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A New Genus of Colubrid Snake from the Upper Miocene of North America

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INTRODUCTION

The oldest colubrid snake remains heretofore known from North America have come from the Republican River formation, lower Pliocene (Quarry E, near Long Island, Kansas; Gilmore, 1938, p. 63). It is thus of considerable interest that a very excellent specimen of fossil snake belonging to this family is now available from the upper Miocene of Montana.

A somewhat fragmentary skull, as well as some articulated anterior and middle thoracic vertebrae, makes this specimen of more than common interest. So complete a fossil snake is rather rare, and I wish to take this opportunity to thank Drs. George Gaylord Simpson and Edwin H. Colbert, the American Museum of Natural History, for the opportunity to examine and describe this interesting specimen. I also wish to thank Mr. Charles M. Bogert and Dr. Richard Zweifel, also of the American Museum, for allowing me to examine modern skeletons in their care. A large part of the delicate task of preparation was accomplished by Mr. Stanley Olsen, for which I am very grateful. Mr. Samuel B. McDowell deserves mention for preparing a skull of *Lystrophis* for my examination. I also wish to thank Mr. Arthur Loveridge, Museum of Comparative Zoölogy, for allowing me to prepare a skeleton of *Arhyton* for comparative purposes. Acknowledgment is certainly due to Dr. Ernest E. Williams for his valuable aid in many ways.

The following abbreviations are used:

A.M.N.H., the American Museum of Natural History, Department of Geology and Paleontology

A.M.N.H.:A.R., the American Museum of Natural History, Department of Amphibians and Reptiles
U.F., the University of Florida

DESCRIPTION

DRYINOIDES,[1] NEW GENUS

DIAGNOSIS: A Miocene snake, similar in certain skull and vertebral characters to the modern colubrid genera *Heterodon, Lystrophis, Conophis,* and *Arhyton.* From *Heterodon* it differs in having sharper subcentral and haemal ridges; lower, longer neural spines, which are less overhanging anteriorly; and neural arches not so strongly depressed. The skull of *Heterodon* differs from that of *Dryinoides* in possessing more elongated nasals; in being shorter, with the posterior and lateral edges of the dorsal spine of the premaxillary being projected, rather than the anterior edge being developed. From *Lystrophis* the fossil genus differs in possessing smaller subcentrum foramina; more flattened haemal keel; premaxillary with no dorsal spine-like process, but flattened and broad. From *Conophis* it differs in possessing a much less projected anterior process on the prefrontal; a wider frontal region; and a more acute posterior end of the haemal keel in the middle thoracic vertebrae. From *Arhyton* it differs mainly in possessing a longer frontal region; a higher, broader dorsal projection of the premaxillary; longer vertebrae with higher neural spines and with flattened haemal keels in the middle thoracic series.

GENOTYPE: *Dryinoides oxyrhachis,* new species.

Dryinoides oxyrhachis,[2] new species

HOLOTYPE: The type (A.M.N.H. No. 7524) consists of a partly articulated skeleton, composed of a fragmentary skull, 10 articulated anterior thoracic vertebrae, and 11 middle thoracic vertebrae, nine of which are articulated. The specimen was collected in 1925 by C. C. Mook and C. S. Williams.

TYPE LOCALITY AND HORIZON: Madison Valley, Gallatin County, Montana; Lower Clay, Madison Valley formation, upper Miocene (Barstovian).

DIAGNOSIS: The sole known species of the genus.

TYPE DESCRIPTION: The skull, though not perfectly preserved, is in fair condition. It is moderate in both size and shape. The parietal, though fractured down the median line, is readily discernible. From

[1] The generic name refers to Dunn's South American stock of New World colubrids (1931), a number of genera which have the Greek stem *Dryinas* in their names.

[2] From the Greek *oxy* (sharp) plus *rhachis* (a ridge or spine).

