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THE SQUAMATE REPTILES OF THE INGLIS IA FAUNA
(IRVINGTONIAN: CITRUS COUNTY, FLORIDA)

PETER A. MEYLAN



UNIVERSITY OF FLORIDA

GAINESVILLE

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THE SQUAMATE REPTILES OF THE INGLIS IA FAUNA (IRVINGTONIAN: CITRUS COUNTY, FLORIDA)

PETER A. MEYLAN¹

ABSTRACT: The early Pleistocene Inglis IA site has yielded the largest and most diverse sample of fossil squamates in eastern North America. About 4000 specimens, including 250 skull elements, represent 26 species of snakes, 4 species of lizards, and 1 amphisbaenian. The herpetofauna is essentially modern; 21 of 26 snake species, 2 of 4 lizard species, and the amphisbaenian survive in Florida today. Three Inglis IA snakes now extinct are *Diadophis elinorae*, *Xenodontinae* (cf. *Dryinoides*), and *Regina intermedia* (n. sp.). The extant species *Opheodrys vernalis* and *Heterodon nasicus* are present in the Inglis IA fauna and have apparently been replaced in Florida by *Opheodrys aestivus* and *Heterodon simus*. The lizards include *Ophisaurus ventralis*, *Sceloporus undulatus*, *Gerrhonotus*, and an extinct new species, *Eumeces carri*. The amphisbaenian is *Rhineura* cf. *R. floridana*.

The ecological requirements of modern counterparts of the fauna suggest that Inglis IA represents a community from a region of high pine with xeric hammock interspersed. This open high pine country was part of a savanna that extended around the Gulf of Mexico during the late Cenozoic. The savanna apparently served as a corridor for mammals going to and from South America, but it did not act in the same capacity for the squamate fauna, which remained essentially autochthonous. The composition of the squamate fauna suggests that this corridor maintained a connection to the west that had previously existed farther north.

SUMARIO: El sitio denominado Inglis IA correspondiente al temprano Pleistoceno ha dejado la más grande y más diversificada muestra de fósiles de reptiles en el Este de Norte América. Cerca de 4000 muestras, incluyendo 250 elementos de cráneo, representan 26 especies de serpientes, 4 especies de lagartijas y 1 especie de anfisbaenido. La herpetofauna es esencialmente moderna: 21 de las 26 especies de serpientes, 2 de las 4 especies de lagartijas y el único anfisbaenido son los sobrevivientes actualmente presentes en Florida. Las tres especies de serpientes extintas pertenecientes al sitio Inglis IA son *Diadophis elinorae*, *Xenodontinae* (cf. *Dryinoides*), y *Regina intermedia* (n. sp.). *Opheodrys vernalis* y *Heterodon nasicus* son especies existentes que están presentes en la fauna del Inglis IA pero que aparentemente, en Florida, han sido reemplazadas por *Opheodrys aestivus* y *Heterodon simus*. Las especies de lagartijas incluyen *Ophisaurus ventralis*, *Sceloporus undulatus*, *Gerrhonotus* sp., y una nueva especie extinta, *Eumeces carri*.

Los requerimientos ecológicos de la presente fauna sugiere que sus antepasados en el Inglis IA representaron una comunidad de región de pino alto intercalada con formaciones xerofíticas de "hammock." Esta área abierta con pinos altos constituyó parte de savana que se extendió alrededor del Golfo de México durante el tardío Cenozoico. Esta savana aparentemente sirvió como corredor para el paso de mamíferos hacia y desde Sur América, pero no actuó con la misma eficacia para los reptiles, los cuales permanecieron esencialmente como autóctonos. La composición de la fauna de reptiles sugiere que este corredor, que previamente había existido más hacia el norte, mantuvo conexión con el Oeste.

¹The author is a Laboratory Technologist in Herpetology, Florida State Museum, and a graduate student in the Department of Zoology, both at the University of Florida, Gainesville 32611. This paper was originally submitted in partial fulfillment for the degree of Master of Science at the University of Florida.

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INTRODUCTION

Studies of fossil squamates in North America have focused largely on two general geographic regions, the High Plains and Florida. Work by Estes, Holman, and others has documented the rich fossil history for squamates in the High Plains states. Although Florida's fossil squamates received much attention during the 1950's and 1960's (Brattstrom 1953; Auffenberg 1955, 1956, 1963; Holman 1958, 1959a, 1959b, 1962; Gut and Ray 1963; Estes 1963), most of the material excavated in the last 15 years has not been described. Unreported fossil squamates are present in at least 8 localities: 1 Oligocene, 6 Miocene, and 1 early Pleistocene (Inglis IA). Of these, Inglis IA (a sinkhole in Citrus County, Florida) has the largest squamate fauna. Biostratigraphic correlations place it in the early Pleistocene (earliest Irvingtonian) (Webb 1974).

When Auffenberg (1963) made his major survey of fossil snakes in Florida, no early Pleistocene sites were known. He recognized the potential value of an early Pleistocene site to the study of Florida's paleoherpetology, and his work showed that the modernization of Florida's snake fauna occurred between the middle Pliocene and middle Pleistocene. The Inglis fauna documents these final steps in the evolution of Florida's snakes and lizards.

Inglis IA is a rich fauna, with over 4000 elements that represent 31 squamate species. This is the largest sample of Squamata known from Florida. The fauna's large size makes it suitable for paleoecological interpretation and allows determination of the zoogeographical affinities of southeastern squamates in the earliest Pleistocene. Furthermore, the Inglis IA fauna contributes to our knowledge of the evolutionary history of 31 taxa.

Inglis IA was discovered by Jean Klein and Robert Martin in 1967, when excavations for the Cross Florida Barge Canal exposed it. After several small collections were made in intervening years, the site was collected in its entirety in 1974. The following description is based primarily on Klein's (1971) account.

The site was exposed on the north bank of the now defunct Cross Florida Barge Canal in Section 8, R.16 E., T.17 S., Citrus County, Florida. The deposit occurred in a sinkhole in the Inglis member of the Ocala Group (or more simply called Ocala limestones) (late Eocene). The fauna accumulated in locally derived clastic sediments, which occupied a volume about 10 m by 20 m and 3 to 4 m deep. In January 1974, approximately 300 cubic meters of fossiliferous sands were removed. The sands were washed through screens at the site and the recovered fossils taken to the Florida State Museum for study.

Klein (1971) recognized six stratigraphic units within the sinkhole.

The lowest, termed the basal conglomerate, included a large quantity of bone fragments, many of which were waterworn and polished. He attributed the wear to the action of waters of a spring boil (see Paleocology). The next four units varied from 1 to 2 m thick. They filled the bulk of the sinkhole and contained the majority of the fossils. Klein said the sediments were deposited during periods of high and low water tables. During high water low energy deposition within the sinkhole produced the deposition of clays, and during a lowered water table sand rapidly accumulated. The entire sequence was capped by a cemented silica sandstone.

Problems in determining the age of Florida's sinkhole faunas are discussed by Webb (1974). The absence of physical stratigraphic control is the major drawback. Because fossils accumulate as isolated deposits in sinkholes and caves, deposits of differing ages can occupy adjacent sinkholes in the same formation. Thus, superpositional data are not available and correlations of their contained faunas must be based wholly on biostratigraphic methods.

In his review of the chronological framework for the Florida Pleistocene, Webb (1974) cited 11 important biostratigraphic indicator lineages, seven of which assist in determining the age of the Inglis IA fauna.

The record of the cotton rat (*Sigmodon*) is perhaps the most valuable. *Sigmodon curtisi*, the most common cricetine rodent in the fauna, is known from late Blancan or early Irvingtonian sites in the American West, including the Curtis Ranch Fauna of Arizona, the Kentuck Fauna of Kansas, and the Vallecito sequence in California (Martin 1979).

Smilodon gracilis, a sabercat present in the Inglis fauna, first appears in the late Blancan or early Irvingtonian of North America. By the late Irvingtonian it is replaced by *Smilodon fatalis* (Webb 1974).

Members of the armadillo lineage *Kraglievichia* to *Chlamytherium* increase in size from the Blancan through the Rancholabrean (Robertson 1976). The Inglis IA chlamythere is intermediate in size between late Blancan *Kraglievichia* and Irvingtonian and Rancholabrean *Chlamytherium septentrionalis*.

The presence of *Hemiauchenia* rather than *Palaeolama* and of *Platygonus bicalcaratus* rather than *Platygonus cumberlandensis* in the Inglis fauna suggests a late Blancan or early Irvingtonian age (Webb 1974). The absence of *Bison* is further evidence that Inglis IA is pre-Rancholabrean.

The freshwater turtle *Pseudemys* is the only reptile that helped date Inglis IA. This genus was examined in detail by Klein (1971), who

determined that the Inglis IA *Pseudemys* was a morphological intergrade between the Blacan *Pseudemys platymarginata* and Irvingtonian *Pseudemys scripta petrolei*. Fossil squamates are too poorly known to be of any help in determining the age of Inglis IA.

Based on the lineages discussed above, Webb (1974) placed the Inglis IA fauna in the earliest Irvingtonian. In particular the fauna from Inglis IA closely resembles that from Curtis Ranch in Arizona, which has been dated at 1.9 million years old.

ACKNOWLEDGEMENTS

The motivation to study fossil squamates and the guidance to see the study through have been provided by Walter Auffenberg. David Webb and Ron Wolff have also advised me, especially in the preparation of this thesis. To them I extend my thanks. Bruce J. MacFadden, Robert Sullivan, J. Alan Holman, and Rhoda J. Bryant also provided comments that improved this contribution.

A number of people helped with specific aspects of this study and deserve recognition and thanks. Tom Van Devender, Richard Zweifel (AMNH), and George Zug (USNM) provided comparative material. Pat Srygley and Howard Kochman helped me with the use of packaged computer programs. Computing was done at the Northeast Regional Data Center of the State University System of Florida, located on the campus of the University of Florida in Gainesville. Ron Wolff and Donna Born Drake provided equipment and advice for the preparation of the included photographs. Esta Belcher prepared Figures 1, 3, 6, 9, 13, 14, and 15. Angela O'Brien and Kelly Howard cheerfully typed the final draft. Special thanks go to all of the people who have helped to assemble the Florida State Museum Herpetological Skeleton Collection, without which this study would have taken much longer.

My wife, Anne, provided endless encouragement and instruction in good English. She diverted time from her own studies to type the first draft of this thesis.

METHODS AND ABBREVIATIONS

IDENTIFICATION. — Most of the material reported here was identified by direct comparison or univariate statistics (student's *t*-test). Diagnostic characters reported in the literature were used when possible. Additional distinguishing features were determined from a large sample of comparative osteological material of lizards (Appendix 1) and snakes (Appendix 2).

Multivariate statistical programs were found to be appropriate for identifying isolated vertebrae. Discriminate analysis was used to distinguish the vertebrae of snake species that show extreme similarity in vertebral form.

Ratios of pairs of linear measurements from single vertebrae were used as the discriminating variables in the analyses. The use of ratios in multivariate statistical analysis has been questioned by Atchley et al. (1976) and requires justification. Ratios are used to remove the effect of individual vertebra size, and their employment has become standard in studies of snake vertebrae (Johnson 1955; Auffenberg 1963). However, there are some statistical consequences of combining two variables to produce a third stemming largely from changes in coefficients of variation (CV) of the denominator variable (Atchley et al. 1976). In the present study such effects were minimized by using variables with approximately equal coefficients of variation.

Heyer (1978) justified the use of ratios in a study of leptodactylid frogs by comparing results from analyses using ratios and linear measurements. In the present study, test comparisons of analyses using ratios and linear measurements produced similar results for two analyses, and better results using ratios in a third (Table 1).

Table 1. — Results of discriminant analysis using measurements and ratios as variables. (Poor discrimination is indicated by a higher percentage of reclassification.)

Analysis	Percentage of Reclassification	
	With Ratios	With Measurements
<i>Elaphe</i> (2 species)	10.6	9.6
"Racers" (3 species)	8.8	7.4
Vipers (4 species)	10.1	24.3

Two types of analyses were used to maximize the information obtained from the discriminant analysis. The Statistical Analysis System (Barr et al. 1976) was used to identify the fossils because it includes a simple test data statement that automatically classifies unknowns. It also produced less reclassification than a similar stepwise BMDP analysis (Dixon and Brown 1979). The BMDP analysis was used to provide information on the relative importance of each of the variables used in the analysis.

TERMINOLOGY. — Terminology of snake bones follows: vertebrae, Auffenberg (1963); skulls, Bullock and Tanner (1966); compound and basiparasphenoid, Estes et al. (1970); basiparasphenoid, Underwood (1967); and compound and palatine, Marx and Rabb (1972). Lizard bone terminology follows: vertebrae, Auffenberg (1963); and skull, Oelrich (1956) and McDowell and Bogert (1954). Measurements of snake vertebrae follow the methods of Auffenberg (1963).

DETERMINATION OF MINIMUM NUMBER OF INDIVIDUALS (MNI). — For lizards, MNI can be determined using the same technique used for mammals, i.e. the most common right, left, or midline element is counted. Estimation accuracy can be increased by considering the size range of elements. The same technique can be used for snakes and amphisbaenians if skull material is common. If skull material is rare, which is typically the case, an estimate of MNI can still be made if the maximum difference in centrum length (or any other measure) from a single column of a given species is known. By subtracting the centrum length of the smallest known fossil of a species from the largest, a range in size for the fossil vertebrae is determined. The MNI is found by dividing the range in size of the fossils by the maximum range in the column of that same species (and rounding up to the next whole number). Some precaution must be taken, because large gaps in the range of centrum lengths of the fossils can produce spurious results. No such gaps are present in data gathered from Inglis material. This method probably greatly underestimates the number of individuals in large samples.

The following abbreviations are used in the text: AMNH, American Museum of Natural History; UF, University of Florida/Florida State Museum; USNM, National Museum of Natural History; CL, centrum length; CTW, cotyle width; NAW, neural arch width; NH, neural spine height; NLU, neural spine length at upper edge; NSB, neural spine length at base; POPR, postzygophyseal to prezygophyseal length; PRPR, width across the prezygophyses; ZW, zygosphenoid width; R, right; L, left; MNI, minimum number of individuals; N, sample size; OR, observed range; \bar{X} , mean; SD, standard deviation.

SYSTEMATIC PALEONTOLOGY

ORDER SQUAMATA OPPELL 1811

SUBORDER LACERTILIA GUNTHER 1867

Four species of lizards, representing three families, are present in

the Inglis IA fauna. Comparisons of the fossils were made only to the lizard families now found in the New World (Anelytropsidae, Anguidae, Gekkonidae, Helodermatidae, Iguanidae, Scincidae, Teiidae, Xantusidae, and Xenosauridae). Statements concerning lizard morphology for which no citation is provided are based on examination of the comparative material listed in Appendix 1.

FAMILY ANGUIDAE COPE 1864
SUBFAMILY GERRHONOTINAE COPE 1900

cf. *Gerrhonotus* WEIGMANN 1828

FIGURE 1 A

REFERRED MATERIAL. — UF 26409, 1 vertebra.

DESCRIPTION. — The single vertebra has a subtriangular centrum 3.35 mm long and 2.1 mm wide. The centrum is gently rounded ventrally with no haemal keel or subcentral ridges. The neural spine is low and rises from the neural arch at an angle of 25°. It projects posteriorly beyond the edge of the neural arch. Rib articulations are not strongly differentiated into parapophyses and diapophyses.

COMPARISONS. — The absence of subcentral ridges indicates that the referred vertebra is not that of a teiid or iguanid. The centrum is longer and more triangular than that of any gekkonids examined. It is more rounded ventrally than in *Ophisaurus* or *Heloderma*. The absence of the haemal keel in the fossil suggests that it is not a scincid or diploglossine anguid. The simple rib articulations eliminate the possibility that *Xenosaurus* is represented. The fossil is very similar to Recent *Gerrhonotus multicarinatus*, but due to a lack of material is not assigned to species.

DISTRIBUTION. — The genus *Gerrhonotus* is found throughout western North America from northern Mexico to southern British Columbia. This genus may be represented by material from upper Cretaceous, upper Paleocene, and lower Eocene of the Midwest (Meszoely 1970). Later records include the Mio-Pliocene of Nebraska (Meszoely 1970), lower Pliocene of Kansas (Wilson 1968), and upper Pliocene (Blancan) of Texas (Rogers 1976).

REMARKS. — Verification of *Gerrhonotus* in the early Pleistocene of Florida is required before any zoogeographical conclusions can be drawn. Its presence in Florida could be a result of the great radiation of anguids that apparently occurred in the Tertiary of North America.

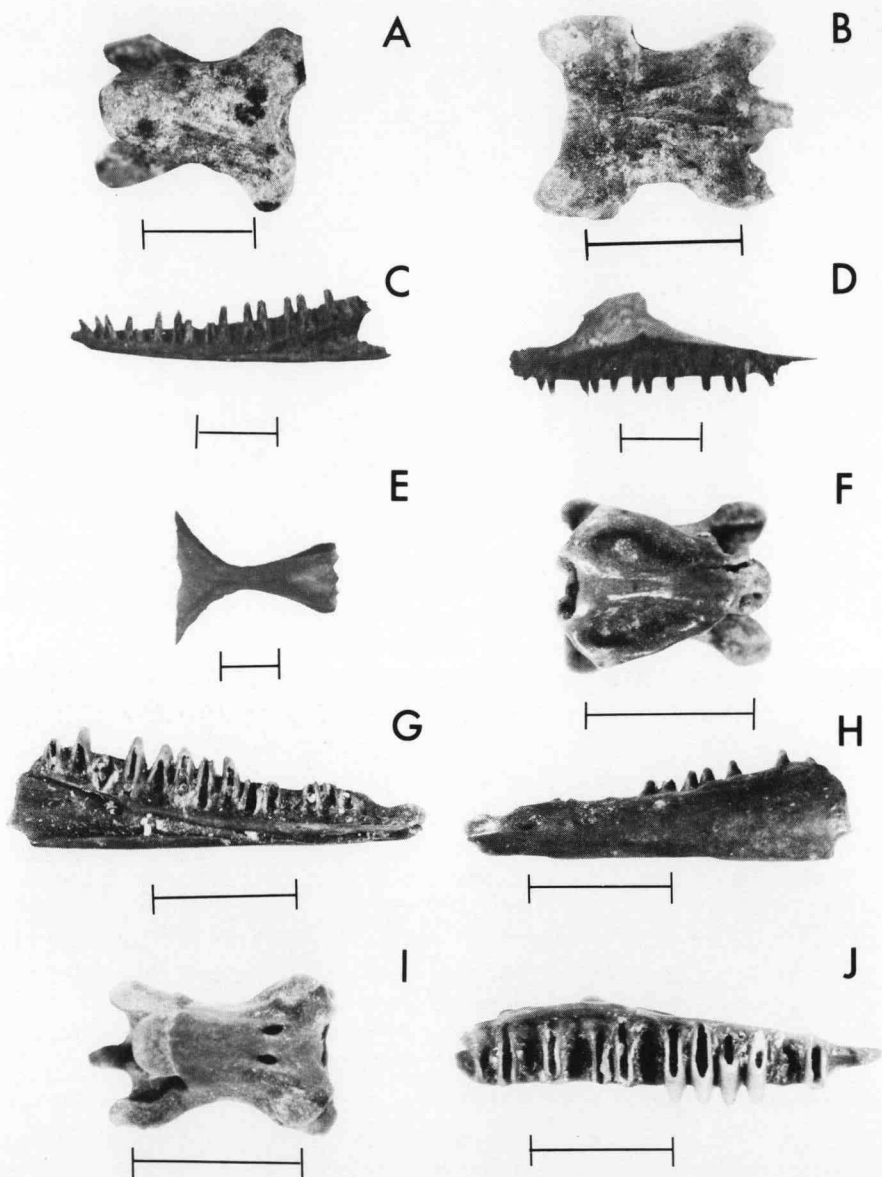


Figure 1. — Limbed lizards and an amphisbaenian from Inglis IA: *Gerrhonotus* (A) vertebra, ventral view, X7. *Rhineura* cf. *R. floridana* (B) vertebra, dorsal view, X10. *Sceloporus undulatus* (C) dentary, lingual view, X4; (D) maxilla, lingual view, X5; (E) frontal, dorsal view, X5; (F) vertebra, ventral view, X10. *Eumeces carri* (n. sp.) dentary, (HOLOTYPE), X10; (G) lingual and (H) labial views; (I) vertebra, ventral view, X10; (J) maxilla, (PARATYPE), lingual view, X10 (each scale = 2 mm).

GENUS *Ophisaurus* DAUDIN 1803
Ophisaurus ventralis (LINNAEUS) 1766

FIGURE 2

REFERRED MATERIAL. — UF 26410, 10 R and 11 L maxillae; UF 26411, 12 R and 11 L dentaries; UF 26412, 3 R and 1 L pterygoids; UF 26413, 3 R and 3 L compounds; UF 26414, 1 R and 1 L frontals; UF 26415, 2 parietals; UF 26416, 3 occiputs; UF 26417, 1 L exoccipital; UF 26418, 2 basisphenoids; UF 26419, 1 quadrate; UF 26420, 1 ilium; and 926 vertebrae including UF 26421, 24 cervicals; UF 26422, 526 presacrals; UF 26423, 22 sacrals; UF 26424, 48 nonautotomic caudals; and UF 26425, 306 autotomic caudals.

DESCRIPTION. — The maxillae have a broad facial flange that contributes to the posterior border of the nares. Premaxillary processes are bifurcate; posterior processes are single. There are 13-17 teeth ($\bar{X} = 15.0 \pm 1.04$) on 12 complete maxillae. The teeth of both the maxillae and dentaries are closely spaced and unicuspid; they have well developed striations on the lingual surface. Thirteen complete dentaries possess 16-21 teeth ($\bar{X} = 17.7 \pm 1.44$); all have a surangular notch that extends anteriorly well beyond the posterior end of the tooth row. A single patch of 30-37 teeth is present on the pterygoids.

The compounds consist of an angular and supra-angular anteriorly, and a splenial on the lingual surface. An articular is fused to the supra-angular. There is a posteroventrally directed retroarticular process. A reduced mandibular foramen is located well anterior to the articular condyle.

The frontals are paired and long, narrow, and pointed anteriorly. The parietals are longer than wide and lack anterolateral processes. The supratemporal processes are robust and nearly meet at their bases.

The occiputs are elongate with the prootic bones extending anteriorly. Crista prootica are poorly developed. The disassociated exoccipital is identical to those of the intact occiputs.

The two fossil basisphenoids have short, robust basiptyergoid processes which extend anterolaterally. The processes originate from the ventral surface of the basisphenoid. The quadrate is triangular in lateral view, and taller than it is thick. The ilium is reduced, consisting of a short, curved shaft with a circular distal expansion.

The thoracic vertebrae are short and wide and have flat centra. The neural spines are broad and low. The sacral vertebrae have flat centra and irregular distal extremities on the transverse processes. The haemal arches of the caudal vertebrae are fused without a trace of suture. Autotomy septa are present in all but the largest (most proximal) caudal vertebrae.

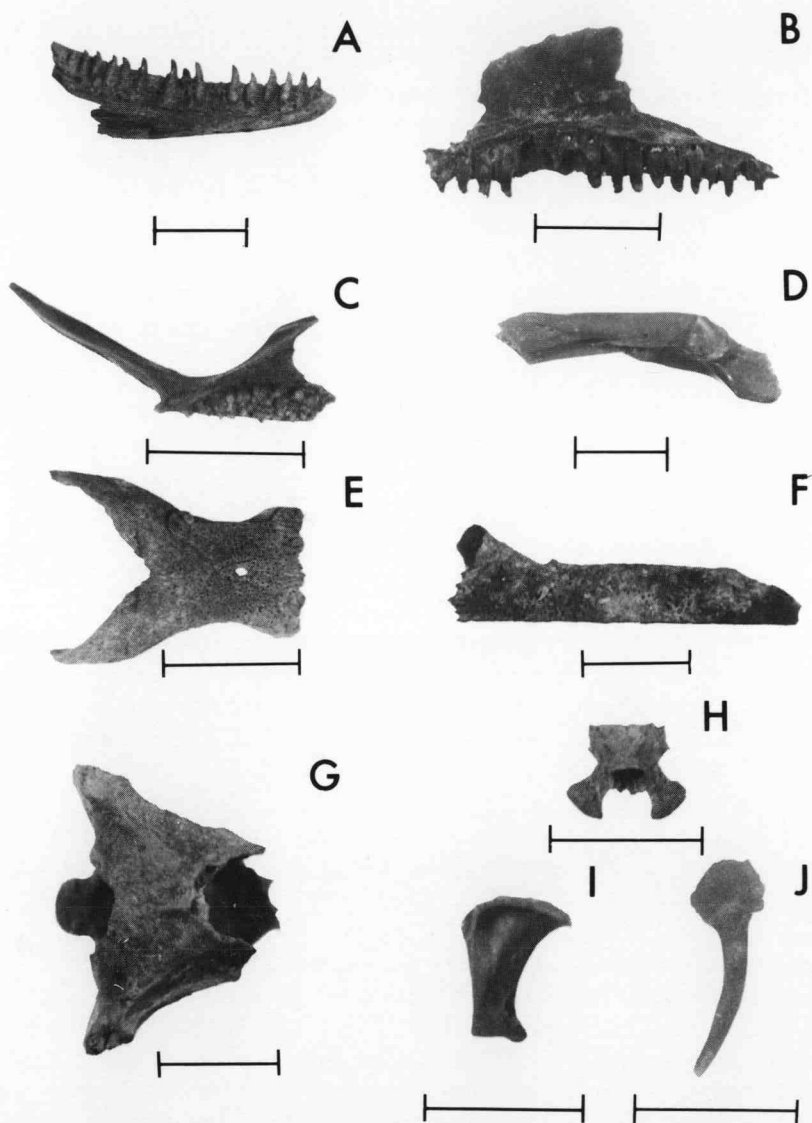


Figure 2. — *Ophisaurus ventralis* from Inglis IA: (A) dentary, lingual view, X3; (B) maxilla, lingual view, X3; (C) pterygoid, ventral view, X3; (D) compound, lingual view, X3; (E) parietal, dorsal view, X3; (F) frontal, dorsal view, X3; (G) occiput, dorsal view, X3; (H) basisphenoid, fronto-dorsal view, X4; (I) quadrate, lateral view, X4; (J) ilium, lateral view, X4 (each scale = 5 mm).

