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# A NEW GENUS AND TWO NEW SPECIES OF MINUTE LEPTODACTYLID FROGS FROM NORTHERN SOUTH AMERICA, WITH COMMENTS UPON *PHYZELAPHRYNE* (AMPHIBIA: ANURA: LEPTODACTYLIDAE)

by

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and

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Hoogmoed, M. S., & J. Lescure: A new genus and two new species of minute leptodactylid frogs from northern South America, with comments upon *Phyzelaphryne* (Amphibia: Anura: Leptodactylidae).

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Key words: Anura; Leptodactylidae; genera; *Adelophryne* gen. nov.; *Eleutherodactylus*; *Phyzelaphryne*; key; Neotropics.

The synonymisation of *Phyzelaphryne miriamae* Heyer with *Eleutherodactylus nigrovittatus* Andersson is denied and it is shown that both species are quite distinct in numerous characters. A new genus (*Adelophryne*) of minute leptodactylid frogs with pointed discs on the toes and a distinctly reduced fourth finger, containing two new species (*A. adiastola* spec. nov. and *A. gutturosa* spec. nov.) is described from northern South America. A key to separate the diminutive leptodactylid frogs with pointed toetips is given. The relationships of the new genus are not clear, but possibly are with one of the species groups of *Eleutherodactylus*, of the subfamily Eleutherodactylinae.

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## RESUMEN

Se niega la sinonimisación de *Phyzelaphryne miriamae* Heyer con *Eleutherodactylus nigrovittatus* Andersson y se muestra que las dos especies son bastante distincta en numerosas características. Se describe un nuevo genero (*Adelophryne*) de ranas leptodactylidos menudas con discos

puntiagudos en los dedos del pie y con el dedo cuarto del mano reducido, conteniendo dos especies nuevas (*A. adiastola* spec. nov. y *A. gutturosa* spec. nov.) del norte de America del Sur. Se presenta una clave para la distinctión de las especies pequeñas de ranas leptodactylidos con dedos del pie puntiagudos. Las relaciones del genero nuevo no son claro, pero tal vez son con uno de los grupos de especies de *Eleutherodactylus*, de los Eleutherodactylinos.

## SOMMAIRE

La mise en synonymie de *Phyzelaphryne miriamae* Heyer avec *Eleutherodactylus nigrovittatus* Andersson n'est pas valable car de nombreux caractères distinguent vraiment les deux espèces. *Adelophryne*, un nouveau genre de très petits Leptodactylidés, identifiable par des disques pointus à l'extrémité des orteils et un quatrième doigt nettement réduit, et ses deux espèces originiaires du nord de l'Amérique du Sud, *A. adiastola* spec. nov. et *A. gutturosa* spec. nov., sont décrites. Une clé est établie pour différencier les petits Leptodactylidés qui ont l'extrémité des orteils pointue. *Adelophryne* est à notre avis un Eleutherodactyliné, mais ses relations avec les autres genres de cette sous-famille ne sont pas encore claires.

## INTRODUCTION

From Amazonian South America several small species of leptodactylid frogs have been described recently. These species, though probably not directly related, agree in being very small, having pointed tips of fingers and toes, lacking webbing between the toes, and probably share the same type of habitat, *viz.*, leaf-litter.

Lynch (1976) described two species from eastern Ecuador and northeastern Peru, which he considered belonging to the genus *Euparkerella,* otherwise only known from the species *E. brasiliensis* (Parker) from southeastern Brazil. The two new species (*E. lochites* and *E. myrmecoides*) differ from *E. brasiliensis* in their more slender habitus, in having a middle ear, in having an inner tarsal tubercle, in having a proportionally longer fifth toe and in being smaller and more slender. Lynch (1976) considered the fact that the three species agreed with each other in having lost one phalanx in the fourth finger, in the condition of the palate and in the arrangement of skull bones, more important than the differences mentioned before and consequently considered them congeneric.

Heyer (1977), on the occasion of the study of a collection of frogs from the Rio Madeira, evaluated the relationships between *Barycholos*, a few species of *Eleutherodactylus* (among which *E. nigrovittatus* Andersson), *Euparkerella brasiliensis, E. myrmecoides* and some specimens of a new frog species. On the basis of his analysis he came to the conclusion that the supposed relationship between *E. brasiliensis* and *E. myrmecoides* was based upon characters of loss

and therefore was suspect. He came to the conclusion that they only shared two derived character states, but differed in eight others. According to Heyer (1977) the shared characters could be consequences of small size and the characters separating them could reflect a functional feeding shift in *E. brasiliensis* and a functional locomotory shift in *E. myrmecoides*. These data induced Heyer to erect the new genus *Phyllonastes* in order to accomodate the two species *myrmecoides* and *lochites*. He ascribed the similarities largely to "convergent adaptations to the leaf litter habitat". Another result of his evaluation was that he described the specimens of his new frog in the new genus *Phyzelaphryne* under the specific name *P. miriamae*. The genus and species are a.o. distinguished by having terminal digital papillae, distinct vomerine teeth, a single subarticular tubercle under the fourth finger and three phalanges in the fourth finger.

Apart from the holotype and the three topotypic paratypes Heyer (1977) studied four additional frogs from the Vaupés River. Because of differences which he attributed to sexual dimorphism, but of which he also said they could represent differentiation at the species level, he excluded these four specimens from the type-series.

Lynch (1980b) considered *P. miriamae* conspecific with *Eleutherodactylus nigrovittatus* and in this decision was followed by Lynch & Lescure (1980). From the text it appears that Lynch (1980b) did not study the holotype, nor any of the paratypes of *P. miriamae,* but solely based his decision on the description and illustration of *P. miriamae*. According to Lynch (1980b), Heyer (1977) wrongly stated than the distal subarticular tubercle under finger IV of *P. miriamae* was lost and he attributed this to the fact that the proximal subarticular tubercles of fingers III and IV in *E. nigrovittatus* are relatively large and more distinct than the distal tubercles under these fingers. Our re-examination of all type-material of *P. miriamae* and direct comparison of it with fresh specimens of *E. nigrovittatus* leads us to disagree with Lynch and to reinstate the genus *Phyzelaphryne*.

Small specimens of frogs, apparently adult, from Roraima and Serra do Navio instigated the present study. Initially we arranged the specimens in the genus *Euparkerella* as defined by Lynch (1976), buth Heyer's (1977) article prompted us to reconsider our former opinion. Direct comparison of these specimens with the paratypes of *P. miriamae* and with the Vaupés specimens mentioned by Heyer (1977) convinced us that the Vaupés specimens were different from the types of *P. miriamae* and together with the new material formed a new genus, containing two species.

## SPECIES ACCOUNTS

### **Phyzelaphryne miriamae** Heyer, 1977
(figs. 1, 3, 4, 11)

*Phyzelaphryne miriamae* Heyer, 1977: 153.

*Eleutherodactylus nigrovittatus*: Lynch, 1980b: 301 (partly); Lynch & Lescure, 1980: 311 (partly); Harding, 1983: 272.

