

Article XXX.—THE SYSTEMATIC STATUS OF SOME BATRACHIANS FROM SOUTH AMERICA.

By G. K. NOBLE.

PLATES XCIII–XCVI.

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INTRODUCTION.

The American Museum has received during the past five years a number of valuable collections of Reptiles and Amphibians from South America. Before attempting a complete report upon any one collection, it has been thought advisable to clear up some of the more important problems connected with this material. In batrachian classification the form of the terminal phalanx has been considered of great importance in some of the groups. It is the purpose of this paper to discuss several groups of South American batrachians represented in the collections and to point out the value of phalanx form in these groups. A correlation of the larval histories of some of the genera has been made from a phylogenetic point of view in order to shed light upon our main problem.

I take pleasure in thanking Dr. Léonhard Stejneger for giving me a part of the type specimen of *Cerathyla panamensis* for histological study. To Dr. Thomas Barbour and to Dr. A. G. Ruthven I am indebted for the privilege of examining specimens of *Eleutherodactylus lineatus* in the collections of the institutions with which they are associated.

1. THE STATUS OF *ELEUTHERODACTYLUS LINEATUS* (SCHNEIDER) AND *ELEUTHERODACTYLUS MILIARIS* (SPIX).

Eleutherodactylus lineatus has been placed in many different genera in the past. After it had been allied first with the genus *Rana* and then with *Bufo*, Duméril and Bibron (1841, p. 625) pointed out its relationship to the genus *Hylodes*. Fitzinger (1843, p. 31) subdivided *Hylodes* and made

lineatus the type of a new genus, *Lithodytes*; but he did not define this genus. Cope (1862, p. 153) followed Fitzinger and later described some new species of the genus *Lithodytes*. Boulenger (1882, p. 207) followed Guenther (1858, p. 91) in accepting the arrangement of Duméril and Bibron. It was not until many years later that Peracca (1904, p. 31) dissected a specimen of *lineatus* and noted its *Leptodactylus*-like pectoral girdle. He pointed out the distinctness of *lineatus* from any *Hylodes* and set up again Fitzinger's *Lithodytes* which Boulenger had considered synonymous with *Hylodes*. Peracca defined *Lithodytes* and made it a monotypic genus transitional between *Hylodes* and *Leptodactylus*. Recently Despax (1911a, p. 40) has disregarded the careful work of Peracca and has referred *lineatus* back again to the genus *Hylodes*. *Eleutherodactylus* is an earlier name for *Hylodes* (see Stejneger, 1902, p. 582).

In a collection of amphibians from British Guiana given to the American Museum by Mr. C. W. Beebe there is a single adult specimen of *Eleutherodactylus lineatus*. The Museum of Comparative Zoölogy has kindly placed at my disposal three smaller specimens of the species. One of these specimens (M. C. Z. 2962) was collected by Rosenberg and was identified by Boulenger as *E. lineatus*. Dr. Ruthven, of the University of Michigan, although engaged himself in a study of the species, has kindly lent me another young specimen. These five specimens form the basis of my work upon the species. The difference in size of the specimens is given below. The measurements are from snout to vent.

- | | |
|---|---------|
| 1. Beebe Collection at A. M. N. H. British Guiana, Tropical Research Station..... | 45.5mm. |
| 2. M. C. Z. 2962. British Guiana..... | 34.5 " |
| 3. Ruthven Collection at Univ. of Mich. British Guiana, Demerara River..... | 29.0 " |
| 4. M. C. Z. 2558. British Guiana, Aremu River..... | 28.5 " |
| 5. Wyman Collection at M. C. Z. Dutch Guiana..... | 22.5 " |

The only character given by Peracca (1904, p. 31) to distinguish *Lithodytes* from *Leptodactylus* is the presence of T-shaped terminal phalanges in the former genus. The pectoral girdle is typical of the genus *Leptodactylus*. Most of the external features of *Lithodytes* are *Leptodactylus*-like, but its coloration is very peculiar. The color pattern is similar to the two-striped variation of *Dendrobates trivittatus* or the typical color form of *Dendrobates braccatus*. Dr. Ruthven informs me that the specimen he secured was very rapid in its movements, which resembled those of a *Dendrobates* more than those of a *Leptodactylus*. But these differences are only of specific value. The generic status of *lineatus* is dependent upon the exact form of its terminal phalanges.

A study of all of the terminal phalanges of the five specimens of *E. lineatus* has led to the following conclusions:

1. The five specimens may be taken as representing four successive stages in the ontogeny of an individual.
2. In this ontogeny the terminal phalanges change from an *Eleutherodactylus*-like, T-shaped type to a *Leptodactylus*-like simple type.
3. The change is brought about by an increase in the length of the phalanges and by a reduction in the extent of the terminal crossbars.
4. This change in form of the terminal phalanges is correlated with a change in form of the digital expansions from a somewhat modified but distinct *Eleutherodactylus* type to a *Leptodactylus* type.
5. The simple phalanges occurring in the adult must be considered typical for the species.
6. The species must be referred to the genus *Leptodactylus*.

In order to study the phalanges of the specimens the tips of the digits were dipped in a solution of glycerin and hydrogen peroxide. They were then dehydrated, and cleared in cedar oil. Subsequent washing in 70% alcohol restored the specimens to nearly their normal condition. The range of variation between the phalanges in young and adult specimens is shown in Fig. 1. For the sake of comparison I have included a figure of a terminal phalanx in a true *Eleutherodactylus*, and two other figures which show the normal range of variation in the ontogeny of *Leptodactylus melanotus*, which is perhaps closely allied to the species under discussion.

An appreciation of the ontogeny in the terminal phalanges of *Leptodactylus lineatus* allows one to interpret the status of *Eleutherodactylus miliaris*. Boulenger (1891, p. 454) removed this species from Cope's genus *Thoropa* and referred it to *Borborocates*. Wandolleck (1907, p. 5) shifted it to the genus *Eleutherodactylus* because he found that the terminal phalanges were T-shaped. I have examined an adult male specimen in the collection of the American Museum. The terminal phalanges are only moderately dilated, similar to those of the young *L. melanotus* (Fig. 1, D). The specimen of *Eleutherodactylus miliaris* which Wandolleck figured was not adult. It seems to me very probable that a change of phalange form takes place as in *L. lineatus* during the life of an individual. As in that species, the simpler type of terminal phalange occurs in the adult. There is no good reason for removing the species from the genus *Borborocates* where Boulenger placed it.

It is generally accepted that in some genera the form of the terminal phalanges is of little diagnostic importance. In *Rana* the terminal phalanges may be pointed or T-shaped. Barbour (1909, Pl. 18) has shown the great range of variation of the terminal phalanges within the genus *Kaloula*.

