

# Fossil snakes of the Penny Creek Local Fauna from Webster County, Nebraska, USA, and the first record of snakes from the Early Clarendonian (12.5-12 Ma) of North America

John J. Jacisin III and A. Michelle Lawing

## ABSTRACT

The Penny Creek Local Fauna in southern Webster County, Nebraska, is an early Clarendonian fossil locality within the Ash Hollow Formation. Undescribed fossils from previously collected Penny Creek material represent the first record of snakes from this time interval and confirm the presence of multiple taxa immediately following the Mid-Miocene Climatic Optimum. We identified eight taxa from the locality, including one booid (*Charina*), three colubrids (*Pantherophis*, *Lampropeltis*, and *Salvadora*), a dip-sadid (*Heterodon/Paleoheterodon*), and several natricids (*Neonatrix elongata*, *Neonatrix magna*, and *Nerodia*). Of these snakes, only *Neonatrix* is an extinct genus, *Charina* and *Salvadora* are presently extirpated from the area, and all other genera are represented in the Central Great Plains today. Habitats occupied by extant members of genera represented in the Penny Creek snake assemblage suggest a relatively open environment with loose substrates and plentiful ground cover near a permanent water source. This further corroborates previous geological and mammalian paleoecological assessments of the Penny Creek area as a somewhat open, woodland-prairie ecotone environment near a permanent, high-energy fluvial water source. Finally, the snakes of Penny Creek help contribute to our understanding of the modernization of North American snake assemblages in the Central Great Plains by providing data for a poorly understood time within the evolution of North American snakes

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## INTRODUCTION

Snakes have a wide geographic distribution in the Cenozoic fossil record, with many modern North American groups first appearing in the Miocene of North America (Rage, 1984; Parmley and Holman, 1995; Holman 2000). Unfortunately, many Cenozoic North American snake faunas are chronically understudied, and specimens remain unidentified or misidentified/overidentified through covert biases such as gestalt or non-apomorphy-based identifications, thereby hindering opportunities to apply a deep time perspective to investigate the effects of environmental change on snake communities (Bell et al., 2010; Szyndlar, 2012; Head et al. 2016). Further complicating matters is the difficulty of identifying unique taxa based on isolated cranial and vertebral elements that may be weathered or otherwise damaged during or after the death of an organism (Rage, 1984). However, it is important to describe and evaluate these taxa because they provide an important key to understanding the evolution of snakes, as well as the deep time effects of environmental change on snake diversification and biogeography. Fossil Cenozoic snakes are potential tools for environmental reconstruction and investigating the long-term biotic effects of climate change, as the physiologies of many reptiles are strongly associated with their habitat (Webb and Shine, 1998; Head et al., 2009; Sinervo et al., 2010; Muthoni, 2010; Huey et al., 2012; Dupoué et al., 2017).

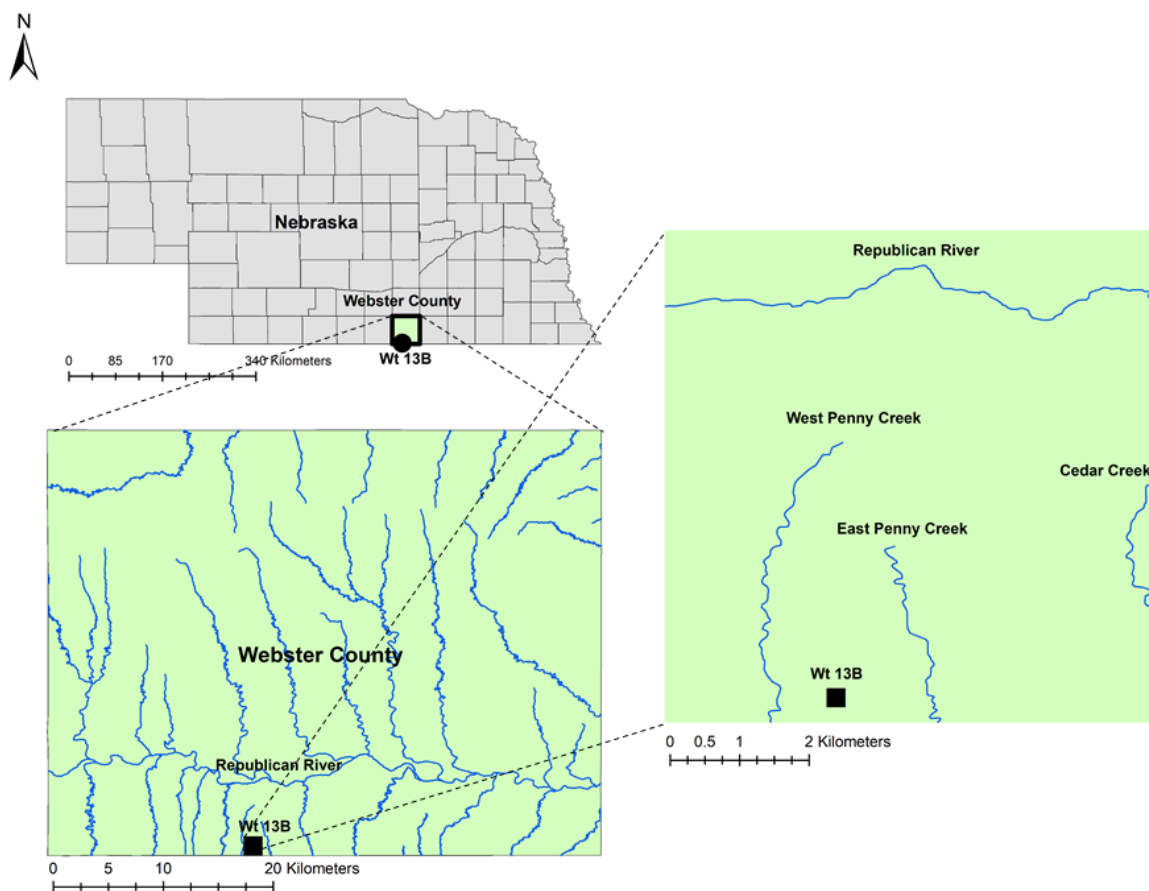
While a relatively small number of mostly diminutive fossil snakes from the Paleogene of the Central Great Plains (South Dakota, Nebraska, Kansas, and Oklahoma) have been described, the Neogene beds of the Central Great Plains – specifically Nebraska – include a comparatively long, well-preserved record of fossil snakes that is unparalleled in illustrating the history of richness, turnover, and modernization of snake assemblages in North America (Holman, 2000; Parmley and Holman, 2007; Parmley and Hunter, 2010). Within the changing environments leading up to, then following the Mid-Miocene Climatic Optimum (MMCO), the “archaic” booid-dominated faunas represented by *Ogmophis*, *Calamagras*, and *Geringophis* gradually gave way to Caenophidian-dominated faunas (Parmley and Holman, 1995; Parmley and Hunter, 2010). More specifically, North American faunas become primarily composed of Colubroidea (sensu

Burbrink et al., 2020). The first recognized appearances of extant genera occur in the early Neogene of the Central Great Plains; these genera include *Lampropeltis*, *Pantherophis* (*Elaphe*), *Salvadora*, *Heterodon*, *Nerodia*, *Thamnophis*, *Crotalus*, *Sistrurus*, and *Charina* (Parmley and Holman, 1995; Parmley and Holman, 2007; Parmley and Hunter, 2010).

Despite the excellent state of the Central Great Plain’s fossil snake record and apparent peaks of genus-level richness in the late Barstovian and late Clarendonian (14.75-12.5 Ma and 10.0 Ma- 9.0 Ma; Holman, 2000; Parmley and Hunter, 2010; Jacisin et al., 2015), a paucity of fossil material has resulted in a knowledge gap on snake assemblages from the earliest Clarendonian (12.5-12 Ma). This temporal gap in the snake fossil record is present throughout North America and highlights a gap in our understanding about the temporal turnover and modernization of snake assemblages immediately following the late Barstovian (including the MMCO) of the Central Great Plains.

Here, we report the first known early Clarendonian snake assemblage in North America Penny Creek Local Fauna in southern Webster County, Nebraska (Figure 1). This fossil material allows us to confirm the presence of a number of snake taxa in Nebraska and the Central Great Plains during the early Clarendonian, providing evidence to evaluate previous geological and biological interpretations of the local paleoenvironment and allowing for a more complete understanding of the modernization of North American snake faunas. Fossil reptiles were reported from this locality, but were unidentified, and the focus of previous studies was primarily given to the geological setting and composition of mammalian assemblages (Turner, 1972; Voorhies et al., 1987; Voorhies, 1990; Corner, 2014). Ours is the first study to explore the differences between Nebraska’s latest Barstovian and earliest Clarendonian snakes and the initial transition into a post-Middle Miocene Climatic Optimum (Zachos et al., 2001; Song et al. 2018) snake assemblage.

**Institutional abbreviations.** UNSM, University of Nebraska State Museum, Nebraska, USA; TCWC, Texas A&M University Biodiversity and Research Teaching Collections, Texas, USA; and TMM, Uni-



**FIGURE 1.** Map showing the geographic position of UNSM locality Wt 13B from the Penny Creek Local Fauna at state (A), county (B), and local (C) scales. The locality is represented by a solid black circle.

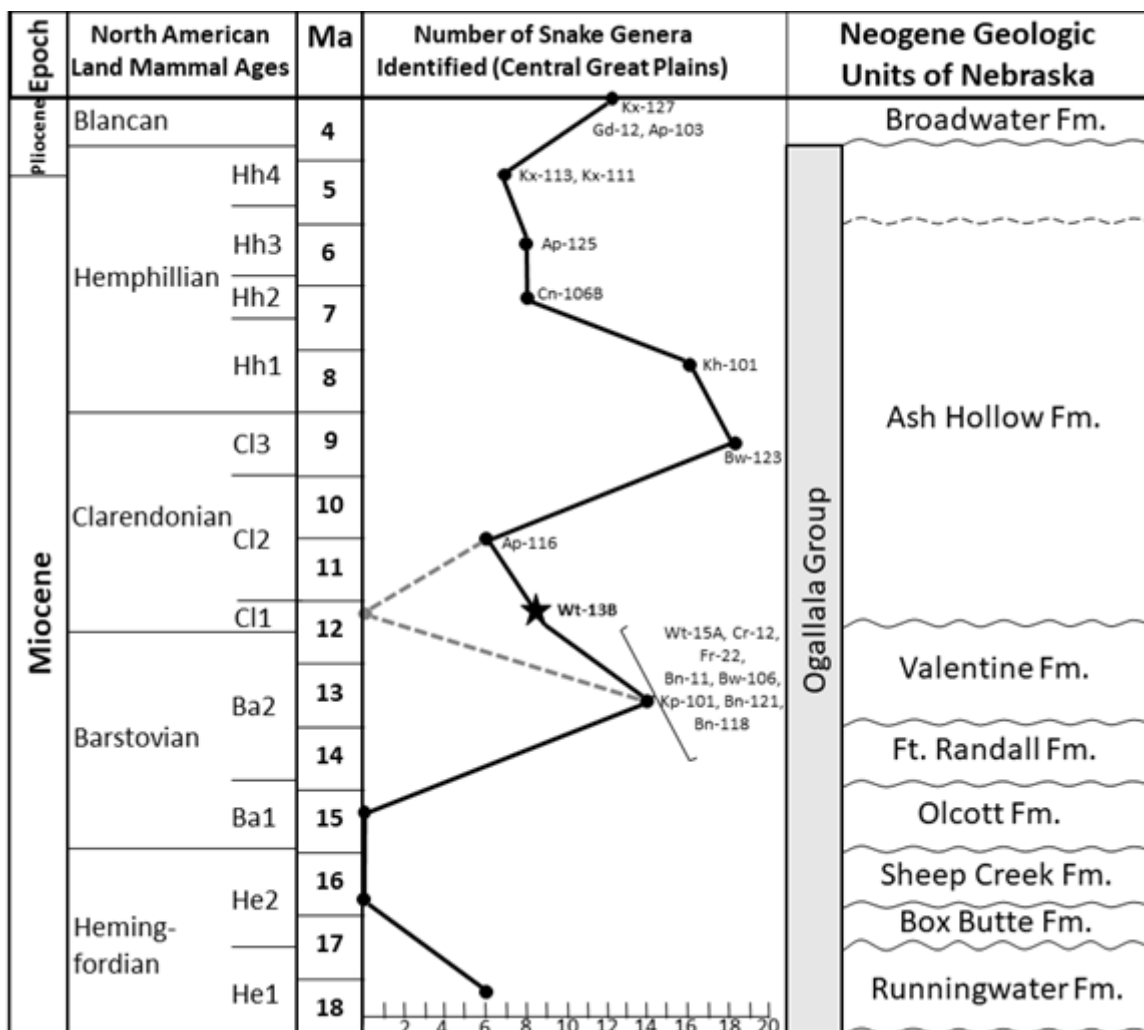
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### GEOLOGIC SETTING

In general, the Ash Hollow Formation is composed of poorly sorted, heterogenous sediments (Diffendal et al., 1996). The basal Ash Hollow Fm. of the Ogallala Group is a cross-bedded conglomerate composed of partially rounded concretions pulled from the underlying Whitney Member of the Brule Formation and is mostly composed of stream-transported and stream-deposited sediments (Diffendal et al. 1996). Boellstorff (1978) first assigned a Miocene age for the formation based on the dates returned during the study of fission tracks in volcanic ash shards. This conglomerate is variable in thickness, and sequences upward into unstratified, massive pebbly sands and calcite-cemented pebbly sandstones (Diffendal et al., 1996; also known as *pudding sands* via Lueninghoener, 1934). These massive sandstones tend to

form massive ledges with the underlying conglomeratic layer. At the type locality of the Ash Hollow Fm., the conglomeratic unit lies upon an erosional surface developed on top of a Whitney Member (Brule Fm.) concretion zone to form an unconformity. Overlying the Ash Hollow Fm. are coarse, stream-deposited sands and gravels that represent the Pliocene Broadwater Formation (Figure 2). While much of the Ash Hollow Fm. is epiclastic, it does contain several diatomite and ash beds (Thomasson, 1980), the latter of which includes the infamous Ashfall Fossil Beds located in Antelope County, Nebraska, although these beds are younger than the locality examined within this study (Voorhies, 1992; Diffendal et al., 1996).

In Webster County, Nebraska, Turner (1972) first reported granitic sand and gravel with cross-bedding indicative of a braided stream fluvial environment for several Nebraska localities collectively named the Penny Creek Local Fauna; this included locality Wt 13B, from which the fossils of this study were collected (Figure 1). Turner (1972) assigned



**FIGURE 2.** Composite time-stratigraphic chart of the Neogene of Nebraska correlated with the number of snake genera presently identified from the Central Great Plains for each North American Land Mammal Age (NALMA) substage. Abbreviations: He (Hemingfordian), Ba (Barstovian), Cl (Clarendonian), Hh (Hemphillian). Each point on the snake richness chart is summarized for each substage at that substage’s midpoint, and is not necessarily correlated with a particular rock unit on the right. Species richness values include fossils from the entire Central Great Plains region, while localities from Nebraska specifically and discussed in this study are listed at each substage point and come from the rock units to the right. The star represents the data from this study, which updates the previous lack of data from Cl1 across North America (represented by the gray hashed line) with data from UNSM Wt-13B. NALMAs and substages are correlated with time based on data and figures from Tedford et al. (2004). Rock Units are adapted from Joeckel et al. (2017) and Tedford et al. (2004). Snake generic richness is modified and updated from Jacisin et al., 2015).

an early Clarendonian age to those localities based on the mammalian fauna. In addition to the dates reported in Boellstorff (1978), work by Swisher (1992) dating the sediments of Nebraska also indicated an early Clarendonian age based on Ar–Ar and K–Ar dates of glass and ash for the lower parts of the Ash Hollow Formation. Reviews of the biostratigraphy and geochronology of the North American Cenozoic further support these dates (Tedford et al., 2004). Research by Voorhies et al. (1987),

Voorhies (1990) and Corner (2014) confirmed the assessment for the locality, and provided additional knowledge on the geology, vertebrate biostratigraphy, and mammalian fossils of Wt 13B as part of larger studies. They concluded that the sediments belonged to the Ogallala Group’s Ash Hollow Fm. and were earliest Clarendonian (middle Miocene) in age, or slightly older than the Ashfall Fossil Beds of northeastern Nebraska (Figure 2). They also noted that the sediments of the Penny Creek local

fauna, and the Ogallala sediments as a whole, were predominantly epiclastic, as opposed to the volcanoclastic sediments of the underlying Arikaree and White River Group rocks in Nebraska (Voorhies, 1990).

## MATERIALS AND METHODS

The fossils assessed in this study were collected from a single locality (Wt 13B), accessioned to the University of Nebraska State Museum's collections, and are part of a diverse assemblage dubbed the "Penny Creek Local Fauna", consisting of several other Webster County localities (Wt 11, Wt 12, Wt 13A, and Wt 15B; Turner, 1972; Voorhies et al., 1987; Corner, 2014). These localities were collected extensively, especially in the 1960's and early 1970's, under the supervision of the UNSM. Wt 13B was quarried annually for several years by students from the Red Cloud Community Schools under the supervision of J. L. Fitzgibbon (Voorhies et al., 1987). Collection methods included surface prospecting, quarrying, and screenwashing during these years (Corner, 2014).

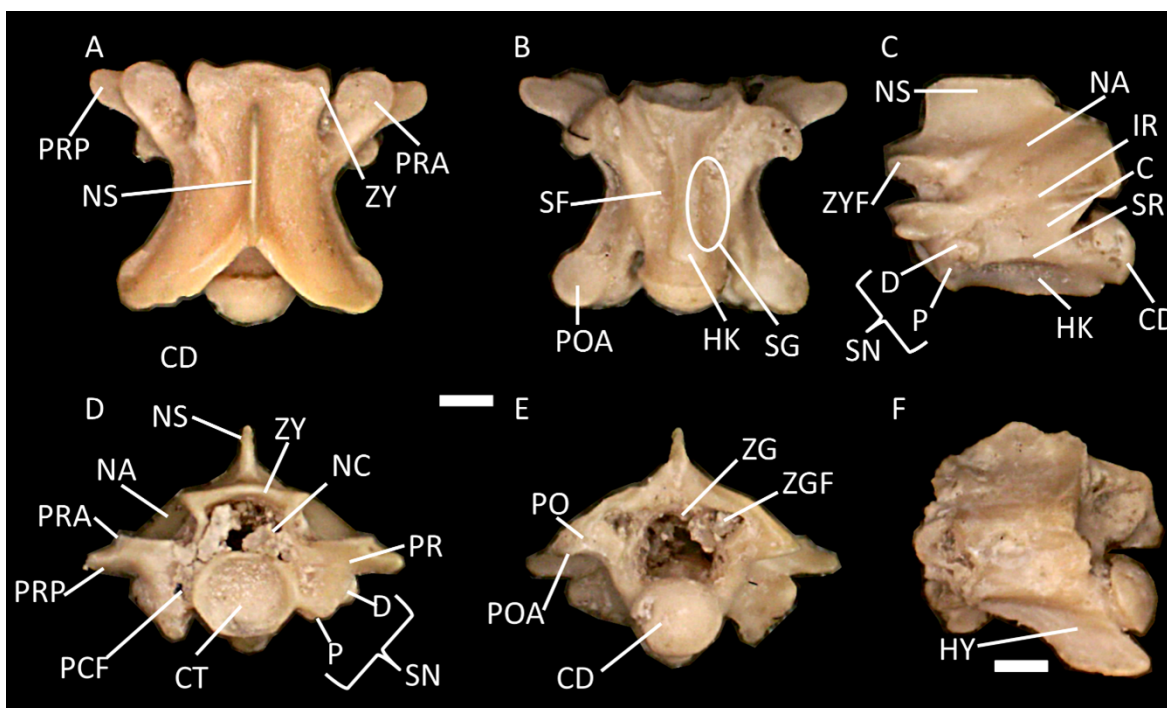
We used a binocular dissecting microscope to examine the snake fossils from Wt 13B, which were predominantly pre-cloacal trunk vertebrae and a small number of caudal vertebrae. Apomorphic characters (such as the presence of a hypapophysis on mid-trunk vertebrae; Holman, 2000) capable of uniquely identifying different snake groups (e.g., natricid vs. colubrine snakes) were used for fossil identification following the recommendations of Bell and colleagues (Bell et al., 2004, 2010). Character tables suggested by Holman (2000) and modified by Ikeda (2007) assisted in the process through generalized descriptions of the range of shape variation for the neural arch, prezygapophyseal articular facets in dorsal view, postzygapophyseal articular facets in ventral view, anterior edge of the zygosphene in anterior and dorsal views, zygosphene articular facets in lateral view, anterior and posterior edges of the neural spine in lateral view, hypapophysis, hemal keel, cotyle, condyle, prezygapophyseal accessory processes in ventral view, developmental degree of the parapophyses, prezygapophyseal accessory processes, interzygapophyseal ridge in lateral view, and subcentral ridge in lateral view (see Figure 3 for morphological position of major vertebral structures). In addition, we made personal observations using comparative methods with available modern and fossil specimens at the UNSM, TCWC, and the TMM collections, as well as previously published literature and figures (including

Gilmore, 1938; Auffenberg, 1963; Rage, 1984 and references therein; LaDuke, 1991; Holman, 2000; Parmley and Walker, 2003; Ikeda, 2007; Parmley and Hunter, 2010; Head et al., 2016; and Zaher et al., 2019). Extinct taxa are denoted by a dagger symbol (†).

