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Early Oligocene (Whitneyan) snakes from Florida (USA), the second oldest colubrid snakes in the North America

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Abstract. A new genus and species, *Floridaophis auffenbergi*, and new species, *Nebraskophis oligocenicus*, of colubrid snakes are reported from the Early Oligocene (Whitneyan) I-75 Local Fauna (Florida Natural History Museum Locality AL018) near Gainesville, Alachua County, Florida, USA. The snakes represent only the second record of the family Colubridae from the Oligocene of North America and are the second oldest colubrid snakes known from the continent. *Floridaophis* is perhaps most similar to *Ameiseophis robinsoni* HOLMAN of the Early to Middle Miocene of North America. *Floridaophis* was a very small snake that is thought to have been a terrestrial species based on its relatively high neural spine. *Nebraskophis*, also a very small snake, was previously known only from the Middle to Late Miocene of Nebraska. It probably was fossorial or very secretive based on its obsolete neural spine. Both fossil snakes appear to be archaic genera with no known modern relatives. The presence of *Nebraskophis* in Florida suggests a connection to the continent during the Paleogene.

Key words: fossil snake, Early Oligocene, Colubridae, USA.

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I. INTRODUCTION

The earliest known North American snake of the Family Colubridae is *Texasophis galbreathi* HOLMAN, 1984, a small snake with a long, narrow vertebral form from the Early Oligocene (Orellan Age) of eastern Colorado. No other colubrid snakes have thus far been reported from the Oligocene of North America, although Miocene colubrids are relatively well known in the region (HOLMAN, 1979, 2000; PARMLEY and HOLMAN, 1995). Here, a new genus of colubrid snake with a short, wide vertebral form, and a new colubrid species of a previously named genus with a long, narrow vertebral forms are reported from the younger Early Oligocene (Whitneyan Age) of northern Florida.

The I-75 Site.– One of the most exciting discoveries in vertebrate paleontology in the southeastern United States in the second half of the 19th century was the discovery of a surprisingly diverse assemblage of Early Oligocene (Whitneyan) terrestrial vertebrates in northern Florida in 1965. The site (Fig. 1) was found during the contruction of Interstate Highway I-75 near Gainesville, Alachua County, Florida. Previous to this discovery, knowledge of pre-Miocene land mammals in the Gulf Coast of North America was based only on the recognition of titanotheres from the Eocene of Mississippi and Texas (GAZIN and SULLIVAN, 1942; PATTON, 1969).

The Florida Oligocene I-75 Local Fauna not only yielded an abundant mammalian fauna, but fishes, amphibians, reptiles, and birds were also collected there. Bones were first recognized from

