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THE STRUCTURE AND SYSTEMATIC RELATIONSHIPS OF THE GENUS *RHINOPHRYNUS*

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ALTHOUGH the genus *Rhinophrynus* has been generally recognized since its discovery nearly a century ago as one of the most specialized salientians of the Neotropical region, it has received relatively little anatomical study. The external features and certain details of the visceral anatomy were well described by Günther (1858), who attached great taxonomic importance to the peculiar structure of the tongue, and erected for the genus a monotypic family which was further distinguished from all other salientians as the sole representative of a division, the "Proteroglossa," in contrast with the Aglossa and Opisthoglossa. Cope (1865: 100) described a peculiar condition of the pectoral girdle of *Rhinophrynus,* which, in combination with the general body form, led him to believe that it was related to the African genus *Breviceps,* a view which he later (1889: 260) abandoned, referring the genus without comment to the family Bufonidae, as did Boulenger (1882). Dugés (1897) gave a brief and incomplete description of the skeleton. More recently Kellogg (1932: 24–25) has added somewhat to our knowledge of the skeletal anatomy and reinstated the family Rhinophrynidae. Noble (1922: 40) described the thigh musculature and later (1931: 500) placed

the genus in the Bufonidae (*sensu latu*), as the sole representative of the subfamily Rhinophryninae.

In preparing a skeleton of a specimen of *Rhinophrynus* in the Museum of Zoology, University of Michigan, collection, I became aware that some details of structure did not agree with any of the published accounts, the discrepancies involving structures of fundamental taxonomic importance. Accordingly, further study was made of the osteology and at the same time certain features of the musculature were examined. Of the latter, the hyolaryngeal muscles have not been previously described. The results of the study tend to confirm the view of Günther and Kellogg that *Rhinophrynus* occupies an isolated position among existing salientians, although this conclusion is based on very different evidence than has been presented before.

Material

Two male skeletons from Petén, Guatemala (Stuart, 1933: 35), have been prepared (U.M.M.Z. Nos. 75290, 75294). Five skeletons, sex unknown, also from Guatemala, in the collection of the United States National Museum (Nos. 71431–35), were kindly loaned by Dr. Leonhard Stejneger and Dr. Doris Cochran. All of the following notes on musculature are based on the examination of a single individual, U.M.M.Z. No. 75290.

Osteology

The vertebrae of *Rhinophrynus* are hour-glass shaped, with a median constriction and expanded ends. Due to the breadth of the centra it is necessary to disarticulate the column in order to determine the relation of the centra to the intervertebral bodies. In a freshly dissected specimen the vertebrae prove to be opisthocoelous, and the intervertebral bodies, which are cartilaginous and strongly notochordal, are consistently attached to the anterior ends of the centra. In dried material, however, the cartilaginous intervertebral body shrinks considerably, and often tends to pull away from the surrounding ring formed by the centrum. The anterior face then may

present a flat or slightly concave surface. The true relation of centrum and intervertebral body is still quite evident when the anterior and posterior ends of a vertebra are compared; the later are deeply concave and contain at most only a trace of cartilage.

The exact extent to which fusion occurs between intervertebral body and centrum cannot be determined from a gross examination. The attachment seems to be firm, and it was not found possible to rotate the intervertebral body in alcoholic specimens. In one dried specimen an intervertebral body was forcibly dislodged from its centrum in a single piece. The inner surface of the centrum thus exposed was rough, indicating that fusion does occur to some degree.

The sacral vertebra has moderately expanded diapophyses and two well formed condyles with which the coccyx articulates (Fig. 1). Normally the coccyx lacks transverse processes,

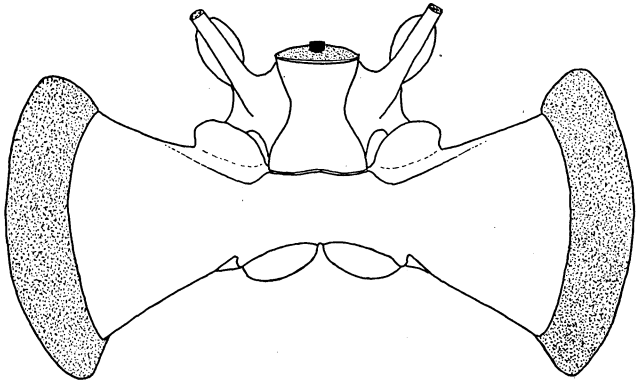

FIG. 1. Sacrum and presacral vertebra, ventral view.

but rudimentary processes were present in one instance. There are eight presacral vertebrae, and none show any trace of ribs.