above, this element is wider anteriorly, being widest at the parieto-postorbital articulation, as in most colubrids, presumably with fairly straight lateral edges. It possesses no indication of a sagittal crest. The frontoparietal articulation presents a rather smooth, rounded appearance, not complicated with interdigitations. The prootic and lateral surfaces of the parietals are badly crushed. The squamosals, if present, are crushed beyond recognition, though a thin, slender fragment on the right side may represent a part of this element. The postorbitals are also badly broken, but a small narrow fragment on the left side pushed forward into the orbit is undoubtedly a portion of this element. The postorbito-parietal articulation apparently extended forward to very near the line of contact between the parietal and the frontals. The latter are wider anteriorly than posteriorly, with a median suture in a linear depression. Where they border the orbit they are very faintly emarginated. Following the contour of the orbit, and medial to the orbital border of the frontal, is a curved depression, provided with a series of small pits and perforations, of unequal size, which continues posteriorly on the parietal. The prefrontal is complete on the right side and is in position. In lateral view it is high and narrow, without a well-developed anterior projection. The lower posterior border is curved posteriorly. The external face is flat, not hollowed out or provided with a ridge as in some colubrid genera. Its articulation with the frontal is short, being more medial anteriorly. The nasals are badly crushed, the shape of which cannot be determined with any degree of accuracy. Each element appears to have been roughly subtriangular in shape, widest near their articulation with the frontal, becoming narrower anteriorly. They are flat, and there is no evidence that they came into contact with the premaxillary so intimately as in the genus *Heterodon*. The premaxillary, though tilted to one side, is in its approximate position and fortunately is rather complete. The dorsal process is broad and thin, slightly thickened medially. From above, the anterior border is broadly obtuse. From the front the process is somewhat subtriangular, truncated dorsally. The lateral processes are acute, slightly flattened, and project slightly posteriorly and ventrally. The ventro-anterior edge is slightly thickened medially. The two horizontal posterior processes are vertically flattened, moderately long, and parallel to the median line.

On the left side of the skull a structure possessing several alveoli is interpreted as an ectopterygoid, largely on the basis of its width and structure. However, it is too fragmentary to be useful in comparative studies of this element.

The only preserved mandibular element is a very broken surangular, of which only the posterior half is available. The laminae are low and not widely divergent from above. There is no coronoid.

The anterior thoracic vertebrae are provided with well-developed hypapophyses, which are moderately long, slender, and slightly compressed laterally. They extend from just posterior to the lip of the cotyle to below and directly under the condylus, where they end in a rather sharp tip directed posteriorly. The centrum is moderate in length, somewhat triangular from below. The subcentral ridges are rounded and weakly developed, extending from the diapophyses about halfway to the condylus. The paradiapophyses are moderate in size, provided with two well-developed articular facets, the upper larger and located more posteriorly than the lower. The anteroventral paradiapophysial process is well developed, extending below and anterior to the lower lip of the cotyle, flattened and ending in an acute tip well forward of the lower articular facets. The neural arch is moderately high and wide, but lacks any indications of the small spines found above the postzygapophyses in many colubrids. The zygapophysial articular facets are covered by articulated vertebrae so that it is not possible to determine their shape. The accessory processes of the prezygapophyses are well developed, extending laterally as a short acute spine on either side of the articular facets, directed slightly downward from the front, slightly anteriorly from above. The zygosphene-zygantrum articulation is hidden because of the articulated nature of the vertebrae. The interzygapophysial ridges are strongly concave and sharp. The anterior edge of the neural spine is almost vertical, overhanging posteriorly, slightly longer at its upper edge than its height at the anterior edge. The neural canal is moderately large, but not unusually so for anterior vertebrae.

The middle thoracic vertebrae are without hypapophyses. The broadly gladiate to oblanceolate-shaped haemal keel is expanded anteriorly so that it blends into the raised margin of the lower lip of the cotyle, extending posteriorly to just in front of the condylus. The entire structure is slightly flattened dorsoventrally. The centrum is moderate to slightly elongate, somewhat triangular from below, being widest at the paradiapophyses, narrowest at the condylar neck, which is short. The condylus is directed more posteriorly than dorsally. The centrum is slightly concave from the side and provided with weak subcentral ridges, extending from the median cleft of the paradiapophysial articular surfaces posteriorly to a little over halfway to the

condylus. The paradiapophysial articular surfaces are well developed, with two facets. The diapophysial surface is larger, more spherical, and posterior to the level of the parapophysial one. The parapophysial process is not greatly projected beyond the parapophysial articular surface, extending only slightly below the level of the centrum, and practically even with the lip of the cotyle. The cotyle is rounded, not distinctly oval. The neural arch is moderate in size, equal to, to slightly less than, the width of the cotyle. The neural arch is somewhat depressed, but not greatly so, and moderate in width, without a short spine above the postzygapophyses. The articular surfaces of the postzygapophyses are wider than long and somewhat oval in outline. The interzygapophysial ridges are strongly developed and concave. The articular surface of the prezygapophyses are oval to slightly subtriangular. A well-developed accessory process extends beyond the articular facets of the prezygapophyses as an acute spine, slightly flattened, directed laterally both from above and from the front. The zygosphene is thin dorsoventrally, with a straight to slightly convex anterior edge from above, convex from the front. The neural spine is long and low, extending from just anterior to the base of the zygosphene to the median, cleft posterior edge of the neural arch laminae, with a straight to slightly overhanging anterior edge, overhanging posteriorly.