Our taxonomic groups follow the terminology used in recent publications on snake systematics, including Burbrink et al. (2020), Georgalis and Smith (2020), and Zaher et al. (2019). These changes in taxonomic nomenclature resulted in a lack of diagnostic characters for some groups. This, combined with the overall rarity of vertebral morphological characters described for higher taxonomic levels in at least North American literature (pers. obs., but see also Holman, 2000 and Ikeda, 2007), hinders comparative morphological studies (see Bell et al., 2010 and Head et al., 2016 for further discussion of identification biases in fossil herpetofauna). As such, we have attempted to resolve more recent nomenclature for groups such as Colubroides (sensu Zaher et al., 2009) and Charinidae (sensu Pyron et al., 2014) with vertebral characters for those groups, rather than vertebral diagnoses of the highest resolution identifications alone (e.g., genus or species).

We assembled occurrences of snakes from 19 sites, Barstovian through Blancan, in the state of Nebraska in order to assess first and last occurrences and the transition to a more modern snake assemblage (Figure 4, Appendix Table 1). We examined the similarity of snake assemblages through time. It is important to note that absences may be representative of true absence, a lack of data or errors in identification. As such, true absences are exceptionally difficult or impossible to be distinguished from false absences, especially when considering communities with numerous rare or difficult to distinguish species (Boulinier et al., 1998).

Beyond identifying taxa at each location, we visualized the similarity between assemblages at these sites by constructing a Euclidean distance matrix and using a principal coordinates analysis (PCoA) for the Nebraska localities. We also used this distance matrix to perform a hierarchical cluster analysis (HCA) with the complete-linkage method to look for groupings of localities that may suggest major shifts in the snake assemblages of Nebraska. Agglomerative HCA is a "bottom-up" analysis where each observation starts in its own cluster, and pairs of clusters are merged as the hierarchy is built up (Hammer et al., 2001). The complete-linkage or farthest neighbor clustering



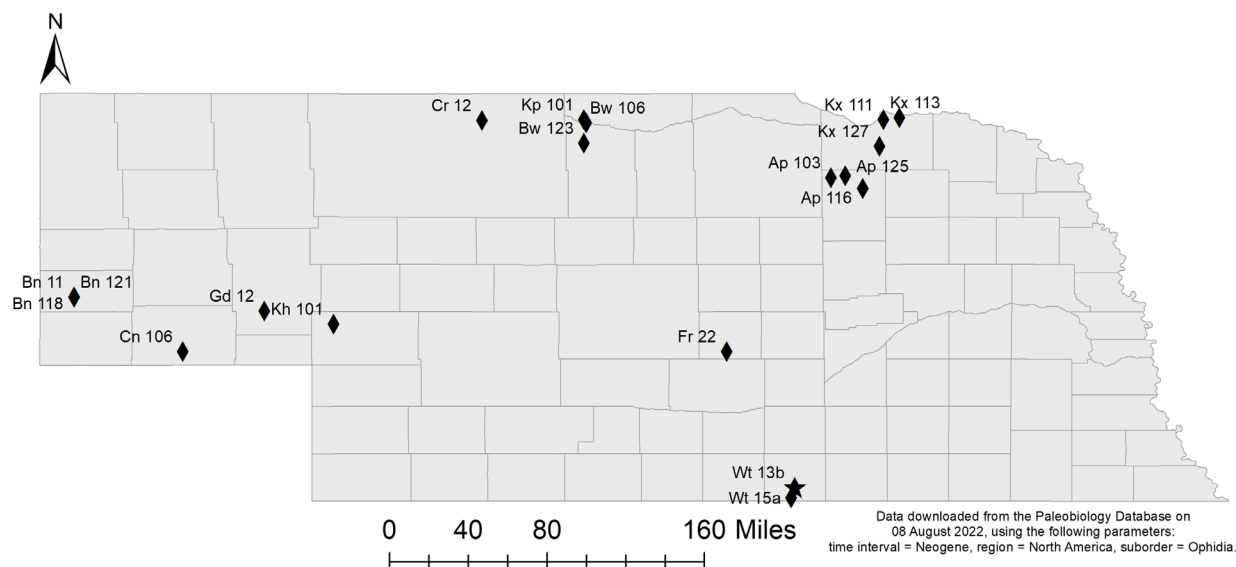
**FIGURE 3.** Basic units of snake trunk vertebrae. **A-E** are from a fossil colubrine, and **F** is from a fossil natricid. **A:** trunk vertebra in dorsal view. **B:** trunk vertebra in ventral view. **C:** trunk vertebra in left lateral view. **D:** trunk vertebra in anterior view. **E:** trunk vertebra in posterior view. **F:** trunk vertebrae in left lateral view. Abbreviations: C, centrum; CD, condyle; CT, cotyle; D, diapophysis; HE, hemapophysis; HK, hemal keel; HY, hypapophysis; IR, interzygapophyseal ridge; LY, lymphapophyses; NA, neural arch; NC, neural canal; NS, neural spine; P, parapophysis; PCF, paracotylar foramen; PLE, pleurapophysis; PO, postzygapophysis; POA, postzygapophyseal articular facet; PR, prezygapophysis; PRA, prezygapophyseal articular facet; PRP, prezygapophyseal accessory process; SF, subcentral foramen; SG, subcentral groove; SN, synapophyses; SR, subcentral ridge; ZG, zygantrum; ZGF, zygantral articular facet; ZY, zygosphene; ZYF, zygosphenal articular facet.

method, which forms compact clusters of near-equal diameters and avoids forcing clusters together based on single elements being close. Complete-link clustering builds clusters where the similarity of two clusters is the similarity of their most dissimilar members (thus, “farthest neighbor”).

Snake ectothermic physiology is highly dependent on ambient temperature and is therefore a practical choice for examining terrestrial climates of the past. To examine the potential climate of the Penny Creek local fauna, we identified area of overlap in climate envelope models for the snake assemblage of the Penny Creek local fauna. Climate envelope models characterize a set of suitable climates for a species or group of species derived from their location in climate space. While these models are constructed from the associations between the geographic location of a species and its climate without consideration of biotic interactions, dispersal, or evolutionary change, past review has suggested that climate envelope mod-

els are capable of producing useful initial approximations of the dynamics of species to climate interactions at appropriate scales (Lawing, 2021). Climate envelope models have been used to evaluate impacts of climate associated changes in the projected geographic distributions of snakes through time to model both the past and future dispersal of a clade (Lawing and Polly, 2011; Lawing et al., 2016).

To create climate envelope models for the Penny Creek snake assemblage, we selected representative congeners of presumed closely related living species for each of the fossil taxa (see Appendix Table 2 for list of congeners used for each fossil taxon). We obtained geographic range maps of those congeners from the IUCN Redlist (IUCN, 2021). Climate data for Mean Annual Temperature (MAT) and Annual Precipitation (AP) from the Worldclim database Version 2.1 (Fick and Hijmans, 2017) at 10-minute resolution were extracted from the polygon overlap of the congeneric species. The two variables described



**FIGURE 4.** Map of the 19 localities in Nebraska, USA with documented occurrences of snake fossils from the Barstovian through Blancan NALMAS.

the mean of temperature and sum of precipitation on an annual basis (Nix, 1986). All congeneric species were combined into a genus-level dataset to decrease the influence of specific differences. Finally, we produced density plot histograms to identify the area of overlap for all generic models across taxa of the Penny Creek local fauna. We used the area of overlap to infer the potential climate envelope of the depositional setting of Penny Creek.

#### SYSTEMATIC PALEONTOLOGY

Class REPTILIA Laurenti, 1768

Order SQUAMATA Oppel, 1811

Suborder SERPENTES Linnaeus, 1758

Infraorder ALETHINOPHIDIA Nopsca, 1923

**Diagnosis.** Vertebrae of Infraorder Alethinophidia are variable, but can typically be identified by the presence of a neural spine, a somewhat high neural arch, and the presence of a median notch on the posterior border of the neural arch has a median notch (Rage, 1984; Holman, 2000).

**Remarks.** While the above characters are true for most of Alethinophidia, both Rage (1984) and Holman (2000) noted exceptions in the Uropeltidae, which lack neural spines, and the genus *Coniophis*, where the vertebrae lack both a neural spine and a median notch in the posterior neural arch. The “higher neural arch” of Rage (1984) is relative to the lower neural arch of Scolecophidia. Ikeda (2007) examined these characters in additional

taxa, and stated that despite the exceptions above, the character states of Rage (1984) and Holman (2000) can be considered diagnostic.

Suprafamily Constrictores Oppel, 1811  
(Georgalis and Smith, 2020)

**Diagnosis.** The vertebrae of the Constrictores clade are massively built and anteroposteriorly short, with a low centrum length / neural arch width ratio ( $< 1.1$ ), and generally have tall neural spines, and thick zygosphenes (Ivanov, 2000; Szyndlar and Rage, 2003; Georgalis and Scheyer, 2019; Georgalis and Smith, 2020).

**Remarks.** Georgalis and Smith (2020) applied the term Constrictores to the group uniting Booidea and Pythonoidea following the taxonomic revisions of Pyron et al. (2014). There are a few broad vertebral characters that unite Booidea and Pythonoidea, and exceptions within and outside of this group exist. Georgalis and Smith (2020) note that the centrum length / neural arch ratio of Constrictores is lower in all ingroup taxa except Ungaliophiinae and *Xenopeltis*, and perhaps some undescribed vertebral morphologies from taxa such as *Xenophidion* (Georgalis and Smith, 2020). Georgalis and Smith (2020) also note that this character is not unique to Constrictores, additionally occurring in Tropidophiidae (Bogert and Rowley, 1968), Madtsoiidae, and specific taxa such as *Acrochordus* (Hoffstetter and Gayard, 1965; Zaher et al., 2019).

Superfamily BOOIDEA Gray, 1825

**Diagnosis.** There are not many vertebral characters defining the diverse group of booid snakes; the most commonly cited characters include the presence of lateral foramina and higher neural arches than those found in Anilioidea (Holman, 2000; modified from Rage, 1984; supported by Ikeda, 2007). Furthermore, in pythonids, the shape of the hemal keel is defined by grooves or depressions beginning at the cotylar rim, but projecting below the centrum only in the posterior part of each vertebra (Scanlon and Mackness, 2001; Szyndlar and Rage, 2003).

**Remarks.** Skeletal characters used to describe Booidea are primarily based on cranial elements (see Georgalis and Smith, 2020). In comparison to colubroids, booid vertebrae are generally less slender and elongate, and tend to have shorter and broader neural spines in at least North American species (Holman, 2000; Smith, 2013). Booidea can often be separated from Pythonoidea based on greater intracolumnar heterogeneity in the former (Szyndlar and Rage, 2003), and thicker zygosphenes in the latter when compared to similarly sized booids, although there is some amount of variability in this character (Georgalis and Smith, 2020).

Family CHARINAIDAE Gray, 1849  
(sensu Pyron et al., 2014)

**Diagnosis.** The following vertebral osteological characters are modified from Brattstrom (1958), Kluge (1993), Bell and Mead (1996), Holman (2000), and Head (2015) to reflect the current nomenclature for Constrictores and Booidea (Reynolds et al., 2014; Zaher et al., 2019; Burbrink et al., 2020; Georgalis and Smith, 2020). The vertebrae possess a flattened neural arch. The neural spines are low, and in the caudal vertebrae are expanded, exhibiting a somewhat distended or distally lobate appearance relative to pre-caudal neural spines (Head, 2015). Prezygapophyseal accessory processes are reduced (Holman, 2000). Paracotylar foramina are absent (Kluge, 1993). Caudal vertebrae are very short, with a variety of processes giving them a complex appearance (with the exception of the genus *Lichanura*; Holman, 2000).

**Remarks.** Snakes of the Charinidae are typically small to medium in size, robust in body form, with short tails and small eyes, all of which assist them in a semifossorial lifestyle (Holman, 2000). Many North American fossil booids, including extant genera *Charina* and *Lichanura*, were previously assigned to the Erycinae, which are generally similar in body form, vertebral morphology, and lifestyle

(Holman, 2000; see Pyron et al., 2014 and ICZN, 2020 for additional details regarding taxonomic nomenclature). Under the most recent taxonomy, North American subfamilies Charininae Gray, 1849 (*Charina* and *Lichanura*) and Ungaliophiinae McDowell, 1987 (*Exiliboa* and *Ungaliophis*) are now grouped within the Charinidae (Pyron et al. 2014; Head, 2015; ICZN, 2020). This further complicates the fossil record of older North American snakes not found in Penny Creek, in that genera such as *Calamagras*, *Ogmophis*, *Geringophis*, *Pterygoboa*, and others are left with a somewhat uncertain taxonomic status, although some research has suggested that the fossil species *Ogmophis compactus* and *Calamagras weigeli* may represent loxocemid and ungaliophiine snakes, respectively (Smith, 2013). An extensive apomorphy-based redescription and reorganization of the older fossil taxa may be necessary to determine if it is possible to morphologically differentiate them at the species or genus level given the newer taxonomy of extant booids (Bell et al. 2010; Pyron et al., 2014; Head, 2015). The absence of paracotylar foramina in Charinidae vertebrae differentiates the group from Boidae (sensu Pyron et al., 2014). This variable character is shared with pythonids and most non-booid booids, and as such does not differentiate Charinidae from those groups (Kluge, 1993; Rage, 2001; Szyndlar and Rage, 2003; Georgalis, 2019; Georgalis and Smith, 2020).

Genus CHARINA Gray, 1849

**Diagnosis.** As diagnosed in Head (2015), *Charina* possesses a lobate neural spine that is laterally expanded similar to other Charininae, and the pterapophyses are anteriorly directed in caudal vertebrae (Kluge, 1993; Szyndlar, 1994). *Charina* also exhibits a non-U-shaped zygosphene in dorsal view, a strongly concave zygosphene in anterior view, a relatively depressed neural arch, an incised posterior edge of the neural arch, and no paracotylar foramina (Holman, 2000).

**Remarks.** The fossils described here are similar in size and morphology to known species of *Charina*. The longer neural spine, the V-shaped (dorsal), strongly concave (anterior) zygosphene, and the depressed neural arch with a relatively deeply incised posterior edge suggest that these vertebrae do not belong to the genus *Lichanura*; however, it should be noted that Bell and Mead (1996) have observed some intraspecific variation in these characters. As in Parmley and Walker (2003), we instead attribute this fossil to the genus *Charina* based on the relative length of the neural spine,



which is greater than that of *Lichanura*, and the lack of juvenile characteristics despite being relatively small in size. Parmley and Walker (2003) have observed that *Lichanura* of a similar size show juvenile characteristics such as a short, high overall morphology, thin neural arch, thin and highly arched zygosphenes, exceptionally short neural spine, enlarged neural canal, and a condyle that appears too large for the centrum, none of which are visible in this specimen.

*Charina* cf. *Charina prebottae* Brattstrom, 1958†  
Figure 5

**Material.** UNSM 139981 (posterior middle trunk vertebra).

**Description.** The vertebra appears near square in shape from dorsal view, but is slightly wider at the prezygapophyses than the postzygapophyses. The postzygapophyses are rounded, while the prezygapophyses are moderately pointed with reduced accessory processes, and are raised antero-laterally. The neural spine is low, broad, and is longer than it is tall or wide. The top of the neural spine is weathered, but this does not appear to affect the overall shape of the neural spine in dorsal view. The neural spine tapers in width anteriorly and is incised posteriorly. The zygosphenes are dorsally flat and v-shaped overall, with somewhat rounded lateral edges that extend slightly forward on the anterior face. In anterior view, the zygosphenes are concave. The neural arch is somewhat flattened and deeply incised posteriorly. The cotyle is round and mildly angled ventrally, with the dorsal edge extending more anteriorly and the ventral edge extending more posteriorly. Paracotylar foramina are absent. The hemal keel is wide, flat, and smooth ending just before reaching the condylar head. It is bordered laterally by a flat indentation, primarily on the anterior end.

**Remarks.** The fossil described here is similar in size and morphology to known species of *Charina* (see above for description and comparisons with *Lichanura*). It is most similar to *Charina prebottae* specimens from other Nebraska localities, as it possesses a more strongly developed hemal keel when compared to the same vertebral region in extant species of *Charina* (Holman, 1987) and no break in the slope of the anterior neural spine in lateral view as it descends to the zygosphenes (Bell and Mead, 1996). Other characters described by Brattstrom (1958) for *C. prebottae* may represent individual and intracolumnar variation as well as differences between his fossils from California and the fossils from Nebraska. Holman (2000) noted that *Charina prebottae* also exhibits notable varia-

tion across a wide geographic area throughout the Miocene. Previous literature suggests that *C. prebottae* may be a catch-all taxon for multiple species, as Brattstrom's (1958) un-illustrated account and subsequent illustrated accounts do not completely match, warranting further in-depth study (Bell and Mead, 1996; Holman, 2000). Although this vertebra is weathered and missing the extreme parts of several of its structures, it exhibits features of the neural spine (Brattstrom, 1958; Bell and Mead, 1996) and hemal keel (Holman, 2000) matching those of *C. prebottae*. As such, we confer this vertebra to *C. prebottae* until the taxon is more comprehensively assessed and re-diagnosed.

