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Early Oligocene (Whitneyan) snakes from Florida (USA): remaining boids, indeterminate colubroids, summary and discussion of the I-75 Local Fauna snakes.

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Abstract. In the third and final report on the snakes of the Early Oligocene (Whitneyan) I-75 Local Fauna near Gainesville, Florida, the remaining unstudied boids and colubroids are detailed and a summary and discussion of the entire snake fauna is given. The boid (subfamily undetermined) *Totlandophis americanus* sp. nov. is only the second named species of *Totlandophis*, a genus previously known only from the Upper Eocene of England. Two extinct erycine boids have North American Great Plains affinities. These are *Calamagras platyspondyla* HOLMAN and *Geringophis robustus* sp. nov. Three indeterminate fragmentary colubroid vertebrae exhibit characteristis at least superficially resembling those of the subfamily Natricinae of the Colubridae or the Elapidae, groups that are not known until the Miocene. A summary of the I-75 Local Fauna snake assemblage first presents a taxonomic checklist and then points out (1) the high taxonomic diversity of this assemblage compared to other North American Oligocene snake faunas, (2) the two endemic genera that are present, (3) a boid snake taxon with a possible Eurasian origin, (4) boid and colubrid taxa with North American Great Plains affinities, (5) the small size and probable secretive or fossorial nature of the I-75 Local Fauna snakes, and (6) the possible taxonomic affinities of the indeterminate colubroids.

Key words: Oligocene, boid, colubroid, snakes, USA

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I. INTRODUCTION

This is the third and final paper on the Early Oligocene snakes of the I-75 Local Fauna, near Gainesville in northern Peninsular Florida, USA. The first paper (HOLMAN, 1999) detailed two new genera of small colubrid snakes, representing the second oldest colubrids known from the New World. The second paper (HOLMAN and HARRISON, 2000) dealt with a unique new genus of boid snake with exceedingly dorsoventrally flattened vertebrae. The present paper documents the remaining boid and indeterminate colubroid snakes, as well as summarizing the I-75 Local Fauna snakes.

The I-75 Local Fauna, discussed in detail by HOLMAN (1999), yielded a quite diverse group of Early Oligocene (Whitneyan) vertebrates. The locality (see HOLMAN, 1999, fig. 1) was discovered during the contruction of Interstate Highway I-75 near Gainesville, Alachua County, Florida. The site represents the remains of a fissure fill in the Eocene limestone of the Crystal River Formation (Ocala Group). The deposit not only produced a large mammalian fauna, but yielded fishes, amphibians, reptiles, and birds (HOLMAN, 1999; PATTON, 1969). Faunal connections between the "Florida Island" and other biotic regions in North America, especially the Great Plains Region, were suggested by the I-75 Local Fauna (HOLMAN, 1999; PATTON, 1969).

A c k n o w l e d g e m e n t s. We express our thanks to B. ALBRIGHT, M. S. FRANC and S. D. WEBB of the Florida Museum of Natural History for allowing us to study the I-75 Local Fauna Oligocene snake material. D. HARRISON made the drawings of the fossil snakes figured in the present publication. We thank J-C RAGE for critically reviewing the manuscript.

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 Booidea GRAY, 1825

Family Boidae GRAY, 1825

Subfamily Indeterminate

Genus *Totlandophis* HOLMAN and HARRISON, 1998

Totlandophis americanus sp. nov.

Figs. 1-3

H o l o t y p e. A trunk vertebra: Florida Natural History Museum Number (UF) 190844 (Fig. 1) collected by Florida Natural History Museum field parties between 1966 and 1967.

P a r a t y p e s. Two trunk vertebrae: UF 190845 and 190870 (Figs. 2 and 3).

R e f e r r e d m a t e r i a l. Three trunk vertebrae: UF 190827, 190842 and 190846.

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 ALO18), 1.5 km WSW Gainesville, Alachua County, Florida.

Early Oligocene (Whitneyan).

E t y m o l o g y. The name reflects the fact that this is the only known American occurrence of a genus formerly known only from a single species (*Totlandophis thomasae* HOLMAN and HARRISON) from the Upper Eocene of Hampshire, England.

D i a g n o s i s. Similar to *Totlandophis thomasae* HOLMAN and HARRISON from the Upper Eocene "Rodent Bed" of the Hordle Site, Hampshire, England, but differs from this species in having the zygosphenal area not as distinctly upraised, the neural spine generally thicker and somewhat longer, the posterior border of the neural spine slightly less undercut, and the subcentral ridges less robust.

