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Late Hemphillian Colubrid Snakes (Serpentes, Colubridae) from the Gray Fossil Site of Northeastern Tennessee

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Abstract.—**The Gray Fossil Site (GFS) of northeastern Tennessee is a late Hemphillian fossil locality in the southern Appalachian mountain region of eastern North America with a diverse vertebrate fauna. Snakes make up a substantial microfossil portion of the GFS herpetofauna, particularly the Colubridae, comprised of members of the Colubrinae and Natricinae. Seven colubrid taxa have been identified from the site so far, including three natricines (cf. *Neonatrix*, *Nerodia*, *Thamnophis*) and at least four colubrines (*Coluber/Masticophis*, *Pantherophis*, *Pituophis*, gen. et sp. nov.). Indeed, cf. *Neonatrix* and the new genus (and species) are the only extinct genera identified. Although *Neonatrix* is tentatively identified for the first time east of Nebraska, the new species represents a distinct taxon. In addition, the oldest reported definitive occurrence of *Masticophis* is presented herein. Some of the snakes suggest a pond or other aquatic habitat at GFS, particularly cf. *Neonatrix* and *Nerodia*, whereas others, such as *Masticophis* and *Pituophis*, tend to prefer more open forested habitats. The GFS represents a poorly understood region of North America at a crucial time period in snake evolution, and its study may help us further understand the modern snake fauna present today in midcontinental and eastern North America.**

Colubridae, the largest living family of snakes (Reptilia, Squamata, Serpentes), is found on every continent today except Antarctica (Vitt and Caldwell, 2008). Although the family consists of numerous subfamilies that are sometimes elevated to family-level status themselves (e.g., Uetz, 2010), they are maintained as subfamilies here (see Pyron et al., 2013a,b) with the two most common subfamilies found as fossils, including the Colubrinae and Natricinae. We identified a large number of snake specimens (>300) as colubrids from the Gray Fossil Site (GFS). The GFS in eastern Tennessee is a rich, late Hemphillian Mio-Pliocene age (7.0–4.5 Ma) fossil locality containing a diverse and unique fossil animal assemblage (see Fig. S1). The site covers ~2.5 ha and is up to 40 m thick (Wallace and Wang, 2004). The GFS paleoenvironment is interpreted as a pond deposit with multiple sinkholes (Shunk et al., 2006; Whitelaw et al., 2008; Zobaa et al., 2011), with the herpetofauna also indicating a lacustrine environment (Parmalee et al., 2002; Schubert and Wallace, 2006; Jasinski, 2013; Bourque and Schubert, 2015), with relatively permanent bodies of water (Boardman and Schubert, 2011b). Algal microremains suggest meso- to eutrophic conditions in a pond setting (Worobiec et al., 2013). A moderately dense ancient forest would have surrounded the pond setting and served as a forest refugium among extensive grasslands, with relatively stable seasonal temperatures (DeSantis and Wallace, 2008). Additionally, it is one of a limited number of Miocene–Pliocene vertebrate localities within eastern North America (Farlow et al., 2001; Tedford et al., 2004; Mead et al., 2012). It is also the only site in the Appalachian region representing the Miocene–Pliocene transition.

The site yields a rich herpetofaunal assemblage, currently consisting of at least 34 taxa (Table 1). Though several extended abstracts have been published (e.g., Schubert, 2006; Schubert and Wallace, 2006; Schubert and Mead, 2011), only a few detailed studies have been conducted on the remainder of the herpetofauna (e.g., Parmalee et al., 2002; Boardman and Schubert, 2011b; Mead et al., 2012; Bourque and Schubert, 2015). Snakes are one reptile clade at the GFS that has received relatively little attention. Numerous snake fossils have been recovered from the site, and cursory examination of the vertebrae by Schubert (2006) indicated that at least two families (Viperidae and Colubridae) were present.

Records of Miocene and Pliocene snakes are common across the mid-western and western United States, but rare outside of that range (e.g., Parmley and Holman, 1995; Holman, 2000). Miocene and Pliocene snake localities in eastern North America have previously been reported in Indiana (e.g., Farlow et al., 2001), Delaware (Holman, 1998), and Florida (Meylan, 1984; Hulbert, 2001). Herein we investigate the colubrid snakes from the GFS. Comparison of the GFS colubrid fauna with other similar-aged localities (e.g., see Brattstrom, 1967; Parmley and Holman, 1995; Parmley and Walker, 2003) may help our understanding of patterns of snake evolution and diversification across North America during the late Neogene.

Methods and Materials

Institutional Abbreviations.—ANSP, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania; ETMNH, East Tennessee State University Museum of Natural History, Gray, Tennessee; ETVP, East Tennessee State University Vertebrate Paleontology Laboratory, Johnson City, Tennessee; UMMP V, University of Michigan Museum of Paleontology Vertebrate Collection, Ann Arbor, Michigan.

Methods.—We focused on fossil snakes within the Colubridae, following the taxonomy of Pyron et al. (2013a,b), unless otherwise stated. Fossil material was collected from the GFS by first hand-collecting specimens found in situ. Removed matrix was then screen-washed and the remaining sample hand-picked under a microscope. Auffenberg (1963), Szyndlar (1984), LaDuke, (1991), and Holman (2000) presented characteristics used to identify vertebrae (see Fig. 1). Common characters of the Colubridae include normally thin neural spine, relatively long, never oval in cross-section, and often as high (dorsally) as long (craniocaudally) or higher than long; cotyle usually round to oval, condyle oriented from nearly straight to oblique, and the centrum often has prominent

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TABLE 1. Fossil herpetofauna known from the Late Hemphillian Gray Fossil Site, Gray, Tennessee, USA. Data collected from multiple studies, including Wallace and Wang (2004), Boardman and Schubert (2011a, 2011b), Mead and Schubert (2011), Schubert (2011), Mead et al. (2012), Jasinski (2013), and Bourque and Schubert (2015). "#" signifies fossil taxon.

Class	Order/Suborder	Family	Genus/species
Amphibia			
	Anura		
		Ranidae	
			Rana sp. Multiple indeterminate spp.
	Urodela		
		Ambystomatidae	
			Ambystoma sp.
		Plethodontidae	
			Plethodon sp. Type A *Plethodon* sp. Type B *Desmognathus* sp. Spelerpinae indeterminate sp.
		Salamandridae	
			Notophthalmus sp.
Reptilia			
	Testudines		
		Chelydridae	
			Chelydra sp.
		Emydidae	
			Chrysemys sp. *Emys/Emydoidea* sp. *Terrapene* sp. *Trachemys* sp. nov.
		Kinosternidae	
			Sternotherus palaeodorus#
		Testudinidae	
			Hesperotestudo sp.# Testudinidae indeterminate sp.
	Crocodylia		
		Alligatoridae	
			Alligator sp.
	Lacertilia		
		Anguidae	
			Anguinae indeterminate sp.
		Helodermatidae	
			Heloderma sp.
		Scincidae	
			Scincidae indeterminate sp.
	Serpentes		
		Boidae	
			Boidae indeterminate sp.
		Colubridae	
			Coluber/Masticophis sp. *Masticophis* sp. cf. *Neonatrix* sp.# *Nerodia* sp. *Pantherophis* sp. *Pituophis* sp. *Thamnophis* sp. *Zilantophis schuberti* gen. et sp. nov.#
		Viperidae	
			Viperidae indeterminate sp.

subcentral ridges; relatively thin hemal keel; hypapophyses on trunk vertebrae of natricines and some dipsadines (Holman, 2000; Pyron et al., 2013b); prezygapophyseal accessory processes at varying lengths, with some colubrids possessing epizygapophyseal spines on the posterior ends of the postzygapophyses; thin zygosphene is variable in shape; and paradiapophyses divided into distinct diapophyseal and parapophyseal processes. Fossil vertebrae identified as colubrids were selected for closer examination, further identified to subfamily, and then to genus and species when possible. We identified 348 specimens as colubrids from ~500 fossil snake vertebrae. Many vertebrae could not be identified to, or beyond, the family level due to incompleteness or poor preservation.

