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## THE IMPORTANCE OF LARVAL CHARACTERS IN THE CLASSIFICATION OF SOUTH AFRICAN SALIENTIA

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In recent years a great number of tadpoles have been described, especially from southern Asia and the Americas. It has gradually come to be realized that a single type of tadpole, at least if highly modified, will be found throughout natural groups of species and even genera. Larval characters are in these cases as important as adult characters in diagnosing relationships (Noble, 1925). Nevertheless, it has been steadfastly denied by some of the leading herpetologists (Boulenger, 1918) that larval characters assist in the elucidation of genetic affinities. It is true that, if one examines the literature alone dealing with the larval Salientia from certain regions, one will find various contradictions. Some of the greatest difficulties are presented by the brevipitid toads of South Africa. The present paper represents an attempt to account for the apparent discrepancies in these forms, but some reference is also made to other South African Salientia.

The present paper would not have been possible had it not been for the generous co-operation of Mr. J. H. Power and Mr. Vincent A. Wager, who have kindly sent the American Museum a representative series of the larvæ they have described. The observations reported below may be considered a supplement to the recent contributions of these investigators.

Certain South African Salientia illustrate admirably the thesis that all forms of a natural group will tend to exhibit the same larval specializations. The tadpoles of three species of *Heleophryne* are known. They are all essentially alike and highly adapted to mountain-stream life (Hewitt, 1926). Their large suctorial mouths help them to cling to rocks in the current. In detailed structure these larvæ do not agree with any other mountain-stream tadpoles. Superficially they resemble the larvæ of *Ascaphus* but Hewitt (1926) has shown that the larval teeth are denticulated, an advanced character, and the mandibles are strikingly unlike those of *Ascaphus*. No other African Salientia have larvæ similar to those of *Heleophryne* and no other African forms are closely allied to this genus (Noble, 1926).

Another South African tadpole of equally distinctive structure has recently been described. This is referable to the wide-ranging *Kassina senegalensis*. Unfortunately, Power (1926) did not emphasize the most distinctive features of this tadpole. The upper lip is in the form of a fairly rigid convex plate (Fig. 1a). Further, a black horny plate lies obliquely on either side and slightly below the lower mandible. Modifica-

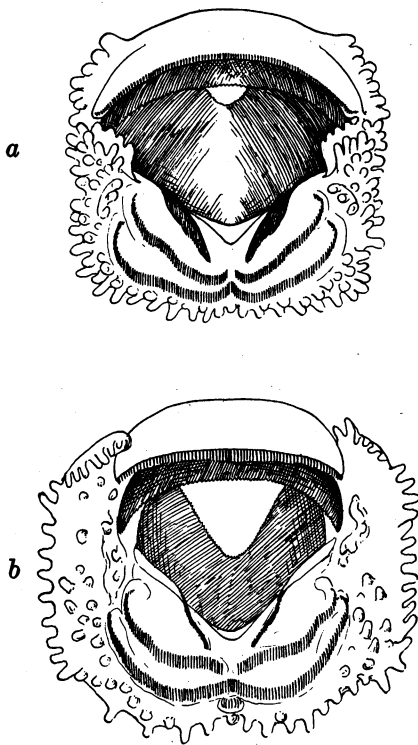


Fig. 1. Larval mouthparts of (a) *Kassina senegalensis* (Duméril and Bibron) and (b) *Hylambates maculatus* A. Duméril. The convex upper lip and oblique horny plates below the jaws are not known in any other Salientia.

tions of exactly this form have not been previously described in the mouthparts of any tadpole.

In recently examining the Amphibian collections in the Berlin Museum I found some tadpoles from East Africa attributed to *Hylambates maculatus* (No. 11451). These tadpoles exhibited the same features described above. Their mouthparts differed slightly from those of *K. senegalensis* in proportion and a minute patch of teeth was present below

the other teeth rows (Fig. 1b). In body form and proportions the tadpoles were much alike but the East African tadpoles were much the larger.

