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SOME PANAMANIAN FROGS¹

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While Mr. C. B. Duryea and I were collecting for the Museum of Comparative Zoology in Panamá and Costa Rica in the summer of 1923 we were so fortunate as to observe the eggs and tadpoles of two species of Hyla, and to collect and make observations on the habits of four species of Phyllobates, one of them new. The latter was also one of the species collected by Mr. and Mrs. Gaige for the University of Michigan in Panamá in the spring of 1923. They worked from the Pacific side and we from the Atlantic, but we both collected in the cloud forest at about 4,500 feet altitude near the volcano of Chiriqui and I am under obligations to them for their courtesy in allowing me to examine their material and to describe the form. I have taken this opportunity to examine all available specimens of Phyllobates from Panamá and Costa Rica. No species of this genus from Central America was known to Barbour and Noble when they revised it (Bull. Mus. Comp. Zool., LXIII, 8, 1920).

¹ Contributions from the Department of Zoology, Smith College, No. 120.

Unfortunately, Mr. Duryea and I did not discriminate between P. talamancae and P. latinasus while in the field, but the fact remains that contrary to the general experience of herpetologists all the frog calls we heard were so nearly identical that we could not certainly tell which of several forms was calling, and this identity of calls included Hyla albomarginata, Hyla uranochroa, Phyllobates latinasus and Phyllobates talamancae at one locality, and the new form from the nearby cloud forest. The call of these five forms was a rather metallic "cheep," a single, brief note, repeated at intervals. There were unquestionably slight differences, appreciable when one watched a calling specimen. Thus Hyla uranochroa had a less metallic note than Hyla albomarginata and both were louder than the Phyllobates, yet the general impression was much the same.

The two Hylas and two of the Phyllobates were observed most carefully at a place called La Loma where we camped for a little over a week. This was in rain forest near the trail from Chiriquicito to Boquete, and at an altitude of about 2,000 feet. Here, in a little brook, we found four sorts of tadpoles. Two of these we traced to two Hylas which we had previously caught; the other two later proved to be Phyllobates. Two lots of eggs were found, and as the Phyllobates males carried their tadpoles to the stream, it seems fair to assume that the eggs were those of the two Hylids. The four tadpoles from La Loma were all traced to their respective adults by complete series of transforming young.

Hyla uranochroa Cope

Eggs assumed to be those of this species were found attached to a leaf overhanging the stream. The eggs when found contained well developed tadpoles. This form of egglaying has been reported for Agalychnis and for Phyllomedusa. Hyla uranochroa has much the appearance of an Agalychnis, as it is uniform green, with very prominent red eyes. The technical characters are those of Hyla. The species was never seen on the ground or in the water, and the calling individuals were always on leaves; even the transforming speci-

mens were caught in such situations. It would seem that *Hyla* uranochroa might well be an approach towards the two more specialized genera in eye color and in habits, while in form of pupil and character of hand still a technical Hyla.

The tadpoles of this species were the first to be assigned correctly to their adults, on account of the red eyes, which were a prominent feature of both stages. They were very common in the stream and possessed well developed power of suction. We often lifted them from the water clinging to our hands in this way. They were occasionally observed elinging to rocks or to the surface film.

Diagnostic characters of mature tadpole: Spiracle sinistral, anus dextral, eyes visible from ventral surface, upper fin crest not extending to anus, spiracle halfway between snout and base of hind limb, labial teeth 2/3, uniform brown, eyes red, greatest length 45 mm., smallest seen 16 mm.

Description of mature tadpole: Length of body contained three times in total length; width of body 1.75 times in its own length; nostril nearer to eye than to snout; eye dorso-lateral, visible from ventral surface, equidistant from snout and from spiracle; distance between nostrils = interorbital width = width of mouth; spiracle sinistral, equidistant from snout and from base of hind legs; anus dextral; depth of the muscular portion of tail at base 1.2 in greatest depth of tail.

Upper labium with two equal uninterrupted rows of teeth; lower labium with three continuous rows, inner two equal, outer about ½ as long as median; a complete lip around the mouth.

General color, uniform brown; crests of tail unpigmented save for a few spots on the dorsal portion. Total length 43 mm., tail 30 mm.

