TAXONOMIC NOTES ON FROGS FROM THE MADEIRA
AND PURUS RIVERS, BRASIL

W. RONALD HEYER

Examination of collections of frogs from the western lowland Amazonian basin has clarified certain taxonomic problems and raised others, as expected for a poorly understood fauna. The collections were made on two expeditions: (1) Joint Museu de Zoologia, Universidade de São Paulo (MZUSP) and Smithsonian (USNM) expedition on the Rio Purus from 2 December 1974 to 19 January 1975. Carlos Roberto F. Brandão, W. Ronald Heyer, and Paulo E. Vanzolini were the collectors on this expedition; (2) Joint Expedição Permanente da Amazônia (EPA) — MZUSP and USNM expedition on the Rio Madeira from 31 October to 19 December 1975. Miriam H. Heyer, W. Ronald Heyer, Paulo E. Vanzolini, and Francisca Carolina do Val were the collectors on this trip. The localities worked and species collected from each locality are presented in Appendices 1 and 2.

The purpose of this paper is to discuss the findings of interest to a taxonomist that have resulted from study of the specimens. An ecological analysis of the collections is presented elsewhere (Heyer, 1976). Comments are arranged alphabetically by species for those species for which specific information is presented. The list of species collected (Appendix 2) is arranged alphabetically within families.

ACKNOWLEDGMENTS

Dr. Paulo E. Vanzolini invited me to join his expeditions. In addition to the educational opportunity of learning from his experience, he made the trips most enjoyable.

Carlos Roberto F. Brandão, Miriam Heyer, Francisca Carolina do Val, and Paulo E. Vanzolini aided in the collection of frogs; their help and companionship continue to be invaluable.

John D. Lynch identified the frogs of the genus Eleutherodactylus. Stephen R. Edwards examined the Colostethus from the Purus. William E. Duellman concurred that the species of Hyla I was unable to identify are presently unidentifiable.

Division of Reptiles and Amphibians, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560, U.S.A.
William F. Pyburn examined some frogs of the *Hyla rubra* group and loaned material of the new genus and species of leptodactylid. James R. Dixon and Max A. Nickerson allowed me to examine specimens in their care. George R. Zug kindly reviewed the manuscript. Barton Kavruck prepared Figures 1 and 2. My participation was supported by MZUSP and the Smithsonian Research Foundation. This is a contribution of the Amazon Ecosystem Research Program (Smithsonian Institution).

### Species Accounts

**Colostethus sp.**

The single specimen listed as *Colostethus sp.* in Appendix 2 represents a new species for which S. R. Edwards has a manuscript name (Edwards, 1974, p. 264). This species was previously known from the Amazonian slopes of the Andes in Bolivia and southern Ecuador.

**Eleutherodactylus sp.**

The specimens listed as *Eleutherodactylus sp.* in Appendix 2 represent a new species being described by Lynch and Hoogmoed. These specimens represent the first record from southern draining affluents of the Amazon.

**Hydrolaetare schmidtii**

There are few reported specimens of *H. schmidtii* (Cochran and Goin), 1959, but specimens are beginning to accumulate in collections. The specimens captured on the Purus and Madeira expeditions represent the first specimens for which reliable habitat data are available. All three specimens were captured at night sitting on the margins of small forest streams. All specimens were located by eyeshine. Individuals were easy to catch; they made no attempt to jump until they were in hand. Two of the specimens gave what sounded like distress calls intermittently for over a half hour after capture. The sound was similar to loud housecat mewing. Although few specimens were captured, all were taken from relatively undisturbed forest, and all were next to 1 to 2 meter wide, slow moving (under non-thundershower runoff conditions) streams. At Beruri, efforts were made to sample the stream where *H. schmidtii* was taken for larvae. The stream was full of fish, ranging from tadpole size to 50 cm size. No tadpoles were collected. If *H. schmidtii* has a stream larva, it must have an adaptation for coexisting with carnivorous fish. Documented specimens are now known from Amazonian Colombia, Peru, and Brasil.

**Hyla acreana**

Bokermann (1964) in describing this species, commented that it might be a subspecies of *H. marmorata* (Laurenti), 1768, as he
had no localities where both occurred sympatrically and some Bolivian specimens appeared to be intermediate between the two forms. Both *Hyla acreana* and *marmorata* were collected at Pauini. *Hyla acreana* was breeding, *H. marmorata* was not at the time of collection. *Hyla acreana* is a full species; the sympatric specimens demonstrate the same differences Bokermann described for allopatric specimens. I have examined one of the Bolivian specimens Bokermann thought might be intermediate (USNM 102665). As Bokermann stated, the specimen is poorly preserved. I think the specimen represents another distinct species in the *H. marmorata* complex.

### Hyla nr. boesemani

Dr. William E. Duellman identified the single specimen as being allied with *H. boesemani* Goin, 1966. I have compared the specimen with the holotype of *H. boesemani* (USNM 159140) and find they are not conspecific. The specimen probably represents a new species.

### Hyla garbei

Specimens show a range of all the types of thigh patterns shown in Figure 1 of Duellman's *Hyla rostrata* group paper (1972). The figured patterns were given as diagnostic characteristics of several species in the group. Additionally, there is variation in the development of the heel tubercle in the specimens at hand. Although this additional material demonstrates that *H. garbei* (Miranda-Ribeiro), 1926, is more variable than previously thought, I think all the specimens refer to a single species.