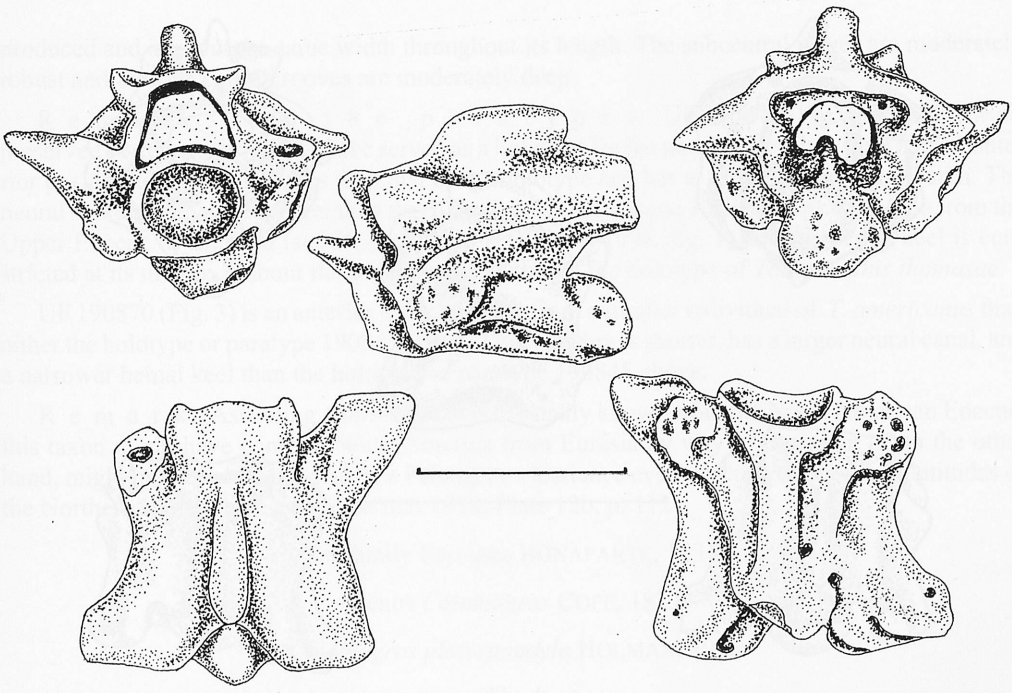

Fig. 1. Holotype trunk vertebra (UF 190844) of *Totlandophis americanus* sp. nov. from the I-75 Local Fauna (Early Oligocene, Whitneyan) of Alachua County, Florida (USA). Upper left, anterior; upper right, posterior; middle, lateral; lower left, dorsal; lower right, ventral. The scale bar = 3.0 mm and applies to all figures.

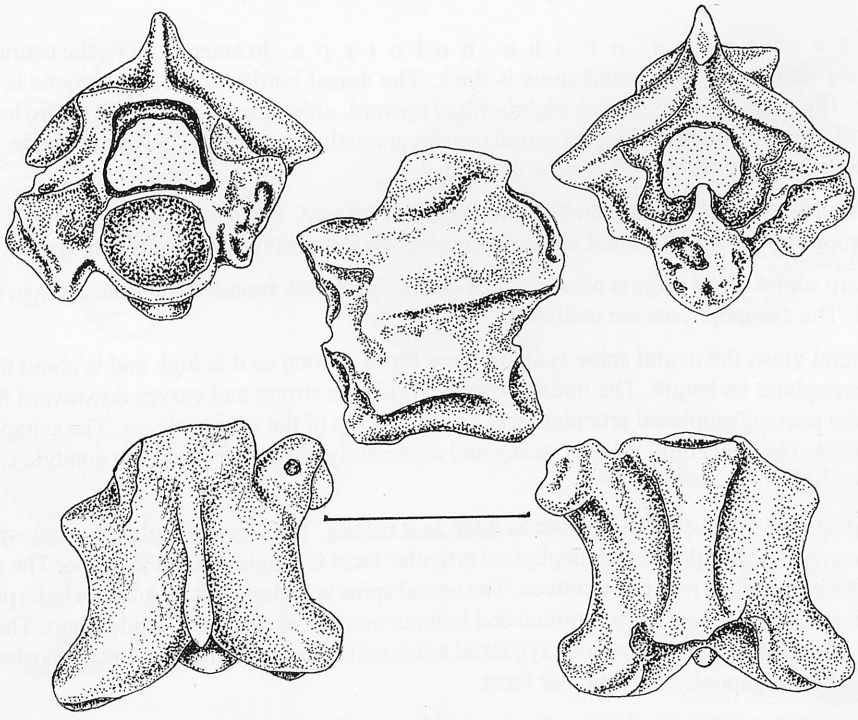

Fig. 2. Paratype trunk vertebra (UF 190845) of *Totlandophis americanus* sp. nov. from the I-75 Local Fauna (Early Oligocene, Whitneyan) of Alachua County, Florida (USA). Upper left, anterior; upper right, posterior; middle, lateral; lower left, dorsal; lower right, ventral. The scale bar = 3.0 mm and applies to all figures.