The fact that the tadpoles of *Kassina* and *Hylambates* should have the same peculiar upper lip and horny accessory plates below the mandibles would seem to indicate that these genera were closely related. *Hylambates* is a tree frog while *Kassina* is strictly terrestrial (Power, 1926). Nevertheless, a recent study of the skeletons of the adults has shown that they are closely allied. *Kassina* may in fact be considered merely a terrestrial *Hylambates* with very small disks, Y-shaped terminal phalanges; and usually a smaller tongue (Noble, 1924). Here again distinctive larval structures would confirm the conclusions derived from a study of the adults.

I have recently had the occasion to discuss some of the types of tadpoles found in the Salientia (Noble, 1925). I have pointed out that one of the most distinctive is that which characterizes all brevicipitids which undergo part of their development in the water. More recently, however, there have been published some data which would seem to show that the brevicipitid larval type is found outside the family. Wager (1926) has described the same tadpole form from "*Rappia marmorata*." Simultaneously with Wager's description there appeared in the same journal a description of the larval *Phrynomerus bifasciata* by Power (1926). This agreed with that of the ordinary brevicipitid larvæ. It occurred to me that there may have been some confusion in the identification of Wager's material. When this was suggested to the author he very kindly sent me a series of the preserved material which he had on hand. The series included an adult, a metamorphosing larva (four legs exposed, but mouth of larval type) and a half-grown tadpole. The adult is unquestionably *Rappia* (= *Hyperolius*) *marmorata*, but the larvæ are those of another species even though they were taken in a pool where only the *Rappias* were calling. A dissection of the metamorphosing individual reveals: (1) the terminal phalanges are Y-shaped, not claw-shaped as in *Hyperolius*; (2) the sacrum is broadly dilated; (3) the clavicles and procoracoids are lacking. The last character shows that the tadpoles are undoubtedly brevicipitids. The presence of Y-shaped terminal phalanges and intercalary cartilages identifies the tadpole as *Phrynomerus*, for no other genera of the family exhibit both these features. It is clear that the tadpole is referable to *Phrynomerus* and very probably to *bifasciata*. I have compared some of the larvæ described as *bifasciata* by Power with Wager's specimens and found them identical.

A dissection has, therefore, cleared up the difficulty presented by Wager's data, but Mr. Powers has sent me some recently described material (Hewitt, 1926) which has presented even a greater problem. The little South African brevicipitid *Cacosternum boettgeri* was originally described as a ranid, a species of *Arthroleptis*. Externally it resembles several species of this latter genus closely but its skeletal anatomy seemed to ally it to the other South African brevicipitids, such as *Phrynomerus*. Power has sent me a series of larvæ of *Cacosternum* at different stages of development. They are of the ordinary ranid type (Noble, 1926) and radically different from all other brevicipitid larvæ so far as known. Why is it that the larvæ of *Phrynomerus* and *Cacosternum* inhabiting the same region should differ so radically, the first having toothless, protrusible jaws, closed external nares (until just before metamorphosis), a median

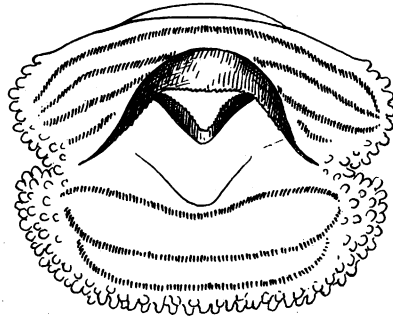


Fig. 2. Larval mouthparts of *Cacosternum boettgeri* (Boulenger).

spiracle and a whip-lash tail, while the second has none of these characters (Fig. 2)? The answer, I believe, is that the genera have descended from totally different stocks.