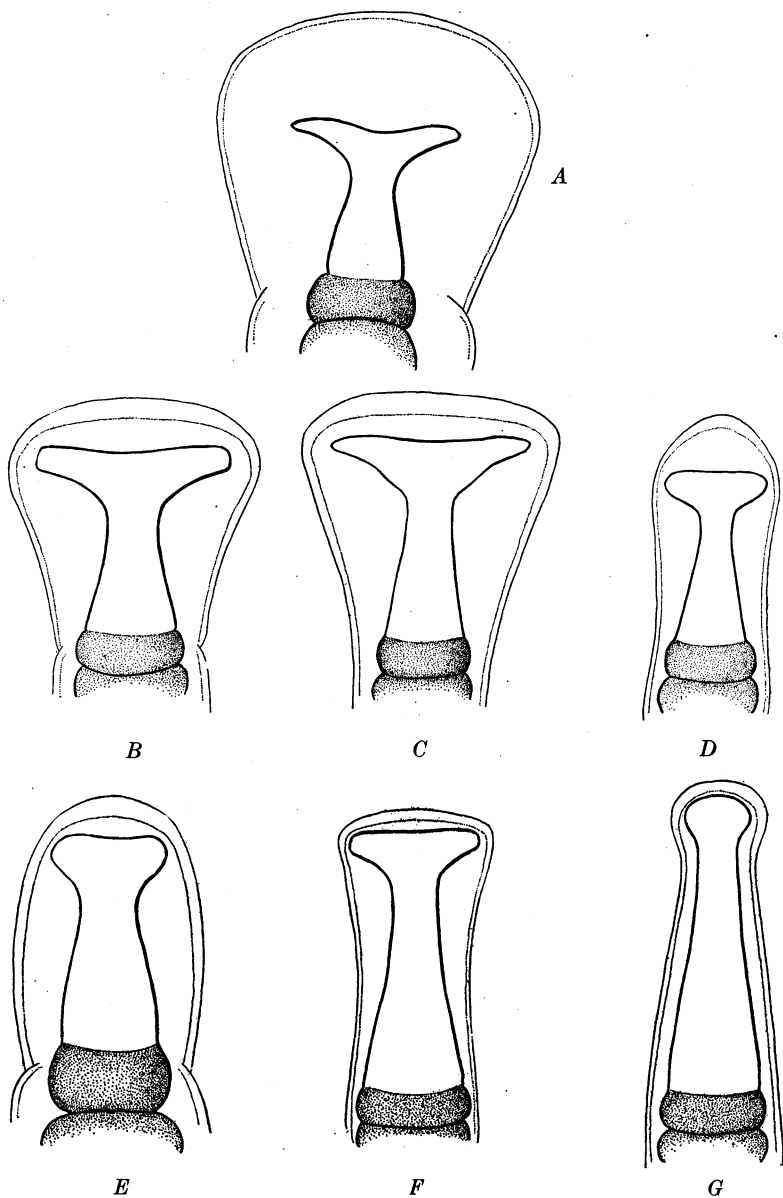


Fig. 1. Ontogeny of terminal phalanges from an *Eleutherodactylus* to a *Leptodactylus* type. A, ADULT, second finger, left manus, *Leptodactylus lineatus*. B, C, D, IMMATURE:—B, second finger, right manus, *Leptodactylus lineatus*; C, third toe, left pes, *Leptodactylus lineatus*; D, third toe, left pes, *L. melanotus*. E, F, G, ADULT:—E, third finger, right manus, *L. lineatus*; F, third toe, left pes, *L. lineatus*; G, third toe, left pes, *L. melanotus*.

It is now probable that the variation of the terminal phalanges is not only due to a difference of species but also to a difference of age of the specimens. Whether the T-shaped terminal phalanges are in all cases more primitive than simple ones is not known, but in *L. lineatus* the simple ones occur only in the adult stage. Moreover, since *Leptodactylus* with its simple phalanges is structurally a more advanced type of batrachian than *Eleutherodactylus* with its T-shaped ones, it is probable that simple phalanges were acquired more recently than T-shaped ones. It is possible, however, that the shape of the terminal phalanges is correlated with the shape of the digital expansion and these in turn with the nature of the environment. Claw-shaped phalanges of the Hylids show little variation. Just how they developed is not known.

It is probable that claw-shaped phalanges are but slightly modified simple ones. There are many species with curved, T-shaped and others with curved, simple phalanges. The most specialized Leptodactylids have not the T-shaped terminal phalanges of the less modified forms but they have simple phalanges. We should expect in over-specialized batrachians of the Leptodactylid stock that their terminal phalanges would be the next degree further along in our scheme of specialization,—or claw-shaped phalanges. That is exactly what we do find in the two specialized genera to be discussed in the following pages.

2. A NEW SPECIES OF *CERATHYLA* FROM COLOMBIA, WITH REMARKS UPON THE GENUS.

The well preserved collection of Amphibians given to the American Museum by Mr. R. D. O. Johnson contains three specimens of a new species of *Cerathyla* from Colombia. Stejneger (1917, p. 31) has said of this genus: "It is not only one of the rarest genera in collections but its aspect is also very singular, due to the large triangular head with its bony casque posteriorly extended as two pointed horns, and the dermal flaps on snout and eyelids."

The occurrence of a *Cerathyla* in Colombia adds a new genus to the batrachian fauna of that country, and it bridges over a gap in the distribution of the genus. It gives *Cerathyla* a continuous range from Panama to Peru. Boulenger (1903, p. 115) in discussing *Cerathyla bubalus* says that it is "an inhabitant of the Andes of Ecuador, Bolivia, and Peru." *Cerathyla* probably occurs in Bolivia but no specimens have been recorded from there.

Cerathyla johnsoni¹ sp. nov.

Plate XCIII.

Diagnosis.—Dorsal surface distinctly granular; upper eyelid covered with tubercles, one of which on the edge of the eyelid near its mid point is larger than the others; third and fifth toes webbed to the penultimate phalanges; tibio-tarsal articulation reaching between the eye and tip of snout. Distance between the anterior angles of the eyes slightly more than twice as long as the greatest diameter of either eye; interorbital width a little more than twice the distance between the nostrils; distance between nostrils just equal to the distance from the tip of snout, slightly more than half the distance to the orbit. Color above dark reddish brown; sides of body ashy reticulated with pale straw color.

Habitat.—Department of Antioquia, Colombia, S. A.

Type.—No. 1341 A. M. N. H. "Limited area in the precipitous valley of the Santa Rita Creek which is located 14 miles north of the little village of Mesopotamia in the southeastern part of the Department of Antioquia, Republic of Colombia, S. A."; R. D. O. Johnson, collector.

Description of type specimen.—(Adult female with gonads well developed.)—Tongue longer than broad; palatine teeth in two slightly oblique series, well separated from each other in the middle but extending on the sides to the maxillary bones; vomerine series V-shaped, the point directed posteriorly; the extreme anterior vomerine teeth on each side longer than the others; snout with a short, compressed, pointed dermal flap; upper eyelid covered with tubercles, one of which on the edge of the eyelid near its mid point is larger than the others but not much larger than one above the posterior angle of the eye. Distance between nostrils just equal to their distance from tip of snout, slightly more than half the distance from orbit; width of upper eyelid nearly equal to the distance of nostrils from tip of snout; interorbital space one and one half times the width of the upper eyelid, a little more than twice the distance between nostrils; interorbital space slightly concave with distinct ridges; distance between points of the occipital horns a little more than the distance from either point to the nostril on the same side, equal to three times the interorbital width; posterior outline of the casque forming an open V but not a semicircle; tympanum turned nearly backward, its greatest diameter almost equal to the diameter of the orbit; a bony tubercle at angle of the mouth. Fingers long with a rudiment of a web and with distinct disks; first finger longer than the second by a distance equal to the width of its disk. Toes one third webbed: 1st (inner) toe barely webbed, 2nd to base of penultimate phalanx, 3rd to base of penultimate phalanx, 4th to point about half the length of proximal phalanx, 5th to base of penultimate phalanx; third toe slightly shorter than fifth, a single metatarsal tubercle; subarticular tubercles extending upon the metatarsal region as three or four flat warts; a small dermal heel flap; the tibio-tarsal articulation extends forward to nearly the tip of the snout. Neural spines of vertebræ raising the skin into a row of six tubercles on the back; skin on the head involved in cranial ossification, distinctly granular; skin of the back covered with slightly smaller granules; the upper side of the forearms covered with granules of the same size and strewn with a number of large tubercles; the