*Hyla garbei* is a nocturnal forest species, but a few specimens were located in the daytime. For example, on 13 November 1975 two specimens were found adpressed to (different) tree trunks in the afternoon. Both specimens were the same color as the trunk and very difficult to see. In both cases, the individuals were pointed head down and were about 20 cm high on the trunk from the ground. One specimen, when approached closely, ran around the tree trunk with the same rapidity as a lizard and escaped. All *H. garbei* seen in the day were on tree trunks.

### Hyla granosa — punctata — rhodoporus complex

Two species of green tree frogs in life were collected on the expeditions. These represent the species usually identified as *H. granosa* Boulenger, 1882 (broader head, no light dorsolateral stripes) and *H. punctata* (Schneider), 1799 (narrower head, light dorsolateral stripes present).

Duellman (1974) discussed the taxonomic status of *Hyla punctata*, synonymizing several names including *Hyla papillaris* Spix, 1824, *Hyla variolosa* Spix, 1824, and *Hyla rhodoporus* Günther, 1869, which actions I interpret to be premature in part. The figures in Spix (1824) of *papillaris* and *variolosa* appear to belong to two species, not one as indicated by Peters (1873) who was the last herpetologist to have seen Spix's specimens. The figure of *Hyla*
papillaris has a broad head and lacks dorsolateral stripes, the figure of Hyla variolosa has a narrower head and has dorsolateral stripes. Both figures are quite stylized. There is no reason to question the synonymy of Hyla variolosa with Hyla punctata. However, the figure of Hyla papillaris certainly suggests what most authors refer to as Hyla granosa. Peters (1873) states that the holotype of H. papillaris is a 30 mm juvenile with a 5 mm tail stub. All juvenile specimens of this complex at hand of the 30 mm size range have no suggestion of a tail stub. Because of the conflicting evidence, the best nomenclatural decision appears to be acceptance of Peters’ arbitrary designation of Hyla papillaris as a synonym of Hyla punctata.

Cochran and Goin (1970) pointed out that H. rhodoporus was distinct from H. punctata. They compared the type with specimens from the USNM. I concur that the USNM specimens Cochran and Goin examined are distinct from both Hyla granosa and Hyla punctata. Hyla rhodoporus lacks dorsolateral stripes, as does granosa. However, the following features distinguish rhodoporus from granosa: rhodoporus has a narrower head, the top of the head is smooth rather than shagreened, a supratympanic fold is present, and rhodoporus has less webbing than granosa. Boulenger’s description and figure (1882) of granosa clearly apply to the broad headed form.

### Hyla leali

Duellman (1974) placed Hyla leali Bokermann, 1964, in the synonymy of H. rossalleni Goin, 1959. He based this decision on comparison of specimens from Bolivia, Peru, and Ecuador with the types of H. rossalleni from Leticia, Colombia. Although not taken in sympatry, specimens that match both species descriptions were taken at adjacent localities along the Purus. The specimens clearly represent distinct species, although only one specimen is available for what I identify as H. rossalleni. The differences previously reported between these species also are found in the present material: H. rossalleni has a distinct light interocular stripe not found in leali, the dorsal pattern of H. rossalleni is nondescript, H. leali usually have distinct scapular and sacral markings.

### Hyla “membranacea”

Duellman (1974) synonymized H. membranacea Andersson, 1975, with Hyla triangulum Gunther, 1869. The specimens here identified as “membranacea” have a fairly uniform patterned dorsum, but differ from the uniform phase of H. triangulum. Hyla “membranacea” has a uniform dorsum with irregular little dark spots, the same pattern is on the sides of the body. The uniform phase of H. triangulum has a contrasting lighter dorsal and darker side of head and body pattern. The Hyla “membranacea” are probably a different species from the species described by Andersson, but I prefer to use “membranacea” to point out the distinctiveness of this form for the next reviser of the H. leucophyllata group. Morphologically, the specimens are similar to H. oliveae Cochran and Goin, 1970, but the “membranacea” did not have the gold spots in life of H. oliveae.
Hyla species

There additionally appear to be at least six new species of *Hyla*, reflecting the fact that the Amazonian frog fauna is still in the discovery phase. A series of specimens representing three species are related to *Hyla blairi* Fouquette and Pyburn, 1972, and are being studied by William F. Pyburn. Two of the other species listed as *Hyla* sp. in Appendix 2 are represented by one or two specimens and the group relationships are unclear (both are small species). One of the species is a distinctive new member of the recently revised *Hyla parviceps* group and is described as:

**Hyla pauiniensis**, new species

(Fig. 1)


*Paratopotypes* — MZUSP 49893, female; USNM 202034-35, male and female. Collected with holotype at same pond.

*Diagnosis* — A member of the *Hyla parviceps* group, differing from *bokermanni* Goin, 1960, *brevifrons* Duellmann and Crump, 1974, *tuteocellata* Roux, 1927, and *subocularis* Dunn, 1934, in lacking light dorsolateral stripes in both sexes. From *brevifrons*, in which most males lack light dorsolateral stripes, *pauiniensis* differs in lacking light spots on the dorsal surface of the thigh and having one rather than two light suborbital spots. From *microps* Peters, 1872, *pauiniensis* differs in having dark dorsal transverse bands (dorsum plain or marked with irregular dashes) and lacking a large light spot on the posterior face of the thigh (orange in life in *microps*). From *parviceps* Boulenger, 1882, *pauiniensis* differs in lacking a proximal discrete large light spot on the ventral surface of the tibia (orange in life in *parviceps*). *Hyla pauiniensis* differs from all members of the group in having a tuberculate dorsum.