The pectoral girdle of *Rhinophrynus* has been briefly described by Cope (1865: 100), and by Kellogg (1932: 24). It is reported by these authors to be unique among salientians in that both clavicles and both coracoids attach to a single, curved epicoracoid cartilage. This character was considered

of family importance by Kellogg. None of the five specimens[1] whose girdles I have examined shows such a condition (Fig. 2). In these the girdle is fully arciferous, and notable chiefly for the absence of sternum and omosternum. The clavicles are strongly curved and extend laterally over the lower end of the scapula. The coracoids are short and stout. The epicoracoid cartilages are narrower than is usual among arciferous forms, but are entirely separate throughout their length. The scapula is moderately long, being only slightly shorter than the clavicle,

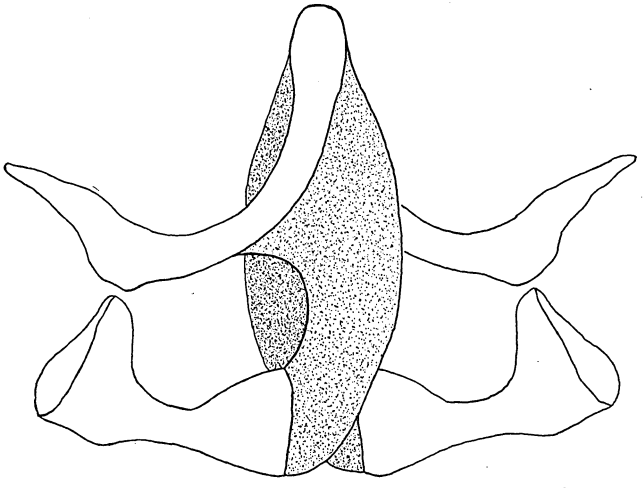

FIG. 2. Pectoral girdle of *Rhinophrynus*, ventral view.

and is deeply notched at its lower end. The suprascapula is strongly ossified, slender, somewhat constricted medially; its anterior and scapular margins are reflected dorsally.

The pelvic girdle is remarkable for the acute angle at which the ilia meet; the whole structure is *V*-shaped. The limb bones are short and stout but not otherwise peculiar. The loss of one phalanx from the first toe results in a phalangeal formula, $\frac{2\text{–}2\text{–}3\text{–}3}{1\text{–}2\text{–}3\text{–}4\text{–}3}$, which seems to be unique.

[1] In addition to the two skeletons listed above a pair of specimens from Petén, Guatemala, and a male from Tehuantepec were partially dissected in order to examine the pectoral girdle. The skeletons in the National Museum collection are at present disarticulated, most of the cartilage apparently having been destroyed in preparation.

The skull of *Rhinophrynus* is specialized and offers few characters of value in tracing relationships. Some of the outstanding peculiarities have been described previously by Kellogg (1932: 25). The ossification in the ethmoid region is notably extensive. The ethmoid is complete below, and dorsally is fused with the frontoparietals. Anteriorly the ethmoid ossification involves the medial part of the nasal capsules, forming a narrow bony tube which encloses the olfactory nerves. At the level of the anterior margin of the nares the ventral wall of this tube bends sharply upwards, fusing with the dorsal wall which extends forward as a narrow bony plate almost to the premaxillaries. The ethmoid is also produced laterally in the palatine region, nearly to the maxillaries. The exoccipital and prootic of each side are fused, and the exoccipitals are narrowly separated from one another in midline.

The exact outlines of the roofing bones of the skull are indeterminable due to the fusion of frontoparietals, nasals, and the anterior extension of the ethmoid. The frontoparietals are also fused with one another in midline throughout the greater part of their length, and are produced laterally in the direction of the squamosals, with which there is a membranous connection, above and anterior to the prootic. The squamosals are normal in relations, but are short and broad in outline, and have a poorly developed prootic process.