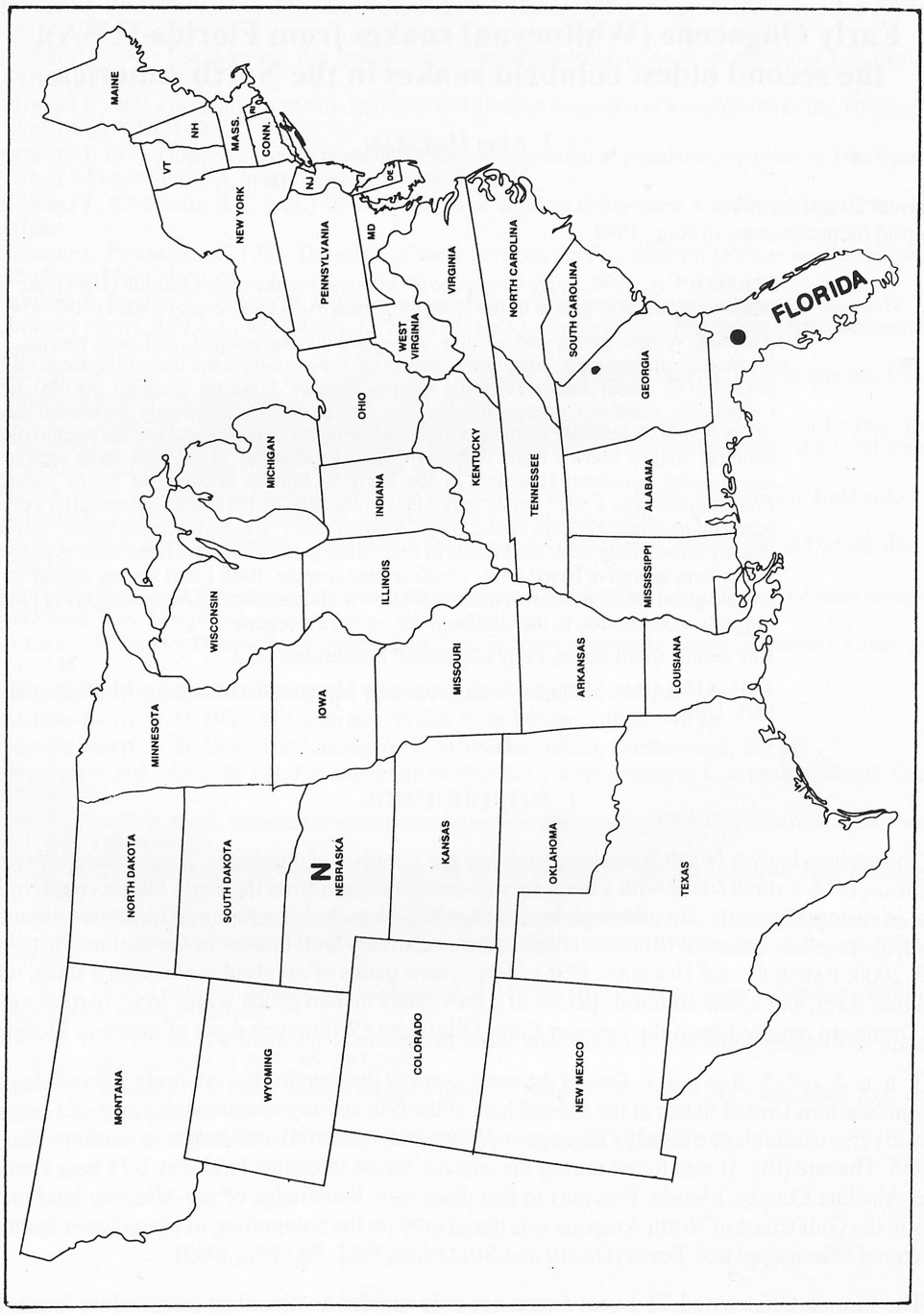

Fig. 1. Location of I-75 Local Fauna in Florida (closed circle) and state where *Nebraskophis* (large N) occurred in the Miocene.

the site in 1965 by Mervin KONTROVITZ of the University of Florida and a preliminary report on the fauna by PATTON (1969) followed.

The location of the fossil site (Florida Museum of Natural History Locality AL018) is in Alachua County, Florida, 1.5 km WSW of Gainesville, on the W side of I-75: Micanopy Quadrangle, NE1/4, Sec. 4, T10S, R19E. The fossil deposit was not detailed geologically by PATTON (1969), but it undoubtedly was a remnant of some type of a fill in the eroded Eocene limestone of the Crystal River Formation (Ocala Group). The deposit was reported to have been of extremely small size considering the wealth of fossil vertebrates that it produced (PATTON, 1969).

Both squaliform and rajiform cartilaginous fishes were collected at the site. Bony fishes were represented by sciaenid and tetradontiform species. Among the amphibia, the anuran genera *Bufo* and *Scaphiopus* were present, and salamanders were represented by generically undetermined sirenids.

Reptiles included turtles of the genus *Floridemys* and *Pseudemys* as well as the lizard genus *Peltosaurus*. Unidentified iguanid lizards were present and amphibaenids were possibly represented in the fauna. PATTON (1969) reported that snakes of the families Boidae and Colubridae occurred at the site, but none of the material was identified below the family level.

Birds were represented by assorted fragments. A diverse terrestrial mammalian fauna included didelphid marsupials; shrews; bats; leporid lagomorphs; cricetid, eomyid, heteromyid, and possibly eutypomyid rodents; possibly two carnivores; the perissodactyl *Mesohippus*; tayassuids; and two kinds of oreodonts.

During the paleogene the Florida limestone platform was alternately submerged, partially submerged, or ephemerely connected to the continent. The I-75 faunal assemblage was especially important in that it suggested that faunal connections between Florida and other biotic regions in North America, especially the Great Plains, were open from time to time in the Paleogene. Moreover, it was suggested that a large and remarkably varied terrestrial fauna was present during a time when such a fauna was thought by many to be composed of waning or relictual populations (PATTON, 1969).