COMPARISONS. — The fossil dentaries and maxillae can be distinguished from North American iguanids (except *Phrynosoma*), helodermatids, teiids, *Anniella*, and xantusids (except *Klauberina*) by the closely spaced unicuspid teeth. They differ from *Klauberina* and gekkonids in having well developed striations on the lingual surface of the teeth. These striations and a more symmetrical tooth shape distinguish the fossil dentaries and maxillae from *Gerrhonotus*. The dentaries differ from *Phrynosoma* and all scincids in having the surangular notch extended anteriorly beneath the tooth row. Bifurcate premaxillary processes distinguish the fossil maxillae from *Phrynosoma*. The fossil maxillae differ from those of scincids in having a single posterior process.

The fossil dentaries and maxillae have significantly fewer teeth than modern samples of *Ophisaurus attenuatus* and *O. compressus* (t -test, $P < .01$) (Fig. 3). They have more teeth than modern *O. ventralis*, but the difference is not significant.

The pterygoids of *O. ventralis*, including the fossils reported here, are apparently unique among North American lizards in having a single patch of 15 or more teeth. *O. attenuatus* has 10-20 teeth arranged

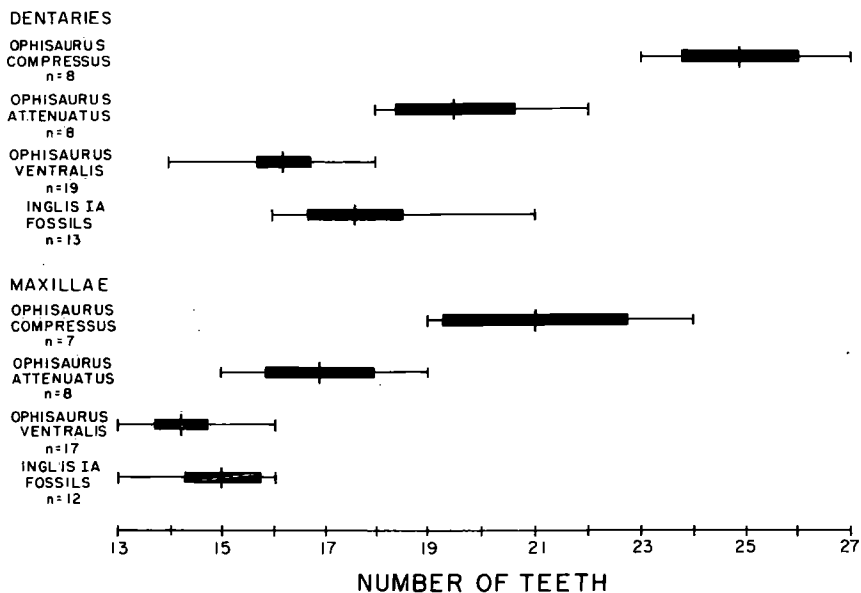


Figure 3. — Number of teeth in the dentaries and maxillae of three Recent North American *Ophisaurus* and the Inglis IA fossils. Mean, 95% confidence limits, and range are indicated.

in one or two rows. *Gerrhonotus* and *O. compressus* have 10 or fewer pterygoid teeth.

The fossil compounds differ from those of all North American lizards except *Ophisaurus* in having a small mandibular foramen located well anterior of the articular condyle. The mandibular foramen is reduced in *Gerrhonotus* but it is also more posteriorly located. There are no apparent differences in the compounds of the modern *Ophisaurus* species examined.

Among extant North American lizards, only the Scincidae, Xantusiidae, Helodermatidae, some diploglossine anguids, and *Ophisaurus* have divided frontals. The divided fossil frontals are as long and narrow as those of *Eumeces* and *Ophisaurus*. As in these two genera, the frontals are more than three times longer than the width at their widest point. The frontals of *Eumeces* are not pointed anteriorly as they are in the fossils and in *Ophisaurus*.

The frontal of *Ophisaurus attenuatus* makes up a larger part of the dorsal edge of the orbit than in *O. compressus* or *O. ventralis* (Wilson 1968). In the Inglis fossil, the proximity of the prefrontal and postfrontal sutures indicates that the frontals made up only a small part of their respective orbits, so the material could represent either *O. ventralis* or *O. compressus*.

The referred parietals are longer and more narrow than those of all North American lizards examined, except *Ophisaurus*. The parietals could not be identified to species, but are referred to *O. ventralis* on the basis of associated material.

A characteristic feature of the occiput of all anguimorph lizards is the extended nature of the prootic bone, which extends anterior to the semicircular canal (McDowell and Bogert 1954). This condition, as well as the near absence of the crista prootica, distinguishes the fossil occiputs from those of all extant North American lizards, except *Ophisaurus* and *Anniella*. *Anniella* differs from the fossils in having reduced spheno-occipital tubercles on the basioccipital. There is no consistent interspecific variation in the occiputs of modern North American *Ophisaurus*. The fossils are referred to *Ophisaurus ventralis* on the basis of associated material.

The fossil basisphenoids were only compared to material of species thought to occur in the Inglis fauna. They differ from *Eumeces*, in which the lateral wall of the abducens canal is continuous with the anterior edge of the basipterygoid process. They differ from *Sceloporus*, which has relatively longer, thinner basipterygoid processes. In *Gerrhonotus* these processes are directed anteriorly rather than anterolaterally.

The quadrates of most North American lizards are D-shaped in

lateral view. Only in scincids, helodermatids, and *Ophisaurus* are they triangular, as they are in the Inglis material. The quadrates of helodermatids are unlike the fossils in having a distinctive T-shape from above. Those of *Eumeces* are thicker than those of *Ophisaurus*. The quadrates of *Ophisaurus* are not diagnostic at the species level.

The reduced size of the ilium of *Ophisaurus* is distinctive. The fossil differs from *O. compressus*, which has a triangular rather than round distal expansion. The expansion is round in *O. attenuatus* and *O. ventralis*.

The body vertebrae of *Ophisaurus* differ from those of all other North American lizards in being short and wide and having a flat centrum and a broad, low neural spine (Etheridge 1961). The absence of articulating surfaces on the transverse processes of the sacral vertebrae indicates that these vertebrae belong to the limbless genus *Ophisaurus*. Only *Anniella* is similar, but it has lower neural spines. The caudal vertebrae differ from all limbed forms in having haemal arches fused to the centrum without a trace of suture. Again, *Anniella* is similar, but it has a much lower neural spine (Etheridge 1961).

In the present study the body vertebrae of modern *Ophisaurus* species were found to show more variation than Etheridge (1961) reported. He separated the three well known modern species in North America by differences in the length to width ratio of the centrum (CL/NAW) and/or by differences in the angle of the posterior border of the neural spine. Two Mexican species are known from a total of three specimens, none of which is prepared as a skeleton. *O. compressus* has distinctly narrower vertebrae than either *O. ventralis* or *O. attenuatus*,

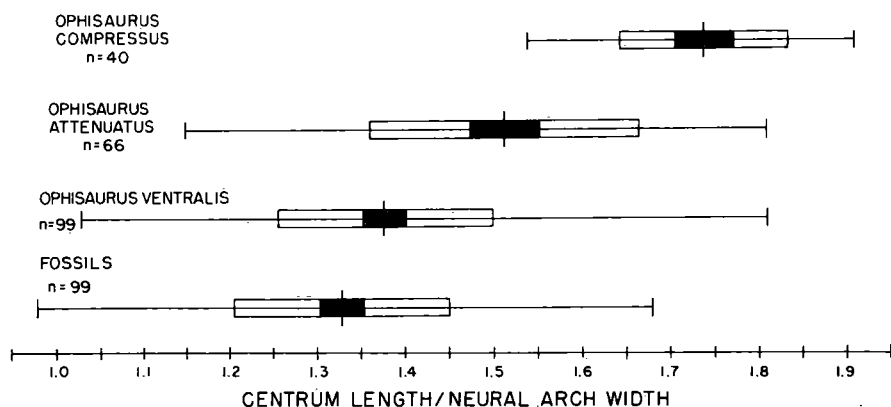


Figure 4. — Vertebrae shape (centrum length/neural arch width) for three Recent North American *Ophisaurus* and Inglis IA fossils. Mean, standard deviation, two standard errors of the mean, and range are indicated.

but there is little difference between the latter two (Fig. 4). A similar figure for separating *O. compressus* and *O. ventralis* in Auffenberg (1955) includes a misleading error — the scale of 0.1 to 1.0 should read 1.1 to 2.0. Etheridge (1961) used differences in the angle of the posterior edge of the neural spine to separate *O. attenuatus* (45° - 65°) from *O. ventralis* (65° - 84°). In the present study, this angle was found to be 65 - 85° in *O. attenuatus* and 70 - 90° in *O. ventralis*. The difference between Etheridge's data and those reported here may be explained in part by the geographical origin of the samples. Etheridge's *O. attenuatus* were from Kansas and Texas and represented only *O. attenuatus attenuatus* (Etheridge, pers. comm.). The sample used in the present study included both *O. a. attenuatus* from Texas and Kansas and *O. a. longicaudus* from Florida.

Although no clear difference exists between the vertebrae of *O. attenuatus*, *O. ventralis*, and the fossils, Figure 4 shows that the mean and the 95% confidence limits for the fossil body vertebrae are more similar to *O. ventralis* than to *O. attenuatus*.

The sacral and caudal vertebrae of *Ophisaurus* are not diagnostic at the species level except in one case. The caudals of *O. compressus* are unique in lacking fracture planes. The presence of these planes in the fossil caudals indicates that *O. compressus* is not represented.

Not all of the material referred to *Ophisaurus ventralis* is diagnostic. However, statistical variation observed in the fossils (see Table 2) is

Table 2. — Diagnostic osteological characters for United States *Ophisaurus* species and Inglis IA fossils.

	Fossil	<i>O. attenuatus</i>	<i>O. compressus</i>	<i>O. ventralis</i>
Maxillary Teeth (mean \pm one S. D.)	15.0 \pm 1.04	16.8 \pm 1.14	21.0 \pm 1.58	14.4 \pm 0.91
Dentary Teeth (mean \pm one S. D.)	17.7 \pm 1.44	19.3 \pm 1.87	24.9 \pm 1.46	16.7 \pm 1.10
Pterygoid Teeth	30-37 (patch)	10-20 (in 1 or 2 rows)	10 (in 1 row)	10-25 (patch)
CL/NAW (body vertebrae) (mean \pm one S. D.)	1.33 \pm .123	1.51 \pm .151	1.74 \pm .097	1.37 \pm .121
Frontals in Orbit	Small	Large	Small	Small
Distal Expansion of Ilium	Round	Round	Triangular	Round
Fracture plane in Caudal Vertebrae	Present	Present	Absent	Present

not greater than that in any one of the modern species examined, suggesting that only one species is present in the Inglis fauna. Analysis of seven characters in combination (Table 2) indicates that *O. ventralis* is the species present in the Inglis fauna.

DISTRIBUTION. — *Ophisaurus ventralis* is found in the southeastern coastal plain and Piedmont from Louisiana to North Carolina. It is known as a fossil from the late Miocene of Nebraska (Holman 1975), the early Pliocene of Kansas (Wilson 1968), middle Pliocene of Florida (Auffenberg 1955), late Irvingtonian of Florida (Holman 1959a,b), and Rancholabrean of Florida (Auffenberg 1955; Holman 1958) and Missouri (Holman 1965). *Ophisaurus attenuatus* has been reported from late Plio-Pleistocene localities in Kansas and Oklahoma (Etheridge 1961). Holman (1970) described *Ophisaurus canadensis* from the upper Miocene of Saskatchewan and suggested that this species might be ancestral to *O. ventralis* and *O. attenuatus*. The Buda Local Fauna (Miocene: Arikareean) and Love Bone Bed (Miocene: Clarendonian) of Florida contain unstudied *Ophisaurus* material.

REMARKS. — The *Ophisaurus* material from Inglis is the most extensive reported for the genus in the New World. It provides previously unavailable morphological data on *Ophisaurus ventralis* in the early Pleistocene. Minor differences between the Inglis *O. ventralis* and a modern sample include higher average numbers of dentary and maxillary teeth, and substantially higher numbers of pterygoid teeth in the fossils. No changes were detected in the cranium or dermal roofing bones. An important consistency is seen in the condition of the ilium. It is evident that *O. ventralis* had reached its present limbless condition by the earliest Pleistocene and has not subsequently reduced the pelvic girdle. Speciation in North American *Ophisaurus* has been attributed to isolation of various stocks during the Pleistocene (McConkey 1954). The fossil record described above shows that this is not the case for *O. ventralis* and *O. attenuatus*, which are both present before the Pleistocene.

FAMILY IGUANIDAE GRAY, 1827

GENUS *Sceloporus* WEIGMANN 1828

Sceloporus undulatus (LATRIELLE) 1802

FIGURE 1 C-F

REFERRED MATERIAL. — UF 26426, 3 frontals; UF 26427, 33 R and 36 L dentaries; UF 26428, 11 R and 10 L maxillae; UF 26432, 2 humeri; UF 26433, 1 femur; and 53 vertebrae including: UF 26429, 42 cervicals and thoracics; UF 26430, 2 sacrals; and UF 26431, 9 caudals.

DESCRIPTION. — The frontals are single, unsculptured, narrow between the orbits, and have poorly developed crista cranii.

The tooth-bearing elements have tricusate teeth posteriorly. The cusps are not strongly developed. The dentaries are long and slender with Meckle's groove open lingually. They have an average of 3.57 teeth per mm. Maxillae have an average of 3.14 teeth per mm.

The vertebrae have trapezoidal centra with moderately developed haemal keels and weakly developed subcentral ridges. Both sacral vertebrae are second members of disarticulated sacral pairs. They have posterolaterally directed tubercles on the posterior margins of the transverse processes.

COMPARISONS. — Among extant North American lizards, only iguanids, teiids, gekkonids, xenosaurids, and *Gerrhonotus* have single frontals (Camp 1923). Unlike the fossils, crista cranii are well developed in the frontals of both gekkonids and xenosaurids. The fossil frontals are relatively shorter than those of the teiid genera *Ameiva* and *Cnemidophorus*. They are narrower between the orbits than the frontals of the iguanid *Anolis carolinensis*, but are very similar to *Sceloporus woodi* and *S. undulatus*. The dentigerous elements possess typically iguanid tricusate teeth. The three cusps are less developed than those of *Leiocephalus*, and the central one is not as pronounced as in *Anolis carolinensis*. The teeth and the long slender shape of the dentary suggest a small *Sceloporus*. The referred vertebrae have centra similar in shape to most iguanid lizards. Subcentral ridges are less well

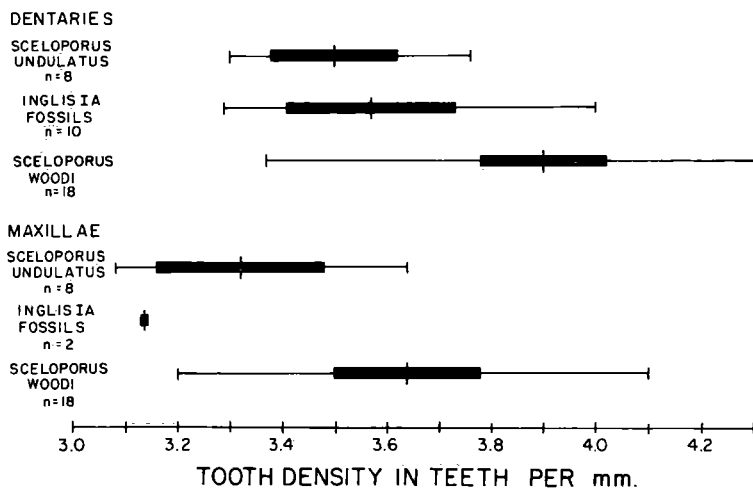


Figure 5. — Tooth density in the dentaries and maxillae of Recent *Sceloporus undulatus*, Recent *Sceloporus woodi*, and fossil *Sceloporus* from Inglis IA. Mean, 95% confidence limits, and range are indicated.

developed than in the teiids *Ameiva* and *Cnemidophorus*, but they and the haemal keels are better developed than in any scincids, gekkonids, or anguids examined. The vertebrae of many small iguanids are similar, and the reference of these fossils to *Sceloporus* is based on the associated skull elements. All of the elements referred to *Sceloporus undulatus* closely resemble *S. undulatus* and *S. woodi*. These two species can be distinguished on the basis of tooth density (Fig. 5). *Sceloporus woodi* has a significantly larger number of teeth on the dentary and maxilla than does *S. undulatus* or the fossils (t test, $P < 0.05$). The fossils do not differ in tooth density from *S. undulatus*. Therefore the frontals and postcranial material, along with the dentigerous elements, are assigned to *S. undulatus*.

DISTRIBUTION. — *Sceloporus undulatus* is found throughout the southern two-thirds of the United States from extreme southeastern Nevada to New Jersey and Florida. It is known as a fossil from the Blanton of Texas (Rogers 1976), Irvingtonian of Maryland (Holman 1977a) and Texas (Holman 1969a), and Rancholabrean of Arizona (Van Devender et al. 1977), Florida (Brattstrom 1953), Georgia (Holman 1967), Missouri (Holman 1974), and Texas (Holman 1968b, 1969a; Gehlbach and Holman 1974). The oldest known sceloporine is from the upper Miocene of Saskatchewan (Holman 1970).

REMARKS. — In their discussion of the evolution of the genus *Sceloporus*, Larsen and Tanner (1975) reported *S. undulatus* to be a member of the *virgatus* group, the most complex and recently derived of three species groups. They suggested that the initial division of this group occurred when its progenitor was isolated in various refugia during the first glacial advance, and that with the first interglacial *virgatus* group stock migrated east and west to produce *occidentalis*, *undulatus*, and *woodi*. The appearance of *S. undulatus* by the Pleistocene indicates that some division of the *virgatus* group had occurred by the end of the Pliocene.

Jackson (1973) found *Sceloporus woodi*, a Florida endemic, to be more similar to southwestern members of the *virgatus* group than to *Sceloporus undulatus undulatus*. He cited the possible late arrival (Sangamonian = late Irvingtonian) of *S. undulatus* as additional evidence that it was a southwestern form which was isolated in Florida during the Pleistocene and gave rise to *S. woodi*. This new evidence of *S. undulatus* in Florida by the earliest Pleistocene renews the possibility that it is ancestral to *Sceloporus woodi*.

FAMILY SCINCIDAE GRAY 1825
GENUS *Eumeces* WEIGMANN 1834
Eumeces carri new species

FIGURE 1 G-J

DIAGNOSIS. — *Eumeces carri* is similar to several small *Eumeces* species (e.g. *E. inexpectatus*, *E. fasciatus*). However, it differs from these and all Recent species examined in features of the teeth and the dentary. The dorsal margin of the dentary in all available *Eumeces* (14 species) is straight. The anterior dilation of the fossil dentary (Fig. 1 G) could be a result of wear, but the presence of a labial ridge, which apparently occurs in no other skink, suggests that the anterior end of the dentary is modified. The teeth are also modified, being rounded or even blunt and unstriated rather than striated and weakly cusped as in most skinks. The high degree of lingual tooth erosion seen in the fossils could be a result of depositional wear, but the identical pattern of wear on both toothed elements suggests a predepositional feature. Such erosion may indicate very rapid tooth replacement.

HOLOTYPE. — UF 26435 (Fig. 1 G, H), a left dentary from Inglis IA, Irvingtonian of Citrus County, Florida.

PARATYPE. — UF 26432, (Fig. 1 J) a right maxilla.

REFERRED MATERIAL. — UF 26434, 11 thoracic vertebrae; 2 pairs of fused sacral vertebrae (tentative).

DESCRIPTION. — The dentary is nearly complete and contains space for 17 teeth. The 10 preserved teeth are blunt, unstriated, and eroded lingually to about two-thirds their height. Meckle's groove is open along the entire length of the bone. In labial view the dentary narrows and then expands anteriorly. A well developed ridge occupies the middle of the labial surface at the same level as this expansion.

The maxilla is nearly complete. The most anterior portion of the tooth row and the facial wing are missing. The maxilla has 15 or 16 tooth positions. The teeth are eroded lingually to about two-thirds of their height.

The referred vertebrae are small (< 2 mm CL) and about twice as long as wide. Centra have nearly parallel sides and are rounded ventrally. Haemal keels are broad and weakly developed. Subcentral ridges are absent. Neural spines rise from the neural arch at an angle of 15-20°. The sacral vertebrae are about as wide as long and have long transverse processes. Each pair is fused at the centrum and at the ends of the transverse processes.

COMPARISONS. — The thoracic vertebrae compare best to those of the scincid genus *Eumeces*. The haemal keels are weaker than in iguanids, but stronger than in *Gerrhonotus* or *Ophisaurus*. The fossil vertebrae

differ from those of the teiids, *Cnemidophorus* and *Ameiva*, which have well developed subcentral ridges. They differ from gekkonid vertebrae, which tend to be relatively shorter and have neural spines that rise more vertically from the neural arch. Sacral vertebrae are fused only in scincids, xantusids, gekkonids, and some teiids (not fused in *Cnemidophorus*). Because no other material was found that could be referred to the Teiidae, Gekkonidae, or Xantusidae, the sacral vertebrae are tentatively referred to this skink.

The lingual erosion of the teeth in the maxilla and dentary suggests non-anguimorph, vertical tooth replacement. Among lizards with vertical tooth replacement, iguanids and teiids have some multicuspid teeth; Meckle's groove is closed in gekkonids and xantusids. The only remaining non-anguimorph New World families are the Scincidae and the Anelytropsidae. It is unlikely that the latter, a small monotypic form known only from central Mexico, is represented.

REMARKS. — The Inglis material represents a new and specialized species of skink. The study of its relationships will require additional comparative material. At least two individuals of this skink are represented in the fauna.

SUBORDER AMPHISBAENIA GRAY 1825
FAMILY RHINEURIDAE VANZOLINI 1951
GENUS *Rhineura* COPE 1861
cf. *Rhineura floridana* (BAIRD) 1858

FIGURE 1 B

REFERRED MATERIAL. — UF 26438, 32 thoracic and 1 caudal vertebra.

DESCRIPTION. — The thoracic vertebrae (Fig. 1B) are dorsoventrally compressed and as long as or slightly longer than wide. The large pre- and postzygapophyses are adjacent to the neural arch and connected by an interzygapophyseal ridge. Zygosphenes and zygantra are absent. Neural spines project posteriorly when enlarged, but typically are reduced to a ridge. On either side of the neural spine is a series of raised striations. The vertebral centra are rounded below and have no haemal keel or subcentral ridges. The paradiapophysis is single. The single caudal vertebra is as above, but, in addition, has anterolaterally directed transverse processes and ventrally fused hemapophyses.

COMPARISONS. — The vertebrae of rhineurids do not differ markedly between species. They are apparently unique among amphisbaenians in bearing numerous longitudinal striations on the neural arch (Berman 1976).

DISTRIBUTION. — *Rhineura floridana* is at present restricted to the northern half of peninsular Florida. Rhineurid vertebrae from the late Irvingtonian (Holman 1962, 1959a) and Rancholabrean (Holman 1958) of Florida are referred to *R. floridana*. The Inglis material extends the fossil record for rhineurids in Florida to the beginning of the Pleistocene, but unstudied material in the Buda Local Fauna (Arikareean) indicates an early Miocene arrival of rhineurids in Florida.

REMARKS. — The identification of fossil rhineurids in the literature has been based completely on skull characters. The absence of skull material from Inglis makes a positive identification of this rhineurid impossible, but because these fossils occur within the present range of *Rhineura floridana* and are identical to recent examples, the Inglis material is tentatively referred to this species.

SUBORDER SERPENTES LINNAEUS 1758

Living members of the suborder Serpentes are divided into three infraorders: the Scolecophidia, the Henophidia, and the Caenophidia (Underwood 1967). Each of these has a diagnostic vertebral form (Holman 1979). The Scolecophidia are primitive burrowing snakes. Their vertebrae are depressed and lack neural spines. The cotyle is oval in shape and the haemal keel and subcentral ridges are absent or poorly developed. The henophidians include boas and pythons. The vertebrae of this group have neural spines that tend to be short and thick, rarely as long as the neural arch. Paradiapophyses tend to be undifferentiated, and accessory processes are poorly developed or absent. The advanced snakes, or Caenophidia, have vertebrae with thin neural spines that are typically longer than those of henophidians; they are often nearly as long as the neural arch. Paradiapophyses are divided into parapophyses and diapophyses. Accessory processes tend to be well developed.

On the basis of these characters, all of the snake vertebrae from Inglis IA are referable to the Caenophidia. Smith et al. (1977) applied the name Colubroidea to this group and recognized four families within it. Members of three of these families, Colubridae, Elapidae, and Viperidae, constitute the snakes of the Inglis fauna.

FAMILY COLUBRIDAE OPPEL 1811

This study was facilitated by dividing American colubrid snake vertebrae into five artificial groups. Four of these morphological groups approximate natural phylogenetic assemblages of species recognized by various authors. These are the Natricinae, Xenodontinae, Lampropeltinae, and Colubrinae.

