

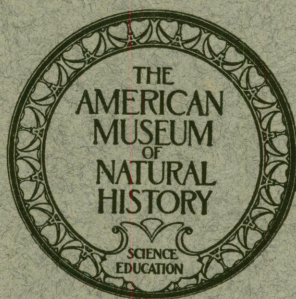
A NEW FOSSIL SNAKE FROM THE NOTOSTYLOPS BEDS OF PATAGONIA

BY GEORGE GAYLORD SIMPSON

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

VOLUME LXVII, 1933

ARTICLE I



NEW YORK

May 26, 1933

BULLETIN
OF
THE AMERICAN MUSEUM OF NATURAL HISTORY

VOLUME LXVII, 1933

56.81, 2 M (1181: 82.9)

**Article I.—A NEW FOSSIL SNAKE FROM THE *NOTOSTYLOPS*
BEDS OF PATAGONIA¹**

BY GEORGE GAYLORD SIMPSON

Among the more remarkable discoveries of the Scarritt Patagonian Expedition is much of the skeleton of a gigantic snake, ranking among the largest known. It is also unusually well preserved in comparison with most of the fragmentary and rare fossil remains of snakes so far discovered.

The drawings in this paper are by Mildred Clemans.

In his list of the *Notostylops* fauna, Ameghino (1906, p. 466) included "des Ophidiens, quelques-uns de taille gigantesque." This perhaps was based on fragmentary specimens of the species here described, although the only specimens found in his collection are probably distinct and are only about one-third as large as ours. He gave no description and did not mention ophidians as occurring in any other Patagonian formation.

In 1901, Smith Woodward described *Dinilysia patagonica*, a rather boa-like snake of moderate size (probably considerably less than ten feet) believed to be related to the recent small, degenerate, burrowing, South American snake *Ilysia*. This has sometimes been recorded as of *Notostylops* or comparable age, but there is nothing in the known data to support this. It was found by Roth in "the red sandstone of Neuquén" and was associated with mesosuchian crocodiles and no mammals. This clearly indicates Cretaceous age and there is now no reason to suppose that it came from the *Notostylops* Beds. It is distinct from the known snakes of Tertiary age. *Dinilysia* appears to be the only fossil snake previously described from South America.

¹Publications of the Scarritt Patagonian Expedition, No. 13.

NOMENCLATURE OF OPHIDIAN VERTEBRAE

As fossil snakes are almost invariably described on the basis of vertebrae, usually the only remains available, their study has become a specialized one with descriptive technique and terminology somewhat different from other branches of palaeontology. The principal works cited below, and particularly those of Owen and Rochebrune, illustrate variations of this method. For convenience and because usage varies somewhat, a brief outline of the nomenclature used is here given.

Considering the vertebral column as a whole, Rochebrune divides it into five regions, which he calls cervical, thoracic, pelvic, sacral, and coccygeal. A convenient grouping is as follows:

1. Cervical. Usually two in number. Without ribs and strongly modified in form.
2. Thoracic. Far the greatest number. With movable ribs.
 - A. Anterior thoracic (thoracic of Rochebrune, in a limited sense). Usually fewer than the posterior thoracic. With long hypapophyses.
 - B. Posterior thoracic (pelvic of Rochebrune). With hypapophyses short or absent.
3. Caudal. Always fewer than thoracic and usually only a fourth or a fifth as many. Without movable ribs.
 - A. Anterior caudal (sacral of Rochebrune). Never more than ten in number. With bifid diapophyses (or fused ribs) and no lymphapophyses.
 - B. Posterior caudal (coccygeal of Rochebrune). Much more numerous than the anterior caudal. With single diapophyses and strong lymphapophyses.

There is little agreement regarding the grouping of these five (or fewer) divisions, still less regarding their names, and they cannot always be clearly recognized. The few vertebrae here placed as 3A, anterior caudals, are often grouped with the thoracic or pre-sacral vertebrae as corresponding more or less to lumbar.

Rochebrune gives the following figures for the various categories of vertebrae in some recent snakes more or less comparable to our fossil.

	1	2A	2B	3A	3B	Total
<i>Python sebae</i>	2	72	228	6	62	370
<i>Python molurus</i>	2	68	296	8	62	435
<i>Liasis amethystinus</i>	2	65	255	10	92	424
<i>Tortrix scytale</i>	2	38	191	5	32	268
<i>Xenopeltis unicolor</i>	2	46	135	7	20	210
<i>Eryx jaculus</i>	2	31	160	7	20	220
<i>Cylindrophis rufa</i>	2	36	125	9	15	187
<i>Boa constrictor</i>	2	55	193	8	44	302

With their twelve articular surfaces, fifteen or more processes, numerous muscle attachments, etc., ophidian vertebrae are very complex objects. Chiefly following Owen, the following are the principal terms used in describing them, with the meaning here employed:

Centrum—the actual body of the vertebra, below the neural canal and between the condyle and glenoid cavity. In snakes, the centrum is usually much outweighed in bulk by the various processes arising from it.

Condyle—the approximately hemispherical posterior articular process of the centrum.

Glenoid cavity—the anterior concavity on the centrum, for the reception of the condyle of the preceding vertebra.

Neural arch—the two plates arising from the top of the centrum, surrounding the neural canal, and meeting in the midline above.

Neural canal—the canal for the spinal cord.

Neural spine—the median dorsal projection above the neural arch.

Aliform processes—wing-like posterior projections, one on each side of the neural arch.

Prezygapophyses—paired anterior processes arising near the junction of the neural arch and centrum on each side, bearing articular facets facing upward (and generally somewhat inward).

Postzygapophyses—similar posterior processes bearing articular facets facing downward (and generally somewhat outward) for articulation with the prezygapophyses of the following vertebra.

Zygosphen—a somewhat wedge-shaped median anterior process from the union of the neural arch above the neural canal, bearing two articular processes facing outward and downward.

Zygantrum—a mortise-like depression on the posterior part of the neural arch above the neural canal, articulating with the zygosphen of the following vertebra.

Diapophyses—paired processes on the two sides of the vertebra, below the prezygapophyses. On the thoracic vertebrae they bear ribs, and on the caudals are variously produced. One division, where these processes are bifid, is sometimes called the parapophysis. Although "diapophysis" in so broad a sense undoubtedly includes various non-homologous structures, the homologies are so uncertain that it is convenient to use the term descriptively to include all lateral processes on this part of the vertebra, its exact application being sufficiently clear from the context.

Hypapophysis—a median ventral process, sometimes double (in tandem) but very seldom distinctly paired (transversely).

Lymnaphophyses—laterally paired ventral processes (occurring only in the posterior caudal region).

The distinguishing of these units rather than any others is in part objective and the supposed homologies and exact applications vary, but used consistently within the group the names as here defined are adequate as a mechanism for description. Haemapophyses, chevron bones, are absent as such in snakes.