*Description of Holotype* — Snout slightly truncate in dorsal outline; snout rounded-acute in profile; canthus rostralis obtuse; tympanum indistinct, greatest diameter about 1/3 eye; vomerine teeth in two transverse patches posterior to choanae; vocal slits present; vocal sac single, external; outer finger disks moderate, about equal to tympanum; finger webbing formula I trace II 1 1/2 — 2 1/2 III 2 1/3 — 2 IV; subarticular tubercles single except for bifid tubercle under finger IV; white glandular nuptial asperities weakly developed; no ulnar ridge or tubercle; moderate patagium; dorsal texture smooth with scattered, large, white-tipped tubercles; throat texture smooth; belly texture granular; outer toe disks moderate, about equal to finger disks; toe webbing formula I 2 — 2 IV 1 — 2 III 1 — 2 IV 2 — 1 V; outer metatarsal tubercle indistinct; no tarsal fold or tubercle; heel very slightly rugose.

Color pattern in preservative. Light rostral stripe joining a light narrow canthal stripe; loreal region uniform tan; one light subocular spot; dorsum tan with brown cross bars (Figure 1); limbs barred; anterior face of thigh dark with a single large light spot (bright golden yellow in life); posterior face of thigh uniform, dark, almost
black; throat suffused with melanophores; belly dotted with melanophores.

Measurements. Snout-vent length 20.2 mm, head width 6.8 mm, femur 9.5 mm, tibia 9.9 mm, foot 7.8 mm.

Variation. The snout is truncate and acute in the paratypes. The webbing variation of all specimens for fingers is

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... the outer metatarsal tubercle is absent. The anterior face of the thigh has small light spots or an irregular light stripe under the dark portion. The posterior face of the thigh may be bordered above and below the black areas by irregular light stripes. The male paratype lacks a distinct rostral stripe and the canthal stripes extend on the eyelid to the tympanic region. The dorsal tranverse bands may be indistinct.

Based on the four specimens, the following appear to be sexual differences. The female disks are large, larger than the tympanum. The females lack a light canthal stripe and the belly is heavily mottled, contrasting with the light male belly. The two females are 23.0 and 24.0 mm SVL, the male paratype is 20.3 mm SVL.

Remarks — The four specimens were taken from a forest pond at night on vegetation over the water. The call is cricket-like.

The species has few derived character states of those analyzed by Duellman and Crump (1974), but the relationships appear to be closest with H. microps and parvicaps.

Etymology — The species is named for the location of Boca do Paulini, the type locality, where several very productive days were spent in profitable collecting and feeding mosquitos.

Family Leptodactylidae, new genus and species

Four small, distinctive leptodactylid frogs were taken from under logs at Puruzinho on the Rio Madeira. In their general aspect upon collecting, my first impression was that they represented a new species of the genus Adenomera. Upon closer examination, the toes had distinctly grooved disks with pointed tips. Lynch (1976) described two small leaf litter frogs from the Amazonian slopes and placed them in the genus Euparkerella. The four specimens are clearly distinct at the species level from the two described by Lynch. In order to determine whether the new species were congeneric with the species described by Lynch, a character analysis was undertaken. At the time the analysis was done, only the four specimens were available, so no specimen was cleared and stained. Osteological observations were made from superficial dissections and X-rays. After the data were gathered, Dr. William F. Pyburn indicated he also had specimens and calls. He kindly loaned these materials to me for inclusion in this paper.

Groups for Comparison. As data were being taken on the new species, the suite of states confirmed that the species is an eleutherodactyline. The question is to which species of lowland eleutherodactyline the species has closest affinities — the genera in question are Barycholos, Eleutherodactylus, and Euparkerella. The character states for Eleutherodactylus come from the species coqui Thomas, 1965, fleischmanni (Boettger), 1892, guentheri (Steindachner), 1864 and nigrovittatus Andersson, 1945, together with previously published
data. I remain convinced that the genus *Eleutherodactylus* as presently constituted is a composite, but for present purposes, the composite nature of the genus does not affect the results of the analysis in terms of the question being asked. As study began, it became apparent that *Euparkerella brasiliensis* (Parker), 1926, and *myrmecoides* Lynch, 1976, should be analyzed separately. Specimens of *E. lochites* Lynch, 1976, were not available for study at the time of the analysis.

**Character analysis.** Data were gathered for the characters used previously by Heyer (1975) and Lynch (1976). Data are available for 18 characters which show variation among the study group and for which data are available for all taxa. Three osteological characters were not discernible for the new species, the nasal-maxillary relationship, squamosal shape, and fusion of the prootic with the frontoparietal bones. Where the determination of primitive and derived states is the same as used previously, the citation only is given for justification. All primitive states are coded as 0.