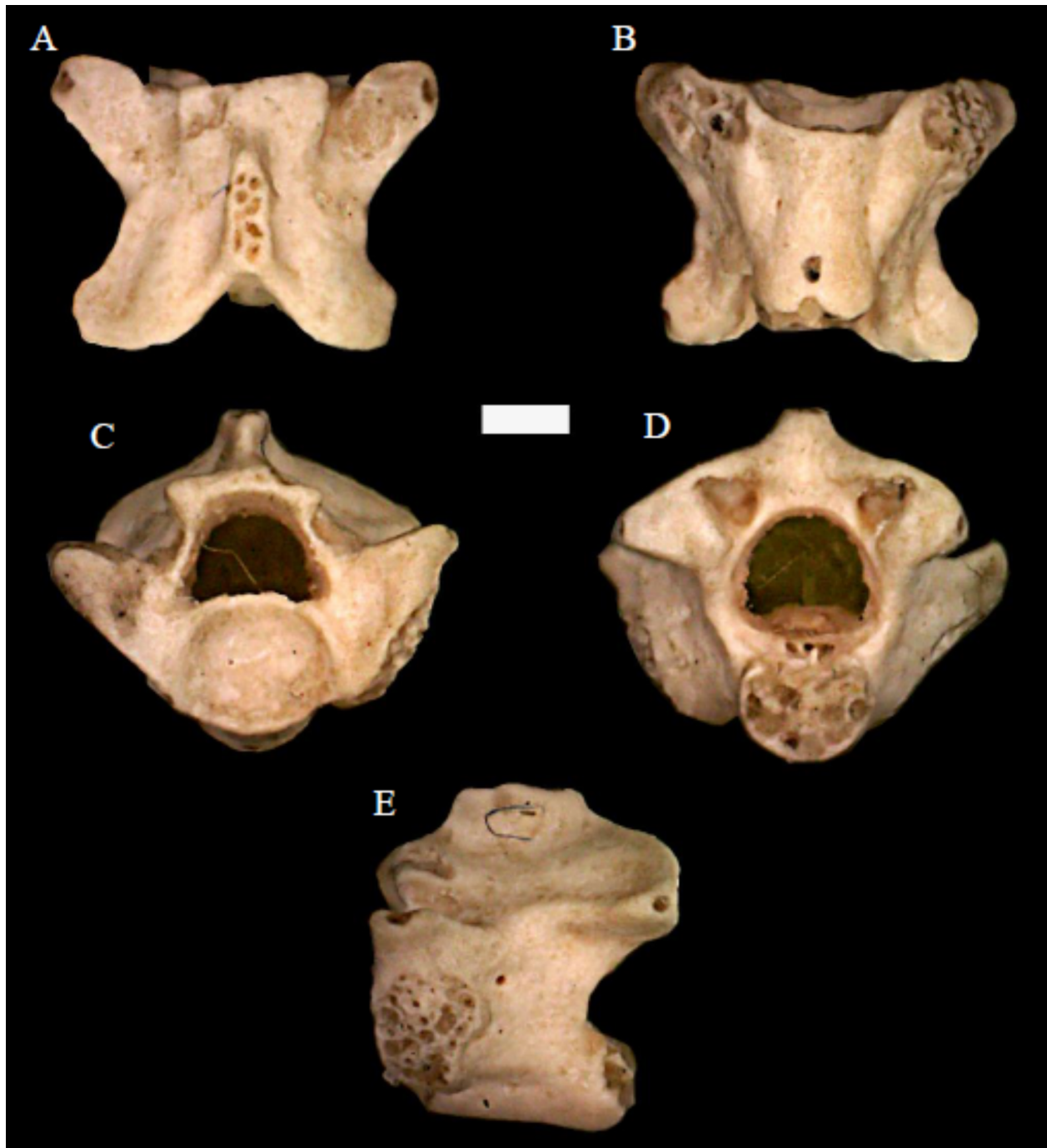
Parvorder CAENOPHIDIA Hoffstetter, 1939

**Diagnosis.** The vertebral synapomorphies of crown Caenophidia include well-developed prezygapophyseal accessory processes, synapophyses that are well-differentiated into para- and diapophyseal articular facets, the presence of pleurocentral hypapophyses throughout the preloacal vertebral column, the presence of one or more paracotylar foramina, a condyle and cotyle that are relatively small (compared to Constrictores) and circular to ovoid and elongate in cross section, and well-developed paralympathic channels that define the lateral margins of a distinct hemal keel (Holman, 2000; Head et al., 2016).

**Remarks.** The vertebral morphologies of Caenophidians is markedly different from that of Booidea, including many of the most notable components of a snake vertebrae (e.g., neural spine, centrum, synapophyses, etc.). The works of Head (2015) and Head et al., (2016) to provide fossil calibration dates for snakes also summarize the morphological synapomorphies that differentiate these groups after the taxonomic restructuring of Caenophidia by Zaher et al. (2009), and Constrictores by Pyron et al. (2014), and Georgalis and Smith (2020).

Suprafamily COLUBROIDES Zaher et al., 2009

**Diagnosis.** Characters that unite Colubroides and exclude Acrochordidae include a highly elongate centrum, the presence of distinct lateral foramina, and large, paired ventrolateral cotylar processes below the ventral margin of the cotyle that may form a paralympathic channel (Head, 2005; Head et al., 2016). Additional vertebral synapomorphies of *Acrochordus* that differentiate Acrochordidae from Colubroides include smaller paired ventrolateral cotylar processes, a greater minimum number of paracotylar foramina (one or more in Colubroides, two or more in Acrochordidae), a shallow fossa or minute lateral foramina as opposed to an



**FIGURE 5.** Trunk vertebra of *Charina* cf. *Charina prebottae* from the Penny Creek local fauna. From top left: dorsal, ventral, anterior, posterior, and lateral views (anterior to the left). Scale bar equals 1 mm.

obvious foramen, synapophyseal articular surfaces with diapophyseal and synapophyseal facets strongly angled relative to each other, ventrally elongate and pendant synapophyses, and a hemispherical, vertically oriented, and blade-like prezygapophyseal accessory process (Head, 2005).

**Remarks.** Vertebral synapomorphies of this group have not been described under the current nomenclature of Colubroidea, perhaps because of confusion between the use of Colubroidea and the previous use of Colubroidea prior to the reorganization of Caenophidian taxonomy (see Zaher et al., 2009 for the history of these taxonomic terms).

Here, we attempted to assemble some vertebral characters by which to define this group; however, some of these characters merely differentiate this group from Acrochordidae, and may not fully match some earlier taxa sometimes assigned to Colubroidea (see Head et al., 2016's discussion of *Procerophis* and *Thaumastophis* under Pan-Colubroidea).

Clade COLUBRIFORMES Günther, 1864  
(sensu Zaher et al., 2019).

**Diagnosis.** Vertebrae can be assigned to Colubri-formes based on the combination of the following features: vertebrae lightly built and elongate (longer than wide), paracotylar foramina and elongated, tapering prezygapophyseal accessory processes present, blade-like and uniformly thin neural spine reaches the roof of the zygosphenon, and synapophyses differentiated into diapophyses and parapophyses (Rage, 1984; Zaher et al., 2019).

**Remarks.** Assigning vertebrae to Colubri-formes is based on a combination of the characters listed above. Other groups may show some similarities, for example, Georgalis and Scheyer (2022) point out that elongate centra can be present in non-colubri-forms, such as in some scolecophidians and ungaliophiids, but are quite different in other aspects of their morphology. The combination of elongate, lightly built and precloacal vertebrae, the presence of tapering prezygapophyseal processes, and blade-like uniformly thin neural spine that reaches the roof of the zygosphenon excludes Colubri-formes from an association with the families Acrochordidae, Russellophiidae, Anomalophiidae, and Xenodermidae (Zaher et al., 2019). The differentiated para- and diapophysial articular facets further distinguishes Colubri-formes from russellophiids and anomalophiids (Zaher et al., 2019). Finally, Xenodermidae differs from Colubri-formes in possessing vertebrae with accessory processes on both zygapophyses and neural spines with broad lateral expansions (Bogert, 1964; Zaher et al., 2019).

Superfamily COLUBROIDEA Opperl, 1811

**Diagnosis.** Vertebral characters used to identify to Colubroidea include: vertebrae longer than wide (length at least 1.2-1.3 times as wide at the neural arch) and relatively lightly built (Holman, 2000; Smith, 2013); neural spines thin and long when compared to other groups (Holman, 2000); zygosphenon and zygantral areas less massive than in booids (Holman, 2000); synapophyses distinctly divided into parapophysial and diapophysial pro-

cesses (Holman, 2000); mid- and posterior trunk vertebrae with sharp, relatively thin hemal keels, with hypapophyses often absent in these regions (Rage, 1984; Holman, 2000; Ikeda, 2007; Smith, 2013; Head et al., 2016). When present, trunk vertebral hypapophyses are relatively long and often pointed (Holman, 2000; Ikeda, 2007); both paracotylar and lateral foramina present (Rage, 1984; Ikeda, 2007).

**Remarks.** There is some disparity in what constitutes the defining characters of colubroid vertebrae because of the vast diversity of the group. As such, we saw it fitting to summarize known characters in this study. Zaher et al. (2009, 2019) point out that no known vertebral synapomorphies currently define Colubroidea, and vertebrae are typically assigned through the combination of the characters listed above. However, Rage (1984) and Ikeda (2007) identified the presence of both paracotylar and lateral foramina together on the vertebrae as consistent throughout the group. Holman (2000) provided a number of additional characters, but some of the proposed characters describe only some groups of colubroids, and as such, are not included in the diagnosis of the group at this time. These disputed characters include the lack of hypapophyses beyond the cervical region in several groups, and possibly the presence of well-developed prezygapophyseal accessory processes, which Ikeda (2007) was unable to find in several Asian viperids. It should be noted that Holman (2000) focused only on North American colubroids, and therefore may have defined the group primarily for North American taxa.

Family COLUBRIDAE Opperl, 1811

**Diagnosis.** Vertebral characters of Colubridae include: trunk vertebrae lightly built and longer than wide (Holman, 2000); neural spines long, thin, uniformly wide, and as high as or higher than they are long (Holman, 2000; Head et al., 2016); subcentral ridges of the centrum are deep (Holman, 2000; Jurestovsky, 2021); prezygapophyseal accessory processes are prominent (Holman, 2000); epizygapophysial spines extending posteriorly from the postzygapophyses present in some species (Holman, 2000); synapophyses distinctly divided into diapophyses and parapophyses (Holman, 2000); cotyle circular-to-oval in shape (Jurestovsky, 2021). The hemal keel is typically thin and may appear similar to one of three types: hemal keels present without parapophysial process development, both hypapophysis and parapophysial processes present, and hemal keel thin with somewhat round pro-

zygophyseal articular processes (Rage, 1984; Holman, 2000; Ikeda, 2007).

**Remarks.** The defining characters for colubrids are complicated by the diversity and degree of variation within the group, and are partially dependent on whether groups such as the natricids and dipsadids are included within the group. Post-cervical hypapophyseal characters would seem to be inappropriate for defining colubrids as a whole if natricids are included because, as noted in Ikeda (2007), several studies have pointed out that some natricids lack hypapophyses on their trunk vertebrae (McDowell, 1961; Malnate, 1972), while a small number of homalopsine snakes exhibit prominent hypapophyses on their trunk vertebrae (Gyi, 1970; McDowell, 1987). Furthermore, Ikeda (2007) noted the highly variable shape of the prezygapophyseal facets and hemal keel within Colubridae, and pointed out that the neural spine is often more long than high in small-bodied species, but more high than long in large-bodied species.

#### Subfamily COLUBRINAE Opperl, 1811

**Diagnosis.** Holman (2000) outlined some general osteological characters for colubrine snakes, which were later examined and modified by Ikeda (2007). The trunk vertebrae are typically longer than wide, are often lightly built, and lack hypapophyses (Holman, 2000; Ikeda, 2007; Ikeda et al., 2016). The neural spines are somewhat thin, tall, mostly uniform in width, and often project posteriorly over adjacent vertebrae (Holman, 2000). The prezygapophyseal accessory processes are well-projected and prominent (Holman, 2000; Ikeda, 2007; Ikeda et al., 2016). The hemal keels are well-projected from the centrum and may or may not be relatively thin (Holman, 2000; Ikeda, 2007; Ikeda et al., 2016), and the subcentral ridges and grooves are distinct (Holman, 2000, Ikeda, 2007; Ikeda et al., 2016). Epizygapophyseal spines may or may not be present (Holman, 2000).

**Remarks.** While Holman's (2000) diagnosis of colubrines appears to fit North American taxa, Ikeda (2007) noted that the lightly build vertebrae and relatively thin hemal keels are not features consistent with some non-North American taxa, as these features show various states amongst extant species. These characters may only be consistently useful for North American taxa, and should not preclude taxa from being assigned to the subfamily Colubrinae if those characters are not present as described in Holman (2000). Furthermore, Head et al. (2016) point out that while a precloacal vertebral column without hypapophyses have been traditionally used to differentiate colubrines from natricids

and elapids (Bell et al., 2004; Szyndlar, 2012), this absence also occurs in a number of dipsadid and elapid taxa as well (Dowling and Duellman, 1978 after Pyron et al., 2013). This character therefore cannot fully diagnose colubrines to the exclusion of other clades on its own (Head et al., 2016).

#### Genus *LAMPROPELTIS* Fitzinger, 1843

**Diagnosis.** *Lampropeltis* vertebrae are somewhat robust, relatively short, and wide for a colubrine (centrum about as wide as long; Parmley, 1987), with long neural spines that are moderate to low in height, overhang posteriorly, and are either straight or overhanging anteriorly (Auffenberg, 1963; Meylan, 1982; Parmley, 1988; Parmley, 1990). The neural spines may also be thickened dorsally (LaDuke, 1991). The neural arches are depressed and wide (Auffenberg, 1963; Meylan, 1982; LaDuke, 1991; Holman, 2000). The hemal keel is well-developed and usually widened posteriorly, with well-developed subcentral ridges that curve inward near the cotyle (Auffenberg, 1963; Meylan, 1982; Parmley, 1988), and may be bordered laterally by fossae (LaDuke, 1991). The cotyle is round (Auffenberg, 1963), the condyle is round and sometimes obliquely tilted upwards (Parmley, 1990), the zygosphenes are flat anteriorly (LaDuke, 1991) and epizygapophyseal spines are absent (Auffenberg, 1963; Holman, 2000).

**Remarks.** *Lampropeltis* vertebrae differ from those of *Pantherophis* and *Pituophis* in exhibiting more pronounced subcentral ridges, less vaulted neural arches, and relatively lower neural spines (Parmley, 1990). They may additionally differ from *Pantherophis* and *Arizona* in being relatively longer and more robust (LaDuke, 1991). *Lampropeltis* vertebrae differ from those of *Rhinocheilus* in being relatively longer, with relatively thinner and taller neural spines that do not project anteriorly beyond the zygosphenes, narrower hemal keels, relatively wider cotyles, larger zygapophyses, and more developed subcentral ridges (Van Devender and Mead, 1978; LaDuke, 1991).

Holman (2000) suggested that *Lampropeltis* vertebrae are more easily diagnosed on a species-by-species basis, as there are greater differences among some species of *Lampropeltis* than there are among some other colubrine genera (such as *Coluber* and *Masticophis*). This idea was reexamined and discussed in Parmley and Hunter (2010), who found that *Lampropeltis alterna* and the *Lampropeltis pyromelana-zonata* grouping have diagnostic vertebral characters distinct from each other and from the rest of the genus, while *Lampropeltis getula*, *Lampropeltis calligaster*, and *Lampropeltis*

*triangulum* form a discernable *L. getula* complex. Furthermore, Auffenberg (1963) noted that smaller species appeared to have neural spines that are relatively shorter in height compared to larger species and that the hemal keel showed variation in development between species and age groups. Where exactly the known fossil species of *Lampropeltis* fall within the genus could therefore be dependent on the ability to discern between these three main morphospaces on a case-by-case basis. A better understanding of these morphospaces and the morphology of fossil species could also help determine when the genus started exploring the various morphologies associated with these groupings.

*Lampropeltis similis* Holman, 1964†  
Figure 6

**Material.** UNSM 139982 (14 pre-cloacal trunk vertebrae).

**Description.** In anterior view, the neural arch is moderately vaulted. The cotyle is a depressed oval bordered by deeply excavated pits, and is slightly larger than the ventrally restricted, inverted U-shaped neural canal. The zygosphene curves dorsally, and the prezygapophyseal articular facets tilt slightly upward. The diapophyses and parapophyses are distinct elements of the parapophyses, with the latter portion more distally pointed than the former; however, they are not as clearly separated as in most other colubrids.

In dorsal view, the vertebrae are approximately as long as they are wide at the prezygapophyses, and the width at the well-developed, rounded prezygapophyseal accessory processes is greater than it is long through the zygapophyses. The neural spine tilts slightly ventrally in its anterior portion. The prezygapophyseal articular facets are oval to ovoid and slightly tilted upward. The epizygapophyseal spines are absent. The anterior edge of the zygosphene is slightly convex to slightly sinuate; the posterior notch of the zygosphene is V-shaped.

In lateral view, the neural spine is significantly longer than it is tall, and dips slightly downward cranially. The hemal keel is visible and quite strong.

In posterior view, the neural arch is moderately vaulted, and the condyle is a dorso-ventrally depressed oval.

In ventral view, the strong hemal keel is spatulate or oblong in shape, but not wide throughout most of its length. Subcentral ridges are present and concave from below, but not exceptionally

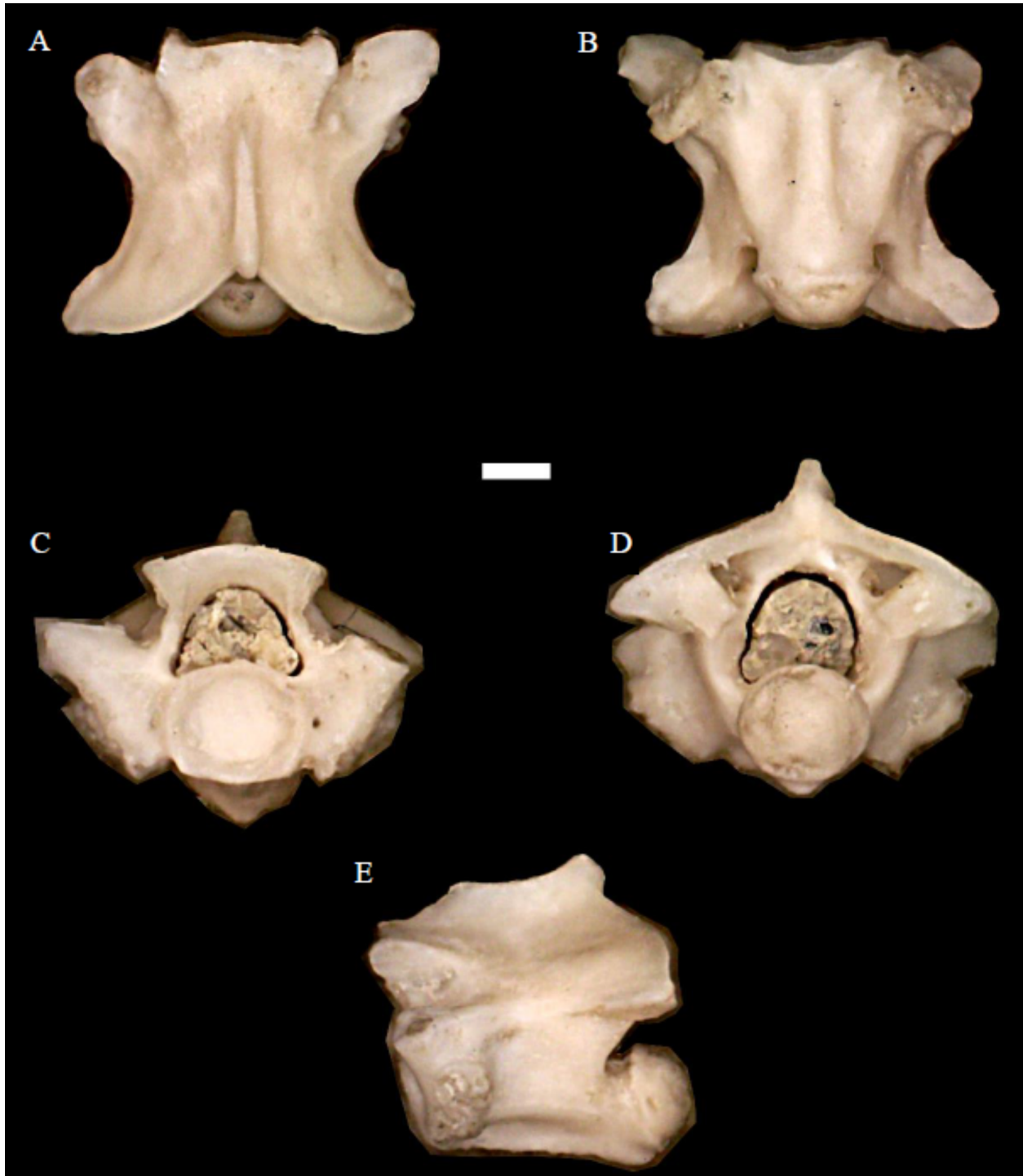
developed. The postzygapophyseal articular facets are ovoid.

