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AN ANALYSIS OF THE REMARKABLE CASES OF DISTRIBUTION AMONG THE AMPHIBIA, WITH DESCRIPTIONS OF NEW GENERA

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It is the practice of zoögeographers to postulate former centers of dispersal and routes of migration of groups of animals after studying their present distributions. If the conclusions in regard to any one group are to be of value, the zoögeographer should take into consideration three questions. First, is the group a natural one? Second, have the genera or species in the group been correctly identified? Third, how far would the fossil record, or more often lack of fossil record, modify the conclusions? As regards the Amphibia, it is unfortunate that certain recent writers on the distribution of this group have not always sufficiently considered the first and third questions (see Noble, 1925). Many of the recorded cases of distribution in the Amphibia are so remarkable that it has seemed probable that the second question as well has been too often neglected.

Recently I have had the opportunity of examining the material on which many of these remarkable cases are based. This material is preserved in various foreign museums, and it is through the courtesy of the custodians of these collections that I have had this privilege. My thanks are due especially to Mr. H. W. Parker of the British Museum, Dr. Ernst Ahl of the Berlin Museum, Dr. Lorenz Müller of the Munich Museum, Dr. Louis Roule and Mr. M. F. Angel of the Paris Museum, Dr. Jean Roux of the Basel Museum, and Dr. Lidth de Jeude of the Leyden Museum. I am greatly indebted to these gentlemen, not only for the opportunity of studying this unique material, but also for the excellent optical equipment which they placed at my disposal permitting me to examine the specimens frequently with much greater detail than had been done previously. The present paper is a brief statement of the most outstanding results of my investigation.

CAUDATA

AMBYSTOMIDÆ

One of the most startling cases of discontinuous distribution in the Urodeles is the reported occurrence of an *Ambystoma*, an otherwise Ameri-

can genus, in Siam. The species is known only from the type specimens, described long ago by Gray (1859) under the name of *Plethodon persimilis*. The species has been generally recognized as closely related to *A. jeffersonianum*. Boulenger (1882) distinguished it from the latter by its head form, less compressed tail, shorter body, and absence of tarsal tubercles.

I have recently examined in the British Museum the type specimens of *A. persimile* and have found that both specimens are sexually immature females measuring respectively 64 and 59 mm. from snout to posterior end of vent. I have compared these specimens with immature specimens of *A. jeffersonianum* in the British Museum, not adults, and have failed to find the differences given by Boulenger. A tarsal tubercle is present in both specimens, but ill defined, because of the poor state of preservation. The tail is identical in form with several specimens of *A. jeffersonianum* in the British Museum. The body length as measured by the approximation of the apposed legs is exactly the same in the young *A. jeffersonianum* and relatively shorter than in the adult of this species. The head form can be matched almost exactly in the series of *A. jeffersonianum* examined. In short, *A. persimile* agrees entirely in the usual external characters of descriptions with the immature *A. jeffersonianum*.

I have further compared the types of *A. persimile* with immature specimens of *A. jeffersonianum* in the British Museum in regard to the following features: extent and form of the vomerine teeth series; papillæ and grooves of tongue; anterior cranial elements (anterior to eyes); hyoid apparatus; number of phalanges; costal grooves; and color. In none of these features was I able to find any difference between *A. persimile* and the immature *A. jeffersonianum*. I am therefore forced to conclude that *A. persimile* must be referred to the synonymy of the latter species.

Does this conclusion make the distribution of the genus *Ambystoma* and of the species *A. jeffersonianum* even more remarkable? What is the evidence that the type specimens of *A. persimile* actually came from Siam? The two specimens are recorded in the British Museum as having been purchased from "Mr. Stevens," and are presumed to have formed part of the collection of reptiles and amphibians made by Mouhot in Siam. This Mr. Stevens is very probably Mr. Samuel Stevens, whom Mouhot mentions in his 'Travels in the Central Parts of Indo-China (Siam), Cambodia and Laos' Mr. Tate Regan of the British Museum has kindly informed me that Mr. Samuel Stevens was a salesman and auctioneer of natural history objects for many years, and that

his company is still doing business in London. Mouhot very probably sold his collection to Mr. Stevens, as many other collectors have since done, and the collection was in turn sold to the British Museum. Although I have not been able to trace fully the history of the type specimens of *A. persimile*, it is certain that these specimens were not sent directly from the field to the British Museum but passed through other hands, apparently those of a dealer in natural history objects.

Anyone who has had much business with even the most careful of natural history dealers knows how frequently specimens are erroneously labeled. Nor are all the errors committed in the natural history shops. I might mention only the case of the common American ribbon snake described by Cope as *Prymnomiodon chalceus* because he thought the specimen before him came from Siam. Such indirect evidence in no way strengthens our argument, but at least it warns us to be skeptical of all remarkable cases of distribution which do not rest upon the soundest kind of evidence.

In the present case, it may be argued that type specimens of *A. persimile* might have come from Louang Prahang, the mountainous region of southern Yunnan, into which Mouhot had penetrated at the time of his death. No amphibian collections have since come from this region and it is possible that the species may exist here. This argument, presented to me verbally by Dr. Malcolm Smith, might seem to receive some support from the remarkable discontinuous distribution of the genus *Hydromantes*, or that of the two closely related genera *Cryptobranchus* and *Megalobatrachus*. When these arguments are, however, weighed against the evidence presented above it seems to me far wiser to assume without further data that Gray's specimens never came from Siam, but were mislabeled before reaching the British Museum.

SALIENTIA

PELOBATIDÆ

Among the more primitive families of frogs and toads there are several instances of discontinuous distribution. Liopelmids, for example, are found only in New Zealand and western America; pipids, only in tropical Africa and tropical America. These are ancient families dating back certainly to the Mesozoic, and we may readily postulate a former continuous distribution in ancient times followed by later extinctions until only a mere remnant of these families survive today. The absence of fossil record in the intervening areas is of little consequence, for frogs do not make good or frequent fossils. We should expect that the more

ancient families would show a more discontinuous distribution than the recent ones and, consequently, we should make some allowance for this time factor when dealing with the distribution of primitive families.

It has always been a strange fact that one comparatively primitive and hence ancient family, the Pelobatidæ, should exhibit a nearly continuous distribution and be limited to only the northern hemisphere (except in the East Indian region). Why do not pelobatids occur today in Africa or Australia? This question cannot be answered today and, in fact, because of our scanty fossil record everywhere, may never be answered. I am, however, at this time able to show that the Pelobatidæ have a much greater range than has been previously supposed.