The premaxillaries and maxillaries are unusually thin, and entirely toothless. The ascending process of the premaxillary is located more posteriorly than usual, arising from the posterior end of the bone. Small but distinct quadratojugals are present. The pterygoids form thin, straight bars, extending from the maxillaries to the quadrate; connections with the prootic are entirely membranous. The prevomers, which form the anterior, medial, and posterior margins of the internal nares, are toothless. Anteriorly, they are well developed, reaching to the maxillaries, medially they fail to meet by an appreciable distance. Distinct palatines are lacking; these elements have been lost, or possibly incorporated by fusion in the postnarial portion of the prevomers. The parasphenoid shows no important peculiarity. Anteriorly it is slender and reaches

to the level of the nares. The basal portion is moderately developed and covers only a small portion of the exoccipitals.

The auditory apparatus is incomplete, as in a number of other fossorial and aquatic salientians. Plectrum, annulus tympani, and Eustachian tubes are absent.

The hyoid skeleton (Fig. 3) is notable for the presence of a

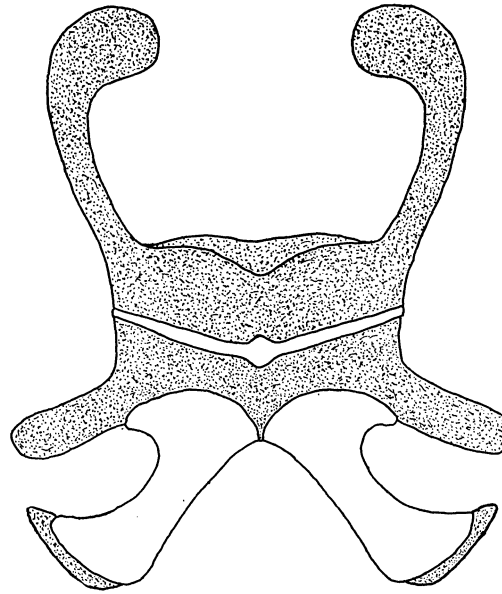

FIG. 3. Hyoid, ventral view.

distinct parahyoid ossification which extends across the body of the hyoid in the form of a narrow, slightly angulate bar, and also for the discontinuous character of the hyalia, which are interrupted anteriorly, the basal (hyoid) portions terminating in spoon-shaped processes turned inwards towards the midline. The anterior margin of the hyoid plate between the hyalia is much thickened. There are no alar processes. The posterior-medial processes are ossified as is usual and are constricted medially. The additus laryngis is directed craniad rather than dorsad.

Musculature

As might be anticipated from the peculiar form of the tongue and hyoid, the hyolaryngeal musculature of *Rhinophrynus* shows a high degree of specialization. The anterior portion of *m. intermandibularis posterior*[2] forms a pair of slips which run forward parallel to the maxillae to attach at the tip of the jaw, ventral to *m. intermandibularis anterior*. *M. interhyoideus* is greatly developed and forms a pair of thick-walled vocal sacs laterally. An extraordinary feature is the presence of a pair of large slips which laterally merge insensibly into the mass of the interhyoideus but medially are very distinct and attach to the dorsal (deep) surface of the pectoral girdle on the membrane covering the epicoracoids. There is no omohyoid muscle. *M. sternohyoideus* presents no unusual features. *M. geniohyoideus* is notable in that it shows no division into medial and lateral parts but forms a single sheet spreading over the hyoglossus and attaching posteriorly in a continuous line along the inner margins of the posteromedial processes and on the hyoarytenoid membrane. There is no trace of any attachment to the hyoid plate in the region of the posterolateral processes. *M. hyoglossus* originates, as usual, on the ventral surface of the posterior part of the posteromedial processes and runs forward into the tongue. *M. petrohyoideus anterior* seems to be absent, although the work of Trewavas (1933) and others would indicate that this muscle is among the most constant of the hyolaryngeal series. There are three *mm. petrohyoidei posteriores,* the first and second attaching to the medial portion of the posterolateral process and the third attaching in part to the tip of that process and in part to the cricoid cartilage. Perhaps the most striking feature of the hyolaryngeal apparatus is the presence of a muscle extending from the median dorsal surface of each posteromedial process to the *dorsal* surface of the hyoid plate. This muscle seems not to have been previously noted among the Salientia and its homologies are problematical.

[2] Terminology of Trewavas (1933).