The axis and atlas have been separated from the base of the skull so that they might be compared with those of modern colubrid genera. Only the left half of the atlas is complete. The neural spine is low. There is a well-developed spine on the posterior edge of the neural arch, dorsolateral in position. A lower spine (as found in some snakes), if present at all, must be very small. Further preparation will weaken these elements considerably, as they are badly cracked.

The axis is relatively long when compared to that of many other colubrid genera, not greatly depressed. The neural arch is fairly short, convex at its anterior edge both from the front and from above. The neural spine is long, low, slightly lower anteriorly, greatly overhanging posteriorly, the anterior edge more or less vertical. The odontoid process is conical, pointed, relatively narrow at its base, directed straight forward, not slightly upward as in some colubrid genera. There are three cranial articular surfaces, the lateral pair with a rounded surface, facing outward and forward, and blending into the base of the odontoid process, with no clear line of demarcation between them. The median ventral articular surface is flattened, directed anteriorly,

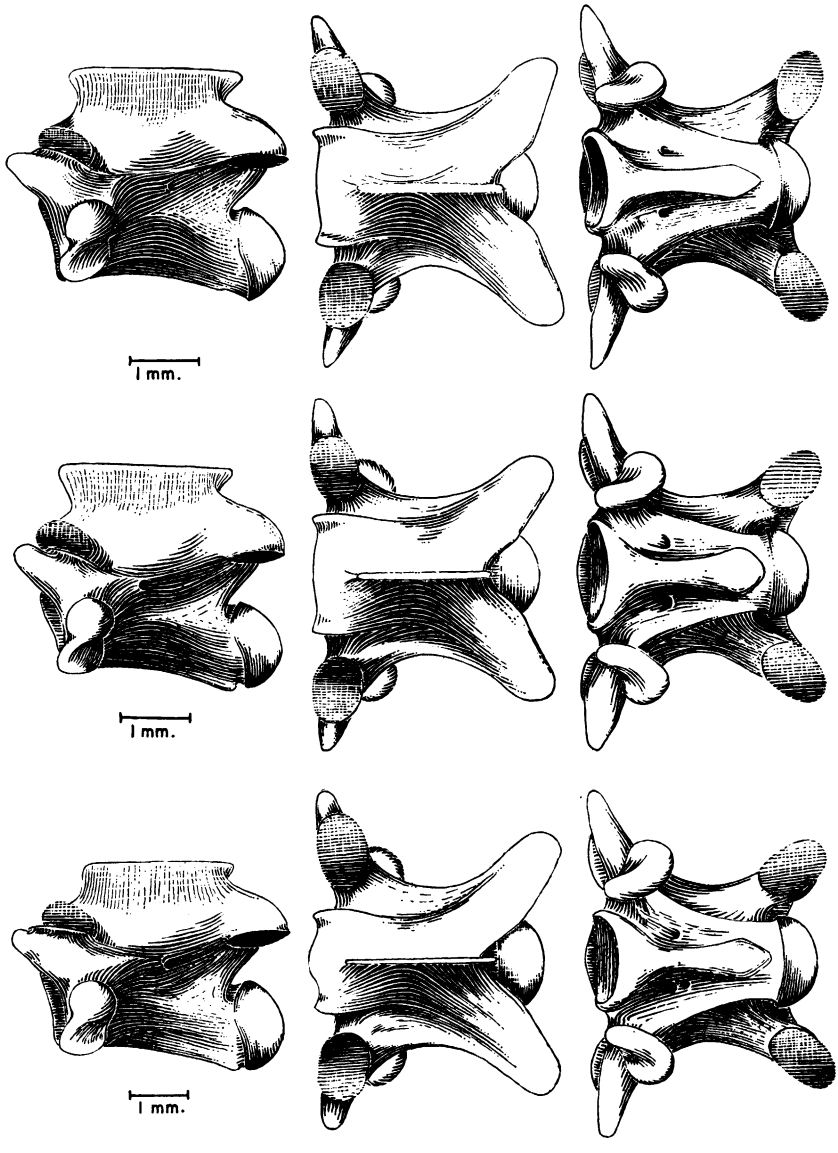

FIG. 1. Lateral, dorsal, and ventral views of middle thoracic vertebrae. Top row: *Dryinoides oxyrhachis,* new genus and species, holotype, A.M.N.H. No. 7524, Madison Valley, Gallatin County, Montana, Madison Valley formation, upper Miocene. Middle row: *Conophis lineatus,* Recent, U.F. No. 7657. Bottom row: *Lystrophis d'orbignyi,* Recent, A.M.N.H.:A.R. No. 71257.