*Cacosternum* is most nearly allied to the brevicipitid *Anhydrophryne*. It agrees externally very closely with the latter, differing chiefly in possessing subarticular tubercles and a blunter snout and in lacking a distinct tympanum. Maxillary teeth are absent in one species of *Cacosternum* (*namaquense*) but present in the other two (Hewitt, 1926). Turning to the skeletons, it is found that *Cacosternum* has a more dilated sacrum than *Anhydrophryne* (Fig. 3), a more reduced pectoral girdle, more pointed terminal phalanges, and a less ossified skull. Although *Cacosternum* is clearly more closely allied to *Anhydrophryne* than to any other brevicipitid, it has advanced in specialization considerably beyond the conditions found in that genus.

*Anhydrophryne* has been referred to the brevicipitids although its sacral diapophyses (Fig. 3) are no more dilated than in many ranids. It differs from the ranid *Arthroleptis*<sup>1</sup> solely in lacking a clavicle. The clavicle is easily lost in the family Brevicipitidæ but it is never entirely lost in any other family of Salientia. In some ranids the clavicle is slightly reduced and in the Chinese *Montorana ahli* it is half gone (Fig. 4). Thus the ranids parallel the brevicipitids in the reduction but not in the loss of this pectoral element.

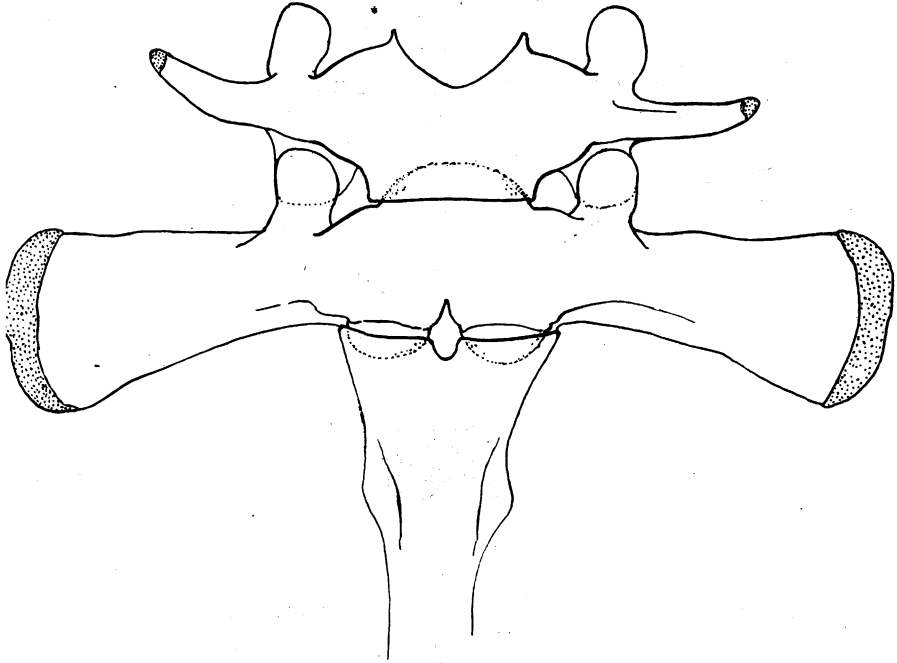


Fig. 3. Sacrum of *Anhydrophryne rattrayi* Hewitt as seen from the ventral surface.

When the entire skeleton of *Anhydrophryne* is compared with the short-webbed species of *Arthroleptis*, such as *A. variabilis*, several remarkable resemblances will appear. Perhaps the most important is found in the ethmoid. As shown in Fig. 5, the ossified sphenethmoid of *Anhydrophryne* extends far forward into the rostral region. The condition of this region is very much the same in *A. variabilis* and its allies. The ossified sphenethmoid is, however, only slightly less extensive in *Phryno-*

<sup>1</sup>I have received Hewitt's recent paper (1926, Ann. S. Afr. Mus., XX, pp. 413-431) after my paper was in page proof. The immediate ancestor of *Anhydrophryne* seems to be Hewitt's *Arthroleptella*, while his *Microbatrachella* helps to bridge the gap between *Cacosternum* and *Arthroleptella*. My figures of the girdles of South African Salientia are based upon material identified by Hewitt and sent to the American and British Museums.