**Remarks.** These vertebrae in particular appear to be more similar to the general morphology of the milksnakes of the *Lampropeltis triangulum* complex or the kingsnake *Lampropeltis calligaster* as opposed to the *L. alterna* or *L. pyromelana-zonata* groupings. They possess long neural spines, moderately depressed neural arches, distinct hemal keels with deep subcentral grooves, and robust, distinct subcentral ridges (Parmley, 1990; Parmley and Hunter, 2010). More specifically, *L. similis* has previously been described as similar in appearance to *L. triangulum*; however, *L. similis* possesses a less depressed neural arch in the trunk region (more similar to that of *L. calligaster*) with an inverse U-shaped rather than depressed ovoid-shaped neural canal, a thinner hemal keel. Holman (2000) also stated a centrum that “is not as triangular from below” as an additional apomorphy for *L. similis*, but we are unable to confirm this as a consistent character throughout the vertebral column of the species.

Genus *PANTHEROPHIS* Fitzinger, 1843

**Diagnosis.** The vertebrae of North American *Pantherophis* are relatively short, but robustly built compared to most of their contemporary colubrids. The vertebrae have wide, high neural spines and broad hemal keels, but lack epizygapophyseal spines (Holman, 2000; Parmley and Hunter, 2010). The parapophyseal process is poorly developed on either side, and the interzygapophyseal ridge is straight in lateral view (Ikeda, 2007).

**Remarks.** The vertebrae of North American *Pantherophis* are similar to some species of other large-bodied colubrine genera. In North America, the vertebrae of *Pantherophis* differ from those of New World *Masticophis* and *Coluber* in that they are relatively shorter and more robustly built, have higher and wider neural spines, have wider hemal keels, and lack epizygapophyseal spines (Holman, 2000). *Pantherophis* generally differs from *Lampropeltis* in possessing a higher, more vaulted neural arch, a higher neural spine (compared to at least some species of *Lampropeltis*), straight and less defined subcentral ridges, and less robust vertebrae (Holman, 2000; Parmley and Hunter, 2010). *Pantherophis* differs from *Pituophis* in having a lower neural spine and a zygosphene that is rarely or never concave (Auffenberg, 1963). *Pantherophis* differs from *Drymarchon* in possessing a zygosphene that is rarely or never concave, greater posterolateral curvature of the neural arch, less posterior curvature of the neural spine, and a

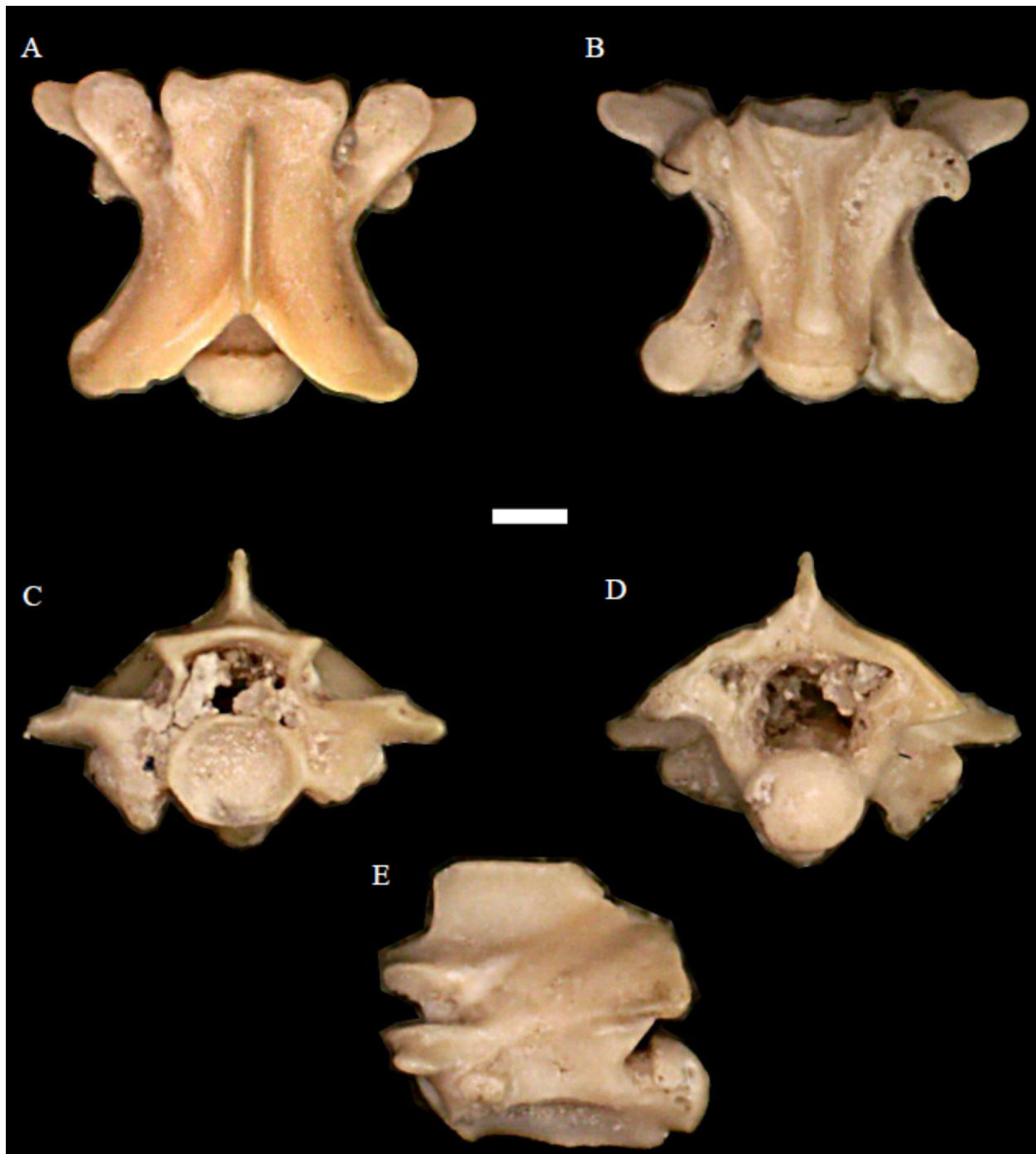


**FIGURE 6.** Trunk vertebra of *Lampropeltis similis* from the Penny Creek local fauna. From top left: dorsal, ventral, anterior, posterior, and lateral views (anterior to the left). Scale bar equals 1 mm.

deeper concavity on the posteromedial portion of the neural arch (Jasinski and Moscato, 2017). There has been no work to definitively separate the vertebral morphology of *Pantherophis* and *Elaphe*, in part because their reclassification as separate

genera has not been morphologically defined since their separation in Utiger et al. (2002).

*Pantherophis kansensis* Gilmore, 1938†  
Figure 7



**FIGURE 7.** Trunk vertebra of *Pantherophis kansensis* from the Penny Creek local fauna. From top left: dorsal, ventral, anterior, posterior, and lateral views (anterior to the left). Scale bar equals 1 mm.

**Material.** UNSM 139983 (21 pre-cloacal trunk vertebrae).

**Description.** In anterior view, the neural spine is relatively low for a colubrid, the neural arch is moderately vaulted, and the zygosphenon is convex dorsally. The zygosphenal articular facets are strongly tilted dorso-ventrally. The neural canal is rounded

and slightly smaller than the cotyle, which is also round. The prezygapophyseal articular facets tilt slightly upward, and the diapophyses and parapophyses are rounded, distinct sections of the synapophyses.

In dorsal view, the neural spine is long and located in the middle of the vertebra. The anterior

edge of the zygosphene is concave. The prezygapophyseal accessory processes are moderately pointed, the prezygapophyseal articular facets are rounded to oval and tilted slightly upward, and the epizygapophyseal spines are absent. The posterior edge of the neural arch in dorsal view is slightly rounded.

In lateral view, the neural spine is approximately twice as long as it is high. The condyle is tilted slightly forward. The hemal keel is distinct from the centrum, and the synapophyses can clearly be divided into diapophyseal and parapophyseal sections. The interzygapophyseal ridge is bowed downward, and the subcentral ridge is bowed upward.

In posterior view, the neural arch is somewhat vaulted. The condyle is round and approximately the same size as the neural canal, which is an inverted U-shape. The zygosphenal articular facets and the postzygapophyseal articular facets are all tilted sharply upward. The diapophyses and parapophyses are distinct parts of the synapophyses.

In ventral view, the centrum is triangular and bordered by visible subcentral ridges. The hemal keel is well-developed, moderately wide, and constricted in the middle relative to the ends. The prezygapophyseal accessory processes are distinct, oblique, and directed anterolaterally. As in other views, the synapophyses are distinctly divided into the diapophyses and parapophyses.

**Remarks.** *Pantherophis kansensis* has vertebrae with a lower neural spine and more anterolaterally directed prezygapophyseal accessory processes than any other known species of *Pantherophis* or *Bogertophis*. This neural spine is relatively taller in some specimens, and is more proportionally more similar to *Pantherophis obsoletus* in that regard; these vertebrae appear to be from a more anterior portion of the vertebral column.

Genus *SALVADORA* Baird and Girard, 1853

**Diagnosis.** Generally, *Salvadora* can be identified by the combination of the following characters: (1) a thin, relatively low neural spine that gets shorter posteriorly through the trunk region; (2) obsolete to absent epizygapophyseal spines; (3) vertebrae that are approximately as wide as they are long; and (4) dorsally convex subcentral ridge in lateral view (Holman, 1973).

**Remarks.** The delicate neural spine and invariably thin hemal keel is similar to that found in other North American colubrids such as *Coluber* or *Masticophis*. However, *Salvadora* can be identified separately from those taxa on the basis of a proportionally shorter vertebra that appears to be

nearly as wide as it is long, whereas the other two taxa appear elongate, more dorsally convex subcentral ridges, and obsolete to absent epizygapophyseal spines. *Pantherophis*, *Pituophis*, and *Lampropeltis* possess more robust and relatively wider vertebrae with less delicate neural spines and broader hemal keels than those of *Salvadora*. Jurestovsky (2021) also noted that extant *Salvadora* differ from *Carphophis*, *Diadophis*, and *Gyalopion* in possessing longer, more pointed accessory processes and a uniformly thinner hemal keel. *Carphophis* also possesses a narrower zygosphene, more elongate centrum, a shorter neural spine, less laterally directed postzygapophyses, and a less dorsoventrally tall cotyle (Jurestovsky, 2021). *Salvadora* has less robust postzygapophyses than *Diadophis* and possesses a more elongate centra, a taller neural spine, and a dorsoventrally taller cotyle than in *Gyalopion* (Jurestovsky, 2021).

*Salvadora paleolineata* Holman, 1973†  
Figure 8

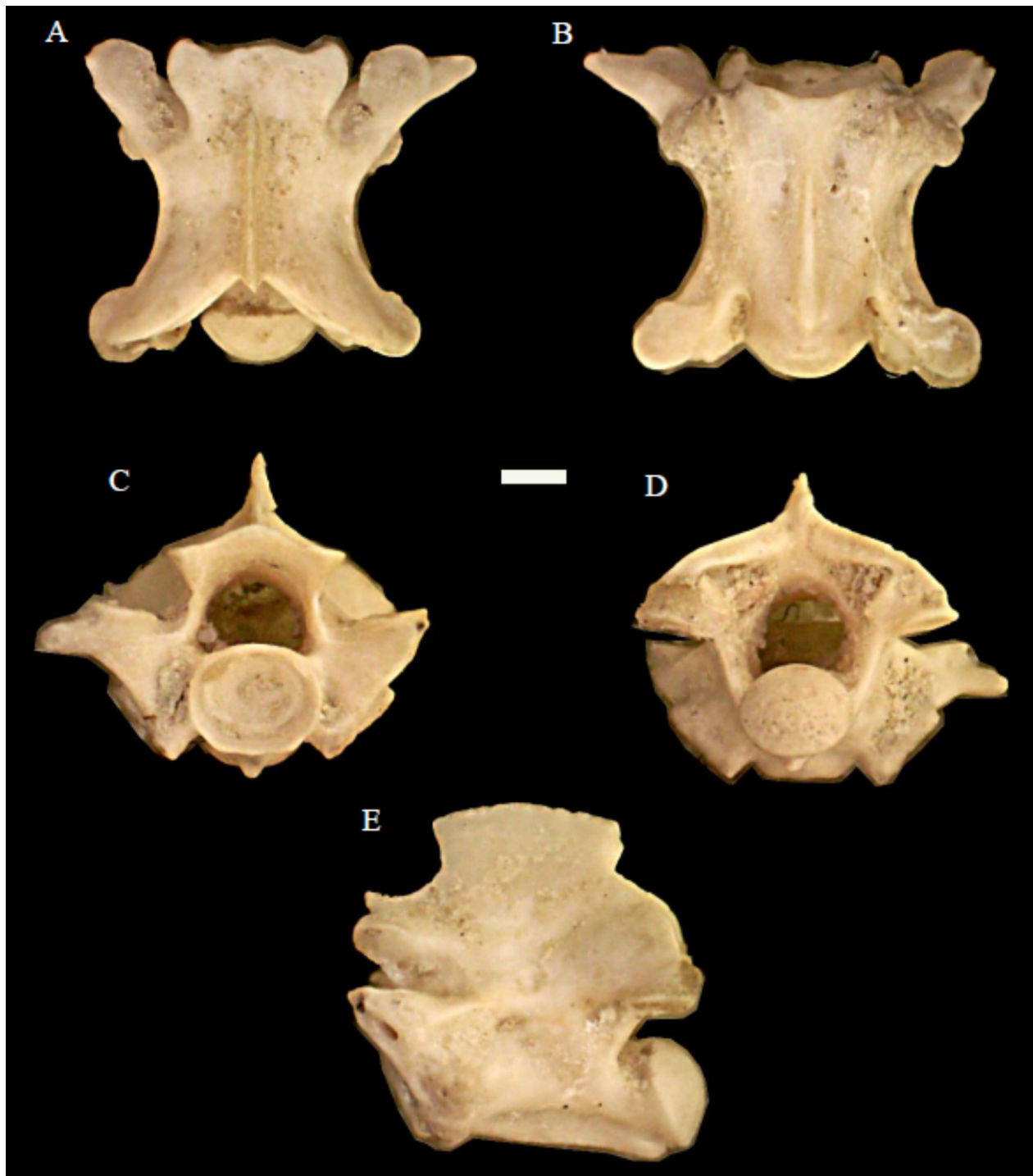
**Material.** UNSM 139984 (8 pre-cloacal trunk vertebrae).

**Description.** The description is similar to Holman (2000) unless otherwise noted. In anterior view, the cotyle is a slightly depressed oval bookmarked by relatively large paracotylar foramen to each side. The neural canal is similar in size to the cotyle and is an inverted U-shape with medially convex sides to the neural arch. The zygosphene is dorsally convex in this view. The prezygapophyses are tilted slightly upward, and the prezygapophyseal accessory processes are well developed.

In dorsal view, the vertebra is approximately as wide as it is long. The neural spine is thin and slightly overhangs the neural arch posteriorly. The zygosphene is slightly convex anteriorly. The prezygapophyseal articular facets are subrounded, and the prezygapophyseal accessory processes are approximately two-thirds as long as the width of the prezygapophyseal articular facets and are well-developed and moderately pointed. The diapophyses are only somewhat directed laterally and are barely visible from this orientation.

In lateral view, the neural spine is delicate and is low, over three times as long as it is tall, with a slight anterior and posterior overhang. The subcentral groove is relatively deep, with dorsally convex subcentral ridges and a clear, uniform hemal keel. The condyle is tilted somewhat postero-dorsally, while the cotyle is oriented slightly antero-ventrally. The lateral foramen is positioned near the center of the vertebrae in this orientation, just below the





**FIGURE 8.** Posterior trunk vertebra of *Salvadora paleolineata* from the Penny Creek local fauna. From top left: dorsal, ventral, anterior, posterior, and left lateral views. Scale bar equals 1 mm.

interzygapophyseal ridge. Epizygapophyseal spines are absent.

In posterior view, the subcentral ridges are well-developed and narrow, and the hemal keel is strongly developed and uniformly thin. The postzygapophyseal articular facets are subrounded. The

condyle is a slightly depressed oval. Epizygapophyseal spines are absent, as also seen in the lateral orientation.

In ventral view, the zygosphenes are slightly convex anteriorly. The prezygapophyseal accessory processes are well developed. The hemal keel is

uniformly thin. Both the cotyle and the condyle are oval in shape and the condyle extends to be approximately even with the postzygapophyseal articular facets.

**Remarks.** According to Holman (2000) and our own comparisons, the vertebrae from Penny Creek assigned to *S. paleolineata* are primarily from the middle trunk region, as noted by neural spines somewhat taller than in the type specimen and the larger condylar-cotylar articulation. As in Holman's description, none of the specimens appear to have epizygapophyseal spines; as such, taxonomic assignment to *S. paleolineata* is possible. *S. paleolineata* is suggested as an ancestral species to modern *Salvadora* species, which differ only in possessing obsolete epizygapophyseal spines (see description of genus above; Holman, 1973). *S. paleolineata* also differs from *Coluber* and *Masticophis* in vertebral proportions, where the former has proportionally shorter, wider vertebrae and less dorsally convex subcentral ridges, as well as in the complete absence of epizygapophyseal spines (Holman, 2000). *Dakotaophis greeni* possesses smaller zygapophyseal articular facets than *S. paleolineata*, and the articular facets are more elongate or oval in shape and oriented less laterally (Holman, 2000). It is possible that, as in *Heterodon/Paleoheterodon*, there may be greater morphological differences in the elements of the skull, should they ever be found for this species.