The most primitive pelobatids are included in the genus *Megalophrys*. I previously assumed (Noble, 1924a) that *Megalophrys* arose from the liopelmids rather than from the discoglossids for their intervertebral disks (centra) are often unattached to either the vertebral ring immediately before or to the one behind. An examination of all the skeletons in the British Museum and the American Museum has shown that this arrangement may possibly be considered to be not a primitive condition but a specialization peculiar to a group of related species, for in such cases where the "ball" is free, the vertebral ring is reduced in width exposing the ball to view. Further, this "free centra" arrangement is found elsewhere among Salientia (excepting certain forms to be discussed below) only in the Australian bufonids (*Heleioporus albopunctatus*, *H. pictus*, *Limnodynastes dorsalis*, etc.) where, however, a remnant of the notochord persists throughout each vertebra. (In *Hymenochirus*, which has the vertebræ irregularly modified, one of the centra is free.) It would seem probable that the ancestral pelobatids received their procœlous vertebræ directly from the amphicœlous type of the liopelmids rather than from the opisthocœlous discoglossid condition and that the "free centra" arrangement of *Megalophrys* was a secondary modification. No matter how we interpret the evidence of the vertebræ, it is generally agreed that *Megalophrys* is not closely related to any genus of discoglossids or liopelmids, but represents a distinct advance over these primitive groups.

From *Megalophrys* the other modern pelobatids have evolved in rather divergent lines. The series which I considered in my earlier paper (Noble, 1924a) most closely related to *Megalophrys* has been the subject of more dispute than any other one. I have assumed on several occasions (Noble, 1922, 1924a) that *Ophryophryne* and *Scutigera* arose directly from

Megalophrys by a loss of their maxillary teeth. Having recently had the opportunity of dissecting both these genera in the British Museum, I can now fully confirm this assumption.

Scutiger differs from most species of *Megalophrys* by its warty skin. There is one recently described species, *M. weigoldi* Vogt, which is almost identical with *Scutiger alticolus* (Procter) in form, color, and rugosity. This species was described from an unknown locality, but Dr. Vogt has more recently determined that the type specimen (Berl. Mus. 27881) actually came from Waschan. If we lay specimens of these high-mountain forms, *Megalophrys weigoldi*, *Scutiger alticolus*, *S. sikkimensis*, and *S. mammatus*, together, we shall find only a few external characters to separate them specifically. The genus *Megalophrys* is characterized internally by a number of distinctive features of skeleton and musculature (Noble, 1924a). A dissection should, therefore, reveal if the above series is a natural one.

In the type specimen of *S. mammatus* in the British Museum (No. 99.11.13.1) the vertebral column has fortunately been dissected free of the surrounding tissues. In this specimen it may be readily demonstrated that all the intervertebral disks or centra are perfectly free and can be rotated in their sockets with a needle. No remnant of a notochord may be seen piercing these intervertebral "balls." This condition, as stated above, is found elsewhere only in *Megalophrys*. The coccyx of this specimen articulates by a single condyle. The sacral diapophyses are greatly dilated. The pectoral and thigh musculature are nearly identical with that of *Megalophrys hasseltii* and readily distinguishable from that of any bufonid (Noble, 1924a). In a specimen of *S. sikkimensis* in the British Museum, I have found the same chordaless type of free centra vertebræ, coccyx with single condyle, dilated sacrum, and *Megalophrys* musculature. There is, therefore, no doubt that *Scutiger* is a pelobatid closely related to *Megalophrys*.

Scutiger has been considered by previous writers to be a bufonid, or an intermediate between bufonids and pelobatids (Procter, 1922). In other families of frogs it has been found that here and there in specialized groups certain species lost their maxillary teeth. In other words, the toothless forms were derived and not ancestral or primitive species. Can we be sure that this holds true for *Scutiger* as well?

In trying to solve this problem, I have turned first to a study of the jaws. In *Megalophrys weigoldi* Vogt, the maxillary teeth are well developed, but the vomerines are absent. In the type specimen of *Scutiger alticolus* (Procter), teeth are also present on the upper jaws.

These teeth are small but project through the gums and have the characteristic bifid tip, enamel cap and pulp cavity of true teeth. In a second specimen of the same species in the British Museum (1923.5.6.1), true teeth are also present on the maxillaries projecting through the gums. In short, there is no generic difference between *M. weigoldi* and *S. alticolus*. Turning to the next species, *Scutiger sikkimensis*, I had no difficulty in finding rudimentary teeth present on the upper jaws of the three type specimens in the British Museum, but these teeth, for the most part, do not perforate the mucosa which covers them. In the type specimen of *S. mammatus* the maxillaries are roughened, but there are no true teeth present. Where in this series from *Megalophrys weigoldi* to *Scutiger mammatus* may a line of generic separation be drawn? The problem was the same in *Telmatobius* and *Batrachophrynus* (Barbour and Noble, 1920) where certain species show a similar gradual loss of teeth.

In order to be consistent in our taxonomic arrangement, *mammatus* must be separated from the other species although it is perfectly clear that this is the terminal form of a natural series. I, therefore, reinstate Boulenger's name *Æluophryne* to include this species alone. For simplicity of identification *sikkimensis* and *alticolus* should be included with *weigoldi* in *Megalophrys*, but they are the intermediate forms of the series described and are characterized by shorter maxillary teeth than *weigoldi*. It might, therefore, be legitimate to use the name *Scutiger* for these two species, although this is a purely arbitrary grouping, since the teeth of *sikkimensis* are smaller than those of *alticolus*. The use of the generic name, *Scutiger*, tends to emphasize the reduction of the teeth, and, as this is the chief point of the present discussion, I refrain at this time from placing *Scutiger* in the synonymy of *Megalophrys*.

Scutiger and its close relative *Æluophryne* have, therefore, arisen directly from the high-altitude species of *Megalophrys* as represented by *weigoldi*. There is a third genus mentioned above as having a similar origin. This genus, *Ophryophryne*, is known only from a single species, *microstoma*. Externally, *Ophryophryne* looks very much like *Megalophrys montana*, except for its smaller head. The color pattern, skin texture, and general proportions are the same.

I have dissected one of the specimens of *O. microstoma* in the British Museum and have found that it has the characteristic pectoral and thigh musculatures of *Megalophrys* (for figures, see Noble, 1924a). There is a slight difference in proportions, the *pectoralis sternalis* is larger than in *M. hasseltii*, the *pectoralis abdominalis* is narrower than in this species and is not indented along its medial margin. The sternum extends farther

posteriorly and the caudal portion of the sternohyoideus is visible from the ventral surface. The vertebral column exhibits the same peculiarities as in *Megalophrys*: namely, a certain freedom of the intervertebral balls (centra). Further, the coccyx and sacrum are fused. All critical internal, as well as external, characters show that *Ophryophryne* is merely a toothless *Megalophrys* more closely related to *M. montana* than to the tubercular-skinned *M. weigoldi*.