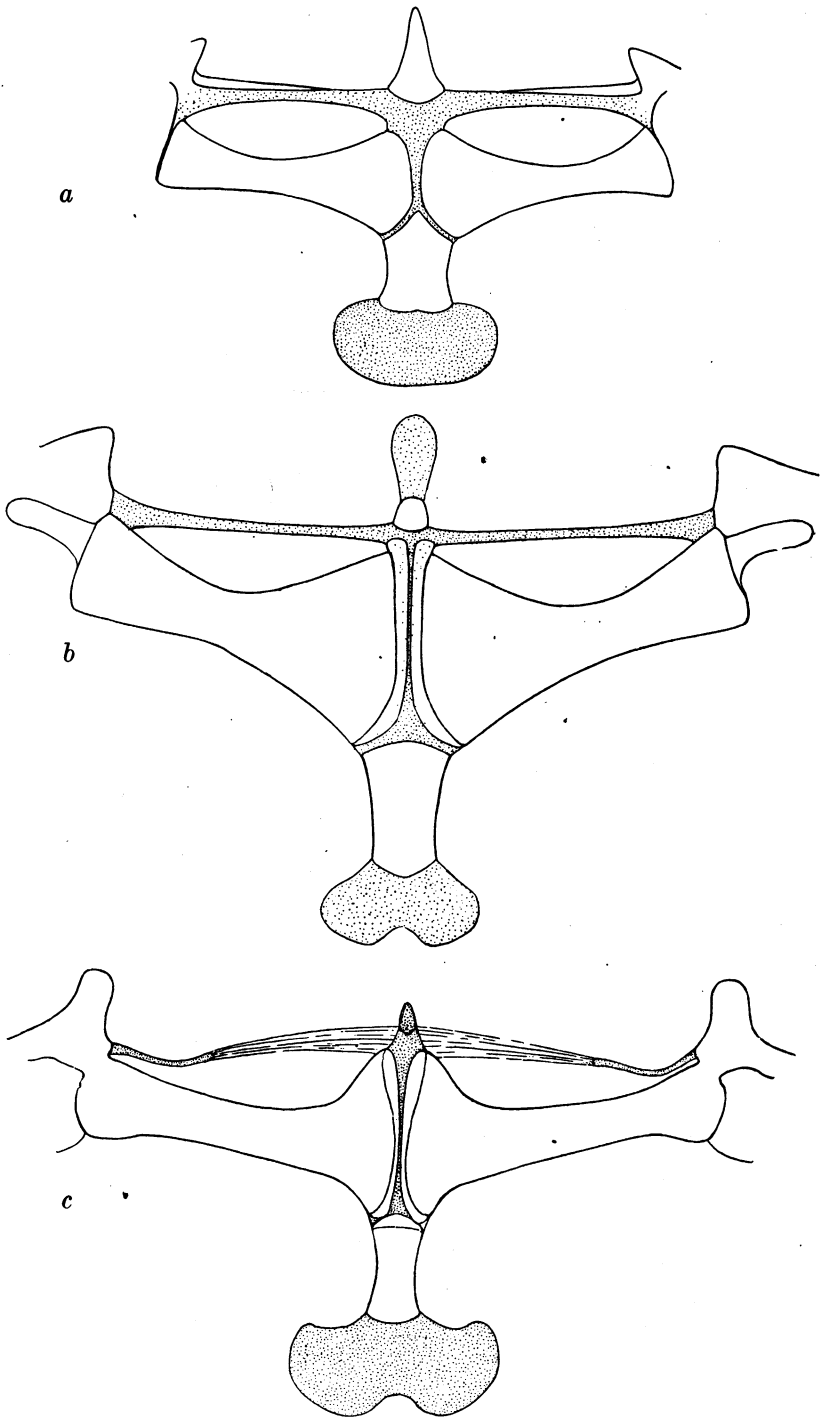


Fig. 4. Pectoral girdles of a ranid and two brevicipitid frogs, showing the gradual loss of the clavicle and the reduction of the procoracoid and omosternum. Girdles viewed from ventral surface.