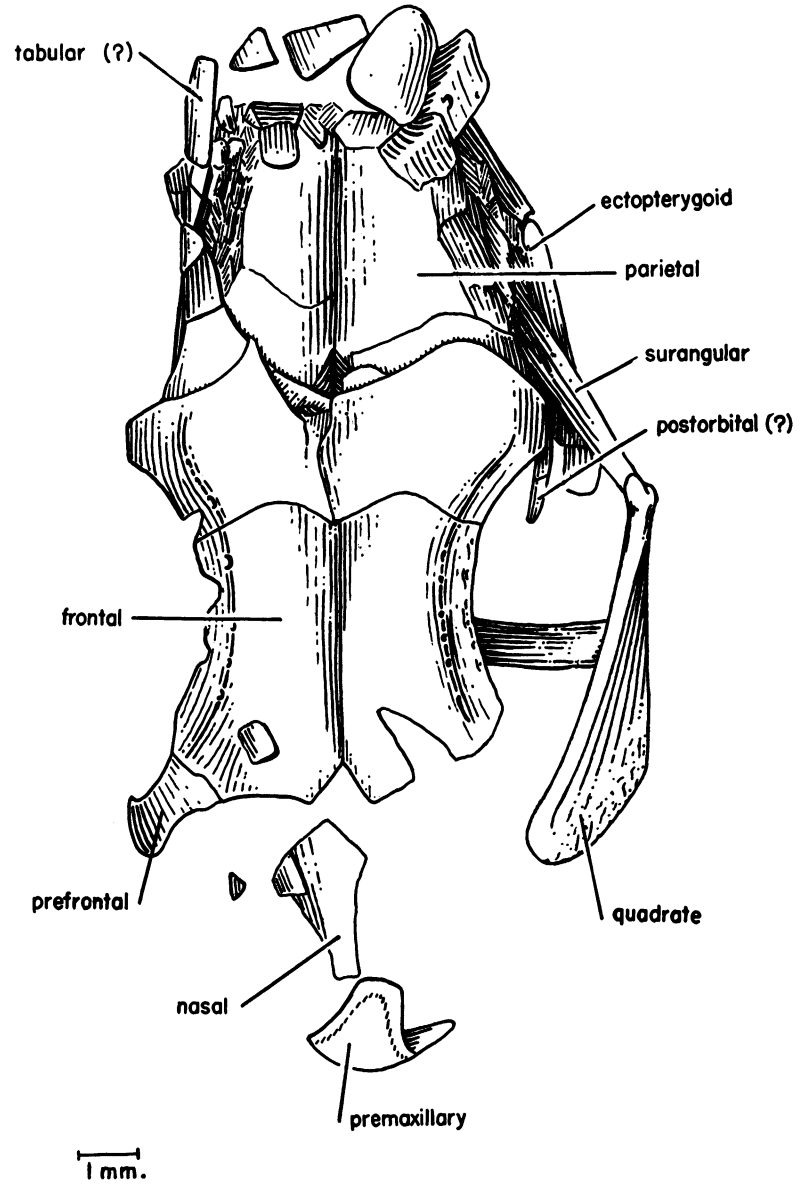

FIG. 2. Dorsal aspect of skull of *Dryinoides oxyrhachis,* new genus and species, holotype, A.M.N.H. No. 7524, Madison Valley, Gallatin County, Montana, Madison Valley formation, upper Miocene. Surrounding matrix not shown.

and vertically oval in shape. The remainder of the element is not discernible, as further preparation would cause it to separate into many small fragments.

The skull of the type, as well as the anterior and middle thoracic vertebrae, is illustrated in figures 1 and 2. Tables 1 and 2 give certain measurements and ratios of the skull and vertebrae.

COMPARISONS AND RELATIONSHIPS

Of particular interest and importance is the relationship of the fossil form to other snake genera, both fossil and Recent. The absence of a coronoid and a sagittal crest, as well as the moderately long vertebrae, which are provided with two well-developed paradiapophysial articular surfaces, and many minor details definitely separate

TABLE 1

MEASUREMENTS IN (MILLIMETERS) AND RATIOS OF THE MIDDLE THORACIC VERTEBRAE OF *Dryinoides oxyrhachis*, NEW GENUS AND SPECIES

Centrum length (cl)	3.13
Centrum width (cw)	2.49
cl/cw	1.26
Zygosphene width (zw)	0.75
zw/cl	4.17
zw/cw	3.32
Glenoid cavity, width (glw)	0.60
Glenoid cavity, height (glh)	0.56
glw/glh	1.07
Neural spine, length (nlu)	3.01
Neural spine, height (nh)	1.08
nlu/nh	2.79
Prezygapophyses to prezygapophyses (pr-pr)	4.68
Postzygapophyses to prezygapophyses (po-pr)	3.82
pr-pr/po-pr	1.23

Dryinoides from the Boidae, Uropeltidae, and Anilidae. It is obviously not a typhlopid or leptotyphlopid, on numerous skull characters, if nothing else. Unfortunately the maxillary is missing, but the absence of hypapophyses on the middle thoracic vertebrae clearly excludes the Elapidae, Hydrophidae, and Viperidae as possible close relatives. Xenopeltids, as well as several of the families mentioned above, have premaxillary teeth. These are absent in the fossil specimen.