No evidence is available to show that *Ophryophryne* arose from *Megalophrys* by a gradual reduction of the teeth, as in the case of *Ælurophryne*, instead of by a sudden disappearance of these structures. In other groups of Salientia exhibiting the same phenomena, some species, apparently, may suddenly and others slowly lose their teeth. *Batrachophrynus microphthalmus* of the Peruvian Andes seems to have slowly lost its teeth for the large *Telmatobius culeus* has very small ones. But another species, *Batrachophrynus brachydactylus*, is a small frog not unlike *T. jelskii* in external characters and may have evolved from this species by a sudden change, for no intermediates exist today. In other families of frogs (Ranidæ, Brachycephalidæ, Bufonidæ, etc.) we have many examples of the apparent sudden loss of teeth (Noble, 1922). All evidence points to *Ælurophryne* having arisen from one group of *Megalophrys* species and *Ophryophryne* from another. It would, therefore, seem that these toothless pelobatids are not ancient types, for they show so little differentiation from the stock from which they were derived.

The Pelobatidæ include two rather different groups of genera: namely, the *Megalophrys*-*Ælurophryne* series and the "Spade-foot" series. One genus, *Pelodytes*, seems externally different from either group, but Boulenger (1899) has suggested its close affinity to the latter group and particularly to *Pelobates*. *Pelodytes* is said to exhibit one character which distinguishes it not only from *Pelobates* but from all the pelobatids: its sacrum is said to have two condyles for the sacrum.

A casual examination of the coccyx head of *Pelodytes* would give the impression of a double condyle, for a slight median projection extends forward from the ventral side of the head. This projection is probably a remnant of the hypochordal cartilage. In bending back the coccyx the projection is apt to scratch the articulation surface of the sacral vertebra. The scratched surface of the condyle makes it appear double.

I have examined the series of skeletons of *Pelodytes punctatus* in the British Museum. Two adult skeletons, a male and a female (Lataste, 1920. 1. 20. 2703 and Lataste, 1920. 1. 20. 1487), had the coccyx still in place. When this was bent gently backward, the sacral condyle was

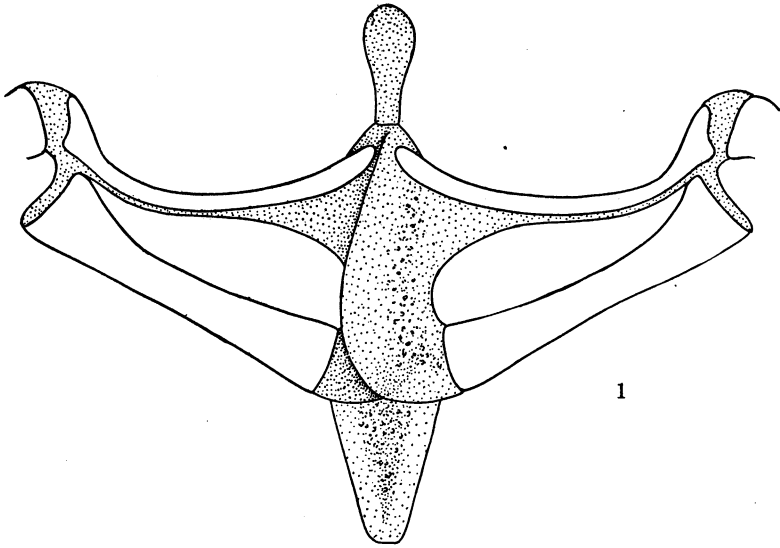
found to be single as in all other pelobatids which do not have the sacrum and coccyx fused. Two other skeletons had the coccyx already turned back and here the sacrum had obviously been scratched. The other three skeletons in the British Museum are immature and the coccygeal condyle not fully formed. From this series it is clear that *Pelodytes* has only a single coccygeal condyle. Moreover, I have dissected an alcoholic specimen of *Pelodytes* in the British Museum and have confirmed this conclusion.

Pelodytes agrees with *Pelobates* in its ossified sternum, bent clavicles, and widely expanded sacral diapophyses. It differs in its exposed ethmoid, frontoparietal foramen, reduced squamosal, and different habitus. *Pelodytes* agrees more closely with *Pelobates* than any other batrachian. It may be considered a specialized member of the spadefoot toad series.

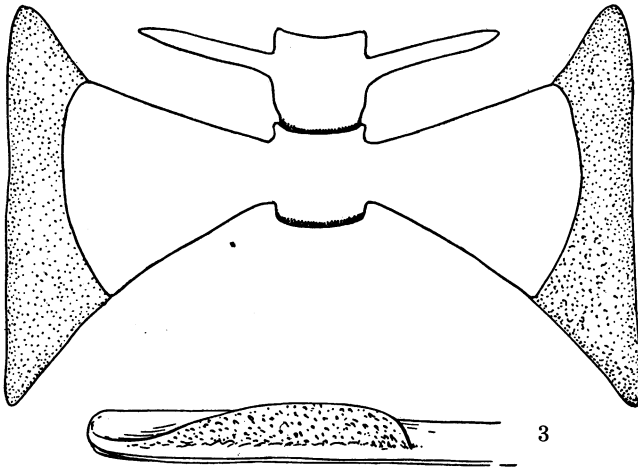
The Pelobatidæ have evolved, therefore, in two directions. First, in the spadefoot toad series which has spread over nearly the entire Palearctic region, and secondly, the *Megalophrys-Elurophryne* series which has a restricted range in southern Asia and neighboring islands. Why has neither series succeeded in penetrating into the southern hemisphere (save in the East Indian region)? Why has this comparatively primitive family such a northern range?

An examination of the large collection of Salientia in the British Museum has revealed that three species indigenous to the Seychelles and referred to three different genera and two families are really pelobatids greatly separated from the previously known range of the family. This discovery raises the question of whether the pelobatids might not have had a much greater distribution in former times, and have more recently been exterminated in most of their southern ranges. It is of great importance, first, to know on what evidence the pelobatid relationship of these species rests.