¹ Named in honor of the naturalist-engineer who made the collection.

outer edge of forearm ornamented with a row of tubercles which are continuous with a seam of skin along the outer edge of the hand; under side of both pairs of appendages smooth; throat covered with granules of the same size as those of the back, and strewn with a number of tubercles of various sizes; belly and sides of body coarsely granular, and provided with a number of thickly-set, low tubercles; a few tubercles on the legs tending to form regular transverse rows as in other species of *Cerathyla*, posterior faces of femurs granular. Color above (in alcohol) a dark reddish brown, head tinged with greyish yellow; six indistinct dark bars on each side of the upper lip; a few indistinct reticulations of the same color about the nostrils and around the tympanum; sides of the body ashy, reticulated with straw color, the large tubercles on the sides of this color; three ashy crossbars extending transversely across the contracted leg and contiguous with the three rows of tubercles. Ground color of throat reddish brown fading into a greenish yellow upon the belly; entire under surface reticulated with dark brown, indistinctly on the throat and definitely on the belly and appendages; the large tubercles of the throat straw color in sharp contrast to the general throat color; under surface of tarsus and metatarsus ashy, the tubercles tinged with white.

Dimensions.

Tip of snout to vent	73.5 mm.
“ “ “ “ nostrils	8
“ “ “ “ anterior rim of orbit	16
“ “ “ “ posterior edge of tympanum	30
“ “ “ “ tip of occipital horn	39.5
Distance between tips of occipital horns	34
“ “ nostrils	4
“ of nostrils from orbit	8.5
Interorbital width	10.5
Width of upper eyelid	6
Greatest width of head	36.5
Forelegs from axilla	47.5
Hindlegs from vent to tip of longest toe	123.5
Tibia	41

Notes on Paratypes.—Two other specimens of the series are males and although smaller than the female they have well developed gonads, associated with small fat bodies. The range of variation exhibited in the three specimens suggests that too great weight has been placed in the past upon the importance of tongue and head form in distinguishing species of *Cerathyla*. The larger of the males has its tongue broader than long and unnotched behind; the smaller longer than broad, but proportionately not so long as that of the female, and notched behind. The larger male is not so well preserved as the other, and this difference of tongue form may be due to shrinkage. The differences in head form may be seen in the illustration (Plate XCIII, Fig. 2). It is evident that some of the measurements given above, such as that from tip of occipital horn to end of snout cannot be of specific value if specimens of different size or sex are compared. There

is probably individual variation in the development of the helmet for the male with the greatest body length has the less curved posterior margin to the casque, but it also has a narrower head than the other and may be a younger individual. The width of the upper eyelid does not vary in proportion to the size of the specimen. It is noteworthy that the tympanum varies little in orientation throughout the series and but slightly in size. The occipital horns are subject to so much variation that their measurements have been left out of the diagnosis while coloration has been given.

The coloration of the sides of the body seems to be a good specific character. In one of the males the coloration is nearly the same as that of the female. Although the color of the other male has faded considerably the dusky and white reticulations of the sides are very distinct. The dark bars on the lips and legs are conspicuous in the males, but there is no constant color difference between the sexes.

Remarks on Related Species.—*Cerathyla johnsoni* is apparently closely allied to *C. bubalus* Espada, but may be distinguished from it by 1. the granular dorsal surface, 2. more extensive webs between the toes, 3. longer snout and 4. different coloration. There may be a constant difference in the head form and leg length of specimens of the same sex. The interorbital width is probably wider in *C. johnsoni* than in *C. bubalus*. The difference in the webbing of the toes of these species is not great but very distinct if the figures of Espada (1875, Pl. 5, fig. 3) and Boulenger (1903, text fig. 8) may be relied upon. In the third and fifth toes of *C. bubalus* the web extends only two thirds the length of the proximal phalanx while in *C. johnsoni* it extends to the base of the penultimate phalanx. In the former species the fourth toe is webbed only to the base of the proximal phalanx while in the latter the web extends half the length of the same phalanx.

Cerathyla johnsoni needs comparison with no other species of *Cerathyla*. Future work may show that the great range of variation in this species is found in other species of *Cerathyla*. In that case some of the species described from Ecuador must be considered synonymous with other forms from the same region. The extreme range of variation in a species of *Cerathyla* is perhaps shown in the differences between the type of *C. panamensis* and the young one associated with it. Through the kindness of Dr. Stejneger I have recently examined these specimens. The tympanum of the young one is laterally not half posteriorly directed. The helmet is very small. The disks and snout flap are proportionately larger than in the adult. The under side is brown, not whitish as in the adult.

Habitat.—We have owed most of our knowledge of the habitat which *Cerathyla* frequents to the work of Espada (1871, p. 64), but even he has only informed us that the type specimens of several of his species were

taken in palm trees or in the woods. We know from the works of travelers that villages like Archidona and Sumaco, the type localities of these species, are surrounded by luxuriant vegetation. But we have no exact information as to the habitat of *Cerathyla*. It was therefore of great interest to me to receive from Mr. R. D. O. Johnson a letter in which he graphically describes the region in which he collected the "arrow-headed frogs" described above. I quote directly from his letter:

"The temperature of this region is cool for the tropics, varying during the day from 58 to 68 degrees F. This might be called the second wet zone, the zones being of different elevations. The elevation of this region lay between 7500 and 8000 ft. above sea level. On account of the coolness and great amount of moisture ferns and mosses flourish. The surface of the ground is covered with a mass of decaying leaves, mosses, and ferns, the mass knitted together with a great abundance of fine roots. This covering is called 'capote' by the natives. It is in eternal shade and is soaked with water at all times. This 'capote' not only covers the ground but extends out on the lower limbs of the trees of the dense forest. Not infrequently when cutting and mowing one's tedious way along the side of a stream, one's foot may break through the 'capote' and through the hole thus made the turbulent stream is visible. It is in this 'capote' that the arrow headed frog makes his home.

"...The rain gauge records that were kept during my stay in the region of the Santa Rita showed a monthly precipitation of from 21 to 36 inches, as I remember now."

The stomachs of two of the specimens contained food. In the stomach of one of the males was a seed capsule 14 mm. long, nearly one half as long as the body cavity. This seed capsule I have not yet succeeded in having identified. It is very hard on the outside but the inside is pulpy with a number of seed arranged around an axial core. The stomach of the female contained a vegetable pulp similar to that inside of the seed capsule. No remains of animal food were present in either stomach.

Phylogenetic Position of Cerathyla.—The mere fact that *Cerathyla* is placed among the Hemiphractidæ chiefly because of the odontoids on the lower jaw tells us little about its phylogenetic position among the Salientia. The modern tendency is to regard as artificial associations several of the genera based upon the presence or absence of teeth. Some of the higher groups may be artificial. The family Dendrophryniscidæ is certainly an unnatural group of two very unlike genera: *Batrachophrynus* being closely related to *Telmatobius* and *Dendrophryniscus* to some genus of burrowing toads. At first glance *Cerathyla* appears to be an over-specialized Hyliid which has developed teeth on all available bones. It has claw-shaped

terminal phalanges, and Stejneger (1917, p. 33) has attributed dilated sacral diapophyses to one of the species.

