discernable features to assign it to a viperid snake. These features include: (1) a relatively short and wide shape (blocky); (2) ventrally directed and spine-like hypapophysis that originates near the condyle (based on remaining basal portion); (3) relatively large cotyle and condyle; and (4) one remaining partial paradiapophysis that is elongate and ventrally projected (Meylan 1982, Parmley and Holman 2007, Szyndlar 1991 [in part]).

Subfamily Crotalinae Opper

With the exception of well-preserved *Sistrurus* vertebrae (Parmley and Holman 2007), there seems to be no reliable characteristics or features that differentiate Viperinae and Crotalinae vertebrae (Parmley and Holman 2007, Parmley and Hunter 2010). Nonetheless, we argue that because all modern New World viperids are crotaline snakes, and there is no biogeographic or paleontological evidence to suggest viperine snakes ever occurred in North America (at least not in the past ca. 25–30 Ma), the CQ fossil is a crotaline snake.

Genus *Agkistrodon* Palisot deBeauvies (Copperhead and Cottonmouth)
Agkistrodon sp. indet. (Fig. 6A, B)

Material—One trunk vertebra (GCVP 17958).

Remarks—This vertebra is damaged. Nonetheless, it is too large to be from *Sistrurus*, but retains enough features to suggest it is an adult *Agkistrodon*. It differs from *Crotalus* (Rattlesnakes) in having deep paracotylar fossae, each with one relatively distinct, large foramen, which *Crotalus* does not have (Holman 1963, Meylan 1995, Parmley and Holman 2007; Fig. 6C). On the basis of its large size, GCVP 17958 most likely represents *A. piscivorus* Lacépède (Cottonmouth), rather than *A. contortrix* Linnaeus (Copperhead).

Results and Discussion

Collectively, the CQ paleoherpetofauna provides an important contribution to the knowledge of amphibian and reptile life during the Late Pleistocene of the southeastern coastal region of North America. Compared with Pleistocene paleoherpetofaunas of mid-continental North America, the overall numerical and taxonomic composition of the CQ paleoherpetofauna is moderate (Holman 1995) consisting of the following taxa: *Rana* sp. indet.; *Bufo* sp. indet.; *Amphiuma* sp. indet.; *Siren* sp. indet.; *Anolis* sp. indet.; *Heterodon* sp. indet.; *Seminatrix* sp. indet.; *Storeria* sp. indet.; *Virginia* sp. indet.; *Thamnophis* sp. indet.; *Nerodia* sp. indet. (given the “Groups” represented, see *Nerodia* accounts, we suggest that at

least two, if not three species were likely present in the paleofauna); *Masticophis-Coluber*; *Elaphe* sp. indet.; *Agkistrodon* sp. indet.

Albeit CQ identifications are to the generic level, as far as we can determine there are no extinct (excluding the tortoise *Hesperotestudo* reported by Clark 2009) or extralimital taxa (of any significance) present in the CQ paleoherpetofauna. This is in strong contrast with the mammalian fauna which contains impressive remains of *Mammuthus columbi* (Patterson et al. 2012) and the giant Woodland Bison *Bison latifrons*. Additionally, preliminary examination of the small mammals from the site clearly indicates at least three extralimital Recent taxa were present (A.J. Mead, in progress).