Material of *P. miriamae*. — 1 ♀, MZUSP 49894 (holotype), Igarapé Puruzinho, Rio Madeira, Amazonas, Brazil, 5-xi-1975, leg. M. H. and W. R. Heyer, F. do Val, P. E. Vanzolini; 2 ♀, 1 ♂, USNM 202607-8, MZUSP 49895 (paratypes), as holotype, but 5/6-xii-1975; 1 ♂, USNM 239363, Parque Rio Tapajos, 75 km SW of Itaituba, Pará, Brazil, 20-i-1979, leg. R. I. Crombie; 1 ex., DZUB not registered, Humaita, Rio Madeira, Amazonas, Brazil, 9-iii-1975, leg. U. Caramaschi.

Comparative material of *E. nigrovittatus*. — Peru. Depto. Loreto. Colonia: 1 ♀, 2 ♂, MNHNP 1978-2839, 2844, 2845, January-March 1978, leg. P. Razon; 1 ♂, MNHNP 1978-2840, 30-v-1978, leg. J. Lescure; 1 ♀, 3 ♂, MNHNP 1978-2841, 2842, 2843, 2846, 12/14-vi-1978, leg. J. Lescure.

Ecuador. Napo Province. Loreto: 1 ♀, RMNH 21638, leg. J. Olalla. Pastaza Province. Shiona: 1 ♀, 2 ex., RMNH 21639-41, 26-iv-1983, 2 ♀, RMNH 21643-4, 13-viii-1983, 1 ♂, RMNH 21645, 14-viii-1983, all leg. M. S. Hoogmoed & A. Almendariz. Montalvo: 1 hgr., RMNH 21646, 16-viii-1983, leg. M. S. Hoogmoed & A. Almendariz. Pozo Huito, 85 km E. Montalvo: 1 ♀, RMNH 21642, 22-iv-1983, leg. M. S. Hoogmoed & A. Almendariz.

Comparative material of *Phyllonastes myrmecoides*. — Peru. Dpto. Loreto. Colonia: 2 ♀, MNHNP 1979-7898/9, January – April 1978, leg. P. Razon.

Brazil. Amazonas. Igarapé Belém (near Rio Solimoes), ± 70 km E. Leticia: 2 ♀, 1 ♂, AMNH 97050-52, 18/28-v-1970, leg. B. Malkin.

These two localities extend the known range of this species, so far only reported from the surroundings of Iquitos, about 400 km to the east.

Description. — The description given by Heyer (1977: 153-154) of this species mostly is correct, but needs some additions and/or corrections on several points. In the following account only those characters are mentioned in which we noticed differences with Heyer's description.

In lateral profile the snout is truncate to rounded. Loreal region nearly vertical, slightly concave. When viewed from above, the eyes project beyond the circumference of the head (fig. 1). The tympanic annulus is complete. There is an oblique glandular ridge from some distance below the tympanum (not in contact with the tympanic annulus) to the insertion of the forelimb (fig. 1). Dorsal and lateral surfaces not granular, but shagreened. The tongue has a short narrow stem, which widens into a large subcircular head, free over its entire length. Vomerine teeth ca. 10. The relative length of the fingers depends on the method used at measuring. When the fingers are pressed against each other, the second finger is slightly longer than the first, when measured from the base of the corresponding basal subarticular tubercle, they are of equal length. Thus, Heyer's formula is correct, but should be interpreted ac-

cording to the above statement. The fourth finger has three phalanges, of which the second one is rectangular. The small discs on top of fingers III and IV are pointed, with shallow lateral grooves, which are interrupted at the tip. Tips of fingers I and II hardly expanded into discs, pointed, without lateral grooves. The metacarpal tubercles oval, three additional palmar tubercles (fig. 3a). Discs of toes deeply grooved laterally, narrowly interrupted at the pointed tip. Subarticular tubercles of both fingers and toes well developed, salient. Fingers I-V with respectively, one, one, two and one tubercles, toes I-IV with respectively, one, one, two, three and two tubercles. Both fingers and toes round in cross-section. Inner metatarsal tubercle oval, no additional solar or tarsal tubercles (fig. 3b). There is a white subtympanic stripe from below the eye to the insertion of the arm, which in its posterior part coincides with the glandular subtympanic ridge. An indistinct, narrow, interrupted darker vertebral stripe.

Colour in life of male USNM 239363 (field notes of R. I. Crombie): "Above yellowish brown, becoming grayish on head and more chestnut on rump. Suggestion of yellow on sides, in groin and on thighs. Indistinct grayish lateral line from eye to just past axilla; darker one from naris-eye. Belly gray with distinct white spots."

The "fourth paratype" mentioned by Heyer (1977: 154) as having a snout-vent length of 14.6 mm and surmised to be a juvenile female, in our opinion is a male (MZUSP 49895). It has vocal slits and a subgular vocal sac which is indicated by longitudinal folds in the posterior part of the throat. The throat also is darker than in the females. According to measurements by MSH in 1981 the snoutvent length of this specimen is 15.1 mm (see table 2).

Discussion. — In our opinion the generic definition should include a statement about the number of phalanges in the fingers (2-2-3-3) and that in the toes (2-2-3-4-3) and it also should be made clear that the terminal phalanges of both fingers and toes are T-shaped. The well defined, oblique subtympanic gland, not in contact with the tympanic annulus (complete), should also be included. From our study of the types (MZUSP 49894-5, USNM 202607-8) of *P. miriamae* it became clear to us that Heyer (1977) was correct in assigning this taxon to a new genus and that Lynch's (1980b) conclusion that *P. miriamae* is synonymous with *Eleutherodactylus nigrovittatus* is wrong, because it is not substantiated by our findings. As stated above, we strongly suspect that Lynch (1980b), being convinced of his right interpretation, did not study the type-specimens of *P. mariamae* and only based himself on the published account and illustration. On this evidence, he brushed aside Heyer's (1977) observation that under the fourth finger only a single subarticular tubercle was present and implied that this was based on defective observation on Heyer's