Hyla albomarginata Spix

A foamy mass of eggs was found under a rock in the small stream. As this was the situation from which *Hyla albomarginata* was calling, it is quite possible, by association and by elimination of the other three species whose tadpoles inhabited the stream, that these were the eggs of this animal.

The dark brownish green adults were all taken under rocks in the water, whence they were calling. One transforming specimen was on a leaf. This was bright green with tiny dark dots, and a white line from the eye over the tympanum.

Diagnostic characters of mature tadpole: Spiracle sinistral, anus dextral, eye not visible from ventral surface, upper fin crest not extending beyond hind curve of body, distance from spiracle to base of hind limb contained 1.5 times in its distance from the snout, labial teeth (6-7/8), brown above, light cross bars on dorsum of tail, crests unpigmented, greatest length of tadpole 60 mm.

Description of mature tadpole: Length of body contained 2.9 times in total length; width of body 1.5 in its own length; nostril nearer to eye than to snout; eye dorsal, nearer to snout than to spiracle; distance between nostrils greater than interorbital width, less than width of mouth; spiracle sinistral, its distance from the base of the hind limb contained 1.5 times in its distance from the snout; anus dextral; depth of the muscular part of tail at base contained 1.5 times in greatest depth of tail. Upper labium with 7 equal rows of teeth, the outer three somewhat fragmented, the innermost narrowly broken in the middle: lower labium with eight rows of teeth, of nearly equal length, the outer four somewhat fragmented; a complete circlet of papillae around mouth; in repose this contracts into a triangle, apex forwards, lateral angles curved in and back. The general color was brown, with three lighter reddish brown cross bars on the muscular part of the tail, the crests unpigmented, and the belly pale; total length 53 mm., head and body 18 mm., tail 35 mm.

These tadpoles were most frequently seen in numbers clinging to the rocks over which a swift current of water was streaming. They had by far the best developed sucking disks of the four forms in the stream.

Phyllobates

Barbour and I (Proc. Biol. Soc. Washington, 34, p. 159, 1921) redescribed *Phyllobates talamancae* (Cope) from two specimens from Santa Cecilia, Costa Rica, and described

Phyllobates beatriciae as new with a single specimen from Zent, Costa Rica. On the basis of more extensive material and re-examination of these specimens the opinions we then expressed require modification.

Phyllobates beatriciae, of which five additional specimens were taken at Almirante, Panamá, and four in the Talamanca Valley, Costa Rica, by Duryea and myself, seems to be identical with the frog described as Dendrobates lugubris by Schmidt (Denksch. Acad. Wien, 14, 1858, p. 250, pl. 2, fig. In the specimen we described the yellow dorso-lateral lines had disappeared, and so had the line from the arm to under the eye. These are quite apparent in the series at hand. Schmidt's specimens are well described and figured, and while his are said to have come from the cloud forest at 5,000-7,000 feet, and ours all came from low rain forest, there seems to be no doubt that the two are identical and the animal must be known as Phyllobates lugubris (Schmidt). We did not take it at La Loma nor in the cloud forest. It was observed to have the tadpole-carrying habit. Its very different coloration, dense black with narrow yellow lines, precludes any confusion with the other forms.

The redescription of *Phyllobates talamancae* by Barbour and myself was based on a male of this species and a female of what seems to be *Phyllobates latinasus* (Cope). This specimen of *latinasus* was assumed to be a female at the time of describing. The male of *talamancae* has a black throat and this specimen was carrying tadpoles; the very similar specimen of *latinasus*, taken in the same stream, with a light throat, and without tadpoles, was assumed to be the female, an assumption which dissection has shown to be erroneous.

The two species were found in both Costa Rica and Panamá last summer, and were supposed to be the same. Two very different sorts of tadpoles at La Loma, which both seemed to us in the field to turn into the same frog, caused a critical examination of all the available material upon our return. Specimens of *Phyllobates latinasus* have been seen from Santa Cecilia, Costa Rica; Almirante and La Loma in western Panamá; Cerro Azul near the Canal Zone (U. S. N. M., 54174–5);

Cana (U. S. N. M., 54231, 63005) and Rio Esnape in extreme eastern Panamá. The last two lots are so near the type locality, the Truando region of Colombia, as to be virtually topotypes.

P. talamancae has been seen from Santa Cecilia and from Suretka, Costa Rica, and from La Loma in Panamá. It was described from Old Harbor on the coast between Limon and Almirante.