If *Cerathyla* is an over-specialized genus it is not because of an over-favorable environment. Anyone who has been in such a region as Mr. Johnson has described must have been impressed by the paucity of vertebrate life. There are a few birds such as Trogons and Hummers which are adapted to this habitat, but the vast majority of the vertebrates occur only along the edge or upon the roof of the jungle.

Our knowledge of the internal structure of *Cerathyla* has been confined almost entirely to the two or three sketches of Espada (1875, pl. 4). A few notes on some of the structures of *C. johnsoni* may be of interest from a systematic point of view. There is practically no variation in the sexes. The figures were made from the type specimen and from the largest male.

The pectoral girdle is very peculiar. Although no omosternum is represented in Espada's figure of the sternal apparatus which he considers typical for the genus, the structure is present but small and weak. There are no muscles attached to it. The most extraordinary feature of the pectoral girdle is the long anterior processes of each of the epicoracoid cartilages. These fit one over the other. They are very firm and each forms the attachment for two well developed muscles. Both muscles are attached at their distal end to the humerus, the most posterior muscle much nearer the glenoid cavity than the other. Not all

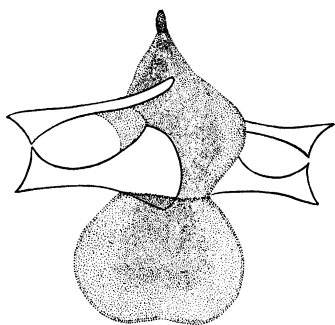


Fig. 2. *Cerathyla johnsoni*, ventral view of shoulder girdle.

of the proximal end of the posterior muscle is attached to the epicoracoid process, about one half of it is attached to the epicoracoid cartilage in the region of the clavicle. While the epicoracoid cartilage is wide it is not so wide as represented in Espada's figure. The pectoral muscles cover the greater part of the epicoracoids and separate them from each other. A few strands of tissue connect the two halves of the girdle at the extreme anterior end of the epicoracoids and at a few points on their edges, but this attachment is elastic and allows a maximum amount of free movement. The ventral half of the girdle may be readily lifted from the dorsal.

The sacral diapophyses, as shown in the figure, are scarcely dilated but they are slightly flattened. The ilia project normally somewhat beyond the diapophyses. The impression of the tissue connecting ilia and diapophyses is made upon the skin, and without dissection one would think

that the sacral diapophyses were strongly dilated. The vertebræ are procœlous, unlike those of *Hemiphractus*. The cœcyx articulates upon two condyles. The terminal phalanges are not typically claw-shaped but are nearly straight and flattened at the base.

Here in *Cerathyla*, a most specialized batrachian, we find a non-dilated terminal phalanx. It is to be expected after the change in phalanx form which we have seen in *Leptodactylus lineatus* that the non-dilated phalanx would be associated with specialization. There are many species of *Eleutherodactylus* having much larger digital pads than *Cerathyla*, and yet retaining the T-shaped terminal phalanges. Phalanx form is probably in this case not due to digital form. The sacral diapophyses and vertebræ are characteristic of the Leptodactylids; the pectoral girdle has some features in common with that of *Hemiphractus*. It is most reasonable to assume that *Cerathyla* owes the sum-total of its internal characters not to any Hyloid stock but rather to Leptodactylid ancestry. If this is a correct assumption, it is interesting that during all the differentiation of head form and phalanx form the sacral diapophyses have remained nearly cylindrical.

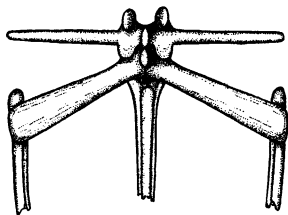


Fig. 3. *Cerathyla johnsoni*, dorsal view of sacral vertebra *in situ*.

3. THE STATUS OF *HYLA FUHRMANNI* PERACCA, WITH REMARKS UPON THE HOMOLOGUE OF ITS LARVAL STRUCTURES.

Plate XCIV.

Hyla fuhrmanni has been known to science only a very short time. Peracca (1914, p. 108) made the single specimen which Fuhrmann and Mayor brought back with them from Colombia the type of the species. This specimen was a female carrying eggs upon its back. Ruthven (1915) secured in the Santa Marta Mountains two more specimens each with eggs upon the back. The broods were in different stages of development and Ruthven made an excellent study of his material. The American Museum has received from Mr. R. D. O. Johnson a series of four specimens of *Hyla fuhrmanni* collected near the type locality. One of these specimens is an adult female carrying eggs upon the back, another is an adult female without eggs, while the remaining two are adult males. These are the first males of the species which have ever been recorded.

The males are much smaller than the females, measuring 51 millimeters

from snout to vent against 67.5 millimeters. They are nevertheless sexually mature. The gonads are well developed, but the fat bodies of one specimen are very much smaller than those of the other. The female without eggs on its back has well developed gonads, the ova being conspicuous although not free in the coelom. There do not seem to be any constant color differences between the sexes, and the relative proportions are about the same.

The habitat of *Hyla fuhrmanni* is evidently the soaking forests which cling to the steep sides of many Colombian ravines. Ruthven, Fuhrmann, Mayor, and Johnson found their specimens under somewhat similar conditions. Ruthven (1915, p. 2) states that both of his specimens were found "on the steep bank of a mountain stream at an altitude of 4500 feet on the mountain of San Lorenzo." Fuhrmann and Mayor (1914, p. 50) show us in their several photographs of the environs of Guaca the kind of habitat in which the type specimen was taken. Johnson found his specimens associated with *Cerathyla* in the Santa Rita Valley. A description of this region has been given above, and some of Mr. Johnson's photographs are reproduced on Plates XCV and XCVI.

One of the adult females contained in its stomach one cockroach, one spider, and two chilopods. Mr. Roy W. Miner has kindly identified the chilopods as *Otosignus scabricaudus* (Humbert and Saussure). Although the bite of chilopods is more or less poisonous, they are sometimes eaten by chickens. It is to be supposed that a tree-toad would be much more susceptible to the poison of a chilopod, and yet this specimen had eaten two. The stomach of one of the males contained fragments of grasshopper legs and wings.

The peculiar transverse vomerine teeth possessed by *Hyla fuhrmanni*, the short stubby head and large eyes impressed me as unlike those of any *Hyla* with which I was familiar. A dissection of one male and one female showed conclusively that this species should no longer be referred to the genus *Hyla*. The sacral diapophyses instead of being dilated are cylindrical. The pectoral girdle is arciferous but the sternum is much reduced. Claw-shaped phalanges are present, but the vomerine teeth are peculiar and apparently do not fall within the range of variation exhibited by the known species of *Hyla*.

The species must be referred to the genus *Hyloscirtus*. Peters (1882, p. 107) described the genus *Hylonomus*, but since that name was preoccupied he changed the name to *Hyloscirtus* (1882a, p. 127). The genus is characterized in part by having sacral diapophyses non-dilated, terminal phalanges with a "simple point." Peters summed up his diagnosis with the remark: (trans.) "next to *Hylodes*, it is distinguished from this genus through its well developed webs." Peters doubtlessly intended *Hyl-*

scirtus to be a new genus of Leptodactylidæ for he compared it with *Hylodes*, but he does not comment upon the family relationship of the genus.