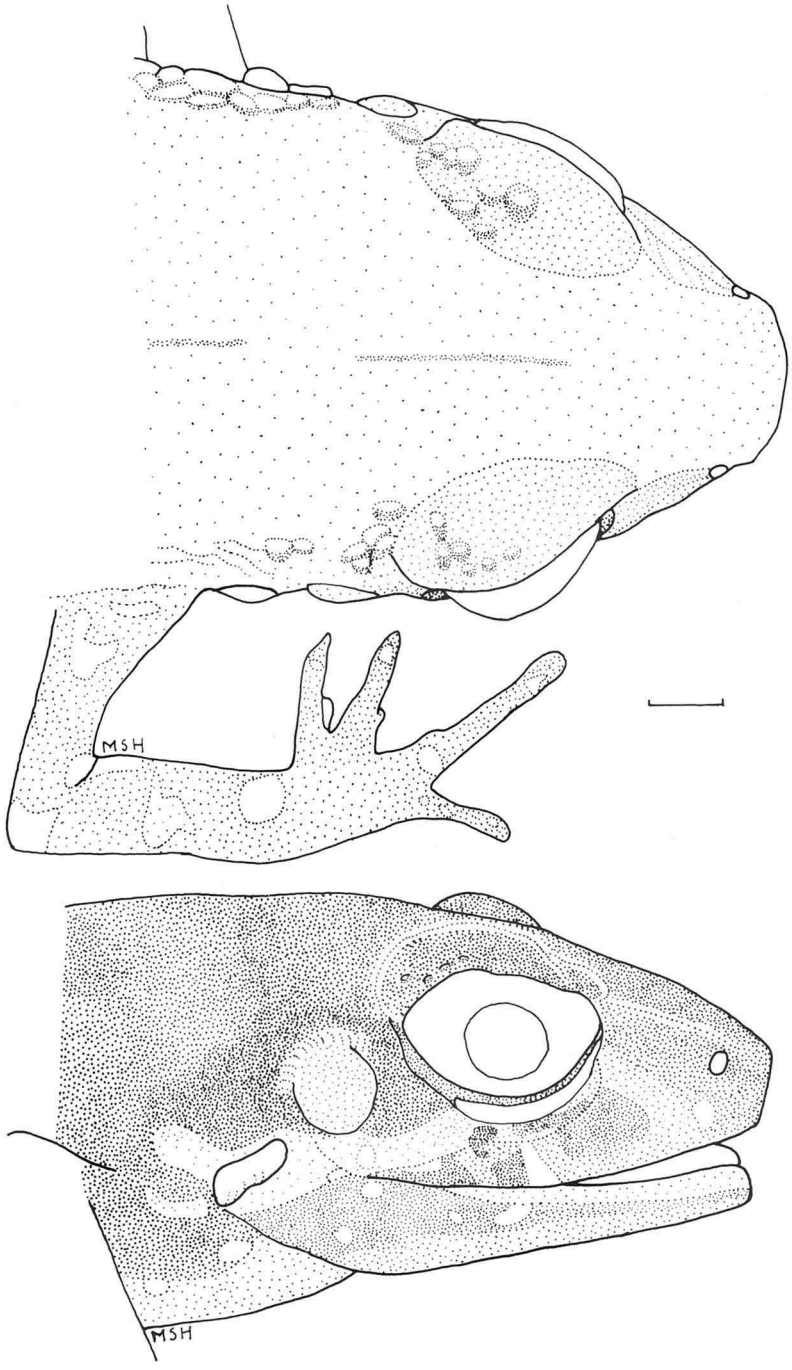


Fig. 1. *Phyzelaphryne miriamae* (USNM 202608). Dorsal (upper) and lateral (lower) view of head. The bar represents 1 mm.

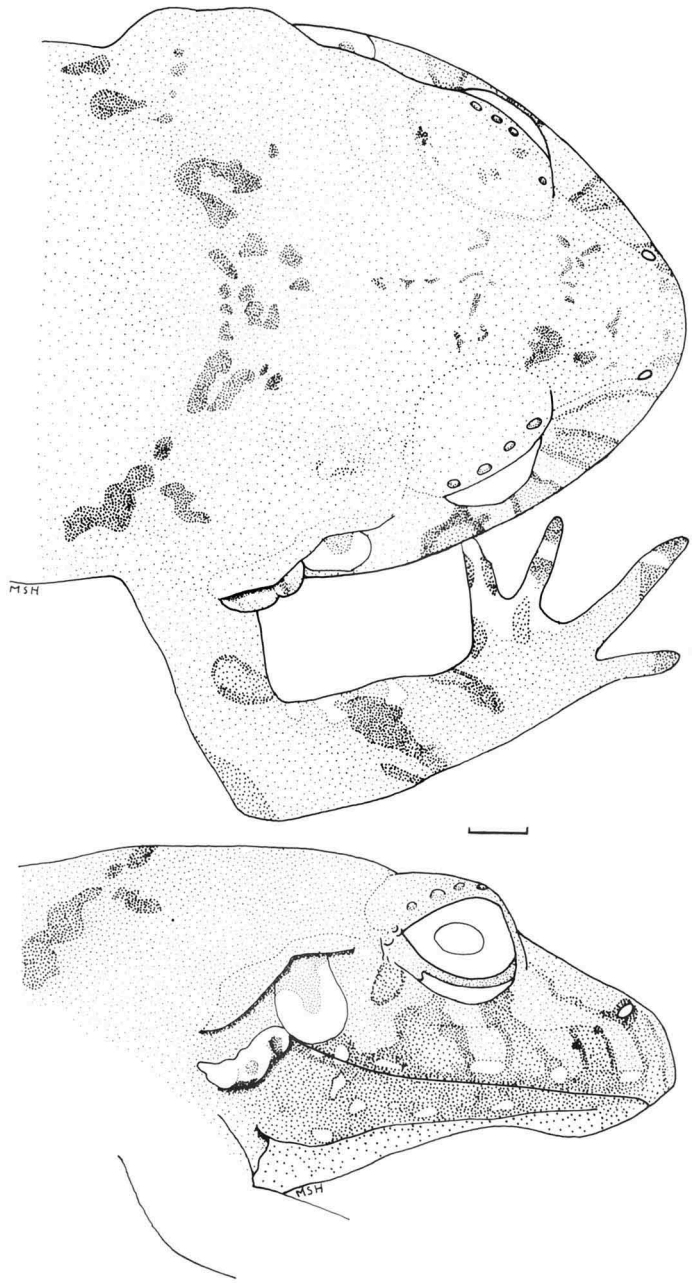


Fig. 2. *Eleutherodactylus nigrovittatus* (RMNH 21642). Dorsal (upper) and lateral (lower) view of head. The bar represents 1 mm.

part. Our recent examination of the types of *P. miriamae* completely corroborates Heyer's observation that there is only a single, well developed subarticular tubercle under the fourth finger. As *P. miriamae* has three phalanges in the fourth finger, in combination with a single subarticular tubercle, this observation is in contradiction with Lynch's (1976) statement that loss of a phalange in leptodactylid frogs is accompanied by loss of a corresponding subarticular tubercle. As Heyer (1977) correctly concluded, *P. miriamae* shows "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".

Lynch's (1980b) statement about the configuration of subarticular tubercles in *Eleutherodactylus nigrovittatus* is correct and we could ascertain it with the material at our disposition (part of which (MNHP 1978–2839/46) was also examined and identified as such by Lynch & Lescure (1980)). However, comparison of figs. 3a and 3c will make clear that they represent completely different situations, which are not due to simple variation. Indeed, the distal subarticular tubercle under the fourth finger in *E. nigrovittatus* (fig. 3c) is less distinct than the proximal one (fig. 3a), but still distinct enough to be observed, whereas in *P. miriamae* this tubercle is completely absent. Another, easily observed difference between the two species is the shape of the head. In *P. miriamae* (fig. 1) the sides are nearly vertical, causing the eyes to project beyond the circumference of the head when viewed from above (also see fig. 2 in Heyer (1977)), whereas in *E. nigrovittatus* (fig. 2) the sides of the head are sloping outward, causing the eyes to fall completely within the circumference of the head (also see fig. 7 in Lynch (1980b)). Moreover, males of *P. miriamae* have snouts that do not differ in shape from those of the females, whereas in *E. nigrovittatus* the males are reminiscent of male *Adenomera* and have a shovel-shaped fleshy ridge on the snout (Lynch, 1980b: fig. 7). These and other differences between the two species have been tabulated in table 1 and in our opinion clearly show that we are dealing with two taxa.

## **Adelophryne** gen. nov.

Type species: *Adelophryne adiastola* spec. nov.