- (a) *Montorana ahli* Vogt.  
 (b) *Anhydrophryne railtrayi* Hewitt.  
 (c) *Cacosternum boettgeri* (Poulenger).

*batrachus dendrobates* and *P. natalensis*. *A. variabilis* has a widely forked omosternum and it is not improbable that the dwindling of the clavicle may have been associated with a further widening of the posterior arms of the omosternum. This would not, however, account for the fact that an ossified rudiment of the omosternum remains in *Anhydrophryne*. Whether or not the genus is closely allied to *A. variabilis*, as its skeleton

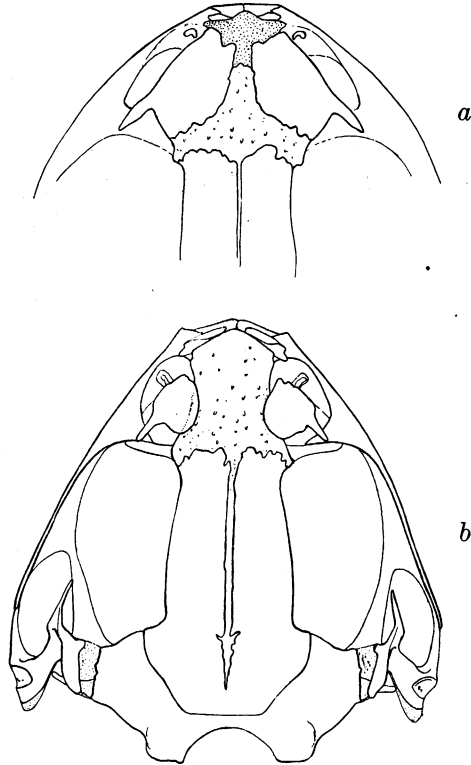


Fig. 5. The enlarged sphenethmoid of *Anhydrophryne* and its allies.  
 (a) The sphenethmoid region of *Arthroleptis variabilis* Matschie, dorsal aspect of skull.  
 (b) The dorsal aspect of the skull of *Anhydrophryne rattraui* Hewitt.

indicates, the fact remains that any species of *Arthroleptis* which by some accident of growth failed to develop a clavicle (and reduced its omosternum) would be referred to *Anhydrophryne*. Certain differences, such as the "anchor shaped" terminal phalanges, were emphasized in the original description of *Anhydrophryne*, but a study of all the terminal phalanges reveals a great variation in form (Fig. 6). Some are as T-shaped as in *A. variabilis*.

Referring back to the life-history data to secure confirmatory evidence of these relationships, it is interesting to note that the life history of *Arthroleptis*, so far as known, agrees fully with that of *Anhydrophryne* (Procter, 1925). The eggs are laid on land and in *Anhydrophryne*, at least, development is direct. Further, Power has very recently written in a letter to me: "The tadpole of *Arthroleptis* is not unlike that of *Anhydrophryne* as figured by Hewitt, no horny beak, no teeth, etc."

At first glance these data, although confirming the *Anhydrophryne*-*Arthroleptis* relationship, seem to disprove any relationship between

