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The Systematic Position of *Loxocemus* *bicolor* Cope (Ophidia)

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INTRODUCTION

The genus *Loxocemus*, probably represented by a single species, *L. bicolor* Cope, has been included by Boulenger (1893, p. 74) in the subfamily Pythoninae of the Boidae. This is a most remarkable allocation, because, if correct, it would establish a strange dispersal pattern for the Pythoninae, a group mainly concentrated in tropical Asia, Australia, and Africa; *Loxocemus* would be the only tropical American representative of the subfamily, occurring in Mexico and Guatemala. As members of the second subfamily, the Boinae, of the Boidae are widely scattered over the Old and New World, this strange isolation of a single pythonine genus in America did not attract special interest.

During the author's stay at the Department of Amphibians and Reptiles of the American Museum of Natural History, he had the opportunity to discuss this remarkable distribution with Mr. C. M. Bogert and Mr. S. B. McDowell, and to learn of their doubts concerning the systematic position of *Loxocemus*, based on many deviations from the other Boidae in the pholidosis and details of the skull. The author proposed an investigation of the jaw muscles of *Loxocemus*, as this might be expected to give important clues to the real relationships of this form. Mr. Bogert kindly agreed and presented a specimen of this rather rare snake to the author. The present paper deals with the results of this investigation, made possible by Mr. Bogert's most generous gift.

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THE VALUE OF THE JAW MUSCLES IN THE TAXONOMY OF SNAKES

In a series of previous papers, the author has demonstrated that the trigeminally innervated muscles of snakes give useful clues for the solution of phylogenetic questions and problems of taxonomic relationship among the different groups of Ophidia. A rather striking result of these investigations is the demonstration that colubrid snakes can be split into two groups which differ in the arrangement of the adductor mandibulae superficialis of Lakjer (1926).

For a long time it has been known that the adductor externus of snakes shows a clear-cut division into three parts: (1) a superficialis, protracting the lower jaw; (2) a medialis, pulling more or less vertically upon the lower jaw; and (3) a profundus, placed postero-laterally and retracting the lower jaw. This pattern was long believed to be the only one in either the colubrids or the boids.

Only the Hydrophinae and Elapinae, both formerly united as "Proteroglypha," were known to deviate in a remarkable way from this pattern. In these forms the superficialis envelops the poison gland in a complicated fashion, thus differing markedly from the situation found in the Solenoglypha. It is noteworthy that in the artificial assembly of forms designated as "Opisthoglypha," the poison gland, although sometimes very bulky, produces no deviations from the normal muscular arrangement, and there is no special muscle for the gland.

The author discovered that while the vast majority of aglyphous colubrids have the normal pattern of an adductor externus with three portions, some genera have four externi, the externus superficialis being represented by two muscles instead of one. The posterior externus superficialis has the same inclined position and the same areas of origin and insertion as the single superficialis of the great majority of snakes. The additional, more anterior, externus superficialis encircles the angle of the mouth more or less completely. This arrangement of the muscles is characteristic of such colubrid snakes as those of the genera *Sibynophis* (= *Polyodontophis*), *Dromicodryas*, *Atractus*, and *Calamaria*, and of the subfamily Dipsadinae.

In addition, many primitive groups, such as the Ilysiidae (= Aniliidae), Uropeltidae, and Xenopeltidae, and the very aberrant Leptotyphlopidae, show complicated patterns in the differentiation of the external adductor muscle, including a double adductor externus superficialis.

On the other hand, the Boidae show the same division of the adductor externus into three portions as is characteristic of the vast majority of colubrids, a fact which seems to contradict their primitiveness among the ophidians. Yet this primitiveness is deduced from a vast number of

external and internal morphological features. Perhaps the simplification of the jaw muscles seen in the Boidae is linked with the mechanical adaptation for the swallowing whole of relatively big prey. Nevertheless, the Solenoglypha are similarly adapted and yet show, in a somewhat modified way, the muscle pattern of the snakes with a double externus superficialis (Haas, 1952). Burrowing boids, such as the pythonine *Calabaria* and the boine *Eryx*, do not deviate from the regular pattern of the Boidae; this would seem to indicate that the tripartite adductor externus constitutes a fixed morphological character of the Boidae, independent of the habits.

OBSERVATIONS ON *LOXOCEMUS*

The dissection of *Loxocemus* disclosed not only a peculiar pattern of the skin muscles intruding into the head region, quite unlike conditions in the Boidae, but also a double adductor externus superficialis. Both these features exclude *Loxocemus* from the Boidae. In the following section a description of the muscular topography of the head of *Loxocemus* is given, in so far as it is relevant to the discussion of the systematic position of this genus.