Diagnosis. — A genus of minute leptodactylid frogs, with asymmetrically pointed, laterally grooved, elongate discs, digits flattened, fourth finger reduced in size, having two or three phalanges and only one subarticular tubercle. This combination of characters distinguishes it from other small leptodactylids with pointed discs (*Euparkerella, Phyllonastes, Phyzelaphryne, Eleutherodactylus*). *Adelophryne* differs from *Phyzelaphryne* in having flat-

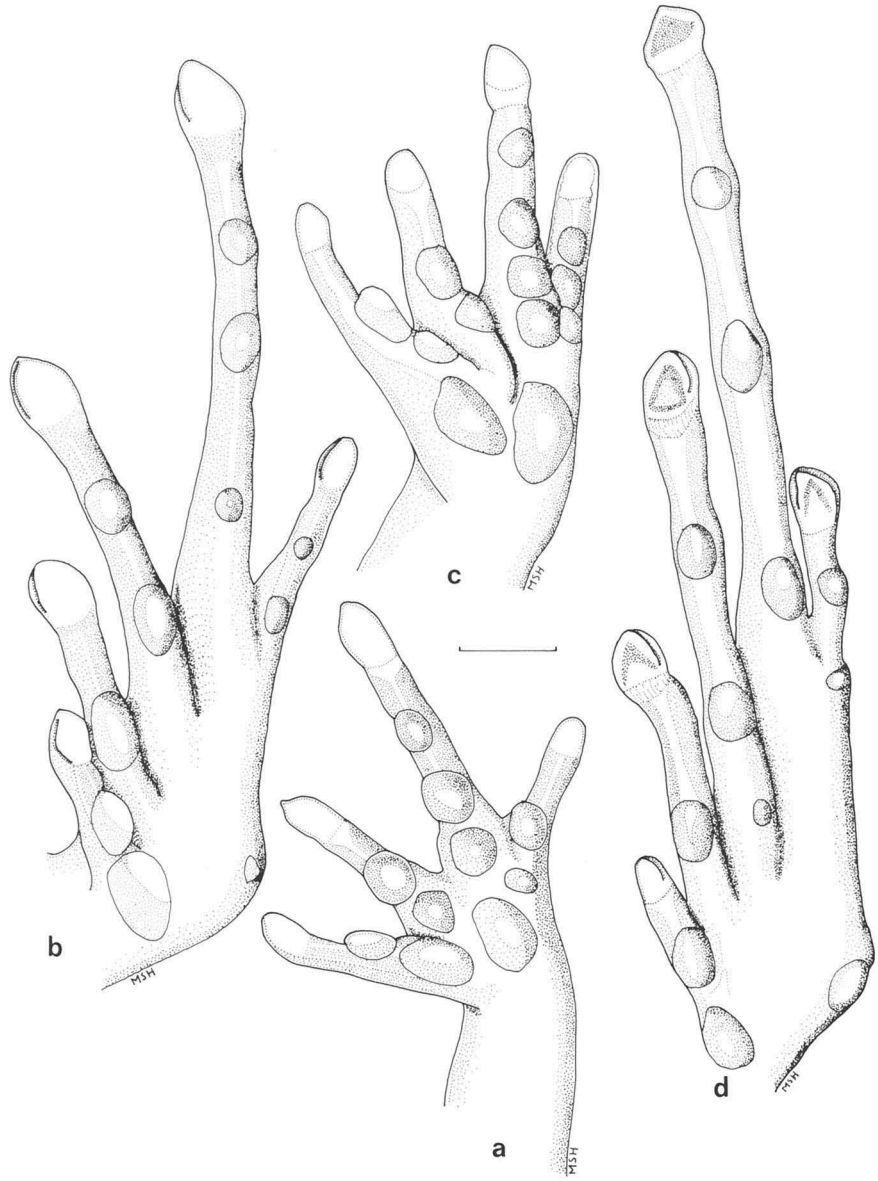


Fig. 3. Palmar (a, c) and plantar (b, d) surfaces of hands and feet. a, b: *Phyzelaphryne miriamae* (USNM 202608); c, d: *Eleutherodactylus nigrovittatus* (RMNH 21642). The bar represents 1 mm.

tened digits, indistinct subarticular tubercles, a long and slender tongue and in showing reduction of the phanlanges in the fourth finger. From *Phyllonastes* and *Euparkerella* it differs in having vomerine teeth, in lacking a tarsal tubercle and in the variable number of phalanges in the fourth finger. From *Eleutherodactylus* it differs in having only one subarticular tubercle under the fourth finger, and in showing a distinct reduction in size of the fourth finger.

Description. — Minute (snout-vent length adults not exceeding 15 mm) leptodactylid frogs, with horizontally oval pupil, a distinct tympanum with an incomplete tympanic annulus, smooth to granular skin, a subtympanic glandular ridge, asymmetrically pointed, narrow, circumferentially (groove narrowly interrupted at the tip) grooved discs on the toes, fingers with asymmetrically pointed tips, indistinct subarticular tubercles, only a single one under the fourth finger, fingers and toes not webbed, smooth tarsus, small, round outer metatarsal tubercle, large, flat inner metatarsal tubercle. Males with a large, external subgular vocal sac, thumb lacking nuptial asperities. Number of phalanges in fourth finger two or three, terminal phalanges of fingers and toes knobbed or T-shaped. Ilium without a dorsal crest. Frontoparietals meet medially, not exposing a fontanelle, vomerine and maxillary teeth present, occipital condyles widely separated, last presacral vertebra about as wide as the sacrum, sacral diapophyses rounded, distally slightly wider, omosternum without bony element.

Etymology. — From the Greek *adelos*, unseen, unknown, obscure and *phryne*, toad, in reference to the fact that these small froglets hardly have been collected for science until recently. The genus is feminine in gender.

Contents. — Two species, *viz.*, *Adelophryne gutturosa* spec. nov. and *A. adiastola* spec. nov.

Distribution. — Northern South America east of the Andes (roughly the Guiana Shield).

Relationships. — It is difficult to say anything well founded regarding this topic, because the seven specimens available were not dissected to study muscle arrangements and the characters used are mainly external, together with a few skeletal features derived from X-ray photographs. Characters like reduction of the number of subarticular tubercles under the fourth finger, and the reduction of the number of phalanges in the fourth finger are characters involving loss of morphological elements and accordingly provide little information in deducing relationships. A character like pointed discs on the toes probably has an adaptive value, though we are not aware what its use could be, and apparently arose independently in several groups, as the final situation appears to have been realised along different routes. Although nothing is known about the mode of reproduction (amplexus, number and size of eggs,

development of eggs), judging by the size only, it seems most reasonable to suppose *Adelophryne* only produces few large eggs having a large vitellin reserve which would facilitate direct or semi-direct development of the juveniles after the eggs have been deposited. This supposition seems to be strengthened by the fact that development is direct in the similarly sized *Euparkerella*/*Phyllonastes* (Lynch, 1976) living under corresponding circumstances.

Solely based on the available morphological data this genus appears to belong to the tribe Eleutherodactylini of the subfamily Telmatobiinae (Lynch, 1971; Dowling & Duellmann, 1974-1978) or to the subfamily Eleutherodactylinae as defined by Laurent (in press) after Lutz (1954).