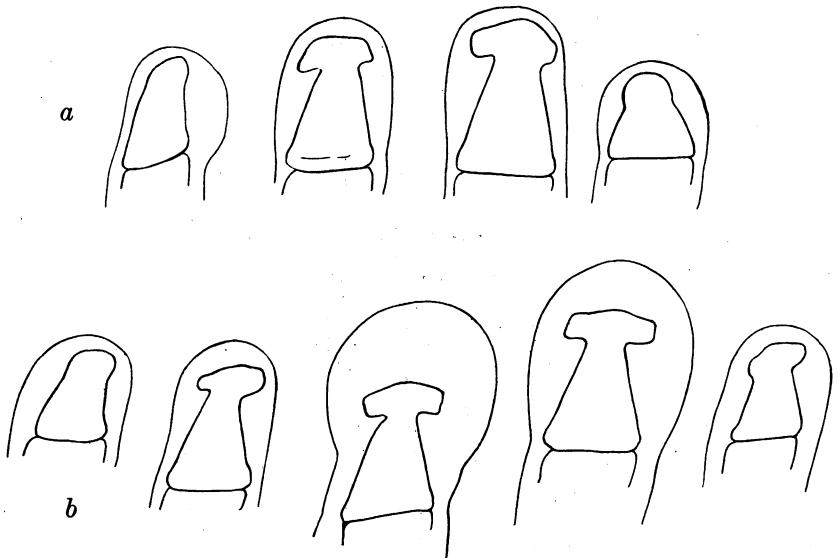


Fig. 6. Terminal phalanges of *Anhydrophryne ratrayi* Hewitt.

(a) Of hand.

(b) Of foot. The first (inner) digit of each series is on the left.

*Anhydrophryne* and *Cacosternum*. When, however, the life histories of all the Salientia are considered, it is found that in many different families species have secondarily developed large-yolked eggs and avoided a larval life in the water (Noble, 1925). Conversely, a few forms such as some species of the marsupial Frog, *Gastrotheca*, have succeeded in reversing this process and produce small eggs although they retain the larval peculiarities (bell gills) of their large-yolked ancestors (*Cryptobatrachus*). It is, therefore, not impossible that *Cacosternum* may have been derived from *Anhydrophryne* even though the latter genus practices direct and the former indirect development. According to this hypothesis, the



larvæ of *Cacosternum* should resemble the undescribed tadpole of *Phrynobatrachus*,<sup>1</sup> or at least that of the closest ally of *Arthroleptis* which passes a larval life in the water. With the data available, it is important to stress the fact that the larvæ of *Cacosternum* is of the ranid, not the brevicipitid type. This fact confirms the conclusion derived from the study of the adults: namely, that *Anhydrophryne* and *Cacosternum* have arisen directly from the ranids and not from other brevicipitids.

There is considerable indirect evidence which supports the above conclusion. Mention may be made of the thinning of the median portion of the coracoid as it approaches the midline in some species of *Cacosternum* (Hewitt, 1926, Fig. 1c). This peculiar condition is found elsewhere among Salientia, so far as my observations go, only in *Schoutedenella*, which is also a derivative of *Arthroleptis* (Noble, 1922). *Schoutedenella* and *Cacosternum* are diplasiocoelous, although some specimens of *Arthroleptis* may be procoelous. *Schoutedenella* has its sacrum dilated considerably more than *Arthroleptis* and about two-thirds as much as *Cacosternum*.

The conclusion that *Anhydrophryne* and *Cacosternum* have been immediately derived from the ranids is supported therefore by the evidence to be derived both from the adult and from the larvæ. All other brevicipitids possess the same type of specialized larva (or practice direct development) and may, therefore, be considered to form a natural group. Most natural families are assumed to have sprung from a single ancestor, that is, from a single species in an ancestral family. As a matter of fact, when the situation is closely analyzed, it is found that the derived family may have arisen from several species or even genera of the ancestral family. The latter was found to be the case in the brachycephalid frogs (Noble, 1926a). Some families may include genera of merely the same grade of organization, the genera in each family having arisen by parallel mutations from the same ancestral stock in different parts of the world. Other families are more truly "natural" for they have arisen in a single region and spread from this point. Obviously it is only the latter type of family which is of value in zoögeographic discussions. In the case of *Anhydrophryne* and *Cacosternum*, the life-history data have not destroyed the value of the whole family Brevicipitidæ in geographical studies, for these genera are only two in a family of many genera. Further typical brevicipitids live in the same region with them.

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<sup>1</sup>Since these notes went to press Mr. Power has sent me a description of the tadpole of *Phrynobatrachus*. It agrees essentially with that of *Cacosternum* but fewer teeth rows are present.

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