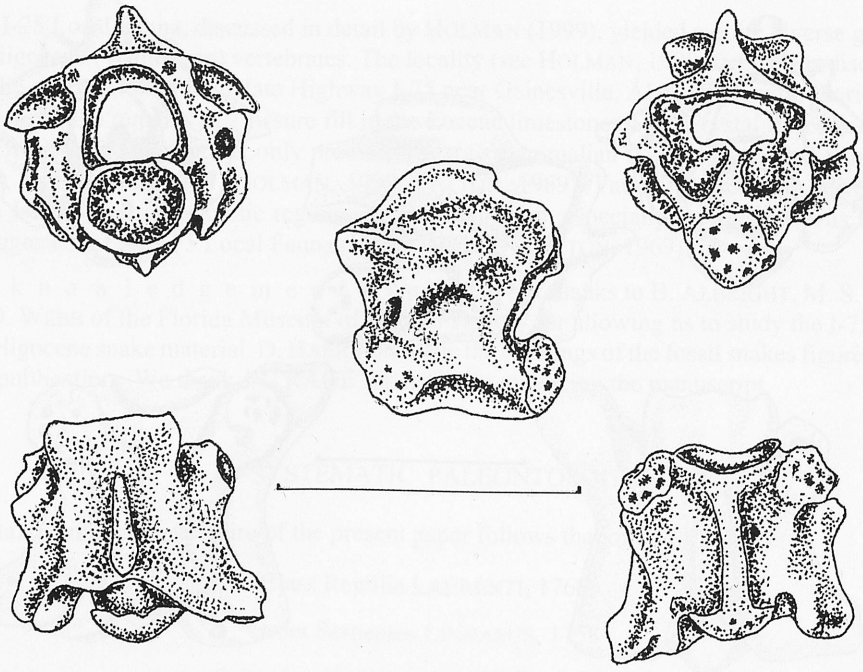

Fig. 3. Paratype trunk vertebra (UF 190870) of *Totlandophis americanus* sp. nov. from the I-75 Local Fauna (Early Oligocene, Whitneyan) of Alachua County, Florida (USA). Upper left, anterior; upper right, posterior; middle, lateral; lower left, dorsal; lower right, ventral. The scale bar = 3.0 mm and applies to all figures.

Description of the holotype. In anterior view, the neural arch is moderately depressed. The neural spine is thick. The dorsal border of the zygosphene is slightly concave. The prezygapophyses are slightly tilted upward, although the distal part of the left one is broken off. The loaf-of-bread shaped neural canal is about the same size as the round cotyle. The left synapophysis is eroded, the right one is undivided.

In posterior view, the neural arch is moderately depressed. The neural spine is thick. The right postzygapophysis is slightly tilted upward, whereas the left postzygapophysis is horizontal.

A sharp supracentral ridge is present. The condyle is roughly rounded and is larger than the neural canal. The synapophyses are undivided.

In lateral view, the neural spine is about three times as long as it is high and is about the same height throughout its length. The interzygosphenal ridge is strong and curves downward from the level of the postzygapophseal articular facet around the top of the synapophysis. The synapophysis is undivided. The subcentral ridge is strong and moderately bowed upward. The condyle is rotated anteroventrally.

In dorsal view, the vertebra is about as wide as it is long. The anterior end of the zygosphene is slightly convex. The right prezygapophyseal articular facet is roughly ovoid in shape. The anterior edge of the zygosphene is slightly convex. The neural spine is widest slightly anterior to its posterior end and tapers anteriorly until its terminal end is about one half as wide as its widest part. The neural spine originates at the apex of the interzygantral notch and extends slightly beyond the posterior end of the right prezygapophyseal articular facet.

In ventral view, the vertebra is about as wide as it is long. The synapophyses are roughly rounded. The centrum is roughly triangular in shape. The hemal keel is moderately wide, strongly

produced and is about the same width throughout its length. The subcentral ridges are moderately robust and the subcentral grooves are moderately deep.

R e m a r k s o n t h e p a r a t y p e s. UF 190845 (Fig. 2) is such a well-preserved vertebra that it could have served as a holotype for the new species. It is from a more anterior position on the trunk series than that of the holotype and has a more vaulted neural arch. The neural spine is somewhat higher than that of both the holotype and *Totlandophis thomasae* from the Upper Eocene of England (see HOLMAN and HARRISON 1998, fig. 1) and the hemal keel is constricted at its middle at about the same degree as that of the holotype of *Totlandophis thomasae*.

UF 190870 (Fig. 3) is an anterior trunk vertebra from a smaller individual of *T. americanus* than either the holotype or paratype 190845 above. This vertebra is shorter, has a larger neural canal, and a narrower hemal keel than the holotype or paratype 190845 above.