Viewing most ophidian vertebrae from the side, three chief surfaces are seen between the hypapophysis and neural spine. The smallest,

usually rather simply concave, is on one side of the ventral part of the centrum, generally bounded on the midline by the hypapophysis or a ventral median keel, or haemal carina, and usually ending above at a rounded ridge or buttress running forward from the side of the condyle to the diapophysis. Above this ridge, which may be absent, is a larger surface facing outward, backward, and downward. The surface is usually slightly and somewhat irregularly concave. It is bounded above by the usually strong angulation or buttress between the prezygapophysis and postzygapophysis. Above this is a still larger surface, on the neural arch, facing upward, forward, and outward. Posteriorly it is produced into the aliform process, if present, and it extends to the base of the neural spine at the midline. Near its middle there is often a slight convexity, above and below which are concavities.

In articulation the vertebrae are very strongly locked, having five articulations with each adjacent vertebra, one large ball and socket joint and four smaller inclined planes. Lateral motion is relatively free, and there is some possible movement arching the back so that it is slightly convex dorsally, but little or no possibility of causing it to be concave dorsally. When articulated, there is a vertical passage running into the neural canal between and below each articulation of pre- and postzygapophyses, which no amount of lateral movement can close completely. There is also a dorsal passage communicating with this near its junction with the neural canal and lying between the zygapophysis and the zygosphene-zygantrum articulations on each side, widely open on the convex side when the body is curved strongly laterally, but almost closed on the concave side. The zygosphene almost completely fills the zygantrum in articulation, leaving only a little space at its deepest middle part, with little or no free passage into the neural canal, but with a large triangular dorsal opening. This deep anterior part of the zygantrum is often divided into two hollows by a vertical median ridge or convexity.

These are the leading structures common to most snakes. Taxonomy is based for the most part on relatively minor differences of proportion, shape, and position rather than on outstanding structural distinctions. Comparisons of fossil snakes are usually and most conveniently based on thoracic, and especially posterior thoracic, vertebrae, as these are the most abundant in the living animals and in collections of their isolated bones.

DISTRIBUTION OF THE BOIDAE

Werner's classification of the Boidae (Werner, 1921) recognizes twenty genera with a distribution extending through practically all the tropical and subtropical parts of the world. There are several remarkable anomalies in the distribution of the family. *Boa* and *Corallus* occur in the Neotropical region and in Madagascar but not in any intervening area. *Casarea* of Round Island, near Mauritius, also appears to be of Neotropical affinities. On the other hand, *Loxocemus* of southern Mexico and Guatemala seems to be more nearly related to the Old World pythons than to any Neotropical boids. The family Ilysiidae, apparently derived from the Boidae or at least allied to it in spite of the very different appearance and habits of its recent members, also has a peculiar distribution, occurring in South America and southern Asia (Ceylon, Malay Archipelago, Indo-China). In other and more distantly related snakes there are some similar examples of discontinuous distribution involving South America and very distant parts of the Eastern Hemisphere.

These distributional anomalies suggest that of *Tapirus* among mammals and must be due to the same cause: survival only at distant and isolated points of groups formerly occupying the whole intervening region.

Some classifications separate the boas, pythons, and their allies into two or more families. There is some question as to the phylogenetic validity of such divisions, and in any event they apparently cannot be recognized in the materials usually available to palaeontologists. In dealing with fossils, there has been a strong tendency to consider those from the Western Hemisphere as boids and from the Eastern as pythonids, but even if these groups are valid the distributional anomalies of recent forms fully prove that at one time or another both have spread widely over both hemispheres. The term Boidae must then be used palaeontologically in a broad sense for all these snakes. They do form a natural unit, and the available material is far too scanty as yet to trace any sure phyletic divisions. It is also doubtful whether some other distinct but more or less nearly allied groups have not been confused with the Boidae in dealing with fossils. This may be true of the Ilysiidae, for instance, which would almost inevitably be confused with the Boidae in the absence of good specimens of the skull.

The boids are a relatively primitive group, almost devoid of any of the various specializations which characterize all other ophidian families. Thus both jaws have teeth, these are simple and nearly equal, the pterygoid reaches the quadrate, an ectopterygoid is present, the coronoid has

not been lost, the squamosal or supratemporal is present, the prefrontal is strongly in contact with the nasal, the vertebrae seldom show any marked compression or aberrant development of processes, and there are vestiges of the hind limbs. Their distribution also implies antiquity, although hardly more remarkable than that of some other groups of snakes.

A large proportion, probably the majority, of fossil snakes have been referred to the Boidae. Some of these references may not be correct, not being verifiable without a revision of the generally fragmentary and widely scattered materials, but most of them probably are. This is not surprising, as the very wide recent distribution of the boïds, their considerable generic differentiation, and their primitive structure testify to a long and widespread career, while the medium to large size of many of them tends to aid their preservation and discovery as fossils. Their recent distribution includes the whole tropical and most of the subtropical zones throughout the world save on strictly oceanic islands. Their known history as fossils extends back to the Eocene and also covers most of the world: fossil boïds have been found on each of the continents, in several cases outside the limits of the climatic zones in which they now occur, for instance in Canada and Patagonia. The recent forms, and also the extinct genera, cover a wide range of size, from two feet or less to about thirty feet, or possibly more, in length. The smallest recent species, for instance of the chiefly Mediterranean and Central Asiatic genus *Eryx*, are smaller than the probable size of any of the known fossils, but it is doubtful whether any of the extinct forms much exceeded the greatest size reached by the recent pythons or anacondas.

In addition to the probable fossil boïds, there are in the Cretaceous and Eocene several other genera of fossil snakes, some of large size, of great interest and importance but not now believed to be boïds: *Pachyophis*, *Symoliophis*, *Archaeophis*, *Palaeophis*, *Pterosphenus*.

The principal known genera of boïds found fossil and their distribution are as follows:

EOCENE:

Western North America:

Boavus Marsh.

Protagras Cope.

Lithophis Marsh.

Lestophis Marsh.

Patagonia:

Madtsoia Simpson. (Described below).

England:

Paleryx Owen.

Germany:

Paleryx Owen.

Palaeopython Rochebrune.

Egypt:

Gigantophis Andrews.

EOCENE TO OLIGOCENE (Phosphorites du Quercy):

France:

Palaeopython Rochebrune.

Scytalophis Rochebrune.

OLIGOCENE:

Western North America:

Aphelophis Cope.

Calamagras Cope.

Ogmophis Cope.

MIOCENE:

Western North America:

Ogmophis Cope.

France:

Scaptophis Rochebrune.

Botrophis Rochebrune.

Sardinia:

Palaeopython Rochebrune. (Reference to this genus doubtful).

Euboea:

Heteropython Rochebrune.

PLIOCENE:

India:

Python.

Burma:

Daunophis Swinton.

PLEISTOCENE:

India:

Python.