An apomorphy-based approach is preferred for fossil identification (e.g., Bell et al., 2004, 2010). Many to most modern snake taxa have not been thoroughly diagnosed osteologically with identified apomorphic characters. This is due, in part, to variation within individuals and intra- and interspecific variation. Therefore, a detailed description of the apomorphies of modern snakes remains incomplete. In this study, we made identifications by comparison to descriptions from the literature and with those specimens in the modern comparative collections of the ANSP and ETVP, with the use of apomorphic characters where applicable. Although a more apomorphy-

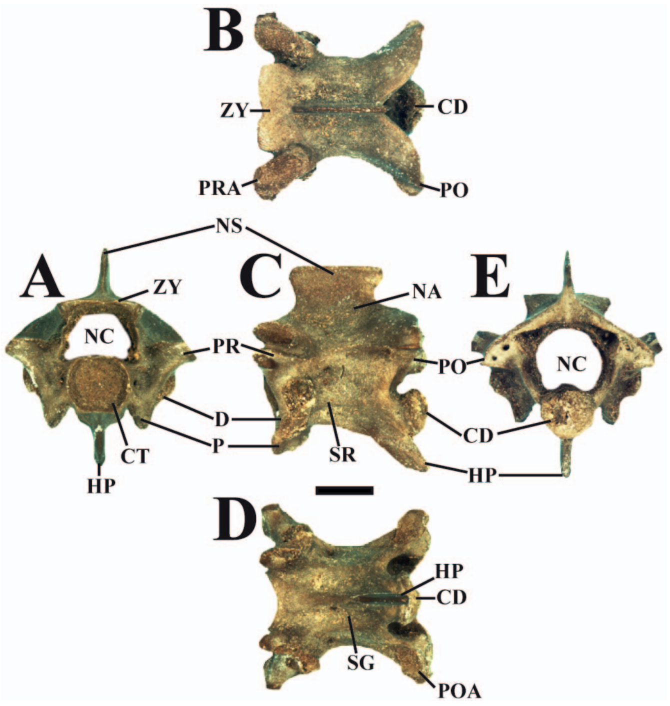

FIG. 1. Terminology of snake vertebrae used in this study, following Auffenberg (1963), LaDuke (1991), and Holman (2000). *Thamnophis* sp., ETMNH-11961, trunk vertebra in A, anterior view; B, dorsal view; C, left lateral view; D, ventral view; E, posterior view. Abbreviations: CD, condyle; CT, cotyle; D, diapophysis; HP, hypapophysis; NA, neural arch; NC, neural canal; NS, neural spine; P, parapophysis; PO, postzygapophysis; POA, postzygapophyseal articular facet; PR, prezygapophysis; PRA, prezygapophyseal articular facet; SG, subcentral groove (=subcentral paramedian lymphatic fossa); SR, subcentral ridge; ZY, zygosphene. Scale bar equals 1 mm.

based approach is desirable, the methods used herein still allow for confident referral of fossil vertebra to snake genera. Terminology of snake vertebral morphology in this study follows Auffenberg (1963), Hoffstetter and Gasc (1969), LaDuke (1991), and Holman (2000), unless otherwise stated. Much of the descriptive terminology (e.g., "elongate," "high," etc.) follows LaDuke (1991). We took photographs with the use of a Z16 APO macroscope (Leica Microsystems, Inc., Wetzlar, Germany), QImaging MicroPublisher 5.0 RTV image capture (Adept Turnkey Pty Ltd., Perth, Australia), and a Zeiss KL200 light source (Carl Zeiss Mfg., Oberkochen, Germany).

SYSTEMATIC PALEONTOLOGY

Class Reptilia Laurenti, 1768
Order Squamata Oppel, 1811
Suborder Serpentes Linnaeus, 1758
Family Colubridae Oppel, 1811
Subfamily Natricinae Bonaparte, 1840
Neonatrix Holman, 1973
cf. *Neonatrix* sp.
(Fig. 2A–C)

Material.—ETMNH-9262, caudal vertebra (Fig. 2A–C).

Remarks.—Precaudal and caudal vertebrae share some characteristics within a taxon, although the latter tend to exhibit more complex processes along with paired hemapophyses. Some work exists on snake caudal vertebrae (e.g., Hoffstetter and Gasc, 1969; Polly et al., 2001; Smith, 2013), but little on investigating intraspecific versus interspecific morphologic change between precaudal and caudal vertebrae among snakes. In modern snake specimens examined we found similarities between precaudal and caudal vertebral features, allowing taxonomic information to be derived from isolated caudal vertebrae.

ETMNH-9262, while similar to *Thamnophis* and *Nerodia*, differs from them in lacking hooked projections on the neural spine; neural spine taller anteriorly; an inconspicuous subcentral ridge; and a well-rounded opening between the neural arch and the condyle in lateral view. The taller neural spine distinguishes it from natricines with low to obsolete neural spines such as *Storeria*, *Tropidoclonion*, and *Virginia*. It differs from *Seminatrix* in possessing a relatively craniocaudally shorter neural spine and more gracile processes; distinct from *Micronatrix* in possessing a taller neural spine, more convex zygosphene, and a small hypapophysis. ETMNH-9262 most closely resembles specimens of *Neonatrix* and *Regina*; it is distinguished from *Regina* in possessing a shorter hemapophysis. Although the zygosphene of *Neonatrix* is convex and less crenate than that of ETMHN-9262, it is still more similar to this genus than other observed natricines. The neural spine resembles that of *Neonatrix magna*, albeit a bit taller in ETMNH-9262. The hypapophysis is like *N. infera* and some specimens of *N. elongata*, and the centrum length of ETMNH-9262 (3.28 mm) lies between *N. elongata* (~2.6–2.7 mm) and *N. infera* and *N. magna* (~4.2 mm each). Therefore, ETMNH-9262 appears most similar to the presacral vertebrae of *Neonatrix*, which possess small hypapophyses (Holman, 2000). Laterally, the hemapophyses appear most similar to the hypapophysis of *N. infera*, especially with their wide contact with the ventral edge of the centrum; however, the neural spine extends farther dorsally than that of *N. infera* and *N. elongata*, agreeing more closely with *N. magna*.

ETMNH-9262 may represent a new, younger, and more eastern species of *Neonatrix*, but because it is a caudal vertebra, we do not think it can be identified to species or diagnosed as a new taxon with certainty, and conservatively identify it as cf. *Neonatrix* indeterminate species. Indeed, we think that ETMNH-9262 does not represent a modern taxon and, if it does not represent *Neonatrix*, likely represents an undescribed extinct taxon. The genus *Neonatrix* is a fossil natricine from the Miocene of Nebraska, Texas, and questionably Wyoming (Holman, 2000; Parmley and Hunter, 2010). If ETMNH-9262 is correctly identified as *Neonatrix*, it would represent the first North American report of this genus east of Nebraska and Texas and younger than the Clarendonian LMA (late Miocene).

Nerodia Baird and Girard, 1853
Nerodia sp.
(Fig. 2D–F)

Material.—ETMNH-9362, midtrunk vertebra (Fig. 2D–F).

Remarks.—ETMNH-9362 is a natricine with a caudally directed and pointed hypapophysis. Because of its robust and relatively prominent hypapophysis and neural spine, ETMNH-9362 is distinct from most natricines, aside from *Regina*, *Nerodia*, and *Thamnophis*. Although ETMNH-9362 does possess a "squarish" hypapophysis, similar to what has been described for *Regina* (Holman, 2000:208), the neural spine, with its strong anterior and posterior undercuts, more closely resembles that of a referred specimen of *Nerodia hibbardi* (UMMP V34446) from the middle Pliocene (see Holman, 2000:fig. 130). The hypapophysis of ETMNH-9362 has a steeper and larger angle in relation to the centrum, more similar to *Nerodia* than *Thamnophis*. ETMNH-9362 has a relatively low neural spine and robust hypapophysis (Fig.