GLANDS

As in other burrowing snakes, the glands of the head are well developed. The rather expanded external nasal, supralabial, and infralabial glands exhibit an identical surface, with a rather coarse pattern of irregular polygons. Both labial glands are remarkably deep in the vertical direction. The roundish, smooth Harderian gland surpasses the orbit by about one and a half times the orbital diameter; the gland remains exposed ventrally. More than the upper half of this postorbital portion of the gland is covered by both external adductores superficiales (by 1a medially and by 1b laterally).

DERMAL MUSCLES

The ligamentum quadrato-maxillare links the lower joint of the quadrate with the postero-external angle of the anterior expansion of the ectopterygoid; the anterior expansion of the ectopterygoid is linked with the maxilla under the orbit. Two flattened fans of a skin muscle converge cranially, each forming a terminal tendon, linked with the skin of the rictal region in the case of the more cranial fan, and linked with the lower lip in the case of the more caudal fan. Both fans overlap the post-rictal flanks of the head, sloping downward from the dorsal median part of the neck.

ADDUCTOR EXTERNUS SUPERFICIALIS: At first glance this muscle appears to correspond to the normal simple superficial adductor of the

Boidae. A slanting muscle begins partly at the posterior face of the post-orbital process of the skull and partly at the most anterior area of the temporal crest of the parietal. Dissection reveals, however, that this muscle is in fact the posterior of two externi superficiales (1b), completely covering the deeper postorbital origin of an anterior superficialis. This latter muscle bends sharply around the rictus oris and follows the infralabial border medial to the infralabial gland (fig. 2), forming a long, flattened insertional tendon that ends at the middle infralabials. The most anterior fibers of this muscle end at the rictal plate. (Such rictal fibers are found in the homologous portion of the adductor in *Xenopeltis*, but they are situated at the posterior end of the muscle.) This portion tapers strongly in its diameter from the origin towards the angle of the mouth, but very inconsiderably from that portion onward to the terminal tendon. The Harderian gland expands at the median surface of this muscle, where the muscle is broadest, and bulges beyond its ventral border (fig. 1). The sloping posterior portion of the adductor externus superficialis (1b) exhibits a sudden constriction somewhat under its origin, expanding slightly again anteroposteriorly (fig. 1) in front of a drastic final constriction at the level of the ligamentum quadrato-maxillare. From this point downward the muscle is continued as a diaphanous aponeurosis that expands on the surface of the adductor externus profundus.

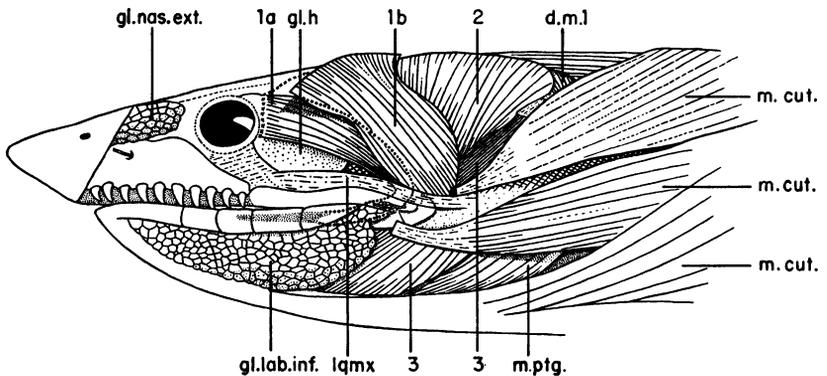


FIG. 1. *Loxocemus bicolor*. The skin and the supralabial gland have been removed, and the posterolateral adductor externus superficialis (1b) has been severed from its origo and slightly bent dorsally (the origo is indicated by a line of small x's) in order to show the origo of the adductor externus superficialis 1a, situated medially of the first. *Abbreviations*: 2, adductor externus medialis; 3, adductus externus profundus; d.m.1, occipital belly of depressor mandibulae; gl.h., Harderian gland; gl.nas.ext., external nasal gland; gl.lab.inf., inferior labial gland; lqmx, ligamentum quadrato-maxillare; m.cut., musculus cutaneus; m.ptg., musculus pterygoideus.