Australia:

Python.

The great majority of the fossil species included in these genera (of which all but *Python* are extinct) are based on isolated vertebrae, or at most five or six in association. The outstanding exceptions are:

Paleryx: twelve associated vertebrae and skull fragments in the referred species *P. spinifer* Barnes.

Gigantophis: about twenty associated vertebrae and a jaw fragment of another individual.

Heteropython: twenty-six associated vertebrae and associated fragment of lower jaw.

Daunophis: nearly complete individual, but so poorly preserved that no one part is clearly exhibited.

Madisoia: see below.

Nothing approaching a complete skull or jaw is known. In *Gigantophis*, *Heteropython*, and *Palaeopython*, lower jaw fragments are known. In *Paleryx spinifer* Barnes, parts of the upper jaw and parietal are known.¹ *Palaeopython sardus* Portis, from the Middle Miocene of Sardinia, is exceptional among fossil boïds in not being known from vertebrae but only from an upper jaw fragment. Its reference to this genus is dubious, as it is not directly comparable with the genotype, *P. cadurensis* (Filhol) of the Phosphorites du Quercy, and is of much later age. In *Daunophis* there is a vague impression of the head region, but no morphological characters could be determined. *Madtsoia* is on the whole the most satisfactory known fossil boïd.

DESCRIPTION OF NEW PATAGONIAN EOCENE BOÏD

Madtsoia,² new genus

TYPE.—*Madtsoia bai*, new species.

DISTRIBUTION.—*Notostylops* Beds, Patagonia.

DIAGNOSIS.—(All characters based on posterior thoracic vertebrae). Centrum triangular, relatively short, wide, and depressed. Glenoid fossa wider than zygosphene, transversely elongate, deep. Condyle moderately oblique, with short neck. Inferior surface of centrum flattened, haemal carina absent as such, a broad, low, rounded median convexity flanked posteriorly by shallow, indefinite depressions. Hypapophysis represented only by a very low, blunt swelling near the posterior border, double transversely on the most posterior thoracic vertebrae. Heavy, low, rounded ridge between condyle and each diapophysis. Zygapophyses with rounded borders and oblique, elongate, oval facets. Zygosphenes stout, deep, facets at small angle to the vertical, superolateral edges somewhat produced. Zygapophyses joined by short, very prominent ridge. Lateral emargination between them sharp but only moderately deep, strongly asymmetrical with deepest part distinctly posterior. Diapophyses directly below prezygapophyses, very prominent and heavy, with larger convex superior part and smaller inferior part concave vertically and convex horizontally, placed relatively very high on the centrum, the lower part projecting little or not at all below the level of the centrum itself, and the strongly protuberant upper part nearly as high as the zygapophysis, from which it is separated by a narrow notch. Neural arch broad, heavy, depressed, with distinct superomedian and inferolateral concavities. No aliform processes. Neural canal nearly as wide as zygosphene, with vague trefoil-like outline but without sharp internal carinae.

¹Some excellent new ophidian material, some of it probably boïd, has been found recently at Barnes locality, Middle Eocene of the Geiseltal near Halle, but it has not yet been described. See Weigelt, 1932.

²*Mad*, valley, *tsoi*, cow, Tehuelche Indian. Freely compounded after the locality name Cañadón Vaca.

Believing that scientific nomenclature will not suffer by deviation from the constant repetition and variation of common Greek and Latin roots, I propose to employ local native roots for some new Patagonian fossil animals. The use of barbarous names is valid (International Rules of Nomenclature, Art. 8, Recommendation j, and recommendation to Art. 14). The Indian languages of aboriginal Patagonia were dialects of Tehuelche and Araucanian. Tehuelche roots will be derived from Father Schmid, or in some cases Musters, and Araucanian chiefly from Augusta.

In addition to the two specimens described below, both from the same locality and almost the same level, in the true *Notostylops* Beds, we found another specimen, Amer. Mus. No. 3156, in the older sandstones. The formation has been called "Pehuenche," Upper Cretaceous, chiefly on lithologic grounds, but the horizon of this specimen is clearly early Tertiary although apparently older than the typical *Notostylops* Beds. This specimen consists of the triangular centrum only, with all the processes broken off. It clearly belongs to this genus, but is smaller than either of the two individuals of *Madtsoia bai* and differs in some

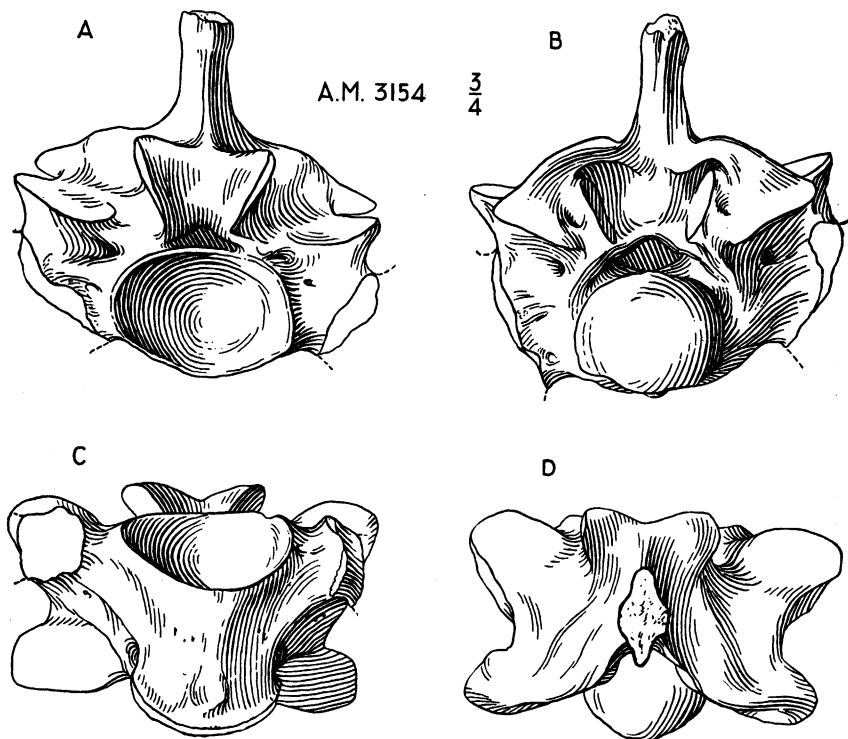


Fig. 1.—*Madtsoia bai*, new genus and species. Type, Amer. Mus. 3154. Vertebrae of the more anterior, shorter series of five articulated vertebrae (see Fig. 6). A, Anterior view of the second of these vertebrae. B, Posterior view of the last. C, Ventral view of the second. D, Dorsal view of the second. Three-fourths natural size.