The Natricinae are easily distinguished by the presence of laterally compressed hypapophyses throughout the column (Underwood 1967). A second group has dorsoventrally flattened (depressed) neural arches. It approximates the Xenodontinae (Ophiinae of Dunn 1928) and includes *Heterodon*, which is clearly a xenodontine, and *Farancia*, which was placed in this subfamily by Dunn (1928) and Neill (1964). Underwood (1967) placed the genus in the Lycodontinae. The extent of vaulting or depression of the neural canal is difficult to determine in very small snakes. They are assembled in a third, clearly unnatural group which includes *Carphophis*, *Diadophis*, *Rhadinaea*, *Tantilla*, *Stilosoma*, and *Sonora*. The remaining larger colubrid vertebrae are of two kinds (Fig. 6, Table 3). One group is short and wide, with poorly developed epizygapophyseal spines and short laterally directed accessory processes. The other group is longer and more narrow, with epizygapophyseal spines that are moderately to well developed and long anterolaterally directed accessory processes. The former group includes *Pituophis*, *Lampropeltis*, *Elaphe*, *Arizona*, *Rhinoceilus*, and *Cemophora*. This assemblage approaches Dowling and Duellman's (1974) Lampropeltiinae, a tribe of their subfamily Colubrinae. Smith et al. (1977) raised this tribe to subfamilial status on the basis that knowledge of snake relationships is too uncertain to recognize tribes. The group with long vertebrae remains in the Colubrinae and includes *Coluber*, *Drymarchon*, *Masticophis*, and *Opheodrys*.

Table 3. — Vertebral characters for the separation of the Colubrinae and Lampropeltinae (as recognized in this study).

Vertebral characters	Lampropeltinae (8 species, 29 columns, 223 vertebrae)	Colubrinae (4 species, 10 columns, 79 vertebrae)
CL/NAW	less than 1.27 (except in <i>Cemophora</i>)	greater than 1.37 (except in <i>Drymarchon</i>)
Epizygapophyseal Spines	weak to absent (96.9%)	moderately to well developed (83.5%)
Accessory Process Length	shorter than prezygapophyseal width (85.4%)	longer than prezygapophyseal width (64.6%)
Accessory Process Direction	laterally directed (65.1%)	anterolaterally directed (87.4%)

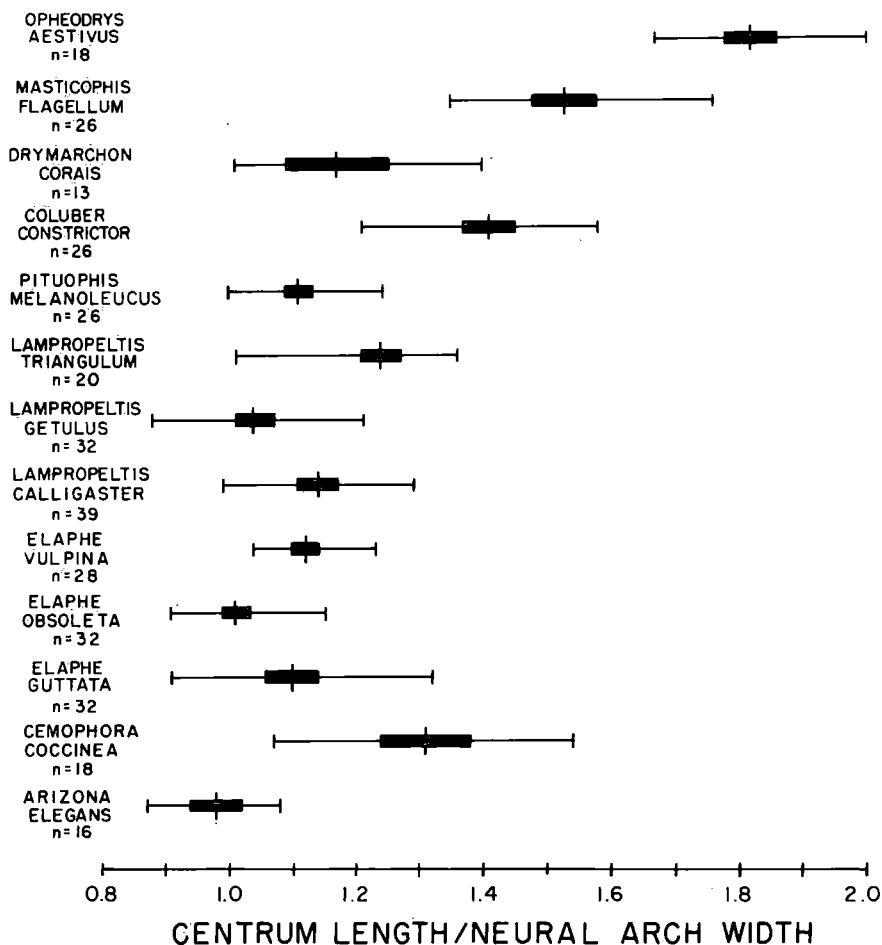


Figure 6. — Centrum length/neural arch width (CL/NAW) for lampropeltine and colubrine snakes. Mean, 95% confidence limits, and range are indicated.

The present study does not address the validity of these natural groups. The subfamilial names Colubrinae, Lampropeltinae, Natricinae, and Xenodontinae are used only to assist in the organization and identification of the fossils.

SUBFAMILY COLUBRINAE OPPEL 1811

For the purpose of this paper, the Colubrinae is considered to include the racer-like snakes *Coluber*, *Masticophis*, *Drymarchon*, *Opheodrys*, and *Salvadora*. The vertebral centra of these snakes are nearly half again as long as they are wide, except in *Drymarchon*. The

accessory processes are long and straight. Epizygapophyseal spines are better developed in this group than in other subfamilies (less so in *Ophedrys* and *Salvadora*).

GENUS *Coluber* LINNAEUS 1758
Coluber constrictor LINNAEUS 1758

FIGURE 7 A-D, TABLE 4

REFERRED MATERIAL. — UF 26360, 334 vertebrae; UF 26361, 1 L pterygoid; UF 26362, 2 R compounds; UF 26363, 1 L and 2 R dentaries.

DESCRIPTION. — The referred vertebrae have long narrow centra that are nearly square across the zygapophyses (Table 4). Accessory processes are long, narrow and anterolaterally directed. Haemal keels are variable, but are typically narrow and straight with a slight lateral expansion just anterior to the condyle. Epizygapophyseal spines are well developed.

The fossil left pterygoid is moderately large. It is broken at the posterior end of the toothrow. The pterygoid flange has a poorly developed, laterally directed ectopterygoid process. The flange is slightly constricted between the ectopterygoid process and the base of the quadrate process. A ridge is present on the dorsal surface; it extends anteriorly beyond the ectopterygoid process.

In the fossil compound bones the labial and lingual flanges are subequal in height, the lingual flange being slightly taller than the labial flange.

All three fossil dentaries are broken posterior to the 12th tooth. Meckle's groove closes completely by the 8th or 9th tooth. The anterior end of these dentaries is very slightly curved.

COMPARISONS. — The referred vertebrae are similar to those of *Masticophis* and, to a lesser extent, *Drymarchon*. In recent individuals of *D. corais* from Florida the anterior edge of the neural spine is bevelled. In *Masticophis*, *Coluber*, and some Mexican and Central American *Drymarchon*, the anterior edge of the neural spine is square. Thus the bevel, used as a standard diagnostic character for *Drymarchon*, does not always hold. This problem, and the fact that neural spines from many of the fossils were broken, encouraged me to include *Drymarchon* in a discriminant analysis with *Coluber* and *Masticophis*.

The analysis developed is independent of neural spine characters. It is based on 26 vertebrae from four *Coluber constrictor*, 16 vertebrae from two *Drymarchon corais* and 26 vertebrae from four *Masticophis flagellum*. Of the 68 vertebrae, 6 (8.8%) are reclassified by the analysis. The most important characters for the separation of these groups (ZW/NAW, PRPR/POPR, PRPR/NAW, PRPR/ZW) are shown in Table 4.

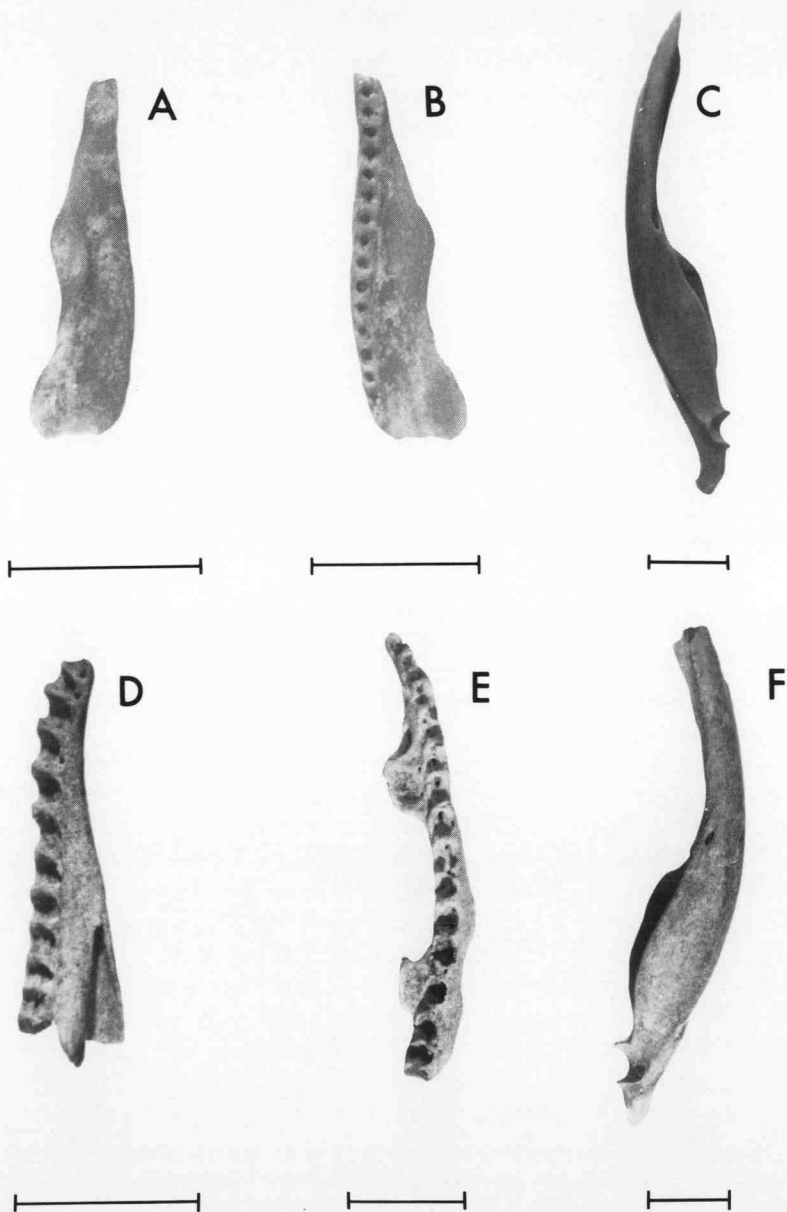


Figure 7. — Fossil *Coluber* and *Masticophis* from Inglis IA: *Coluber constrictor* (A) pterygoid, dorsal view, X5; (B) pterygoid, ventral view, X5; (C) compound, labial view, X2; (D) dentary, lingual view, X3. *Masticophis flagellum* (E) maxilla, occlusal view, X3; (F) compound, labial view, X2 (each scale = 5 mm).

Table 4. — The four most important ratios for the discrimination of *Coluber constrictor*, *Drymarchon corais*, and *Masticophis flagellum* (mean \pm one standard deviation).

	(ZW/NAW) ¹	(PRPR/POPR) ²	(PRPR/NAW) ³	(PRPR/ZW) ⁴
<i>Coluber constrictor</i>				
Recent (N = 27)	.98 \pm .04	1.04 \pm .04	1.79 \pm .10	1.83 \pm .11
Fossils (N = 334)	.96 \pm .98	.99 \pm .05	1.74 \pm .11	1.90 \pm .15
<i>Masticophis flagellum</i>				
Recent (N = 26)	.98 \pm .05	.98 \pm .05	1.81 \pm .05	1.84 \pm .11
Fossils (N = 331)	.95 \pm .08	.97 \pm .05	1.80 \pm .11	1.89 \pm .13
<i>Drymarchon corais</i>				
Recent (N = 14)	.81 \pm .02	1.12 \pm .06	1.65 \pm .07	2.03 \pm .06
Fossils (N = 29)	.84 \pm .03	1.03 \pm .06	1.72 \pm .06	2.04 \pm .06

¹Zygasphene Width/Neural Arch Width

²Prezygapophysis to Prezygapophysis Width/Prezygapophysis to Postzygapophysis Length

³Prezygapophysis to Prezygapophysis Width/Neural Arch Width

⁴Prezygapophysis to Prezygapophysis Width/Zygasphene Width

The fossil pterygoid is broken posteriorly. The presence of an ectopterygoid process (Fig. 7) indicates that it is not that of a viperid (see Figs. 5, 29, 30; Brattstrom 1964). The process in the fossil is less developed than that of the larger North American natricines and *Farancia* (App. 3-4). It differs from *Heterodon* in being laterally, rather than anteriorly, directed (Fig. 12B). From the large lamppropeltines, the fossil differs in having the dorsal ridge extended anteriorly beyond the ectopterygoid process. It is most similar to *Coluber*, *Masticophis* and *Drymarchon*, differing from the latter two only in having the ectopterygoid flange rise from the tooth row at a high angle and in having the ectopterygoid process more anteriorly located.

Among larger North American snakes very few genera have subequal flanges on the compound bone (Marx and Rabb 1972). The lingual and labial flanges are subequal in the referred fossils, as they are in *Masticophis* and *Coluber*. In both *Masticophis* and *Coluber* the lingual flange is slightly the larger, and in both the extension of these two flanges increases with age. However, the lingual flange of *C. constrictor* is always more dorsally expanded than in individuals of *M. flagellum* of the same size. Based on this criterion, the fossils are referred to *C. constrictor* rather than *Masticophis*.

The fossil dentaries are most similar to *Coluber* and *Masticophis*, which have Meckle's groove closed completely between the 8th and 11th teeth (App. 3-6). They are assigned to the former because they do not show the more distinct curve at the anterior end of the dentary of *Masticophis*.

DISTRIBUTION. — *Coluber constrictor* is found throughout the United States, except in the desert southwest. Its extensive fossil record must

be regarded with caution because of the difficulty involved in distinguishing it from *Masticophis flagellum*. The oldest referred material is from the early Pliocene of Nebraska. Blancan fossils are known from Idaho (Holman 1968a), Kansas (Brattstrom 1967), and Texas (Rogers 1976). Irvingtonian specimens are reported from Arizona (Brattstrom 1955a; Lindsay and Tessman 1974), Florida (Holman 1959a), Kansas (Brattstrom 1967), and Maryland (Holman 1977a). Rancholabrean records occur in at least 10 states from coast to coast (see Holman 1981).

Extinct, but possibly related forms include *Paraoxybelis floridanus* from the early Miocene of Florida (Auffenberg 1963), *Paracoluber storeri* from the late Miocene of Wyoming and Saskatchewan (Holman 1970), and *Coluber plioagellus* from the late Pliocene of Kansas (Wilson 1968).

REMARKS. — It is apparent from the fossil record that *Coluber constrictor* is widely distributed by the Irvingtonian. The referred skull material from Inglis shows that the skull of this species has not changed over the last two million years.

GENUS *Drymarchon* FITZINGER 1843

Drymarchon corais (BOIE) 1827

REFERRED MATERIAL. — UF 26367, 29 vertebrae.

DESCRIPTION. — The fossil vertebrae differ from those of *Coluber constrictor* only in being relatively wider. Neural spines, if present, are squared off anteriorly.

COMPARISONS. — Long accessory processes and well developed epizygapophyseal spines identify these as colubrine vertebrae. The vertebrae were identified as *D. corais* by the discriminant analysis described under *Coluber constrictor*. They differ from modern *D. corais* from Florida, in which the anterior edge of the neural spine is bevelled. Specimens from other parts of the range often have unbevelled neural spines (UF 11467, 11782, 11784).

DISTRIBUTION. — At present *D. corais* is found from southern Texas to northern Argentina, with a disjunct subspecies in Florida, Alabama, and Georgia. It is known as a fossil from 10 middle or late Pleistocene and 6 late Pleistocene localities in Florida (see Holman 1981). Material from the Pleistocene of Texas that may represent this species has been lost (Holman 1969a).

REMARKS. — Florida's Recent *D. corais* is clearly a relict of a once more widely distributed species. The Inglis fossils referred to *D. corais* show greater similarity to Recent populations from Mexico and Central America than to those in Florida. Apparently differentiation of Florida's *D. corais* populations has occurred since the early Pleisto-

cene. This suggests that *Drymarchon* became isolated in Florida after Inglis time.

GENUS *Masticophis* BAIRD AND GIRARD 1853

Masticophis flagellum (SHAW) 1802

FIGURE 7 E,F, TABLE 4

REFERRED MATERIAL. — UF 26364, 331 vertebrae; UF 26265, 2 R, 1 L maxillae; UF 26366, 1 R, 2 L compounds.

DESCRIPTION. — In most respects the *Masticophis* vertebrae fit the description of *Coluber constrictor* above, but they are slightly narrower across the zygapophyses and the centrum (Table 4).

The complete left maxilla is from an adult snake; the two right maxillae are from subadults and are missing their anterior halves. The complete maxilla has space for 15 teeth with no diastema. The prefrontal process is located at the 5th and 6th teeth; the ectopterygoid process is located at the 12th tooth. There are three tooth sockets posterior to the latter process. A dorsal constriction of the maxillary ramus is present at the level of the ectopterygoid process. The constriction of the maxillary ramus is more pronounced in the smaller specimens than in the complete adult maxilla.

The three compound bones are complete. Labial and lingual flanges are subequal in height; the lingual flange is slightly higher than the labial flange.

COMPARISONS. — The fossil vertebrae were identified using discriminant analysis (see *Coluber constrictor*). The most important characters for distinguishing *M. flagellum* from *Coluber constrictor* and *Drymarchon corais* appear in Table 4. Lack of adequate comparative material prevented the inclusion of *Masticophis taeniatus* in this analysis. However, the largest referred vertebrae are much larger than those of Recent *M. taeniatus*.

The number and placement of teeth and the position of the two maxillary processes distinguish the referred maxillae from most other colubrids (App. 3-1). In the lampropeltine genera these processes are closer to one another and are located more posteriorly than in the fossils. North American natricines have more teeth; the minimum observed is 19 in *Seminatrix*. *Heterodon* has a diastema in the tooth row. The maxillae of *Farancia* are more robust and have the two processes more widely separated. Forms similar to the fossils include *Drymarchon*, which has more teeth (ca 22) in adults and *C. constrictor*, which differs only in lacking the constriction of the maxillary ramus at the level of the ectopterygoid process. Both *M. flagellum* and *M. taeniatus* have the constriction described in the fossils. Four maxillae of the latter differ from the fossils in having more (17-18) teeth.

The three fossil compound bones are referable to *Masticophis* based on the characters discussed under *Coluber constrictor*.

DISTRIBUTION. — *M. flagellum* is found throughout the southern half of the United States and in northern Mexico. The fossil record of *M. flagellum* must be regarded with caution because of the difficulty involved in distinguishing this species from *C. constrictor* and other species of *Masticophis*. Vertebrae of this species have been reported from the Blanton of Arizona (Lindsay and Tessman 1974) and Texas (Rogers 1976), the Irvingtonian of Florida (Holman 1959a; Auffenberg 1963) and Arkansas (Dowling 1958), and the Rancholabrean of Arizona, Arkansas, California, Florida, New Mexico, Nevada, and Virginia (see Holman 1981).

REMARKS. — The Inglis material is the earliest reported from Florida and includes the oldest known cranial material. It substantiates the appearance of *Masticophis flagellum* by the earliest Pleistocene.

GENUS *Opheodrys* FITZINGER 1843

Opheodrys vernalis (HARLAN) 1827

REFERRED MATERIAL. — UF 26368, 29 vertebrae.

DESCRIPTION. — These vertebrae have centra which are longer than wide (CL/NAW $\bar{X} = 1.54 \pm .145$). They are nearly square across the zygapophyseal faces (POPR/PRPR $\bar{X} = 1.03 \pm .061$). The cotyle is oval and epizygapophyseal spines are present. The accessory processes are short and often laterally directed. The haemal keel and subcentral ridges are poorly developed.

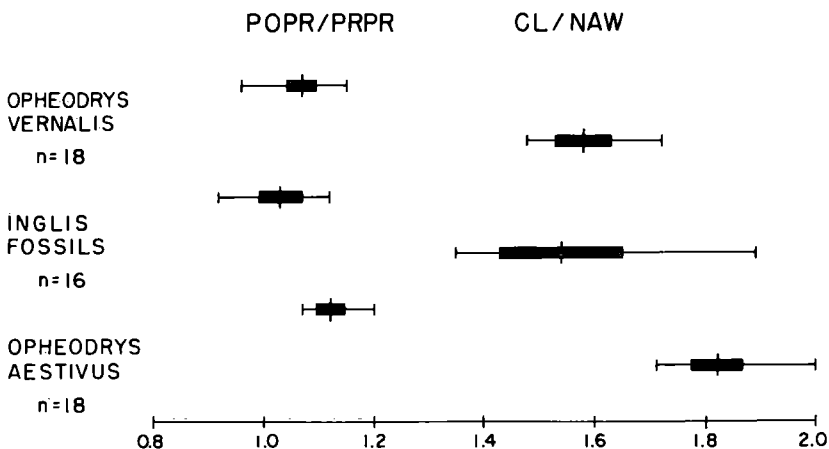


Figure 8. — Diagnostic ratios for the vertebrae of North American *Opheodrys*. Mean, 95% confidence limits, and range are indicated. POPR/PRPR = postzygapophyseal to prezygapophyseal length/width across the prezygapophyses, CL/NAW = centrum length/neural arch width.

COMPARISONS. — The lack of development of the accessory processes and subcentral features serves to distinguish *Opheodrys* from other North American colubrids with long narrow vertebrae.

The two extant species of *Opheodrys* can be distinguished by differences in their centrum and neural arch shapes (CL/NAW and POPR/PRPR) (Auffenberg 1963). The fossils differ significantly from *O. aestivus* in both these ratios (Fig. 8). They do not differ from *O. vernalis* and thus are assigned to this species.

DISTRIBUTION. — *O. vernalis* is at present restricted to the northeastern portion of the United States from northeastern Kansas to Maine. Isolated populations occur at medium to high elevations in several western states, North Carolina, the eastern coastal plain of Texas, and northern Mexico. *O. aestivus* occupies a nearly complimentary range from Florida to Texas, north to the Ohio River Valley and southern New Jersey. *O. aestivus*, and not *O. vernalis*, is present in the vicinity of Inglis IA today. *O. vernalis* is known as a fossil only from the Irvingtonian of Maryland (Holman 1977a). *O. aestivus* is known from Rancholabrean localities in Florida (Auffenberg 1963) and Texas (Holman 1969a).

REMARKS. — The Inglis *Opheodrys vernalis*, together with the large number of Recent isolated populations, is evidence of a once greater range for this species. The Inglis material indicates that in the early Pleistocene this species occurred as far south as Florida. The complimentary range of modern *Opheodrys aestivus* suggests that it has replaced *O. vernalis* over much of its former range. In light of the present fossil record, this would have had to occur in the middle or late Irvingtonian.

SUBFAMILY LAMPROPELTINAE DOWLING 1975

The subfamilial name Lampropeltinae is the best available for the North American constricting colubrids. In the present study, *Arizona*, *Elaphe*, and *Pituophis* have been added, on the basis of vertebral morphology, to the genera considered by Dowling and Duellman (1974) to be members of this group. Possibly the similarity in vertebral form of these snakes is due to convergence.

GENUS *Cemophora* COPE 1860

Cemophora coccinea (BLUMENBACH) 1788

APPENDIX 3-5, TABLE 5

REFERRED MATERIAL. — UF 26269, 28 vertebrae.

DESCRIPTION. — The vertebrae are moderately small (CL = 1.75-2.35 mm) and slightly longer than wide. The cotyles are as large or larger than the neural canal. Epizygapophyseal spines are absent.

Neural spines are almost as high as long, and are not undercut anteriorly. The haemal keels are narrow and not expanded posteriorly. The accessory processes are as long or longer than the prezygapophyseal width, and are directed laterally.

COMPARISONS. — The vertebrae are from a moderately small lampropeltine snake. The relative size of the neural canal indicates that the fossils are not those of juveniles of a larger species. The fossils differ from *Rhinoceilus*, which has neural spines undercut anteriorly (App. 3-5). *Arizona* is similar, but has wider vertebrae (CL/NAW, Table 4). The vertebrae of *Cemophora coccinea* can be separated from those of *Lampropeltis triangulum* only with great difficulty. The best character for separation is the ratio of the height to the length of the neural spine (NLU/NH). The neural spine of modern *L. triangulum* is not as high as that of *C. coccinea* (Table 5). Vertebrae thought to represent one or the other of these forms are referred to *C. coccinea* if NLU/NH is ≤ 2.6 and to *L. triangulum* if NLU/NH is > 3.0 . Vertebrae falling in the region of overlap ($2.6 < \text{NLU/NH} < 3.0$) were not referred to species unless they were very narrow ($\text{CL/NAW} \geq 1.40$), as in modern *C. coccinea*.

DISTRIBUTION. — Recent populations of *C. coccinea* occur throughout the southeastern United States from southern New Jersey and central Missouri to Louisiana and Florida. An isolated population occurs in southern coastal Texas. This species has been reported from a single Rancholabrean locality in Florida (Auffenberg 1963). A form with similar vertebral morphology, *Pseudocemophora antiqua*, is known from the Hemingsfordian of Florida (Auffenberg 1963) and Wyoming (Holman 1976). It is similar to both *Cemophora* and *Lampropeltis*, but its relationship to these two genera remains unclear.

Table 5. — Diagnostic ratios for the vertebrae of *Cemophora coccinea*, *Lampropeltis triangulum*, and *Arizona elegans*.