All available evidence points to the fact that *Dryinoides* definitely belongs in the family Colubridae. On the basis of the known fossil snakes, this family was already well differentiated in the Miocene. By

TABLE 2

MEASUREMENTS (IN MILLIMETERS) AND RATIOS OF THE SKULL OF *Dryinoides oxyrhachis*, NEW GENUS AND SPECIES

Length of frontal (lf)	4.38
Narrowest width of frontal (fw)	4.24
lf/wf	1.03
Greatest width of parietal	7.24
Length of quadrate	7.54
Height of prefrontal	3.51

the Pliocene at least some modern genera were well established. The possibility of finding a close relative to *Dryinoides* among modern genera is, therefore, not remote.

Unfortunately comparative series of the vertebral columns of snakes are rather inadequate in most collections, so that certain important Old World colubrid genera have not been compared with the fossil. Of the New World colubrids I have examined adequate material of all the currently recognized subfamilies.

The position of many genera in the Colubridae is not at all certain. Subfamilial categories are not always clearly defined. Phyletic lines are not easily demonstrated. It is, therefore, somewhat difficult to place *Dryinoides* in any particular subfamily with any real degree of assurance.

Probably the most important single character exhibited by the fossil is the absence of hypapophyses in the middle thoracic vertebrae. It is a characteristic feature of several modern subfamilies of Colubridae. Whether the structure is primitive in the colubrid snakes is unknown. More than likely it was derived independently in several phyletic lines. In any event, hypapophyses in the middle thoracic region were present in at least some Miocene snakes, as a natricine is known from this epoch in Europe. The Sibynophiinae apparently represent a primitive group, perhaps close to the Natricinae. They possess hypapophyses throughout the column. On these bases they are excluded from consideration as a possible subfamilial position for *Dryinoides*. The Acrochordinae differ greatly from *Dryinoides* in various ways, chiefly in their short, wide vertebrae and the spine-like neural spine. The xenodermines have fairly high neural spines which are frequently T-shaped in cross section and may be ornamented dorsally with pustulations. In addition the prezygapophysial or postzygapophysial process is greatly expanded laterally. The fossil genus possesses none of these characteristics.

The anterior vertebrae of *Dryinoides* are not highly modified, as in the Dasypeltinae or Elachistodontinae. However, these may be rather recent specializations in these two subfamilies. In addition, the skull of the fossil form differs markedly from that of at least *Dasypeltis.*

The subfamily Colubrinae serves partly as a "catch-all," though for the most part it seems to form a fairly definitive and natural group. On the other hand the Xenodontinae and Coronellinae are somewhat less clearly defined and seemingly do not form, as a whole, natural groups. *Dryinoides* seems closest to these three subfamilies, none of which possess hypapophyses on the middle thoracic vertebrae.

Of these three subfamilies I have examined at least the middle thoracic vertebrae of 82 genera, representing 132 species. The vast majority of these are New World forms. Adequate comparisons between *Dryinoides* and various genera referred to the three subfamilies above have thus been possible only with genera from the New World.

The vertebral type is quite varied in the Colubrinae and Xenodontinae, and I find it impossible to separate them into two groups on this basis alone. There is, however, a fairly definitive series of approximately nine groups which can be recognized on vertebral characters. These nine groups suggest Bogert's (1940) tentative arrangement of African colubrids. It is not within the scope of the present paper to arrange the New World Colubridae on the basis of vertebrae, but it seems pertinent to point out that Dunn's separation of the Colubrinae and Xenodontinae (1928) is not entirely compatible with an arrangement based on the anatomy of the vertebral column alone. For the present it seems best to compare the fossil directly with various genera from both of these subfamilies.