The first of the three species was originally classified as an *Arthroleptis*. But Boulenger, in 1906, pointed out that it differed from the known species of that genus in its entire tongue and he proposed the name *Sooglossus*. The second species was named the type of another genus *Nesomantis*, but Boulenger (1909), realized that it was closely related to *Sooglossus*, differing chiefly in its larger size, less pointed digits, and the possession of vomerine teeth. Boulenger assumed that both these genera were ranids presumably allied to *Arthroleptis* or related African stocks. Boulenger had in the same collection with *Nesomantis* a little batrachian very similar to *Sooglossus* but with fleshy webs at the base of the fingers. In this, Boulenger thought he spied evidence of



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Fig. 1. Pectoral girdle of *Nesomantis thomasseti*, ventral aspect.
 Fig. 2. Sacrum of *Nesomantis thomasseti*, ventral aspect.
 Fig. 3. Cephalic end of ilium of *Nesomantis thomasseti* showing the cartilaginous appendage.

relationship to the viviparous toads of east Africa, for he described it as a new species of *Nectophryne*.

I have dissected cotypes of all three species. All possess the following pelobatid characters: true teeth present in the upper jaws, pectoral girdle arciferal, supracoracoideus muscle not differentiated into an episternocleidohumeralis longus and a supracoracoideus profundus, presacral vertebræ procœlous, a single condyle to the coccyx, sacral diapophyses broadly dilated, terminal phalanges simple, no intercalary. These genera cannot be ranids because of the arciferal girdle, nor bufonids because of the single coccygeal condyle. Further, neither ranids nor bufonids have the simple pectoral musculature found in these genera and the pelobatids. They agree with the Pelobatidæ in all critical characters, except one, the thigh musculature.

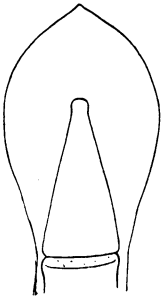


Fig. 4. Outline of the digital disk of the third finger of *Nesomantis thomasseti* showing the form of the terminal phalanx.

After examining the thigh musculature in an enormous series of Salientia, I was led to the conclusion (Noble, 1922, 1924a) that the characters exhibited by it are among the most conservative and diagnostic of all those utilized in the classification. Oddly enough, the thigh musculature of the three species under discussion agrees not with that of the next "higher" family, the Bufonidæ, as one might expect, but with that of the Ranidæ.

What is the meaning of this difference? Are these thigh musculature characters, which I have found to be so important in a primary division of the Salientia, sometimes variable and useless in our classification? It must be recognized that the three species have been isolated on the Seychelles for a long time. In general form or habitus they approach closely to ranids, such as *Arthroleptis*, and are different from all pelobatids. Further, their life history so far as known is also very peculiar. Such evidence would confirm our conclusion as to their long isolation. In one family of Salientia, the Pipidæ, the distal tendons of the thigh of the several species of *Xenopus* show considerable differences. The distal tendon complex (Noble, 1922) of *X. muelleri* has reached the same degree of specialization found in *Rana*. It is therefore possible for a batrachian to have assumed the thigh musculature characteristic of the Ranidæ while retaining all the other characters of a more primitive family. I believe this acquisition of specialized thigh muscles has occurred again in

these Seychelle frogs which, while retaining the pelobatid organization of pectoral girdle and vertebræ, have diverged in developing a ranid habitus and thigh musculature.

The three species under discussion are not alike externally and, before concluding this discussion of their relationship, some statement should be made as to their taxonomy. Boulenger recognized that *Sooglossus* and *Nesomantis* were closely related. The differences between them are very trivial. It may, nevertheless, be well to utilize these generic names until the anatomy of *N. thomasseti* and *S. sechellensis* is

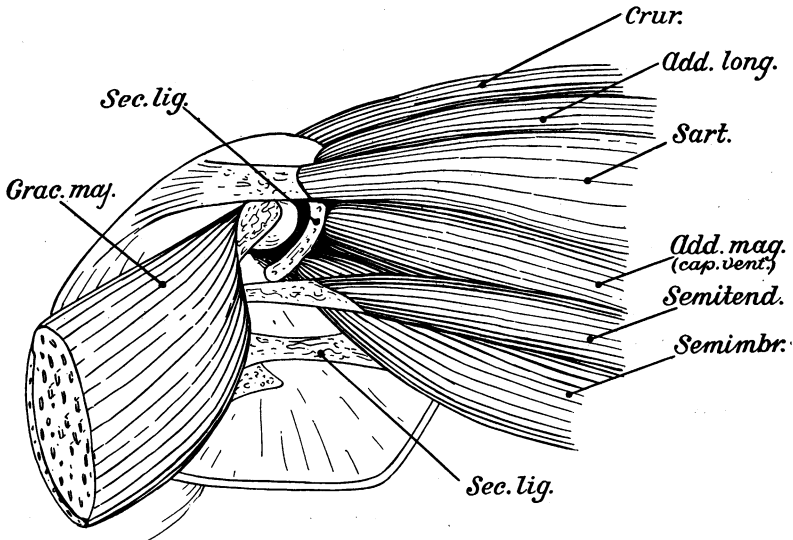


Fig. 5. Distal portion of the thigh musculature of *Nesomantis thomasseti*, ventral aspect; the *Gracilis major* has been cut and turned back to show the deeply lying *Semitendinosus*.

Add. long., Adductor longus; *Add. mag. (cap. vent.)*, Adductor magnus (ventral head); *Crur.*, Curalis; *Grac. maj.*, Gracilis major; *Sart.*, Sartorius; *Sec. lig.*, Secondary ligament; *Semimbr.*, Semimembranosus; *Semitend.*, Semitendinosus.

better known. The third species, *Nectophryne gardineri*, cannot possibly be a *Nectophryne* because of the presence of maxillary teeth, a single coccygeal condyle, simple terminal phalanges, and ranid thigh musculature. It agrees in size and body proportions to *Sooglossus*. Further, it agrees with that genus in all the internal characters listed above. It differs from *Sooglossus* in its shorter toes, one third webbed, and in its fingers with fleshy webs at their base. Such differences are often considered of generic value. Thus *Nectodactylus* is a *Chiasmocleis* with modi-

fications of the finger webbing parallel to those of *gardineri*. *Nectophryne tornieri* of East Africa differs from *Pseudophryne vivipara* of the same region by more or less the same characters. A genus might well be erected for *gardineri* for the sake of consistency. But *gardineri* is obviously closely related to *Sooglossus sechellensis* and occupies the same isolated range. I, therefore, consider it more advisable to extend the generic limits of *Sooglossus*, which has never been fully defined, in order that it may include *gardineri*. The genus, *Sooglossus*, may therefore consist of two species, *sechellensis* and *gardineri*, and be defined as follows: size small, teeth in upper jaw, no vomerine teeth, anomocœlous with a single condyle to coccyx, sacral diapophyses greatly dilated, arciferal with a cartilaginous unforked omosternum and sternum, pupil horizontal, tongue entire, not nicked behind, fingers and toes free or with fleshy webs extending about one third their length, outer metatarsals united, digits terminating in very small pointed disks, terminal phalanges simple, sharply pointed, ending in a very small knob, no intercalary cartilage.