	(NLU/NH) ¹				(CL/NAW) ²			
	N	OR	\bar{X}	SD	N	OR	\bar{X}	SD
<i>Cemophora coccinea</i>								
Recent	21	1.8-3.0	2.44	.42	23	1.05-1.55	1.33	.13
fossil	27	1.4-2.8	2.00	.33	27	1.05-1.55	1.18	.13
<i>Lampropeltis triangulum</i>								
Recent	26	2.6-5.0	3.46	.77	19	1.10-1.35	1.24	.07
fossil	10	3.0-4.0	3.34	.46	10	1.0-1.29	1.19	.08
<i>Arizona elegans</i>								
Recent					16	.87-1.08	.96	.11

¹Neural Spine Length/Neural Spine Height

²Centrum Length/Neural Arch Width

REMARKS. — Williams and Wilson (1967) suggested that *Cemophora* is a specialized derivative of some member of the *L. triangulum* group, though *L. triangulum* has the lowest neural spine of any *Lampropeltis*. This apparent specialization for burrowing would have had to be reversed in order to arrive at the higher neural spines of *C. coccinea*. Thus it is more likely that *Cemophora* diverged from some earlier form of *Lampropeltis*. The Inglis fossils constitute the oldest record of *Cemophora coccinea*.

The observed range in centrum lengths of the referred vertebrae indicates that at least two individuals of *C. coccinea* were preserved in the Inglis IA fauna.

GENUS *Elaphe* FITZINGER 1833
Elaphe guttata (LINNEAUS) 1766

FIGURE 9 A-C, TABLE 6

REFERRED MATERIAL. — UF 26370, 71 vertebrae; UF 26371, 1 L pterygoid; UF 26372, 1 L compound.

DESCRIPTION. — The referred vertebrae lack hypapophyses. The centra are as wide as long (Table 6). Haemal keels are moderately to well developed and have posterior expansions. Subcentral ridges are moderately developed and straight. Accessory processes are not longer than the prezygapophyseal width. Neural spines are as tall as long. Epizygapophyseal spines are very weak or absent. Zygosphenes are usually flat or convex from above.

Only the anterior third of the large left pterygoid is preserved. The anterior margin of the ectopterygoid flange rises from the toothbearing ramus at an angle of 25°. The ectopterygoid process is not well developed. The tooth row is straight. No ridge is evident on the dorsal surface of this fragment.

The referred compound is large and nearly complete. The lingual flange is highly arched. Its dorsal edge is twice as high as the dorsal edge of the labial flange.

COMPARISONS. — The pterygoid fragment has a pterygoid flange and thus cannot represent a viperid; it is too large to be *Micrurus*. Unlike the pterygoids of the colubrine group and *Lampropeltis getulus*, there is no ridge on the dorsal surface at the level of the ectopterygoid process. The weak development of this process indicates that the fossil is not a xenodontine or natricine. The extension of the pterygoid flange is more anterior in the fossil than in *Elaphe obsoleta*, less anterior than in *Pituophis melanoleucus* and identical to *E. guttata* (see App. 3-3).

The compound differs from colubrines in having only one flange developed. The lingual flange is unlike *E. obsoleta*, *Pituophis melano-*

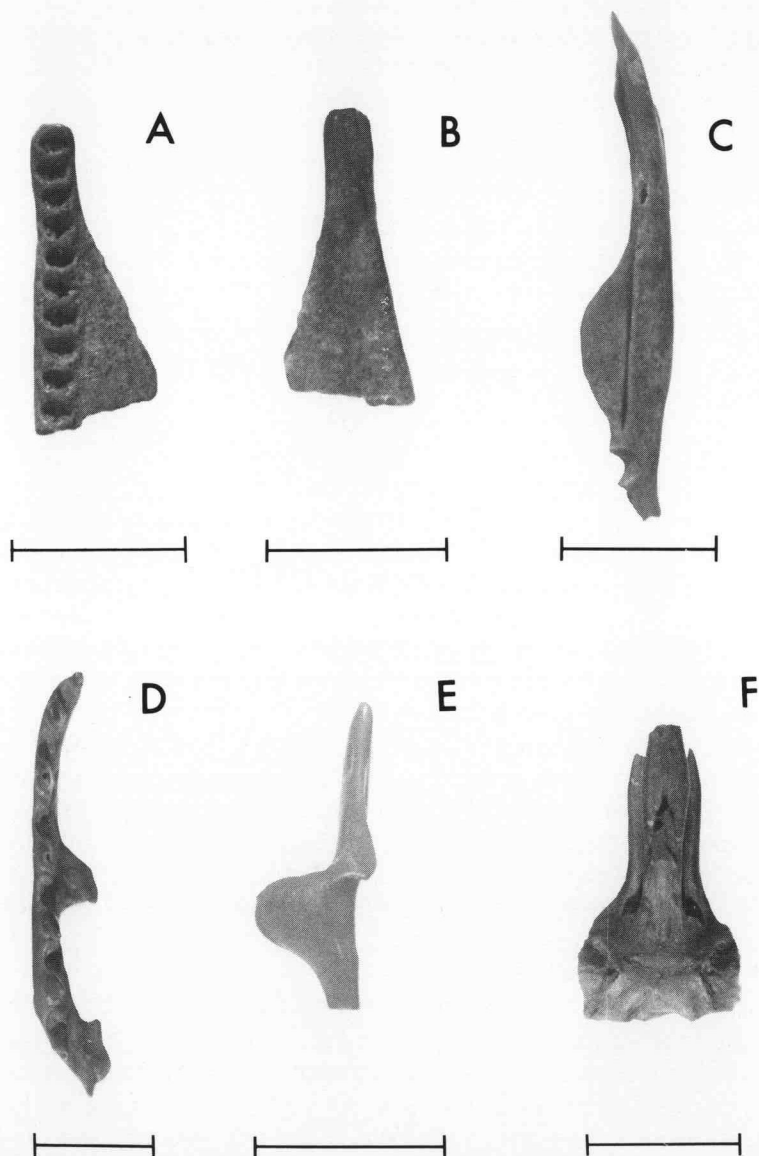


Figure 9. — Fossil *Elaphe* from Inglis IA: *Elaphe guttata* (A) pterygoid, ventral view, X5; (B) pterygoid, dorsal view, X5; (C) compound, labial view, X4. *Elaphe obsoleta* (D) maxilla, occlusal view, X2; (E) palatine, dorsal view, X5; (F) parasphenoid, dorsal view, X4 (each scale = 5 mm).

leucus, and *Lampropeltis calligaster* in being highly arched. This condition is present in *Farancia abacura*, *Lampropeltis getulus*, *Elaphe guttata*, and viperids. The two former have taller labial flanges than the fossil. Viperids have a less symmetrically arched labial flange (see Figs. 31-32, Brattstrom 1964).

The referred vertebrae are of the lampropeltine type. *Lampropeltis getulus* differs from the fossils in having better developed subcentral ridges (strong in 83% of *L. getulus* and 47% of *E. guttata*) that curve inward near the condyle (Brattstrom 1955a; Auffenberg 1963). *Pituophis* is unlike the fossils in having higher neural spines and zygosphenes that are usually concave from above (Auffenberg 1963). The fossils have better developed subcentral ridges than *Arizona*. They are larger than the vertebrae of *Lampropeltis triangulum* and *Cemophora coccinea* (1.6-2.45 mm CL in *L. triangulum*, 1.75-2.35 mm CL in *C. coccinea*, and 3.2-6.6 mm in the fossils). The fossil vertebrae are similar to several species of *Elaphe*.

The vertebrae of various *Elaphe* species have been separated on the basis of the height of the neural spine (Auffenberg 1963; Holman 1968a). *E. vulpina* has a lower neural spine than *E. guttata* or *E. obsoleta*. It is not present in the Inglis fauna. Discriminant analysis was used to assign the vertebrae to *E. obsoleta* or *E. guttata*. The analysis is based on 28 vertebrae from four individuals of *Elaphe guttata* and 38 vertebrae from five individuals of *Elaphe obsoleta*. Of the 66 original observations, 7 (10.6%) were reclassified. Values for the most important measurements and ratios are found in Table 6.

DISTRIBUTION. — *Elaphe guttata* is found throughout the southern half of the United States from New Mexico, Colorado, and northeastern Mexico to New Jersey and Florida. Fossils of this species are known from the Blanton of Texas (Rogers 1976) and Kansas (Brattstrom 1967), the Irvingtonian of Kansas (Brattstrom 1967), and the

Table 6. — The four most important ratios for the separation of *Elaphe obsoleta* and *Elaphe guttata* by discriminant analysis.

	(CL/NAW) ¹	(CL/CTW) ²	(ZW/NAW) ³	(CL/ZW) ⁴
<i>Elaphe guttata</i>				
Recent (N = 32)	1.10 ± .11	1.74 ± .11	.81 ± .06	1.35 ± .14
fossils (N = 71)	1.08 ± .09	1.49 ± .19	.81 ± .06	1.34 ± .13
<i>Elaphe obsoleta</i>				
Recent (N = 33)	1.01 ± .06	1.71 ± .15	.81 ± .07	1.25 ± .09
fossils (N = 98)	.98 ± .06	1.41 ± .18	.82 ± .06	1.19 ± .09

¹Centrum Length/Neural Arch Width

²Centrum Length/Cotyle Width

³Zygasphene Width/Neural Arch Width

⁴Centrum Length/Zygasphene Width

Rancholabrean of Kansas, Missouri, Texas, and Florida (see Holman 1981).

Four extinct species of *Elaphe* have been described from the Miocene and Pliocene of North America (Holman 1979). There is no evidence that any of these are closely related to *Elaphe guttata*.

REMARKS. — The Inglis IA fossils establish the presence of *E. guttata* in Florida by the earliest Pleistocene. The observed range in centrum lengths of the fossils shows that at least three individuals are present.

Elaphe obsoleta (SAY) 1823

FIGURE 9 D-F, TABLE 6

REFERRED MATERIAL. — UF 26373, 98 vertebrae; UF 26374, 1 L maxilla; UF 26375, 1 R palatine; UF 26376, 1 parasphenoid.

DESCRIPTION. — The vertebrae fit the description of *Elaphe guttata*. The only qualitative difference is that the neural spines tend to be higher than long.

The maxilla is nearly complete (Fig. 9 D). There is a diagonal break at the 13th tooth; probably a 14th tooth is lost. There is no diastema. The maxilla is large, but not robust. The shaft is curved medially anterior to the 4th tooth, posterior to that point it is straight. The prefrontal process is at the level of the 7th and 8th teeth. The ectopterygoid process is at the level of the 12th and 13th teeth. Both processes are subrectangular.

The palatine is moderately large. It is worn and broken posterior to the medial process. The posterior edge of the lateral process and the anterior edge of the medial process are opposite. There are four tooth positions anterior to the lateral process. The maxillary nerve foramen passes through the lateral process. The posterior opening of this foramen lies below the dorsal surface of the lateral process.

The base of the parasphenoid is missing posterior to the middle of the pituitary fossa. The cultriform process is stout, widens anteriorly, and extends beyond the suborbital flanges, which are well developed. There is a frontal step at the midpoint of the cultriform process. The suborbital flange has a smooth margin.

COMPARISONS. — The referred vertebrae have been identified by the discriminant analysis discussed under *Elaphe guttata*.

The fossil maxilla is that of a large colubrid (App. 3-1). It has fewer teeth than any natricine. The absence of a diastema indicates that it is not *Heterodon* (Fig. 12 A). Either one or both of the maxillary processes are more posteriorly located in the fossil than in *Farancia*, *Coluber*, *Drymarchon*, or *Masticophis*. Most of the maxillary ramus of the fossil is straight, unlike that in *Lampropeltis getulus* or *Pituophis melanoleucus*, which is gently curved. The maxilla of *E. guttata* and *E.*

obsoleta are similar to the fossil. That of the former differs slightly from both the fossil and *E. obsoleta* in having a posteriorly projecting prefrontal process.

The palatine differs from that of most large North American snakes in its basic form (App. 3-2). The two processes are absent in all viperids (Brattstrom 1964, Fig. 10). In *Heterodon* the base of this lateral process extends to the anterior end of the bone. The medial process of all large *Nerodia* species has a shorter base than the fossil. *Drymarchon*, *Coluber*, and *Masticophis* have medial and lateral processes that arise from the same section of the toothed ramus. In the fossil the base of the lateral process lies completely anterior to the base of the medial process. The fossil differs from the remaining large lampropeltines, except *E. obsoleta* and *E. vulpina*, in the placement of the maxillary nerve foramen in the lateral process. In the fossil the posterior opening of the foramen is below the dorsal surface of this process. In *Elaphe guttata*, *Pituophis melanoleucus*, *Lampropeltis getulus*, and *Lampropeltis calligaster*, this opening is in the dorsal surface of the lateral process. The final assignment of the fossil to *E. obsoleta* rather than *E. vulpina* is based on the presence of vertebrae of the former.

The fossil parasphenoid differs from those of viperids in being narrower and in lacking the ventral keel found in that group (see Figs. 25-26, Brattstrom 1964). Unlike the fossil, larger natricines have no frontal steps on the cultriform process. The fossil differs from *Heterodon*, in which orbital flanges are absent or restricted to the basal part of the bone. The cultriform process is narrower than in *Farancia*, but wider than in *Drymarchon*, *Coluber*, and *Masticophis*. The latter three also have suborbital flanges reaching the anterior end of the cultriform process. The suborbital flanges in *Lampropeltis getulus* and *Elaphe guttata* are poorly developed, which results in a narrower cultriform process than in the fossil. The fossil is very similar to *Pituophis melanoleucus* and *E. obsoleta*, but it lacks the small notches present in the suborbital flanges on either side of the parasphenoid in *Pituophis*, and thus is assigned to *E. obsoleta* (see App. 3-4).

DISTRIBUTION. — *Elaphe obsoleta* is found today throughout the eastern half of the United States. It is known as a fossil from the Blancan and Irvingtonian of Kansas (Brattstrom 1967) and Blancan of Texas (Rogers 1976). It is also present in seven middle to late Pleistocene sites in Florida (see Holman 1981). Holman (1973) provided a tentative phylogeny for *Elaphe* in which he designated *E. buisi* Holman from the middle Pliocene of Oklahoma and *E. kansensis* (Gilmore) from the lower Pliocene of Kansas as ancestors to *E. obsoleta*.

REMARKS. — The Inglis material documents the presence of this species in Florida at the beginning of the Irvingtonian. *E. obsoleta* is

thus widely distributed by the early Pleistocene. At least two individuals are represented in the fauna.

GENUS *Lampropeltis* FITZINGER 1843
Lampropeltis getulus (LINNEAUS) 1766

REFERRED MATERIAL. — UF 26377, 58 vertebrae.

DESCRIPTION. — The referred vertebrae are short and wide with moderate to low neural spines. The neural arches are slightly depressed. The subcentral ridges are very well developed (in most they are so strong that the ventral surface of the centrum appears to be excavated between the subcentral ridges and haemal keel). Subcentral ridges curve inward near the cotyle. Haemal keels are usually widened posteriorly.

COMPARISONS. — The extreme development of the subcentral ridges of *Lampropeltis getulus* distinguishes it from most other large lampropeltines (Auffenberg 1963). *Lampropeltis calligaster* is similar, but has haemal keels that remain uniformly narrow to the condyle (100% vs. 23% in *L. getulus*). It also has less well developed subcentral ridges (88% moderate to weak vs. 83% strong in *L. getulus*). *Farancia* also has similar vertebrae, but has more depressed neural arches and wider, blunter accessory processes (Auffenberg 1963).

DISTRIBUTION. — *L. getulus* ranges from coast to coast across the southern United States and northern Mexico. This species is known as a fossil from Blancan localities in Kansas (Brattstrom 1967) and Texas (Rogers 1976), Irvingtonian localities in Kansas (Brattstrom 1967), Texas (Holman 1969b), and Florida (Holman 1959a), and Rancholabrean localities in Arizona, California, Florida, Georgia, Kansas, New Mexico, Nevada, Tennessee, and Texas (see Holman 1981). Two extinct species of *Lampropeltis* have been described, but they are more closely related to the tricolored king snakes, including *L. triangulum* (Holman 1970), and are discussed under that heading.

REMARKS. — Blanchard (1921) and Blaney (1977) suggested that the Recent subspecies, *Lampropeltis getulus splendida*, from Texas and Mexico best approximates the ancestor of now widely dispersed and highly variable *Lampropeltis getulus*. Blaney (1977) considered the peninsular Florida form, *L. g. floridana*, to be a direct and closely related derivative of *L. g. splendida*. Thus a *splendida*-like form was probably once widespread. The Inglis record now indicates that this had occurred by the earliest Pleistocene.

At least two individuals of *L. getulus*, one large and one of medium size, were preserved in the Inglis fauna.

Lampropeltis triangulum (LACEPEDE) 1788

TABLE 4

REFERRED MATERIAL. — UF 26378, 10 vertebrae.

DESCRIPTION. — These vertebrae are slightly longer than wide, moderately small, and have cotyles as large or larger than the neural canal. Neural spines are low. Accessory processes are moderate to long and typically anterolaterally directed. Haemal keels are usually narrow and not flared posteriorly. Subcentral ridges are not well developed.

COMPARISONS. — The vertebrae represent a moderately small lampropeltine snake. The relative size of the neural canal indicates that they are not juveniles of large species. The only moderately small lampropeltine with a neural spine as low as that of the fossils is *L. triangulum* (see Comparisons under *Cemophora coccinea*).

DISTRIBUTIONS. — *L. triangulum* is presently distributed throughout the eastern three-quarters of the United States and ranges south to northern South America. The species is known from the Blanton of Kansas and Oklahoma (Brattstrom 1967) and Texas (Rogers 1976); the Irvingtonian of Kansas (Brattstrom 1967) and Maryland (Holman 1977a); and the Rancholabrean of Arkansas, Florida, Georgia, Kansas, Missouri, Pennsylvania, Tennessee, Texas, and Virginia (see Holman 1981). Two related forms are the extinct species *Lampropeltis similis* Holman, known from the late Miocene and early Pliocene of the Midwest (Holman 1979), and *Lampropeltis intermedius*, known from the late Pliocene and earliest Pleistocene of Mexico and Arizona (Brattstrom 1955a, b).

REMARKS. — Brattstrom (1955a) considered *Lampropeltis intermedius* to be ancestral to *L. triangulum* and the mountain kingsnakes *Lampropeltis pyromelana* and *Lampropeltis zonata*. Holman (1964) suggested that *Lampropeltis similis* is ancestral to *L. intermedius*. It is noted that *L. intermedius* is limited to the southwest, the suggested center of origin for *L. triangulum* (Blanchard 1921). Blanchard (1921) hypothesized a pre-Pleistocene radiation of *L. triangulum* from the southwest into the southeast. The Inglis material supports this hypothesis. Blanchard also suggested a postglacial migration of the northern forms of *L. triangulum*, but the fossil record indicates that this dispersal was a pre-Pleistocene or, at least an early Pleistocene event.

All the referred vertebrae could have come from a single vertebral column.

GENUS *Pituophis* HOLBROOK 1842
Pituophis melanoleucus (DAUDIN) 1803

REFERRED MATERIAL. — UF 26379, 129 vertebrae.

DESCRIPTION. — These vertebrae have high neural spines which do not overhang anteriorly and overhang only slightly posteriorly. The zygosphenes are convex from anterior, and flat to concave from above. Subcentral ridges are moderate to weak.

COMPARISONS. — Large lamppropeltine snakes other than *Elaphe* can be distinguished from adult *Pituophis* by their lower neural spines alone (Auffenberg 1963). *Elaphe* also has relatively lower neural spines but some overlap occurs (see Tables 15 and 16; Auffenberg 1963). The fossils are referred to *Pituophis melanoleucus* on the presence of very high neural spines, zygosphenes that are always convex from anterior (concave or flat in 41% of *Elaphe*), and poorly developed subcentral ridges (weak in 78% of *P. melanoleucus*, strong to moderate in 67% of *Elaphe*).

DISTRIBUTION. — *P. melanoleucus* ranges from coast to coast, from New Jersey to Florida and British Columbia to northern Mexico, with a significant hiatus in the Mississippi Valley.

Fossils are known from the Blanton of Texas (Brattstrom 1967) and Kansas (Rogers 1976), the Irvingtonian of Florida (Holman 1959a) and Kansas (Brattstrom 1967), and the Rancholabrean of Arizona, Arkansas, California, Florida, Illinois, Kansas, Missouri, Nevada, New Mexico, Oklahoma, and Texas (see Holman 1981).

REMARKS. — The Inglis material indicates that *P. melanoleucus* was already widespread by the beginning of the Irvingtonian. The observed range in centrum length indicates that at least three individuals are present in the Inglis fauna.

GENUS *Stilosoma* BROWN 1890
Stilosoma extenuatum BROWN 1890

REFERRED MATERIAL. — UF 26380, 5 vertebrae.

DESCRIPTION. — The referred vertebrae are small. The oval cotyles are about equal in size to the neural canal. The centra are nearly as wide as long. Accessory processes are pointed and laterally directed. Haemal keels are well developed but do not widen posteriorly.

COMPARISONS. — The size of these vertebrae and the relative size of the neural canals suggest a small but mature snake. All small snakes extant in the eastern United States have anterolaterally directed accessory processes except *Rhadinaea flavilata* and *Stilosoma extenuatum*, in which they are laterally directed. *R. flavilata* differs from the fossils in having blunt accessory processes and haemal keels that

broaden posteriorly. The Pliocene form, *Stilosoma vetustum* Auffenberg, differs from the extant species and from the Inglis fossils in having a narrower, more ridge-like haemal keel.

DISTRIBUTION. — *Stilosoma* is endemic to northern peninsular Florida. Records of this genus as a fossil fall within its present range. *S. extenuatum* may be represented by vertebrae from two middle to late Pleistocene sites near Gainesville, Florida (Auffenberg 1963; Martin 1974). *S. vetustum* is known only from the middle Pliocene, Haile VI locality (Auffenberg 1963).

REMARKS. — The Inglis material is the first clearly referable to *Stilosoma extenuatum*. The material could represent a single individual.

SUBFAMILY *Natricinae* BONAPARTE 1838

Various caenophidians, including all natricines, viperids, and elapids, have hypapophyses present throughout the vertebral column. In the natricines they are wide in lateral view and somewhat laterally compressed. The hypapophyses are fin-like, rather than cylindrical as in viperids and elapids. Because all caenophidians have hypapophyses present in the anterior portion of the column, natricine vertebrae are easily confused with the anterior precaudals of many species. Although no simple character will distinguish them, anterior precaudals of non-natricine colubrids can often be identified by their wide neural canals, reduced accessory processes, posteriorly sloping neural spines, or distinctly non-natricine hypapophyseal shapes.

GENUS *Nerodia* BAIRD AND GIRARD 1853

Nerodia cyclopion (DUMERIL, BIBRON AND DUMERIL) 1854

REFERRED MATERIAL. — UF 26381, 5 vertebrae.

DESCRIPTION. — These are moderately large vertebrae. The centra are short and wide. Neural spines are high and overhang anteriorly and posteriorly to the same extent, giving the neural spine a nearly symmetrical outline in lateral view (see Fig. 42 in Auffenberg 1963). Hypapophyses are short and broad.

COMPARISONS. — The vertebrae are assigned to *Nerodia* on the basis of their size, short, broad hypapophyses, and short, wide centra (Brattstrom 1967). Holman (1962, 1968a, 1970, 1971) and others separated *Nerodia* into three artificial groups based on the length-height relationship of the neural spine. *Nerodia sipedon*, *N. fasciata*, and the extinct forms *N. hibbardi*, *N. hillmani*, and *Neonatrix elongata* have neural spines that are longer than high. *Nerodia erythrogaster* has neural spines that are as long as high. *Nerodia cyclopion*, *N. taxispilota*, and *N. rhombifera* have neural spines that are higher than long.

The referred vertebrae belong to this last group. They differ from *N. taxispilota* and *N. rhombifera*, which have neural spines that overhang more posteriorly than anteriorly. Only *N. cyclopion* shows the near symmetry seen in lateral view of these fossils. Thus, this sample is assigned to *N. cyclopion*.

DISTRIBUTION. — *Nerodia cyclopion* is present today along the coastal plain from eastern Texas to southern South Carolina and up the Mississippi Valley to southern Illinois. *N. cyclopion* is known as a fossil from three Rancholabrean localities in Florida (Auffenberg 1963). Eight vertebrae from the late Blancan Beck Ranch locality in central Texas represent *N. cyclopion* or *N. rhombifera* (Rogers 1976).

REMARKS. — *N. cyclopion* is not common as a fossil. The Inglis material is the first evidence of its presence in the Irvingtonian. It and the material from the Beck Ranch (Rogers 1976) indicate that one or two high-spined forms of *Nerodia* had evolved by the Irvingtonian.

Nerodia erythrogaster (FORSTER) 1771

REFERRED MATERIAL. — UF 26382, 1 vertebra.

DESCRIPTION. — This short, wide natricine vertebra has a neural spine which is as high as it is long. Accessory processes are longer than the prezygapophyseal width and are anterolaterally directed.

COMPARISONS. — The fossil resembles *Nerodia erythrogaster* in the size of the neural spine (see *Nerodia cyclopion*). It can be distinguished from *N. fasciata* and *N. sipedon* by its longer, more anteriorly directed accessory processes.

DISTRIBUTION. — *N. erythrogaster* is present throughout the south from Texas and Mexico to southern Illinois and the Delmarva Peninsula. As a fossil it is known from the late Blancan of Texas (Rogers 1976), the Irvingtonian of Texas (Holman 1969b), and the Rancholabrean of Texas (Holman 1969a) and Florida (Auffenberg 1963).

REMARKS. — As in the *Nerodia cyclopion* group discussed above, *N. erythrogaster* appears to be distinct and widely distributed by the beginning of the Pleistocene. A single individual is represented in the fauna.