R e m a r k. Assuming *Totlandophis* is not really known from the North American Eocene, this taxon might have come to North America from Eurasia by way of Beringia; or on the other hand, might possibly be a product of a Paleogene vicariance event in the western upper latitudes of the Northern Hemisphere (see SANCHIZ, 1998, Plate 12b, p. 112).

Subfamily Erycinae BONAPARTE, 1831

Genus *Calamagras* COPE, 1873

Calamagras platyspondyla HOLMAN, 1976

Fig. 4

Calamagras platyspondyla, represented only by a single well-preserved vertebra UF 190830 (Fig. 4), has previously been reported only from the Late Oligocene of Nebraska and Wyoming and

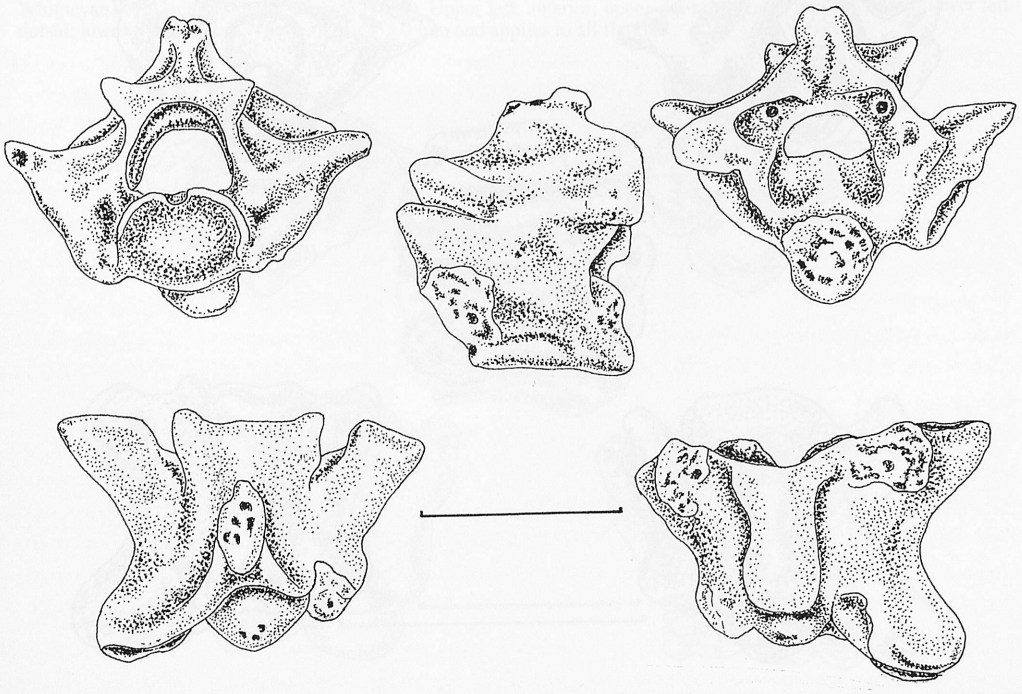

Fig. 4. Trunk vertebra (UF 190830) of *Calamagras platyspondyla* HOLMAN from the I-75 Local Fauna (Early Oligocene, Whitneyan) of Alachua County, Florida (USA). Upper left, anterior; upper right, posterior; middle, lateral; lower left, dorsal; lower right, ventral. The scale bar = 3.0 mm and applies to all figures.

has tentatively been reported from the Early Miocene of Nebraska (HOLMAN, 2000, pp. 64-65 and fig. 13). *Calamagras platyspondyla* is easily distinguished from other species in the genus by its much wider hemal keel. We can find no differences between the Florida Oligocene *Calamagras* and the western *C. platyspondyla*. This is yet another western snake taxon in this Early Oligocene Florida fauna.

Calamagras floridanus AUFFENBERG, 1963 from the Early Miocene (Early Hemingfordian) of the Thomas Farm Locality of Gilchrist County, Florida, differs from *C. platyspondyla* in having a narrow, gladiate-shaped hemal keel and a neural spine with its posterior border straight rather than undercut (see HOLMAN, 2000, fig. 31).

Genus *Geringophis* HOLMAN, 1976

Geringophis robustus sp. nov.

Figs. 5-7

H o l o t y p e. A trunk vertebra: Florida Natural History Museum (UF) 190837 (Fig. 5) collected by Florida Natural History Museum field parties between 1966 and 1967.

P a r a t y p e s. Two trunk vertebrae UF 190847 and 190848 (Figs. 6 and 7) both collected by Florida Natural History Museum field parties between 1966 and 1967.