One of the cotypes of *S. gardineri* in the British Museum is an adult female only 15 mm. in head and body length. This minute specimen contains unpigmented ovarian eggs 2 mm. in diameter! It is, therefore, highly probable that *S. gardineri* will be shown to have an abbreviated life history, and very probably one similar to that of its relative *S. sechellensis*.

BUFONIDÆ

The Bufonidæ, including both the toothed and toothless forms, exhibit a number of remarkable cases of discontinuous distribution. Some of these cases have been known a long time, but the specimens on which they were based have been described only in part.

The most discussed case of discontinuous distribution in the Bufonidæ is that of a toothed form, *Heleophryne*, in South Africa. It has been suggested that this genus may have arisen from some ranid stock of Africa by "arrested development" of its shoulder girdle. No ranid is known to possess an arciferal shoulder girdle during any stage of its development (Villiers, 1924, p. 206). Further, I have emphasized (Noble, 1922) that the known skeletal features of *Heleophryne* show that it cannot be closely allied to any African ranid nor, in fact, to any bufonid living today. In short, the known anatomical evidence would confirm the zoögeographic evidence, as interpreted by some workers, that *Heleophryne* has been isolated in Africa for a long time.

The discovery of pelobatids in the Seychelles demanded a re-examination of *Heleophryne* with a view to determining if it could possibly be considered a relative of *Nesomantis*. Thanks to the kindness of Mr. H. W. Parker, I have dissected one of the specimens of *H. regis* in the British Museum and have found that it agrees in both its skeleton and musculature with the primitive bufonids and has no affinity with either the Pelobatidæ nor the Ranidæ.

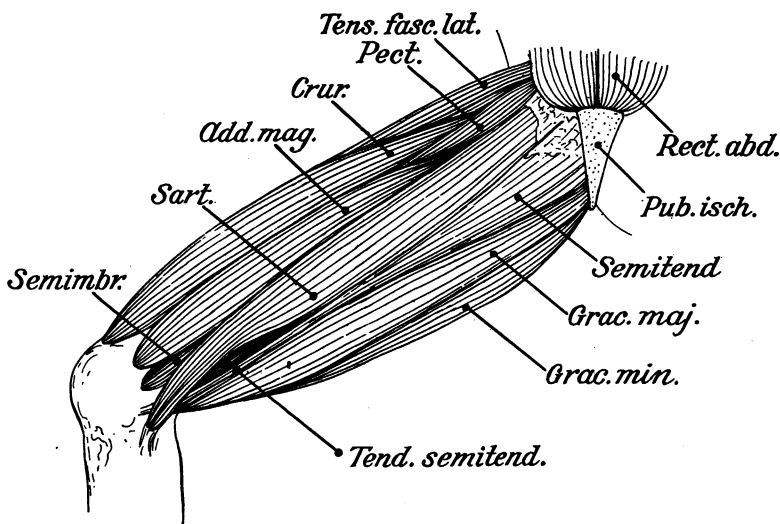


Fig. 6. Thigh musculature of *Heleophryne regis*, ventral aspect.

Add. mag., Adductor magnus; *Crur.*, Cruralis; *Grac. maj.*, Gracilis major; *Grac. min.*, Gracilis minor; *Pect.*, Pectineus; *Pub. isch.*, Puboischium; *Rect. abd.*, Rectus abdominis; *Sart.*, Sartorius; *Semimbr.*, Semimembranosus; *Semitend.*, Semitendinosus; *Tend. semitend.*, Tendon of the Semitendinosus; *Tens. fasc. lat.*, Tensor fasciæ latæ.

Heleophryne regis exhibits the following critical characters: vertebræ procelous (the first and second fused as in various other families), sacrum slightly dilated with a double condyle for the coccyx, no persistent notochord, a large frontoparietal foramen, nasals not in contact but separated by the ethmoid, maxillary teeth present, vomerine teeth in two straight series between the choanæ, pectoral girdle arciferal with a broad procoracoid cartilage, omosternum and sternum cartilaginous, pectoral muscle essentially as in *Lechriodus melanopyga* (Noble, 1924a), terminal phalanges broadly T-shaped, no intercalary, thigh musculature halfway between that characteristic of most pelobatids and that of bufonids (Fig. 6, the semitendinosus is exposed on the ventral surface, but distally it is

perfectly distinct from the sartorius, the tendons of both muscles lie ventral to that of the gracilis major distally).

Heleophryne differs from the primitive bufonids as represented by *Ranaster* in its T-shaped terminal phalanges, solid vertebræ, more dilated sacrum, and more anterior vomerine teeth. Its pectoral musculature is exactly like that of *Lechriodus melanopyga* (Noble, 1924a) except that the rectus abdominis does not overlap the sternum, the coracobrachialis longus is attached only to the posterior edge of the coracoid, the coracobrachialis brevis extends less than half the length of the coracoid. These differences are only matters of proportion. The distinctive thigh musculature shows clearly that *Heleophryne* cannot be closely related to any other bufonid. It represents the ancestral stock of toothed bufonids in Africa and shows that these forms reached Africa before they acquired the thigh musculature characteristic of all other bufonids.

Heleophryne cannot be considered a pelobatid, because it possesses an episternocleidohumeralis longus, a supracoracoideus profundus, a double condyle to the sacrum, and broadly T-shaped terminal phalanges. In these features it represents a distinct anatomical advance over any described pelobatid. It may be further remarked that the phylogenetic isolation of *Heleophryne* is further reflected in the tadpole, which is highly specialized for life in mountain streams.

Until recently, *Heleophryne* was the only genus of toothed bufonids known from Africa, but Ahl (1923) has described a second species as possibly coming from "Ndjiri Sümpfe" East Africa, and has given this species a new generic and specific name, *Niedenis spinulifer*. Through the kindness of Dr. Ahl, I have had the privilege of examining the two type specimens of this species which are preserved in the Berlin Museum (No. 26867) and have recognized them as the Brazilian frog *Cycloramphus asper*. In order to confirm this identification, I have compared Dr. Ahl's types with a specimen of the latter species in the Berlin Museum (No. 28028) and have found them to agree fully. All three specimens are females and possess the usual indistinct inguinal gland of that sex. They agree in the most minute details of color, proportions, rugosity, and digital webbing. *Niedenis spinulifer* must be referred to the synonymy of *Cycloramphus asper*, and one more case of mislabeling added to our list.