In Figs. 1-4 the vertebrae are drawn essentially as they are, without correction of crushing or distortion and without any hypothetical restoration, but in some cases details have been completed by comparison with the other side of the same vertebra or with parts preserved on an immediately adjacent vertebra.

minor morphological details. It may merely be a younger individual of that species, but is probably a distinct, somewhat older form. I prefer not to name or describe this single imperfect specimen. We also have a centrum of a snake vertebra of a different genus found in wash at Cabeza Blanca and either from the *Notostylops* or, more probably, from the *Pyrotherium* Beds, but its imperfect preservation and dubious horizon deprive it of interest beyond the bare mention that at least one more genus of fossil ophidians does occur in the Lower Tertiary of Patagonia.

***Madtsoia bai*,¹ new species**

TYPE.—Amer. Mus. No. 3154, forty-five posterior thoracic vertebrae, forty in one series and five in another, with most of the corresponding ribs, all of one individual. Found by G. G. Simpson.

REFERRED SPECIMEN.—Amer. Mus. No. 3155, two nearly complete vertebrae and fragments of a third, in articulation. Found by C. S. Williams.

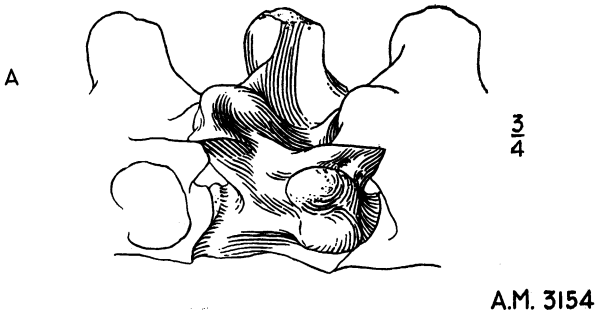
HORIZON AND LOCALITY.—*Notostylops* Beds, Cañadón Vaca, Chubut, Argentina.

DIAGNOSIS.—Sole known species of the genus as defined above.

The forty vertebrae in articulation have, as nearly as can be determined in their curved position and with some of them partly restored, a length of about 97 cm. The best four of the five others have a length together of 10.5 cm., measured not as maxima on the outstanding processes but between the lower edges of the articular faces of the first and last along the ventral surfaces of the centra in articulation. It is probable that there were at least 300 vertebrae in all, and possible that the number greatly exceeded that, so that those present are almost surely less than a sixth of the total, and possibly only about a tenth. The missing vertebrae probably averaged larger than those present, as the great majority of them were the powerful anterior and median dorsals. Both on this basis and on comparison with recent boïds, the total length of the snake was probably around ten meters. This is, of course, a rough guess, as the total number of vertebrae is not known and cannot be at all accurately estimated, and as the vertebrae differ in proportions from those of recent boïds. Yet it is clear that this individual is among the largest known snakes, recent or fossil. None of the fossil boïds yet discovered has surely and significantly exceeded the maximum authentic reported sizes of recent boïds, but both *Gigantophis garstini* and *Madtsoia bai* were of about that maximum size and far above the average for even the large species of recent boïds.

¹*Bai*, grandfather, Tehuelche.

As found, the series of forty vertebrae lay upright in a single plane, slightly tilted onto the left side, and all tightly locked together as in life. The first eight and the twelfth to twenty-second were nearly straight, but the others were curved, convex on the left side, most of them as strongly flexed as the articulations allow. The ribs of the left side were all present and in order, but bent so strongly backward that their heads no longer were in workable contact with the diapophyses. Their distal ends curved under the vertebrae and were crushed up against the ventral surfaces of the centra. The ribs of the right side, the concave side as preserved, were, on the contrary, spread out more irregularly away from the vertebral column and in the same plane with it. Some were nearly or quite articulated, but others were misplaced or missing. The shorter

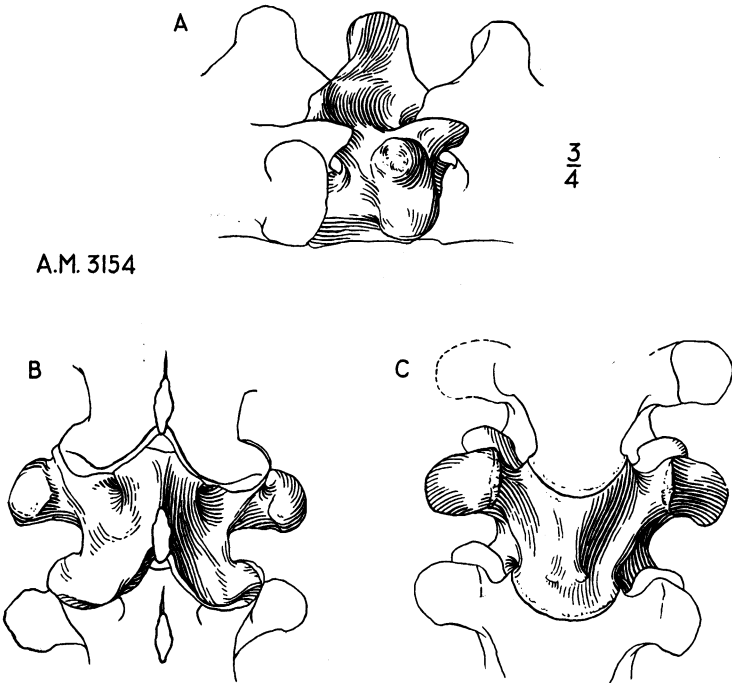


A.M. 3154



Fig. 2.—*Madtsoia bai*, new genus and species. Type, Amer. Mus. No. 3154. The sixth vertebra of the long series (see Fig. 6), as preserved in articulation with the fifth and seventh. A, Right lateral view. B, Dorsal view. C, Ventral view. Three-fourths natural size.

series of five vertebrae lay in the large open loop formed by the others, somewhat oblique to the latter, and pointing nearly in the opposite direction. These vertebrae were also strongly flexed, but in the opposite direction, concave on the left side. Their ribs had become disconnected. Several loose large ribs were found in the matrix, some below the other ribs and vertebrae.



A.M. 3154

Fig. 3.—*Madtsoia bai*, new genus and species. Type, Amer. Mus. No. 3154. The thirty-sixth vertebra of the longer series (see Fig. 6), as preserved in articulation with the thirty-fifth and thirty-seventh. A, Right lateral view. B, Dorsal view. C, Ventral view. Three-fourths natural size.

When found, the shorter series of vertebrae and the ends of the long series were exposed at the surface. Conditions were such as to promote the rapid removal and destruction of weathered fragments, and nothing of value was found in the wash below. As the vertebrae found were so well articulated, with the only free ends at the surface, it is probable that these two series were parts of the two sides of a long, nearly closed loop of a skeleton complete or nearly so, the other parts weathered out and destroyed.

The second specimen, two vertebrae and fragments of another, is not of the same individual. It was in the next *zanjón* (draw or coulee), and while not in place lay above the exact level of the better specimen and so can hardly have been buried at the same time.