Nothing more appears in literature in regard to these peculiar tree-toads until Ruthven (1916, No. 33) described a new genus and species of Leptodactylids from the Santa Marta Mountains of Colombia. This genus, *Cryptobatrachus*, is synonymous with *Hyloscirtus* for it has the same cylindrical diapophyses and non-dilated terminal phalanges. The species are apparently closely related. The presence of a tympanum in *Cryptobatrachus boulengeri* and the absence in *Hyloscirtus bogotensis* is a character

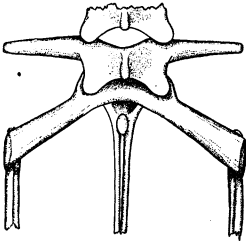


Fig 4.

Fig. 4. *Hyloscirtus fuhrmanni*, dorsal view of sacral vertebra in situ.

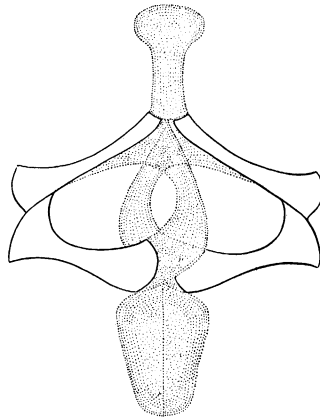


Fig 5.

Fig. 5. *Hyloscirtus fuhrmanni*, ventral view of shoulder girdle.

of hardly specific value in many genera of mountain frogs, *e. g.*, *Telmatobius*.

The three species of *Hyloscirtus* may be distinguished from one another by the following key.

- a. Tympanum hidden. *H. bogotensis* Peters.
- a¹. Tympanum distinct.
 - b. Interorbital space much broader than upper eyelid. *H. boulengeri* (Ruthven).
 - b¹. Interorbital space less than width of upper eyelid. *H. fuhrmanni* (Peracca).

Hyloscirtus fuhrmanni has several features in common with the Hylids, especially with species of the genus *Hyla*. There is a constant difference in size between the sexes,—a difference such as that in *Hyla baudinii*. The terminal phalanges of *H. fuhrmanni*, as well as those of *H. boulengeri* are claw-shaped, while the same condition probably exists in *H. bogotensis*. Several species of *Hyla* carry eggs attached by their membranes to the back of the nurse. The pectoral girdle is *Hyla*-like but the sternum is reduced even more than that of *H. albomarginata*.

Ruthven referred *Cryptobatrachus* without comment to the Leptodactylidæ. Peters pointed out the relationship of *Hyloscirtus* to *Eleutherodactylus*. There are several reasons why *Hyloscirtus* should be referred to the Leptodactylidæ. In that family the range of generic variation is greater than in the Hylidæ. The sacral diapophyses of the Leptodactylids are cylindrical or only slightly dilated. A wide webbing between the toes exists in several species of *Hylodes*. Boulenger (1898, p. 119) commenting upon the status of *Hylodes anomalous* says:

"This species differs so much from the other members of the genus *Hylodes* in the extensive web between the toes that it might be made the type of a new genus. I am, however, unwilling to adopt such a course at present in view of the existence of the species *H. palmatus* and *H. raniformis* which afford a link between this and the more typical forms, and render the character of the development of the web between the toes one of very doubtful value in this group, a conclusion which is further strengthened by a study of several other genera of tailless Batrachians."

Hyloscirtus possesses non-dilated phalanges,—claw-shaped in at least two of the species. Is that not what we should expect in a highly specialized Leptodactylid if we hold to our theory of phalanx evolution stated above? *Hyloscirtus* is a genus confined to the forested ravines of Colombia. This environment has developed several giant species of *Eleutherodactylus* as well as a *Cerathyla*. It is evidently an environment which fosters overdevelopment and specialization. *Hyloscirtus* has the cylindrical sacral diapophyses of the Leptodactylids but the claw-shaped terminal phalanges of the Hylids. We have already concluded that in *Cerathyla* the form of the sacral diapophyses was of more diagnostic value than the shape of the terminal phalanges. To be consistent we must consider *Hyloscirtus* a highly specialized Leptodactylid genus.

When I received the specimens of *H. fuhrmanni* only one egg was in place upon the back of the female. But there were twenty-six shallow hollows in the dorsal integument of the specimen. Several eggs were free in the container. All of the eggs proved to be in a late gastrula stage.

The embryo in this stage is modeled very low upon the large yolk, suggesting a ganoid type of egg. In most specimens the neural tube is closed over and the embryo is marked off from the yolk by a slight furrow on either side. The embryo is banjo shaped. The neural fold ends in a pair of optic lobes resting upon the large circular head piece which is also separated from the yolk by a slight furrow. The blastopore is closed. A curved furrow extends posteriorly from the embryo, probably marking the gastrula lips. The embryo is pigmented with black, which places it in strong contrast with the yellowish unpigmented yolk. In *Hyloscirtus*

fuhrmanni the embryo is much smaller in comparison with the yolk than in *Phyllomedusa hypochondrialis* as described by Budgett (1899, Pl. 30). This condition is to be expected since both Peracca and Ruthven have shown that the young undergo their entire metamorphosis while enclosed within the egg membranes upon the nurse's back.

That the young receive all of their nutriment from the yolk is very probable. Not only do the several egg membranes separate the young from the nurse, but the dorsal integument is in no way differentiated. The squamous epithelial cells and stoma cells are similar to those on other parts of the integument. Ruthven and Peracca have both shown that the eggs are "glued to the nurse frog by a gelatinous substance." The substance is histologically undifferentiated and apparently is part of the egg membranes. Several of the eggs which had been torn from the nurse had a thin layer of epithelial cells attached to their tertiary membranes. This shows how firmly the eggs are attached to the integument.

The observations made by Ruthven upon the later embryonic life of *Hyloscirtus fuhrmanni* are of especial interest from a phylogenetic point of view. He has shown that the young are provided while in the egg membranes with special cup-shaped gills. These are of course homologous with the bell-shaped gills of *Gastrotheca oviferum* described by Weinland (1854, p. 457) and of *G. cornutum* considered by Boulenger (1898, p. 124, pl. 18). Similar organs are found in the larvæ of *G. marsupiatum* and *G. plumbeum* (see Brandes and Schoenichen, 1901, p. 444). *Cerathyla bubalus* and *Hyloscirtus fuhrmanni* have no dorsal pouch and yet they possess these peculiar bell-shaped gills. Ruthven has figured the gills *in situ* and has shown that they cover the embryo like an allantois. It is certain that these gills are breathing organs but it is not so certain why similar organs have developed in those species which take oxygen from the air and those which apparently absorb it from the body of the mother.

There are other species of tree-toads which carry the eggs upon their back like *Hyloscirtus fuhrmanni*. Their larval histories have not been studied so fully as in the case of *Gastrotheca oviferum*. Goeldi (1895, p. 95) worked out the life history of *Hyla goeldii* and compared its larval stages with those of *Hylodes martinicensis*. In this he implied that the development was direct and that no gills were found. But Boulenger (1904, p. 106) in describing *Hyla evansi* states:

"The unique specimen, a female, carries its eggs on the back, fitting into shallow hexagonal impressions in the skin; these eggs, 22 in number, measure 8 or 9 millimeters in diameter and contain tailed larvæ with rudimentary limbs, and with allantois-like, membranous, respiratory organs. In this it agrees with *Hyla goeldii* Blgr., to which it is nearly related and with *Ceratothyla bubalus* Esp."

One of the more recently described egg-carrying tree-toads, *Hyla ohausi* Wandolleck, is unique in having a superabundance of "jelly" which not only glues the eggs to the back of the female nurse but holds the eggs together in a single mass. Wandolleck (1907, p. 15) comments briefly upon the larval history comparing it with that of *Hyla goeldii*, but he says nothing about the form of gills.