Family DIPSADIDAE Bonaparte, 1838

**Diagnosis.** Vertebrae can be assigned to Dipsadidae through a combination of characters that individually are not necessarily exclusive to the group. Dipsadid snakes generally have vertebrae that are square to slightly longer than wide in dorsal view, an elongated centrum, and long, low, and narrow neural spines that overhang posteriorly (some taxa also overhang anteriorly) (Holman, 2000; Parmley and Hunter, 2010; Holman et al., 2011; Mead and Steadman, 2017; Jurestovsky, 2021; Syromyatnikova et al., 2021). The neural arch is depressed to moderately vaulted in different species, and the zygosphenes are usually crenate, but can be concave in some species when viewed dorsally (Holman, 2000; Mead and Steadman, 2017). The prezygapophyses generally protrude only slightly beyond the ovoid prezygapophyseal facets to form small points (Mead and Steadman, 2017). The cotyle and condyle are round to slightly dorsoventrally compressed, where the cotyle is flattened on the ventral portion in anterior view (Mead and Steadman, 2017; Jurestovsky, 2021) Epizygapophyseal spines are absent (Holman, 2000; Mead and

Steadman, 2017; Jurestovsky, 2021). The synapophyses are divided into distinct diapophyses and parapophyses (Holman, 2000; Syromyatnikova et al., 2021). Distinct hemal keels with adjacent subcentral ridges are present, and hypapophyses are absent from trunk vertebrae except potentially in a few species (Holman, 2000; Ikeda, 2007; Head et al., 2016; Mead and Steadman, 2017; Syromyatnikova et al., 2021)

**Remarks.** The vertebrae of many extant dipsadid snakes have not yet been described and is outside the scope of this study, making it difficult to confirm the above characters across the entire group. We have, however, assembled the common characters expressed across several publications (Holman, 2000; Parmley and Hunter, 2010; Holman et al., 2011; Mead and Steadman, 2017; Jurestovsky, 2021; Syromyatnikova et al., 2021) – and our personal observations of some North American and West Indian taxa – as a way to delimit dipsadids from colubrids and natricids through a combination of characters .

Genus *HETERODON* Latreille, 1801  
(in Sonnini and Latreille, 1801) or  
*PALEOHETERODON* Holman, 1964†

**Diagnosis.** The trunk vertebrae of *Heterodon* and *Paleoheterodon* can exhibit a very depressed to slightly more vaulted neural arch (though relatively depressed overall compared to other dipsadids), a narrow neural spine that is longer than it is high, and a wide but flattened hemal keel (Holman, 2000). The vertebrae are slightly more long than wide, including the centrum, but still somewhat squarish appearance (Holman, 2000). The zygapophyseal articular facets are ovoid, and the prezygapophyseal accessory processes are moderately well-developed, end in somewhat obtuse points, and extend just beyond the prezygapophyseal articular facets (Holman, 2000; Mead and Steadman, 2017; Jurestovsky, 2021). The condyle and cotyle are mostly round but may be slightly dorsoventrally compressed and flattened on the ventral side; both are similar in size to the neural canal (Holman, 2000). The synapophyses are divided into distinct diapophyses and parapophyses. Subcentral ridges are present adjacent to the hemal keel but are not prominent, the epizygapophyseal spines are absent, and hypapophyses are absent from post-cervical vertebrae (Holman, 2000). The zygosphenes are variably crenate/convex or concave (Holman, 2000).

**Remarks.** Though it is possible to identify trunk vertebrae to genus for *Heterodon* or possibly *Paleoheterodon*, individual vertebrae of this group

are difficult to distinguish at the species level. They share most diagnostic features with the genus *Farancia*, but the vertebrae of *Farancia* generally exhibit greater anteroposterior compression (leading to a laterally wider appearance overall; Jurestovsky, 2021) a more vaulted neural arch, and a neural spine that is more deeply undercut both anteriorly and posteriorly than in *Heterodon* (Holman, 2000). Vertebrae associated with specimens previously assigned to *Paleoheterodon* may show the same differences from *Farancia* as *Heterodon*, except in the neural arch, which overlaps with both *Farancia* and *Heterodon* in how depressed/vaulted the shape of that region is (Holman, 2000; Parmley and Hunter, 2010; Head et al., 2016). *Farancia* and the *Heterodon/Paleoheterodon* group are both identifiable within Dipsadidae in possessing comparatively flattened and depressed neural arches (Head et al., 2016), longer than high neural spines (Jurestovsky, 2021) and wide, relatively flat hemal keels (Holman, 2000, Jurestovsky, 2021).

*Heterodon* Latreille in Sonnini and Latreille, 1801  
or *Paleoheterodon* Holman, 1964† sp. indet.

Figure 9

**Material.** UNSM 139985 (12 pre-cloacal trunk vertebrae).

**Description.** In dorsal view, the vertebrae are nearly square to slightly longer than wide. The anterior edge of zygosphenes is convex, and the prezygapophyseal facets, when preserved, are ovoid in shape. The prezygapophyseal accessory processes are well-developed and the tips are moderately pointed to obtuse. Epizygapophyseal spines are absent. The postzygapophyseal accessory processes are ovoid in shape.

In anterior view, both articular facets are visible on the synapophyses. The cotyle is mostly round, but sometimes slightly taller than wide. The neural arch is depressed. The neural canal is similar in shape to a ventrally restricted semi-cylinder, even somewhat squarish, and similar in size to the cotyle. The cotyle is somewhat dorso-ventrally compressed, with well-excavated pits on either side.

In lateral view, the neural spine is longer than it is tall, somewhat depressed, and is typically more undercut posteriorly than anteriorly. In posterior view, the shape of the condyle is a dorso-ventrally compressed oval, and similar overall to the cotyle.

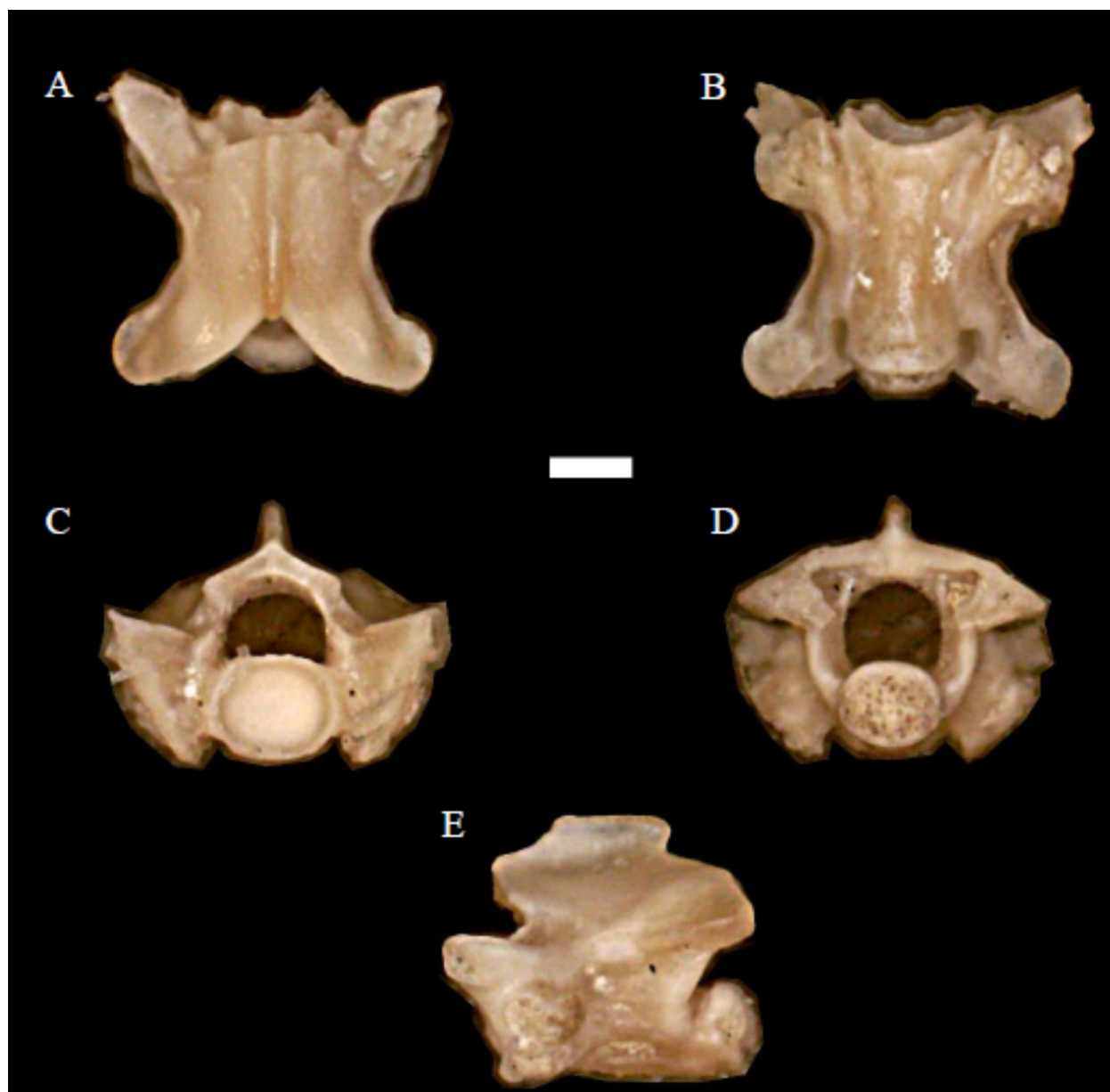
In ventral view, the hemal keel generally is weak, wide, and oblong, and very depressed to flat. In some specimens, the hemal keel is slightly more distinct, and is slightly constricted between

the synapophyses, indicating a more anterior trunk position for these vertebrae. The subcentral ridges are indistinct. The centrum itself is longer than it is wide.

**Remarks.** The somewhat more vaulted nature of the neural arch in the specimens from Wt 13B when compared to extant *Heterodon* vertebrae (a morphological difference also shared with *Farancia*, as stated by Head et al., 2016) would previously have suggested that these fossils belong to or are comparable to *Heterodon* (or *Paleoheterodon*) *tihenii*, a species that is more easily determined based on skull morphology, rather than vertebral morphology (Holman, 1964; Holman, 2000; Parmley and Hunter, 2010). However, Parmley and Hunter (2010) determined that this neural arch character showed considerable and overlapping variation in specimens assigned to *Paleoheterodon* and *Heterodon*, and that vertebral characters are not sufficient to differentiate between the two taxa. Unfortunately, we lack reproducible or statistical data on both the variation and the degree of overlap between these taxa, as both Holman (1977; 2000) and Parmley and Hunter (2010) included only personal observations on the topic. Furthermore, these vertebrae lack the apomorphies of the fossil species *Heterodon meadi*, which exhibits a zygosphenal groove and antero-posteriorly directed sculpturing on the neural arch, but lacks skull elements to clarify its association with *Heterodon/Paleoheterodon* (Jurestovsky, 2021). Similarly, the unnamed but potentially different taxon from the Sappa Creek Fauna in Kansas also lacks cranial elements (Holman et al., 2011). Because we presently do not have enough information regarding both vertebral and skull characters to confidently differentiate these taxa, and because these taxa overlap temporally (albeit in younger deposits; Parmley and Hunter, 2010), we describe it here as *Heterodon* or *Paleoheterodon* of an indeterminate species. Future work using quantitative and morphometric methods with isolated skeletal elements may potentially help untangle this taxonomic issue.

Family NATRICIDAE Bonaparte, 1840

**Diagnosis.** North American natricid vertebrae have well-developed, pointed hypapophyses directed posteriorly on the trunk vertebrae (Holman, 2000). These hypapophyses are usually sigmoid in shape (Szyndlar, 1991). The vertebrae overall are lightly built and elongate, with long centra, strong subcentral ridges, posteriorly vaulted neural arches, and somewhat short parapophyseal processes (Szyndlar, 1991).



**FIGURE 9.** Middle trunk vertebra of *Heterodon* cf. *Heterodon* (*Paleoheterodon*) *tihen*i from the Penny Creek local fauna. From top left: dorsal, ventral, anterior, posterior, and lateral views (anterior to the left). Scale bar equals 1 mm.

**Remarks.** Szyndlar (1991) differentiated natricid snakes from other snake groups known to possess hypapophyses on their trunk vertebrae. Natricids differ from viperids in exhibiting hypapophyses that are somewhat sigmoidal in shape, and in possessing a relatively longer centra, posteriorly vaulted neural arches, and shorter parapophyseal processes. They differ from elapids in being more lightly build overall, with much longer centra and prominent subcentral ridges. Despite the hypapophyses being presented as a definitive character for natricids as a whole, McDowell (1961), Malnate

(1972), and Ikeda (2007) showed that there are a few exceptions to this rule outside of North America, possibly representing a loss of this character later in the evolution of some species.

Genus *NEONATRIX* Holman, 1973†

**Diagnosis.** *Neonatrix* trunk vertebrae are most easily characterized by very short hypapophyses that strongly project posteriorly, are ventrally beveled in most North American species (except *Neonatrix elongata*) but are weakly developed, terminally rounded, and do not extend beyond the

end of the condyle. Furthermore, they are relatively small and distinctly longer than wide. The neural spines of *Neonatrix* are much longer (up to 4x) than wide (Holman, 1973, 2000; Parmley and Hunter, 2010), with reduced or absent hooked projections at each terminal end. The zygosphenes are convex, but less so in caudal vertebrae (Jasinski and Moscato, 2017).

**Remarks.** The hypapophyses of North American species of *Neonatrix* are less well-developed than the reported species from Europe (Holman, 1973, 1982, 1996; Rage and Holman, 1984) and shorter than in any other natricid genus (Holman, 1973, 2000). *Neonatrix* also differs from *Thamnophis* and *Nerodia* in possessing an anteriorly taller neural spine that lacks hooked projections and a less prominent subcentral ridge (Jasinski and Moscato, 2017). The neural spine of *Neonatrix* is also taller than in *Storeria*, *Tropidoclonion*, *Virginia*, and *Micronatrix*, but shorter than in *Seminatrix* (Parmley and Hunter, 2010; Jasinski and Moscato, 2017)

*Neonatrix elongata* Holman, 1973†

Figure 10

**Material.** UNSM 139986 (17 pre-cloacal trunk vertebrae).

**Description.** The diagnosis follows that of Holman (2000) and is only modified where otherwise noted. *Neonatrix elongata* trunk vertebrae are longer than wide, with a neural spine that is drastically longer than tall or wide. The vertebrae possess poorly developed hypapophyses reaching only the posterior portion of the centrum, and unbeveled neural spines that end just short of the posterior end of the cotyle.

In anterior view, the neural canal is shaped like a ventrally restricted semi-cylinder, is medially convex at the sides, and is slightly narrower than the round cotyle. The zygosphenes are convex dorsally. The synapophysis is developed. For the first time in this genus and species, we confirm the presence of paracotylar foramina in anterior view, adjacent to the cotyle on each side, approximately half-way down the cotyle. Previous descriptions exhibited excavated cavities on either side of the cotyle, but could not observe any foramina based on the specimens available.

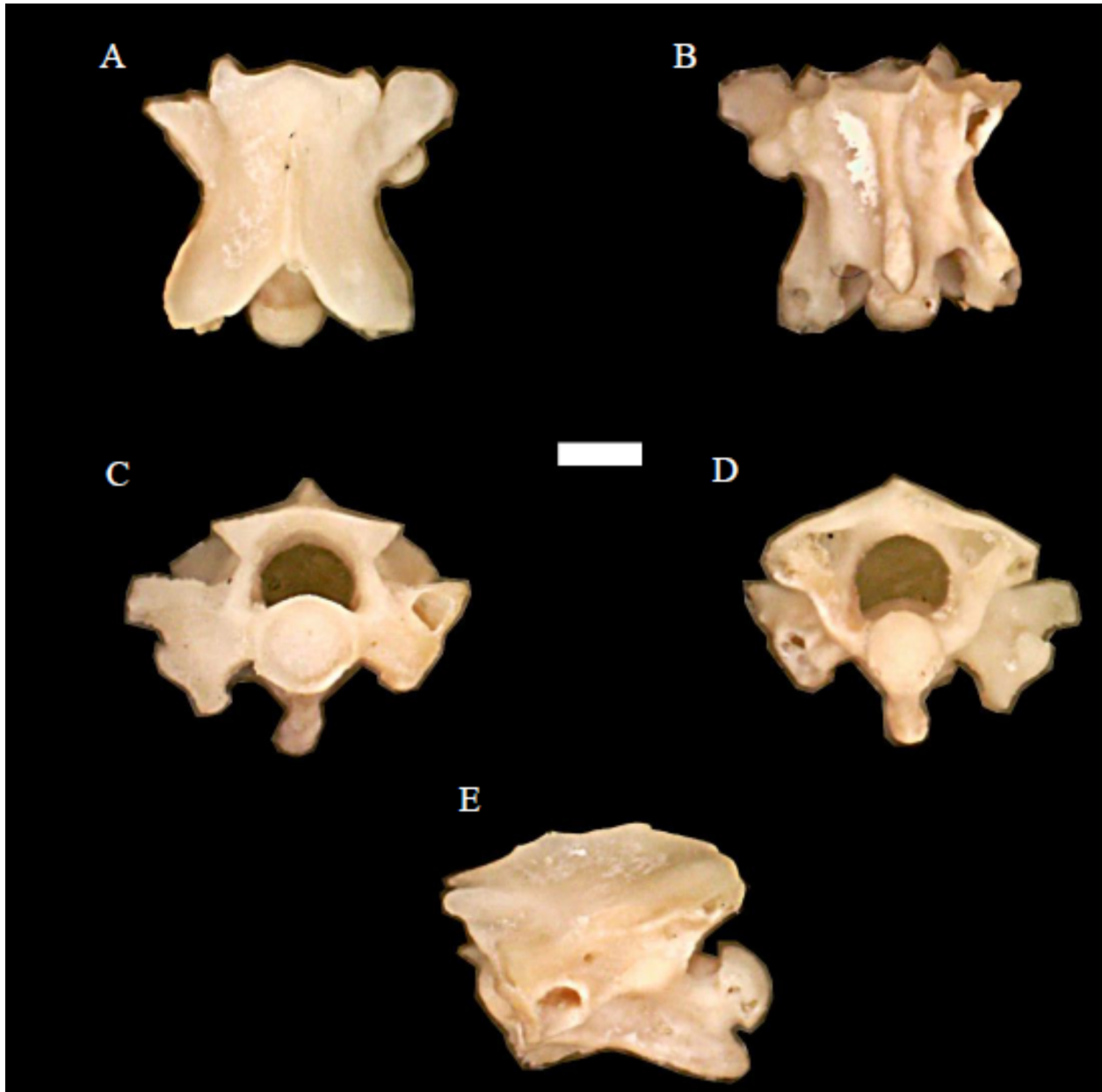
In dorsal view, the centrum is longer than wide. The prezygapophyseal articular facets are ovoid in shape. This is a correction of Holman (2000), which appears to have mistakenly labeled the prezygapophyseal processes as ovoid, rather than the articular facets. The prezygapophyseal processes are long and somewhat pointed on the anterior end. The diapophyses only slightly extend

out laterally. The epizygapophyseal spines are absent or obsolete.

In lateral view, the vertebrae are elongate. The neural spine is over two times as long as it is high. The neural spine is rarely preserved at the ends in Penny Creek fossils and in *Neonatrix* throughout the fossil record, and so is difficult to observe, but a few mostly preserved neural spines from Penny Creek material allow us to determine the absence of an anterior projection, and an extremely reduced to absent – typically absent – posterior overhang. The subcentral ridge is convex dorsally. The prezygapophyses tilt somewhat dorsally. The hypapophysis is short and ends short of the posterior-most part of the condyle; we find that it does not extend past even the anterior-most part of that articulation in these specimens.

In posterior view, we find that the condyle is near circular, but is slightly depressed and closer to an oval shape in some vertebrae. The neural arch is vaulted, steeply incised by the zygantral articular facets, and similar in size to the condyle. The hypapophysis is visible below the condyle around one-half of the condyle's height when undamaged. The postzygapophyses tilt slightly upward, just as in the prezygapophyses. In ventral view, the centrum is long and narrow. The subcentral grooves are shallow, and the hemal keel narrows slightly anteriorly to the robust but truncated hypapophysis.