In the series of forty vertebrae, the width across the prezygapophyses of the third (somewhat less than the width across the diapophyses, but more accurately determinable) is 51 mm. On the last, the same measurement is 36 mm. On the middle of the five other vertebrae it is 65 mm. It is thus certain that these largest vertebrae are more anterior than the long series and probable that at least thirty-five, and possibly many more, intervening vertebrae have been lost. This arrangement and relative size, together with the facts that all these vertebrae had normal ribs, that they are relatively depressed, and that the ventral surfaces are almost flat and have extremely small hypapophyses, show clearly that these are all posterior thoracic vertebrae. The long series belongs well back in the thoracic region, probably not very far from the anterior caudal or so-called sacral vertebrae, and the five larger vertebrae are probably from near the middle of the whole thoracic series.

As the general characters of ophidian, and especially boïd, vertebrae and the more diagnostic peculiarities of those of this genus have already been given, it will suffice to bring out some of the details of structure and the characters progressively modified in the series, without thorough description.

Although the most anterior vertebrae preserved are nearly twice the size of the most posterior, they do not differ much in proportions or gross structure. The most noteworthy change is that posteriorly the neural arch becomes more depressed and the neural spine relatively lower.

The character of the hypapophyses is very distinctive. On the largest vertebrae, the hypapophysis is a low, blunt swelling, projecting only to about the level of the rim of the articular surface. Anteriorly it passes into the convexity which in this genus replaces the haemal carina usual in large boïds. Posteriorly it has a more abrupt, somewhat denticulate, rounded rim. It is flattened and not keeled. In the longer, more posterior series, it undergoes a still more remarkable modification. On the more anterior of these, it is hardly present at all as such, but is represented by a slight swelling on the posterior half of the surface, tending to rise into two more definite, but still very low, points which are paired transversely and about 7-8 mm. apart. More posteriorly, these

become more definite and slightly more prominent and are about 5 mm. apart on the most posterior vertebra preserved.

The gentle convexity functionally replacing a haemal carina is narrower and more definite on the largest vertebrae, very broad and vague in the anterior part of the long series, and slightly more distinct on the most posterior of these vertebrae.

Instead of being divided sharply into a pair of distinct concave surfaces, the ventral face of the centrum in all these vertebrae is essentially an undivided relatively flattened surface, mostly convex but with shallow concavities at the anterolateral angles.

The remarkably large, stout, and high diapophyses were mentioned in the diagnosis. Both upper and lower ends are produced beyond the

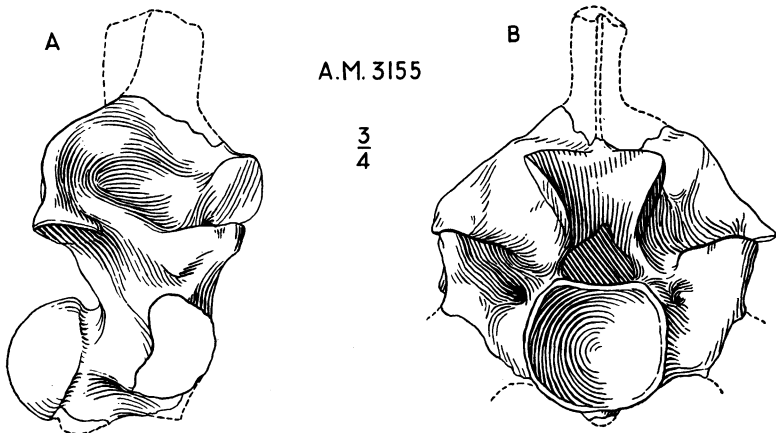


Fig. 4.—*Madtsoia bai*, new genus and species. Amer. Mus. No. 3155. Anterior thoracic vertebra. A, Right lateral view. B, Anterior view. Three-fourths natural size.

restricted pedicel that fixes the process to the centrum, leaving between each end and the adjacent part of the vertebra a well defined notch. In the upper notch, between the diapophysis and prezygapophysis, there is in most cases a pit for muscular origin.

The anterior rim of the diapophysis is also produced beyond the pedicel, but less so, and the posterior rim, at least in its median part, passes smoothly into the pedicel. The diapophyses are of very spongy bone, and the articulation has no smooth, hard surface, doubtless being covered with cartilage. These circumstances have militated against their preservation, but enough of them are complete to leave no doubt as to their characters.

The roughly rectangular lateral surface between the rounded ridge from the condyle to the lower end of the diapophysis and the sharper and much more prominent ridge between the zygapophyses is somewhat irregularly sculptured and has a vascular foramen below the middle of the last mentioned ridge. This foramen is much more distinct on the larger vertebrae, but seems always to be present. The pair of foramina on the ventral surface of the centrum are much smaller and less constant than is usual.

The non-articular anterior face of the zygosphenes is smooth and passes evenly into the roof of the neural canal, without the development of the usual lip and small median spine. The corresponding fundus of the zygantrum, while somewhat rough, is more flat, undivided, less strongly sculptured than is usually the case. Its vascular foramina are very conspicuous. In all cases there is a large prominent foramen near the median end of the triangular posterior surface between the zygantrum and postzygapophysis. This is seen in several of the fossil boïds (e.g., *Gigantophis*) but is absent in at least some recent boïds, where it may be represented by a sharp notch, absent in these fossils. As in most boïds, there is a deep, sharply defined, small circular pit on each side on the anterior face of the vertebrae, near the superolateral rim of the glenoid fossa.

The other vertebrae, Amer. Mus. No. 3155, appear to belong to an individual of the same species and about the same size but to belong farther forward in the column, as evidenced by the less depressed neural canal and centrum, higher neural arch, and more definite ventral longitudinal ridge, which does not, however, even here become a true carina. The hypapophyses are broken, but from their bases it is evident that they were somewhat larger and more definite than on the other vertebrae. These are all characters that would be expected in vertebrae of the anterior thoracic region of *Madtsoia bai*. Aside from the development of a tubercle, directed somewhat posteriorly, between the diapophysis and prezygapophysis, the vertebrae are otherwise closely similar to those already described.

The ribs are generally similar to those of modern boïds, but are very stout and differ in some other details consonant with the peculiar diapophyses and the general great size and strength of this species. The heads are nearly twice as wide dorsoventrally as anteroposteriorly and the posterior edge is produced into a thin sharp flange. At the dorsal side there is, as usual, a projecting process at the posterior corner, and there is also a larger but less projecting process at the anterior corner, the

two enclosing a groove between them. Just distal to the dorsoposterior process is a strong muscular pit, with a foramen in the bottom.

All essential characters not mentioned in diagnosis or description differ little or not at all from the conditions usual in boïds generally.