I shall not at this time discuss the toothless bufonids of Africa in any detail, although some, such as *Pseudophryne*, represent striking cases of discontinuous distribution. The anatomy of these species is not sufficiently known for us to be sure that we are dealing with natural assemblages. There are, to be sure, certain natural groups of species. *Necto-*

phryne afra and *N. batesii*, for example, may be distinguished from their East Indian relatives by the lamellated ventral surface of their feet and by the fused coccyx and sacrum. A second group would be *Nectophryne tornieri* and *Pseudophryne vivipara*, characterized by viviparity, an omosternum, and simple T-shaped but not flattened or spatulated terminal phalanges. Obviously, *Nectophryne tornieri* has nothing to do with *N. afra* and I therefore designate it the type of a new genus which may be known as **Nectophrynoides**. I provisionally assign *vivipara* to this genus, although I know no anatomical character to separate it from *Pseudophryne* except the more dilated sacrum. It would seem that we were begging the question of discontinuous distribution by erecting a new name. This, however, seems justified in the present case because the life history shows conclusively that *tornieri* and *vivipara* are closely related. How closely these species are related to the Australian bufonids will be made clear when the anatomy of the latter is better known.

HYLIDÆ

Of all the families of Salientia the Hylidæ present the most remarkable cases of discontinuous distribution. It was, therefore, highly advisable for this review to re-examine the more important material on which the reported cases were based.

Until 1911, no hylid was known from Africa south of the Sahara. In that year Nieden described, under the name of *Hyla wachei*, a large tree frog reported to have come from Dire Dawa, Abyssinia, although it was apparent from Nieden's description that the species closely resembled certain large hylas of South America. This remarkable record met with no comment in the literature until I had occasion to review the amphibian faunas of Africa (Noble, 1922, p. 65). More recently, Ahl (1924, p. 254) has described a second species from the Ethiopian region, giving it the name of *Hyla africana*. A zoögeographer studying the literature alone would be led to believe that the genus *Hyla* is widely spread in the Ethiopian region but that for some reason the earlier collectors were not successful in finding any specimens.

Upon my recent visit to the Berlin Museum, I had the opportunity, through the kindness of Dr. E. Ahl, of examining the type and unique specimen on which the record of *H. wachei* in Abyssinia is based. To my surprise, I found the species identical with *Hyla faber*, a form well represented in the collections of America. I selected for detailed comparison a series of *H. faber* (Berl. Mus. 21871) probably collected in Brazil but without definite locality. The type specimen of *H. wachei* falls well within

the limits of variation shown by this series in (1) size and proportions, (2) extent of webbing on fingers and toes, (3) form of the prepollex, (4) peculiar shape of the vomerine teeth series, (5) large size of the choanæ, (6) shape and relations of the elements of the skull roof, (7) very small size of the frontoparietal foramen, and (8) color and color pattern. In even the most minute details of head form, tympanum size and form, dorsal median stripe, etc., the type of *H. wachei* agrees with this series of *H. faber*. Further, the type of fixation is identical. It is, therefore, highly probable that *H. wachei* never came from Africa at all. At least, we may conclude that *H. wachei* is identical with *H. faber*, and it would be a bold zoögeographer, indeed, who would attribute a range of northern South America and Abyssinia to this species. There is no *Hyla* of the Australian-New Guinean or Asiatic regions which approaches *H. faber* structurally. Hence, "parallel evolution" could not be introduced here to save the situation. It seems clear that *H. wachei* is one more of these unfortunate mislabeling cases.

This solution of the *Hyla wachei* problem in no way explains the case of *H. africana*. The latter species was said to have been collected by Baumann, an officer in the German colonial army during the Great War. Dr. E. Ahl informs me that the collector died during the war and hence we shall never know exactly under what conditions the type specimen of *H. africana* was captured. It was merely included in a lot of specimens shipped from Misahöhe, Togo, and is assumed to have been collected in the vicinity. However, it was clear from Dr. Ahl's description that *H. africana* was in no way related to *H. wachei* but approached *Hyla arborea* closely in structure. With Dr. Ahl's permission, I have compared the type of *H. africana* (Berl. Mus. 27012) with a large series of *Hyla arborea meridionalis* (Berl. Mus. 18060) from Algiers in the Berlin Museum. I find that *H. africana* is practically identical with the adult females in this series. In proportions, webbing of the toes, and color they are exactly the same. The only difference that I can find is in the vomerine teeth. In the type of *H. africana*, they are slightly more posterior than in any specimens of *H. a. meridionalis* in this series, but fall within the limits of variation for the species. *H. africana* must, therefore, be referred to the synonymy of *H. a. meridionalis*.

The question arises at once, does *H. a. meridionalis* actually occur in Togo? Was Baumann's specimen collected there or did he pick it up on his way to that country, possibly at some point of call in Morocco? It must be remembered, however, that a newt larva has also been collected near Diéké, French Guinea. Mr. Angel at the Paris Museum very kindly

permitted me to compare this larva with a series of *Molge walli* in that Museum. It is certainly very similar to that species. There is good geological evidence that the Niger once flowed northward into the "Sahara Sea," but that by river capture its course has been turned in comparatively recent times to the southward (Schwarz, 1918). It is possible that *H. a. meridionalis*, as well as *M. walli*, has extended its range southward along the new course of the Niger, and that these species originally living near the edge of a Sahara Sea have succeeded in following up this river along its new course through Ethiopian forests to the Gulf of Guinea beyond.

It is also possible that both *M. walli* and *H. a. meridionalis* did not follow the course of the Niger as suggested above, but rather have made their way southward along the semiforested coastal regions from Morocco to Togo. Dr. J. P. Chapin has informed me that there are a number of birds which have a somewhat similar distribution (*Melierax metabates*, *Fancolinus bicalcaratus*, *Pycnonotus barbatus* and *Tschagra senegala*). Further, the Guinea Fowl, a typical forest bird of Africa, has a representative in Morocco (*Numida sabyi*). This discovery, therefore, raises the question of whether it would not be well for descriptive purposes to draw an arm of the north African (European) zoögeographic province extending southward around the Sahara and penetrating what has been previously considered a typical Ethiopian region.

Only future collecting can determine definitely whether or not *H. a. meridionalis* occurs in the Ethiopian region. In view of the occurrence of *M. walli* in this region, the possibility can not be rejected without further observations.

In reviewing the genera of Hylidæ known from South America, no remarkable cases of discontinuous distribution appear. The most peculiar feature of their distribution seems to be the very limited ranges reported for some groups. It is to be expected that the more bizarre genera such as *Diaglena*, *Lophyohyla*, and *Triprion* would not be widely distributed, but the ranges of most of the genera other than *Hyla* are restricted.