GENUS *Regina* BAIRD AND GIRARD 1853

Regina intermedia new species

FIGURE 10 A-C, J, K

DIAGNOSIS. — An early Pleistocene natricine snake closely resembling *Regina rigida*. It differs from all modern members of the genus in features of the dentary. The teeth are stout and blunt like those of *R. alleni* and *R. rigida*, but they are not hinged as in those species (Rojas and Godley 1979). The teeth are well ankylosed as in *R. septemvittata*.

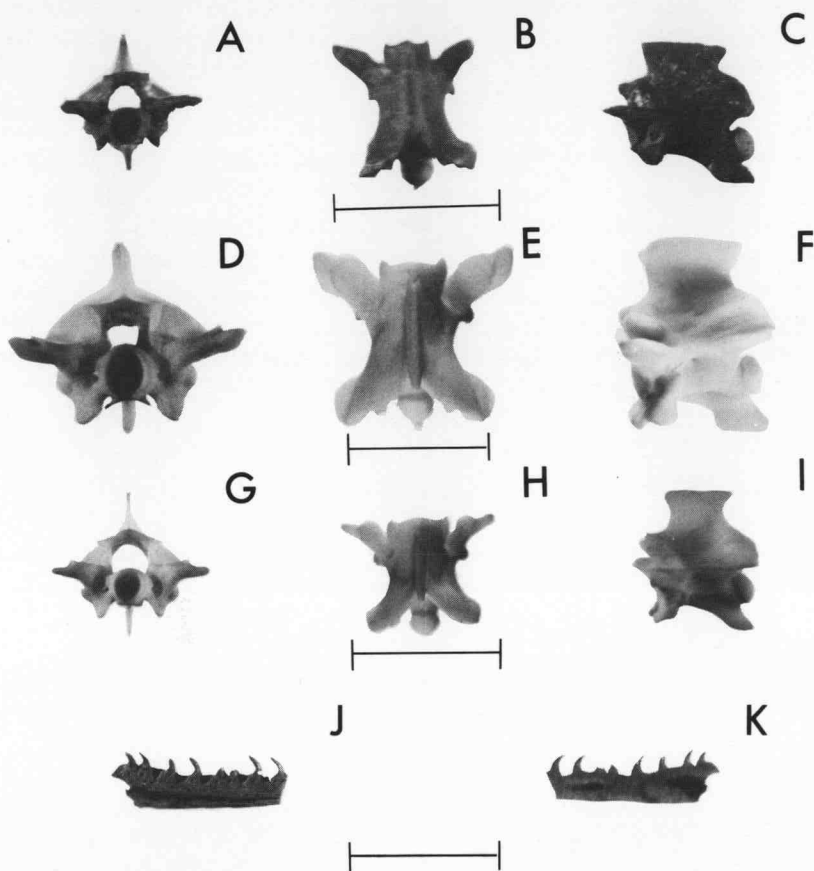


Figure 10. — Fossil and Recent *Regina*: *Regina intermedia* (n. sp.) vertebra, X4; (A) frontal, (B) dorsal, and (C) lateral views. Recent *Regina rigida* vertebra, X4; (D) frontal, (E) dorsal, and (F) lateral views. Recent *Regina alleni* vertebra, X4; (G) frontal, (H) dorsal, and (I) lateral views. *Regina intermedia* (n. sp.) dentary (HOLOTYPE), X4; (J) lingual and (K) labial views (each scale = 5 mm).

and *R. grahami*. These two species differ from *R. intermedia* in having thinner, sharper teeth.

HOLOTYPE. — UF 26383; the middle third of a left dentary from the early Irvingtonian Inglis IA Local Fauna, Citrus County, Florida.

REFERRED MATERIAL. — UF 26384, 7 vertebrae.

DESCRIPTION. — The holotype is broken anteriorly and posteriorly. It is straight and shallow. Meckle's groove is open throughout its length. Thirteen tooth positions are present; eight retain well ankylosed teeth. Five unbroken teeth are short, stout, and blunt.

The referred vertebrae have neural spines that are slightly flattened on the dorsal edge (= "ground off" of Auffenberg 1963). The neural spines are long and low and undercut anteriorly and posteriorly. The vertebrae have small hypapophyses and short blunt accessory processes.

COMPARISONS. — The presence of an open Meckle's groove so far anterior in the dentary (App. 3-6), and short, stout, blunt teeth are not common among North American snakes. These characters do occur in the crayfish-eating snakes of the genus *Regina*. The type differs from all living members of the genus in having blunt and firmly ankylosed teeth.

Neural spines with flattened dorsal edges have been reported for the vertebrae of two natricine species, *Storeria dekayi* and *Regina alleni* (Auffenberg 1963). They also occur in adult *Regina rigida* (Fig. 10 D-F). The referred vertebrae are too large (2.75-3.50 mm CL) to be *S. dekayi* (1.13-2.13 mm CL). They differ from *R. alleni* in having shorter, more blunt accessory processes and lower neural spines (Fig. 10 G-I). No apparent difference is evident between the vertebrae of *R. rigida* and *R. intermedia*.

DISTRIBUTION. — The genus *Regina* occurs throughout most of the midwest and eastern United States. The fossil record for the genus includes *R. alleni* from the Rancholabrean of Florida (Auffenberg 1963) and *R. grahami* from the Irvingtonian of Kansas (Holman 1972).

REMARKS. — Wilson (1968) described an extinct natricine, *Natrix hillmani*, from the late Miocene of Kansas. He assigned it to *Natrix* only because he questioned the validity of the genus *Regina*, but he implied that its affinities lie with *Regina*. Thus, it appears that the genus *Regina* was established by the late Miocene and had begun diversification by the Pleistocene, with two species known in the Irvingtonian and three by the Rancholabrean.

Regina intermedia receives its name from its intermediate position between primitive and advanced *Regina*. The primitive forms have thin unhinged teeth and eat only freshly molted crayfish (Branson and Baker 1974). The advanced forms have evolved stout, blunt, hinged teeth and, at least in the case of *R. alleni*, distinctive behavior which allows them to capture and eat hardshelled crayfish (Franz 1977).

A scenario for the phylogeny of *Regina* is presented in Figure 11. The presence of *R. intermedia* in the Inglis IA fauna indicates that the split between the primitive and the advanced forms of the genus must have occurred by the end of the Pliocene as suggested by Rossman (1963b). *Regina alleni* is depicted as arising from the proto-*rigida* (*R. intermedia*)-*Regina rigida* line following Rossman.

Table 7. — The four most important ratios in the discrimination of *Thamnophis sirtalis*, *Thamnophis proximus*, and *Thamnophis sauritus*.

	POPR/NAW ¹	POPR/CL ²	CL/NAW ³	PRPR/CL ⁴
<i>Thamnophis proximus</i>				
Recent (N = 22)	1.84 ± .11	1.19 ± .04	1.55 ± .10	1.17 ± .06
<i>Thamnophis sirtalis</i>				
Recent (N = 27)	1.94 ± .10	1.21 ± .06	1.61 ± .10	1.16 ± .06
<i>Thamnophis sauritus</i>				
Recent (N = 25)	2.00 ± .11	1.19 ± .03	1.69 ± .11	1.16 ± .09
fossils (N = 17)	1.93 ± .17	1.18 ± .06	1.64 ± .12	1.15 ± .11

¹Postzygapophysis to Prezygapophysis Length/Neural Arch Width²Postzygapophysis to Prezygapophysis Length/Centrum Length³Centrum Length/Neural Arch Width⁴Prezygapophysis to Prezygapophysis Length/Centrum Length

out that this practice may produce some error. A highly aquatic garter snake like *Thamnophis melanogaster* could be present in the later Cenozoic of North America, yet remain undetected because it has the short, wide vertebrae typical of *Nerodia*.

COMPARISONS. — The vertebrae referred to *Thamnophis* were identified to species using discriminant analysis. Discriminant functions were created using 25 vertebrae from four *T. sauritus*, 27 vertebrae from four *T. sirtalis* and 22 vertebrae from three *T. proximus*. The program reclassified 15 of 74 (20.2%) of these vertebrae. The most important characters for the separation of these species are given in Table 7.

DISTRIBUTION. — *T. sauritus* occurs today throughout the United States east of the Mississippi River. The closely related form *T. proximus* occurs in the Great Plains states and the Mississippi Valley as far north as Wisconsin. Because of the difficulty in distinguishing species of *Thamnophis*, much material has been referred to *Thamnophis* sp. The genus may be present as early as late Miocene (Holman 1977b; Webb et al. 1981). There are numerous late Pliocene and Pleistocene records for *Thamnophis* sp., but the only material referred to *T. sauritus* is from the Rancholabrean of Tennessee (Guilday et al. 1978).

REMARKS. — Rossman (1963a) suggested that *T. sauritus* evolved from *T. proximus* or its prototype. He felt that the longer tail and reduced supralabial scale count in *T. sauritus* indicate specialization. Speciation was thought to have occurred during the Pleistocene, when the ribbon snake stock was isolated in Floridian and Mexican refugia. If Rossman's suggestion that *T. sauritus* is derived from *T. proximus* is correct, then the Inglis material clearly indicates a pre-Pleistocene separation, but if a *sauritus*-like form, at least in vertebral characters, is ancestral to *T. proximus*, this separation could have occurred during the Pleistocene.

GENUS *Virginia* BAIRD AND GIRARD 1853

REFERRED MATERIAL. — UF 26386, 3 vertebrae.

DESCRIPTION. — The vertebrae are short ($< 1.75\text{mm}$) in centrum length. Hypapophyses are small. Neural canals are about equal in width to the cotyle. Neural spines are twice as long as they are high, and are not flattened dorsally.

COMPARISONS. — The vertebrae represent a very small but mature natricine snake. *Seminatrix* has a neural spine which is as tall as long. The fossils ($\text{CL/NAW} = 1.22\text{--}1.50$) are wider than *Storeria* ($\text{CL/NAW} = 1.67\text{--}1.83$) and *Tropidoclonion* ($\text{CL/NAW} = 1.62\text{--}2.00$). The width of the fossils falls into the range of modern *Virginia* ($\text{CL/NAW} = 1.20\text{--}1.66$). Like the fossils, the neural spines of *Virginia* are long and low and not dorsally flattened. As no diagnostic characters for the two extant species of *Virginia* were found, no attempt was made to assign the fossils to species.

DISTRIBUTION. — *Virginia* is presently found throughout the eastern United States from Iowa and Texas to New Jersey and North Florida. There are records of *Virginia* from the late Pleistocene of Texas (Holman 1963) and Virginia (Guilday 1962).

REMARKS. — The Inglis material extends the record of this genus into the early Pleistocene. Thus *Virginia*, like the natricines discussed above, had differentiated by the earliest Pleistocene.

SUBFAMILY XENODONTINAE BONAPARTE 1845

GENUS *Diadophis* BAIRD AND GIRARD 1853*Diadophis elinorae* AUFFENBERG 1963

REFERRED MATERIAL. — UF 26387, 3 vertebrae.

DESCRIPTION. — The vertebrae are very small, but represent a mature snake. Accessory processes extend anteriorly beyond the prezygapophyseal facets, but are not longer than the width of the facet. They are hooked anteriorly and are not markedly pointed. The neural spine is nearly as tall as the cotyle and overhangs posteriorly. The zygosphenes are crenate from above and flat or nearly flat from anterior. The haemal keel is narrow and the subcentral ridges are weakly to moderately developed.

COMPARISONS. — The shape and position of the accessory processes distinguish *Diadophis* from *Stilosoma*, *Tantilla*, *Sonora*, and *Rhadinæa* (App. 3-5). The shape of the zygosphenes and the taller neural spine with a posterior overhang separates it from *Carphophis* (Auffenberg 1963). The Inglis material compares more closely to Auffenberg's *Diadophis elinorae* (Hemiphillian, Florida) than to Recent *D. punctatus*. As described for *D. elinorae*, the haemal keel of the fossil is narrower and the subcentral ridges better developed than in *D. punc-*

tatus. Neural spines are taller than those in *D. punctatus* and overhang only slightly in one of the three vertebrae.

DISTRIBUTION. — Recent *Diadophis punctatus* is found throughout most of North America. It is absent from the northern Rocky Mountains, the northern Great Plains, and coastal Mexico. Fossils of *D. punctatus* are recorded from the Rancholabrean of Florida (Holman 1959a; Auffenberg 1963), Georgia (Holman 1967), Maryland (Holman 1977a), and Texas (Holman 1969a) and from the Irvingtonian of Kansas (Brattstrom 1967).

REMARKS. — Haemal keels and subcentral ridges tend to be better developed in terrestrial rather than fossorial snakes. Extreme reduction of these features occurs in burrowers (scolecophidians, *Heterodon*) (Holman 1979). Thus the slight difference between *D. elinorae* and *D. punctatus* may indicate a minor shift in the ecology of ringneck snakes from the Irvingtonian to present times. The slightly higher neural spine and the greater development of subcentral features suggest that *D. elinorae* was less fossorial and perhaps less secretive than modern *D. punctatus*.

All three vertebrae could be from a single individual.

cf. *Dryinoides* AUFFENBERG 1958

FIGURE 12 F-H

REFERRED MATERIAL — UF 26388, 26 vertebrae; UF 26389, 1 R, 1 L maxillae (tentative).

DESCRIPTION — The vertebrae are dorsoventrally compressed. Haemal keels and subcentral ridges are moderately to well developed. Subcentral ridges extend three-quarters or more of the length of the centrum. In some vertebrae the subcentral ridges are so well developed that the area between them and the haemal keel appears to be excavated. Neural spines are low.

The right maxilla is unbroken but lacks teeth. It has sockets for eight teeth. No diastema is present. The sockets for the two posterior-most teeth are slightly enlarged. The entire bone is short and straight. The prefrontal process is at the level of the 3rd and 4th teeth. The ectopterygoid process is at the level of the 6th and 7th teeth. The left maxilla is broken across the prefrontal process. It is slightly larger than the right maxilla, and has an additional tooth socket posterior to the prefrontal process. It is also very straight. Teeth are present in the last and the third-to-last sockets. The last tooth is broken but is larger at its base than the single tooth anterior to it.

COMPARISONS. — The dorsoventrally flattened or depressed neural arches of the vertebrae are typical of the xenodontine genus *Heterodon*, but in *Heterodon* the subcentral ridges, if present, do not extend

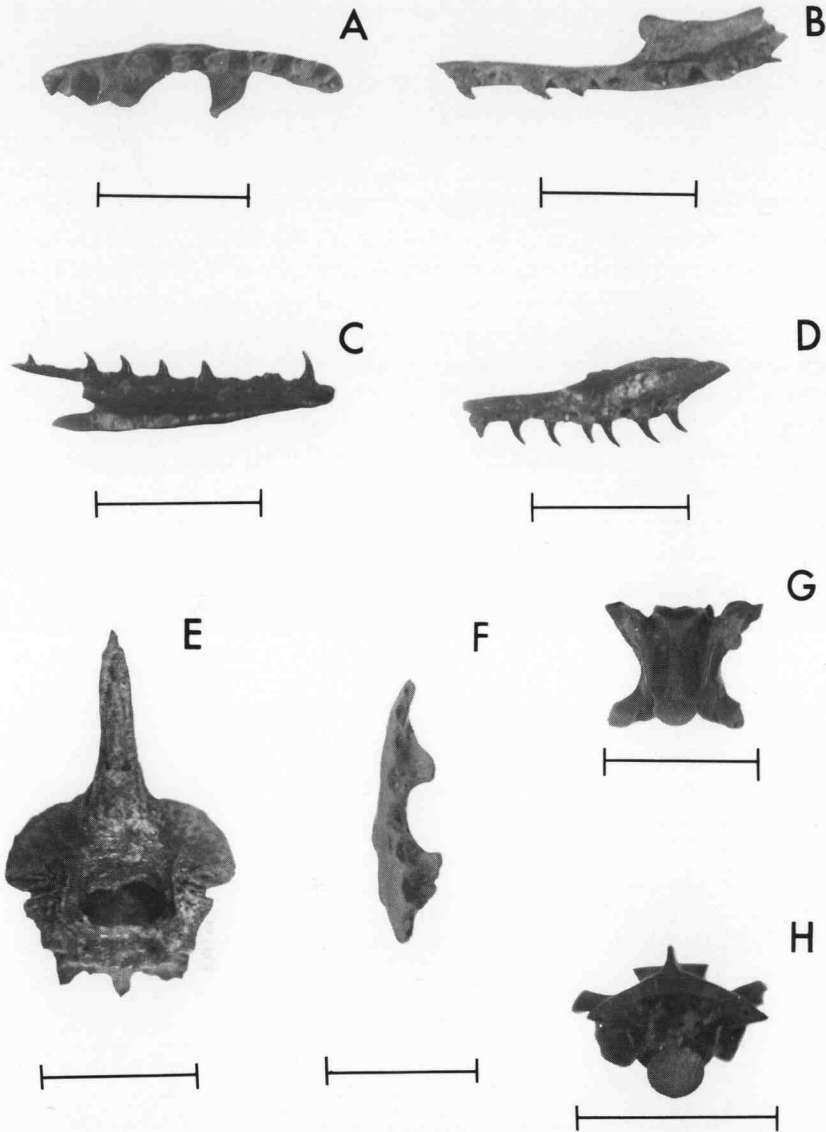


Figure 12. — Fossil xenodontine snakes from Inglis IA: *Heterodon platyrhinos* (A) maxilla, oclusal view, X4; (B) pterygoid, ventral view, X4; (C) dentary, labial view, X4; (E) basiparasphenoid, dorsal view, X4. *Heterodon nasicus* (D) pterygoid, ventral view, X4. Xenodontine, cf. *Dryinoides* (F) maxilla, oclusal view, X5; and (G) ventral and (H) posterior views of vertebrae, X3 (each scale = 5 mm).

more than halfway down the centrum. The development of subcentral ridges allowed Auffenberg (1958) to distinguish the vertebrae of a new genus, *Dryinoides*, from *Heterodon*. The referred vertebrae compare well with Auffenberg's (1958) description of the middle thoracic vertebrae of *Dryinoides oxyrachis* from the Miocene of Montana.

The fossil maxillae have fewer teeth than any colubrid examined, except *Arrhyton* and *Lystrophis*. These two genera have a maxillary diastema that is lacking in the fossils. The fossil maxillae are similar to those of *H. nasicus* and *H. simus* in length and proximity of the two maxillary processes, but they are much straighter and lack the diastema present in all *Heterodon*. The type and only known specimen of *Dryinoides oxyrachis* lacks maxillae, so comparison is impossible. Auffenberg (1958) found *Arrhyton*, *Lystrophis*, and *Heterodon*, as well as *Conophis*, to be similar to *D. oxyrachis* in certain skull and vertebral characters.

REMARKS. — It is possible that the maxillaries and the vertebrae represent two different snakes, but considered separately, each suggests a snake similar to *Heterodon*, *Arrhyton*, or *Lystrophis*. Just such a snake is *Dryinoides oxyrachis* Auffenberg. The vertebrae are the best evidence for assigning the material to *Dryinoides*.

The Inglis fossils probably represent a new species. The skull of the type of *D. oxyrachis* is longer than that of *Heterodon*. The short, complete maxilla described above suggests that the Inglis fossil had a short skull, similar to *Heterodon*.

If the maxillae are correctly associated with the referred vertebrae, they suggest that the Inglis *Dryinoides* may be the relict of an ancestor to *Heterodon* as indicated in Figure 14. To derive a *Heterodon* maxilla from the Inglis cf. *Dryinoides* (Fig. 12 F) requires only that a diastema and a gentle curve be added. The species of *Heterodon* vary only in the degree of curvature and the number of teeth anterior to the diastema. The vertebrae are also easily imagined as a model for *Heterodon*, requiring only reduction of subcentral ridges and an additional depression of the neural arch.

GENUS *Farancia* GRAY 1832
Farancia abacura (HOLBROOK) 1836

FIGURE 13 A, C

REFERRED MATERIAL. — UF 26390, 1 L maxilla; UF 26391, 5 thoracic vertebrae.

DESCRIPTION. — The single maxilla is complete. It has space for 17 teeth and no diastema. The prefrontal process is simple and located anteriorly at the level of the 6th and 7th teeth. The ectopterygoid process is nearly terminal, located at the 15th and 16th teeth. The

entire bone is heavy and only very slightly curved.

The vertebrae are nearly square across the centrum and have depressed neural arches. They have well developed haemal keels, moderate to strong subcentral ridges, and blunt, laterally directed accessory processes.

COMPARISONS. — Among North American snakes only *Farancia* has such a stout maxilla with the prefrontal process so anterior in location (Fig. 13 A, B, App. 3-1). The anterior location of this process undoubtedly adds structural strength to the skull of this burrowing snake. The maxilla of *F. abacura* differs from *F. erythrogramma* in having a simple rather than recurved or hooked prefrontal process (Fig. 13 B).

In the past, isolated vertebrae of the two species of *Farancia* have been considered difficult, if not impossible, to separate (Auffenberg 1963; Holman 1978, 1981). To distinguish these species, a discriminant analysis was developed using 49 vertebrae, 31 from four individuals of *F. abacura* and 18 from three individuals of *F. erythrogramma*. The analysis reclassified three of the *F. abacura* vertebrae, indicating reliable discrimination. The analysis assigned all of the fossil vertebrae to *F. abacura*.

DISTRIBUTION. — *F. abacura* is at present limited to the Gulf coastal plain of the United States, the Mississippi Valley, and the Atlantic coastal plain as far north as Maryland. The fossil record of *Farancia* is so far restricted to the Rancholabrean of Florida (see Holman 1981).

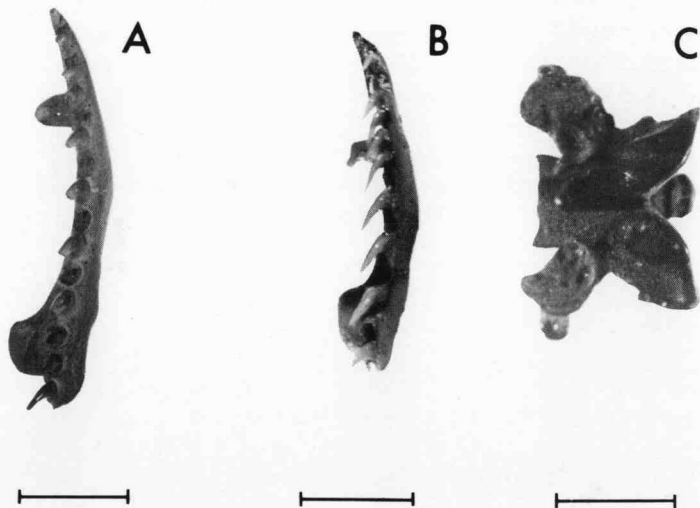


Figure 13. — Fossil and Recent *Farancia*: Fossil *Farancia abacura* (A) maxilla, occlusal view, X3; (C) vertebra, dorsal view, X3. Recent *Farancia erythrogramma* (B) maxilla, occlusal view, X3 (each scale = 5 mm).

The closely related snake *Paleofarancia brevispinosa* was described from a single vertebra from Lithia Springs, Florida, a site that includes material thought to be middle Pliocene in age.

REMARKS. — The Inglis material establishes the presence of *Farancia abacura* in the early Pleistocene of Florida. If *Paleofarancia* is ancestral to *Farancia*, it suggests modernization of the lineage by the late Pliocene.

The material probably represents a single individual. Apparently this individual had serious vertebral pathologies in the cervical region (Fig. 13 C).

GENUS *Heterodon* LATREILLE 1802

Heterodon nasicus BAIRD AND GIRARD 1852

FIGURE 12 D, TABLE 8

REFERRED MATERIAL. — UF 26392, 57 vertebrae; UF 26393, 1 L pterygoid.

DESCRIPTION. — The vertebrae are depressed and have flattened haemal keels. The subcentral ridges are weak.

The single left pterygoid has a moderately developed ectopterygoid process on the pterygoid flange. The anterior border of the flange between the ectopterygoid process and the tooth-bearing ramus is straight (Fig. 12 D).

COMPARISONS. — The specific identification of the vertebrae was carried out using discriminant analysis. The analysis is based on 21 vertebrae from three *H. nasicus*, 28 vertebrae from four *H. platyrhinos* and 30 vertebrae from four *H. simus*. The program reclassified two (2.5%) of these 79 vertebrae. The four most important variables in

Table 8. — The four most important ratios for the discrimination of *Heterodon nasicus*, *Heterodon platyrhinos*, and *Heterodon simus* (mean \pm one standard deviation).

	POPR/NAW ¹	CL/NAW ²	PRPR/CL ³	PRPR/ZW ⁴
<i>Heterodon nasicus</i>				
Recent (N = 22)	1.59 \pm .13	1.68 \pm .20	1.40 \pm .12	2.35 \pm .18
fossils (N = 57)	1.62 \pm .17	1.70 \pm .19	1.40 \pm .11	2.37 \pm .23
<i>Heterodon platyrhinos</i>				
Recent (N = 27)	1.72 \pm .16	1.57 \pm .17	1.41 \pm .08	2.20 \pm .18
fossils (N = 128)	1.75 \pm .17	1.62 \pm .15	1.39 \pm .11	2.23 \pm .16
<i>Heterodon simus</i>				
Recent (N = 30)	1.33 \pm .08	1.56 \pm .15	1.49 \pm .14	2.30 \pm .12

¹Postzygapophysis to Prezygapophysis Length/Neural Arch Width

²Centrum Length/Neural Arch Width

³Prezygapophysis to Prezygapophysis Width/Centrum Length

⁴Prezygapophysis to Prezygapophysis Width/Zygasphene Width

this analysis are POPR/NAW, CL/ZW, PRPR/CL, and PRPR/ZW (Table 8).

The pterygoid is referred to *Heterodon* because of the anterior orientation of the ectopterygoid process. It is similar to *H. nasicus* and *H. simus* in the moderate development of this process. *H. simus* has a curved anterior border to the pterygoid flange, thus the assignment to *H. nasicus*.