Stejneger has very recently described from Panama a new *Cerathyla* which had young attached to the back previous to capture. He says (1917, p. 33) in part:

"With the adult specimen described above, there is a very young one only 17 mm. long but fully developed. It has evidently just been severed from its mother, as two strings, issuing on either side from the chest near the shoulder look as if they had just been ruptured. When received, the mother specimen had the back covered with a loose flap of skin which came off easily when gently lifted by the forceps. On the exposed side of this flap there are about 12 pairs of whitish cords, apparently freshly ruptured and similar to the ones on the chest of the young one, which indicate that at least so many young ones had been attached to the mother's back just previous to capture. This condition fully bears out the account given by Boulenger of the closely related *Cerathyla bubalus* carrying its eggs on the back.... The young ones evidently undergo their entire development while attached to the mother, after which the skin of her back, to which the eggs adhered sloughs off. On the piece of skin shed there are distinct impressions of the outlines of the eggs, apparently at least 14. This would indicate a larger number of eggs than in *C. bubalus*, in the specimen of which recorded by Boulenger there were only 9."

Dr. Stejneger has very kindly not only allowed me to study the type specimen and young one, but he has given me to section a piece of the skin which he lifted from the adult. For staining some of the serial sections made from this piece I used Hansen's Hæmatoxylin and for others Delafield's. The counterstain was eosin. In Figs. 6 and 7 there are represented different parts of a single section made through the sheet of tissue at a point where the cord joined it.

The sections show conclusively that this dorsal sheet of tissue which looks very much like skin is really a mass of egg membranes, very much shriveled and covered with dirt. Each hollow in the sheet contains a single gill homologous no doubt to those of the tree-toads already discussed. The gills lie in their normal positions, separated from the ventral surface of the sheet by several thick layers of structureless substance,—the egg membranes. Each gill extends only the length of one hollow. The outer edge of a gill is shown in Fig. 7. The gelatinous layers are not continuous between

hollows, although the basal sheet is very regular. The gill consists largely of capillaries. Each gill has two cords associated with it. The capillaries of the gills are supplied usually by four blood vessels from each cord, but I have not examined enough material to state if this number is constant for every gill cord. The blood vessels of each cord apparently anastomose in the gill with those of the other. The cords contain striated muscle fibers of

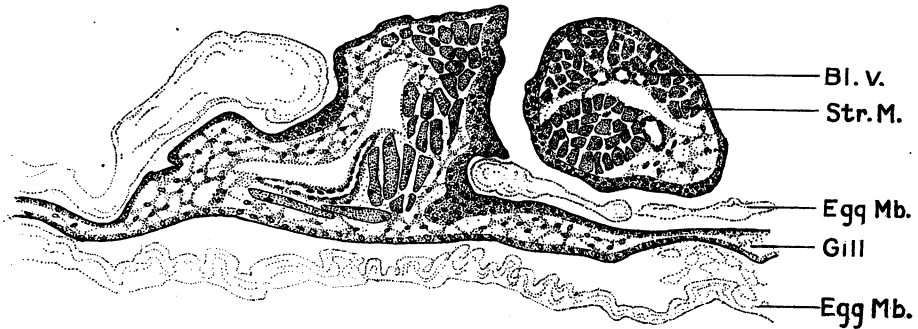


Fig. 6. $\frac{106}{1}$.

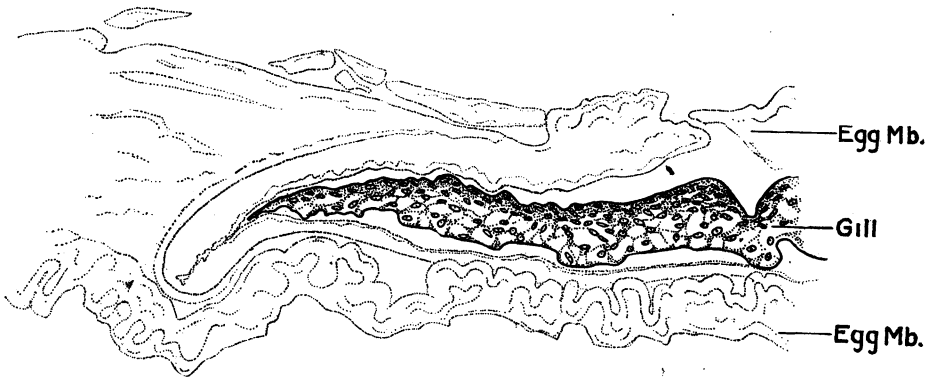


Fig. 7. $\frac{184}{1}$.

Figs. 6 and 7. Sections through dorsal cover of the type specimen of *Cerathyla panamensis* Stejneger.

a simple type having only a few large nuclei to each fiber. As shown in Fig. 7, the muscle fibers crowd the blood vessels into the center of the cords. The muscle fibers do not extend deeply into the gill, but end abruptly near the point of junction of the cord with the gill. The lumen in the cords may be due to the poor fixation of the tissue. The lumen between the gill and egg membranes is often filled with coagulated lymph containing white

blood corpuscles. For the sake of clearness this lymph is not represented in the drawings.

Each of the two strings issuing from the neck of the young one is really a double string twisted in the fashion of a curtain cord. The two components of each string are widely separated at their point of fusion with the gill, and form the pair of cords described above. Stejneger has pointed out that there were at least 12 pairs of cords issuing from the sheet of tissue. Corresponding with these 12 pairs of cords, there could have been only six young ones attached to the mother. Each hollow does not mark the position of an egg but rather of half an egg. It is the depression formed by the gill after it has collapsed with the egg membranes.

It was impossible to float the gills in water to study their exact shape. Probably the whole sheet of tissue is an abnormal structure,—a mass of egg membranes and their associated gills very much distorted by unnatural causes. In no species of tree-toad carrying eggs on the back has it been shown that the gill cords are ruptured to free the young ones from the egg membrane. (The work of Brandes and Schoenichen, 1901, is diagrammatic and untrustworthy). There is no information available as to the treatment which the type specimen of *Cerathyla panamensis* received just after capture.

The serial sections of the gills have brought out the close similarity between the larval structures in *Cerathyla panamensis* and *Gastrotheca oviferum*. Weinland (1854, pp. 451–463) has studied the anatomy of the larvæ of the latter species. The gills in *G. oviferum* are cup-shaped and are connected with the neck of the young one on each side by two cords which as in *C. panamensis* contain striated muscle fibers. Weinland suggests that the striated muscle of these organs may be functional only in later larval life. By analogy with what occurs in *Hyloscirtus fuhrmanni* it seems more probable that these muscles are used for pulling the huge “bell gills” into the gill chamber just after the young tree toad has escaped from the egg membranes. It is indeed hard to imagine what function the muscle tissue could have during the embryonic life of the individual. In each gill cord of *G. oviferum* there are only two blood vessels, while in *C. panamensis* there are apparently four. Whether this is a constant difference has not been determined. In both species there occurs the same anastomosing capillaries, the same lymph space separating the gills from the egg membranes, and probably some of the egg membranes from one another. It is evident that no different larval structures are required for taking oxygen from the air as in the case of *Cerathyla*, or for absorbing it from the body of the parent as in *Gastrotheca*.