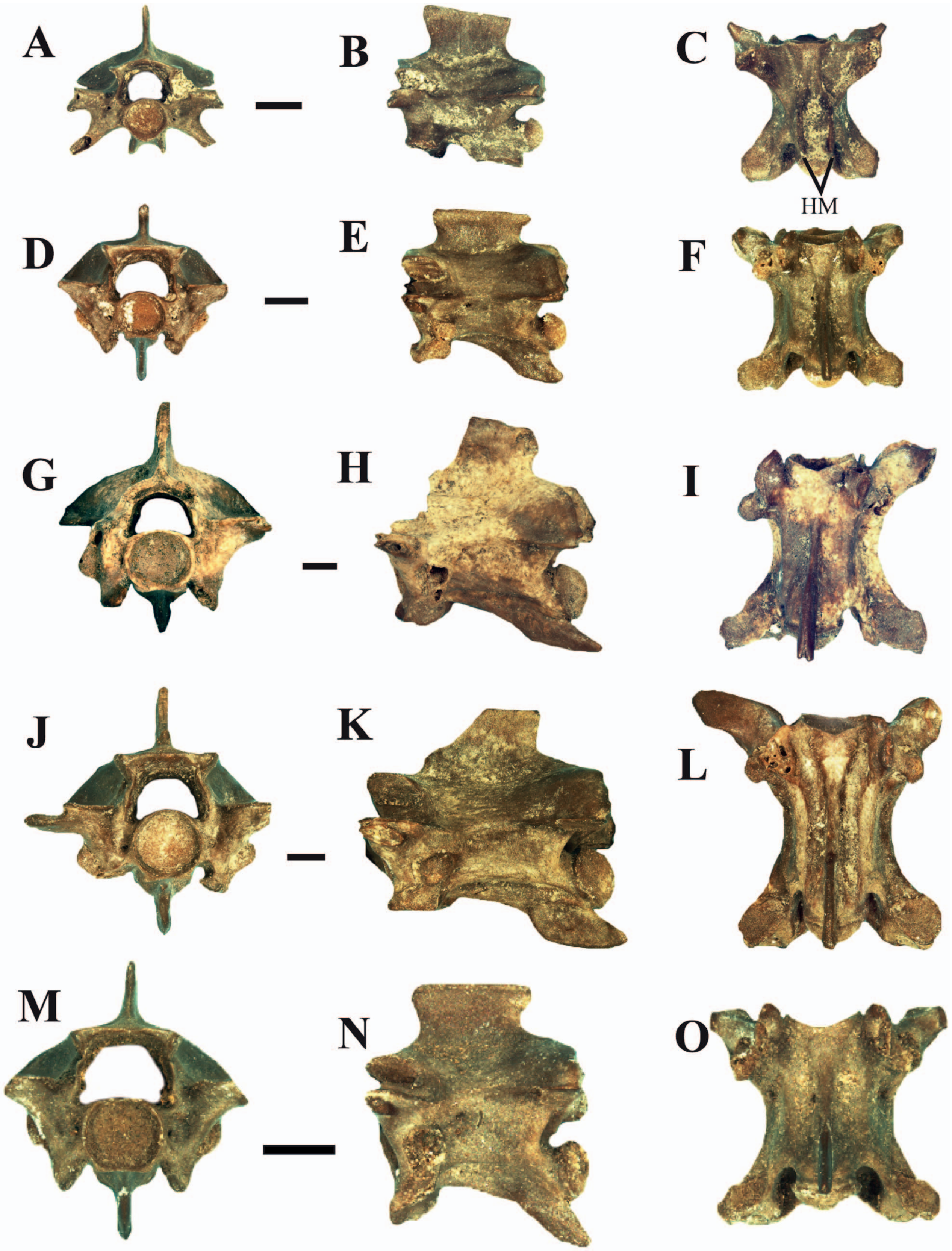

FIG. 2. Natricines from the late Hemphillian of eastern Tennessee. A–C, cf. *Neonatrix* sp., ETMNH-9262, caudal (=postcloacal) vertebra in A, anterior view; B, left lateral view; C, ventral view; D–F, *Nerodia* sp., ETMNH-9362, trunk vertebra in D, anterior view; E, left lateral view; F, ventral view; G–I, *Thamnophis* sp., ETMNH-9261, posterior trunk vertebra in G, anterior view; H, left lateral view; I, ventral view; J–L, *Thamnophis* sp., ETMNH-9448, trunk vertebra in J, anterior view; K, left lateral view; L, ventral view; M–O, *Thamnophis* sp., ETMNH-11961, trunk vertebra in M, anterior view; N, left lateral view; O, ventral view. Abbreviation: HM, hemapophyses. Scale bars equal 1 mm and each scale bar corresponds to the three consecutive images representing each individual specimen.

2D–F), both suggest either *Nerodia* or *Thamnophis* rather than *Regina*. Distinguishing trunk vertebrae of *Nerodia* and *Thamnophis* (Holman, 2000) often is difficult, other than the generality that vertebrae of *Thamnophis* are more elongate (as defined by LaDuke, 1991). LaDuke (1991) defined an elongate vertebral form as one with a centrum length/neural arch width ratio as being >1.2, and ETMNH-9362 has a ratio of 1.8 (centrum length 3.85 mm). *Nerodia* has a broader and more robust hypapophysis and more slender and gracile prezygapophyseal processes than *Thamnophis*. Additionally, *Nerodia* tends to have a moderately vaulted neural arch versus flatter in *Thamnophis*.

Other than the elongate nature of the vertebra, all other characters observed on ETMNH-9362 agree with the abovementioned features for *Nerodia*, as opposed to *Thamnophis* and *Regina*. Some fossil species of *Nerodia* (e.g., *N. hibbardi*) often have more elongate vertebrae than modern *Nerodia* species. Indeed, here ETMNH-9362 is identified as an indeterminate species of *Nerodia* based on its similarities with *N. hibbardi* and modern specimens of *N. sipedon*. The water snake *Nerodia* ranges today from Canada to Mexico and commonly occupies quiet aquatic habitats, such as ponds or lakes (Conant and Collins, 1998). The earliest known record of *Nerodia* is from the Barstovian (middle Miocene) of Nebraska (Holman, 2000).

Thamnophis Fitzinger, 1843
Thamnophis sp.
(Fig. 2G–O)

Material.—ETMNH-9261, posterior trunk vertebra (Fig. 2G–I); ETMNH-9448, posterior trunk vertebra (Fig. 2J–L); ETMNH-11961, midtrunk vertebra (Fig. 2M–O).

Remarks.—ETMNH-9261, -9362, and -11961, all follow the general characteristics of *Nerodia* and *Thamnophis* trunk vertebrae. A higher neural spine distinguishes them from those of other natricines such as *Storeria*, *Tropidoclonion*, and *Virginia*. The hypapophyses are not short and/or "squarish," distinguishing them from *Neonatrix* and *Regina*. The posterior angle of the hypapophysis, in relation to the centrum, is much smaller and more reminiscent of *Thamnophis*. *Thamnophis* possesses more elongate centra than *Nerodia* (Auffenberg, 1963; Holman, 2000). Toward the posterior of ETMNH-9261 (Fig. 2G–I), the hypapophysis has a slight median depression, implying it is a posterior trunk vertebra at the beginning of the transition into the cloacal and postcloacal regions. Whereas the vertebra is somewhat elongate, the hypapophysis is also relatively long and gracile, agreeing closely with *Thamnophis*. ETMNH-9448 is larger (centrum length 5.81 mm) and more robust than ETMNH-9362 (3.85 mm) and ETMNH-9261 (5.6 mm). Its slightly convex zygosphene is similar to *Nerodia* and *Thamnophis*. It is truncated with an elongate hypapophysis, distinguishing it from ETMNH-9261, where it is quite smooth and gently angled. Whereas ETMNH-9448 is large and elongate, reminiscent of *Thamnophis*, the hypapophysis is strongly "squared-off," reminiscent of *Nerodia* and *Regina*. Additionally, the posterior angle of the hypapophysis is larger than that of ETMNH-9261 and -11961, but still smaller than ETMNH-9362 (*Nerodia* sp.) and more reminiscent of *Thamnophis*. Both ETMNH-9261 and -9448 are probably more properly identified as cf. *Thamnophis*, although they are included here with *Thamnophis* until more specimens are found.