The ranges of some groups may, however, be much more extensive than recorded. Thus, *Centrolenella* has been reported to include, besides the type species (*C. antioquiensis*), only *C. parabambæ* and *C. buckleyi* of Ecuador and *C. fleischmanni* of Panama and Costa Rica. I can now add two additional species from two widely different parts of the South American continent.

The first species is *Hyla cappellei*, described by Lidth de Jeudę from Surinam. Through the kindness of the describer, I have examined the type specimen in the Leyden Museum. A dissection has revealed the species to be a typical *Centrolenella*, for T-shaped terminal phalanges are present, an intercalary cartilage, but no omosternum nor vomerine teeth. Further, it has the typical rounded head of *Centrolenella* and the eyes are directed partly upward in the usual way. So, *cappellei* should be referred to *Centrolenella*.

The second species referable to *Centrolenella* was recently described by Lorenz Müller (1924) from the state of Santa Catharina, Brazil. He called it *Hyla (Hylella) uranoscopa*, but a dissection of the type specimen in the Munich Museum has revealed all the characters listed above as characteristic of *Centrolenella*. We may, therefore, conclude that the genus *Centrolenella* has a very wide distribution in South and Central America from southern Brazil and Ecuador northward to Costa Rica.

A second genus previously reported to be restricted to northeastern South America (including Panama) is *Cerathyla*. This genus is so distinctive that it could not possibly be confused with any other hylid. There is, however, another genus, *Hemiphractus*, very similar externally to *Cerathyla* but placed in another family because it is supposed to have "diapophyses of sacral vertebra not dilated" (Boulenger, 1882, p. 451). *Hemiphractus* is known to occur in Ecuador, Colombia, and Brazil.

When abroad, I made an effort to examine the skeletons of every specimen of *Hemiphractus* preserved in the museums visited, for the skeleton of *H. scutatus* as described by Brocchi (1877) was peculiar in several respects. The type of *H. scutatus* (Spix) is still preserved in the Munich Museum and I am indebted to Dr. Lorenz Müller for his kindness in permitting me to make a partial dissection of this specimen. To my surprise, I found that the specimen is uniformly procelous, with two condyles to the coccyx; the sacrum is slightly dilated and flattened as in *Cerathyla johnsoni* (Noble, 1917). The terminal phalanges are claw shaped with an intercalary cartilage present. In short, this specimen of *Hemiphractus* differs from *Cerathyla* only in having smaller digital disks, shorter body and legs, and in lacking the canthal ridges.

Two additional specimens of *H. scutatus* are contained in the collections of the British Museum. These agree entirely with the type in vertebral column, digital skeleton, sacrum, and pectoral girdle. The very broad overlapping coracoid cartilages of *Hemiphractus* are found elsewhere only in *Cerathyla*. Externally and internally there is no more generic difference between *Hemiphractus* and *Cerathyla* than between

Hyla goughi and *H. versicolor*, *Leptopelis anchietæ* and *L. rufus*, or between the species in any genus of tree frogs having narrow disks and the species having wider ones. The head is somewhat different in that the casque of *Hemiphractus* lacks the canthal ridges. But in other hylids having a casque, such as *Diaglena*, the canthal ridges may vary enormously from species to species.

Further, *Cerathyla* seems to grade into *Hemiphractus*. *Cerathyla fasciata* (Peters) has very slight webbing between the toes, small disks, and very small canthal ridges. The type of this species agrees with other species of the genus and with *Hemiphractus* in its skeletal features. The genus *Hemiphractus* may be maintained only on body (and canthal ridge) proportions. As such an arrangement would be quite inconsistent with generic distinctions as utilized today in the Salientia, I propose to unite *Hemiphractus* and *Cerathyla*. As the former is the older name, the combined group may be known as *Hemiphractus*. *Hemiphractus* and *Centrolenella* have, therefore, a much wider distribution in South America than previously supposed.

BREVICIPITIDÆ

Among the narrow-mouthed toads there are several reported cases of remarkable distributions which I have critically studied.

The first I had occasion to discuss in a recent paper (Noble, 1922, p. 64). Only one genus of African brevicipitids is said to have its present range extended beyond the continent. This genus, *Phrynomantis*, is said to have a representative on Amboyna and Batanta Islands in the East Indies, but as I pointed out, there are a number of characters given in the original description which would lead one to suspect that the form was not congeneric with the African species.

Through the kindness of Dr. E. Ahl, I have had the opportunity of examining the type specimen of *Phrynomantis fusca* (Berl. Mus. 5648) and have found that the species can no longer be maintained in the same genus as the African species. *P. fusca* differs from *P. bifasciata* in the following particulars: vomers large bearing a crenulated ridge along their posterior margins transverse to the body axis instead of small and confined to the anterior mesial edge of the choanæ; a denticulated fold between the Eustachian tubes instead of a smooth ridge; tongue entire, instead of prominently notched; sacrum moderately dilated, instead of greatly so; terminal phalanges T-shaped, no intercalary, instead of Y-shaped with an intercalary; pupil horizontal instead of vertical (Fig. 7).

The clavicles and procoracoids are absent in both species. *P. fusca* agrees essentially with several of the smaller species of *Hylophorbus* as defined by Van Kampen (1923). *P. fusca* is the type species of the genus, hence the name *Phrynomantis* which has priority over *Hylophorbus* should be used for the species usually referred to the latter genus.

The African species form a uniform group so far as they have been investigated anatomically. No generic name is available for these species, since the earlier name *Brachymerus* is preoccupied. I, therefore, propose the name **Phrynomerus** for these African species and designate *P. bifasciata* as the type. It is clear from the above that the African *Phrynomerus* has arisen from a different brevicipitid stock than the East Indian *Phrynomantis*.

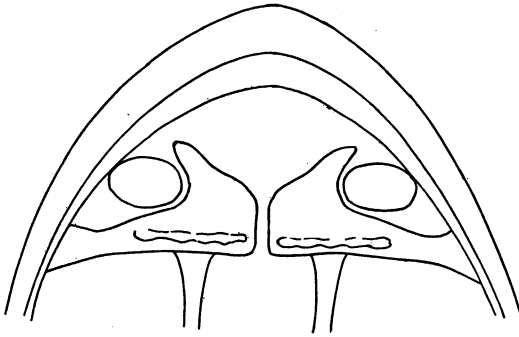


Fig. 7. Vomers (prevomers) of *Phrynomantis fusca*, ventral aspect.