COMPARISON AND AFFINITIES

Comparison of *Madtsoia* with its compatriot *Dinilyisia* is an obvious first step, but the vertebrae of the latter are too poorly known for detailed collation. The facts that *Dinilyisia patagonica* is much smaller, that it is (with great probability) considerably older geologically, and that it seems to have had the neural spines less developed and the zygapophyses more extended laterally, more slender, and separated by a deeper emargination seem, however, to exclude the possibility that the genera are identical. To this may be added the indirect evidence that *Dinilyisia* is placed, on cranial characters, in the Ilysiidae and *Madtsoia*, on vertebral characters, in the Boidae.

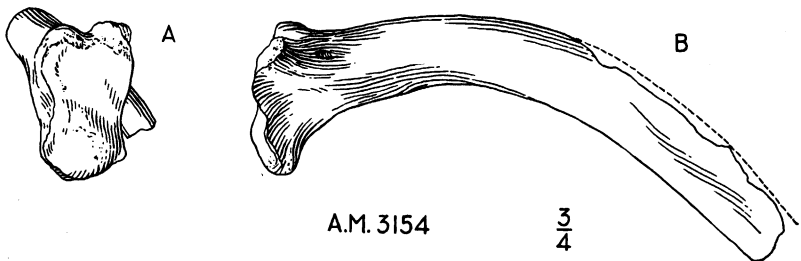


Fig. 5.—*Madtsoia bai*, new genus and species. Type, Amer. Mus. No. 3154. Rib. A, Proximal view. B, Posterior view. Three-fourths natural size.

It is at once obvious that *Madtsoia* does not belong to any of the three mutually related families Pachyophidae, Symoliophidae, and Palaeophidae which include late Cretaceous and early Eocene snakes, some of which were formerly confused with the Boidae. (On these groups see especially Andrews 1906; Cope 1869, 1882; Janensch 1906B; Leriche 1926; Lucas 1898; Marsh 1869; Nopcsa 1923, 1925; and Owen 1841, 1853). It has even less resemblance to the Archaeophidae (see Janensch 1906A). Close comparison can be only with the Boidae, *sensu lato*, and *Madtsoia* may be referred to that family as an isolated and very distinctive genus.

The supposed fossil boïds from the Eocene and Oligocene of North America are all very much smaller than *Madtsoia*, and all differ markedly from the latter in many ways. Thus in *Protagrass*, *Ogmophis*, *Calamagras*,

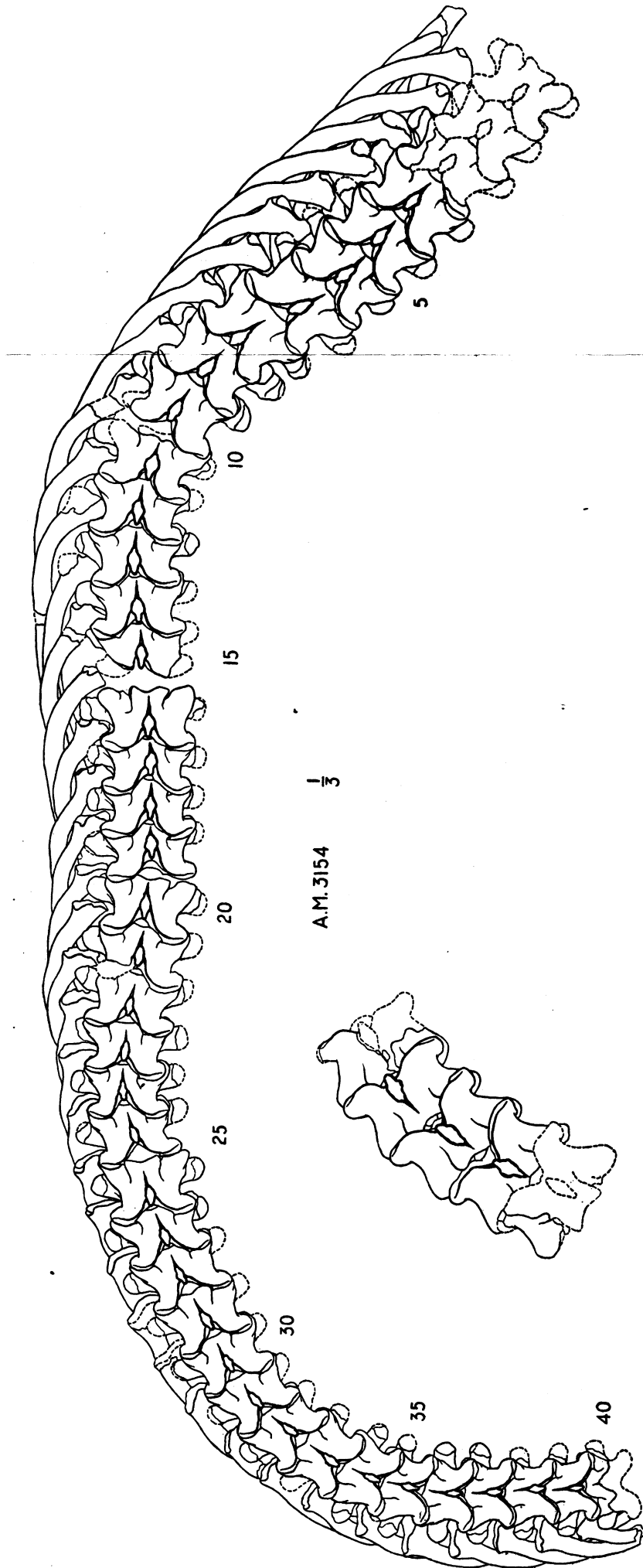


Fig. 6.—*Madisoia bai*, new genus and species. Type, Amer. Mus. No. 3154. The entire series of vertebrae, seen from above, as they were preserved in the matrix. The ribs of the left side of the long series have been drawn as they are preserved, but for clearness those of the other side have been omitted, as well as the ribs of the shorter series and those found disarticulated and scattered in the matrix. In each series the terminal vertebrae lay at the surface and so were damaged by weathering, as shown by the discontinuous restored outlines. The vertebrae at the anterior end of the long series, shown here as wholly restored, preserve part or all of the centrum, not visible in this aspect. One-third natural size.

Boavus, and *Lithophis*, a haemal carina is present. In at least *Ogmophis*, *Calamagras*, and *Lithophis* the centrum is deeper relative to its width. The condylar articulation is said to be nearly vertical in *Boavus*, *Lithophis*, and *Lestophis*. The diapophysis is simple and convex throughout in *Boavus* and *Lestophis*, while in *Protagras* it has a marked median constriction, and in at least *Aphelophis*, *Ogmophis*, and *Calamagras*, and probably in most or all of the others, the diapophysis is relatively smaller and more ventral than in *Madtsoia*. The anterior and posterior articular surfaces were narrower relative to the zygosphenes in *Protagras*, *Aphelophis*, *Boavus*, and possibly some others. The ridges which run posteriorly on each side from the lower end of the diapophysis are lacking in *Lithophis*, *Lestophis*, and *Calamagras*. The neural spine was apparently less developed in *Aphelophis*, *Ogmophis*, *Calamagras*, and *Boavus*. In short, from these and other distinctions it is clear that *Madtsoia* is unlike any known North American genus, and there is no evidence of special affinity between the known Eocene boids of the two continents.