ETMNH-11961 is similar to ETMNH-9261, with a more elongate centrum than ETMNH-9262 (cf. *Neonatrix* sp.) and ETMNH-9362 (*Nerodia* sp.), and is within the range of variation expected of *Thamnophis* as discussed by Auffenberg (1963) and Holman (2000). The posterior angle of the hypapophysis is smaller and more reminiscent of *Thamnophis*. Indeed, the flatter cranial edge of the zygosphene, strongly pointed and relatively straight hypapophyses, elongate nature of the centrum, and relatively flat neural arch also suggests ETMHN-11961 belongs to *Thamnophis*. *Thamnophis*, a genus of snakes that includes garter and ribbon snakes, range today from southern Canada south to Costa Rica and occupy habitats close to water (e.g., Conant and Collins, 1998; Holman, 2000). The earliest known specimens of *Thamnophis* have been identified from the Barstovian of Nebraska (Holman, 2000).

Subfamily Colubrinae Oppel, 1811
Genera *Coluber* Linnaeus, 1758
and *Masticophis* Baird and Girard, 1853
Coluber sp. or *Masticophis* sp.
(Fig. 3A–F)

Material.—ETMNH-9244, midtrunk vertebra (Fig. 3A–C), ETMNH-9401 midtrunk vertebra (Fig. 3D–F).

Remarks.—*Coluber* and *Masticophis* have often been considered congeneric (e.g., Utiger et al., 2005; Figueroa et al., 2016), but universal agreement still is lacking and many workers maintain them as distinct genera (e.g., Krysko et al., 2016). We here maintain them as distinct genera, but note that distinction between the two in the current study may deal with specific, rather than generic, differences (e.g., *C. coluber* versus *M. flagellum*). Multiple workers (e.g., Parmley and Walker, 2003; Parmley and Hunter, 2010) have determined trunk vertebrae of *Coluber* and *Masticophis* are indistinguishable, and we include them together here as well. ETMNH-9244 is referred to a colubrine with strongly pronounced epizygapophyseal spines, common features of the trunk vertebrae of *Coluber* and *Masticophis* (see Holman, 2000). *Drymarchon* and *Salvadora* also possess epizygapophyseal spines, but ETMNH-9244 is distinguished from these genera by a relatively longer vertebral form and lower neural spine. Additionally, ETMNH-9244 is distinguished from *Miocoluber* and the new species (discussed below) by the relatively large size and anteroposteriorly long neural spine of the former versus the latter two, and further from *Miocoluber* based on a presumably lower neural spine. ETMNH-9244 is distinct from *Paracoluber* based on its less robust and more distinct hemal keel and in possessing epizygapophyseal spines, which the latter lacks.

ETMNH-9401 possesses a slightly sinuate zygosphene, often present in *Coluber*. The moderately vaulted neural arch agrees more strongly with *Coluber* than with *Masticophis*. ETMNH-9401 and -9244 have different neural spine heights, which is quite low in the former, although the neural spine in the latter is incomplete. This neural spine height difference may reflect an intraspecific, or even an interspecific, distinction between these two specimens. *Coluber* and *Masticophis* (racers and whipsnakes) are found in a wide variety of habitats across most of the United States and south into Mexico (Conant and Collins, 1998; Holman, 2000). The earliest known specimens identified as *Coluber/Masticophis* are known from the Clarendonian of Nebraska (Parmley and Hunter, 2010).

Masticophis Baird and Girard, 1853
Masticophis sp.
(Fig. 3G–I)

Material.—ETMNH-11115, axis (2nd cervical vertebra) (Fig. 3G–I).

Remarks.—Little work exists on identifications based on cervical vertebrae, although it is possible based on comparison

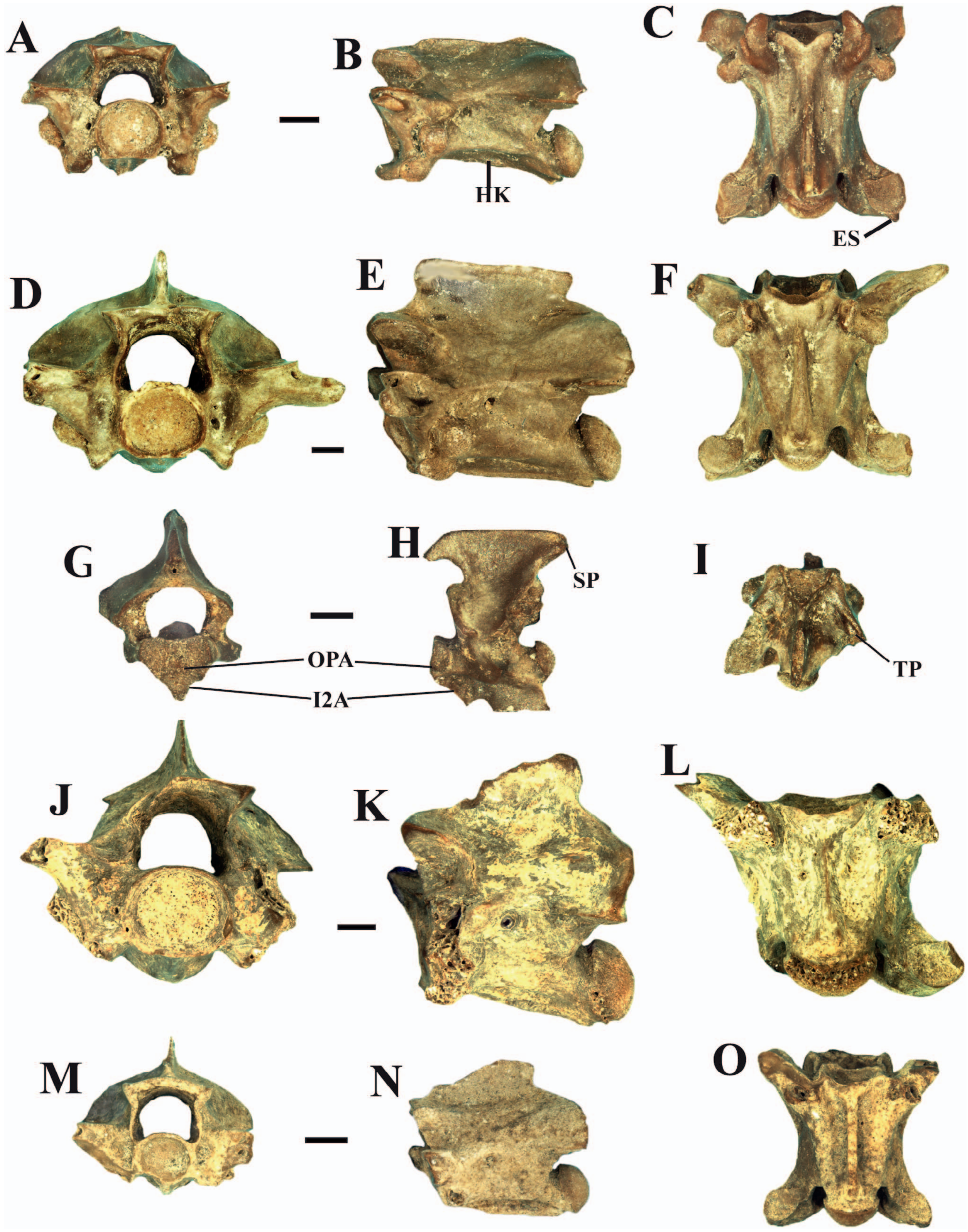

FIG. 3. Colubrines from the late Hemphillian of eastern Tennessee. A–C, *Coluber/Masticophis* sp., ETMNH-9244, trunk vertebra in A, anterior view; B, left lateral view; C, ventral view; D–F, *Coluber/Masticophis* sp., ETMNH-9401, trunk vertebra in D, anterior view; E, left lateral view; F, ventral view; G–I, *Masticophis* sp., ETMNH-11115, axis (=second cervical) vertebra in G, anterior view; H, left lateral view; I, ventral view; J–L, *Pantherophis* sp., ETMNH-9510, trunk vertebra in J, anterior view; K, left lateral view; L, ventral view; M–O, *Pituophis* sp., ETMNH-9451, trunk vertebra in M, anterior view; N, left lateral view; O, ventral view. Abbreviations: ES, epizygapophyseal spine; HK, hemal keel; I2A, intercentrum 2 attachment area; OPA, odontoid process attachment area; SP, spinal process; TP, transverse process. Scale bars equal 1 mm and each scale bar corresponds to the three consecutive images representing each individual specimen.