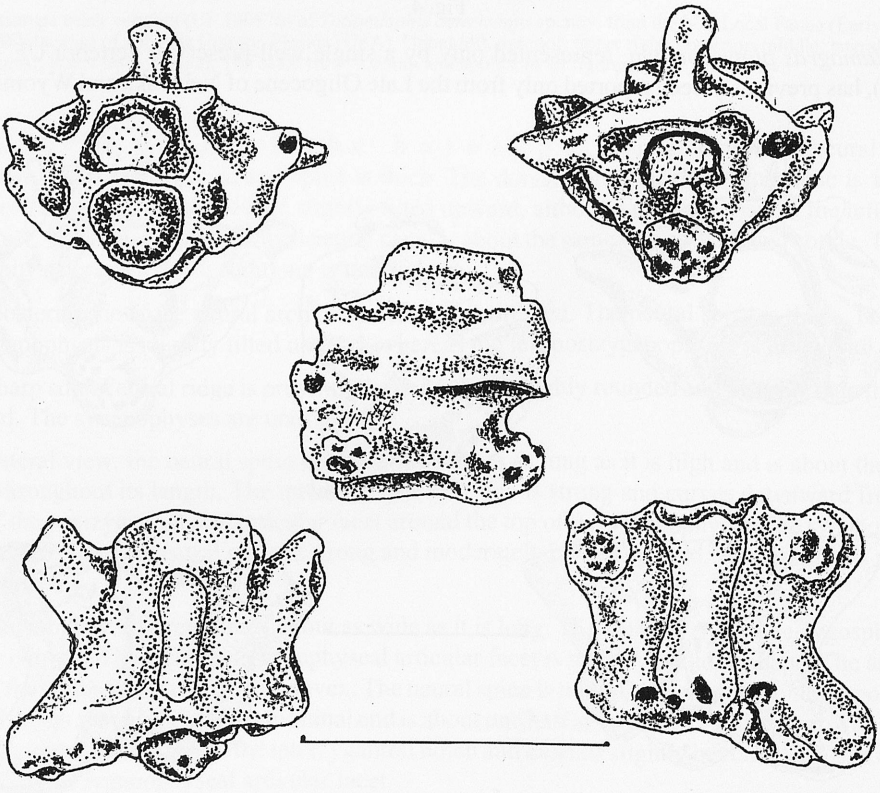

Fig. 5. Holotype trunk vertebra (UF 190837) of *Geringophis robustus* sp. nov. from the I-75 Local Fauna (Early Oligocene, Whitneyan) of Alachua County, Florida (USA). Upper left, anterior; upper right, posterior; middle, lateral; lower left, dorsal; lower right, ventral. The scale bar = 3.0 mm and applies to all figures.

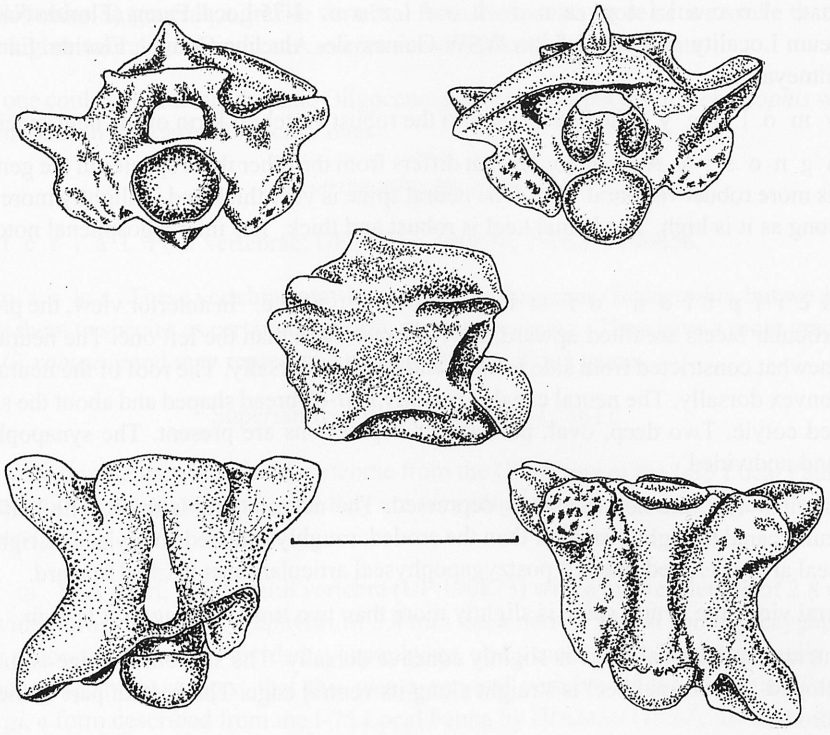

Fig. 6. Paratype trunk vertebra (UF 190847) of *Geringophis robustus* sp. nov. from the I-75 Local Fauna (Early Oligocene, Whitneyan) of Alachua County, Florida (USA). Upper left, anterior; upper right, posterior; middle, lateral; lower left dorsal; lower right, ventral. The scale bar = 3.0 mm and applies to all figures.