In all of the various species of tree-toads which carry eggs on the back those larvæ which have been critically studied have been found to possess

cup-shaped gills. Some species of *Gastrotheca* complete their larval development in the water. This does not destroy the similarity of the early larval structures in these species. If Boulenger's statement is correct in regard to the gills of *Hyla goeldii*, the one doubtful case is eliminated and we may conclude that direct larval development is not associated in tree-toads with the type of nursing habit under consideration. It is therefore not probable that the mode of development exhibited by *Eleutherodactylus martinicensis* is transitional to that of *Hyla goeldii*.

Boulenger (1895, p. 209) has shown that the skin on the back of *H. goeldii* "is expanded into a feebly reverted fold which borders and supports the egg mass on the sides, thus suggesting an incipient stage of the dorsal pouch of the allied genus *Nototrema*." Boettger (1893, p. 41) considered *Gastrotheca pygmaeum* to have developed its dorsal pouch from just such inverted folds. On the other hand Andersson (1911, p. 5) maintains that the pouch of *Gastrotheca* was formed by an invagination on the posterior end of the back. It would be vain to speculate on that problem now; there is nothing in the ontogeny of *Hyloscirtus fuhrmanni* which suggests how the invagination might take place. In no species of non-pouched forms has the dorsal integument been found to be specialized. Boulenger (1903, p. 116) says of *C. bubalus*:

"The eggs in this *Cerathyla* simply stick to the back, leaving shallow hexagonal impressions on the much thinned dorsal skin, through which the neural processes project to such an extent as to leave marks on the vitelline sacks with which they are in contact."

But since the neural processes project in a similar manner in both sexes of *C. johnsoni* although the specimens were apparently well preserved, we may conclude in default of histological study that the skin of Boulenger's specimen of *C. bubalus* was probably normal.

What is the significance of the fact that in all tree-toads carrying eggs on the back the larval structures developed are practically the same? These structures are very different from those of *Pipa*, which, as is well known, carries the eggs on the back. In this discussion we have limited ourselves to the genera *Hyla*, *Gastrotheca*, *Amphignathodon*, *Cerathyla*, and *Hyloscirtus*. The first three of these genera undoubtedly came from a Hylid stock, but it has been the purpose of this paper to show that the other two genera arose from a very different stock, or perhaps stocks. Does this identical embryonic life show that our system of classification is inadequate and that after all the five genera form a natural group?

If we consider the breeding and nursing habits in other batrachians, we shall find cropping out similar larval histories in entirely unrelated groups (see Sampson, 1900). *Chiromantis rufescens* and *Phyllomedusa iheringii*

both deposit their eggs on trees in nests made of leaves. *Dendrobates braccatus* and several species of *Prostherapis* are nearly alike in form and color. It is well known that they carry their young while in the tadpole stage upon their backs. Under adverse conditions many different groups of batrachians have abbreviated larval histories. *Eleutherodactylus martiniensis* and *Rana opisthodon* have direct development. *Eleutherodactylus petropolitanus* and *Hyla abbreviata* are said to have larvæ adapted to living among moist rocks. These tadpoles are provided with a ventral adhesive disk and are the color of stone. *Rhacophorus schlegeli* and *Leptodactylus mystacenus* deposit their eggs in damp holes in the ground. The later histories of the larvæ are somewhat the same. In *Xenopus laevis* and *Pipa americana*, although only distantly related, the tadpoles agree in having fore limbs free from the operculum and in having two spiraculæ. This similarity may be due to the aquatic habits of the two species. Few of the life histories of the mentioned batrachians have been intensively studied, and we are not able to draw the close comparison which we can in the case of *Gastrotheca* and *Cerathyla*.

If *Cerathyla* and *Hyloscirtus* are not related to the Hylids, it is evident that the bell-shaped gills and related larval organs of these batrachians which carry their eggs on the back, have no real genetic relationship but have developed independently in different groups. We do not know whether this convergent evolution has been brought about by external or internal factors. Is the bell-gilled larva a form moulded in different groups by some potent factor in the environment, or is it the one end of several distinct lines of internal specialization? This question cannot be answered satisfactorily. We can only conclude that *Hyloscirtus*, *Cerathyla*, and *Gastrotheca* are the ends of three lines of specialization and in spite of this fact they have developed similar larval breathing organs. In the last two genera, although the eggs of one are exposed to the air, and of the other are covered by a fold of skin, these larval structures are nearly identical.

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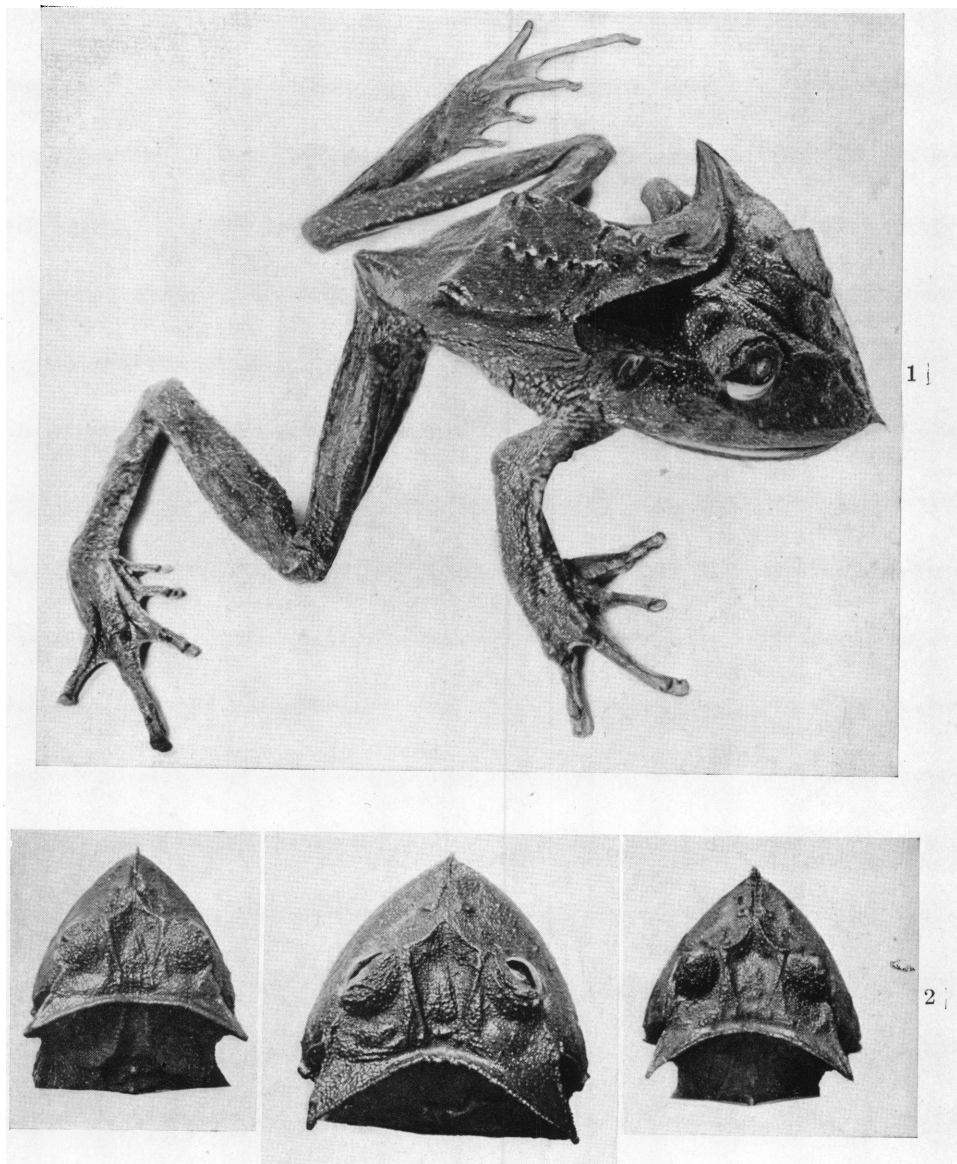


Fig. 1. *Cerathyla johnsoni* sp. nov. Type, A. M. N. H. No. 1341.