to modern specimens. Hoffstetter and Gasc (1969) and Holman (2000), among others, discussed the atlas–axis complex in snakes, and the terminology used here follows these studies. ETMNH-11115 has a small centrum, a subtriangular anterior articular surface, a large neural canal, and a distinct neural spine, and represents the axis (2nd cervical vertebra). The pronounced anterior hook of the neural spine and remnants of a craniocaudally long and enlarged hypapophysis are consistent with observed specimens of *Coluber*, *Drymarchon,* and *Masticophis* from the ETVP and ANSP. ETMNH-11115 exhibits a more ventrally oriented anterodorsal-projecting hook of the neural spine, a flatter neural arch, and presumably enlarged posteroventral projections, characters present in *Masticophis* but not *Coluber*.

Another large colubrid, *Drymarchon*, can also be clearly distinguished from ETMNH-11115, *Masticophis*, and *Coluber*. In *Drymarchon*, the cranial edge of the zygosphene is concave with its lateral portions curving cranially, different from the flat edge and caudally curving lateral portions in ETMHN-11115. The dorsal edge of the neural spine in *Drymarchon* angles ventrally in its cranial portion, and this cranioventral–caudodorsal angle is common in North American colubrid axises (e.g., *Coluber*, *Lampropeltis*, *Nerodia*, *Pantherophis*, *Pituophis*, *Regina*, *Seminatrix*, *Storeria*, *Thamnophis*, *Virginia*). This can lead to a smaller concavity in the cranial portion of the neural spine and larger and more gentle concavity caudally, features present in *Masticophis* but absent in other colubrid axises. The enlarged and pronounced hypapophysis also distinguishes *Masticophis* (and ETMNH-11115) from other North American colubrids. Other than a single specimen identified as *Masticophis* cf. *M. flagellum* from the middle Pliocene of Texas (Holman, 2000), ETMNH-11115 represents the earliest reported occurrence of *Masticophis*. Parmley and Hunter (2010) identified two trunk vertebrae from the Clarendonian of Nebraska as either *Coluber* or *Masticophis*, but because this identification was not certain, they cannot be considered to represent the earliest known occurrence of *Masticophis*.

Pantherophis Wagler, 1833 (Fitzinger, 1843)
Pantherophis sp.
(Fig. 3J–L)

Material.—ETMNH-9510, midtrunk vertebra (Fig. 3J–L).

Remarks.—ETMNH-9510 is distinguished from most genera by its moderately high neural spine and broad hemal keel (Fig. 3J–L). Its features agree strongly with those of *Pantherophis* (sensu Utiger et al., 2002) trunk vertebrae in overall morphology as discussed by Holman (2000). Holman (2000) discussed *Pantherophis* (=New World *Elaphe*) vertebrae and distinguished them from the *Coluber/Masticophis* complex by their shorter and more robust vertebrae, wider and higher neural spines, wider hemal keels, and a lack of epizygapophyseal spines. ETMHN-9510 differs from *Drymarchon* by possessing a concave cranial edge of the zygosphene, deep cranial concavity on the posteromedial portion of the neural arch, pronounced posterolateral curvature, and less posterior curvature of the neural spine. Auffenberg (1963) separated *Pantherophis* (*Elaphe*) from *Lampropeltis*, *Arizona*, and *Pituophis* by straight and less well-developed subcentral ridges (versus *Lampropeltis*), lower neural spine, and rarely or never concave zygosphene (versus *Pituophis*) in *Pantherophis*. The posterolateral curvature of the neural arch and hemal keel morphology are most similar to *Pantherophis*. *Pantherophis* is a genus of medium to large colubrines that occurs throughout the central and eastern United States and south to Costa Rica (Conant and Collins, 1998; Holman, 2000). Fossils of the genus are known from the Clarendonian through present (Holman, 2000).

Pituophis Holbrook, 1842
Pituophis sp.
(Fig. 3M–O)

Material.—ETMNH-9451, posterior trunk vertebra (Fig. 3M–O).

Remarks.—The hemal keel of ETMNH-9451 projects far ventrally. Because of the prominence of the hemal keel and subcentral grooves, this vertebral morphology is a rare component of the GFS colubrid fauna and is most similar to *Pituophis*, especially those figured by Holman (2000:fig. 115). The pronounced subcentral grooves often are present on more posterior trunk vertebrae, and this may imply that ETMNH-9451 lies more posterior. Van Devender and Mead (1978) discussed *Pituophis melanoleucus* and reported several important characteristics, including vertebral centrum length up to 7.5 mm; vertebrae slightly longer than wide; vaulted neural arch; high and thick neural spine, moderately to strongly convex zygosphene in anterior view; short and pointed prezygapophyseal accessory processes; and a round, relatively large, and slightly oblique condyle. Although ETMNH-9451 agrees with most of these observations, it appears distinct from *P. melanoleucus* because of a lower and potentially more gracile neural spine and a potentially sinuate zygosphene. Nevertheless, it agrees most strongly with *Pituophis* and is here referred to an indeterminate species of *Pituophis*. *Pituophis* are a group of relatively large snakes present throughout most of North America today, including eastern Tennessee (Conant and Collins, 1998; Holman, 2000). The earliest known occurrence of *Pituophis* is from the Clarendonian of Nebraska (Parmley and Hunter, 2010).

Zilantophis, gen. nov

Type Species.—*Zilantophis schuberti*, sp. nov.

Etymology.—Generic epithet is a combination of *Zilant*, a Russian word that refers to a legendary creature, akin to a dragon, wyvern, or winged snake, which itself refers to the broad, wing-like lateral processes of the vertebrae, and *ophis*, a Greek word for snake or serpent. Pronounced "zee-lahn-TOE-phis."

Diagnosis.—As for the type species (currently monotypic).

Zilantophis schuberti, sp. nov.
(Figs. 4 and S2)

Holotype.—ETMNH-9557, posterior trunk vertebra (Fig. 4).

Type Locality and Horizon.—Gray Fossil Site at East Tennessee State University and General Shale Natural History Museum, 2.9 km west of Gray, Washington County, northeastern Tennessee. Age is late Hemphillian North American Land Mammal Age (latest Miocene–earliest Pliocene).

Paratype Material.—ETMNH-9245, caudal vertebra; ETMNH-9273, midtrunk vertebra; ETMNH-9292, caudal vertebra (Fig. S2G–I); ETMNH 9324, anterior trunk vertebra (Fig. S2A–C); ETMNH-9413, trunk vertebra (Fig. S2D–F); ETMNH-9431, anterior trunk vertebra.

Etymology.—Specific epithet is in honor of Blaine Schubert for his support, his contributions to herpetology and paleontology, particularly at the Gray Fossil Site, and for inspiring the authors and furthering our understanding of fossil reptiles and amphibians.