On the basis of vertebral form and structure *Conophis* approaches the fossil more closely than all the other modern genera I have examined (fig. 1). From this genus the fossil vertebrae are mainly distinguished on the basis of the shape of the haemal keel, which is more flattened and has a more acute posterior tip in *Dryinoides.*

A flattened haemal keel occurs with some frequency in genera placed in both the Colubrinae and Xenodontinae. However, almost all these genera are considerably different from *Dryinoides* in that the keel usually has a rounded posterior tip *(Sonora, Toluca, Rhadinea, Enulius,* and *Carphophis);* or, if the haemal keel is nearly like that in *Dryinoides,* the centrum is longer *(Oxybelis, Leptophis),* or has a higher neural spine *(Pseutes, Tomadon, Stenorhina, Philodryas, Chironius, Drymarchon,* and *Leimadophis),* or has more prominent subcentral ridges *(Rhadinea, Lampropeltis,* and *Drymarchon).*

Flattening of the haemal keel may vary with age, so that in young specimens of *Drymarchon corais* this structure is ridge-like, becoming flattened with increasing size. On the other hand, the character may be found in some species of a single genus but not in others *(Leimadophis, Tomadon, Philodryas,* and *Lampropeltis).* An intermediate condition is characteristic of some forms, so that not all species are clearly placed in one category or the other *(Lampropeltis, Tantilla,* and *Sonora).*

Therefore, the character, though it possesses some diagnostic value, cannot be relied on very heavily.

Of considerably more value is the angle formed at the posterior tip of the keel. In the fossil form it is very acute, as it is in many genera placed in the Xenodontinae. However, an acute tip is not confined to this subfamily, as it also occurs in the Colubrinae, but to a limited extent.

A combination of these two characters, i.e., a flattened, gladiate-shaped haemal keel with an acute posterior tip, is most common in Central and South American genera, being most frequent in the Xenodontinae.

Besides *Conophis,* the vertebral characters of *Dryinoides* are basically similar to those in *Lystrophis, Heterodon,* and *Xenodon. Lystrophis* and *Heterodon* have frequently been placed close to each other. An examination of not only the vertebrae but the skull as well seems to complement certain external similarities, such as the upturned rostrum. The differences in hemipenial characters and the respiratory system may be specializations derived quite recently in the evolution of this group.

Most of the modifications of the skull of *Heterodon* are apparently brought about by the shortening of the length of the head and strengthening of the naso-premaxillary area. The very specialized vertebrae of *Heterodon* can readily be derived from a condition similar to that found in *Lystrophis.* The vertebrae of *Xenodon* bear some resemblances to those of *Lystrophis.*

Of the three modern genera, *Dryinoides* is closest to *Lystrophis.* It differs from *Xenodon* in possessing a shorter centrum, lower neural spine, and more flattened haemal keel. From the vertebrae of *Lystrophis* those of *Dryinoides* differ mainly in the smaller subcentral foramina, a more flattened haemal keel, and a lower neural spine. From the vertebrae of *Heterodon platyrhinos* those of *Dryinoides* differ in having a higher neural arch, a more anterior position of the subcentrum foramina, and a lower neural spine. From *Heterodon*

simus and *H. nascicus* the fossil form differs in having a higher neural arch and a much narrower haemal keel. In addition the neural spine is much lower.

Among North American colubrine genera the fossil is approached most closely by the *doliata* group of *Lampropeltis*. The similarities include moderate size and proportions of the vertebrae, a low neural spine, absence of small spines above the postzygapophyses, and the tendency towards a flattened haemal keel. However, *Lampropeltis doliata* and closely related species are distinguished from *Dryinoides* in possessing much more well-developed subcentral ridges, and a haemal keel which, even when flattened, is more ridge-like. In addition, the vertebrae of *Lampropeltis* are almost always shorter. The fossil form is quite distinct from *Lampropeltis getulis* in a number of characters, including, among other things, a much lower neural spine, smaller size of the vertebrae, more flattened haemal keel, and much less well-developed subcentral ridges.

The vertebrae of *Dryinoides* bear some resemblances to those of *Rhadinea*. However, as pointed out above, in the latter the haemal keel, though frequently flattened, is provided with a rounded posterior tip. In addition, the fossil form is larger, with less well-developed subcentral ridges and a lower neural spine.

The slight similarity of *Dryinoides* to *Rhadinea* suggests a possible relationship between the former and *Liophis*. In the latter the neural spine is much higher and the haemal keel is not flattened, but strong and ridge-like.

Unfortunately many bones of the skull of the type specimen have been crushed beyond recognition, or beyond hope of comparison with modern genera. Some elements are, however, fairly good. Chief among these are the premaxillary, the prefrontals, and the frontals. Unfortunately, the nasals are badly broken.

Of the unbroken skull elements the premaxillary and prefrontals are probably the most important. In many colubrid genera the premaxillary is provided with a narrow, high, dorsal spine (fig. 3L). This is highly modified in certain genera. It may be thickened anteroposteriorly, even ridge-like and projected anteriorly, as in *Pituophis*. In *Heterodon* the basic structure is modified by the development of two fan-like processes, each arising from the posterolateral surface of the dorsal spine (fig. 3L). These and similar modifications have led to the suggestion by Bogert (1947) that premaxillary shape may be a useful tool in a determination of the relationships between at least some colubrid genera.