In the width of the glenoid cavity relative to the zygosphenes, the development of the lateral emarginations, the general proportions of neural arch and spine, and some other features, *Paleryx* makes an approach to *Madtsoia*, but even *Paleryx* is quite distinct, as shown, among numerous other details, by its deeper centrum, well developed haemal carina, and shorter, more ventral diapophyses.

Palaeopython has a strong haemal carina, more elevated neural arch, more slender spine, more symmetrical and subquadrate lateral emarginations, and many other characters that exclude close relationship to *Madtsoia*. The same may be said of *Scytalophis*, with its squared postzygapophyses with denticulate edges, its broader posterior emargination of the neural arch, and its less prominent and somewhat different muscular sculpturing.

With *Gigantophis*, discussed below, the genera already contrasted with *Madtsoia* are the only ones of at all comparable antiquity. Among the later forms, *Scaptophis* and *Botrophis*, from the French Miocene, are both very different, the former especially in its very shallow zygosphenes and low, hook-like neural spine, and the latter most strikingly in its wide, thick zygosphenes and heavy neural arch with spine developed only as a low blunt ridge. *Heteropython* also differs markedly, for instance in its more circular glenoid cavity, haemal carina, and more ventral and smaller diapophyses.

Dawnophis langi, in spite of the enticing completeness of its type specimen, is so poorly preserved that there is hardly any basis for com-

parison, but its comparatively minute size and very different provenience, Pliocene of Burma, make identity with or even close relationship to *Madtsoia* almost impossible.

So far as known, all the above genera include only relatively small species, the largest less than half the size of *Madtsoia bai* and most of them much smaller than this. Even allowing for the variation in size of vertebrae in one individual and their growth with age, it is improbable that any of them approached the size of our Patagonian species. *Gigantophis garstini* Andrews, from the Egyptian Fayûm, on the other hand, is of about the same size as *Madtsoia bai* and the two are similar in several features. It is probable, however, that these are mostly adaptive, as they are offset by important differences, such as the presence in *Gigantophis* of less developed and more posterior neural spines, less prominent diapophyses farther removed from the prezygapophyses, zygosphenes more evenly truncate above, or proportionately much smaller neural canal. Although the similarity in size, general aspect, and a few more detailed features make resemblance of *Madtsoia* to *Gigantophis* somewhat closer than to other known genera, it is impossible without further evidence to conclude that these two are definitely more closely related to each other than to other fossil boids.

Madtsoia is likewise quite distinct from any recent boid. Its resemblance is rather with the largest forms, chiefly species of *Python*, *Boa*, and *Eunectes*, than with the more numerous smaller species. But accompanied as it is by very marked differences apparently not dependent on size, I take this resemblance to be rather mechanical or adaptive than indicative of special affinity. Nor is any evidence detected that would tend to relate *Madtsoia* to the ancestry of any one group of recent boids. It differs more from both *Python* and *Boa*, for instance, than they do from each other and seems to be without any definite characters present in one and not in the other. If it is ancestral to any particular modern form, this must be through a long series of unknown annectant forms and cannot even be guessed at present. Its striking divergence in some characters, such as those of the ventral surface of the centrum and of the diapophyses, makes direct ancestry seem improbable.

CONCLUSIONS

1. *Madtsoia bai* from the *Notostylops* Beds of Patagonia is named and described on the basis of a specimen which is, on the whole, more satisfactory than any other known fossil boïd.

2. It must be referred to the Boidae on present evidence, and in this family it forms a distinctive, well characterized genus.

3. No definite palaeogeographic conclusion should be drawn from the present evidence, beyond the fact, already probable on other grounds, that South America was not an isolated continent when the early (Upper Cretaceous or Paleocene) radiation of the Boidae occurred. *Madtsoia* is not especially related to any known North American snakes, although knowledge of the latter is lacking in the Paleocene and very poor in the Eocene so that this negative conclusion has no positive force. It is somewhat more like some Eocene European snakes, e.g., *Paleryx*, than like later forms, a condition to be expected in following the divergent lines of a group back toward their point of common origin.

4. It is on the whole more like *Gigantophis* of the Egyptian Eocene than any other known genus, but even here there are significant differences, and present data do not permit proper evaluation of convergence and habitus as against true affinity, especially as *Gigantophis garstini* is the only known fossil boïd as large as *Madtsoia bai* and hence particularly likely to show convergence toward it.

5. On the same basis, *Madtsoia* does not at present assist in determining the phylogeny of the boïds. It is not clearly closer to any particular modern form or group, and is probably aberrant. Other equally good or better records are lacking and without them phylogenetic study is premature and doomed to failure.

6. As a carnivore capable of attacking almost any of the contemporaneous mammals, *Madtsoia bai* occupies an important ecological position in the *Notostylops* fauna. This is especially true as the mammalian carnivores of that period all belonged to one archaic family, distinctly limited in scope and perhaps not very abundant in numbers. The presence of a large boïd so far outside the present range of the Boidae agrees with other evidence that the Eocene climate of central Patagonia was subtropical.¹

¹It is interesting that this region seems to be very unfavorable to snakes now. In the region where *Madtsoia* was found, the natives are acquainted with only one species of snake, and even this is extremely rare—in seven months we saw only a single individual, and it was dead. Lizards, on the other hand, are abundant.