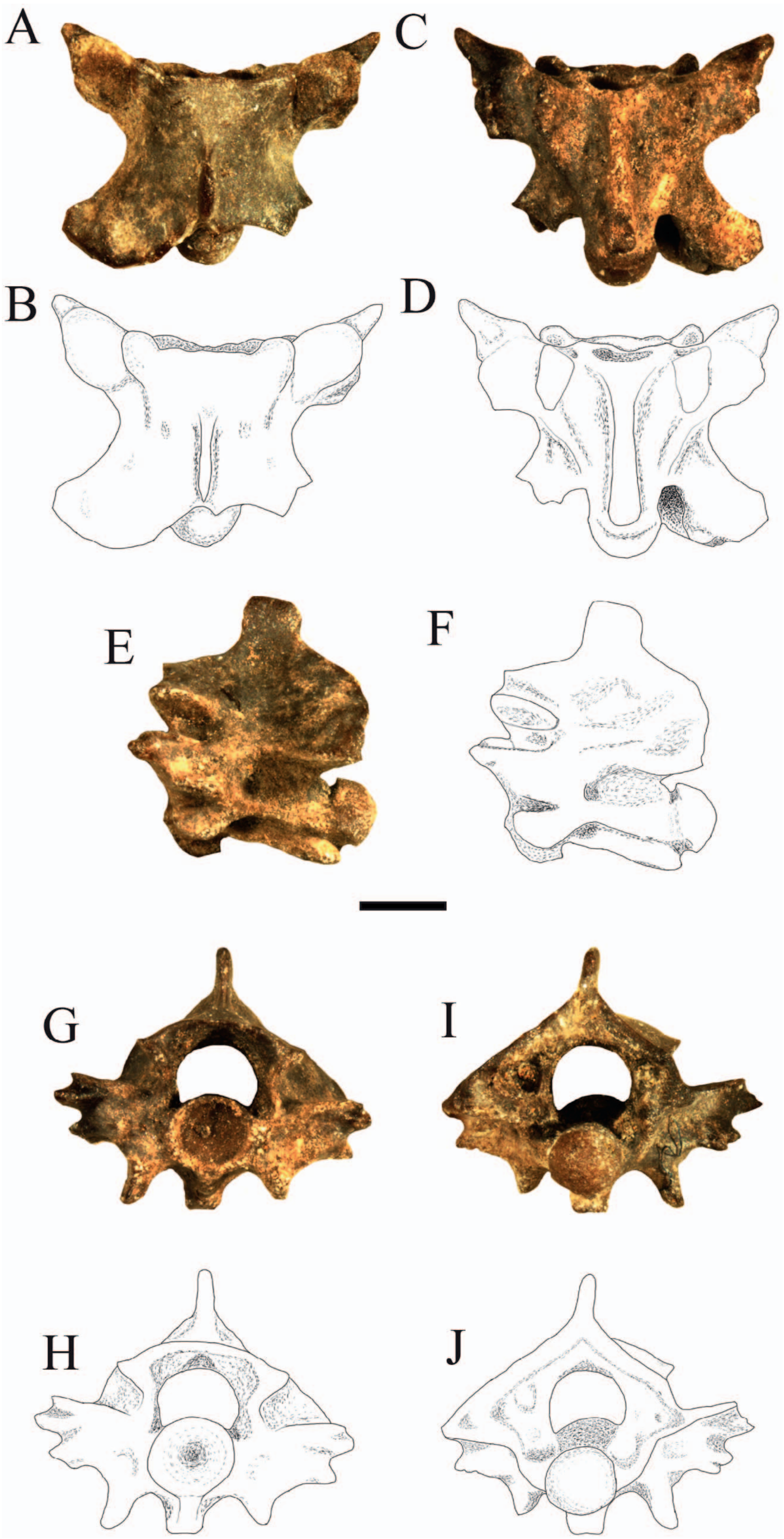

FIG. 4. Holotype vertebra of *Zilantophis schuberti* (ETMNH-9557), trunk vertebra in A–B, dorsal view; C–D, ventral view; E–F, left lateral view; G–H, anterior view; I–J, posterior view. Scale bar equals 1 mm.

Diagnosis.—A small colubrine distinguished from all other North American colubrid snakes by the following combination of vertebral characteristics: 1) vertebra in dorsal view short and wide; 2) short and high neural spine, with the anterior edge at approximately the halfway point of the prezygapophyseal–postzygapophyseal length (52% posterior in ETMNH-9557), with a straight anterior edge and a slight posterior undercut; 3) distinct, narrow hemal keel for most of its length, the posterior portion of the hemal keel is wider and teardrop shaped (=spatulate) in ventral view and extends slightly ventrally (posteroventral projection believed to be only on anterior vertebrae plus cloacal and caudal vertebrae); 4) moderately vaulted neural arch with a well-rounded posterodorsal edge (which possess postzygapophyses); 5) relatively wide zygosphene with a flat to gently convex anterior edge; 6) moderately pointed prezygapophyseal accessory processes; 7) ovoid prezygapophyseal articular facets; 8) horizontally broad, dorsoventrally flat diapophyses on trunk, cloacal, and caudal vertebrae; 9) prominent parapophyses that are pointed in anterior view; and 10) lacks epizygapophyseal spines on precaudal vertebrae while having inconspicuous epizygapophyseal spines on caudal vertebrae.

Comparisons.—Trunk vertebrae assigned to *Zilantophis* appear superficially similar to the cloacal or caudal vertebrae in many snakes because of features including the craniocaudally short length, a (slight) ventral projection of the hemal keel, a relatively small cotyle and condyle with a potentially wide zygosphene, a large neural canal, and large paradiapophyses potentially leading to lymphapophyses. In contrast, although some of the lateral projections appear broken, and in some cases are inferred to represent lymphapophyses broken near the base, in other specimens (e.g., ETMHN-9273, -9324, and -9431), these projections are clearly intact paradiapophyses, representative of trunk vertebrae. Although the neural spine can become craniocaudally shorter in the cloacal-caudal region (e.g., *Coluber*, *Pantherophis*, *Nerodia*, *Regina*, *Virginia*), this is not always the case (e.g., *Drymarchon*, *Storeria*), and is not consistent within or between the two key subfamilies (Colubrinae and Natricinae). Additionally, the morphology of the neural spine often becomes more uniformly square moving caudally, with the anterior and posterior edges becoming more parallel, generally losing the potential undercuts and curvature present more anterior in the series. The neural spine also tends to decrease in dorsoventral height in the cloacal and caudal region, including those of *Zilantophis* in relative terms, although they remain quite tall throughout the column of *Zilantophis*. Indeed, even accounting for variation in neural spine morphology, the shape and position of the neural spine in *Zilantophis* is distinct among colubrids.

Zilantophis is distinguished by the following two apomorphies from all other colubrines: 1) a tall and axially short neural spine whose anterior edge lies at approximately the halfway point (craniocaudally) on the vertebra; and 2) possessing prominent diapophyses on trunk vertebrae that are wide in dorsal and ventral views, but thin in anterior and posterior views. *Zilantophis* also can be distinguished from several colubrines by its tall neural spine, including *Cemophora*, *Chionactis*, *Coluber*, *Dakatophis*, *Ficimia*, *Gyalopion*, *Liochlorophis*, *Masticophis*, *Nebraskophis*, *Opheodrys*, *Oxybelis*, *Paraoxybelis*, *Pollackophis*, *Pseudocemophora*, *Stilosoma*, *Tantilla*, *Tauntonophis*, *Texasophis*, and *Trimorphodon*. Additionally, its teardrop-shaped hemal keel helps easily distinguish it from *Ameiseophis*, *Arizona*, *Drymarchon*, *Paracoluber*, *Pituophis*, *Proptychophis*, *Rhinocheilus*, *Salvadora*, and *Sonora*. *Zilantophis* can be further distinguished from *Drymobius* by its anteroposteriorly short neural spine, and from *Phyllorhynchus* by its anteroposteriorly short neural spine and its tapered (or pointed) prezygapophyseal accessory processes.