1. Tympanum visibility. 0 = tympanum present, visible, 1 = tympanum absent (Heyer, 1975, character 2).
2. Toe disks. 0 = disks lacking circumferential grooves, 1 = disks with circumferential grooves (Heyer, 1975, character 5).
3. Tarsal decoration. 0 = tarsus smooth, 1 = tarsal tubercle present in at least some species (Heyer, 1975, character 6).
4. Adductor mandibularis muscle. 0 = s + e condition, 1 = s only condition in at least some species (Heyer, 1975, character 11).
5. Depressor mandibulae muscle. 0 = muscle origin tripartite, 1 = muscle origin bipartite or single (Heyer, 1975, character 12).
7. Anterior petrohyoideus muscle. 0 = attachment on ventral body of hyoid, 1 = attachment on lateral edge of hyoid (Heyer, 1975, character 14; justification of polarity, Heyer and Liem, 1976).
8. Sternohyoideus muscle insertion. 0 = some attachment near midline of hyoid plate, 1 = attachment near lateral edge of plate in at least some species (Heyer, 1975, character 15; justification of polarity, Heyer and Liem, 1976).
9. Omohyoideus muscle. 0 = muscle present, 1 = muscle absent in at least some species (Heyer, 1975, character 16).
10. Iliacus externus. 0 = muscle extends from 1/2-3/4 anterior on ilium, 1 = muscle extends from 3/4 to full length of ilium (Heyer, 1975, character 17).
11. Tensor fasciae latae muscle. 0 = muscle inserts posterior to anterior extent of iliacus externus muscle, 1 = muscle inserts on anterior end of ilium immediately anterior to iliacus externus and the tensor fasciae latae and iliacus externus are contiguous for considerable length in at least some species (Heyer, 1975, character 18).
12. Semitendinosus muscle. 0 = exterior head not rudimentary, 1 = exterior head rudimentary, attached by tendon to interior portion (Heyer, 1975, character 19).
13. Adductor longus muscle. 0 = muscle present, 1 = muscle absent (Heyer, 1975, character 20).
14. Vomerine teeth. 0 = present, 1 = absent (Heyer, 1975, character 26).
15. Alary process of the hyoid. 0 = alary process narrow, stalked, 1 = process rudimentary, 2 = process absent in at least some species (Heyer, 1975, character 31).
16. Posterior sternum. 0 = simple cartilaginous plate, sides of plate broaden posteriorly, 1 = cartilaginous plate, sides parallel or narrow posteriorly, 2 = similar to 1 with deposition of mineral in the mesosternum in at least some species (Heyer, 1975, character 32).
17. Number of phalanges in digit 4 of hand. 0 = 3, 1 = 2, (Lynch, 1976).
18. Tips of fingers and toes. 0 = rounded, 1 = with distinct drawn out tips in at least some species. State 1 is found only in a few eleutherodactyline among all leptodactylid frogs and is clearly a derived condition.

The distribution of states among the taxa are presented in Table 1.

As explained previously (Heyer, 1975), I concur that relationships are best expressed by shared derived states. The total numbers of shared derived states among the taxa are:

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<tr>
<td>A — Barycholos</td>
<td>10</td>
<td>10</td>
<td>3</td>
<td>8</td>
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<tr>
<td>B — Eleutherodactylus</td>
<td>15</td>
<td>6</td>
<td>10</td>
<td>8</td>
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<tr>
<td>C — E. brasiliensis</td>
<td>10</td>
<td>7</td>
<td>2</td>
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<td>D — E. myrmecoides</td>
<td>13</td>
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<td>E — new species</td>
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Hecht and Edwards (1976) recently proposed a method of grouping characters into categories of different phylogenetic weight. Several of the characters used herein can not be assigned to the groupings they propose. However, 2 kinds of characters can be identified, corresponding to their groups I and II, involving loss of morphological elements. As they document, these characters carry little information in deducing relationships because there is usually no developmental evidence to indicate that loss occurred independently or was the result of directional selection on a common ancestor. Characters 1, 4, 9, 13, 14, 15, 17 are group I and II characters of Hecht and Edwards (1976). When these characters are deleted, the matrix of numbers of shared derived states appears as:

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<tr>
<td>A — Barycholos</td>
<td>8</td>
<td>8</td>
<td>1</td>
<td>6</td>
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<tr>
<td>B — Eleutherodactylus</td>
<td>12</td>
<td>3</td>
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<td>7</td>
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<tr>
<td>C — E. brasiliensis</td>
<td>3</td>
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<td>D — E. myrmecoides</td>
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<td>E — new species</td>
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Comparison of these two matrices allows the following conclusions to be drawn: (1) Most of the evidence for close relationships between *E. brasiliensis* and *E. myrmecoides* is based upon characters of loss, therefore the relationship is suspect; (2) *E. myrmecoides* has a closer relationship with *Barycholos* and *Eleutherodactylus* than with *E. brasiliensis*; (3) The new species is not closely related to *E. brasiliensis*; and (4) The new species has its closest relationships with *Barycholos*, *Eleutherodactylus* or *E. myrmecoides*.

Before discussing the generic allocation of the new species, additional comment is needed on the generic allocation of *E. myrmecoides* as the results of this analysis clearly indicate that *myrmecoides* is not congeneric with *E. brasiliensis*, conflicting with Lynch's arrangement.

Lynch gave the following list of shared characters of the two species as evidence of both belonging to a common genus: (1) presence of two large metatarsal tubercles, (2) no digital webbing, (3) pointed disks on the toes, (4) a reduced phalangeal formula for the fourth finger, (5) lack of vomerine teeth, (6) short, broad head, (7) small adult size, (8) partially fused epicoracoid cartilages. The only skeletal differences Lynch (1976) listed between the two were: (1) presence of a plectrum (and tympanum) in *E. myrmecoides*, absent in *E. brasiliensis*, (2) terminal phalanges are more knob-like in *E. myrmecoides*, (3) minor proportional differences.

Both species are leaf litter frogs with certain adaptive complexes reflecting this habitat specialization, including large metatarsal tubercles, no digital webbing, pointed disks on toes (also found on leaf litter *Eleutherodactylus* in the West Indies, clearly a result of convergence), and small adult size. The reduced phalangeal formula and lack of vomerine teeth could well be due to independent loss rather than reflecting relationships as pointed out by Hecht and Edwards (1976). The question is then, are the leaf litter adaptations due to common ancestry or convergence. The way to answer the question is to examine the characters which unite and separate the taxa excluding those characters associated with the leaf litter habitat and characters of loss.

The remaining derived character states that unite the two species are: (1) short, broad head, (2) partially fused epicoracoid cartilages. Partially fused epicoracoid cartilages are also found in a few other species of leptodactylids, all of which are small species, suggesting a locomotory skeletal compensation for small size. No shared derived states are added from this analysis.