The most obvious difference between the two is the marking of the sides. In both species the dorsal region is gray and the sides are an intense black. There is an ill-defined light line where the gray and black meet. In both species a white streak starts from the groin and passes obliquely forward and upward toward the upper eyelid. In latinasus it dies out about halfway between leg and arm, but in talamancae it reaches the eye, and rather supersedes the ill-defined line which separates the black from the gray. The result is that talamancae apparently has a single white streak on the side and that latinasus has one and a half.

The marking of the thigh in *talamancae* is a hooked or "anvil-shaped" affair, owing to the dark line along the dorsal surface of the thigh running into a black area in the knee-pit which extends along the posterior aspect of the thigh. In *latinasus* this latter is absent and there is merely a dark streak on the dorsal surface.

The legs of *latinasus* are barred, while the legs of *tala-mancae* are not barred.

There are various differences in the length of toes and size of disks. These differences are essentially that the inner and outer toes of talamancae are reduced. Thus the tip of toe I reaches the penultimate joint of II in latinasus but not in talamancae and beyond it in latinasus. Two phalanges of IV are in latinasus but only the antepenultimate in talamancae. The tip of III reaches the antepenultimate joint of IV in talamancae and beyond it in latinasus. Two phalanges of IV are beyond the tip of V in latinasus and $2\frac{1}{2}$ in talamancae. The tip of V reaches the penultimate joint of III in talamancae and beyond it in latinasus. The disk of V is equal to half the

disk of IV in talamancae, but in latinasus they are the same size.

There is marked sexual dimorphism in talamancae. The throat of the male is black and the third finger of the male is so swollen that the disk is no larger than the rest of the finger. These characters are not apparent in latinasus.

Finally, while latinasus has the normal tadpole of the genus, with labial teeth 2/3, as described for subpunctatus, sylvatica, and trinitatis, the tadpole of talamancae has no labial teeth, but a highly developed labial disk, like that of Microhyla achatina and Megalophrys montana and entirely different from anything hitherto described from America.

Phyllobates kingsburyi Boulenger, a large species with grayish mottling on throat and chest, seems to occur east of the Canal Zone. Specimens considered to be this form have been seen from Rio Calobre about south of the Gulf of San Blas (U. S. N. M., 53737-8), and from Cana (U. S. N. M., 50177, 50197-50200).

In the cloud forest above the Chiriqui lagoon, on the slopes of Chiriqui and Horqueta, and in the drier forest down as far as Boquete lives another species allied to *talamancae* and having the same sort of tadpole. It may be called

Phyllobates nubicola, new species

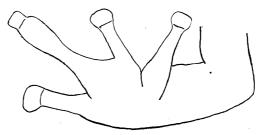
Diagnosis: Closely related to P. talamancae (Cope) from which it may be distinguished by the following characters: the black line on the dorsal surface of the thigh is not hooked, the thigh is red in life and the belly yellow, the tip of toe V reaches past penultimate joint of toe III, two phalanges of toe IV reach beyond the tip of toe V, the tip of toe I reaches the penultimate joint of toe II.

From *P. latinasus* it may be distinguished by the white line from the groin reaching the eye, and by the disk of toe V being half the size of the disk of toe IV, as well as by the black throat and swollen third finger of the male, in which characters it agrees with *talamancae*.

Type specimen: Cat. No. 58292, Museum of Zoology, University of Michigan. Adult male, collected in rain forest above

Boquete on the trail to Chiriqui Grande, 4,500 feet, by F. M. Gaige, May 15, 1923.

Description of type specimen: Snout moderate, as long as orbit; loreal region vertical, somewhat concave; nostril nearer tip of snout than eye; interorbital space much broader than upper eyelid; tympanum indistinct, 1/3 the size of eye; disks well developed, smaller than tympanum; third finger swollen, as wide as disk; disk of toe I half as large as that of toe II;



Right forefoot of male of Phyllobates nubicola, ventral surface, x71/2.

disk of toe V half as large as that of toe IV; tip of toe I reaches penultimate joint of toe II; tip of toe II reaches antepenultimate joint of toe III; tip of toe III reaches antepenultimate joint of toe IV; two phalanges of toe IV beyond tip of toe V; tip of toe V reaches past penultimate joint of toe III; two small metatarsal tubercles; a tubercle in the middle of the tarsus; tibiotarsal articulation reaching eye; skin smooth. Head and body black above and on sides; a light line from above eye to groin; a light line under eye above insertion of arm to groin; chin and throat black, belly mottled black and white; a dark line on anterior edge of thigh; a dark line on dorsal surface of thigh; a dark triangle, apex at vent, corners along thigh; light portions of thigh red, legs and arms uniform dusky; snout to vent 21 mm.; head width 7 mm.; head length 7 mm.; arm 13 mm.; leg 28 mm.