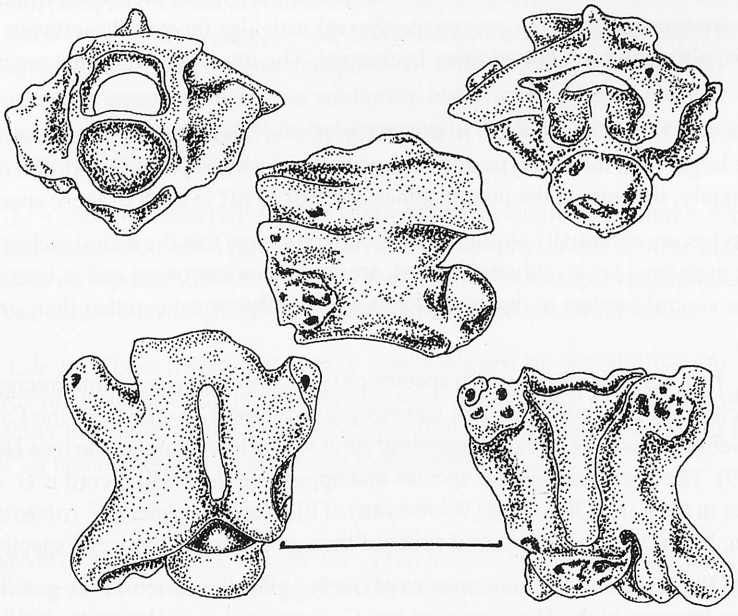

Fig. 7. Paratype trunk vertebra (UF 190848) of *Geringophis robustus* sp. nov. from the I-75 Local Fauna (Early Oligocene, Whitneyan) of Alachua County, Florida (USA). Upper left, anterior; upper right, posterior; middle, lateral; lower left, dorsal; lower right , ventral. The scale bar = 3.0 mm and applies to all figures.

Type locality and horizon. I-75 Local Fauna (Florida Natural History Museum Locality AL018), 1.5 km WSW Gainesvile, Alachua County, Florida. Early Oligocene (Whitneyan).

Etymology. The name refers to the robust vertebral form of the new species.

Diagnosis. A *Geringophis* that differs from the other three species in the genus on the basis of its more robust vertebral form. The neural spine is very thick and is slightly more than two times as long as it is high. The hemal keel is robust and thick. The interzygosphenal notch is very shallow.

Description of the holotype. In anterior view, the prezygapophyseal articular facets are tilted upward, the right one more than the left one. The neural spine is thick, somewhat constricted from side to side, and swollen dorsally. The roof of the neural canal is slightly convex dorsally. The neural canal is roughly loaf-of-bread shaped and about the size of the subrounded cotyle. Two deep, oval, paracotylar depressions are present. The synapophyses are massive and undivided.

In posterior view, the neural arch is depressed. The neural spine is thick. The loaf-of-bread shaped neural canal is slightly smaller than the eroded, roughly rounded condyle. The right postzygapophyseal area is eroded, the left postzygapophyseal articular facet is tilted upward.

In lateral view, the neural spine is slightly more than two times as long as it is high.

The interzygapophyseal ridge is slightly concave dorsally. The subcentral ridge is moderately well-developed. The hemal keel is straight along its ventral edge. The bottom part of the synapophysis is eroded.

In dorsal view, the anterior edge of the zygosphene is moderately convex. The prezygapophyses are directed anterolaterally. The neural spine is thick and slightly constricted in its posterior half. It extends from a little beyond the end of the dorsal roof of the apex of the zygosphenal notch to well beyond the posterior edges of the prezygapophyseal articular facets. These facets are generally ovoid in shape, although each one of them is chipped. The interzygapophyseal notch is very shallow.

Comments on the paratypes. The paratype specimens (Figs. 6 and 7) are somewhat larger than the holotype and may come from a more posterior portion of the trunk series. Unfortunately, the tops of the neural spines are broken off in each of these specimens.

Both paratypes are essentially similar to the holotype except that the neural arches are somewhat more vaulted; the hemal keels, although robust, are somewhat narrower; and in lateral view in both specimens, the ventral borders of the hemal keels are slightly concave, rather than straight as in the holotype.