The remaining character state separating the two species as given by Lynch (1976) is the nature of the shape of the terminal phalanges. Both are distally expanded, but as Lynch shows (1971, figs. 42-43, pp. 65-66), the condition of *E. brasiliensis* is distinctive and difficult to homologize with other T-shaped conditions. Contrary to Lynch, I find the following skeletal differences between the two species. 1) Nature of the nasal-maxillary relationship. The nasals of *E. brasiliensis* are large and in contact with the maxilla. The nasals of *E. myrmecoides* are small and well separated from the maxilla. The condition of *E. myrmecoides* is derived with respect to *E. brasiliensis* (Heyer, 1975). 2) The prootic and frontoparietal bones are fused in *E. brasiliensis* as Lynch indicated, but I find the elements to be separate in *E. myrmecoides*. The fused condition is derived (Heyer, 1975). 3) Lynch and I have different interpretations of sternal con-
ditions; whereas he considers the styles similar between the species, I interpret the states as distinct (Table 1). In addition, I find the following muscle and hyoid derived states that separate the two: *E. brasiliensis* 5, 7 (character numbers as used above); *E. myrmecoides* 10, 12.

In summary, excluding characters that involve loss and characters that are associated with the leaf litter habitat, the following derived states are common to the two taxa:

1. short broad head.
2. partially fused epicoracoid cartilages.

The derived states that differentiate the two species are:

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<th><em>E. brasiliensis</em></th>
<th><em>E. myrmecoides</em></th>
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<tr>
<td>1. terminal phalanges</td>
<td>1. terminal phalanges</td>
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<td>spade shaped</td>
<td>T-shaped</td>
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<td>2. frontoparietal-prootic fusion</td>
<td>2. small nasal bones</td>
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<td>3. depressor mandibulae origin single</td>
<td>3. derived sternal apparatus</td>
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<td>4. anterior petrohyoideus attached to lateral edge of hyoid plate</td>
<td>4. derived iliacus externus state</td>
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<td>5. derived semitendinosus state</td>
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In comparing the summary characters that unite the species with those that separate, the following arguments could be made: (1) the characters that are shared could all be consequences of small size; (2) the characters that separate the two could reflect a functional feeding shift in *E. brasiliensis*, a functional locomotory shift in *E. myrmecoides*. I conclude that *E. brasiliensis* and *E. myrmecoides* belong to distinct genera and the similarities are due in large part to convergent adaptations to the leaf litter habitat.

As indicated by the matrices, *Barycholos*, *E. myrmecoides*, *Eleutherodactylus* and the new species share the closest relationships. I consider the leaf litter adaptive complex a sufficient complex to warrant generic recognition if morphological differences are consistent with such action. It seems reasonable that both *E. myrmecoides* and the new species shared a common ancestor that was similar to *Eleutherodactylus* and *Barycholos*. Three taxonomic conclusions are possible: (1) All four belong to a single genus. The morphological differences argue against this; (2) *E. myrmecoides* and the new species belong to a single genus distinct from *Eleutherodactylus* and *Barycholos*. This would be the best conclusion if the two shared a common ancestor that had already adapted to the leaf litter habitat; (3) *E. myrmecoides* is generically distinct from the new species and both are generically distinct from *Barycholos* and *Eleutherodactylus*. This would be the best conclusion if the common ancestor to *E. myrmecoides* and the new species was not adapted to the leaf litter habitat.

In order to choose between the last two alternatives, the leaf-litter adaptive characters and characters of loss need to be deleted.
from a comparison of the characters that unite and distinguish the two species. The derived states that the two species share are:

1. grooved toe disks
2. derived state of iliacus externus

The derived states that distinguish the two species are:

**E. myrmecoides**  
1. tarsal tubercle
2. derived state of semitendinosus
3. derived sternal apparatus

**E. myrmecoides** new species
1. derived sternohyoideus state
2. derived geniohyoideus state
3. derived tensor fasciae latae state
4. derived sternal apparatus

The sternal apparati of the two species are very different. The posterior sternum of *E. myrmecoides* is very short and broad with some mineral deposition in the mesosternum (similar to Fig. 4, L, p. 18, Heyer, 1975, except xiphisternal region barely indented). The posterior sternum of the new species is similar in shape to the leptodactyline style except that it is entirely cartilagenous (similar to Fig. 4, J, p. 18, Heyer, 1975, except no calcification). The reason the new species shares so many derived states with *Eleutherodactylus* is due to the polyphyletic nature of *Eleutherodactylus*. For example, when the new species is compared to each species of *Eleutherodactylus* used in the study, the new species has from 2-5 distinct derived states with respect to each *Eleutherodactylus* species and each species of *Eleutherodactylus* has 3-5 distinct derived states with respect to the new species. The evidence suggests that *E. myrmecoides* and the new species have been derived from different species groups within the *Eleutherodactylus*-complex and thus are best represented as belonging to separate genera.

As one of the conclusions of this study is that *myrmecoides* requires a new genus name, it is described as:

**Phyllonastes**, new genus


**Diagnosis:** The only leptodactyloid genera with a combination of no vomerine teeth and toes with circumferentially grooved disks are *Phyllonastes*, *Syrrophus* and *Tomodactylus*. Both *Syrrophus* and *Tomodactylus* lack the tarsal tubercle found in *Phyllonastes*.