A c k n o w l e d g e m e n t s. I would like to express my thanks to B. ALBRIGHT, M. S. FRANC and S. D. WEBB of the Florida Museum of Natural History for allowing me to study the I-75 Local Fauna Oligocene snakes. Rachael WALKER made the drawings of the snake vertebrae. I thank J. C. RAGE for suggestions that improved the manuscript and Z. SZYNDLAR for his editorial help.

II. SYSTEMATIC PALEONTOLOGY

The taxonomic nomenclature of the present paper follows that of RAGE (1984).

Class: Reptilia LAURENTI, 1768

Order Serpentes LINNAEUS, 1758

Suborder: Alethinophidia NOPCSA, 1923

Superfamily Colubroidea OPPEL, 1811

Family Colubridae, OPPEL, 1811

Subfamily Colubrinae, OPPEL, 1811

Genus *Floridaophis* gen. nov.

T y p e s p e c i e s: *Floridaophis auffenbergi*

E t y m o l o g y. The generic name refers to the state of Florida where the type specimen was collected.

D i a g n o s i s. The diagnosis is the same as for the type and only known species.

Floridaophis auffenbergi sp. nov.

Fig. 2

H o l o t y p e. A single trunk vertebra: Florida Natural History Museum Number 190884 collected by Florida Natural History Museum field parties between 1966 and 1967.

T y p e l o c a l i t y a n d h o r i z o n. I-75 Local Fauna (Florida Natural History Museum Locality AL018), 1.5 km WSW Gainesville, Alachua County, Florida. Early Oligocene (Whitneyan).

E t y m o l o g y. The species is named in recognition of the pioneering work on Florida fossil snakes done by Walter Auffenberg.

D i a g n o s i s. A small colubrid trunk vertebra that is wider (width through prezygapophyseal accessory processes) than long (length through anterior and posterior zygapophyses); neural arch vaulted; anterior edge of zygosphene sharply convex in dorsal view; neural spine well developed and thin, a little less than twice as long as high, anterior portion rising higher from neural arch than posterior portion; a distinct depression with a foramen in it occurs just posterior to the

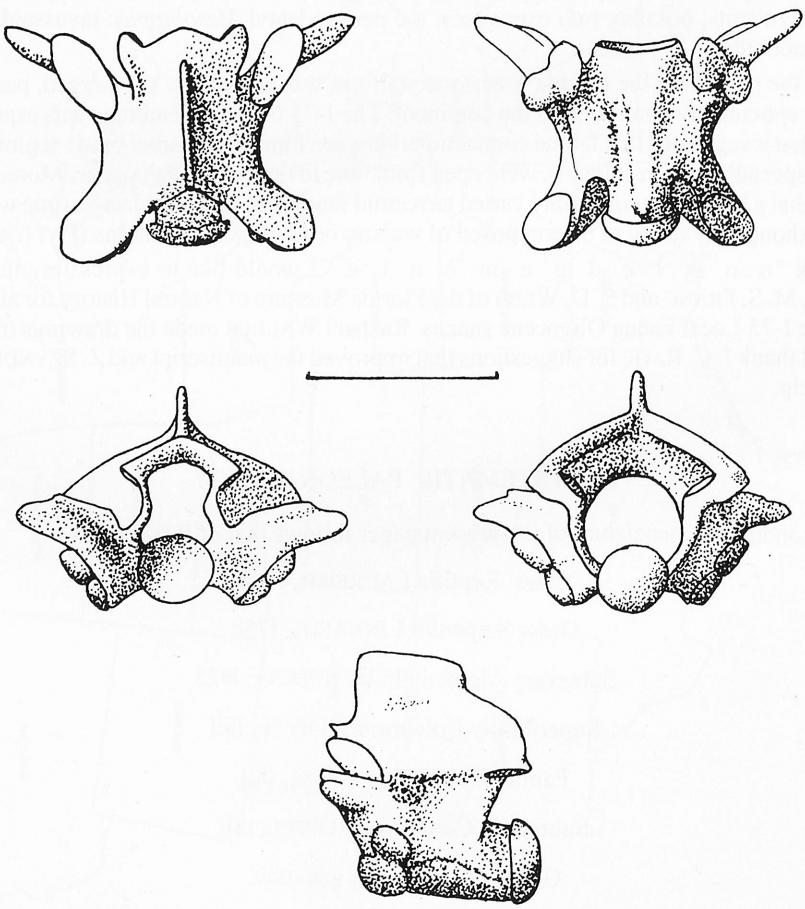

Fig. 2. Holotype trunk vertebra of *Floridaophis auffenbergi* gen. et sp. nov. from the I-75 Local Fauna (Early Oligocene, Whitneyan) of Alachua County, Florida (USA). Upper left, dorsal; upper right, ventral; middle left, anterior; middle right, posterior; bottom, lateral. The scale bar = 2.0 mm and applies to all figures.

prezygapophyses in lateral view; hemal keel well-defined from centrum, only moderately wide, tapering slowly from anterior to posterior to a narrowly rounded terminal end; subcentral grooves moderately well-developed; epizygapophyseal spines absent.