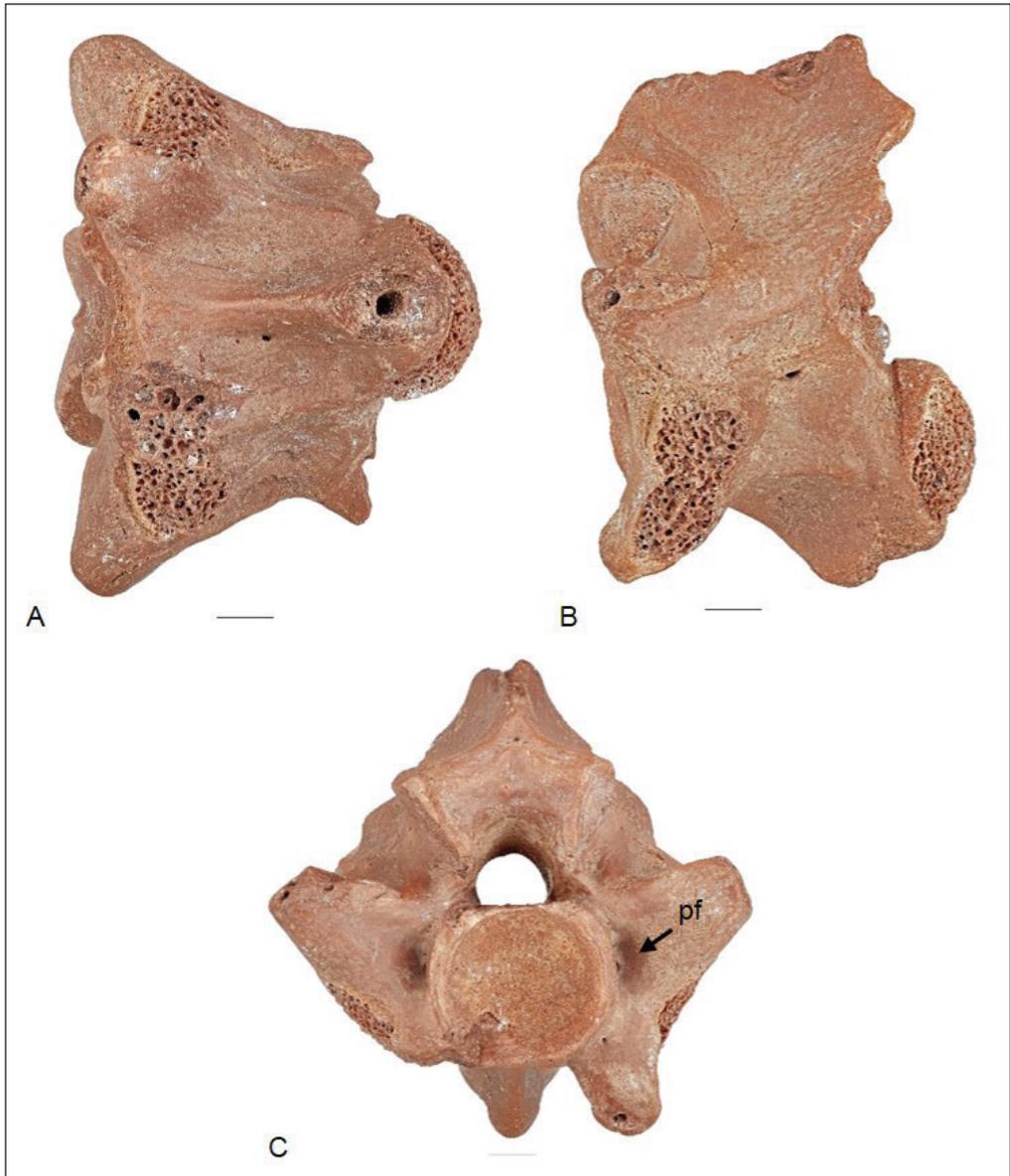


Figure 6. Snake fossils from Clark Quarry, Glynn Co., GA. *Agkistrodon* sp. indet. trunk vertebra (GCVF 17958) in ventral (A), lateral (B) and anterior (C) view; pf = paracotyler fossa.

Paleoecology

Based on known habitat preferences of the modern counterparts of the CQ amphibians and reptiles (albeit at the generic level; Jensen et al. 2008, Petranka 1998) and the presence of large grazer mammals (mammoths and bison), some type of swamp, marsh or small pond habitat set in an area of open woodlands and grasslands (parkland) is clearly indicated at the time of deposition. It was perhaps a setting like depicted in Figure 7. The aquatic habitat is based on the fact that both of the anurans (*Rana* and *Bufo*) require non-ephemeral freshwater for reproduction with *Rana* being more water dependent and *Bufo* more terrestrial. *Amphiuma* and *Siren* are obligate aquatic organisms that often occur sympatrically in the same aquatic habitat (Parmley, pers. observ.). Also, two of the eight snakes identified are aquatic (*Seminatrix* and *Nerodia* [again, both of these taxa can co-occur with *Amphiuma* and *Siren*]), one or two are semi-aquatic (*Thamnophis* and possibly *A. piscivorus*) and the remaining two small natricine snakes *Storeria* and *Virginia* require at least damp microhabitats. The three most terrestrial taxa identified are *Heterodon*, *Elaphe* and *Masticophis-Coluber*. The vertebrae of these snakes likely washed into the aquatic habitat from the surrounding terrestrial lands or the snakes entered the aquatic habitat for water or to forage for prey. Nonetheless the fossils indicate the presence of near-by woodlands and/or woodland/grassland settings (Fig. 7). Moreover, *Heterodon* is a noted burrower

Figure 7. Depiction of parkland (A) and aquatic (B) habitat likely present in the CQ area during the time of deposition (based on habitats on the south end of St. Catherines Island, GA).



and its presence in the CQ herpetofauna suggests nearby sandy or friable soil such as might be found in oak-pine forests or oak hammocks of the South today (see Jensen et al. 2008). The overwhelming majority of fossil snake vertebrae, however, are those of natricines. This coupled with the amphibian fauna discussed above is evidence that an aquatic habitat was clearly present during the time of deposition, as previously noted. In summary the CQ paleoherpetofauna and the mammalian fauna (as thus far known) indicate an aquatic habitat set in a parkland.

Acknowledgments

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