**Remarks.** Like other species of North American *Neonatrix*, *N. elongata* have less well-developed hypapophyses that do not extend as far posteriorly (relative to the condyle) than found in the European species (Rage and Holman, 1984). *N. elongata* occurs earlier than other North American species of *Neonatrix* and is known to occur more broadly in a temporal and geographic manner throughout the Miocene. In the Penny Creek specimens, the unbeveled neural spine and unbeveled hypapophysis that end just short of the posterior end of the cotyle indicate that these fossils belong to *N. elongata*, as opposed to other known species of *Neonatrix*. There is some variation on how rounded (or pointed) the posterior tips of the hypapophyses are, likely indicating a small amount of intracolumnar variation in the hypapophyseal morphology of the species (LaDuke, 1991; McCartney, 2015). Nonetheless, we have not observed more variation within an individual taxon than between species, and the morphology is generally consistent with what is described above. *Neonatrix elongata* is typically smaller than *Neonatrix magna* and *Neonatrix infera*, but the taxon's relative length and neural spine height are intermediate between the



**FIGURE 10.** Posterior trunk vertebra of *Neonatrix elongata* from the Penny Creek local fauna. From top left: dorsal, ventral, anterior, posterior, and lateral views (anterior to the left). Scale bar equals 1 mm.

other two species, which are either more elongate with a shorter neural spine (*N. infera*) or less elongate with a taller neural spine (*N. magna*; Holman, 2000). It is noteworthy that these specimens show some measure of variation in terms of the neural spine height and the shape of the hypapophyses, some of which appear similar to some morphologies known in the other North American species. Given that *N. elongata* was considered to have “intermediate” morphologies by Holman (2000), it may be necessary to further study the intracolumnar variation with *Neonatrix* for additional definitive

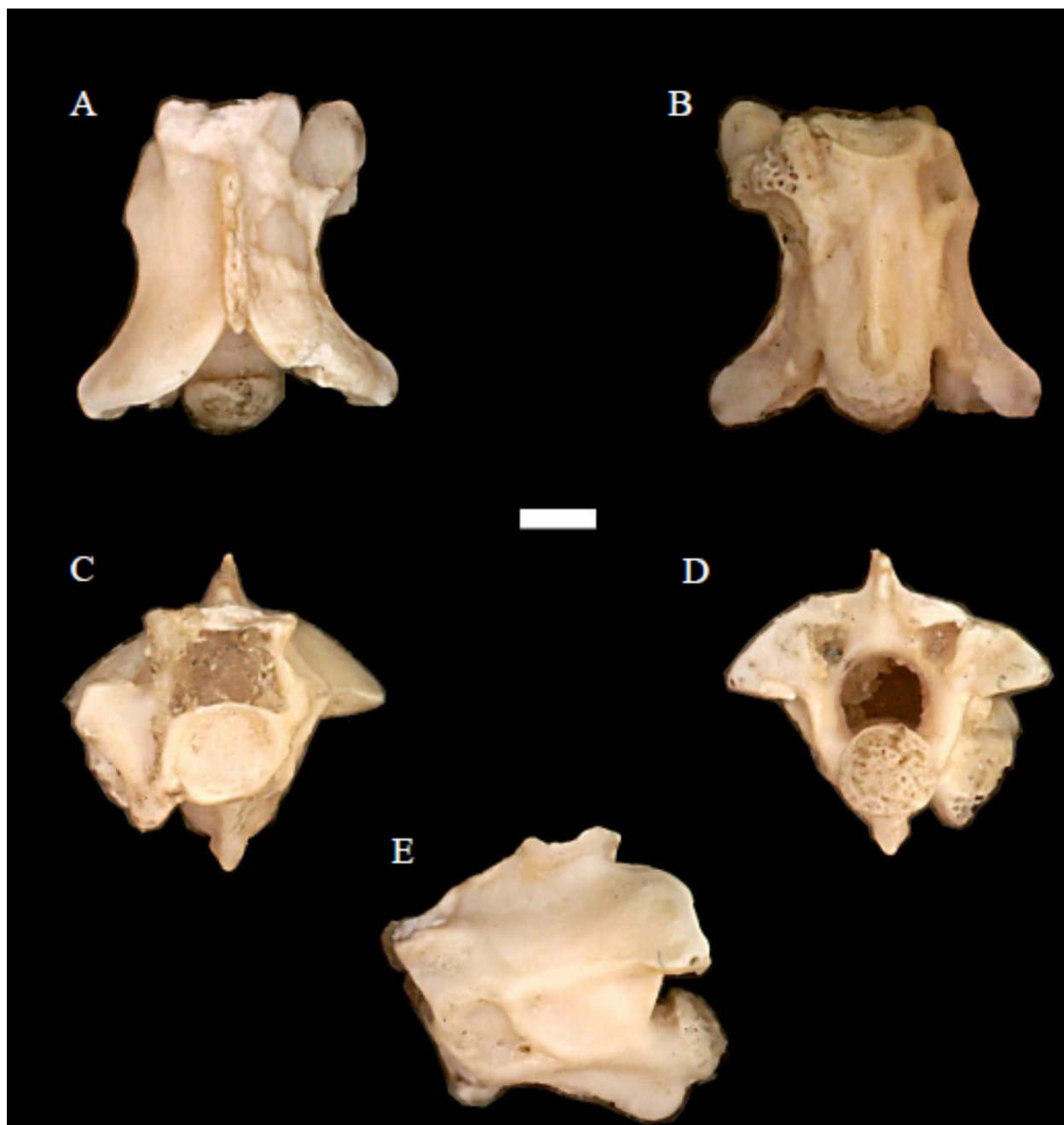
characters and consider potential changes to the taxonomy of the species within.

*Neonatrix magna* Holman, 1982†

Figure 11

**Material.** UNSM 139987 (8 pre-cloacal trunk vertebrae).

**Description.** The diagnosis is based on that of Holman (2000) but is modified where noted. The vertebrae are mainly distinguished by (1) a very poorly developed hypapophysis that typically terminates near the posterior part of the centrum; (2)



**FIGURE 11.** Trunk vertebra of *Neonatrix magna* from the Penny Creek local fauna. From top left: dorsal, ventral, anterior, posterior, and lateral views (anterior to the left). Scale bar equals 1 mm.

ventral portion of the hypapophysis beveled and ending well anterior to the condyle; (3) vertebral size relatively large (at least relative to other North American *Neonatrix* at >5 mm); (4) vertebrae nearly the same width and length; and (5) neural spine near same height and length.

In anterior view, the cotyle is round and similar in size to the neural canal, which is an inverted U-shape with slightly convex lateral sides. The zygo-

sphene is dorsally straight. The prezygapophyses are slightly tilted dorsally. Short excavations with single, centered paracotylar foramen border each side of the cotyle. We observe that the synapophyses that are missing from previous descriptions are moderately well developed and differentiated.

In dorsal view, the centrum's length and width are similar. The prezygapophyses are ovoid. The neural spine is somewhat thick and slightly over-

hangs posteriorly when preserved. Epizygapophyseal spines are absent. The zygosphene is slightly convex anteriorly. The diapophyses are produced laterally enough to be seen from the dorsal orientation.

In lateral view, the vertebra is only slightly elongate. The neural spines are not completely preserved but appear as though they are similar in height and length. There is a slight overhang on the posterior border of the neural spine. The hypapophysis is beveled ventrally, about as tall as it is long, and ends anterior to the condyle, but appears to have rounded rather than the pointed tips observed by Holman (1982; 2000).

In posterior view, the neural arch is significantly vaulted. We observed that the condyle is mostly round and slightly compressed, rather than truly oval, and is similar in size to the neural canal. The hypapophyses strongly projects ventrally and is clearly visible below the condyle.

In ventral view, the hypapophysis is somewhat narrow, ends clearly anterior to the anterior end of the condyle, and is beveled on the ventral surface. The subcentral ridges are well developed.

**Remarks.** *Neonatrix magna* has the shortest relative length and widest appearance, the highest neural spine, and most anteriorly terminating hypapophyses of any species of *Neonatrix* in North America or Europe. It also has somewhat less strongly developed subcentral ridges and deep subcentral groups than *N. elongata* or *N. infera*.

Several of our observations contribute to or differ slightly from previous descriptions of the species. We observe that the synapophyses are moderately developed. The hypapophyses of our specimens have rounded rather than pointed tips, and the condyle, while slightly depressed, is better described as round rather than oval. Comparison with specimens of *N. elongata* and examination of intracolumnar differences in vertebral morphology in extant natricid snakes suggest that the hypapophysis does change shape along the column; however, the differences in the hypapophysis alone between the two species described from fossils seems to be greater than generally seen in other natricids, except between anterior or middle trunk vertebrae and precloacal vertebrae. Given other morphological differences discussed above and the observation that *N. magna* is not smaller but would appear to have a morphology more similar to the smaller posterior trunk and precloacal vertebrae, we do not believe that these vertebrae represent the same species. Nonetheless, little is known about the intracolumnar variation of *Neonatrix* at

this time, as preserved elements are mainly trunk vertebrae; this would seem to warrant a more complete investigation, as also suggested by Jasinski and Moscato (2017).

Genus *NERODIA* Baird and Girard, 1853

**Diagnosis.** The trunk vertebrae of *Nerodia* are typically medium to large in size and relatively short and wide, with an elongate centrum (Holman, 2000). The neural spines and hypapophyses are prominent (Holman, 2000). The neural spine is tall and undercut on both the anterior and posterior sides. The robust hypapophyses on each precaudal vertebra are well-developed, laterally compressed, directed posteriorly, and usually end in a somewhat pointed tip extending beyond the condylar head (Holman, 2000). Epizygapophyseal spines are absent (Holman, 2000).

**Remarks.** The trunk vertebrae of *Nerodia* relative to other North American natricids are typically medium to large in size, relatively robust in appearance, and exhibit higher neural spines (Holman, 2000). The vertebrae are still elongate relative to large North American colubrids (Holman, 2000). *Nerodia* vertebrae are typically less elongate than *Thamnophis* vertebrae, with a more ventrally-oriented hypapophysis with a steeper angle relative to the centrum (LaDuke, 1991; Holman, 2000; Jasinski and Moscato, 2017). *Nerodia* also exhibits a more vaulted neural arch, broader and more robust hypapophyses, but more gracile prezygapophyses compared to *Thamnophis* (Jasinski and Moscato, 2017). They possess higher neural spines than *Storeria*, *Tropidoclonion*, and *Virginia* (but relatively shorter than *Regina*), and the hypapophyses are longer and less squared in shape when compared to *Regina* (Holman, 2000). It should be noted that the degree to which the hypapophysis extends beyond the condylar head appears to differ between some taxa, and perhaps between individuals, though this has not been extensively studied at this time. Other characters of *Nerodia*, such as neural spine height, hypapophysis shape, and the degree to which the neural spine is undercut all vary to some degree at least between species of the genus (Holman, 2000; pers. obs.).

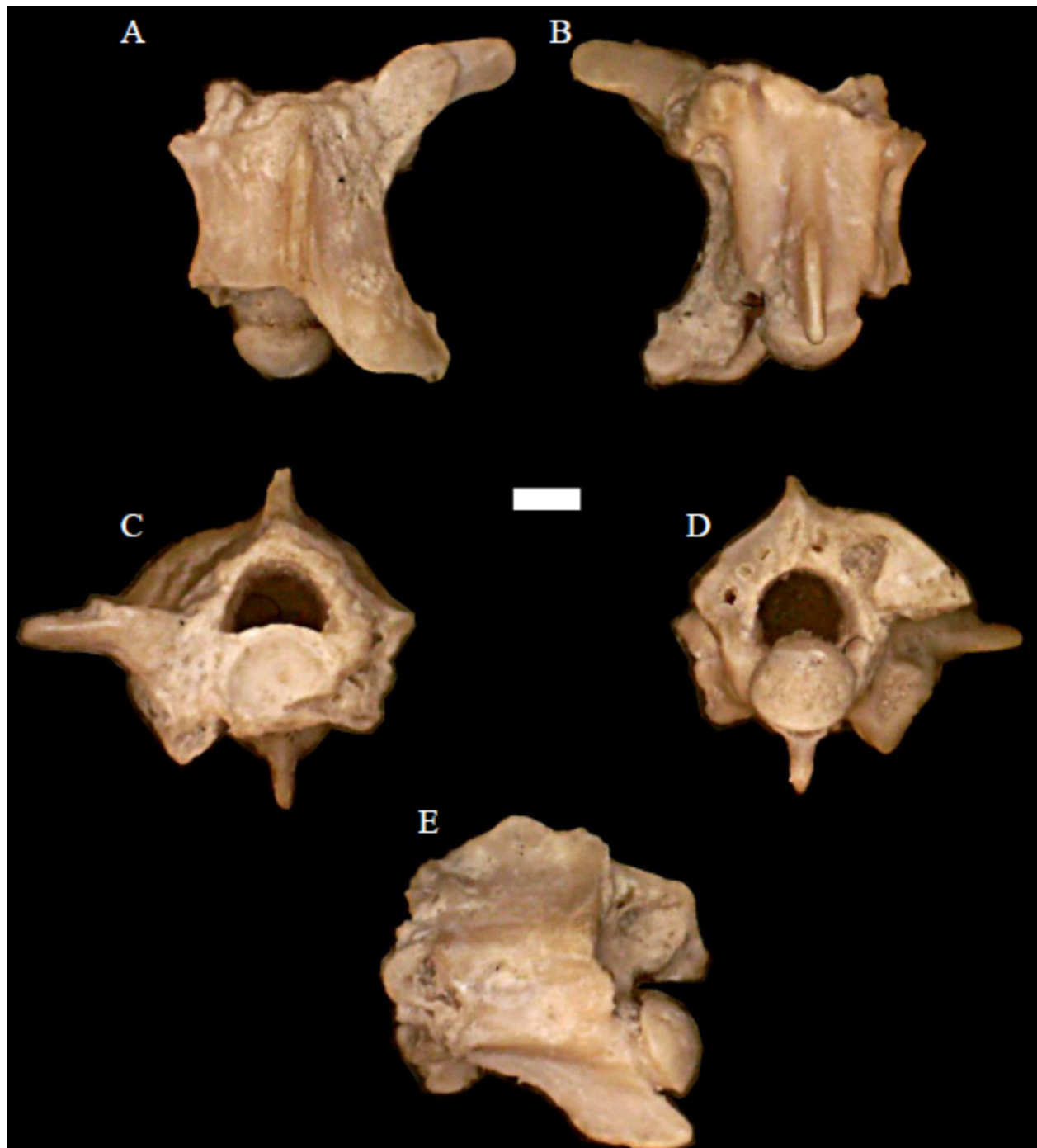
*Nerodia* sp. indet.

Figure 12

**Material.** UNSM 139988 (24 pre-cloacal trunk vertebrae).

**Description.** These trunk vertebrae are large in size and relatively wide when including the prezygapophyseal accessory processes, but are still rel-





**FIGURE 12.** Posterior middle trunk vertebra of *Nerodia* sp., from the Penny Creek local fauna. From top left: dorsal, ventral, anterior, posterior, and lateral views (anterior to the left). Scale bar equals 1 mm.

actively elongate along the centrum. The neural spines are tall and straight dorsally and somewhat undercut both anteriorly and posteriorly, but are rarely preserved in their entirety, hindering full comparisons between neural spine height and length. The neural arch is vaulted. The zygosphenes is convex when viewed dorsally. The con-

dyle and cotyle are round, and larger than the neural canal. The prezygapophyseal and postzygapophyseal facets are ovaloid in shape (sensu Holman, 2000) and oblique to the long axis of the centrum. The epizygapophyseal spines are absent. The subcentral ridges are pronounced and form deep grooves along the hypapophysis. The hypa-

pophyses on each precaudal vertebra are well-developed, laterally compressed, directed posteriorly, and end in a somewhat pointed tip that extends posteriorly beyond the condylar head when complete.

**Remarks.** The only other concurrent species during the Miocene is *Nerodia hillmani* and an indeterminate species from the Pratt Slide (Bw 123) locality, which is ~10.5-9.5 Ma (Clarendonian 3). Based on the larger size, longer hypapophysis, and longer prezygapophyseal articular facets, the *Nerodia* fossils described here are more similar to the unnamed Pratt Slide species than to *N. hillmani*. Comparison to more specimens, extant *Nerodia sipedon* and the somewhat younger *Nerodia hibbardi* from the Pliocene of Idaho and possibly Texas (Holman, 1968, 2000) may be necessary before assigning a species-level classification to these fossils.

## RESULTS AND DISCUSSION

The Neogene fossil record of the Central Great Plains has produced the most significant and continuous record of the evolution and modernization of snakes in North America (Figure 2). While the number of taxa represented in Penny Creek locality Wt 13B is low when compared to other Nebraska localities, such as the older Late Barstovian Myers Farm Local Fauna or the younger Late Clarendonian Pratt Slide Local Fauna (Holman, 1977; Parmley and Hunter, 2010), the Penny Creek snake assemblage is a crucial piece of evidence to understand diversification and modernization of North American snake faunas. As the only described snake assemblage from the earliest Clarendonian (12.5-12.0 Ma), the presence of the snake species identified here can now be confirmed as having been present in the area, whereas the presence of these taxa could previously only be assumed based on bracketing snake assemblages from older and younger localities (Figure 2). Furthermore, the snakes of Wt 13B represent the first documentation of non-testudine reptiles documented in a period temporally bracketed by the earlier peak of reptilian diversity in the warmer, more humid, and likely more closed environments of the Late Barstovian of the Central Great Plains (Holman, 1977) and the later Yellowstone hotspot eruption that preserved the Ashfall Fossil Beds lagerstätten in an opening, cooler, and more arid northeastern Nebraska (Voorhies, 1992). Penny Creek, therefore, provides the first opportunity to look at not only what snakes were present during this period, but also allows for paleoenviron-

mental predictions based on their poikilothermic physiologies and modern proxies.

Of the eight taxa identified at Penny Creek, all taxa identified to the species level are extinct; however, only *Neonatrix* is extinct at the genus level. *Charina* persists in western North America and *Salvadora* persists in the southwestern United States and Mexico, but are extirpated from Nebraska and the Central Great Plains. All other genera described from Penny Creek currently persist in the Central Great Plains. Thus, approximately 88.9% of this assemblage can be considered taxonomically “modern” (i.e., extant at the genus level). Furthermore, the low abundance of booid relative to colubroid taxa supports the idea of a taxonomically “modern” assemblage. This site bridges the previous temporal gap in the transitional modernization of North American snake assemblages.