D e s c r i p t i o n. In dorsal view, the vertebra is wider than it is long. The prezygapophyseal accessory processes are well-developed and slightly shorter than the prezygapophyseal articular facets; they are relatively robust and are moderately pointed. The prezygapophyseal articular facets are ovaloid and oblique. The anterior edge of the zygosphene is sharply convex. The zygosphenal articular facets are strongly produced anteriorly. The neural spine is thin and extends from the posterior notch in the neural arch to well beyond the posterior level of the zygosphenal articular facets. The posterior notch in the neural arch is widely U-shaped. Epizygapophyseal spines are absent.

In ventral view, the centrum is slightly triangular in shape. The prezygapophyseal accessory processes are well-developed, relatively thick, and moderately pointed. The synapophyses are clearly divided into dorsal diapophyses and ventral parapophyses. The parapophyses project anterior to the diapophyses. The hemal keel is well-defined, only moderately thick, and well produced from the centrum. The hemal keel tapers gently from anterior to posterior and is narrowly rounded terminally. The subcentral grooves are moderately well developed. The postzygapophyseal articular facets are ovaloid.

In anterior view, the neural spine is well developed and thin. The zygosphene is convex dorsally. The neural canal is roundly eroded, constricted at its middle, and larger than the round and small cotyle. The prezygapophyseal articular facets are tilted slightly upward. The parapophyses are strong and produced ventrally to slightly below the level of the bottom of the cotyle. Moderately well-developed small depressions occur on either side of the cotyle, but it is not possible to determine whether they have paracotylar foramina within them or not due to the fact that the depressions are obscured by particles of adherent matrix.

In posterior view, the neural arch is vaulted. Some of the sidewall structure of the neural arch is broken on each side above the condyle, thus the shape of the neural canal is enlarged and obscured. The neural spine is thin. The zygantral articular facets are moderately tilted upward. The condyle is round. The synapophyses appear massive in this view.

In lateral view, the vertebra is about as long as it is high. The anterior part of the neural spine rises distinctly higher from the neural arch than does the posterior part. A distinct depression with a lateral foramen in it occurs just posterior to the prezygapophyses. The interzygapophyseal ridge is sharp and well developed. The synapophyses are distinctly divided into dorsal diapophyseal and ventral parapophyseal portions. The subcentral ridges are well developed and bowed strongly upward.

O t h e r m a t e r i a l. No other *Floridaophis* material is known.

R e m a r k s. The vertebra of *Floridaophis* clearly belongs in the family Colubridae on the basis of: (1) the lightly built vertebral structure; (2) the long, thin, relatively high neural spine; (3) the well-developed prezygapophyseal accessory processes; and (4) division of the synapophyses into very distinct diapophyseal and parapophyseal processes. The vertebra of *Floridaophis* is similar to the subfamily Colubrinae and differs from the subfamily Xenodontinae on the basis of its vaulted neural arch and the distinct, only moderately wide hemal keel. It differs from the subfamily Natricinae whose trunk vertebrae bear hypapophyses rather than hemal keels.

Floridaophis differs from the only other previously reported North American Oligocene colubrid snake, *Texasophis galbreathi* HOLMAN, 1984, on the basis of (1) having a short and wide rather than a long and narrow vertebral form, (2) having a higher neural spine, (3) having a more vaulted neural arch, and (4) having dorsally curved rather than straight subcentral ridges.

Floridaophis is perhaps most similar to the Early and Middle Miocene *Ameiseophis robinsoni* HOLMAN, 1976 which ranged from Wyoming to Delaware (HOLMAN, 1976, 1979, 1998). It is similar to *Ameiseophis* in the thin neural spine that is somewhat longer than high and rises higher from the

neural arch anteriorly than it does posteriorly. It is also similar to *Ameiseophis* in the moderately thick hemal keel that is quite distinct from the centrum. *Floridaophis* differs from *Ameiseophis* in having a shorter and wider vertebral form, a well developed depression with a foramen in it just posterior to the prezygapophyses in lateral view, less deep subcentral grooves, a dorsally curved subcentral ridge, and more massive synapophyses (compare Fig. 2 with HOLMAN, 1979, Fig. 20).