Variations: Females are white below. Many males have only the throat dark. Many specimens have the lower light line continuous around upper lip. Specimens seen: 30, as follows: Cloud forest above Gutierrez, 6,000 feet on trail from Chiri-

quicito to Boquete, Atlantic slope, 6; Pacific slope, same trail, under stones and debris along edge of stream 2 miles above Boquete, 3,900 feet, 11 (U. Mich., 58286); same trail, wet forest 4,500–5,500 feet, 8 (U. Mich., 58289, 58291); rain forest by last creek on trail on Pacific slope, 4,500 feet, 5.

Key to Central American forms of Phyllobates

- AA. Dorso-lateral line white.
- BB. Throat and chest of female always immaculate, disk of toe I = $\frac{1}{2}$ disk of toe II.
- CC. White line from groin reaching eye, disk of toe $V=\frac{1}{2}$ disk of toe IV, throat of male black.
 - D. Anvil-shaped black marking on thigh, thigh not red in life, tip of toe V not reaching penultimate joint of toe IV......P. talamancae (Cope) (Costa Rica, western Panamá).

Save for P. kingsburyi we saw all these carrying their tiny tadpoles. Tadpoles of latinasus, talamancae, and nubicola are at hand. Similar habits have been described for trinitatis and for subpunctatus. Apparently the male carries the very young tadpoles to the stream and leaves them there. There is no evidence that the male of Phyllobates gets the tadpoles from the water. The stream at La Loma contained all stages from the tiny young ones 10-12 mm. long to the transforming specimens. Males carrying tadpoles were put into water and the tadpoles left the parent and swam away. Nothing was seen of the eggs or the mating. The tadpoles of latinasus are similar in all respects to the described tadpoles of sylvatica, trinitatis and subpunctatus. The tadpoles of talamancae and of nubicola are very different.

Diagnosis of the mature tadpole of P. latinasus: Spiracle sinistral, anus dextral, eye invisible from the ventral surface, upper fin crest extending to end of body, distance from spiracle to base of hind limb contained 1.2 times in its distance from the snout, labial teeth 2/3, light grayish brown, fine dots on tail and on crests, greatest length 36 mm.

Description of mature tadpole of P. latinasus: Length of body contained 2.9 times in total length; width of body 1.4 in its own length; nostril equidistant between eye and snout; eye dorsal, not visible from below, nearer to snout than to spiracle; distance between nostrils = interorbital width = width of mouth; spiracle sinistral, its distance from the base of the hind legs 1.2 times in its distance from the snout; anus dextral; depth of the muscular portion of the tail contained twice in greatest depth of tail. Upper labium with two series of teeth equal in length, inner divided in the middle for a distance equal to 1/4 the length of either half; lower labium with three equal series of teeth; papillate border of mouth broadly absent anteriorly, upper row of teeth forming border; light grayish brown above, darker spots on base of tail and on crests. Total length 32 mm., head and body 11 mm, tail 21 mm.

Diagnosis of mature tadpole of P. talamancae: Spiracle sinistral, anus dextral, eye invisible from the ventral surface, upper fin crest well developed only on distal 2/3 of tail, spiracle equidistant between snout and base of hind limb, no labial teeth, brownish with a black streak on upper edge of muscular part of tail, greatest length 33 mm.

Description of mature tadpole of P. talamancae: Length of body contained 3.4 times in total length; width of body 1.3 in its own length; nostril equidistant between eye and snout; eye dorsal, not visible from below, nearer to snout than to spiracle; distance between nostrils less than interorbital width, less than width of mouth; spiracle sinistral, equidistant between snout and base of hind legs; anus dextral; depth of muscular portion of tail at base contained 1½ times in greatest depth of tail; no labial teeth; a broad labial disk, the posterior portion of which is twice as deep as the anterior, papil-

late throughout; brown, posterior half of tail with black line on upper edge of muscle, some mottlings on other parts of muscle and a few dots on crests; total 31 mm., head and body 9, tail 22. Many of the tadpoles are lighter in color than the described one but in all the dark line on the tail can be made out.