For a key to the known species of *Adelophryne*, we refer to the fifth couplet of the general key at the end of this paper.

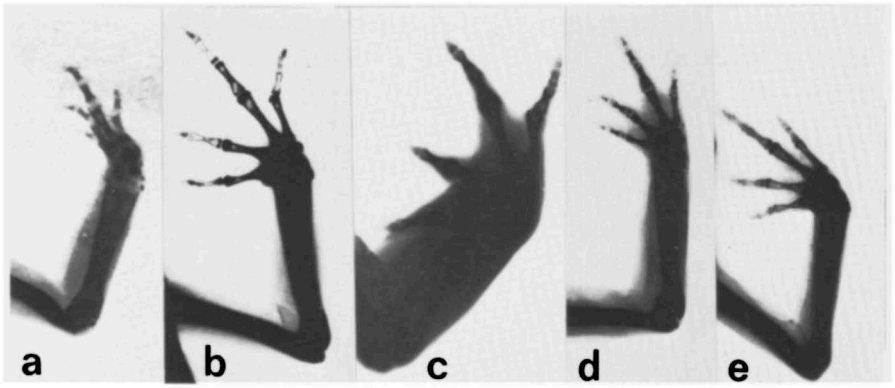


Fig. 4. Radiographs of hands of small eleutherodactyline frogs. a. *Phyllonastes myrmecoides*, b. *Phyzelaphryne miriamae*, c. *Eleutherodactylus nigrovittatus*, d. *Adelophryne adiastola*, e. *A. gutturosa*. The pictures are not to scale and only serve to show the different arrangements of phalanges.

## **Adelophryne adiastola** spec. nov.
(figs. 4, 5, 6, 7, 11)

*Phyzelaphryne miriamae* Heyer, 1977: 154 (partly, referred material only).

Holotype. — ♂, UTACV 4943, Yapima, Vaupés River, Vaupés, Colombia (69°28'W 1°03'N), 21-iv-1976, leg. W. F. Pyburn.
Paratypes. — 1 ♀, 2 ♂, UTACV 4940-42, same data as holotype.

Diagnosis. — A minute (maximum snout-vent length 13.9 mm) frog, fourth finger distinctly reduced, only having two phalanges and one indistinct subarticular tubercle. Fingers and toes depressed, Tips of fingers without discs, with

asymmetrically pointed tips. Tips of toes expanded into circumferentially grooved, asymmetrically pointed discs. Terminal phalanges of fingers bluntly pointed or T-shaped, of toes T-shaped. Skin of back shagreened to granular. Adult males with large subgular vocal sac.

Description. — Snout-vent length 13.0-13.9 mm. Head longer than wide, head slightly wider than adjacent part of body. Snout rounded in dorsal, rounded to truncate in lateral profile, tip of snout round. Distance between eye and tip of snout equal to or slightly longer than the diameter of the eye. Distance between eye and nostril less than the distance between the nostrils, distance between nostril and tip of snout slightly less than 1/3 the distance between eye and tip of snout. Canthus rostralis indistinct, rounded, straight; loreal region sloping steeply to the upper lips, flat. Lips not flaring. Nostrils inferolateral of canthus rostralis, not projecting, a vertically oval opening in a round translucent area, directed laterally. Eye with horizontally oval pupil. Interorbital space more than 1.5 times as wide as an upper eyelid, slightly convex. Temporal region vertical; tympanum small but distinct, round, 0.3–0.4 times the diameter of the eye, surrounded by a distinct, incomplete tympanic annulus; distance between tympanum and eye slightly less than, or equal to, the tympanum diameter. A skinfold from the corner of the mouth to the lower margin of the tympanum; postero-dorsal margin of tympanum obscured by an indistinct supratympanic fold; a glandular series of warts forming an interrupted ridge from the tympanum to the insertion of the forelimb.

Choanae medium-sized, round; prevomerine processes present, bearing a transverse row of two to eight teeth each, posteriorly of the choanae, just anteriorly of the palatine bones. Tongue mushroom-shaped, the capitum only slightly wider than the stem, not notched behind, completely free, except at its anterior margin. Males with long, curved vocal slits and a large, subgular vocal sac, extending onto the anterior part of the chest and to the insertion of the forelimbs.

Skin of back and flanks granular or shagreened, skin of venter smooth, skin of throat at sides granular and wrinkled, the central area smooth, skin of limbs smooth. Discoidal folds absent. Posteroventral aspect of thighs coarsely areolate. Indistinct transverse folds of skin present on the upper surface of the wrists and on the posterior aspect of the heels.

Hand with a large, undivided, flat, oval outer and a smaller, flat, oval inner metacarpal tubercle. Subarticular tubercles present, but indistinct, large, flat and oval, one under each finger, except under the third, which has two of them. A single, indistinct, flat, round supernumerary palmar tubercle at the base of the third finger. Fingers free of web, no lateral fringes, fingers not expanded into pads or discs, with an asymmetrically pointed tip, distinctly de-