Texasophis galbreathi, the only other North American Oligocene colubrid previously identified, occurred in the Orellan Age which lasted from about 34 to about 32 million years ago. *Floridaophis auffenbergi* and the other snake of this report occurred in the Whitneyan Age which lasted from about 32 to 29.5 million years ago (PROTHERO et al., 1996).

It is generally believed that snakes with relatively high neural spines tend to be more terrestrial than those with very low or obsolete neural spines which tend to indicate secretive or fossorial species (HOLMAN, 2000). Based on this character, *Floridaophis* would appear to have been a more active, more terrestrial snake than *Texasophis galbreathi*, the only other North American Oligocene colubrid snake previously identified.

Nebraskophis oligocenicus sp. nov.

Fig. 3

H o l o t y p e. A single trunk vertebra: Florida Natural History Museum Number 190833 collected by Florida Natural History Museum field parties between 1966 and 1967.

T y p e l o c a l i t y a n d h o r i z o n. I-75 Local Fauna (Florida Natural History Museum Locality AL018), 1.5 km WSW Gainesville, Alachua County, Florida. Early Oligocene (Whitneyan).

D i a g n o s i s. A *Nebraskophis* that differs from the only other species in the genus, *Nebraskophis skinneri* HOLMAN, 1973 in having an even more obsolete neural spine with both its anterior and posterior borders sloping gently into the neural arch. The posterior part of the hemal keel flares somewhat at the level of the condyle, unlike *N. skinneri* where it remains about the same width. The condyle is oval and dorsoventrally depressed, unlike *N. skinneri* which has a round condyle.

D e s c r i p t i o n. In dorsal view, the vertebra is long and narrow. The anterior edge of the zygosphene is broken on the left side, but what remains on the right side indicates that it was convex. The prezygapophyseal articular facets are small and ovaloid in shape. Both facets are oriented obliquely to the long axis of the centrum. The right prezygapophyseal accessory process is missing, the left one is short and has a somewhat truncated end. The edges of the interzygapophyseal areas on both sides of the vertebra are shallowly concave. The neural spine in thin and begins just at the terminal point of the posterior notch in the neural arch and extends anteriorly to well beyond the posterior edge of the prezygapophyseal articular facet. The posterior notch in the neural arch is widely U-shaped.

In ventral view, the synapophyses are distinctly divided into diapophyseal and parapophyseal processes. The hemal keel is well-developed and distinct from the centrum. It is only moderately wide and very gradually increases in width until it flares somewhat near the condyle. The subcentral grooves are only moderately deep. The left postzygapophyseal articular facet is broken, the right one is ovaloid in shape.

In anterior view, the neural spine is obsolete. The top of the zygosphene is straight. The prezygapophyseal articular facets are tilted slightly upward. The neural canal is internally eroded and enlarged and constricted at its middle. The cotyle is depressed and oval. In posterior view, the neural arch is moderately vaulted. The loaf-of-bread shaped neural canal is larger than the oval, depressed condyle. The postzygapophyseal articular facets are tilted slightly upward.

In lateral view, the neural spine is very obsolete with both the anterior and posterior portions sloping gently into the neural arch. The interzygapophyseal ridge is well-developed, sharp, and