**Definition:** Pupil horizontal; tympanum distinct; male thumb without nuptial asperities; single subarticular tubercle under fourth finger; body without well defined glands; toes disked, circumferentially grooved, tip of digit pointed or drawn out as tear-shaped papilla; inner tarsal tubercle present; inner and outer metatarsal tubercles large, rounded, not cornified; toes free, not fringed or webbed; adductor mandibularis muscle s only (adductor mandibulae posterior subexternus only present); depressor mandibulae condition DFSQAT (origin from dorsal fascia, squamosal and otic region, and annulus tympanicus); geniohyoideus medialis muscle separated medially;
anterior petrohyoideus muscle insertion on ventral body of hyoid plate; sternohyoideus muscle insertion of narrow band of fibers extending to midline of hyoid body; omohyoideus muscle insertion on edge of hyoid plate adjacent to posteromedial process; iliacus externus muscle extends to anterior end of ilium; tensor fasciae latae muscle inserts posterior to the anterior extent of the iliacus externus on the ilium; semitendinosus muscle with rudimentary exterior head, attached by tendon to interior portion; adductor longus muscle absent; quadratojugal present, contacting maxilla; nasals small, widely separated from maxilla and each other, in contact with frontoparietals; frontoparietals meet medially, not exposing fontanelle; otic ramus of squamosal much longer than zygomatic ramus; vomer reduced, lacking teeth, vomers widely separated from each other, not in contact with premaxillae; prootic not fused with frontoparietal; occipital condyles widely separated; anterior process of hyale present; no alary process of hyoid; posterior sternum short, broad, shallowly bifurcate posteriorly, light mineral salt deposition in mesosternal area; last presacral vertebra same width as sacrum; sacral diapophyses essentially rounded although minor expansion present; terminal phalanges T-shaped; fourth finger with two phalanges: dorsal crest of ilium well developed.

*Etymology:* From the Greek *phyllon*, leaf, and *nastes*, dweller, in reference to the leaf litter habitat characteristic of members of the genus. The genus is masculine in gender.

*Content:* Two species presently known: *Phyllonastes lochites* (Lynch) and *P. myrmecoides* (Lynch). As Lynch (1976) observed, several more species of small leaf litter frogs are likely to be found in collections and in nature. The size and habitat make them easy to overlook. Dr. Lynch has recently identified further specimens of *lochites* in collections and is currently studying the osteology of this species.

A second conclusion of this study is that the new species also requires erection of a new genus, which is proposed as:

**Phyzelaphryne**, new genus

*Type species:* *Phyzelaphryne miriamae*, new species.

*Diagnosis:* The only leptodactylid genera in which some of the species have terminal digital papillae are *Phyzelaphryne*, *Phyllonastes*, *Eleutherodactylus* and *Euparkerella*. *Phyzelaphryne* differs from *Phyllonastes* and *Euparkerella* in having distinct vomerine teeth. From those few species of *Eleutherodactylus* with digital papillae, *Phyzelaphryne* differs by having a single subarticular tubercle under the fourth finger (two in *Eleutherodactylus*).

*Definition:* Pupil horizontal; tympanum distinct, vocal sac external; male thumb without nuptial asperities; single subarticular tubercle under fourth finger; body without well defined glands; toes disked, circumferentially grooved, tip of digit drawn out as tear-shaped papilla; tarsus smooth, lacking folds or tubercles; outer metatarsal tubercle pointed; inner metatarsal tubercle large, rounded, not cornified; toes free, not fringed or webbed; adductor mandibularis muscle condition $s + e$ (adductor mandibulae posterior subexternus and adductor mandibulae externus superficialis present); depres-
sor mandibulae muscle condition DFSQAT; geniohyoideus muscle contiguous medially; anterior petrohyoideus insertion on lateral edge of hyoid plate anteriorly, on ventral body of hyoid plate medially and posteriorly; sternohyoideus muscle insertion entirely near edge of hyoid body; omohyoideus muscle absent; iliacus externus muscle extending almost to anterior tip of iliac; tensor fasciae latae muscle insertion on anterior end of ilium immediately anterior to iliacus externus, tensor fasciae latae and iliacus contiguous for a considerable length; semitendinosus muscle with equal interior and exterior heads; adductor longus muscle insertion on knee; quadratojugal present, contacting maxilla; frontoparietals meet medially, not exposing fontanelle; vomerine teeth present; occipital condyles widely separated; anterior process of hyale present; alary process of hyale rudimentary (as in Fig. 1, F, Heyer, 1974); posterior sternum a cartilagenous style; last presacral vertebra about same width as sacrum; sacral diapophyses rounded; terminal phalanges T-shaped; fourth finger with 3 phalanges; dorsal crest of ilium present.

**Etymology:** From the Greek phyzelos, shy, and phryne, toad, in reference to members of the genus avoiding capture or recognition by scientists until recently. The genus is feminine in gender.

**Content:** Monotypic.

**Remarks:** Lynch (1976) stated that the reduction of a subarticular tubercle under the fourth finger indicated a loss of a phalanx in leptodactylid frogs. This new material indicates that a shortening of the digit, reflected by loss of a subarticular tubercle need not be necessarily accompanied by a loss of a skeletal element.

**Phyzelaphryne miriamae,** new species

*(Fig. 2)*

**Paratopotypes:** MZUSP 49895, USNM 202607-08, collected 17 November and 5-6 December 1975.

**Diagnosis:** As for genus.

**Description of holotype:** Dorsal outline of snout truncate; snout profile rounded; canthus rostralis indistinct; loreal slightly concave; tympanum distinct, greatest diameter 1/2 eye; vomerine teeth in long, transverse series posterior to choanae; finger lengths IV < I ≅ II < III; finger tips pointed with small disks, circumferentially grooved; large, flat inner metacarpal tubercle just smaller than large, flat outer metacarpal tubercle; dorsal surfaces of body and limbs granular; weak supratympanic fold, no other folds on body; belly smooth, weak belly fold; toe tips with distinct disks, larger than finger disks, disks circumferentially grooved, tips with terminal papillae; toes lacking fringe or web; subarticular tubercles moderately developed; large, ovoid, flattened inner metatarsal tubercle much larger than rounded, pointed outer metatarsal tubercle; tarsus smooth; sole of foot smooth; heel smooth.