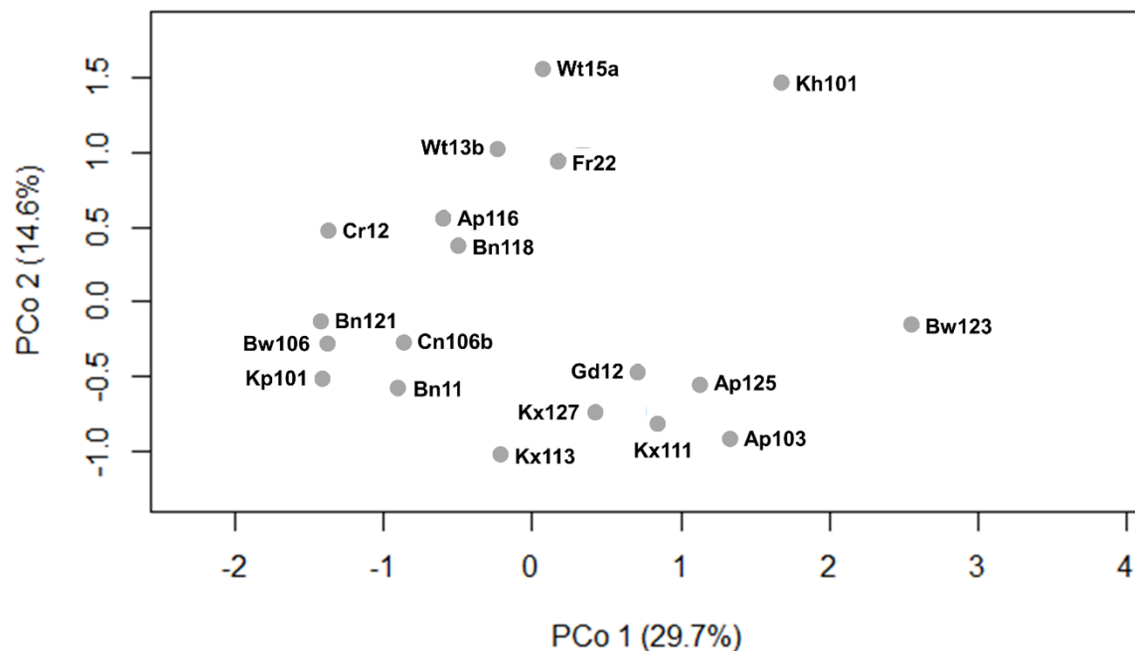
The lack of identified material for other previously common booids, such as *Calamagras*, *Gerin-gophis*, *Ogmophis*, *Pterygoboa*, and *Tregophis*, does not reject the possibility of these taxa persisting over a wide geographic range in the post-Barstovian Central Great Plains, but their absence (or relative rarity) at both this locality and nearly all other published younger Miocene localities in the Central Great Plains is notable. Only two documented younger Clarendonian localities in the Central Great Plains have identified booids not attributable to *Charina* or *Lichanura* and these localities are associated with environmental settings that differ from similarly-aged localities in the same region. The WaKeeney local fauna preserves a “small stream-filled basin” depositional environment with vegetation and climate apparently comparable to present-day southeastern Texas during the Middle Clarendonian (Holman, 1975). One vertebra each – both of which represent the type specimens for both taxa – of *Tregophis brevirachis* and *Ogmophis pliocompactus* were described out of 1230 total snake vertebrae, an exceptionally low occurrence rate for the total number of snake fossils (Holman, 1975). The Pratt Slide local fauna has been suggested as a wooded valley occupied by a riparian stream that is adjacent to a savanna landscape; this idea is supported by geological, paleontological, and isotopic data and differs from other localities of the Late Clarendonian in Nebraska (Rudnick, 1994; Parmley and Hunter, 2010; Parmley et al., 2015; Kita et al., 2014). This assemblage contains *Calamagras* sp. indet. or *Ogmophis* sp. indet., along with the second documented occurrence of *Tregophis bre-*

*virachis*. Both taxa are represented at Pratt Slide by three identifiable vertebrae each. As far as we are currently able to determine based on known occurrences and the above information, it seems possible that the state of the North American booid fossil record represents a true decline in extinct booid taxa in terms of both geographic range and relative abundance, rather than a lack of preservation during the Clarendonian and later. In broader terms, it is possible that the Clarendonian of North America represents a near-complete decline (but not complete loss) of now-extinct booid taxa as soon as the Central Great Plains began transitioning to a more open, arid, cooler, and seasonal environment from more closed, humid Barstovian environments. If that is the case, then the aforementioned examples above may represent a few persistent pockets containing relatively rare holdovers, where environmental conditions were more reminiscent of those in the Late Barstovian of the same region.

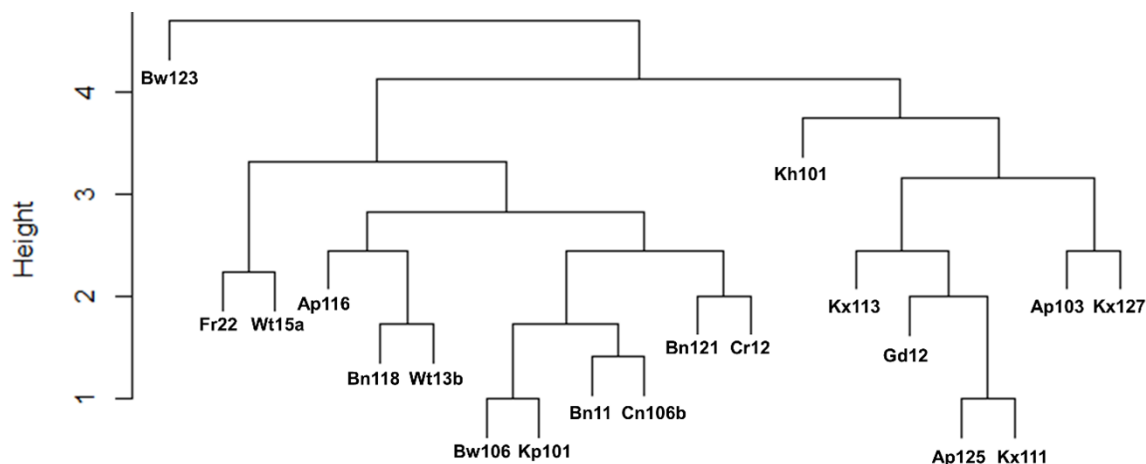
The transition away from extinct colubroids, for the most part, appears more prolonged. Starting with the Late Barstovian, *Dakotaophis* makes its last appearance in the Bijou Hills local fauna of South Dakota (Holman, 1978), and *Micrurus* is extirpated from the region (Holman, 1977), and then does not reappear until the Early Pleistocene (Irvingtonian I) Inglis IA site of Florida and the Mid-

dle to Late Pleistocene (Irvingtonian 2) Fyllan Cave Fauna of Texas (Meylan, 1982; Holman and Winkler, 1987). As in the booids above, *Texasophis* and *Ameiseophis* make their final appearances at the unique Wakeeney, Ashfall, and Pratt Slide localities in the Middle and Late Clarendonian of the Central Great Plains (Parmley and Hunter, 2010). *Paracoluber* and *Nebraskophis* last appear in the Hemphillian (Late Miocene) Lemoyne Quarry of Nebraska; and *Salvadora* is extirpated from the region following the Hemphillian. Finally, *Neonatrix* makes its last known appearance in the Central Great Plains at Lemoyne Quarry, but may potentially be present in the Hemphillian Mio-Pliocene Gray Fossil Site of Northeastern Tennessee as well (Parmley and Holman, 1995; Jasinski and Moscato, 2017).

Our PCoA (Figure 13) and complete-linkage HCA (Figure 14) produced similar results regarding the dissimilarity of the 19 selected fossil localities from Nebraska. The PCoA axes 1 and 2, which represented 29.7% and 14.6% (44.3% total) of the variation in the dataset, indicate that the loss of “archaic” booids and colubroids (particularly natricids) and the introduction of “modern” colubroids – including a more diverse crotaline and colubrine presence – lead to the separation of the localities into multiple groups (Figures 13-14). Our HCA further clarifies these clusters based on a dissimilarity



**FIGURE 13.** Principal coordinates analysis showing the relative similarity of snake assemblages from 19 Barstovian-Blancan localities in Nebraska based on presence-absence.

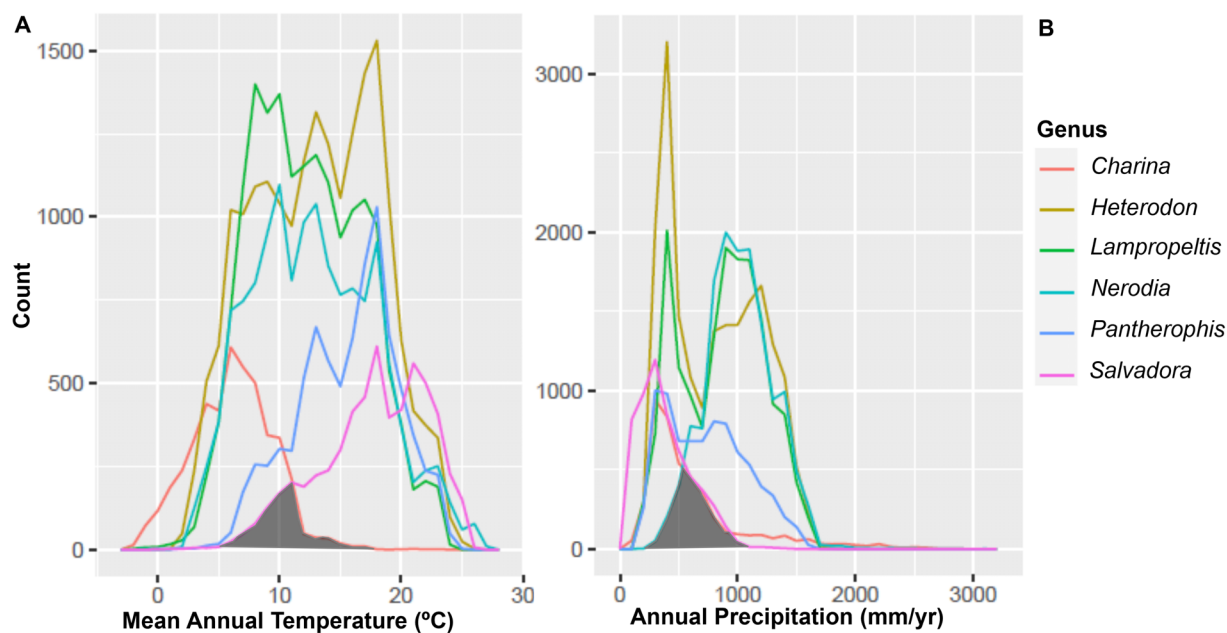


**FIGURE 14.** Complete-linkage hierarchical cluster analysis showing the relative similarity of snake assemblages from 19 Barstovian-Blancan localities in Nebraska based on presence-absence. Three major clusters are visible. From the left, the first cluster contains only Bw 123, the unique Pratt Slide local fauna; the second cluster contains all Barstovian and Clarendonian faunas minus Bw 123, but with the addition of Hemphillian Cn 106b (*Thamnophis* + Colubrinae indet.); and the third cluster, containing all Hemphillian through Blancan sites except Cn 106b.

matrix of each locality (Figure 14). The Pratt Slide local fauna (Bw 123) was an outlier for the localities and forms the first main cluster. This is likely because of its high genus-level richness, which includes an uncommon combination of extinct, novel, and extant taxa. Our second main cluster contains the ten other localities from the Barstovian through the Clarendonian, with the addition of the Hemphillian Cn 106b, which only has *Thamnophis* and indeterminate colubrids identified. All other localities in this cluster seem to be defined by the presence of now extinct or extirpated taxa, including taxa such as *Neonatrix* and *Pterygoboa*. Our third and final cluster includes all seven remaining Hemphillian through Blancan snake assemblages, with appearances from extant taxa such as *Regina*, *Storeria*, and *Rhinocheilus*, and more consistent identifications of extant crotaline genera. These results imply that the major compositional shift of the Central Great Plains occurred through the Clarendonian and the snake fauna was functionally a group of near extant assemblages by the Hemphillian.

Our climate envelope models using congeners produced clear ranges of temperature and precipitation overlap, with differences on which specific congeners provided the upper and lower bounds (Figure 15). The MAT variable (Figure 15a) suggests that the lowest overlapping values are bounded by *Salvadora*, while the highest overlapping values are bounded by *Charina*, as these taxa respectively have higher minimum MAT and lower maximum MAT tolerances today. The overlapping

MAT values range from just below 5°C to 16°C, with a maximum density between 11°C-12°C. The maximum density of the area of overlap may suggest that MAT in the earliest Clarendonian of Webster Co., NE was higher than the present (~10.55°C); however, the range of projections encompasses higher and lower temperatures. Additionally, this would suggest that MAT in the early Clarendonian of the Penny Creek local fauna was lower than proposed for the older Late Barstovian Myers Farm local fauna, which has been considered warm and temperate to sub-tropical (Holman, 1977; Holman, 2000; Corner, 2014), and supports an overall cooling climate in the early Clarendonian. The AP variable (Figure 15b) is bounded at the lower values by *Nerodia* and at the higher values by both *Charina* and *Salvadora*, although *Nerodia* and *Charina* respectively occupy the lower and upper limits at peak density. The overlapping AP values range from approximately 200-1100 mm, with maximum density at 550-600 mm. While these values range from well-below to well-above the present AP of Webster Co., the maximum density suggest a slightly drier environment in the earliest Clarendonian, again indicating a more open, temperate, and cooler environment after the MMCO. The combined MAT and AP values suggest that the most likely biome of the Penny Creek local fauna was a shrubland/woodland (Bailey, 1998; 2005), especially given the maximum density values for each. Slightly less likely biomes based on maximum and minimum values of MAT and AP also include temperate



**FIGURE 15.** Climate envelope models of MAT (A) and AP (B) based on the congeners of the snake assemblage of the Penny Creek local fauna. The gray-filled spaces signify the areas of overlap for all taxa included in the models.

grassland/cold desert (lower AP) or temperate seasonal forest (higher AP); however, the majority of MAT and AP combinations suggest the shrubland/woodland biome.

The results of the climate envelope models are supported by previous research using phytoliths (Strömberg 2004, 2006, 2011), vertebrate faunal composition (Turner, 1972; Corner, 2014), mammal hypsodonty (Janis et al., 2000, 2002, 2004; Strömberg, 2006), paleosols (Retallack, 2007), carbonate isotopes (Fox and Koch, 2004), and isotope values for mammalian teeth from the late Miocene (Wang et al., 1994; Kita et al., 2014), as well as the snakes in this study. Interestingly, *Charina* and *Salvadora* impose opposing limits for MAT, but share much of the upper limit for AP in our climate envelope models. While both snakes are presently located in western North America and overlap somewhat in the southwestern United States today, *Charina* is adapted to cooler temperatures and *Salvadora* to warmer temperatures compared to all other congeners in this analysis, thus limiting the overlap area of MAT. The shared upper limit of AP composed of *Charina* and *Salvadora* likely reflects the high degree of drier biomes occupied by those taxa; the long tail of *Charina*'s data in AP when compared to *Salvadora*'s signifies the former's presence in the Pacific Northwest of the United States and Canada. Conspicuously,

both taxa were the only genera from this assemblage to be extirpated from Nebraska to the West and South during the Neogene, likely during the Hemphillian based on the last appearance datum for each (Jacisin et al., 2015). *Nerodia*, on the other hand, is typically found near permanent sources of water, which likely imposes a lower limit on AP in our plots. It should be noted that the results of our climate envelope models are slightly complicated by the lack of extant species identified from the Penny Creek material. By choosing closely related congeneric species from the present, we assume that our fossil species share similar ecologies and ecomorphologies, to their extant relatives, as suggested by niche conservatism. It is possible that directional trends of evolution related to climate are not detected when fossils are not included, as seen in other squamates such as *Sceloporus* (Lawing et al., 2016). Stronger predictions can be made by incorporating the entire known fossil record of a group in these models, but that is beyond the scope of this study.

Based on the ecologies of extant relatives for the taxa present at Penny Creek, the recovery of *Charina*, *Lampropeltis*, *Pantherophis*, *Heterodon*, and multiple natricid genera allows us to make a few assumptions on what the Penny Creek environment may have looked like. Extant *Charina*, *Heterodon*, *Lampropeltis*, and *Salvadora* all prefer

loose substrates such as sandy soils, along with areas with plenty of ground-level cover (Holman, 1977; St. Clair, 1999; Plummer and Mills, 2000; Pyron and Burbrink, 2009; Davis and LaDuc, 2018). *Nerodia*, *Thamnophis*, and some species of *Lampropeltis* generally prefer to reside near permanent sources of water and the surrounding grassy areas (Holman, 1977; Holman and Schroeder, 1991; McVay et al., 2015). Finally, the presence of *Charina* may indicate a relatively mild, temperate-to-semi-arid environment, as extant members of that genus are relatively cold-adapted booids (St. Clair, 1999; Holman, 2000; Rodriguez-Robles et al., 2001). Most of these snakes, including *Pantherophis* and crotaline vipers, are found across wide geographic swaths of North America today. The majority of the taxa would today be consistent with a transitional or mosaic woodland and prairie ecotone, making it somewhat similar to the Barstovian Egelhoff fauna (Holman, 1987); however, there is notably less amphibian and turtle material presently known from Wt 13b. This difference suggests a permanent stream or river as a local water source, instead of a pond or lake. Furthermore, the severely weathered state of the fossil vertebrates at Wt 13B additionally suggest a high energy fluvial source as a depositional environment.

The interpretation of a somewhat open, permanent fluvial environment surrounded by a transitional or mosaic prairie and woodland is consistent with previous studies focused on the geology and mammalian paleoecology of the Penny Creek Local Fauna (Turner, 1972; Voorhies et al., 1987; Voorhies, 1990). Furthermore, the Penny Creek fossil snakes represent the only presently described snake assemblage from 12.5–12.0 Ma in

North America, providing us with an initial glimpse into the Clarendonian 1 North American Land Mammal Age for small herpetofauna. The description of the Penny Creek fossil snakes confirms the persistence of multiple taxa across the MMCO and contributes to our understanding of the interactions between post-MMCO environmental changes and the gradual modernization and evolution of North American snakes. Extensive future work is a requirement to better understand the radiation of the modern North American snake fauna, particularly in time intervals with sparse material and in regions outside of the Central Great Plains, but Penny Creek is a significant step towards filling the extensive gap of knowledge in our present understanding of ophidian history.

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## APPENDIX

**APPENDIX TABLE 1.** List of Middle Miocene-Pliocene fossil snakes from Nebraska and their localities. A dagger symbol (†) indicates an extinct taxon or group.