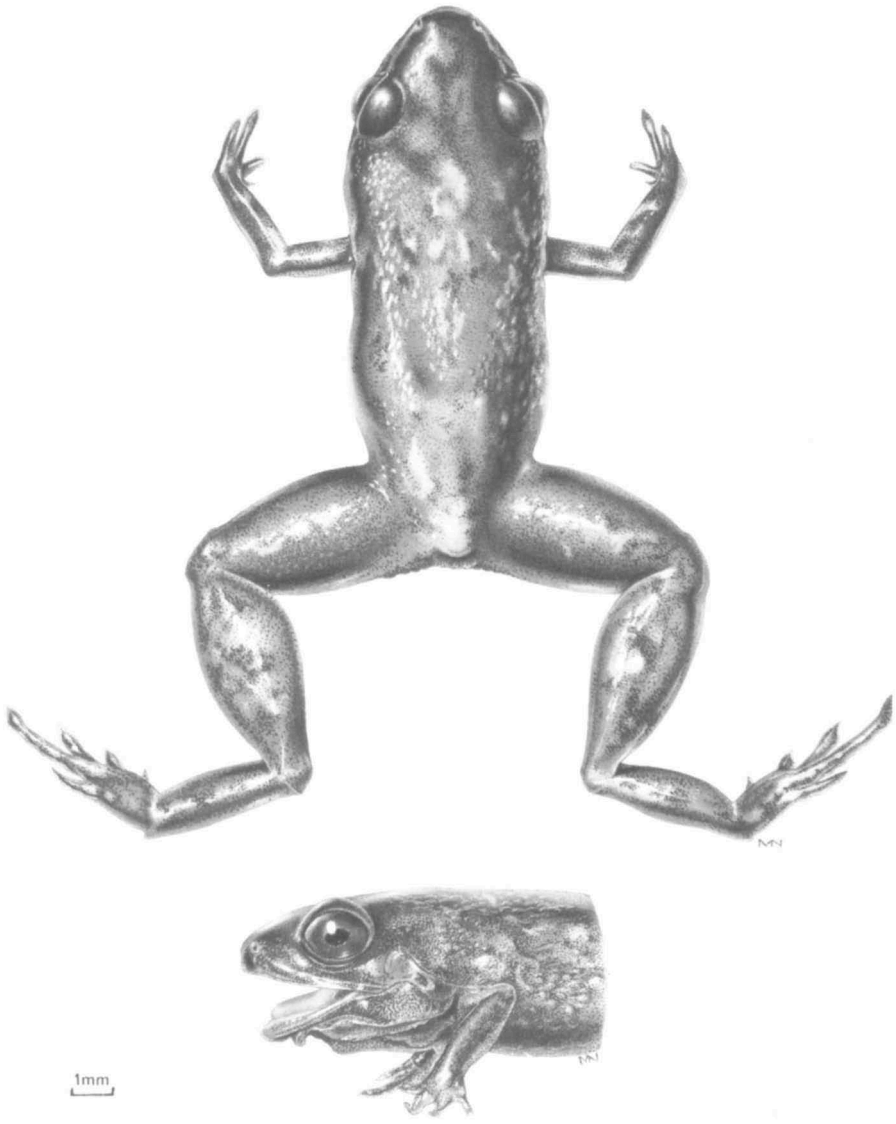


Fig. 5. *Adelophryne adiastola* (UTACV 4943). Dorsal habitus and lateral view of left side of head.

pressed, without circumferential groove. Fingers: I < IV < II < III, fourth finger very small, free part less than half the free part of the third finger. Phalangeal formula 2-2-3-2, terminal phalanges of fingers II and III T-shaped, of fingers I and IV knobbed or bluntly pointed.

Tarsus smooth, without a tarsal ridge or tubercle. A large, flat, oval inner and a smaller, protruding, round outer metatarsal tubercle, approximately half the size of the inner one. Subarticular "tubercles" flat, oval, indistinct, the basal ones of toes IV and V most distinct. Tips of toes dilated into small asymmetrical discs, slightly wider than the toes, ending in an asymmetrical papillate point; discs with a circumferential groove which is narrowly interrupted at the tip. Toes distinctly depressed, free of webs and lateral fringes. Toes: I < II < V <IV <III. Phalangeal formula 2-2-3-4-3, terminal phalanges T-shaped.

When the hindlimbs are flexed at right angles to the sagittal plane, the heels slightly overlap. Tibia 46-48% of the snouth-vent length.

In preservative the back is light brown with diffuse darker brown spots, of which a few in the scapular region seem to be rather constant, snout with indistinct dark brown reticulation. Sides of head dark brown, a dark brown supratympanic spot. One or two glands in the ridge between tympanum and insertion of the forelimb may be white-tipped. Indications of a faint light dorsolateral line seem to be present. Lower arm with a wide dark brown transverse band an a narrower one on the wrist. Tibia and tarsus with three transverse dark brown bands, posterior surface of the thighs appears immaculately dark brown. Belly white, dusted with minuscule brown spots (melanophores), leaving immaculate white areas; throat brown with white spots. Subgular sac in males dark brown, blackish towards the sides, with white spots. A series of larger white spots along the margin of the lower jaw.

For measurements, see table 2.

Remarks. — UTACV 4940 does resemble the other three specimens of the series in most characters, but it shows a number of important differences as well. Though it is a male, with well developed testes and curved vocal slits, and was caught calling in leaf-litter (label data; Heyer, 1977) it lacks the large subgular vocal sac present in the other two males. The tympanic annulus is lacking, there is no supratympanic fold and there is no row of distinct glands between the tympanum and the insertion of the forelimb. Also, the tongue seems to be shaped differently, with a shorter stem and a greater mushroom-shaped head, but this might very well be an artifact of preservation and we donot attach much value to it. Moreover, UTACV 4940 shows rather large epiphyses, indicating it is a young specimen in which the bony elements of fingers and toes are still growing. In the other two males (UTACV 4941 and 4943) the phalanges are full-grown and lack these epiphyses. As in all other

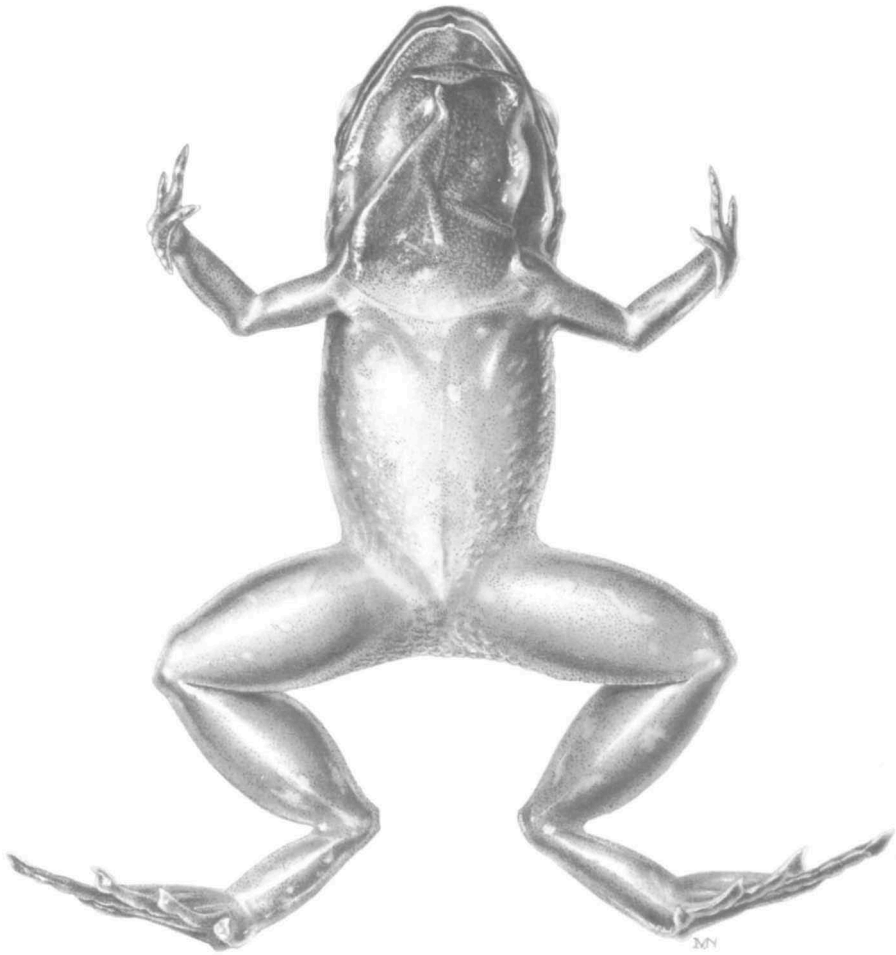


Fig. 6. *Adelophryne adiastola* (UTACV 4943). Ventral habitus.


Fig. 7. *Adelophryne adiastola* (UTACV 4943). Plantar (left) and palmar (right) surfaces of right foot and hand.

characters: body proportions, skin texture, morphology of head, hands and feet, colour pattern and, as far as we could ascertain from X-ray photographs, skeleton, there are no differences, we consider UTACV 4940 conspecific with the other three specimens in the type-series and assume that there is rather extensive age variation in the characters mentioned above. Of course we cannot rule out the possibility that sexually dimorphic characters are involved that have not yet expressed themselves completely, due to differences in the sexual cycle.