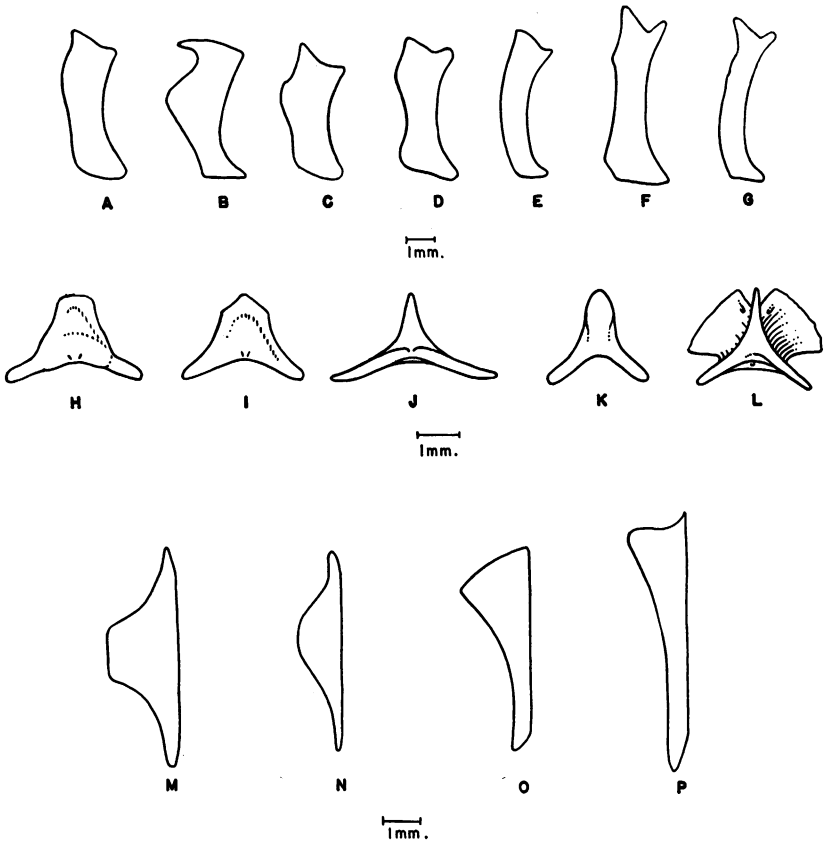

FIG. 3. A–G. Left prefrontals from right side. A. *Dryinoides oxyrhachis,* holotype, A.M.N.H. No. 7524. B. *Conophis lineatus,* U.F. No. 7657. C. *Rhadinea cobela,* A.M.N.H.:A.R. No. 4402. D. *Xenodon merremii,* U.F. No. 7658. E. *Lystrophis d'orbignyi,* A.M.N.H.:A.R. No. 71257. F. *Heterodon platyrhinos,* U.F. No. 7656. G. *Heterodon simus,* U.F. No. 7655. H–L. Premaxillae, anterior view. H. *Dryinoides oxyrhachis,* holotype, A.M.N.H. No. 7524. I. *Conophis lineatus,* U.F. No. 7657. J. *Xenodon merremii,* U.F. No. 7658. K. *Lystrophis d'orbignyi,* A.M.N.H.:A.R. No. 71257. L. *Heterodon platyrhinos,* U.F. No. 7656. M–P. Right nasals from above. M. *Dryinoides oxyrhachis,* holotype, A.M.N.H. No. 7524. N. *Conophis lineatus,* U.F. No. 7657. O. *Lystrophis d'orbignyi,* A.M.N.H.:A.R. No. 71257. P. *Heterodon platyrhinos,* U.F. No. 7656.

In *Dryinoides* the premaxillary is thin, broad, and flattened anteroposteriorly (fig. 3H). A somewhat similar shape is found in the genera *Farancia, Sonora, Carphophis, Elaphe, Lampropeltis, Rhadinea, Liophis,* and *Conophis* (fig. 3I). Within these genera there is considerable

variation, so that in *Elaphe* it is much higher than in *Dryinoides,* and not nearly so flattened. In the *Lampropeltis doliata* group, which in vertebral form approaches the fossil, the premaxillary is usually much broader than in the latter. The remaining genera are close to *Dryinoides* in this particular character. In *Lystrophis* the premaxillary dorsal spine is thickened anteroposteriorly, not flattened as in the fossil (fig. 3K).

Most of the genera that are provided with an anteroposteriorly flattened dorsal spine of the premaxillary are fossorial or semi-fossorial forms. A structure of this type may be correlated with burrowing, though many fossorial or semi-fossorial genera do not possess this type of dorsal spine (*Micrurus,* etc.).