Color pattern in preservative: Dorsum brown, snout with white cast on brown; scattered light spots along upper lip; limbs barred; belly gray with several distinct, small, light spots; posterior face of thigh uniform brown.
Measurements: SVL 19.6 mm; head length 7.7 mm, head width 7.0 mm, femur 9.4 mm, tibia 8.9 mm, foot 8.5 mm.

Variation: Two other adult female paratypes measure 19.7 and 20.0 mm SVL. The fourth paratype appears to be a juvenile female, 14.6 mm SVL. Four specimens (University of Texas at Arlington A 4940-4943) from Colombia, Vaupés, Yapima are referred to this species. Three of these are males, the fourth appears to be a small, poorly preserved female. Two of the males have large external vocal sacs and measure 13.3 and 13.8 mm SVL. The males are similar to the females in body proportions, coloration, and texture. The male fingers are notably reduced (especially the fourth), the finger tips more drawn out and the toe papillae more pronounced than in the females. These differences probably represent sexual dimorphism, but could represent differentiation at the species level. As the critical material is lacking (unquestionable males and females from the same locality), the conservative decision of referring the Colombian specimens rather than including them in the type series is taken.

Mating call: Each call consists of from 1 to 10 notes. Each note is diphasic; the first portion of the note lasts for about .009 s with a .001 s interval between the second portion which lasts about .014 s (Fig. 3). The fundamental frequency of the note is about 1600 hz for the first phase, 1650 hz for the second. The dominant (harmonic) frequency is about 3200-3700 hz (Fig. 4).

Etymology: Named for Miriam Heyer, an industrious field collector whose quick reflexes result in captures of many forest floor frogs.

**Leptodactylus “pentadactylus”**

There appear to be two closely related large species of the *pentadactylus* (Laurenti), 1768, complex in the Amazon basin. All of the specimens from the Madeira belong to a single species. The proper allocation of these specimens is deferred pending a planned revision of the group.

**Microhylid**

A single 27 mm specimen of a microhylid has the following external features: no tympanum; finger tips swollen; 5 toes; toes disked, disks not grooved; toes with basal web; posterior face of thigh with a light pin stripe joining a very short mid-dorsal stripe above the anus.

An X-ray of the animal provides the following osteological information: digit tips simple; 8 presacral vertebrae; last presacral vertebra procoelous; maxillary arch incomplete. The X-ray appears to also show the following, although the X-rays are ambiguous: a clavicle present; posterior prevomer questionably absent; palatine absent; coccyx without processes.

There is only one genus of New World microhylids with the eighth presacral vertebra procoelous: *Myersiella*. The specimen at hand clearly differs at the species level in that the toes are distinctly disked and basally webbed (*Myersiella microps* (Duméril and Bibron), 1841, has toes lacking disks and web). The specimen probably differs at the genus level in that it appears to lack coccygeal processes but has a clavicle, which both differ from *Myersiella*.
Clearly, what is required to ascertain the identity of the specimen is a cleared and stained preparation to resolve some of the osteological interpretations. At this time, I prefer to point out the availability of the specimen so that when a second is located, the relationships of the species can be clarified.

**Osteocephalus taurinus**

Certain specimens identified as *O. taurinus* Steindachner, 1862, do not match published descriptions well; two species may be included in the material.

**Phyllomedusa nr. boliviana**

The specimens from Restauração match specimens identified as *P. boliviana* Boulenger, 1902, in the USNM. The type locality of Chuñumani, Bolivia, 2000 m, suggests that *P. boliviana* pertains to an upland, not lowland species, however. The iris was black in life and the light lateral markings were salmon pink.

**References**


Table 1. Distribution of states among taxa

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<thead>
<tr>
<th>Taxa</th>
<th>Character number and state</th>
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<tr>
<td>E. myrmecoides</td>
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<tr>
<td>new species</td>
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</table>
Appendix 1. List of Localities

Rio Acre: Acre
1. Igarapé do Nico, 9° 49' S, 67° 36' W

Rio Purus: Amazonas
2. Boca do Acre, 8° 45' S, 67° 24' W
3. Boca do Pauini, 7° 47' S, 67° 05' W
4. Pauini, 7° 40' S, 66° 58' W
5. Seringal América, 7° 39' S, 65° 35' W
6. Paciá, 7° 09' S, 64° 39' W
7. Mucuripe, 7° 05' S, 64° 36' W
8. Açaituba, 7° 01' S, 64° 35' W
9. Novo Areal, 6° 41' S, 64° 35' W
10. Canutama, 6° 33' S, 64° 21' W
11. Tapauá, 5° 46' S, 63° 02' W
12. Santa Luzia, 4° 43' S, 62° 41' W
13. Beruri, 3° 54' S, 61° 22' W

Rio Solimões: Amazonas
14. Manacapuru, 3° 18' S, 60° 36' W

Rio Madeira: Rondônia
15. Cachoeira de Santo Antônio, 8° 43' S, 63° 55' W
16. Porto Velho, 8° 46' S, 63° 55' W
17. Foz do Jamari, 8° 28' S, 63° 30' W
18. São Carlos, 8° 28' S, 63° 30' W
19. Calama, 8° 04' S, 62° 52' W