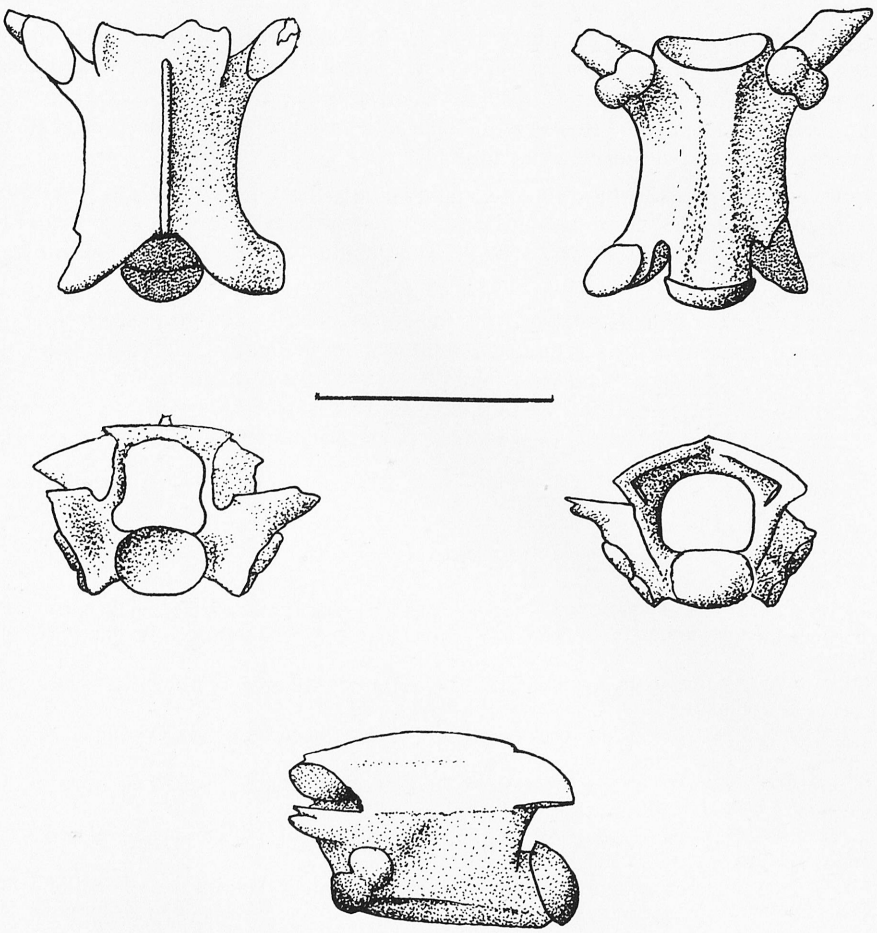

Fig. 3. Holotype trunk vertebra of *Nebraskophis oligocenicus* sp. nov. from the I-75 Local Fauna (Early Oligocene, Whitneyan) of Alachua County, Florida (USA). Upper left, dorsal; upper right, ventral; middle left, anterior;, middle right, posterior; bottom, lateral. The scale bar = 2.0 mm and applies to all figures.

straight. The condyle is slightly directed anteriorly. The subcentral ridges are straight. The zygosphenal articular facets are tilted slightly upward.

R e m a r k s. The vertebra is easily assigned to the genus *Nebraskophis* on the basis of (1) its elongate shape; (2) its obsolete neural spine; (3) its moderately vaulted neural arch; (4) its short prezygapophyseal accessory process; and (5) a well-developed, distinct hemal keel.

Nevertheless, even though the neutral canal is eroded, it appears to be quite large. This, correlated with the depressed condyle and cotyle, indicates that the vertebra belongs to a juvenile individual.

Previous to this record, *Nebraskophis* was known only on the basis of a single species, *N. skinneri*, from the Middle and Late Miocene of Nebraska (HOLMAN, 2000). *Nebraskophis* is a member of the subfamily Colubrinae (see HOLMAN, 1973, p. 131). Both species of *Nebraskophis* are small snakes that, based on their obsolete neural spines, were probably secretive or fossorial species. Differences between the two species are in the diagnosis above.

III. DISCUSSION

The two colubrid snakes reported here from the Early Oligocene (Whitneyan) of Florida are both very small forms. *Floridaophis auffenbergi* has a high neural spine and probably was terrestrial. *Nebraskophis oligocenicus* has an obsolete neural spine and probably was a secretive or fossorial taxon. Neither of these small snakes would appear to have had much of an ecological impact on the larger terrestrial biota of Florida at the time.

The presence of *Nebraskophis*, previously known only from the Middle and Late Miocene of Nebraska, would certainly speak to a connection between the Great Plains and Florida (see Fig. 1) in the Paleogene as suggested by PATTON (1969). The geographic affinites of *Floridaophis* are not known.

All of the Oligocene colubrid snakes from the North American Oligocene, *Floridaophis*, *Nebraskaophis*, and *Texasophis* are considered to represent the subfamily Colubrinae. Thus, the North American fossil record indicates that the colubrid xenodontine and natricine invasion into North America did not take place until Miocene times (see HOLMAN, 2000). All three of these genera probably represent archaic phylectic lines with no modern ancestors (see PARMLEY and HOLMAN, 1995).

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