Fig. 2. *Cerathyla johnsoni* sp. nov. Type and paratypes, showing differences in head form. A. M. N. H. Nos. 1341-1343.



HYLOSCIRTUS FUHRMANNI (*Peracca*). A. M. N. H. No. 1337.

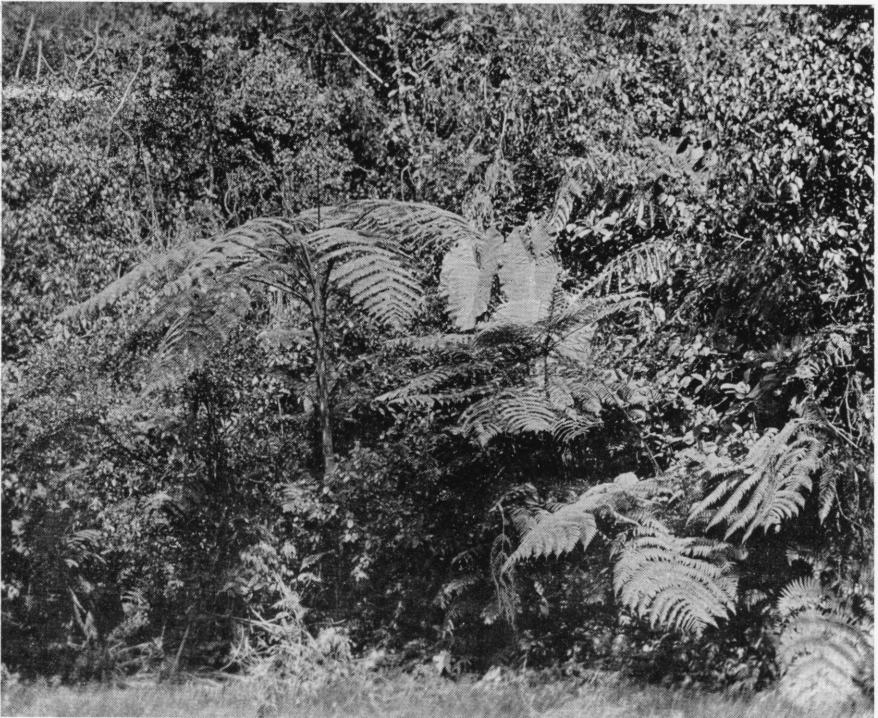
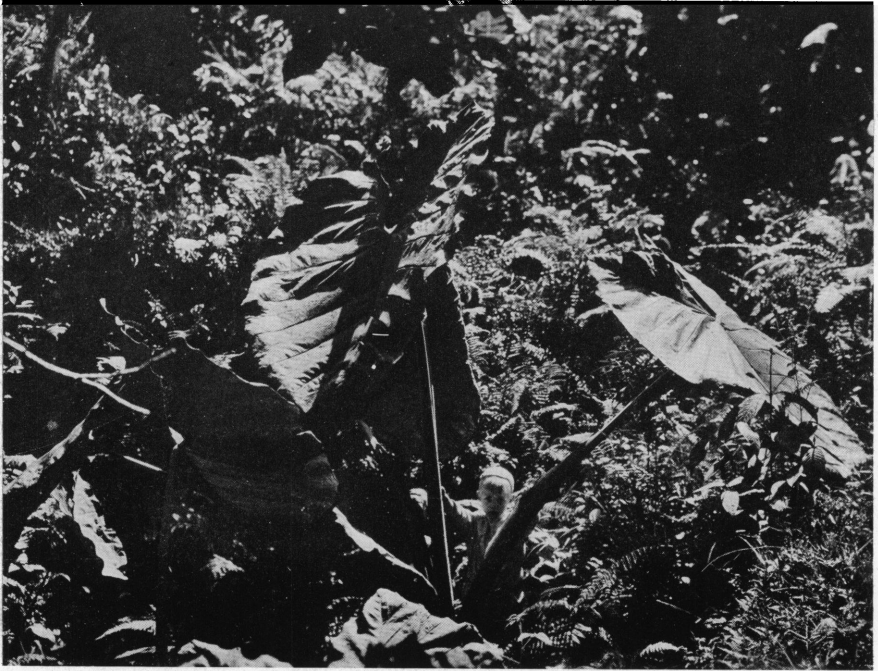


Fig. 1. Luxuriant vegetation in the Santa Rita Valley, the type locality of *Cerathyla johnsoni* sp. nov. Photographed by R. D. O. Johnson.

Fig. 2. The jungle viewed from the Santa Rita Creek, near spot where one specimen of *Cerathyla johnsoni* sp. nov. was collected. Photographed by R. D. O. Johnson.

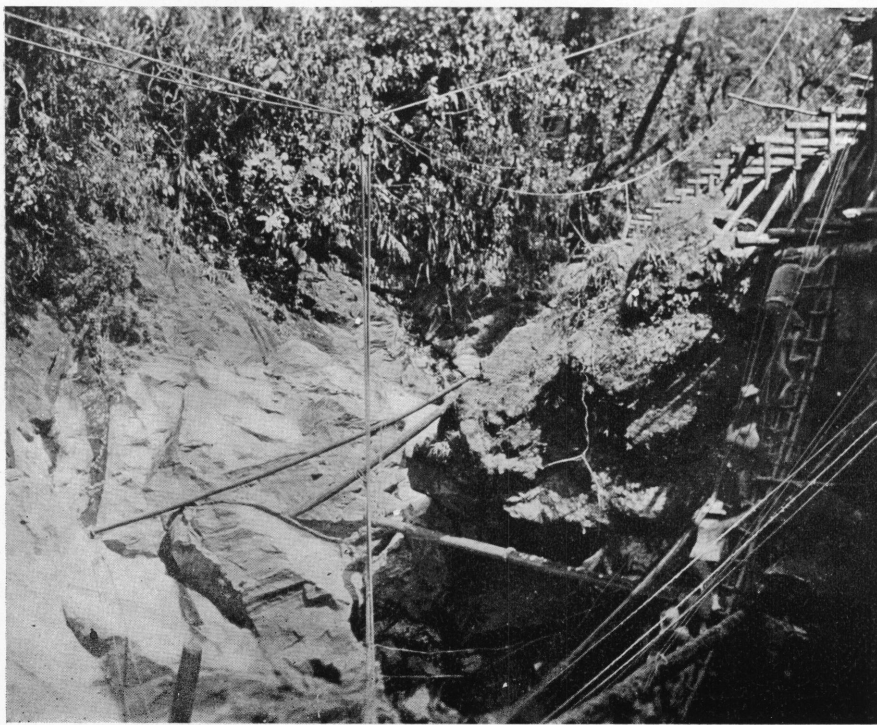


Fig. 1. Santa Rita Creek, showing the habitat of *Hyloscirtus fuhrmanni* (Peracca). Photographed by R. D. O. Johnson.

Fig. 2. Bed of Santa Rita Creek. *Hyloscirtus fuhrmanni* (Peracca) was taken in the "capote" shown in the upper left hand corner of the picture. Photographed by R. D. O. Johnson.