Zilantophis schuberti appears most morphologically similar to *Miocoluber*, *Bogertophis*, *Pantherophis*, and some species of *Lampropeltis*. Although *Miocoluber* also possesses a tall and anteroposteriorly short neural spine, *Zilantophis* differs in its more robust nature and the teardrop and spatulate shape of the hemal keel, together with the more rounded posterior postzygapophysis portions of the neural arch. *Zilantophis* is similar to *Bogertophis* because of its high neural spine, spatulate hemal keel, and relatively short but wide vertebral form, but can be distinguished by its well-rounded centrum, pronounced and robust diapophyses and parapophyses, and dorsally tall and anteroposteriorly short neural spine. *Zilantophis* is similar to *Pantherophis* for the same reasons as *Bogertophis*, but distinct from most species of *Pantherophis* by its tall and anteroposteriorly short neural spine, including *Pantherophis kansensis* (=*Elaphe kansensis*), *Pantherophis obsoletus*, *Pantherophis pliocenica* (=*Elaphe pliocenica*), and *Pantherophis vulpina*. *Zilantophis* trunk vertebrae are wider and shorter than those of *Pantherophis buisi* (=*Elaphe buisi*). *Pantherophis guttatus* has an anteroposteriorly longer neural spine, concave zygosphene, and less prominent diapophyses and parapophyses. All *Pantherophis* vertebrae tend to be longer and laterally less broad than *Zilantophis*, have more prominent subcentral ridges, and neural spines that are longer and located farther anteriorly. *Zilantophis* is similar to some species of *Lampropeltis* because of its tall neural spine, spatulate hemal keel, and generally short but wide vertebral form. It can be distinguished from *Lampropeltis calligaster* by its unique neural spine, possessing a rounder cotyle and condyle, and the slight medial constriction of its hemal keel. Its higher and anteroposteriorly shorter neural spine distinguish it from *Lampropeltis mexicana* and *Lampropeltis similis*. *Zilantophis* is distinguished from *Lampropeltis triangulum* by the flat anterior edge of its neural spine, height and length of its neural spine, its position (located farther posteriorly in *Zilantophis*), and the more rounded cotyle and condyle. It is distinguished from *Lampropeltis getula* by having an anteroposteriorly shorter neural spine that possesses no undercut anteriorly and is positioned farther posteriorly, a wider zygosphene, and the prezygapophyseal accessory processes are more pointed. *Lampropeltis pyromelana* and *Lampropeltis zonata* have lower neural spines than *L. getula*, also distinguishing them from *Zilantophis*. When present, the posterior undercut of the neural spine is more prominent in *Lampropeltis* than in *Zilantophis*. As with other colubrids, the diapophyses are more prominent and pronounced on trunk vertebrae of *Zilantophis* than in *Lampropeltis*.

Description of Holotype.—The holotype of *Zilantophis* (ETMNH-9557) is a small vertebra with a tall and axially short neural spine. The neural spine has flat anterior and posterior edges. It has a moderately vaulted neural arch with a flattened to slightly convex zygosphene. It possesses prezygapophyseal accessory processes that are moderately pointed and slightly anteriorly deflected and ovoid prearticular facets. The cotyle and condyle are both well rounded, and the neural canal is "loaf-of-bread" shaped. As part of the synapophyses, both the diapophyses and parapophyses are robust and prominent. The diapophyses are expanded and bladelike in ventral view, and project farther laterally than in other snake taxa. The parapophyses are thin and gracile in anterior view, and broad in lateral view. While maintaining this blade-like appearance, the parapophyses project

TABLE 2. Vertebral measurements of *Zilantophis schuberti* gen. et sp. nov. and other vertebrae identified in this study. Abbreviations: CL, centrum length; GCW, greatest centrum width; GNSH, greatest neural spine height; NAW, neural arch width; NSL, neural spine length; PPL, length through prezygapophysis–postzygapophysis. Measurements are in millimeters.

		Vertebral measurements					
Genus	ETMNH-	CL	GCW	NAW	PPL	NSL	GNSH
cf. *Neonatrix*	9262	3.28	1.69	1.65	3.72	2.07	1.1
Nerodia	9362	3.85	2.35	2.11	4.23	2.5	0.71
Thamnophis	9261	5.6	2.51	2.7	5.98	?	1.83
Thamnophis	9448	5.81	2.64	2.9	6.92	~3.24	1.79
Thamnophis	11961	2.81	1.75	1.94	3.28	1.79	0.73
Coluber/Masticophis	9244	5.44	2.52	2.46	5.83	2.97	?
Coluber/Masticophis	9401	6.85	4.27	3.66	7.86	5.04	1.48
Masticophis	11115	3.15	1.65	3.1	2.53	3.4	1.41
Pantherophis	9510	6.76	4.86	4.08	8.08	3.56	1.53
Pituophis	9451	4.89	2.91	2.85	5.78	3.37	1.2
Zilantophis	9245	2.45	0.81	1.54	2.53	1	1.18
Zilantophis	9273	2.22	0.69	1.6	1.99	0.92	?
Zilantophis	9292	2.56	1.31	1.85	2.77	1.24	1.4
Zilantophis	9324	2.48	0.82	1.86	2.96	0.78	1.26
Zilantophis	9413	?	1.27	2.15	3.32	1.14	1.58
Zilantophis	9431	?	0.76	1.64	2.18	0.82	1.14
Zilantophis (holotype)	9557	2.37	1.03	1.8	2.67	0.81	1.68

anteroventrally and diverge from each other slightly. The subcentral ridges are inconspicuous, although they are slightly curved and mostly obstructed from view by the enlarged parapophyses anterolaterally. The dorsoposterior border of the neural arch is well rounded, with no epizygapophyseal spines, although the right posterior portion of the neural arch possessing the postzygapophysis is not preserved in ETMNH-9557. It exhibits a relatively broad hemal keel that expands posteriorly into a well-rounded and pronounced teardrop or spatulate shape. No parazygantral foramina are present.

Measurements.—Centrum length 2.37 mm; greatest centrum width 1.04 mm; neural arch width 1.8 mm; length through prezygapophyses–postzygapophyses 2.67 mm; neural spine length 0.81 mm; greatest neural spine height 1.68 mm. For full list of measurements see Table 2.

Description of Paratypes.—The paratype material displays the key features of *Zilantophis schuberti*, with some variation depending on vertebral position. ETMNH-9273 maintains the key features although its neural spine is incomplete and its prezygapophyseal accessory processes are not preserved. In ETMNH-9292 and -9324 the zygosphene is slightly convex with moderately pointed prezygapophyseal accessory processes. The subcentral ridge is relatively inconspicuous and curved in ETMNH-9324. ETMNH-9431 is incomplete, missing the posteroventral portion of the vertebra and the diapophyses and parapophyses, with moderately pointed prezygapophyseal accessory processes. In dorsal view the zygosphene for all the specimens is either flat to gently convex. All of these specimens possess the above-mentioned characteristics of *Zilantophis schuberti* for the preserved portions.