Remarks. In the four known species of *Geringophis* we see some interesting trends in vertebral structure. In the earliest known *Geringophis* species, *G. vetus* from the Early Oligocene (Orellan) of Nebraska, we see a gracile vertebral form with a low neural spine (see HOLMAN, 2000, figs. 38 and 39). The next *Geringophis* species that appears in the fossil record is *G. robustus* from somewhat later in the Early Oligocene (Whitneyan) of Florida (this paper). *G. robustus* has a robust vertebral form, but retains the low neural spine of the earlier Early Oligocene species.

In the Late Oligocene and Miocene species of *Geringophis* the vertebrae are gracile and the neural spines have become high. These species are *G. depressus* (see HOLMAN, 2000, fig. 37) first known from the Late Oligocene (Early Arikareean) of Nebraska and Wyoming and continuing on into the Miocene and *G. yatkolai* (see HOLMAN, 2000, fig. 40) from the Early Miocene (Hemingfor-

dian) of Nebraska. In general, a gracile vertebral form indicates a more active snake than a robust one and a higher neural spine indicates a more active snake than a lower one.

Thus, one could suggest that the Late Oligocene and Miocene species of *Geringophis* were more active animals than the Early Oligocene ones.

Geringophis sp. indet.

M a t e r i a l. Four vertebrae: UF 16737, 190838, 190850, 190856.

R e m a r k s. These vertebrae may be assigned to the genus *Geringophis*, but we are unable to identify them to species as certain diagnostic parts are missing. They have a more gracile structure than *G. robustus* and may represent a second species of this genus.

Superfamily Colubroidea OPPEL, 1811

Three very fragmentary colubroid vertebrae from the Oligocene of the I-75 Local Fauna cannot be assigned with certainty to family, but they are very important from a zoogeographic and evolutionary standpoint.

F o r m 1. A short, lightly built vertebra (UF 190873) with a greatest length of 2.8 mm and a greatest width through the prezygaphyses of 3.4 mm has a narrow neural spine, prezygapophyseal accessory processes, distinctly divided synapophyses, and a moderately long, terminally blunt hypapophyses. One might suggest that this was a cervical vertebra of the colubrid *Floridaophis auffenbergi*, a form described from the I-75 Local Fauna by HOLMAN (1999), although there is the possibility it could be a cervical of the family Elapidae.

F o r m 2. A moderately elongate vertebra (UF 16886) with a greatest length of 4.1 mm, but unfortunately with many of the vertebral structures dorsal to the centrum missing, has a lightly built form, remnants of a broken prezygapophyseal accessory process on the left prezygapophysis, divided synapophyses, and a thin, elongate hypapophysis that is broken off terminally. It is possible that this vertebra might represent either the subfamily Natricinae of the Colubridae or the family Elapidae, although both of these families do not appear until the Miocene in other fossil localities in North America (see HOLMAN, 2000).

F o r m 3. A short vertebra (UF 190885) with a greatest length of 2.8 mm is very eroded, but has a very vaulted neural arch and a proximal part of a hypapophysis that is more than half as wide as the condyle. The right postzygapophysis bears a small, but distinct epizygapophyseal spine. This specimen is taken to be a cervical vertebra from an unidentified colubroid taxon.

R e m a r k s. These fragmentary snake fossils suggest the possibility of an earlier origin than the Miocene in North America of the Elapidae or of the subfamily Natricinae of the Colubridae. The possibility that these groups could have occurred first in North America in the Paleogene "Florida Island" is tantalizing, but awaits much more fossil evidence.

III. SUMMARY AND DISCUSSION OF THE I-75 EARLY OLIGOCENE SNAKE FAUNA

The Early Oligocene (Whitneyan) snakes from the I-75 Local Fauna, Alachua County, Florida consists of the following taxa:

Superfamily Booidea

Boidae (subfamily indeterminate)

Conantophis alachuaensis

Totlandophis americanus sp. nov.

Boidae (subfamily Erycinae)

Calamagras platyspondyla

Geringophis robustus sp. nov.

Geringophis sp. Indet.

Superfamily Colubroidea

Colubroidea indeterminate (elapids? natricines?)

Colubridae (subfamily Colubrinae)

Floridaophis auffenbergi

Nebraskophis oligocenicus

The I-75 vertebrate fauna is especially important because it suggests Paleogene faunal connections existed between the sometimes isolated "Florida Island" and other biotic regions in North America, especially the Great Plains; and because it suggests a richer assemblage of vertebrates existed than would be expected during this time in the Oligocene (PATTON, 1969). The snakes of the I-75 Local Fauna support both of these suggestions, as well as being important in other ways.

Island Endemics

Conantophis alachuaensis, a small boid from the I-75 Local Fauna, has exceedingly flattened vertebrae with the posterior trunk vertebrae being completely flat across the top (see HOLMAN and HARRISON, 2000, fig. 4). This condition appears to be unique among all snakes. These flat vertebrae also have odd short, blunt hypapophyses that are just slightly narrower than the condyle. Small boids in the subfamily Erycinae tend to have depressed neural arches, but none are as flattened as those in *Conantophis*, and as far as we are aware, the blunt hypapophyses are absent.