Natural history. — Only few data are available. All specimens were collected in the leaf litter near streams (pers. com. W. F. Pyburn). As explained above, UTACV 4940 is a young adult male, which was caught calling among leaf-litter. A sonagram and a strip chart recording of the call (at 22°C) were published by Heyer (1977: figs. 3, 4). The other two males in the type-series have large, extended vocal sacs the adult female (UTACV 4942) has well developed oviducts and some rather large, white ovarian eggs. Apparently the specimens were in breeding condition. From remarks by Pyburn (1977) it might be concluded that the types were collected during the rainy season.

The female had swallowed a small harvest-man (Sironidae, Opilionida, Chelicerata) of a group of soil and leaf litter inhabitants.

The region of Yapima is in the tropical lowland rainforest zone ("Bosque muy húmedo premontano (Transición cálida)") (I.G.A.C., 1977) of Colombia, close to the Brazilian border, in the Amazonian drainage.

Etymology. — From the Greek *adiastolos*, not separated, confused, in reference to the fact that originally these specimens were referred to *Phyzelaphryne miriamae*.

## **Adelophryne gutturosa** spec. nov.
(figs. 4, 8, 9, 10, 11)

*Euparkerella* sp. "A" Hoogmoed, 1979: 269.

Holotype. — ♂, BM 1983. 1139, between camp IV and V, northern slopes of Mount Roraima, Guyana (60°46'W 5°17'N), 3000 feet (914 m), 26-viii-1971, leg. A. N. Warren.

Paratypes. — 1 ♀, 1 juv., LACM 44277-8, Serra do Veado, Serra do Navio, hills E. of mines, Territorio Amapá, Brazil (52°5'W 1°N), 300 m, vii-1968, leg. P.A. Silverstone.

Diagnosis. — A minute (maximum snout-vent length 14.5 mm) frog, with a slightly reduced fourth finger, having three phalanges and one indistinct subarticular tubercle. Fingers and toes depressed. Tips of fingers without discs, with asymmetrically pointed tips. Tips of toes expanded into circumferentially grooved, asymmetrically pointed discs. Terminal phalanges of fingers and

toes bluntly pointed, knobbed or T-shaped. Skin of back smooth. Adult males with large subgular vocal sac.

Description. — Snout-vent length adults 13-14.5 mm. Head slightly longer than wide, slightly wider than adjacent part of body. Snout truncate in dorsal and lateral profile, tip of snout with an obtuse median point. Distance between eye and tip of snout equal to the diameter of the eye, distance between eye and nostril about twice the distance between nostril and tip of snout. Canthus rostralis indistinct, rounded, straight; loreal region sloping steeply to the upper lips, flat. Lips not flaring. Nostrils inferolateral of canthus rostralis, not projecting, forming a vertical oval opening in a round, translucent area, directed laterally, internarial distance slightly less than interorbital distance. Eye with horizontally oval pupil. Interorbital space 1.5 times as wide as an upper eyelid, slightly convex. Temporal region vertical, tympanum small but distinct, round, 1/3 the diameter of the eye, surrounded by a distinct, incomplete tympanic annulus, which is obscured by skin in its upper part; distance between tympanum and eye equals the tympanic diameter. No supratympanic fold in the male, a horizontal one present in the female; a skin fold from the corner of the mouth to the underside of the tympanum and a glandular ridge (♂) or series of pustules (♀) from the tympanum to the insertion of the forelimb.

Choanae medium-sized, round; prevomerine processes present, each bearing four to six teeth in the male, indistinct, with two teeth per process in the female, placed in long transverse rows, posteriorly of the choanae, just anteriorly of the palatine bones. Tongue ribbon-like, with slightly expanded posterior part, not notched behind, completely free, except its anterior margin. Male with long, slightly curved vocal slits, flanking the tongue, and a large subgular vocal sac, extending onto the anterior part of the chest and to the insertion of the forelimbs.

Skin of back and venter smooth, skin of throat in male wrinkled. Skin of limbs smooth, posteroventral aspect of thighs coarsely areolate. Discoidal folds absent.

Hand with a large, undivided, irregularly shaped, flat, outer and a smaller, oval, flat inner metacarpal tubercle. Subarticular tubercles present, though flat and indistinct, large, oval, one under each finger, except under the third, which has two tubercles. Three indistinct, flat, oval supernumerary palmar tubercles, one each at the base of fingers II, III and IV. Fingers depressed, free of web, narrow, transparent lateral fringes present. Tips of fingers ending in an asymmetrically pointed tip, no discs, no circumferential groove. Fingers: I $<$ II $\leqslant$ IV $<$ III, fourth finger short, free part more than half the free part of the third finger. Phalangeal formula 2-2-3-3, the second phalange in the fourth finger cubic (♀) or a short rectangle (♂), terminal phalanges of fin-