A second remarkable case of discontinuous distribution is that recorded by Boulenger (1897) of a *Gastrophryne*, an otherwise American genus, in Borneo. Thanks to the kindness of Mr. H. W. Parker, I have had the privilege of examining the type (Brit. Mus. 97. 3. 4. 26). The latter looks superficially like a *Gastrophryne*, especially like *G. atterimum*. (The latter is a large species referred to the genus *Glossostoma* by some workers but its palate differs scarcely from that of *Gastrophryne carolinensis*.) A closer comparison reveals that the snout of *G. borneënsis* is proportionately longer than that of any species of *Gastrophryne*, and the digits end in distinct disks.

The resemblances and differences between *borneënsis* and the other species of *Gastrophryne* may be tabulated for the sake of clearness.

RESEMBLANCES

- 1.—General body form, including pointed snout.
- 2.—No webbing between the toes (rarely present in *Gastrophryne*).

- 3.—A smooth fold between the Eustachian tubes, a glandular fold anterior to this (sometimes reduced in *Gastrophryne* to an oval shaped swelling).
- 4.—Vomers small, restricted to a small crescent anterior to the choanæ.
- 5.—No palatines, but the ethmoid ossified and extending out below the palatine region (rarely present in *Gastrophryne*).

DIFFERENCES. *G. borneënsis* as contrasted to other species has

- 1.—Procoracoid cartilage present.
- 2.—T-shaped terminal phalanges.
- 3.—Digits terminating in small disks.
- 4.—Snout longer.
- 5.—Pupil round (widely dilated).

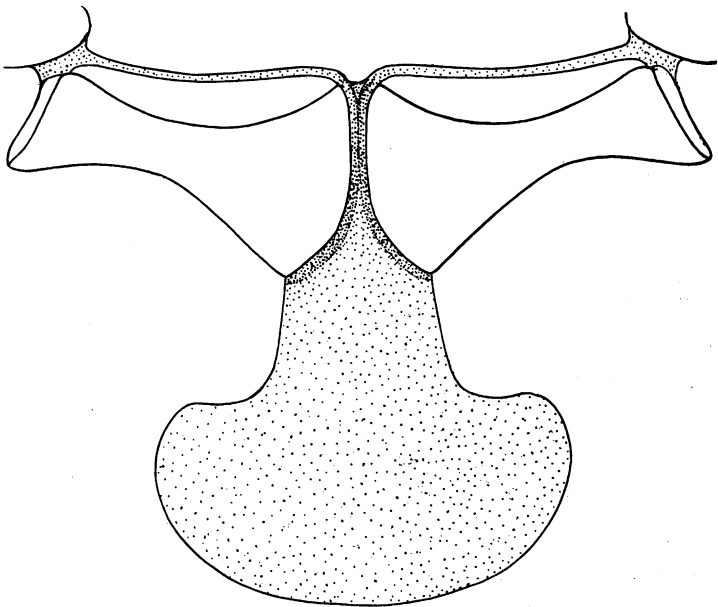


Fig. 8. Pectoral girdle of *Gastrophrynoides borneënsis*, ventral aspect.

In evaluating these characters, it must be kept in mind that there are several other East Indian brevicipitids of nearly the same body form as *borneënsis*. *Copiula oxyrhina* differs chiefly in the slightly longer leg and slightly shorter snout. The vomers in the latter species, however, are extensive and are raised into a sharp edge. In the closely allied *Choerophryne proboscidea*, the vomers, to judge from descriptions, are reduced; but no information is available as to their exact form. *Xenorhina oxycephala* has a habitus similar to that of *G. borneënsis*, but here again the snout is shorter and there are several important structural differences.

If we were to judge from the external characters alone, all of these species might be placed together in one genus, but we realize from their internal anatomy that they are not closely related. Hence, it is the differences rather than the resemblances between *borneënsis* and the other species of *Gastrophryne* which are the more important. It would seem that *borneënsis* has arisen from a different stock than that which gave rise to the American species of *Gastrophryne*. It is therefore highly advisable to place the former in a different genus.

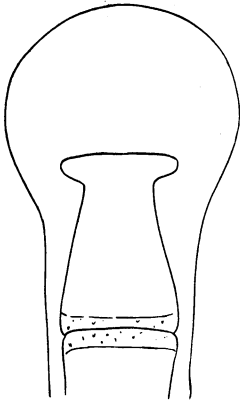


Fig. 9. Outline of the digital disk of the fourth toe of *Gastrophrynoides borneënsis* showing the form of the terminal phalange.

Of the described species of brevicipitids, *borneënsis*, as made known above, seems most closely allied to *Microbatrachus pusillus* Roux. The latter species was based on what appears to be a very young individual. Further, I am informed that the shoulder girdle of the type and only known specimen was removed for study and has been lost. Hence, the critical characters of the genus will remain unverifiable until another specimen is captured. Nevertheless, *borneënsis* seems to differ from *M. pusillus* in its digital disks and T-shaped phalanges. A new genus may well be created for *borneënsis*. I propose the name **Gastrophrynoides** because of the superficial resemblance of *borneënsis* to the species of *Gastrophryne*.

So far as I am aware, there are only three specimens of *G. borneënsis* extant: the type, which is described above; a poorly preserved specimen in the Basel Museum; and a very young individual in the British Museum. I am not at all sure that the Basel specimen is identical with the two others. It is apparently an adult female (partly eviscerated), measuring only 30 mm. from snout to vent, while the type of the species is also an adult female, but measures 38 mm. The snout is distinctly smaller in this specimen. Unfortunately, the pectoral girdle was broken during its capture. The structure which I assume to be the procoracoid is more reduced than in the type. The capture of additional specimens of *borneënsis* will clear up the status of this specimen.

It may be noted in passing that, even if evolution had proceeded one step farther in the reduction of the pectoral girdle and the procoracoid had been lost, this modified *Gastrophrynoides* stock would not merge into

Gastrophryne but would still remain distinguished by the T-shaped terminal phalanges.

There is a third genus of brevicipitids said to have representatives in widely separated regions. This is the well-known case of *Kalophrynus* which, while widely spread across southeastern Asia and the neighboring islands, is said to have three species in Madagascar. Mr. H. W. Parker and I have in preparation a review of the brevicipitids of Madagascar. In this we shall show that the Madagascan species are not related to the typical species of *Kalophrynus* but should be referred to another genus.

In brief, almost every striking case of discontinuous distribution in the Brevicipitidæ has revealed upon close scrutiny that the species grouped together were not at all congeneric and should never have been placed in the same genus. I have come to this conclusion not by juggling values: that is, by picking up small characters and redefining our genera, but merely by dissecting type specimens and describing, for the first time, the usual characters which should have been described long ago. If the present study has no other purpose it will perhaps emphasize the value of internal characters in the classification and phylogeny of the Amphibia.

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