An identical form of dorsal overlap of the portion 1a by portion 1b occurs among some dipsadine snakes such as *Tropidodipsas sartori* and *Petalognathus nebulatus* and in the aglyphous colubrid *Atractus elaps*. A distinct separation of both portions is found more frequently, with the origin of 1a immediately anterior to the origin of 1b. In still other cases the origin of 1a shifts from the postorbital more or less completely onto the maxilla, reaching a suborbital or even a preorbital position (*Amblycephalus carinatus*, *Xenopeltis unicolor*).

ADDUCTOR EXTERNUS MEDIALIS: This muscle (2 in the figures) rises mostly from the temporal crests of the sides of the parietal, but caudally from the supraoccipital and the shield-shaped supratemporal (the tabular of Camp and of Williston) anterior to the articulation of the latter bone with the quadrate. This adductor is posterolaterally overlapped widely by the sloping adductor externus profundus (3 in the figures). The medialis inserts mostly in the dorsal excavation of the posterior half of the mandible from the coronoid to the mandibular joint.

ADDUCTOR EXTERNUS PROFUNDUS: This muscle (3 in the figures) inserts on an extensive area of the lateral surface of the mandible, extending partially to the ventral margin of the mandible. Both this muscle and the adductor externus medialis have a bipinnate arrangement of the externally visible fibers.

Many primitive snakes exhibit an approximation to this bipinnate arrangement of the two muscles; examples are *Xenopeltis*, *Calamaria*,

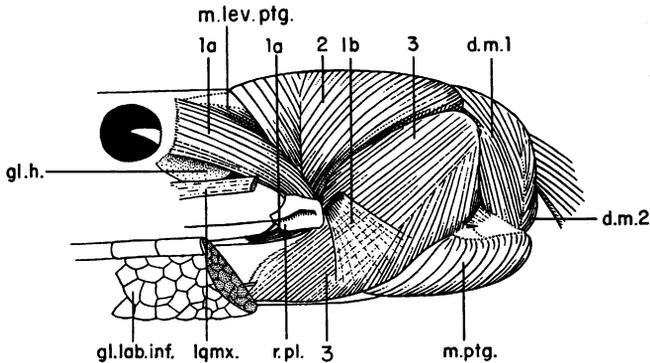


FIG. 2. *Loxocemus bicolor*. A part of the inferior labial gland, the cutaneous muscles, and the dorsal part of the posterolateral adductor externus superficialis (1b) have been removed. *Abbreviations:* d.m.2, deep belly of depressor mandibulae; m.lev.ptg., musculus levator pterygoidei; r.pl., rectal plates. (For other abbreviations, see fig. 1.)

Atractus, the Ilysiidae, and the Uropeltidae. In the Ilysiidae, and to a slighter degree in the Uropeltidae, extensive aponeuroses subdivide these muscles. Probably a bipinnate arrangement of the fibers is a last vestige of such internal aponeuroses, which are frequent in the Sauria and other reptiles. In "higher" snakes, more or less parallel long fibers build up both muscles.

DEPRESSOR MANDIBULAE: Another remarkable feature of *Loxocemus* is the development of two portions of this muscle. In addition to the normal deeper belly arising along the posterior surface of the quadrate, there is a long-fiber occipital belly descending from the sagittal crest of the supraoccipital. This latter portion is confluent with shorter cranial fibers descending from a tendon originating from the dorsal articulation of the quadrate.

Such a double depressor mandibulae has been found in both *Ilysia* and *Cylindrophis*, in *Xenopeltis*, in *Calamaria*, and in the boid *Eryx*.

The deeper head muscles, being rather stereotyped among snakes, may be ignored in a taxonomic discussion.

DISCUSSION AND CONCLUSIONS

Three points in the muscular anatomy of *Loxocemus* separate it from the Boidae: (1) the presence of two distinct parts of the adductor externus superficialis; (2) the bipinnate arrangement of the fibers of the adductor externus medialis and of the adductor externus profundus; and (3) the presence of an occipital belly of the depressor mandibulae.