DISTRIBUTION. — At present *H. nasicus* ranges throughout the Great Plains from northern Mexico to southern Canada. The closely related form *H. simus* occupies the southeastern coastal plain from Mississippi to North Carolina.

The hognose snakes have a long fossil record. *H. nasicus* is known from one Blancan and two Irvingtonian sites in Kansas (Brattstrom 1967). It is also known from the Irvingtonian of Texas and from Rancholabrean sites in Kansas, New Mexico, Oklahoma, and Texas (see Holman 1981). *H. simus* is known as a fossil only from the Rancholabrean of Florida (Holman 1981). Likely ancestors of *H. nasicus* include *Heterodon plionasicus* Peters from the Blancan of Texas (Rogers 1976) and Kansas (Peters 1953; Brattstrom 1967) and *Paleoheterodon tihenii* from the upper Miocene of Nebraska and South Dakota and the lower Pliocene of Kansas (Holman 1964, 1977b).

REMARKS. — The fossil record of *H. nasicus* and its ancestors is surprisingly complete. It suggests the evolution of *H. nasicus* and *H. plionasicus* from *Plioheterodon tihenii* (Fig. 14). As a final step in this sequence, the evolution of *Heterodon simus* from *H. nasicus* is indicated by the present study. This supports Platt's (1969) rebuttal of Edgren's (1952) conclusion that *H. nasicus* evolved from *H. simus* or the two evolved in parallel fashion from *H. platyrhinos*.

The fossil record suggests that two lines of *Heterodon* have been separate since the late Miocene (Fig. 14). Two forms of *Heterodon* are present in the recently discovered Love Bone Bed of Clarendonian age in Florida (Webb et al. 1981). Although the material has not been thoroughly studied, it is apparent that both the *H. nasicus* and *H. platyrhinos* lines are represented. At the time the Inglis fauna was trapped, gene flow between western populations and the southeast was apparently unrestricted. It seems likely that the isolation of eastern populations, probably caused by increased interglacial sea levels, resulted in the differentiation of *H. simus*.

Heterodon platyrhinos LATREILLE 1802

FIGURE 12 A-C, E, TABLE 8

REFERRED MATERIAL. — UF 26344, 128 vertebrae; UF 26395, 2 L dentaries; UF 26396, 2 R maxillae; UF 26397, 1 L and 1 R pterygoids;

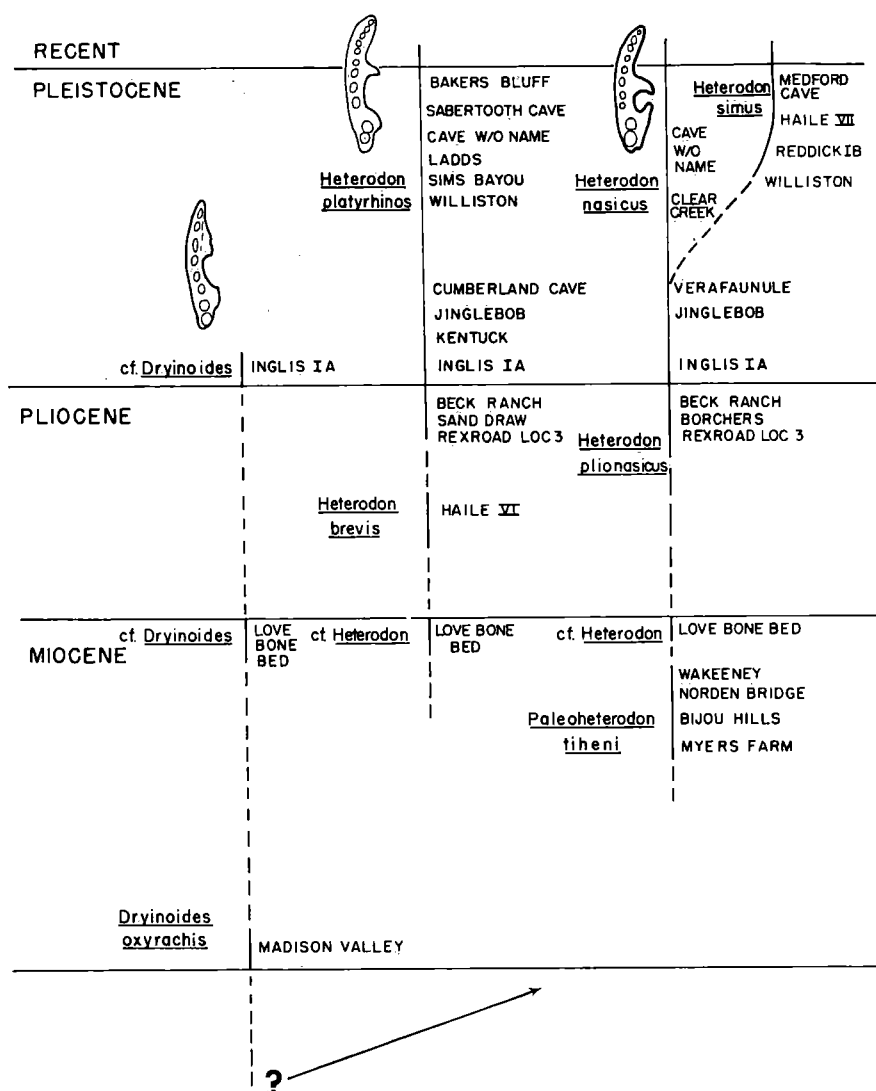


Figure 14. — A phylogenetic scenario for the North American xenodontine genera *Dryinoides* and *Heterodon*.

and UF 26398, 1 basiparaspheoid.

DESCRIPTION. — The referred vertebrae fit the description of *Heterodon nasicus*. Measurements and ratios important in the identification of the vertebrae of this species are given in Table 8.

One maxilla is complete, the other consists of only the central portion. Each possesses a diastema at the level of the ectopterygoid pro-

cess. The complete specimen is a gently curved bone with space for two enlarged teeth posterior to a diastema, and 11 smaller teeth anterior to the diastema. In neither specimen do the tips of the prefrontal and ectopterygoid processes approach each other. In the dentaries, Meckle's groove is open widely to the level of the 4th tooth; from that point to the symphysis it is reduced to a narrow slit. These bones are moderately long and narrow, tapering gradually to a point anteriorly. The compound notch on the labial surface approaches the level of the 9th tooth. The dental foramen lies at the level of the 7th tooth.

The pterygoids exhibit an anteriorly directed, round ectopterygoid process for the articulation of the posterior end of the ectopterygoid.

The basiparasphenoid has a short cultriform process. The basisphenoid and the pituitary fossa are distinctly wider than long, and suborbital flanges are well developed, but do not extend onto the cultriform process.

COMPARISONS. — The four most important characters in the discrimination of vertebrae of the extant species of *Heterodon* appear in Table 8.

Among North American snakes, only the maxillae of *Heterodon* fit the description of the fossils given above. *H. simus* and *H. nasicus* have fewer maxillary teeth and shorter, more curved maxillae with the prefrontal and ectopterygoid processes closely approaching each other.

Among snakes examined in this study, only the dentaries of *Heterodon* and a few natricines were found to have Meckle's groove present to the symphysis, but reduced to a slit at some point posterior to it (App. 3-6). This reduction in natricines varies with the species and the individual, but generally occurs posterior to the level at which it occurs in *Heterodon*. The dentaries of *H. simus* and *H. nasicus* are shorter, deeper and less tapered than *H. platyrhinos*. Among North American colubrid snakes *Heterodon* is apparently unique in having the ectopterygoid process of the pterygoid anteriorly directed. The shape of this process is variable, but it always consists of an anteriorly produced portion of the pterygoid flange. This process is best developed in *H. platyrhinos* (see Fig. 6 in Weaver 1965).

The shortened *Heterodon* skull includes a short, wide basisphenoid with a very short cultriform process. *Heterodon* is extreme among the examined colubrids in this regard (App. 3-4). The suborbital flanges in the referred fossils are more developed than those in any *H. simus* or *H. nasicus* examined. They are similar to the condition seen in adult *H. platyrhinos*.

Auffenberg (1963) described a related form, *H. brevis*, from the middle Pliocene of Florida. Its shorter neural spine distinguishes it

from *H. platyrhinos*. The ratio of centrum length to basal neural spine length (CL/NSB) for the type of *H. brevis* is 2.07. This ratio for 25 Inglis fossils ranges from 1.35 to 1.85, similar to the range of 1.32 to 1.82 for *H. platyrhinos* given by Auffenberg (1963).

DISTRIBUTION. — *H. platyrhinos* is found throughout the United States east of the Great Plains. It is present as a fossil in the Blencoe of Kansas and Nebraska (Brattstrom 1967) and Texas (Rogers 1976), the Irvingtonian of Florida, Kansas, and Maryland, and the Rancholabrean of Florida, Georgia, Kansas, Missouri, Tennessee, and Texas (see Holman 1981).

The related and possibly ancestral form *H. brevis* is known only from the middle Pliocene of Florida (Auffenberg 1963).

REMARKS. — In view of the fossil record, the presence of *H. platyrhinos* in the early Pleistocene of Florida is not unexpected. However, it is of interest for two reasons. First, it suggests the replacement of *H. brevis* by *H. platyrhinos* in Florida between middle Pliocene and early Pleistocene. Second, the referred skull material shows that *H. platyrhinos* had reached its present degree of specialization by the earliest Pleistocene.

GENUS *Rhadinaea* COPE 1863

Rhadinaea cf. *R. flavilata* (COPE) 1871

REFERRED MATERIAL. — UF 26399, 3 vertebrae.

DESCRIPTION. — The referred vertebrae are small (CL < 2.0 mm). Accessory processes are laterally directed, short, straight, and blunt. Haemal keels extend well below the centrum, and are very slightly expanded posteriorly.

COMPARISONS. — The vertebrae have shorter, blunter accessory processes than *Stilosoma*, *Tantilla*, or *Sonora* (App. 3-5). The processes are not curved in the fossils as in *Diadophis punctatus* and *Carphophis amoenus*. The ventral extension of the haemal keel in the fossils is identical to that in modern *R. flavilata*.

DISTRIBUTION. — The 45 modern members of this genus are found from Argentina to the southeastern United States. A single species, *Rhadinaea flavilata*, is known from the southeastern United States. Fossils referred to *R. flavilata* were previously reported from the late Irvingtonian (Holman 1959a) and Rancholabrean (Auffenberg 1963) of Florida.

REMARKS. — Myers (1974) considered the *flavilata* group of the genus *Rhadinaea* unique in having no semblance of geographic unity. The two Recent members, *Rhadinaea flavilata* from the southeastern United States and *Rhadinaea laureata* from western Mexico, are peripheral relicts of a once widespread species that Myers suggested

had its origin in Mexico. He speculated that *R. flavilata* became isolated in Florida in the late Pleistocene and spread to its present range in postglacial times, but Inglis material indicates that *Rhadinaea* had already arrived in Florida by the earliest Pleistocene.

SUBFAMILY — — INCERTAE SEDIS
GENUS *Tantilla* BAIRD AND GIRARD 1853

REFERRED MATERIAL. — UF 26400, 6 vertebrae.

DESCRIPTION. — The referred vertebrae are small (< 1.75 mm CL), with cotyles equal in size to the neural canals. Neural spines are long and low. Subcentral ridges are poorly developed or absent. Accessory processes are straight, anterolaterally directed, and as long as or longer than the prezygapophyseal facet width.

COMPARISONS. — The size of the cotyle relative to the neural arch identifies the fossils as those of a very small adult snake. The accessory processes are like those of *Tantilla relicta*, which are longer and straighter than in any small North American snakes examined (App. 3-5). The vertebrae of *Sonora* are similar to the fossils, but have shorter and more laterally directed accessory processes and stronger subcentral ridges. The fossils compare well with *T. relicta*, but because of the similarity in vertebrae of a number of North American *Tantilla* species no specific identification was attempted.

DISTRIBUTION. — The present distribution of *Tantilla* includes the southern United States from coast to coast, and Central and South America to northern Argentina. The only reported fossils of this genus are from the late Pleistocene of Florida, New Mexico, and Texas (see Holman, 1981).

REMARKS. — The Inglis material is the oldest fossil record of this genus. It confirms Telford's (1966) suggestion that *Tantilla* had arrived in Florida by the early Pleistocene and thus was present during interglacial periods. Telford (1966) suggested that during these interglacials various populations of *Tantilla* became isolated, and then differentiated into the various forms found in Florida today.

FAMILY ELAPIDAE BOIE 1827
GENUS *Micrurus* WAGLER 1824

Micrurus cf. *Micrurus fulvius* (LINNAEUS) 1766

REFERRED MATERIAL. — UF 26401, 6 vertebrae.

DESCRIPTION. — These are small elongate vertebrae with long, low neural spines. Hypapophyses are long, sharp, and posteriorly projected. Accessory processes are short, laterally directed and subtriangular.

COMPARISONS. — Among North American snakes, only the natri-cines, viperids, and elapids have hypapophyses on all precaudal vertebrae. No viperids have vertebrae with such low neural spines or hypapophyses as sharp and posteriorly projected as in this material from Inglis. Two small natricine genera, *Virginia* and *Storeria*, are similar. The former differs from *Micrurus* in having longer, sharper, and more anteriorly projecting accessory processes. The latter has dorsally flattened neural spines (Auffenberg 1963) and broader hypapophyses.

DISTRIBUTION. — *M. fulvius* occurs from northeastern Mexico and central Texas to southern North Carolina and Florida. It is known as a fossil from the later Irvingtonian of Florida (Holman 1959a) and the Rancholabrean of Florida and Texas (see Holman 1981). Material referred to *Micrurus* sp. is known from the upper Miocene of Nebraska (Holman 1977a) and Pliocene of Florida (Auffenberg 1963).

REMARKS. — The specific assignment to cf. *M. fulvius* is based on geographical considerations. The lack of comparative material and incomplete knowledge of this large genus has deterred closer examination of the Inglis material at the species level.

The great diversity of *Micrurus* in South America suggests that the center of origin of the genus may be in that continent, but the oldest known fossils are from the Miocene of Nebraska. Whatever the origin, the Inglis material, along with that from Haile VI referred to *Micrurus* sp. by Auffenberg (1963), documents the arrival of coral snakes in Florida by the Pleistocene.

The material could represent a single individual.

FAMILY VIPERIDAE OPPEL 1811

Viperid vertebrae are short and wide and have short accessory processes. Throughout the column they have hypapophyses that are thick, but narrow in lateral view. They are usually long, and tend to point ventrally in the anterior portion of the column. In the rear portion of the column they point more posteriorly.

The viperid skull is highly modified to incorporate a venom delivery system. This has resulted in a number of skull elements that are diagnostic at the family level.

GENUS *Crotalus* LINNAEUS 1758
Crotalus adamanteus (BEAUVOIS) 1799

FIGURE 15 A-D, TABLE 9

REFERRED MATERIAL. — UF 26402, 979 vertebrae; UF 26403, 5 R and 4 L maxillae; UF 26404, 1 R and 1 L dentaries; UF 26405, 1 R and 1 L palatines; and UF 26406, 3 R and 3 L compounds.

DESCRIPTION. — The vertebrae all have long and narrow hypapophyses that are laterally thickened. Cotyles are oval. Accessory processes are much shorter than prezygapophyseal widths.

The maxillae are short, massive, and modified to hold a fang. From the basal portion of each maxilla rises a vertical flange (= dorsal process of Holman 1959b) which forms the medial wall of the facial pit cavity (= loreal fossa). At the top of this flange is a laterally directed process (= dorsal process) that extends to about the midline of the maxilla. On the anterior border of the flange is a short lateral extension in the frontal plane. There is a small tubercle in the middle of this extension. The anterior expansion and a similar posterior one form the lateral walls of the facial pit cavity.

The dentaries are short and deep with Meckle's groove open to the symphysis. Three complete dentaries average 9.3 teeth.

The palatines are small, thin sheets of bone that bear teeth on their ventral edges. Both fossil palatines are triangular but are broken posteriorly.

The compounds have expanded lingual and reduced labial flanges. The labial flange is dorsally directed.

COMPARISONS. — The maxillae are typically viperid (Brattstrom 1964). They differ from *Agkistrodon* in having anterior and posterior margins to the facial pit cavity. In North American *Agkistrodon* only the medial wall is evident in the maxilla. The fossils differ from *Crotalus atrox* and *Crotalus horridus* in having the basal portion of the bone dorsally expanded at the distal edge. The maxilla of *Sistrurus* can be distinguished from the fossils by a feature visible in the frontal plane. The labial margin of the basal portion tends to be directed dorsomedially rather than dorsally. The maxillae are most similar to *Crotalus adamanteus*.

Marx and Rabb (1972) include several *Crotalus* in a group of snakes with fewer than 9.5 dentary teeth. *Crotalus adamanteus* is the only large snake included in their list. Although they report a dentary of *C. atrox* that has seven teeth, most dentaries examined in this study have 10 teeth. The fossils are identical to *C. adamanteus* in the configuration of Meckle's groove and in the tooth shape.

The thin, high palatines are typical of crotaline snakes (Brattstrom 1964). They are triangular with a longer trailing edge. They do not have a step in the anterior margin, as in *C. horridus*, *Sistrurus*, and *Agkistrodon*. The compounds are indistinguishable from *C. adamanteus* and *C. atrox*. In *Crotalus horridus* and *Agkistrodon* the reduced labial flange is more laterally directed.

The fossil vertebrae can be distinguished from *Sistrurus miliarius* by their wider cotyles and less vaulted neural arches (see *S. miliarius*).

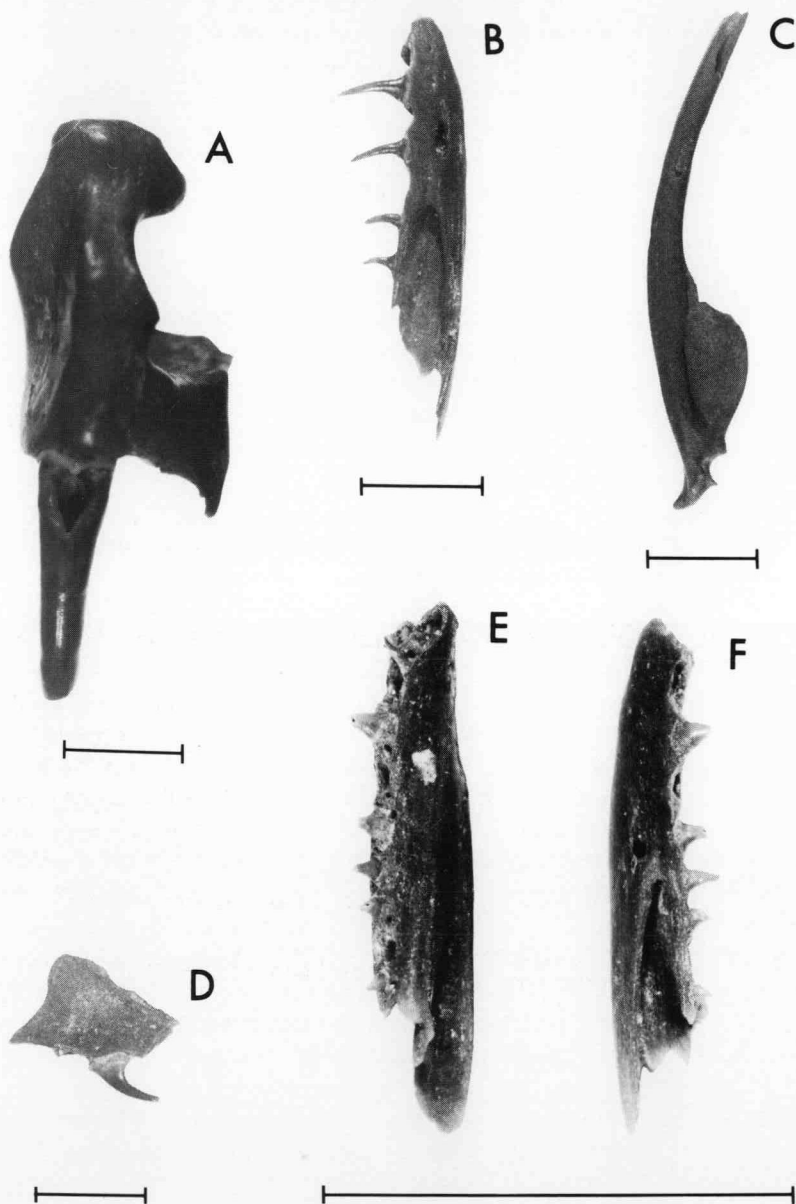


Figure 15. — Fossil crotalids from Inglis IA: *Crotalus adamanteus* (A) maxilla, frontal view, X3; (B) dentary, labial view, X3; (C) compound, labial view, X3; (D) palatine, labial view, X3. *Sistrurus miliarius* dentary, X12; (E) lingual and (F) labial views (each scale = 5 mm).

Separation from other North American viperid snakes is more difficult. The vertebrae of large *Crotalus* and *Agkistrodon* are very similar. Holman (1963) distinguishes *Agkistrodon* from *Crotalus* by the presence in the former of distinct pits on either side of the cotyle. *Agkistrodon* is reported to have one large fossa in each pit; *Crotalus* has one or more small fossae. Examination of two complete vertebral columns of *C. adamanteus* reveals intracolumnar variation in pitting and in the presence of fossae. Pits are present in the anterior one-third and posterior one-third of both columns. They are strongly developed in the vertebrae just anterior to the vent. Two small fossae are present in the pit throughout the column in one specimen but single larger fossae are present throughout the other. Holman's characters would correctly identify a majority of midbody vertebrae, but discriminant analysis was used here in an effort to identify all of the precaudal vertebrae. The fossils were identified using discriminant functions developed from 30 vertebrae from four *A. piscivorous*, 31 vertebrae from four *C. adamanteus*, 31 vertebrae from seven *C. atrox*, and 16 vertebrae from two *C. horridus*. Of the original 108 observations, 11 (10.1%) were reclassified; 10% of *C. adamanteus* were reclassified as *A. piscivorous*, and 10% were reclassified as *C. atrox*. Twelve ratios were used to separate these species. The most important are ZW/NAW, PRPR/POPR, CL/CW, and PRPR/CTW (Table 9).

In a sample of 100 fossil viperid vertebrae, 60% were referred to *Crotalus adamanteus* by this analysis, 30% were referred to *C. atrox*, and 10% to *Agkistrodon piscivorous*. The small number referred to *Agkistrodon* is within the error known to occur in this analysis. Thus the presence of *A. piscivorous* remains uncertain. The absence of any

Table 9. — The four most important ratios for the discrimination of *Crotalus adamanteus*, *Crotalus atrox*, *Crotalus horridus*, and *Agkistrodon piscivorous* (mean \pm one standard deviation).

	ZW/NAW ¹	PRPR/POPR ²	CL/NAW ³	PRPR/CTW ⁴
<i>Agkistrodon piscivorous</i>				
Recent (N = 32)	.88 \pm .07	1.41 \pm .12	1.25 \pm .17	2.92 \pm .14
<i>Crotalus atrox</i>				
Recent (N = 31)	.80 \pm .06	1.36 \pm .12	1.27 \pm .12	2.80 \pm .33
<i>Crotalus horridus</i>				
Recent (N = 17)	.85 \pm .07	1.28 \pm .14	1.44 \pm .24	2.68 \pm .14
<i>Crotalus adamanteus</i>				
Recent (N = 31)	.82 \pm .06	1.43 \pm .14	1.24 \pm .17	2.70 \pm .31
fossils (N = 100)	.79 \pm .06	1.46 \pm .11	1.20 \pm .13	2.75 \pm .27

¹Zygasphene Width/Neural Arch Width

²Prezygapophysis to Prezygapophysis Width/Postzygapophysis to Prezygapophysis Length

³Centrum Length/Neural Arch Width

⁴Prezygapophysis to Prezygapophysis Width/Cotyle Width

skull material of *Agkistrodon* and the paleoecology of the Inglis site are further evidence for the absence, or at least extreme rarity, of this species in the fauna.

The 30% referred to *Crotalus atrox* cannot wholly be attributed to error. It suggests that vertebrae with a morphology more similar to *C. atrox* than to *C. adamanteus* are present in the early Pleistocene of Florida. *C. adamanteus* is also clearly represented among the vertebrae. Although it is possible that *C. atrox* and *C. adamanteus* are sympatric in Florida in the earliest Pleistocene, it seems more likely that *adamanteus* evolved from *C. atrox* and that the vertebrae of early Pleistocene *C. adamanteus* had not differentiated to the extent seen in the modern members of the species.

The skulls of *Crotalus adamanteus* and *C. atrox* are very similar. Of the four elements representing *Crotalus* found preserved in the Inglis fauna, only the maxillae and dentaries show more similarity to *C. adamanteus* than to *C. atrox*. This is further evidence of a close relationship between these forms.

DISTRIBUTION. — *Crotalus adamanteus* is found today in the eastern coastal plain of the United States from the Mississippi River to North Carolina. Klauber (1972) listed the complete fossil record of the genus. He includes 12 middle to late Pleistocene and 10 late Pleistocene to Recent localities for *Crotalus adamanteus* in Florida. Ten late Pleistocene to Recent records are listed for New Mexico, Nevada, and Texas for *Crotalus atrox*.

REMARKS. — At one time *Crotalus atrox* was considered a subspecies of *C. adamanteus*. At present their relationship is considered to be one of direct common ancestry (Fig. 3:4 in Klauber 1972). The similarity of some of the Inglis vertebrae to *C. atrox* supports this relationship. It seems likely that the two were once a single species which was split by a Mississippi Embayment. The Inglis IA record is the oldest for the species.

Differences in the size of the maxillae indicate the presence of at least seven individuals.

GENUS *Sistrurus* GARMEN 1883
Sistrurus miliarius (LINNAEUS) 1766

FIGURE 15 E, F

REFERRED MATERIAL. — UF 26407, 384 vertebrae; UF 26408, 2 L dentaries.