Rio Madeira: Amazonas
20. Igarapé Puruzinho, 7° 24' S, 63° 00' W
21. Restauração, 7° 04' S, 62° 53' W
22. Curuçá, 6° 02' S, 61° 42' W
23. Manicoré, 5° 50' S, 61° 17' W
24. Remanso, 5° 38' S, 61° 15' W
25. Barreiro do Matupiri, 5° 34' S, 61° 07' W
26. Cachoeirinha, 5° 30' S, 60° 56' W
27. Novo Aripuanã, 5° 07' S, 60° 23' W
28. Guajarã, 4° 20' S, 59° 42' W
29. Borba, 4° 25' S, 59° 35' W

Appendix 2. List of Species and Locality Numbers

Bufonidae

Bufo granulosus 16, 18, 19, 20, 22, 23, 26, 27, 29
Bufo marinus 2, 3, 10, 11, 15, 17, 18, 19, 20, 21, 22, 23, 26, 29
Bufo typhonius 1, 7, 8, 10, 11, 13, 17, 19, 20, 21, 25, 26, 28, 29
Dendrophryniscus minutus 13, 22, 29

Dendrobatidae

Colostethus peruvianus 1, 3, 17, 19, 21, 25, 26, 29
Colostethus sp. 7
Papeis Avulsos de Zoologia

Dendrobates quinquevittatus 13, 20
Phyllobates femoralis 1, 20, 22, 29
Phyllobates pictus 7, 10, 13, 20, 29
Phyllobates trivittatus 21

Hylidae

Hyla acreana 3, 4
Hyla boans 12, 17, 21
Hyla nr. boesemani 11
Hyla brevifrons 20
Hyla calcarata 7
Hyla fasciata 3, 4, 7, 10, 11, 17, 19, 20, 21, 22, 24, 26
Hyla garbei 8, 13, 19, 20, 21, 22, 26, 29
Hyla geographic a 13
Hyla granosa 4, 6, 7, 8
Hyla haraldschultzi 13
Hyla lanciformis 2, 4, 11, 13, 20, 22, 29
Hyla lealii 2, 3, 11, 15, 18, 19, 21, 27
Hyla leucophyllata 2, 4, 5, 6, 8, 10, 20, 21
Hyla marmorata 4
Hyla "membranacea" 10, 20
Hyla parviceps 6, 8, 11
Hyla pauiniensis 3
Hyla punctata 2, 10, 18, 22, 25, 29
Hyla raniceps 13, 14, 17, 18, 19, 20, 21
Hyla rhodopepla 4, 22
Hyla riveroi 4, 8, 9, 10, 11
Hyla rossalleni 5
Hyla rubra 2, 3, 4, 10, 11, 13, 18, 19, 20, 21
Hyla sarayacuensis 4
Hyla triangulum 2, 8
Hyla walfordi 14, 15, 21, 22, 23, 27, 29
Hyla nr. blairi A 17, 22
Hyla nr. blairi B 17, 19, 20, 21
Hyla sp. C 3, 10, 19, 22
Hyla sp. D 4
Hyla sp. E 4, 7
Osteocephalus buckleyi 3, 7, 11, 25
Osteocephalus taurinus 2, 7, 10
Phrynophyias venulosa 2, 3, 4, 19, 25
Phyllomedusa nr. boliviana 21
Phyllomedusa palliata 2, 4
Phyllomedusa tomopterna 4, 10
Phyllomedusa vaillanti 10, 11, 13, 20, 25, 26
Sphaenorhyncus carneus 3, 5
Sphaenorhyncus dorisae 3, 5, 13
Sphaenorhyncus eurhostus 2, 3, 5, 8, 10, 13, 20, 29

Leptodactylidae

Adenomera andreae 7, 10, 15, 17, 19, 20, 21, 22, 25, 29
Adenomera hylaedactyla 18, 22, 23, 29
Ceratophrys cornuta 17, 20
Edalorrhina perezi 20
Eleutherodactylus fenestratus 2, 3, 8, 15, 20, 21, 22
Eleutherodactylus nr. martiae 11, 13, 22, 25, 29
Eleutherodactylus nr. variabilis 7, 11
Eleutherodactylus sp. 15
Hydrolaetare schmidti 10, 13, 29
Leptodactylus bolivianus 1, 2, 17, 18, 19, 29
Leptodactylus fuscus 18, 19, 20, 21
Leptodactylus mystaceus 13, 19
Leptodactylus ocellatus 13, 23
Leptodactylus "pentadactylus" 19, 25, 26, 27
Leptodactylus stenodema 21
Leptodactylus wagneri 1, 2, 3, 4, 5, 7, 10, 11, 13, 17, 18, 19, 20, 21, 22, 23, 29
Lithodytes lineatus 11, 20
Physalaemus petersi 11, 20
Phyzelaphryne miriamae 20

Microhylidae

Elachistocleis ovalis 17, 18, 19, 20
Hamptophryne boliviana 10, 17, 25, 28
microhylid 25

Pseudidae

Lysapsus limellus 13, 29
Fig. 1. Hyla panamensis, holotype, dorsal view.
Fig. 2. Physalaephryne miriamae, holotype, dorsal view.
Fig. 3. Sonagram of mating call of *Phylaphryne miriamae*. Vertical scale marks at 1 KHz intervals. Horizontal scale mark indicates 1 second. Recording of William F. Pyburn number 12-76 from Yapima, Colombia. Recorded on 21 April 1976, air temperature 22.0°C.
Fig. 4. Strip chart recording of mating call of *Pheronemomiranda*. Line indicates 0.01 second. Recording data same as for Fig. 3.