The laryngeal muscles are well differentiated. *M. dilatator laryngis* extends, as is usual, from the dorsal surface of the posteromedial process to the summit of the arytenoid, but also has a small deep slip from arytenoid to cricoid. *M. constrictor externus* extends from a more anterior position on the posteromedial process to a raphe with its fellow and with *m. constrictor anterior* over the anterior surface of the arytenoids. The differentiation of anterior and posterior constrictors is quite evident at their posterior raphes. *M. constrictor posterior* runs forward to the cricoid cartilage where it is attached at the tip of a small muscular process.

The musculature of the thigh has been described and figured by Noble (1922). The sartorius is distinct. The arrangement of the distal tendons is, according to Noble's interpretation, a minor variation of the typical bufonid plan, the tendon of the gracilis major attaching ventral to that of the semitendinosus. The single specimen which I have dissected agrees with Noble's figures in the arrangement of the muscles but has the tendons of the gracilis major and semitendinosus fused at a point proximal to their attachment. Noble makes no mention of an adductor longus; in my specimen this muscle is apparently not differentiated from the pectineus mass.

Although the characters of pectoral musculature that were once thought to be of value in classification (Noble, 1924: 11) have since been shown to be unreliable (Jones, 1933) it is perhaps worth while to note that *Rhinophrynus* lacks an episternohumeralis but has a distinct supracoracoideus profundus.

Discussion

An allocation of *Rhinophrynus* in the phylogenetic system involves an evaluation of vertebral structure as the basis of taxonomic distinction. It is at once evident that in its vertebral characters *Rhinophrynus* conforms exactly to none of the previously described salientian types and that it cannot be referred to the order Procoela as defined either by Nichols (1916) or Noble (1922: 22; 1931: 495). In the structure of the individual vertebra there is a resemblance to *Ascaphus*

(Liopelmidae). There are important differences, however, in that *Rhinophrynus* lacks any trace of ribs, has one less presacral vertebra, and has well-developed intervertebral bodies. There is also a degree of resemblance to the free-disked, notochordal vertebrae of many Australian bufonids. Granting the primitiveness of the Liopelmid vertebra, it would seem that in *Rhinophrynus* there is represented a stage only slightly more advanced, a stage from which it is theoretically possible to derive in one line the solid opisthocoelous vertebra of the Discoglossidae and Pipidae, and in another line the free-disked structure of the Criininae and Megophryinae. The apparently constant association of intervertebral body with the anterior end of the centrum makes it doubtful that there can be any close relationship with those salientians which have solid procoelous vertebrae.

Additional features, which although of minor significance, might be considered primitive are the parahyoid ossification and the apparent absence of an adductor longus muscle. A parahyoid ossification is known to occur occasionally in some of the more advanced families, but is constantly present only in the Liopelmidae and Discoglossidae.

On the other hand, there is abundant evidence that *Rhinophrynus* has advanced considerably beyond the primitive salientian groups. The presence of a double coccygeal condyle, a distinct sartorius muscle, the absence of ribs, the structure of the scapula, the specialization of the laryngeal musculature and the posterior attachment of the geniohyoid muscle, considered together make impressive evidence of specialization which warns us against placing too much emphasis upon vertebral characters alone. In these points there is probably closest agreement with certain of the procoelous genera, although the hyoid skeleton is strikingly that of *Pelodytes* (Pelobatidae). That the latter resemblance is due to convergence is indicated by the differences in the structure of the vertebrae, in articulation of the coccyx, and by several characters of musculature.

The sum of the characters which have been investigated serves to emphasize the isolated position which *Rhinophrynus* occupies. In our present knowledge it differs from any other American genus not only in the possession of specialized characters but also in characters that are considered of fundamental importance in classification. It thus seems necessary to refer *Rhinophrynus* to a monotypic family which may be distinguished on vertebral characters alone and which may be briefly characterized as follows:

Vertebrae notochordal, intervertebral bodies cartilaginous, adhering to anterior ends of centra; no ribs; normally arciferous, sternum and omosternum lacking; coccyx free, articulating by two condyles; no teeth; tongue free in front; a distinct satorius muscle; no Bidder's organ;[3] pelvis *V*-shaped; phalangeal formula $\frac{2\text{–}2\text{–}3\text{–}3}{1\text{–}2\text{–}3\text{–}4\text{–}3}$.

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