Locality	NALMA	Geologic Age	Taxon	Genus or Group
Bn-118	Barstovian 2	Middle Miocene	<i>Dakotaophis greeni</i> †	<i>Dakotaophis</i> †
Bn-118	Barstovian 2	Middle Miocene	<i>Lampropeltis similis</i> †	<i>Lampropeltis</i>
Bn-118	Barstovian 2	Middle Miocene	<i>Heterodon tihenii</i> †	<i>Heterodon</i>
Bn-118	Barstovian 2	Middle Miocene	<i>Pantherophis (Elaphe) kansensis</i> †	<i>Pantherophis (Elaphe)</i>
Bn-118	Barstovian 2	Middle Miocene	<i>Salvadora paleolineata</i> †	<i>Salvadora</i>
Bn-118	Barstovian 2	Middle Miocene	<i>Nerodia</i> sp.	<i>Nerodia</i>
Bn-121	Barstovian 2	Middle Miocene	<i>Pantherophis (Elaphe) kansensis</i> †	<i>Pantherophis (Elaphe)</i>
Bn-121	Barstovian 2	Middle Miocene	<i>Salvadora paleolineata</i> †	<i>Salvadora</i>
Bn-121	Barstovian 2	Middle Miocene	<i>Dakotaophis greeni</i> †	<i>Dakotaophis</i> †
Bw-106	Barstovian 2	Middle Miocene	<i>Natricidae</i> sp. indet.	<i>Natricidae</i> sp. indet.
Bw-106	Barstovian 2	Middle Miocene	<i>Colubrinae</i> sp. indet.	<i>Colubrinae</i> sp. indet.
Bw-106	Barstovian 2	Middle Miocene	<i>Nebraskophis skinneri</i> †	<i>Nebraskophis</i> †
Bw-106	Barstovian 2	Middle Miocene	<i>Natricidae</i> sp. indet.	<i>Natricidae</i> sp. indet.
Bw-106	Barstovian 2	Middle Miocene	<i>Colubrinae</i> sp. indet.	<i>Colubrinae</i> sp. indet.
Kp-101	Barstovian 2	Middle Miocene	<i>Natricidae</i> sp. indet.	<i>Natricidae</i> sp. indet.
Kp-101	Barstovian 2	Middle Miocene	<i>Colubrinae</i> sp. indet.	<i>Colubrinae</i> sp. indet.
Bn-11	Barstovian 2	Middle Miocene	<i>Pantherophis (Elaphe) kansensis</i> †	<i>Pantherophis (Elaphe)</i>
Bn-11	Barstovian 2	Middle Miocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Cr-12	Barstovian 2	Middle Miocene	<i>Salvadora paleolineata</i> †	<i>Salvadora</i>
Cr-12	Barstovian 2	Middle Miocene	<i>Neonatrix elongata</i> †	<i>Neonatrix</i> †
Cr-12	Barstovian 2	Middle Miocene	<i>Colubrinae</i> sp. indet.	<i>Colubrinae</i> sp. indet.
Fr-22	Barstovian 2	Middle Miocene	<i>Salvadora</i> sp.	<i>Salvadora</i>
Fr-22	Barstovian 2	Middle Miocene	<i>Salvadora</i> sp.	<i>Salvadora</i>
Fr-22	Barstovian 2	Middle Miocene	<i>Heterodon</i> sp.	<i>Heterodon</i>
Fr-22	Barstovian 2	Middle Miocene	<i>Pterygoboa miocenica</i> †	<i>Pterygoboa</i> †
Fr-22	Barstovian 2	Middle Miocene	<i>Neonatrix</i> sp. †	<i>Neonatrix</i> †
Fr-22	Barstovian 2	Middle Miocene	<i>Crotalus</i> sp.	<i>Crotalus</i>
Fr-22	Barstovian 2	Middle Miocene	<i>Crotalinae</i> sp. indet.	<i>Crotalinae</i> sp. indet.
Fr-22	Barstovian 2	Middle Miocene	<i>Nerodia</i> sp.	<i>Nerodia</i>
Fr-22	Barstovian 2	Middle Miocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Fr-22	Barstovian 2	Middle Miocene	<i>Natricidae</i> sp. indet.	<i>Natricidae</i> sp. indet.
Wt-15A	Barstovian 2	Middle Miocene	<i>Heterodon tihenii</i> †	<i>Heterodon</i>
Wt-15A	Barstovian 2	Middle Miocene	<i>Pantherophis (Elaphe) kansensis</i> †	<i>Pantherophis (Elaphe)</i>
Wt-15A	Barstovian 2	Middle Miocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Wt-15A	Barstovian 2	Middle Miocene	<i>Salvadora paleolineata</i> †	<i>Salvadora</i>
Wt-15A	Barstovian 2	Middle Miocene	<i>Salvadora paleolineata</i> †	<i>Salvadora</i>
Wt-15A	Barstovian 2	Middle Miocene	<i>Nebraskophis skinneri</i> †	<i>Nebraskophis</i> †
Wt-15A	Barstovian 2	Middle Miocene	<i>Heterodon tihenii</i> †	<i>Heterodon</i>

Locality	NALMA	Geologic Age	Taxon	Genus or Group
Wt-15A	Barstovian 2	Middle Miocene	<i>Nerodia</i> sp.	<i>Nerodia</i>
Wt-15A	Barstovian 2	Middle Miocene	<i>Pantherophis (Elaphe) kansensis</i> †	<i>Pantherophis (Elaphe)</i>
Wt-15A	Barstovian 2	Middle Miocene	<i>Neonatrix elongata</i> †	<i>Neonatrix</i> †
Wt-15A	Barstovian 2	Middle Miocene	<i>Crotalinae</i> sp. indet.	<i>Crotalinae</i> sp. indet.
Wt-15A	Barstovian 2	Middle Miocene	<i>Micrurus</i> sp.	<i>Micrurus</i>
Wt-13B	Clarendonian 1	Late Miocene	<i>Neonatrix elongata</i> †	<i>Neonatrix</i> †
Wt-13B	Clarendonian 1	Late Miocene	<i>Neonatrix magna</i> †	<i>Neonatrix</i> †
Wt-13B	Clarendonian 1	Late Miocene	<i>Heterodon</i> sp.	<i>Heterodon</i>
Wt-13B	Clarendonian 1	Late Miocene	<i>Nerodia</i> sp.	<i>Nerodia</i>
Wt-13B	Clarendonian 1	Late Miocene	<i>Lampropeltis similis</i> †	<i>Lampropeltis</i>
Wt-13B	Clarendonian 1	Late Miocene	<i>Pantherophis (Elaphe) kansensis</i> †	<i>Pantherophis (Elaphe)</i>
Wt-13B	Clarendonian 1	Late Miocene	<i>Charina prebottae</i> †	<i>Charina</i>
Wt-13B	Clarendonian 1	Late Miocene	<i>Salvadora paleolineata</i>	<i>Salvadora</i>
Ap-116	Clarendonian 2	Late Miocene	<i>Crotalinae</i> sp. Indet.	<i>Crotalinae</i> sp. Indet.
Ap-116	Clarendonian 2	Late Miocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Ap-116	Clarendonian 2	Late Miocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Ap-116	Clarendonian 2	Late Miocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Ap-116	Clarendonian 2	Late Miocene	<i>Ameiseophis robinsoni</i> †	<i>Ameiseophis</i> †
Ap-116	Clarendonian 2	Late Miocene	<i>Nerodia</i> sp.	<i>Nerodia</i>
Ap-116	Clarendonian 2	Late Miocene	<i>Heterodon tihen</i> †	<i>Heterodon</i>
Ap-116	Clarendonian 2	Late Miocene	<i>Salvadora paleolineata</i> †	<i>Salvadora</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Tregophis</i> sp. †	<i>Tregophis</i> †
Bw-123	Clarendonian 3	Late Miocene	<i>Ogmophis</i> † or <i>Calamagras</i> †	<i>Ogmophis</i> † or <i>Calamagras</i> †
Bw-123	Clarendonian 3	Late Miocene	<i>Ogmophis</i> † or <i>Calamagras</i> †	<i>Ogmophis</i> † or <i>Calamagras</i> †
Bw-123	Clarendonian 3	Late Miocene	<i>Heterodon</i> sp.	<i>Heterodon</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Tregophis</i> sp. †	<i>Tregophis</i> †
Bw-123	Clarendonian 3	Late Miocene	<i>Ameiseophis</i> sp. †	<i>Ameiseophis</i> †
Bw-123	Clarendonian 3	Late Miocene	<i>Heterodon</i> sp.	<i>Heterodon</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Paracoluber</i> sp. †	<i>Paracoluber</i> †
Bw-123	Clarendonian 3	Late Miocene	<i>Coluber</i> or <i>Masticophis</i> sp.	<i>Coluber</i> or <i>Masticophis</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Ameiseophis</i> sp. †	<i>Ameiseophis</i> †
Bw-123	Clarendonian 3	Late Miocene	<i>Lampropeltis</i> cf. <i>L. getula</i>	<i>Lampropeltis</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Pantherophis (Elaphe)</i> sp.	<i>Pantherophis (Elaphe)</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Pantherophis (Elaphe) kansensis</i> †	<i>Pantherophis (Elaphe)</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Lampropeltis triangulum</i> or <i>L. similis</i> †	<i>Lampropeltis</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Micronatrix juliascottae</i> †	<i>Micronatrix</i> †
Bw-123	Clarendonian 3	Late Miocene	<i>Crotalinae</i> sp. indet.	<i>Crotalinae</i> sp. indet.
Bw-123	Clarendonian 3	Late Miocene	<i>Crotalus</i> sp.	<i>Crotalus</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Agkistrodon</i> sp.	<i>Agkistrodon</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Tropidoclonion</i> sp.	<i>Tropidoclonion</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Nerodia</i> sp.	<i>Nerodia</i>

Locality	NALMA	Geologic Age	Taxon	Genus or Group
Bw-123	Clarendonian 3	Late Miocene	<i>Neonatrix</i> sp.	<i>Neonatrix</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Nerodia hillmani</i> †	<i>Nerodia</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Pituophis</i> sp.	<i>Pituophis</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Texasophis</i> sp. †	<i>Texasophis</i> †
Bw-123	Clarendonian 3	Late Miocene	<i>Opheodrys</i> sp.	<i>Opheodrys</i>
Bw-123	Clarendonian 3	Late Miocene	<i>Sistrurus</i> sp.	<i>Sistrurus</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Crotalus horridus</i>	<i>Crotalus</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Arizona</i> sp.	<i>Arizona</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Virginia</i> sp.	<i>Virginia</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Nebraskophis skinneri</i> †	<i>Nebraskophis</i> †
Kh-101	Hemphillian 1	Late Miocene	<i>Crotalus</i> sp.	<i>Crotalus</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Agkistrodon</i> sp.	<i>Agkistrodon</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Pantherophis (Elaphe) kansensis</i> †	<i>Pantherophis (Elaphe)</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Salvadora paleolineata</i> †	<i>Salvadora</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Paracoluber</i> sp. †	<i>Paracoluber</i> †
Kh-101	Hemphillian 1	Late Miocene	<i>Charina prebottae</i> †	<i>Charina</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Charina prebottae</i> †	<i>Charina</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Lichanura</i> sp. indet.	<i>Lichanura</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Colubrinae</i> sp. indet.	<i>Colubrinae</i> sp. indet.
Kh-101	Hemphillian 1	Late Miocene	<i>Coluber</i> or <i>Masticophis</i> sp.	<i>Coluber</i> or <i>Masticophis</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Lampropeltis getulus</i>	<i>Lampropeltis</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Lampropeltis triangulum</i>	<i>Lampropeltis</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Thamnophis proximus</i>	<i>Thamnophis</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Thamnophis cyrtopsis</i>	<i>Thamnophis</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Thamnophis marcianus</i>	<i>Thamnophis</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Heterodon tihen</i> †	<i>Heterodon</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Heterodon platyrhinus</i>	<i>Heterodon</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Heterodon</i> sp.	<i>Heterodon</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Neonatrix elongata</i> †	<i>Neonatrix</i> †
Kh-101	Hemphillian 1	Late Miocene	<i>Nerodia hillmani</i> †	<i>Nerodia</i>
Kh-101	Hemphillian 1	Late Miocene	<i>Nerodia</i> sp. indet.	<i>Nerodia</i>
Cn-106B	Hemphillian 2	Late Miocene	<i>Colubrinae</i> sp. indet.	<i>Colubrinae</i> sp. indet.
Cn-106B	Hemphillian 2	Late Miocene	<i>Thamnophis</i> sp. Indet.	<i>Thamnophis</i>
Cn-106B	Hemphillian 2	Late Miocene	<i>Heterodon tihen</i> †	<i>Heterodon</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Heterodon platyrhinus</i>	<i>Heterodon</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Heterodon tihen</i>	<i>Heterodon</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Heterodon nasicus</i>	<i>Heterodon</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Heterodon</i> sp.	<i>Heterodon</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Thamnophis sirtalis</i> or <i>proximus</i>	<i>Thamnophis</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Thamnophis marcianus</i>	<i>Thamnophis</i>



Locality	NALMA	Geologic Age	Taxon	Genus or Group
Ap-125	Hemphillian 3	Late Miocene	<i>Nerodia</i> sp.	<i>Nerodia</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Crotalus</i> sp.	<i>Crotalus</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Coluber</i> or <i>Masticophis</i> sp.	<i>Coluber</i> or <i>Masticophis</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Pantherophis (Elaphe) guttata</i>	<i>Pantherophis (Elaphe)</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Lampropeltis triangulum</i>	<i>Lampropeltis</i>
Ap-125	Hemphillian 3	Late Miocene	<i>Pituophis melanoleucus</i>	<i>Pituophis</i>
Kx-113	Hemphillian 4	Late Miocene	<i>Crotalus</i> sp.	<i>Crotalus</i>
Kx-113	Hemphillian 4	Late Miocene	<i>Lampropeltis getulus</i>	<i>Lampropeltis</i>
Kx-113	Hemphillian 4	Late Miocene	<i>Lampropeltis triangulum</i>	<i>Lampropeltis</i>
Kx-113	Hemphillian 4	Late Miocene	<i>Pantherophis (Elaphe) guttata</i>	<i>Pantherophis (Elaphe)</i>
Kx-111	Hemphillian 4	Late Miocene	<i>Coluber</i> or <i>Masticophis</i> sp.	<i>Coluber</i> or <i>Masticophis</i>
Kx-111	Hemphillian 4	Late Miocene	<i>Heterodon</i> sp.	<i>Heterodon</i>
Kx-111	Hemphillian 4	Late Miocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Kx-111	Hemphillian 4	Late Miocene	<i>Thamnophis proximus</i>	<i>Thamnophis</i>
Kx-111	Hemphillian 4	Late Miocene	<i>Lampropeltis</i> sp.	<i>Lampropeltis</i>
Kx-111	Hemphillian 4	Late Miocene	<i>Lampropeltis getulus</i>	<i>Lampropeltis</i>
Kx-111	Hemphillian 4	Late Miocene	<i>Pituophis melanoleucus</i>	<i>Pituophis</i>
Kx-111	Hemphillian 4	Late Miocene	<i>Pantherophis (Elaphe) sp.</i>	<i>Pantherophis (Elaphe)</i>
Kx-111	Hemphillian 4	Late Miocene	<i>Pantherophis (Elaphe) obsoleta</i>	<i>Pantherophis (Elaphe)</i>
Kx-111	Hemphillian 4	Late Miocene	<i>Crotalus</i> sp.	<i>Crotalus</i>
Gd-12	Blancan 1	Early Pliocene	<i>Thamnophis sirtalis</i>	<i>Thamnophis</i>
Gd-12	Blancan 1	Early Pliocene	<i>Thamnophis radix</i>	<i>Thamnophis</i>
Gd-12	Blancan 1	Early Pliocene	<i>Nerodia sipedon</i>	<i>Nerodia</i>
Gd-12	Blancan 1	Early Pliocene	<i>Crotalus</i> sp. indet.	<i>Crotalus</i>
Gd-12	Blancan 1	Early Pliocene	<i>Lampropeltis triangulum</i>	<i>Lampropeltis</i>
Gd-12	Blancan 1	Early Pliocene	<i>Storeria</i> sp. Indet.	<i>Storeria</i>
Gd-12	Blancan 1	Early Pliocene	<i>Heterodon</i> sp. Indet.	<i>Heterodon</i>
Gd-12	Blancan 1	Early Pliocene	<i>Heterodon</i> sp. Indet.	<i>Heterodon</i>
Gd-12	Blancan 1	Early Pliocene	<i>Pantherophis (Elaphe) vulpina</i>	<i>Pantherophis (Elaphe)</i>
Gd-12	Blancan 1	Early Pliocene	<i>Pantherophis (Elaphe) vulpina</i>	<i>Pantherophis (Elaphe)</i>
Ap-103	Blancan 1	Early Pliocene	<i>Nerodia</i> sp.	<i>Nerodia</i>
Ap-103	Blancan 1	Early Pliocene	<i>Natricidae</i> sp. indet.	<i>Natricidae</i> sp. indet.
Ap-103	Blancan 1	Early Pliocene	<i>Nerodia sipedon/hibbardi?</i>	<i>Nerodia</i>
Ap-103	Blancan 1	Early Pliocene	<i>Regina grahamii</i>	<i>Regina</i>
Ap-103	Blancan 1	Early Pliocene	<i>Sistrurus catenatus</i>	<i>Sistrurus</i>
Ap-103	Blancan 1	Early Pliocene	<i>Crotalus horridus</i>	<i>Crotalus</i>
Ap-103	Blancan 1	Early Pliocene	<i>Agkistrodon contortrix</i>	<i>Agkistrodon</i>
Ap-103	Blancan 1	Early Pliocene	<i>Pantherophis (Elaphe) vulpina</i>	<i>Pantherophis (Elaphe)</i>
Ap-103	Blancan 1	Early Pliocene	<i>Pantherophis (Elaphe) guttata</i>	<i>Pantherophis (Elaphe)</i>
Ap-103	Blancan 1	Early Pliocene	<i>Rheinocheilus lecontei</i>	<i>Rheinocheilus</i>
Ap-103	Blancan 1	Early Pliocene	<i>Coluber constrictor</i>	<i>Coluber</i>
Ap-103	Blancan 1	Early Pliocene	<i>Masticophis flagellum</i>	<i>Masticophis</i>

Locality	NALMA	Geologic Age	Taxon	Genus or Group
Ap-103	Blancan 1	Early Pliocene	<i>Lampropeltis</i> sp.	<i>Lampropeltis</i>
Ap-103	Blancan 1	Early Pliocene	<i>Lampropeltis doliata</i>	<i>Lampropeltis</i>
Ap-103	Blancan 1	Early Pliocene	<i>Lampropeltis calligaster</i>	<i>Lampropeltis</i>
Ap-103	Blancan 1	Early Pliocene	<i>Lampropeltis getulus</i>	<i>Lampropeltis</i>
Ap-103	Blancan 1	Early Pliocene	<i>Heterodon platirhinos</i>	<i>Heterodon</i>
Ap-103	Blancan 1	Early Pliocene	<i>Heterodon nasicus</i>	<i>Heterodon</i>
Ap-103	Blancan 1	Early Pliocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>
Ap-103	Blancan 1	Early Pliocene	<i>Thamnophis proximus</i>	<i>Thamnophis</i>
Ap-103	Blancan 1	Early Pliocene	<i>Thamnophis sirtalis</i>	<i>Thamnophis</i>
Ap-103	Blancan 1	Early Pliocene	<i>Thamnophis radix</i>	<i>Thamnophis</i>
Kx-127	Blancan 2	Early Pliocene	<i>Crotalus horridus</i>	<i>Crotalus</i>
Kx-127	Blancan 2	Early Pliocene	<i>Pantherophis (Elaphe) guttata</i>	<i>Pantherophis (Elaphe)</i>
Kx-127	Blancan 2	Early Pliocene	<i>Nerodia rhombifera</i>	<i>Nerodia</i>
Kx-127	Blancan 2	Early Pliocene	<i>Nerodia</i> sp.	<i>Nerodia</i>
Kx-127	Blancan 2	Early Pliocene	<i>Regina grahamii</i>	<i>Regina</i>
Kx-127	Blancan 2	Early Pliocene	<i>Nerodia sipedon/hibbardi</i>	<i>Nerodia</i>
Kx-127	Blancan 2	Early Pliocene	<i>Agkistrodon contortrix</i>	<i>Agkistrodon</i>
Kx-127	Blancan 2	Early Pliocene	<i>Thamnophis proximus</i>	<i>Thamnophis</i>
Kx-127	Blancan 2	Early Pliocene	<i>Thamnophis radix</i>	<i>Thamnophis</i>
Kx-127	Blancan 2	Early Pliocene	<i>Thamnophis sirtalis</i>	<i>Thamnophis</i>
Kx-127	Blancan 2	Early Pliocene	<i>Thamnophis</i> sp.	<i>Thamnophis</i>

**APPENDIX TABLE 2.** List of congeners used for climate enveloped models, grouped by genus.

<i>Charina</i>	<i>Lampropeltis</i>	<i>Pantherophis</i>	<i>Salvadora</i>	<i>Heterodon</i>	<i>Nerodia</i>
<i>Charina bottae</i>	<i>Lampropeltis calligaster</i>	<i>Pantherophis emoryi</i>	<i>Salvadora grahamiae</i>	<i>Heterodon nasicus</i>	<i>Nerodia cyclopion</i>
<i>Charina umbratica</i>	<i>Lampropeltis getula</i>	<i>Pantherophis obsoletus</i>	<i>Salvadora hexalepis</i>	<i>Heterodon platirhinos</i>	<i>Nerodia rhombifer</i>
	<i>Lampropeltis holbrooki</i>	<i>Pantherophis ramspotti</i>		<i>Heterodon simus</i>	<i>Nerodia sipedon</i>
	<i>Lampropeltis triangulum</i>				