Another character of apparent taxonomic importance is the shape of the prefrontal. Fortunately this element is present and not broken, so that comparison with modern genera is possible. Among the skulls that I have examined there is considerable variation in the shape of this element. Of apparently particular importance is the fact that the anterior projection, directed towards the nasals (a common condition in colubrids) is virtually absent in *Dryinoides.* In this regard the fossil is most closely approached by *Lystrophis, Heterodon,* and *Ahryton* (fig. 3E, F). Both *Heterodon* and *Lystrophis* possess a slight notch on the dorsal edge. Although present in the fossil, it is much more weakly developed. This notch is absent in *Ahryton.* Of the three genera, the structure in *Dryinoides* is closest to that in *Lystrophis.*

The absence of an anteriorly directed process on the prefrontal is not an uncommon feature in colubrids. However, in most of the genera in which this process is missing or weakly developed a ridge is present on the lateral external surface of the element (as in *Sonora*). This lateral external ridge is absent in *Dryinoides.*

In *Conophis,* the modern genus most similar to *Dryinoides* in vertebrae and premaxillary shape, the prefrontal is provided with an anteriorly directed process, but not so well developed as in many colubrid genera (fig. 3B).

The contact of this element with the frontal is longer in *Conophis* than in the fossil. In addition, the frontal is not provided with pits and perforations, and the supraorbital area is more indented and narrower from above than in *Dryinoides. Lystrophis* possesses small and isolated frontal pits and perforations which become even more pronounced in *Heterodon.*

The shape of the prefrontal in *Lampropeltis doliata* is intermediate between that in *Dryinoides* and that in *Conophis.* In *Xenodon* this

element has a well-developed anterior process. In *Rhadinea* and *Liophis* the prefrontals and premaxillae are similar to those in *Dryinoides.*

It is perhaps too early to ascertain with certainty the relationships of *Dryinoides* to our modern snake fauna. There are, however, some interesting facts and problems that the fossil brings to attention.

First of all, a larger number of genera currently placed by some workers in the Xenodontinae bear resemblances to *Dryinoides* than genera placed in the Colubrinae. If the supposedly South American-derived Xenodontinae form a natural group, and *Dryinoides* is a Miocene member of that group, then (1) the subfamily is probably older than the known fossil history of snakes would tend to indicate, because the Colubridae would have had to have been well differentiated before the Eocene, or (2) *Dryinoides* is a form that through waif dispersal reached North America over the then flooded Isthmus of Panama. On the basis of present evidence the former seems highly unlikely, as the earliest definite record for the family is in the Miocene. The latter remains as a possibility.

There is, on the other hand, evidence (Bogert, 1940; Smith, 1942) that some genera placed in the Xenodontinae are incorrectly placed there, or that the group is an unnatural one. On the basis of vertebral structure the latter seems most reasonable. If true, then the apparent relationship of *Dryinoides* to certain Recent genera placed in the Xenodontinae raises no paleozoogeographic problems.

Dryinoides may, however, be related to *Lampropeltis,* and the suggested relationship to such forms as *Conophis* and *Lystrophis* may be merely the results of convergence. However, the extreme similarity of the fossil vertebrae to those of *Conophis,* as well as a general agreement in skull characters, suggests a closer relationship to this genus than to *Lampropeltis.* Furthermore, a probable close relative of *Lampropeltis,* perhaps even an ancestral form, is already known from the lower Miocene of Florida (Auffenberg, MS).

Lystrophis certainly seems close to *Heterodon* on the basis of at least the skull and vertebrae. *Dryinoides* bears some resemblances to both *Lystrophis* and *Heterodon,* especially *H. platyrhinos;* less so to the more specialized species, *H. simus* and *H. nascicus.* The differences in the lungs, premaxillae, and hemipenial characters between these two genera may be lately derived specializations in one or the other.

As an alternative, *Conophis, Lystrophis,* and *Heterodon* may be incorrectly placed in the Xenodontinae, in which case no serious paleozoogeographical problems are raised by *Dryinoides.*

The entire problem of taxonomic units in the Colubridae is in need of at least some re-evaluation. The relationships of many genera remain obscure. Subfamilial characteristics are based on characters of which virtually nothing is known concerning their variability; or the characters are interpreted differently by several workers in the same group. Osteological characteristics have not been thoroughly explored, and the fossil history is all but unknown except for the Pleistocene. Thus, without a firm taxonomic foundation in the Colubridae, the full importance of the discovery of *Dryinoides* cannot be realized at this time. More detailed study in the osteology of snakes may shed considerable light not only on the relationships of modern snake genera but on fossil forms such as *Dryinoides* as well.

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