These two sorts of tadpoles were common in the stream at La Loma. Those of *latinasus* were similar to Rana tadpoles in appearance and in actions. The tadpoles of *talamancae* seemed to remain in the depest parts of the pools and were very active and darter-like in their movements.

Three tadpoles from near Boquete: "under low stones in washed out cavity at edge of small stream, 4,100 feet," collected by the Gaiges, February 26, 1923, are much like the tadpoles of talamancae, but with quite obvious differences. They are probably the larvae of nubicola.

Diagnosis of mature tadpole of P. nubicola: Spiracle sinistral, anus dextral, eye invisible from the ventral surface, upper fin crest well developed only on distal 2/3 of tail, distance from spiracle to base of hind limb contained 1.2 times in its distance from the snout, labial teeth 1/0, uniform brown, largest of the three 32 mm. long.

Description of mature tadpole of P. nubicola: Length of body contained 3.2 times in total length; nostril nearer snout than to eye; eye dorsal, not visible from below; eye nearer snout than to spiracle; distance between nostrils = interorbital width, less than width of mouth; spiracle sinistral, its distance from the base of the hind limb contained 1.2 times in its distance from the snout; anus dextral; depth of muscular portion of tail at base is the greatest depth of tail; labial teeth 1/0; the row of teeth not as long as width of beak; a few teeth between tooth row and beak perhaps represent a rudimentary inner upper row; a broad labial disk, posterior part twice as deep as anterior, papillate throughout; brown, practically uniform, crests pale; total length 32 mm., head and body 10 mm., tail 22 mm.

In both adult and tadpole *nubicola* is intermediate between *latinasus* and *talamancae*.

Matters of considerable general biological interest are suggested by the forms described above. A Hyla with the habits but not the structure of an Agalychnis; Phyllobates whose adults are so similar as to have been considered conspecific by three observers but whose tadpoles differ in the most extraordinary fashion; these support the precedence in time of function over form, and the possibility of apparent reversal of the biogenetic law, owing to different larval habits and similar adult habits.

The case of Megalophrys seems much like that of Phyllobates. Adult and larva live in two different worlds, and while the general environment and habits of most species are more alike as larvae than as adults, the reverse may be, and in these cases undoubtedly is, true.

The much more profound changes which attend metamorphosis in frogs than in salamanders lead one to marvel why neoteny is unknown in the former while fairly common in the latter.



PLATE I

- 1. Tadpole of Hyla uranochroa, side view, x2.
- 1a. Mouth of tadpole of Hyla uranochroa, x6.
- 2. Tadpole of Hyla albomarginata, side view, x2.
- 2a. Mouth of tadpole of Hyla albomarginata, x6.

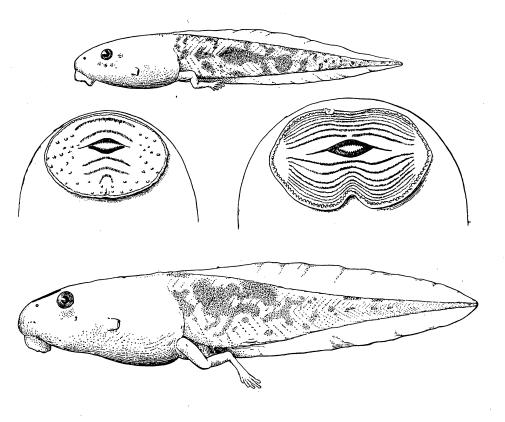


PLATE II

- 3. Tadpole of Phyllobates talamancae, side view, x21/2.
- 3a. Mouth of tadpole of Phyllobates talamancae, x7.
- 4. Tadpole of Phyllobates nubicola, side view, x21/2.
- 4a. Mouth of tadpole of Phyllobates nubicola, x7.
- 5. Tadpole of Phyllobates latinasus, side view, x21/2.
- 5a. Mouth of tadpole of Phyllobates latinasus, x7.