REFERENCES

- AMEGHINO, F. 1906. 'Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie.' An. Mus. Nac. Buenos Aires, XV [(3) VIII], pp. 1-568.
- ANDREWS, C. W. 1906. 'A descriptive catalogue of the Tertiary Vertebrata of the Fayûm, Egypt.' British Museum, London. [Ophidia, pp. 306-312. References and résumé of preliminary publications, not here cited separately.]
- BARNES, B. 1927. 'Eine ezoäne Wirbeltier-Fauna aus der Braunkohle des Geiseltals.' Jahrb. Halleschen Verb. Erforsch. Mitteldeutschen Bodensch., N. F. VI, pp. 5-24. [*Paleryx*, *Palaeopython*.]
- COPE, E. D. 1869. 'Synopsis of the extinct Batrachia, Reptilia, and Aves of North America.' Trans. Amer. Phil. Soc., XIV, pp. i-viii, 1-252. [*Palaeophis*.]
1872. 'Third account of new Vertebrata from the Bridger Eocene of Wyoming Territory.' Amer. Phil. Soc., XII, pp. 469-472. [*Protogras*.]
1873. 'Synopsis of new Vertebrata from the Tertiary of Colorado, obtained during the summer of 1873. Washington, 1873. (Issued as from 7th Ann. Rept. U. S. Geol. Surv. Terr., Hayden, but not in that volume.) [*Calamagras*, *Aphelophis*, *Ogmophis*, pp. 15-16.]
1874. 'Report on the vertebrate palaeontology of Colorado.' Ann. Rept. Geol. Geog. Surv. Terr. (Hayden) for 1873, pp. 427-533. [*Calamagras*, *Aphelophis*, pp. 517-518.]
1882. 'The reptiles of the American Eocene.' Amer. Nat., XVI, pp. 979-993. [*Palaeophis*.]
1884. 'The Vertebrata of the Tertiary Formations of the West.' Rept. U. S. Geol. Surv. Terr. (Hayden) for 1884, III, pp. i-xxxv, 1-1009. [Boïds, pp. 102-103, 781-785.]
- DOUGLASS, E. 1903. 'New vertebrates from the Montana Tertiary.' Ann. Carnegie Mus., II, pp. 145-199. [*Ogmophis*, p. 171.]
- FILHOL, M. H. 1877. 'Recherches sur les phosphorites du Quercy.' Ann. Sci. Géol., VIII, pp. 1-340. [Ophidia, pp. 270-273.]
- JANENSCH, W. 1906A. 'Über *Archaeophis proavus* Mass., eine Schlange aus dem Eocän des Monte Bolca.' Beitr. Pal. Geol. Österr.-Ung. und des Orients, XIX, pp. 1-33.
- 1906B. '*Pterosphenus schweinfurthi* Andrews und die Entwicklung der Palaeophiden.' Arch. f. Biontol., I, pp. 311-350.
- LAMBE, L. M. 1908. 'The Vertebrata of the Oligocene of the Cypress Hills, Saskatchewan.' Cont. Canad. Pal., III, Pt. iv, pp. 1-65. [*Ogmophis*, pp. 20-21.]
- LERICHE, M. 1926. 'Sur les vertébrés de l'Argile d'Ypres (Yprésien) et sur les "*Palaeophis*" de l'Éocène de la Belgique.' Bull. Soc. Belge Géol. Pal. Hydr., XXVI, pp. 13-24.
- LONGMAN, H. A. 1925. 'Ophidian vertebrae from cave deposits at Marmor Quarry.' Mem. Queensland Mus., VIII, Pt. II, pp. 111-112. (*Python*.)
- LUCAS, F. A. 1898. 'A new snake from the Eocene of Alabama.' Proc. U. S. Nat. Mus., XXI, pp. 637-638. [*Pterosphenus*.]

- LYDEKKER, R. 1886. 'Siwalik Crocodilia, Lacertilia, and Ophidia.' Paleont. India, Ser. X, III, Pt. 7. [*Python*.]
- 1888A. 'Note on Tertiary Lacertilia and Ophidia.' Geol. Mag., (3) V, pp. 110-113.
- 1888B. 'Catalogue of fossil Reptilia and Amphibia in the British Museum.' Part I.
- MARSH, O. C. 1869. 'Description of a new and gigantic fossil serpent (*Dinophis grandis*) from the Tertiary of New Jersey.' Amer. Journ. Sci., XLVIII, pp. 397-400. [= *Palaeophis*.]
1871. 'Description of some new fossil serpents, from the Tertiary deposits of Wyoming.' Amer. Journ. Sci., (3) I, pp. 322-329. [*Boavus*, *Lithophis*, *Limnophis* (= *Lestophis*).]
1885. 'Names of extinct reptiles.' Amer. Journ. Sci., (3) XXIX, p. 169. [*Lestophis* for *Limnophis* preoc.]
- MERRIAM, J. C., AND W. J. SINCLAIR. 1907. 'Tertiary faunas of the John Day region.' Bull. Dept. Geol. Univ. Calif., V, pp. 171-205. [*Ogmophis*, p. 187.]
- NOPCSA, F. 1923. '*Eidolosaurus* und *Pachyophis*, zwei neue Neocom-Reptilien.' Palaeontographica, LXV, pp. 97-154.
1925. 'Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens.' II. Wirbeltier-Reste der Baharija-Stufe (unterstes Cenoman). 5—Die *Symoliophis*-Reste. Abhandl. Bayer. Akad. Wissen., XXX, Abh. 4.
- OWEN, R. 1841. 'Description of some Ophidiolites (*Palaeophis toliapicus*) from the London Clay at Sheppey, indicative of an extinct species of serpent.' Trans. Geol. Soc., (2) VI, p. 209.
1853. 'A history of British fossil reptiles.' London, Cassell and Co., 1849-84. [Ophidia, pp. 134-154. Supplements and reprints various preliminary papers and other editions, not separately cited.]
- PORTIS, A. 1901. 'Il *Palaeopython sardus* Port., nuovo pitonide del Miocene medio della Sardegna.' Boll. Soc. Geol. Ital., XX, pp. 247-253.
- ROEMER, F. 1870. 'Über *Python euboicus*.' Zeits. deutsch. geol. Ges., XXII, pp. 582-590. [= *Heteropython*.]
- DE ROCHEBRUNE, A. T. 1880. 'Révision des ophidiens fossiles du Muséum d'Histoire Naturelle.' Nouv. Arch. Mus. d'Hist. Nat., (2) III, pp. 271-296. [With résumé and references of all previous work.]
1881. 'Mémoire sur les vertèbres des ophidiens.' Journ. Anat. Physiol., XVII, pp. 185-229.
- SCHMIDT, K. P. 1927. 'New reptilian generic names.' Copeia, 1927, issue 163, pp. 58-59. [*Palaeoboa* for *Limnophis* Marsh, preoc., but *Palaeoboa* is antedated by *Lestophis* Marsh.]
- STEFANO, G. 1905. 'Appunti sui batraci e sui rettili del Quercy appartenenti alla Collezione Rossignol.' Boll. Soc. Geol. Ital., XXIV, pp. 17-67.
- SWINTON, W. E. 1926. '*Daunophis langi*, gen. et sp. n. (Pliocene, Burma.)' Ann. Mag. Nat. Hist., (9) XVII, pp. 342-348.

- WEIGELT, J. 1932. 'Das Lebensbild zur Bildungszeit der mitteleozänen Braunkohlen des Geiseltals.' *Pal. Zeitschr.*, XIV, pp. 4-24. [New snake material mentioned but not described, p. 13.]
- WERNER, F. 1921. 'Synopsis der Schlangenfamilie der Boiden auf Grundlage des Boulenger'schen Schlangenkatalogs (1893-96).' *Archiv. Naturg.*, LXXXVII, Abt. A, Heft 7, pp. 230-265.
- WOODWARD, A. SMITH. 1901. 'On some extinct reptiles from Patagonia, of the genera *Miolania*, *Dinilysia*, and *Genyodectes*.' *Proc. Zool. Soc. London*, Mar. 5, 1901, pp. 169-184.