One may suggest that *Conantophis* is an "island specialty" that evolved in isolation on the "Florida Island" from some unknown boid ancestor with a well-depressed vertebral neural arch. It is somewhat difficult to suggest the adaption associated with such an odd vertebral morphology. One might speculate that this small snake was able to squeeze into very thin cracks in order to find shelter or prey. Also, one could suggest such a morphology might be associated with flattening for thermoregulation or even for the intimidation of predators.

Floridaophis auffenbergi, a very small snake about 349 mm (about 13 and l/2 inches long) has vertebrae that are generically diagnostic, but that are not in any way bizarre in shape like those of *Conantophis*. *Floridaophis* is one of the at least three I-75 Local Fauna snakes that represent the second oldest colubrid snakes known from the New World (HOLMAN, 1999). *Floridaophis* appears to be restricted only to the I-75 Local Fauna and has no known living relative, thus it may also be considered to be a dead-end island endemic.

The USA Great Plains Connection

Several mammalian species recovered from the I-75 Local Fauna indicate a Great Plains connection with the "Florida Island" in the Paleogene (PATTON, 1969). The same is true of the snakes. Two I-75 snake genera previously known only from the Oligocene/and or Miocene of the Great Plains are *Geringophis*, a boid and *Nebraskophis*, a colubrid (HOLMAN 2000). *Calamagras platyspondyla*, a boid species of the I-75 fauna, has previously been reported only from the Late Oligocene of Nebraska and Wyoming and has tentatively been reported from the Early Miocene of Nebraska (HOLMAN, 2000).

The Eurasian Connection

Boid snakes are thought to have first reached North America from South America (HOLMAN, 2000). But one I-75 Local Fauna boid snake, namely *Totlandophis* (previously known only from a single Late Eocene record from England), could possibly have moved from western Europe through Asia and Beringia into North America. On the other hand, the presence of *Totlandophis* in North America might have been the product of a Paleogene vicariance event in the upper western latitudes of the Northern Hemisphere. Either one of these suggestions, of course, assumes that *Totlandophis* did not actually exist in the Eocene of North America..

The family Colubridae appeared in the fossil record in the form of vertebrae from the Late Eocene of southern peninsular Thailand (RAGE et al., 1992). Colubrids spread from this Asian center of origin to the Arabian Peninsula, Western Europe and North America (RAGE, 1988). The first New World colubrid snake, *Texasophis galbreathi*, was described from the Early Oligocene (Orellan) of Colorado (HOLMAN, 1984). *Floridaophis auffenbergi* and *Nebraskophis oligocenicus* from the I-75 Local Fauna of Florida are the second oldest New World colubrids and occurred a little later (Whitneyan) in the Early Oligocene. All three of these snakes are thought to have arrived from Eurasia via Beringia and are in the Colubrid subfamily Colubrinae (in the broad sense of HOLMAN, 2000). The other colubrid subfamilies did not arrive in North America until the Miocene (HOLMAN, 2000).

Paleoecology

Oligocene snake faunas in North America are taxonomically poor (HOLMAN, 2000), thus the I-75 Local Fauna with 4 boid and 2 colubrid genera is unexpectedly varied. Nevertheless, all of the I-75 snakes are of small or very small size, and could be considered as an ecologically insignificant component of the fauna compared to modern snake assemblages in the southeastern United States. Based on vertebral size (see scale bars on figures in HOLMAN, 1999; HOLMAN and HARRISON, 2000; and the present paper). *Totlandophis americanus* and *Calamagras platyspondyla* would have been species large enough to have eaten small reptiles and the young of small rodents. The other snake species would have probably mainly fed upon invertebrates and possibly some very small vertebrates such as very small anurans or newborn individuals of other snakes. Because of their small size, most of the I-75 fauna snakes would probably have been secretive or even fossorial.

The Provocative Indeterminate Colubroids

Elapid and natricine snakes have not been reported before the Miocene in North America (HOLMAN, 2000), thus some fragmentary indeterminate colubroid vertebrae from the I-75 Local Fauna are of much interest. A short, lightly built colubroid vertebra with a hypapophysis may represent a cervical of the colubrid *Floridaophis auffenbergi*, but there is the possibility it could represent a cervical of a of the family Elapidae. A more elongate colubroid vertebra with a relatively thin hy-

papophysis may possibly represent either the subfamily Natricinae of the family Colubridae or the Elapidae. A third vertebra is short, has a vaulted neural arch, the remnants of thick hypapophysis, and a small, but distinct epizygapophyseal spine. This vertebra is taken to represent the cervical vertebra of an unidentified colubroid taxon.

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