DESCRIPTION. — These small vertebrae have relatively small, round cotyles. The hypapophyses are long, straight, and posteroventrally directed. The neural arches are highly vaulted and not distinctly wider than long. Neural spines are about as high as they are long.

The dentaries are small. Meckle's groove is open to the symphysis. The dental foramen lies immediately adjacent to the anterior end of the compound notch.

COMPARISONS. — Long, straight, posteroventrally directed hypapophyses are typical of the Viperidae. The fossil vertebrae can be distinguished from young *Crotalus*, *Agkistrodon*, and *Sistrurus catenatus* by their smaller, round cotyles.

Few snakes have dentaries with Meckle's groove open to the symphysis (App. 3-6). This condition occurs in *Heterodon* and some natri-cines, but the dentaries of these species differ from the fossils in having the groove reduced to a slit by the 4th tooth. In pit vipers it is open to the symphysis, although it may become ventrally oriented and not laterally visible. Among the crotalines examined, only *Sistrurus miliarius* is similar to the fossils in having the dental foramen immediately adjacent to the compound notch (Fig. 15 F). Its exact position is variable, but it is typically much closer than in any other pit vipers examined.

DISTRIBUTION. — *Sistrurus miliarius* is found today in the southeastern United States from eastern Texas and Oklahoma to southern North Carolina and Florida. The only records of the species as a fossil are from the middle to late Pleistocene of Florida (see Holman 1981). A related form, *Sistrurus catenatus*, is known from the Blaccan of Kansas (Brattstrom 1967) and Texas (Rogers 1976) and the Irving-tonian of Kansas (Holman 1972).

REMARKS. — The Inglis material represents the oldest record of *Sistrurus miliarius*. Klauber (1972) suggests that the most primitive living member of the genus, *Sistrurus ravus*, gave rise to both *S. miliarius* and *S. catenatus* in the Miocene or Pliocene. The Inglis material verifies at least a Pliocene arrival, presumably from the west, of *S. miliarius*. Material reported by Rogers (1976) shows that *S. catenatus* lived in Texas during the Blaccan.

PALEOECOLOGY TAPHONOMY¹

Geological evidence (*vide* Klein 1971) indicates that the Inglis IA sample accumulated in a sinkhole trap. Webb (pers. comm.) suggested that additional material may have been added by local slope wash. Excavations revealed that in cross-section the sinkhole had a hemispherical roof with a 3-meter breach in the center. Such a sinkhole would have been an ideal trap. Indeed the sediments were thickest directly below the opening and thinned out toward the edges. The clastic sediments were locally derived and appear to have been washed or blown in through the roof.

¹Literally the study of burials (for a good example see Behrensmeier 1975).

The excellent preservation of the fossils is also an indication of a natural trap. Many fragile specimens, including pterygoids, dentaries, and maxillae of both lizards and snakes, have been well preserved. These elements would presumably bear evidence of any transportation. Furthermore, the occiputs of several *Ophisaurus* and short sections of snake vertebral columns remain articulated, suggesting limited maceration and transport. Klein (1971) suggested that wind-blown sands may have filled the sinkhole at a rapid rate. The covering of newly trapped animals by these sands would account for the crisp detailed preservation of much of the recovered material (Behrensmeyer 1975).

Further evidence of a natural trap is drawn from the large *Ophisaurus* sample. The 11 left and 10 right maxillae, 11 left and 12 right dentaries (1 each per individual), 926 body vertebrae (50-55 per individual), 22 sacral vertebrae (2 per individual), and 48 nonautotomic caudal vertebrae (5 per individual) all provide an MNI of 9 to 12. This equality of counts suggests that each *Ophisaurus* was preserved completely. Complete preservation would be best accounted for by entrapment.

Few of the fossils are waterworn. Only 11 snake vertebrae are too waterworn to be identified. Klein (1971) gave several reasons why he thought abrasion by water had occurred within the sinkhole after deposition. He considered that the shape of the deposit was incompatible with the concave cross-section of a stream, and noted the absence of crossbedding, graded bedding, or lenticular bedding that is usually associated with stream deposits. During the 1974 excavation some crossbedding was discovered (Webb, pers. comm.), which indicates that water-lain sediments were present in portions of the deposit not seen by Klein. Klein also noted the lack of stream-dwelling forms among the mammals preserved in the fauna. Although one stream- and three marsh- or pond-dwelling snake species are represented, they are clearly in the minority.

Further evidence that Inglis was a sinkhole trap comes from a study of the frogs (Meylan, MS) which reveals a scarcity of hylids. Their rarity in the Inglis fauna may reflect their ability to escape a natural trap by climbing the vertical walls.

Most numerous among the Inglis anurans is a new species of *Bufo* that is related to modern *Bufo terrestris*. At least 168 individuals are represented. A comparison of the population structure of the fossil toads to Recent populations reveals a surplus of adults. Several explanations are possible, but the most plausible seems to be that the surplus adults were trapped during breeding migrations.

Animals would be expected to accumulate in a natural trap in proportion to their density, though differences in trapability could affect the observed results. Larger snakes are less likely to be trapped, being better able to climb out, but any bias toward small snakes in the fauna might be offset by their ability to leave the sinkhole via small crevices or holes. The effects of such possibilities cannot be measured, so it is assumed that the squamates were preserved in the fauna in proportion to their abundance in the vicinity of the sinkhole.

DIAGENETIC FACTORS

Between the time a fauna is deposited and excavated a number of factors can modify it. Destruction of bone can result from a variety of processes (Behrensmeyer 1975). Most of the Inglis fauna was preserved in fine sands and sandy clays (Klein 1971). Bones in a sandy matrix are rarely subject to compaction and fracturing, and have little chance of being perturbed, provided that the sands are not too coarse (Behrensmeyer 1975). At Inglis there was no evidence of slumping, differential settling, or reworking of the sediments (Klein 1971). Thus, diagenetic factors appear to have had little effect on the fauna.

COLLECTION BIAS AND SAMPLE SIZE

The 100 tons of sediment excavated from the Inglis IA site were screened through both coarse and fine screens. Unfortunately the finest screen used was ordinary window screen (16 meshes per inch). Trials with modern skeletons of *Carphophis*, *Diadophis*, *Rhadinaea*, *Stilosoma*, and *Tantilla* showed that some vertebrae and most of the longer skull elements (maxillae, pterygoids, compounds, etc.) of these species pass through window screen. Others become trapped in the screen. Fossils trapped in such a fashion would most likely be broken and lost during washing. This may account for the absence of the small scincids *Scincella laterale*, *Neoseps reynoldsi*, and *Eumeces egregius* in the Inglis fauna. *Neoseps* occurs only in isolated areas of fine sands which may not have been present near Inglis IA, but *Eumeces egregius* and *Scincella laterale* are common in high pine and xeric hammock (Carr 1940) and should have been present in the Inglis fauna. It is possible that *Scincella* had not yet arrived in Florida by the early Pleistocene. The diversification of *Eumeces egregius* into four subspecies in peninsular Florida is attributed to isolation during Pleistocene interglacials (Mount 1965).

It is fortunate that vertebrae of some of the very small snakes were recovered. However, because of the probable bias created by the screening procedure, they do not weigh heavily in the following paleoecological interpretation of the fauna.

The tremendous quantity of matrix recovered and washed from Inglis IA insures that the faunal sample is large enough to provide a valid picture of all but the smallest vertebrates of the surrounding communities. In a discussion of sampling and sample sizes for paleoecological interpretations using fossil mammals, Wolff (1975) considered it necessary to have a sample of 5,000-10,000 kg of bulk sediment, based on the density of fossils in several localities in California. He concluded that for mammalian taxa, the relative abundance of the most common forms are roughly approximated when at least 500 identifiable specimens have been recovered. This represents a minimum of 25 specimens and three individuals per taxon of mammals at the California sites. In the present study, more than 3,500 elements, with an average of 125 specimens per species, represent squamate reptiles. This certainly qualifies as an adequate sample for paleoecological interpretation.

FAUNAL REQUIREMENTS

The use of fossil faunas to identify ancient environments can only be successful when the habitat requirements of the faunal members are known. These requirements must be inferred for more than half of the 98 Pleistocene mammal genera from North America because they are now extinct. North American squamate taxa have experienced far fewer extinctions since the Pleistocene (1 genus, *Dryinoides*), and because they have survived, often to the species level, they are more useful than mammals for paleoecological studies.

Of 31 squamate species identified from Inglis, four are extinct. The remainder, with two exceptions, live in Florida today. The specific Florida habitats occupied by these species have been recorded by Carr (1940) and others (Table 10). Recorded habitat preferences and the relative abundance of the taxa in the Inglis IA fauna are used below in an attempt to classify the community from which the Inglis fauna was trapped.

An often unstated assumption in paleoecological studies is that the habits of a species do not change through time, but just as the habitats occupied by species may change through space (e.g. *Rana areolata*), they can also change through time (Van Devender et al. 1976). Still the Inglis sample is large enough so that many changes would have had to occur to confound the observed results.

ECOLOGICAL INTERPRETATION

It has been suggested that the Inglis IA fauna sampled a savanna that extended around the Gulf of Mexico during the late Cenozoic and expanded markedly during the early Pleistocene (Webb 1978). Evidence from the squamates, presented below, supports this thesis, and

Table 10. — Preferred habitats of Inglis IA squamates. A number in a given column indicates that the species is found in that community. The number is the MNI for that species in the Inglis fauna. Data are largely from Carr (1940), but habits of *Diadophis* and *Rhadinaea* are taken from Myers (1965 and 1967), data for *Tantilla* is taken from Telford (1966), and data for *Cemophora* is taken from ± 60 individuals trapped by National Fish and Wildlife Service in various habitats in Wakulla County, Florida.

Species	MNI	Longleaf Pine (= High Pine)	Xeric Hammock (= Upland Hammock)	Mesophytic Hammock	Flatwoods	Swamps, Marshes, Ponds (Near Water)	Rivers
<i>Nerodia erythrogaster</i>	1						1
<i>Nerodia cyclopion</i>	1					1	
<i>Virginia</i> sp.	1		1	1	1		
<i>Regina</i> sp.	1					1	
<i>Thamnophis sauritus</i>	1					1	
<i>Heterodon platyrhinos</i>	2	2	2				
<i>Diadophis</i> sp.	1			1	1	1	
<i>Farancia abacura</i>	1					1	
<i>Rhadinaea flavilata</i>	1		1		1		
<i>Coluber constrictor</i>	4	4	4	4	4	4	
<i>Masticophis flagellum</i>	3	3			3		
<i>Drymarchon corais</i>	2	2			2		
<i>Elaphe obsoleta</i>	2		2				
<i>Elaphe guttata</i>	3	3	3		3		
<i>Lampropeltis getulus</i>	2		2		2		
<i>Pituophis melanoleucus</i>	3	3					
<i>Lampropeltis triangulum</i>	1	1	1	1			
<i>Cemophora coccinea</i>	1	1	1		1		
<i>Stilosoma extenuatum</i>	1	1	1				
<i>Tantilla</i> sp.	1	1	1	1			
<i>Crotalus adamanteus</i>	7	7	7	7	7		
<i>Sistrurus miliarius</i>	3	3	3		3		
<i>Sceloporus undulatus</i>	36	36	36				
<i>Ophisaurus ventralis</i>	12	12	12		12		
<i>Rhineura floridana</i>	1	1	1	1			
		80	78	16	40	9	1

provides further information as to the nature of this savannah in the earliest Pleistocene of Florida.

In an attempt to analyze the communities represented by the Inglis fauna, the occurrence of each species (or living equivalent) was recorded for six general habitat types (Table 10). Data are almost entirely from Carr (1940), but other sources have been used for taxa not conclusively covered by him. The minimum number of individuals (MNI) for all of the taxa occurring in a single habitat was added. The resulting scores appear in the last line of Table 10. The two xeric habitats, longleaf pine and xeric hammock, receive the highest scores (80 and 78 respectively). Flatwoods are next (40), although 6 of the taxa and 31 of the individuals so assigned could have come from the two more xeric habitats. Another species, *Sistrurus miliarius*, is found in longleaf pine and xeric hammock. Carr's reference to this snake occurring in flatwoods probably reflects its greater abundance in that community. Seven of the eight species recorded from mesophytic hammock are also recorded for xeric hammock. Data for the eighth, *Diadophis elinorae*, has been inferred from *Diadophis punctatus*. It is possible that the minor changes in morphology discussed in the account of *Diadophis elinorae* coincided with a change in habitat preference of ringneck snakes.

The seven taxa that usually occur near water are represented by a minimum of 11 individuals. Three of them may also be found in xeric hammock and/or longleaf pine. The other four species are each represented by a minimum of one individual. *Nerodia cyclopion* and *Thamnophis sauritus* are both active snakes that often leave water. I have found both along the borders of isolated, seasonally dry ponds in north-central Florida. *Farancia abacura* and Recent *Regina* species also travel overland, especially during heavy rain. The single stream dweller, *Nerodia erythrogaster*, is also known to travel far from water (Conant 1975). The few occurrences of these normally aquatic species in the Inglis fauna could thus be attributable to chance entrapment during terrestrial movements. This view is in accord with the apparent subsurface flow of water that deposited the Inglis site (see p. 4).

The composition of the squamate fauna overwhelmingly indicates longleaf pine and/or xeric hammock as the principle community sampled. Longleaf pine, when mature, is open and savanna-like; xeric hammock is not, having a more closed canopy. True grasslands are not present in Florida, thus the only habitat more open is wet treeless marsh maintained by seasonal flooding. The fauna clearly shows that this latter type of habitat did not make a significant contribution to the Inglis fauna.

Klein (1971) cited the abundance of *Capromeryx* (pronghorns), *Odocoileus* (deer), *Platygonus* (peccary), *Hemiauchenia* (llama), and *Lepus* (jackrabbit) in the Inglis fauna as evidence of open habitat, but he noted that these grazers, as well as the carnivores in the fauna, probably required cover for resting spots. The very large sample of *Geomys* indicates dune-like sandy terrain well above the water table.

The combined evidence of the herpetofauna, other vertebrates, and the sedimentary context suggests a mixed habitat of mature longleaf pine with xeric hammock interspersed. Xeric hammock would be expected in the depressions characteristic of a karst topography. That one or more of these depressions contained water at least seasonally, is suggested by the presence of *Nerodia*, *Regina*, *Thamnophis*, *Alligator*, *Pseudemys*, and *Rana catesbeiana*.

ZOOGEOGRAPHY

With few exceptions, the Inglis squamates have ancestors in the fossil record of North America. Thus the fauna is autochthonous and shows no South American or West Indian influence. The Inglis IA fauna shows continuity with the widespread mid- to late Tertiary xeric communities of North America. Post-Inglis changes in Florida's squamates appear to result largely from the variation in climate and sea level resulting from glaciation.

The mid-Tertiary fossil record of temperate North America includes probable ancestors for 84% of the Inglis squamates (Table 11). Twenty-four Inglis genera and 11 species are known from earlier localities. Two genera, *Cemophora* and *Farancia*, are known from morphologically similar forms. Thus, nearly all the species known from Inglis could have evolved in North America.

Only five genera present in Inglis IA do not have known ancestors in the North American fossil record. Three of these, *Drymarchon*, *Rhadinæa*, and *Tantilla*, appear to have a Central American origin. A detailed study of *Rhadinæa* (Myers 1974) reveals that only 12 of 45 known species are present in South America. The primitive and probably ancestral *godmani* group has its center of dispersal and probable place of origin in Nuclear Central America. Similarly, only 8 of 47 known *Tantilla* species and 3 of 8 subspecies of *Drymarchon corais* are found in South America. It seems likely that studies of these genera would reveal Central American origins.

Ophedrys vernalis and *Virginia* sp. also lack ancestors in the fossil record. *Virginia* is only found in North America and undoubtedly evolved on this continent. The genus *Ophedrys* includes four Asian species, which suggests the possibility that it evolved in the Old World (Schmidt and Necker 1936).

Table 11. — A listing of the probable closest relative for members of the Inglis IA fauna known from the previous fossil record (citations given in species accounts).

Inglis IA	Previous Record
<i>Coluber constrictor</i>	<i>Coluber constrictor</i> (Blancan, Texas)
<i>Drymarchon corais</i>	NONE
<i>Masticophis flagellum</i>	<i>Masticophis flagellum</i> (Blancan, Texas)
<i>Opheodrys vernalis</i>	NONE
<i>Cemophora coccinea</i>	<i>Pseudocemophora antiqua</i> (Arikareean, Florida)
<i>Elaphe guttata</i>	<i>Elaphe guttata</i> (Blancan, Texas)
<i>Elaphe obsoleta</i>	<i>Elaphe obsoleta</i> (Blancan, Texas)
<i>Lampropeltis getulus</i>	<i>Lampropeltis getulus</i> (Blancan, Kansas)
<i>Lampropeltis triangulum</i>	<i>Lampropeltis triangulum</i> (Blancan, Kansas)
<i>Pituophis melanoleucus</i>	<i>Pituophis melanoleucus</i> (Blancan, Texas)
<i>Stilosoma extenuatum</i>	<i>Stilosoma vetustum</i> (Pliocene, Florida)
<i>Diadophis elinorae</i>	<i>Diadophis elinorae</i> (Pliocene, Florida)
cf. <i>Dryinoides</i>	<i>Dryinoides oxyrachis</i> (Miocene, Montana)
<i>Farancia abacura</i>	<i>Paleofarancia brevispinosa</i> (Pliocene, Florida)
cf. <i>Rhadinaea flavilata</i>	NONE
<i>Tantilla</i> sp.	NONE
<i>Heterodon nasicus</i>	<i>Heterodon plionasicus</i> (Blancan, Kansas)
<i>Heterodon platyrhinos</i>	<i>Heterodon brevis</i> (Pliocene, Florida)
<i>Nerodia cyclopion</i>	<i>Nerodia cyclopion</i> or <i>N. rhombifera</i> (Blancan, Texas)
<i>Nerodia erythrogaster</i>	<i>Nerodia erythrogaster</i> (Blancan, Texas)
<i>Regina intermedia</i>	<i>Regina hillmani</i> (Lower Pliocene, Kansas)
<i>Virginia</i> sp.	NONE
<i>Thamnophis sauritus</i>	<i>Thamnophis</i> sp. (Hemphillian, Florida)
<i>Crotalus adamanteus</i>	<i>Crotalus atrox</i> (Blancan, Texas)
<i>Sistrurus miliaris</i>	<i>Sistrurus catenatus</i> (Blancan, Texas)
<i>Micrurus fulvius</i>	<i>Micrurus</i> sp. (Miocene, Nebraska; Pliocene, Florida)
<i>Rhineura floridana</i>	<i>Rhineura marslandensis</i> (Miocene, Kansas)
<i>Sceloporus undulatus</i>	<i>Sceloporus undulatus</i> (Blancan, Texas)
<i>Ophisaurus ventralis</i>	<i>Ophisaurus ventralis</i> (Miocene, Nebraska; Pliocene, Kansas)
<i>Eumeces carri</i>	<i>Eumeces</i> sp. (Miocene, Florida)
<i>Gerrhonotus</i> sp.	<i>Gerrhonotus</i> sp. (Blancan, Texas)

The only substantial evidence of a West Indian influence in the squamate history of Florida is seen in the Miocene Thomas Farm Fauna. The presence of *Pseudoepicrates* (Auffenberg 1963), *Leiocephalus*, a possible iguanine, and a gecko (Estes 1963) documents this influence in the early Miocene. No West Indian squamates except *Anolis* are present in the fossil record after that time. The Inglis fauna is the next oldest of sufficient size to be examined for the presence of a West Indian influence in Florida. It documents a complete disappearance of the West Indian faunal elements by the early Pleistocene.

Anolis was not found in the Inglis IA fauna, though it should have been if it occurred in Florida at that time. It is common in longleaf pine

and in xeric hammock, thus its absence cannot be attributed to ecological factors. Perhaps *Anolis carolinensis* had not yet arrived in Florida by the earliest Pleistocene. It is known from Rancholabrean deposits in Florida (Auffenberg 1956).

The modernization of Florida's squamates can easily be seen by comparing the Thomas Farm and Inglis IA faunas. The Thomas Farm fauna includes four boid snakes and two colubrid snakes. Inglis IA includes 23 colubrids, 2 viperids, 1 elapid, and no boids. This change in the squamate fauna is similar to that reported for western North America where domination by colubrids and disappearance of boids (except two species on the west coast) occurs by the end of the Blancan. The Thomas Farm lizards are dominated by iguanids, with at least four species present. An anguid, a gecko, a skink, and *Cnemidophorus* are also present (Estes 1963). Unlike the Thomas Farm fauna, the Inglis lizard fauna is reduced in comparison to the snakes. This could reflect collecting bias in the Thomas Farm, but more likely indicates a change from nearly equal diversity of lizards and snakes (8:6) in the Miocene to a greater diversity of snakes by Inglis time (4:26), which still is evident today (14:36).

All the subfamilies (family, in the case of *Rhineura*) represented in Inglis IA are known in North America by the end of the Miocene (Estes 1963; Holman 1970, 1979; Berman 1976). Thus, the change in Florida's squamate fauna between the early Miocene (Thomas Farm) and early Pleistocene (Inglis IA) is largely due to dispersal and evolution of an established North American fauna rather than immigration and mixing of North and South American faunas, as is apparent in the mammals from Inglis IA (Webb 1978). The participation of colubrids in the faunal interchanges that began seriously in the late Blancan was apparently one-way — south. There is no evidence of South American snakes arriving by Inglis time along with the mammals.

The Inglis fauna documents an important late Tertiary link between the savannas of Florida and those of the American West. Savannas were widespread in North America during the Miocene (Webb 1977). The snakes *Aniliodes*, *Calamagras*, *Pseudocemophora*, and *Ogmophis*, the lizards *Ophisaurus*, *Eumeces*, and *Cnemidophorus* (or a similar form), and the rhineurid amphisbaenians are found in deposits of Miocene age in both the High Plains and in Florida. Thus it is assumed that ecological continuity between the east and west existed in the late Tertiary and was an important factor in the arrival of many forms in the southeastern United States (Blair 1958). Such an east-west corridor would help explain an emerging pattern of survival in the Southeast for some forms that were widespread in the Miocene of the High

Plains. *Dryinoides*, the rhineurid amphisbaenians, the tortoise genus *Stylemys*, and the lizard *Ophisaurus ventralis* are present in the mid-Tertiary of the western United States and have their last surviving members in the Southeast. The rhineurid amphisbaenians are present from the Eocene to the Miocene in the middle and far West (Berman 1976). A single extant species, *Rhineura floridana*, exists today in peninsular Florida. *Stylemys* is known from the Eocene to Miocene of the western United States, but one of its most specialized members, the related genus *Floridemys*, is known from the Miocene of Florida. *Ophisaurus ventralis* is known from the Miocene of Nebraska and Pliocene of Kansas but is now limited to the Southeast. *Dryinoides*, from the Miocene of Montana (Auffenberg 1958), is now apparently present in the earliest Pleistocene of Florida.

These and other squamates were members of mid-Tertiary xeric communities that were widespread in North America. They probably survived longer in Florida because the peninsula acted as a refuge during periods of climatic deterioration. Further investigation of the fossil record may reveal other species that fit this pattern. Perhaps such endemics as *Stilosoma* and *Neoseps* are relicts of widespread mid-Tertiary faunas.

The present distribution of 15 xeric-adapted North American squamates may reflect the past distribution of xeric communities. Their ranges (taken from Conant 1975) are similar in that they all avoid the area of Tertiary Mississippi Embayments (Clark and Stearn 1968). *Crotaphytus collaris*, *Heterodon nasicus*, *Sonora episcopa*, *Tantilla gracilis*, and *Crotalus atrox* all approach the Southeast from the West, but are now restricted north of the area of most Mississippi Embayments. *Cnemidophorus sexlineatus*, *Sceloporus undulatus*, *Cemophora coccinea*, *Lampropeltis calligaster*, and *Micrurus fulvius* are found east and west of the Mississippi River but are absent in much of the embayment area. *Eumeces anthracinus*, *Masticophis flagellum*, and *Pituophis melanoleucus* are completely separated by the Mississippi Basin.

In the early Pleistocene, when the climate was perhaps more arid and sea levels lower, this embayment may have been breached by savanna biotas. But during the late Tertiary the main avenue for east-west connection of xeric faunas was probably across higher latitudes.

A mid-continent corridor, xeric in nature, is thus indicated. It apparently provided an east-west dispersal route for late Tertiary faunas. The presence in Inglis IA of *Heterodon nasicus* and an undifferentiated *Drymarchon corais*, suggests that gene flow was at least periodically maintained with western populations until the end of the

Pliocene. The separation of at least three xeric-adapted genera (*Ophisaurus*, *Sistrurus*, and *Crotalus*) into eastern and western entities by the early Pleistocene may have occurred during isolation when this corridor was closed.

Few species present in the modern squamate fauna of xeric Florida habitats are missing from Inglis IA. The absence of small scincids may be due to screening techniques and is discussed under Paleoecology. *Ophisaurus attenuatus*, *Cnemidophorus sexlineatus*, and *Opheodrys aestivus*, which would be expected in xeric settings, are apparently post-Inglis arrivals. *Sceloporus woodi*, *Ophisaurus compressus*, and *Heterodon simus* all have close relatives in the Inglis fauna, which suggests that speciation of these forms occurred by post-Inglis evolution in peninsular Florida.

Climatic fluctuations during the Pleistocene undoubtedly produced important changes in Florida's squamate fauna. Lowered sea levels during each glacial interval produced broad circum-Gulf corridors of savanna habitat (Auffenberg and Milstead 1965) and probably provided an avenue for the arrival of *Ophisaurus attenuatus*, *Cnemidophorus sexlineatus*, and *Opheodrys aestivus*. During interglacials, higher sea levels would have separated parts of peninsular Florida from the mainland providing the isolation necessary for speciation to occur in *Sceloporus undulatus* (to *S. woodi*), *Heterodon nasicus* (to *H. simus*), and *Ophisaurus ventralis* (to *O. compressus*). Inglis IA represents one of the first glacial intervals and therefore, in a broad sense, the beginning of the Pleistocene mode of herpetofaunal evolution in Florida.