Remarks.—*Zilantophis schuberti*, gen. et sp. nov., is a small colubrine, a group partially characterized by possessing noncervical trunk vertebrae with hemal keels and lacking hypapophyses. It would have measured roughly 300–400 mm in total length, based on vertebral measurements and the estimated total length of *Micronatrix* by Parmley and Hunter (2010). It has a distinct short and wide vertebral form not often present in colubrine snakes, living or extinct (see Table S1). Some of the features present in *Zilantophis* are thought to be present only in more posterior vertebrae, such as cloacal and postcloacal vertebrae, as discussed by LaDuke (1991). Although these features (discussed above) often are found in cloacal and postcloacal vertebrae, they can also potentially be present in more anterior vertebra, particularly if the paradiapophyses described above are not simply broken lymphapophyses. Indeed, the features discussed above are present in all referred vertebrae where the feature is preserved, including the more anterior vertebrae that were less complete, or showed less features, than those figured. This means that some features considered to be present more posteriorly in some snake taxa can be found more anteriorly in others. Indeed, LaDuke (1991) mentioned that distinct subcentral grooves, considered to be features of more posterior vertebrae, can be found throughout the vertebral column in at least one colubrid taxon (e.g., *Lampropeltis getula*). The changes in the neural spine, including slight change in morphology and height, still retain some features throughout the column, and the common features of the neural spine of *Zilantophis*, including its morphology and position on the centrum, help differentiate it from other colubrid taxa. Not all features present in *Zilantophis* are considered present only in more posterior vertebrae, including the height, shape, and position of the neural spine, only moderately vaulted neural arch with a well-rounded posterodorsal edge, nonsinuate (or noncrenate) zygosphene, shape of the diapophyses, and lack of epizygapophyseal spines anteriorly. *Zilantophis* is distinct from all other taxa, but appears most similar, and perhaps most closely related, to *Pantherophis* (and *Bogertophis*), and *Lampropeltis* based on the generally high neural spine that tends to possess a posterior undercut, lack of epizygapophyseal spines (anteriorly), and generally spatulate hemal keel. Fossil *Pantherophis* have been identified from the late Clarendonian or early Hemphillian of Kansas (Gilmore, 1938; Holman, 2000), although they appear more common during the Irvingtonian and Rancholabrean (Holman, 2000). Fossil *Lampropeltis* have been identified from the middle Barstovian (Holman, 1964), although they appear more common during the Irvingtonian and Rancholabrean as well (Holman, 2000). Therefore, *Zilantophis* occurs temporally along with some of the earliest members of *Pantherophis* and *Lampropeltis*. Given its morphological similarity, *Zilantophis* represents a distinct, but perhaps related, taxon, possibly

Table 3. Comparison of several Miocene–Pliocene colubrid faunas from Nebraska and eastern North America. Data for the GFS come from this study, and information for other sites and ranges came from Holman (1964, 1976, 1996, 1998, 2000) Meylan (1984), Woodburne (1996), Conant and Collins (1998), Farlow et al. (2001), Hulbert (2001), and Parmley and Hunter (2010). Abbreviations for localities: elM, early late Miocene; eM, early Miocene; eP, early Pliocene; DE, Delaware; FL, Florida; GFS, Gray Fossil Site, Tennessee; GT, Glad Tidings, Nebraska; HVI, Haile VI, Florida; LBB, Love Bone Bed, Florida; lM, late Miocene; MF, McGehee Farm fauna, Florida; mM, middle Miocene; MET, modern colubrids in eastern Tennessee; Others, other colubrid subfamilies aside from Colubrinae and Natricinae; NE, Nebraska; PCSh, Pipe Creek Sinkhole local fauna, Delaware; PFS, Pollack Farm Fossil Site, Delaware; PS, Pratt Slide fossil site, Nebraska; TN, Tennessee; VF, Valentine Formation. "/" refers to the fact that Parmley and Hunter (2010) identified multiple specimens as either *Coluber* or *Masticophis*, and "\" refers to specimens being identified as *Heterodon* or *Paleoheterodon*.

		Fossil localities and ages										
	Locality	PFFS	GT	VF	PS	MF	HVI	LBB	FL	PCSh	GFS	MET
	State	DE	NE	NE	NE	FL	FL	FL	FL	IN	TN	TN
	Time period	eM	mM	elM	lM	lM	lM	lM	lM-eP	lM-eP	lM-eP	Modern
Subfamily	Genus											
Colubrinae	*Ameiseophis*	×			×							
	Cemophora											×
	Coluber				/	×			×	×	/	×
	Pantherophis		×	×	×	×		×	×	×	×	×
	Lampropeltis		×	×	×	×		×	?	×		×
	Masticophis				/						×	
	Nebraskophis			×								
	Opheodrys				cf.							×
	Paracoluber				×					×		
	Pituophis				×						×	×
	Pollackophis	×										
	Salvadora		×	×								
	Tantilla											×
	Texasophis				×							
	Zilantophis										×	
Natricinae	*Micronatrix*				×							
	Neonatrix			×	×						cf.	
	Nerodia				×		×	×	×	×	×	×
	Regina							×	×			×
	Storeria											×
	Thamnophis			?	×	×		×	×	×	×	×
	Tropidoclonion				cf.							
	Virginia											×
Others	*Carphophis*											×
	Diadophis						×		×			×
	Dryinoides							×	?			
	Heterodon				\		×	×	×	×		×
	Paleofarancia								×			
	Paleoheterodon		×	×	\				×	×		
	Stilosoma						×		×			

endemic to the southern Appalachian region during the late Hemphillian.

Discussion

Currently, the GFS colubrid fauna is comprised of at least seven colubrid taxa, including cf. *Neonatrix*, *Nerodia*, *Thamnophis*, *Coluber/Masticophis*, *Pantherophis*, *Pituophis*, *Zilantophis* (gen. nov.), and indeterminate natricines and colubrines. The presence of *Nerodia*, as well as the tentative presence of cf. *Neonatrix*, would suggest a pond or other aquatic habitat; however, the pond (or pondlike) environment directly at the GFS is known to have been surrounded by an oak–hickory subtropical forest with grasslands nearby (DeSantis and Wallace, 2008; Mead et al., 2012). Although most of the other snake taxa have relatively wide habitat ranges presently and in the fossil record (see Holman, 2000), *Masticophis* and *Pituophis* prefer more open-forested habitats, which are believed to have been present around the GFS. Additionally, gomphotheres, *Tapirus*, and *Teleoceras* from the GFS had C_4 grasses in their diet, indicative of nearby grasslands (DeSantis and Wallace, 2008).

Few sites are similar to GFS and its snake fauna that allow for more detailed comparisons of the colubrids present (Table 3). The Pollack Farm Fossil Site in Delaware is from the early Miocene (Holman, 1998). Holman (1996) reported on the herpetofauna from Glad Tidings in Nebraska (middle Miocene, Barstovian LMA). In earlier studies, Holman (1964, 1976) reported on snakes from the Valentine Formation of Nebraska (late middle to early late Miocene by Woodburne, 1996). Parmley and Hunter (2010) discussed the fossil snakes from the late Miocene (Clarendonian) Pratt Slide fossil site in Nebraska. Meylan (1984) reported on relatively smaller snake faunas from the late Miocene McGehee Farm fauna, Haile VI site, and Love Bone Bed localities in Florida. In a more recent study, Hulbert (2001) reviewed the fossil snake record from the late Miocene–early Pliocene of Florida and reiterated most taxa listed by Meylan (1984), although he listed the presence of the genera *Dryinoides* and *Lampropeltis* as questionable. Perhaps the biggest difference between these Florida sites and the GFS is the presence of so many noncolubrine and nonnatricine colubrids in the Florida sites. Farlow et al. (2001) reported on the late Miocene–early Pliocene (Hemphillian–Blancan) Pipe Creek

Sinkhole local fauna from Indiana. It represents the only site of this age in eastern North America other than those in Florida and the GFS, and differs from the others. Most of these faunas are older than the snake fauna at the GFS.

The Miocene was an important time in the evolution of the North American snake fauna (e.g., Auffenberg, 1963; Savitsky, 1980; Parmley, 1988). Savitsky (1980) suggested this evolutionary transition was a response to the spread of open habitats that allowed colubrids to become dominant. Parmley (1988) mentioned the transition occurred approximately coeval with a major mammalian extinction. Parmley and Holman (1995) offered potential reasons, including a temporal succession of midcontinental forest communities to arid grasslands, immigration of modern colubrid genera from Eurasia, radiation of a new food source, and competition for the new resources. These changes seemed to be occurring within the Appalachian regions at this time as well, and the GFS, and its colubrid fauna, concur with those changes. At the GFS, colubrid specimens make up the majority of snake fossils (91%), whereas boids are a very small percentage (1%), and viperids are only slightly higher (8%) (see Table S2). These values hint at increasing colubrid diversity in North America during this time. The GFS falls toward the end of this time period and provides further data for this evolution of the modern North American snake fauna.

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Supplementary Data

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