Xenopeltis has many resemblances to *Loxocemus*. If the similarity in habitus, especially of the head, is disregarded, both forms have a double adductor externus superficialis, although portion 1a is more specialized in *Xenopeltis*. (In *Loxocemus*, as described above, portion 1a is not subdivided and encompasses the rictus oris, reaching by means of a long tendon the middle part of the lower labial series; few cranial fibers stop at the inside of the inner rictal plate. In *Xenopeltis* fibers arise post-orbitally that end mostly in the rictal area and form the caudal part of a complex muscle; more cranial fibers of a second suborbitally and pre-orbitally located head arise from the external surface of the maxilla; these fibers insert on the pointed, freely movable posterior end of the dentary.) Not much phylogenetic importance is to be given to this difference between *Loxocemus* and *Xenopeltis* in the origin of portion 1a, for among the dipsadine snakes this same muscle shows various intermediate stages between a purely postorbital origin and a preorbital origin from the maxilla. The special differentiation of muscle 1a in *Xenopeltis* is unique, as is the high motility of the dentary, and probably these two features are correlated.

In both *Loxocemus* and *Xenopeltis* the Harderian gland penetrates deeply into the temporal region and is covered in identical manner by both externi superficiales. It may be mentioned in this connection that this gland often deeply penetrates the temporal area in snakes, but with different relations to the various adductors. For instance, in *Dasypeltis scaber* and *Oligodon subgriseus* the postorbital part of the gland protrudes laterally from the outermost adductor.

The differentiation of both the adductor externus medialis and the adductor externus profundus does not lend itself easily to useful comparison, because in *Xenopeltis* both muscles are completely fused into a compound temporal muscle (unique in snakes), in which the anterior fibers maintain the normal course of the medialis, gradually merging posteriorly into a group of fibers with the typical position of a profundus. However, in *Loxocemus* the normal sharp division into a medialis and a profundus is found, and each of the muscles exhibits the pinnate arrangement of fibers denoting an archaic muscular pattern (see above).

Some importance must be given to the presence of an occipital portion of the depressor mandibulae in both *Xenopeltis* and *Loxocemus*, in addition to the normal portion linking the quadrate with the retro-articular process of the mandible. This peculiarity is known in *Ilysia* and *Cylindrophis* (perhaps the most primitive snakes in existence), in one boid genus, *Eryx*, and in the colubrid genus *Calamaria*. Other groups of primitive snakes, such as the Uropeltidae, Typhlopidae, and Leptotyphlopidae, should be excluded from this discussion, as they show an aberrant position of the quadrate that precludes the development of an occipital belly of the muscle.

There is no doubt that a considerable similarity exists between *Loxocemus* and *Xenopeltis*, but the latter genus shows in several respects a higher degree of muscular and skeletal specialization, namely, in these respects:

1. Subocular origin of parts of muscle la.
2. Fusion of the adductor externus medialis and adductor externus profundus.
3. Reduction of the postorbital bar.
4. Great motility of the dentary.
5. Fusion of several mandibular dermal bones with the articular in a way foreshadowing the colubrid stage.

On the other hand, *Loxocemus* has many cranial features in common with the Boidae, and especially with the Pythoninae. Other characters, such as the muscle arrangements discussed here, point to a pre-boid ancestry. In spite of their primitiveness in other respects, the Boidae have so far proved disappointing in the differentiation of the head musculature and show a less primitive pattern than is seen in some mem-

bers of higher groups of snakes. We have in *Loxocemus* a real boid precursor, still exhibiting more archaic traits in the head muscles than are seen in the remainder of the Boidae.

A sharper systematic separation of *Loxocemus* from the Boidae seems advisable. This genus proves the existence of a pre-boaeform stock with a muscular arrangement still surviving, astonishingly, in several genera of aglyphous colubrids, dipsadines, *Xenopeltis*, and the Solenoglypha. In certain ways (for example, the compound bone in the mandible) *Xenopeltis* has surpassed the pre-boid stage in skeletal differentiation, but it has retained a certain primitiveness of head musculature. How the simplification of the mandibular adductors independently could follow the same pattern in both the modern boids and the more advanced colubrids remains a fascinating problem.

It is not easy to illustrate the complicated relationship of *Loxocemus* and *Xenopeltis* in a "tree" as given in the diagrams of snake phylogeny in Schmidt (1950) and in Bellairs and Underwood (1951). In the diagram given by Bellairs and Underwood, the present author would propose placing *Loxocemus* at the point where the Boidae and Xenopeltidae start to diverge. All the groups preserving a double adductor externus superficialis should be placed nearer to the Xenopeltidae than to those Colubridae with a simple superficial adductor. However, such an arrangement would split the vast array of the Aglypha into one relatively small group with relations to the dipsadines and Solenoglypha (see Haas, 1952) and another, very big group, comprising the rest of the Aglypha, the Opisthoglypha, and, somewhat more distantly, both proteroglyphous groups.

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