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APPENDIX 1

LIZARD SKELETONS EXAMINED

Anniellidae

Anniella pulchra (1)

Anguidae

Celestus costatus (1)
C. cruscus (2)
Gerrhonotus multicarinatus (3)
Ophisaurus apodus (2)
O. attenuatus (7)
O. compressus (5)
O. ventralis (14)

Gekkonidae

Aristelliger praesignis (2)
Coleonyx variegatus (2)
Hemidactylus garnoti (2)
H. turcicus (2)
Gekko gecko (3)
Phyllodactylus tuberculatus (2)
Sphaerodactylus cinereus (1)
Thecadactylus rapicaudus (2)

Helodermatidae

Heloderma horridum (2)
H. suspectum (2)

Iguanidae

Amblyrynchus suberistatus (2)
Anolis bimaculatus (1)
A. carolinensis (1)
A. distichus (1)
A. equestris (2)
A. garmani (1)
A. scriptus (1)
Basiliscus vittatus (2)
Callisaurus draconoides (2)
Corythophanes cristatus (1)
Crotaphytus collaris (2)
Ctenosaura pectinata (1)
Cyclura carinata (1)
C. cornuta (1)
Dipsosaurus dorsalis (1)
Holbrookia maculata (2)
Iguana iguana (1)
Leiocephalus carinatus (3)
Phrynosoma cornutum (2)
P. solare (2)
Sceloporus clarki (3)
S. cyanogenys (1)

S. jarrovi (1)
S. magister (1)
S. occidentalis (2)
S. poinsetti (1)
S. scalaris (1)
S. undulatus (7)
S. woodi (8)
Uta stansburiana (2)

Scincidae

Eumeces brevilineatus (3)
E. callicephalus (1)
E. copei (1)
E. egregius (3)
E. fasciatus (2)
E. gilberti (2)
E. inexpectatus (4)
E. laticeps (4)
E. multivirgatus (2)
E. obsoletus (3)
E. parvulus (1)
E. septentrionalis (3)
E. skiltonianus (2)
E. tetragrammus (1)
Leiolopisma cherrei (1)
Mabuya mabouya (2)
Neoseps reynoldsi (2)
Scincella laterale (2)

Teiidae

Ameiva ameiva (2)
A. griswaldi (2)
A. quadrolineata (3)
Cnemidophorus sexlineatus (6)
C. sonora (2)
C. tigris (2)

Xantusiidae

Klauberina riversiana (2)
Lepidophyma flavimaculatum (2)
Xantusia vigilis (2)

Xenosauridae

Xenosaurus platyceps (4)

APPENDIX 2

SNAKE SKELETONS EXAMINED

Colubridae

Alsophis cantherigerus (2)
Antillophis parvifrons (1)
Arizona elegans (4)
Carphophis amoenus (3)
Cemophora coccinea (6)
Coluber constrictor (6)
Diadophis punctatus (7)
Drymarchon corais (6)
Drymobius margartiferus (1)
Elaphe guttata (6)
E. obsoleta (8)
E. vulpina (4)
Farancia abacura (6)
F. erythrogramma (3)
Heterodon nasicus (3)
H. platyrhinos (8)
H. simus (6)
Hypsirynchus ferox (1)
Lampropeltis calligaster (5)
L. getulus (9)
L. triangulum (5)
Leptodeira annulata (1)
L. septentrionalis (1)
Lystrophis dorbigny (1)
Masticophis flagellum (6)
M. taeniatus (2)
Nerodia cyclopion (6)
N. erythrogaster (3)
N. fasciata (6)
N. rhombifera (2)
N. sipedon (2)
N. taxispilota (4)
Opheodrys aestivus (4)
O. vernalis (4)
Oxybelis fulgidus (1)
Phyllorhynchus decurtatus (2)
Pituophis melanoleucus (7)
Pseudoeryx plicatilis (1)
Regina alleni (4)
R. grahami (2)
R. rigida (3)
R. septemvittata (2)
Rhadinaea decorata (1)
R. flavilata (4)
Rhinoceilus lecontei (3)
Salvadora hexalepis (3)
Scaphiodontophis annulatus (1)
Seminatrix pygea (5)
Sibon nebulata (2)

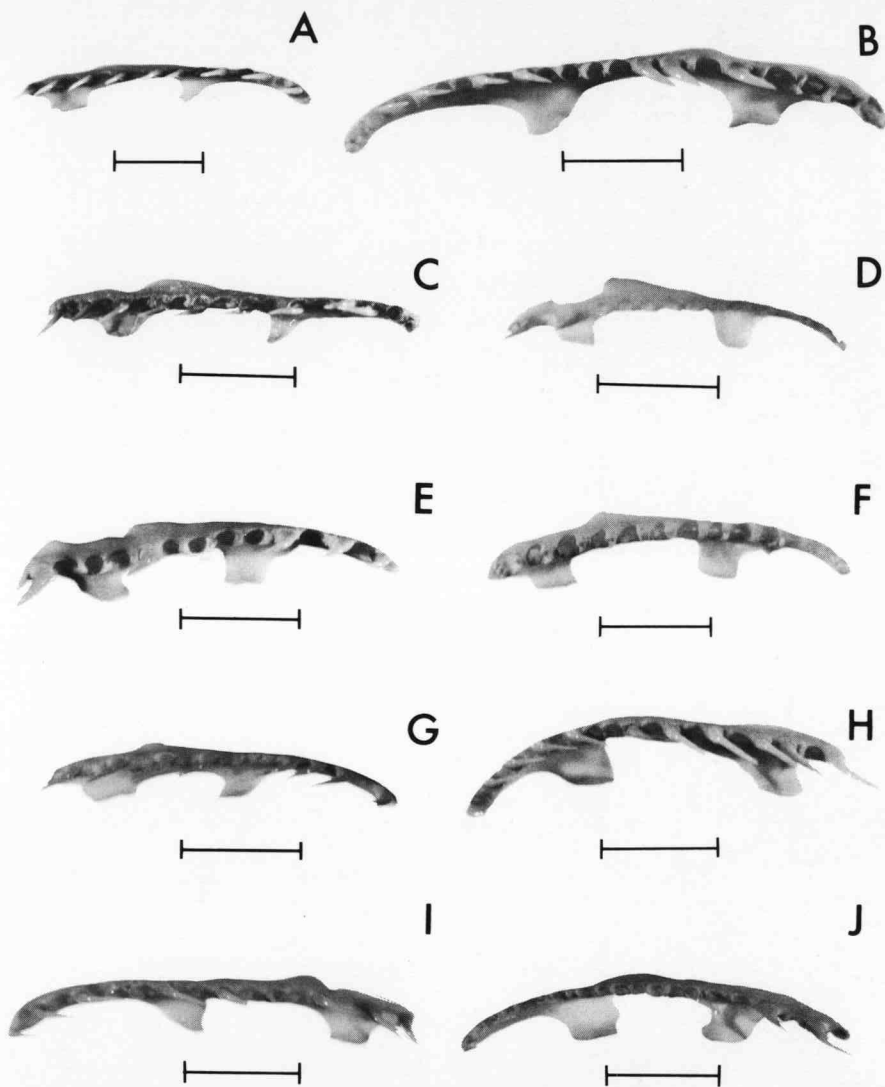
Spilotes pullatus (2)
Stilosoma extenuatum (3)
Storeria dekayi (4)
S. occipitomaculata (2)
Tantilla atriceps (1)
T. planiceps (1)
T. relicta (5)
T. semicincta (1)
T. taeniata (1)
Thamnophis cyrtopsis (2)
T. marcianus (2)
T. melanogaster (2)
T. proximus (4)
T. sauritus (4)
T. sirtalis (4)
Trimorphodon tau (2)
Tropidoclonion lineatum (1)

Elapidae

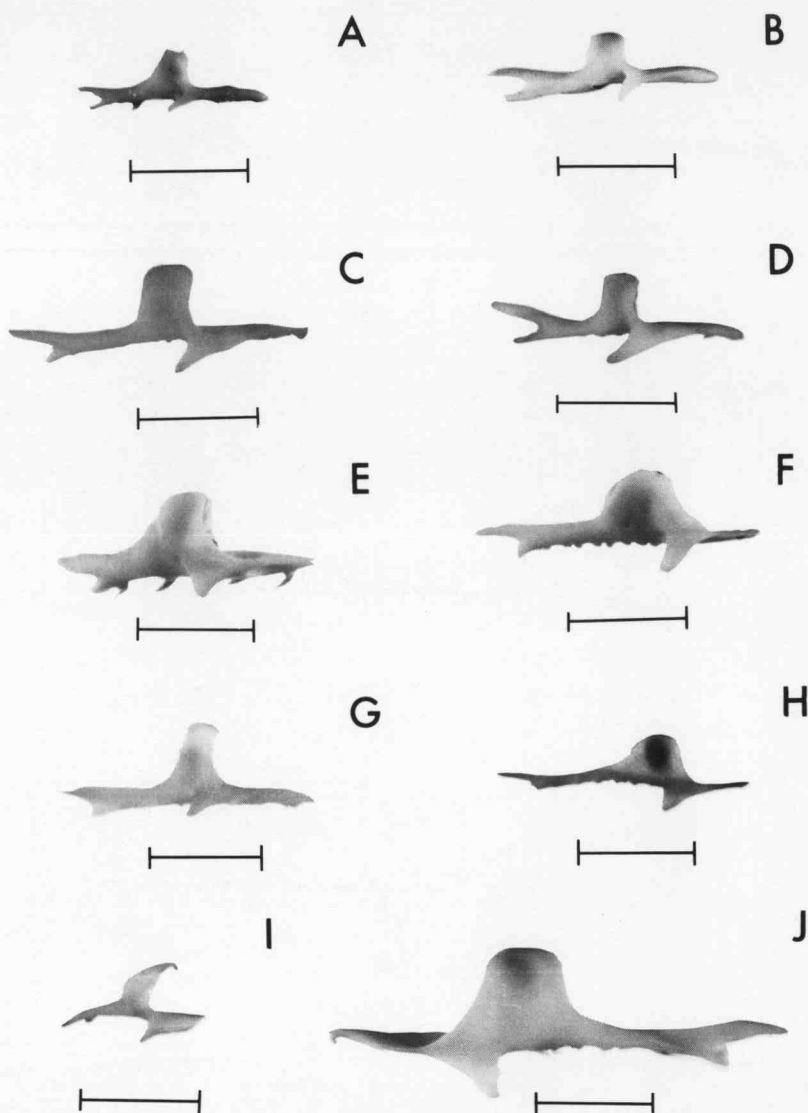
Micrurus affinis (1)
M. fulvius (8)

Viperidae

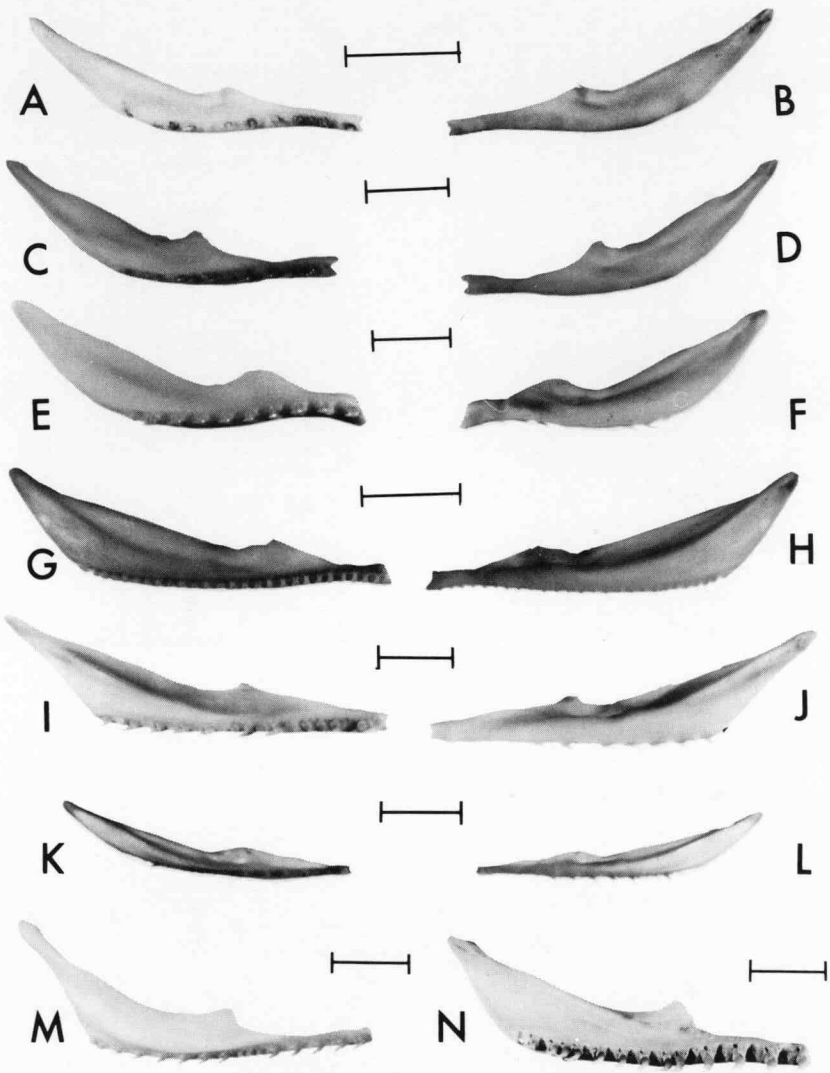
Agkistrodon contortrix (3)
A. piscivorus (6)
Bothrops asper (2)
B. schlegelii (1)
Crotalus adamanteus (10)
C. atrox (7)
C. horridus (5)
C. molossus (2)
C. viridis (2)
Sistrurus catenatus (4)
S. miliarius (7)

APPENDIX 3
SELECTED COMPARATIVE MATERIALS

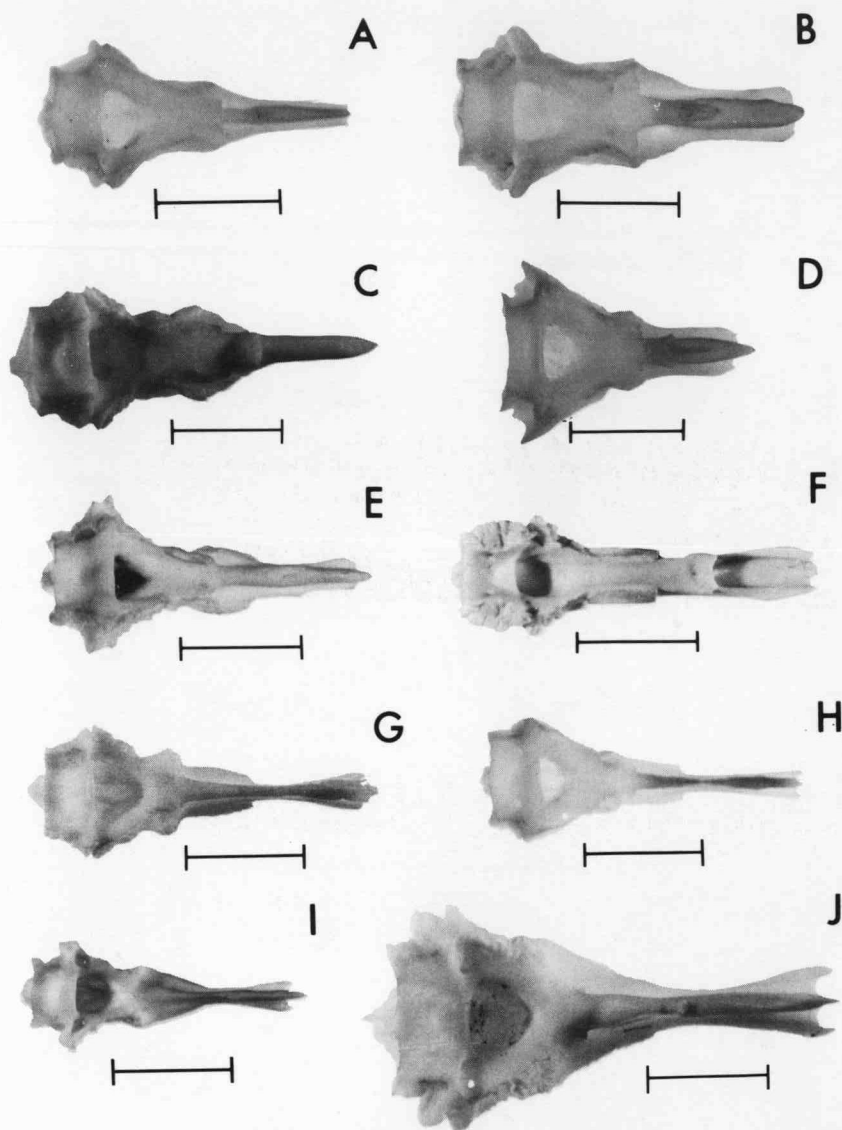
3-1. — Maxillae of selected Recent North American snakes: (A) *Elaphe guttata*. (B) *Drymarchon corais*. (C) *Elaphe obsoleta*. (D) *Masticophis flagellum*. (E) *Lampropeltis getulus*. (F) *Coluber constrictor*. (G) *Pituophis melanoleucus*. (H) *Nerodia cyclopion*. (I) *Thamnophis sirtalis*. (J) *Nerodia fasciata*. All in occlusal view, X3 (each scale = 5 mm).



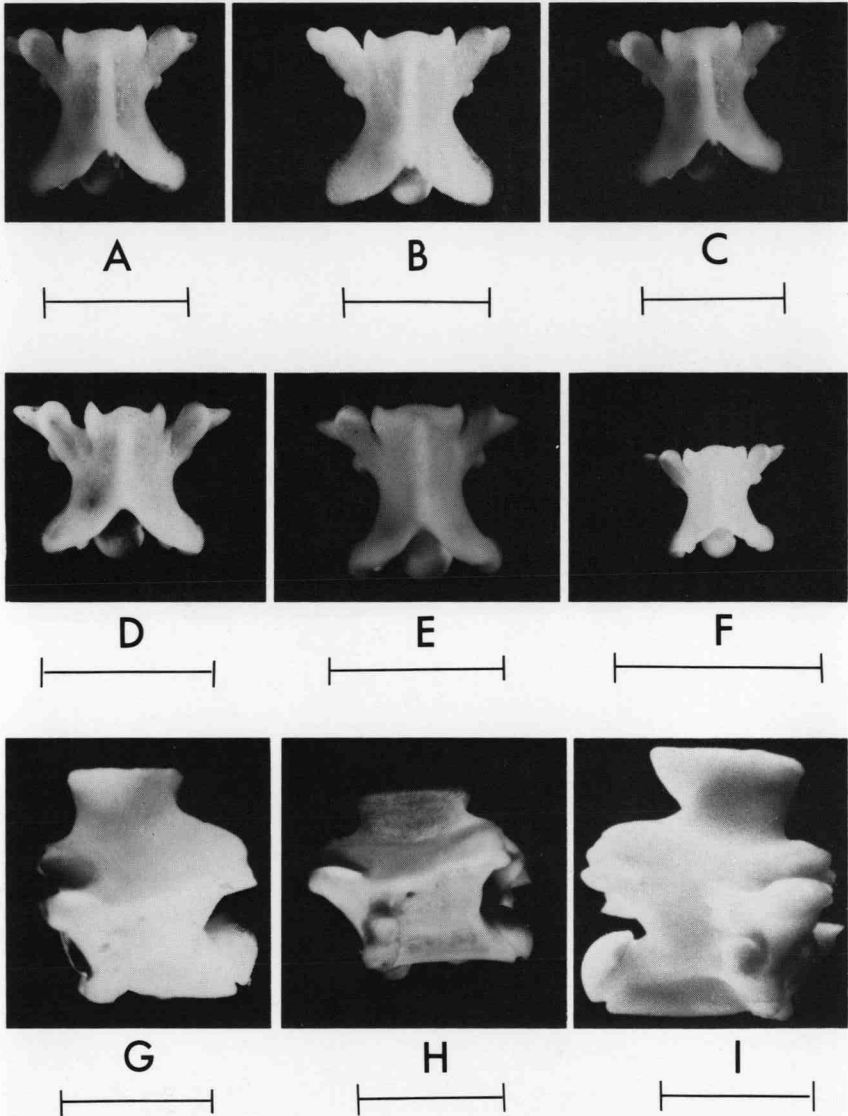
3-2. — Palatines of selected Recent North American snakes: (A) *Elaphe guttata*. (B) *Nerodia fasciata*. (C) *Elaphe obsoleta*. (D) *Nerodia cyclopion*. (E) *Lampropeltis getulus*. (F) *Coluber constrictor*. (G) *Pituophis melanoleucus*. (H) *Masticophis flagellum*. (I) *Heterodon platyrhinos*. (J) *Drymarchon corais*. All in dorsal view, X3 (each scale = 5 mm).



3-3. — Pterygoids of selected Recent North American snakes: *Elaphe guttata* (A) ventral view, (B) dorsal view. *Elaphe obsoleta* (C) ventral view, (D) dorsal view. *Lampropeltis getulus* (E) ventral view, (F) dorsal view. *Drymarchon corais* (G) ventral view, (H) dorsal view. *Coluber constrictor* (I) ventral view, (J) dorsal view. *Masticophis flagellum* (K) ventral view, (L) dorsal view. *Nerodia fasciata* (M) ventral view. *Farancia abacura* (N) ventral view. All X3 (each scale = 5 mm).



3-4. — Basiparasphenoids of selected Recent North American snakes: (A) *Elaphe guttata*. (B) *Elaphe obsoleta*. (C) *Lampropeltis getulus*. (D) *Pituophis melanoleucus*. (E) *Nerodia fasciata*. (F) *Farancia abacura*. (G) *Thamnophis sirtalis*. (H) *Coluber constrictor*. (I) *Masticophis flagellum*. (J) *Drymarchon corais*. All in dorsal view, X3 (each scale = 5 mm).



3-5. — Vertebrae of selected Recent North American snakes: (A) *Carphophis amoenus*. (B) *Diadophis punctatus*. (C) *Rhadinaea flavilata*. (D) *Sonora episcopa*. (E) *Stilosoma extenuatum*. (F) *Tantilla relicta*. (G) *Arizona elegans*. (H) *Cemophora coccinea*. (I) *Rhinocellus lecontei*. A-F dorsal views; G-I lateral views, all X10 (each scale = 2 mm).

3-6. — Number of teeth and condition of Meckle's groove in the dentary of selected North American snakes. A zero in the right hand column indicates that Meckle's groove is open to the symphysis.

Species	N	Number of Teeth	Meckle's Groove	
			Reduced to Slit at Tooth Number	Closed at Tooth Number
<i>Arizona elegans</i>	2	14-15	7 (1 case), not reduced (1 case)	6
<i>Cemophora coccinea</i>	1	10	not reduced	4
<i>Coluber constrictor</i>	7	19-22	not reduced	8-9
<i>Drymarchon corais</i>	5	17-19	7 (1 case), not reduced (4 cases)	5-8
<i>Elaphe guttata</i>	7	19-22	7-10 (6 cases), not reduced (3 cases)	4-6
<i>Elaphe obsoleta</i>	7	21-23	10-12	3-6
<i>Elaphe vulpina</i>	2	18-19	7	3-4
<i>Farancia abacura</i>	6	20-23	not reduced	4-6
<i>Heterodon platyrhinos</i>	7	16-18	3-4	0
<i>Heterodon simus</i>	3	14-15	3-4	3-0
<i>Lampropeltis calligaster</i>	2	14-15	6	4
<i>Lampropeltis getulus</i>	4	13-17	7 (2 cases), not reduced (2 cases)	3-5
<i>Lampropeltis triangulum</i>	2	16-17	not reduced	4-5
<i>Masticophis flagellum</i>	5	19-23	9 (1 case), not reduced (4 cases)	6-9
<i>Nerodia cyclopion</i>	11	19-23	not reduced	7-8
<i>Nerodia erythrogaster</i>	1	28	not reduced	6
<i>Nerodia fasciata</i>	9	26-29	not reduced	6-9
<i>Nerodia rhombifera</i>	1	25	not reduced	8
<i>Nerodia taxispilota</i>	4	22-26	not reduced	6-9
<i>Opheodrys aestivus</i>	3	22-24	12 (1 case), not reduced (2 cases)	6-8
<i>Pituophis melanoleucus</i>	6	17-19	7-9	3-4
<i>Regina alleni</i>	5	27-30	11-12 (4 cases), not reduced (1 case)	3-8
<i>Regina grahami</i>	1	34	18	0
<i>Regina rigida</i>	2	29	10-11	0-5
<i>Regina septemvittata</i>	4	23-27	5-9	0-4

<i>Rhinoceilus lecontei</i>	6	13-16	6-7 (2 cases), not reduced (4 cases)	3-5
<i>Seminatrix pygea</i>	6	20	not reduced	6-8
<i>Thamnophis eques</i>	1	31	not reduced	9
<i>Thamnophis marcianus</i>	1	29	not reduced	8
<i>Thamnophis melanogaster</i>	2	26-27	not reduced	6
<i>Thamnophis sauritus</i>	4	33-39	not reduced	8
<i>Thamnophis sirtalis</i>	5	26-30	not reduced	6-8
<i>Trimorphodon tau</i>	2	16-17	8	7
<i>Agkistrodon mokeson</i>	5	15-17	3 (2 cases), not reduced (3 cases)	0
<i>Agkistrodon piscivorous</i>	7	16-19	2-4 (6 cases), not reduced (1 case)	0-1
<i>Crotalus adamanteus</i>	8	8-10	1-5 (6 cases), not reduced (2 cases)	0
<i>Crotalus atrox</i>	4	9-10	1-2	0
<i>Sistrurus miliarius</i>	2	9-10	not reduced	0

1982

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