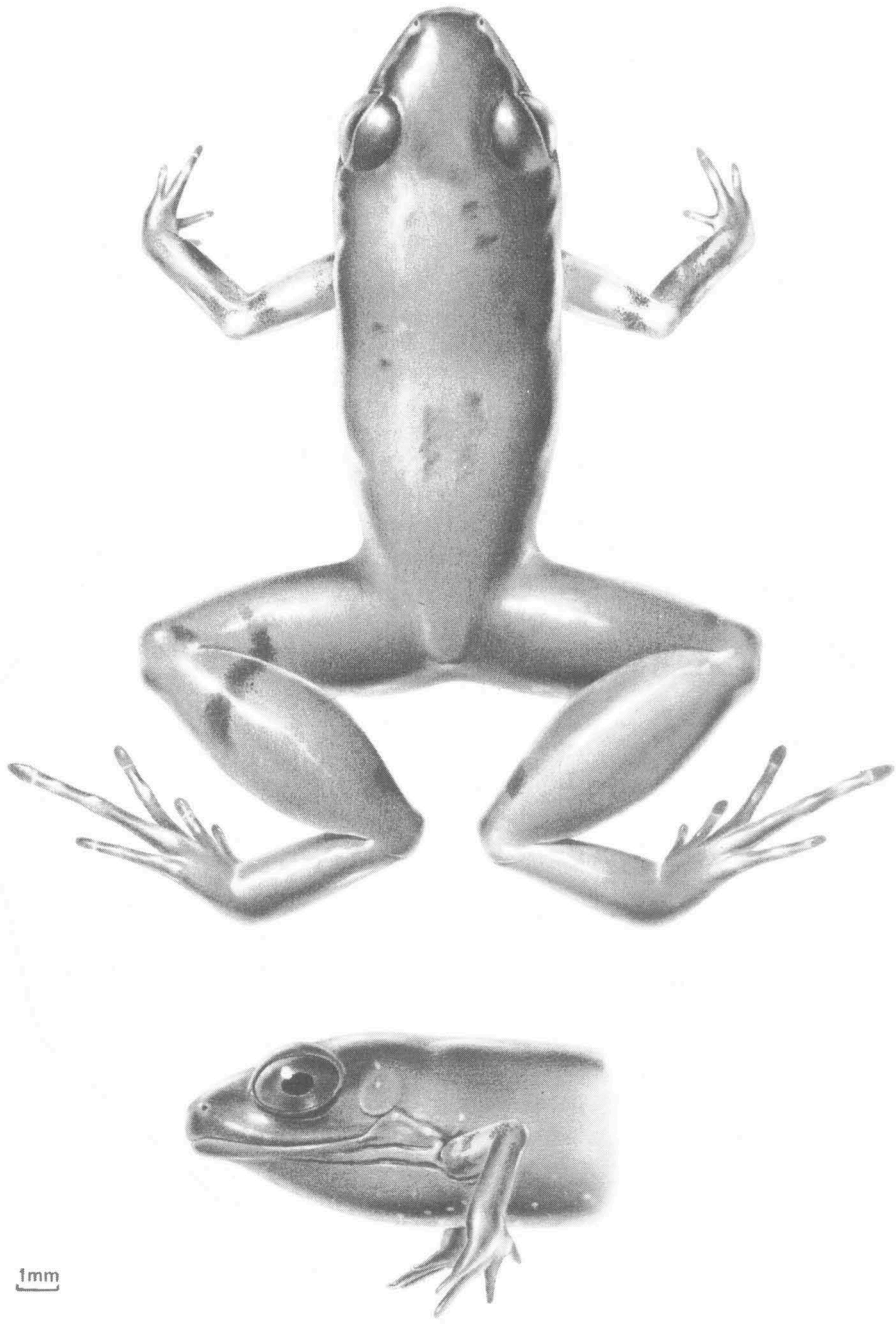


Fig. 8. *Adelophryne gutturosa* (BM 1983.1139). Dorsal habitus and lateral view of left side of head.

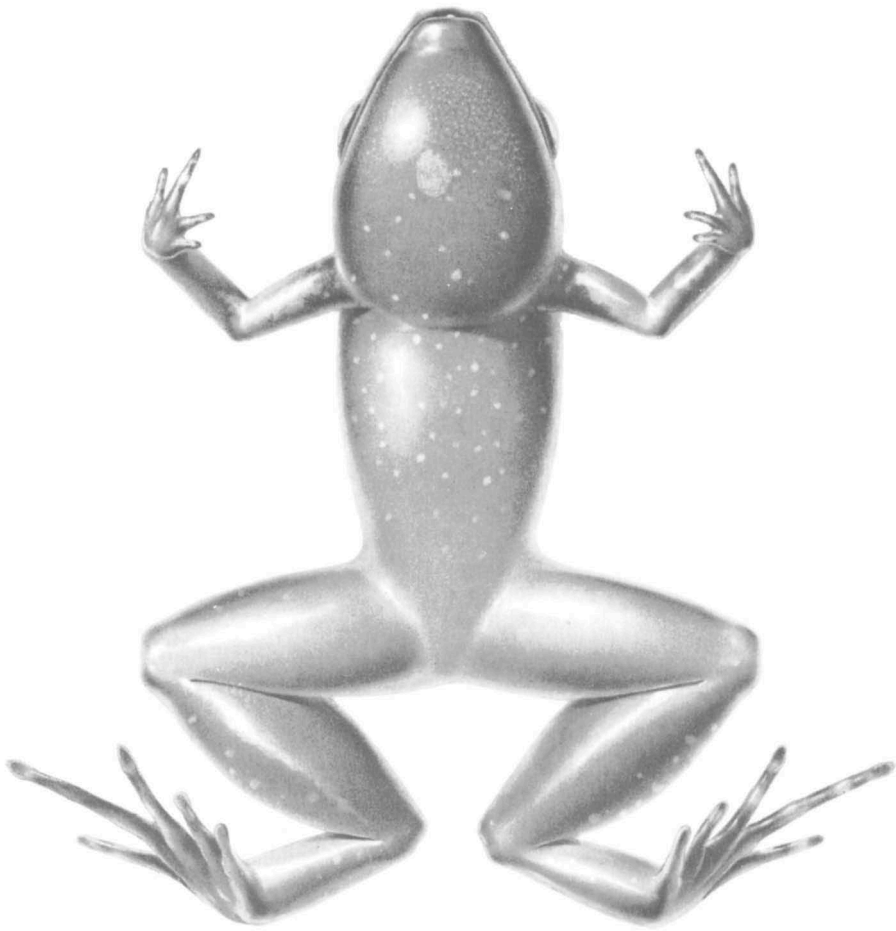


Fig. 9. *Adelophryne gutturosa* (BM 1983.1139). Ventral habitus.

gers I, II and IV bluntly pointed to knobbed, of finger III knobbed (♂) or T-shaped (♀).

Tarsus smooth, without tarsal ridge or tubercle. A large, distinct, oval, flat inner and a smaller, distinct, round, conical outer metatarsal tubercle, approximately half the size of the inner one. Subarticular tubercles flat, oval, indistinct, but more prominent than those on hands. No supernumerary tubercles. Toes depressed, free of web, narrow, transparent lateral fringes present. Tips of toes dilated into small, narrow discs, slightly wider than the toes, ending in an asymmetrically pointed tip. Discs with a circumferential groove, which is narrowly interrupted at the tip. Toes I < II <V <III < IV. Phalangeal formula 2-2-3-4-3, terminal phalanges knobbed (♂) or T-shaped (♀).

Heel of adpressed hindlimb reaches the nostril. When hindlimbs are flexed at right angles to the sagittal plane, the heels slightly overlap. Tibia 45–53% of the snout-vent length, relatively slightly longer in the juvenile (51–53%) than in the adults (45–49%).

In preservative the back is brown with some irregularly dispersed dark brown spots and with scattered white spots in the scapular region. Flanks brown with small white spots. Upper arm white, or brown with white spots, forearm dark brown. Thigh and tibia brown above with an oblique, narrow dark brown band near the knee. Fingers and toes dark brown above, with a white spot over the ultimate articulation. Throat in male dark brown with a few large, central and numerous very small white spots on the anterior part; in the female the throat is like the belly, but darker. Chest, belly and ventral surfaces of limbs lighter brown than the throat, with small white spots. Posteroventral surface of the thighs with numerous tightly packed round white spots.

Natural history. — Hardly any data on this subject are available. The holotype was collected in daytime (10.00 a.m.) on the forest floor in montane forest. A more detailed description of the general habitat is provided by Warren (1973) and Philcox (1973: 70). The male holotype has an extended subgular vocal sac, indicating it was in breeding condition. The period in which it was caught normally forms the transition between the heavy rains of the wet season (May, June, July) and the dry season starting in October. However, 1971 turned out to be an exceptionally wet year, with heavy rains continuing through into September (Chapman, 1973). The female (LACM 44277), with well developed oviducts, was collected in July, which in Amapá is at the end of the great rainy season. Thus, probably, this species breeds during the so-called great rainy season, occurring from April to August in northern South America.

Distribution. — This species, at that time the male only, was reported as a


Fig. 10. *Adelophryne gutturosa* (BM 1983.1139). Plantar (left) and palmar (right) surfaces of right foot and hand.

Guianan lowland endemic by Hoogmoed (1979: 269) under the name *Euparkerella* sp. "A". The two widely separated localities from which it is now known (fig. 11) do not alter this opinion on its distribution and status. At present it is known from altitudes between 300 and 914 m on the Guianan Shield.

Etymology. — From the Latin *gutturosus*, with enlarged throat, in reference to the gigantic subgular vocal sac in adult males.

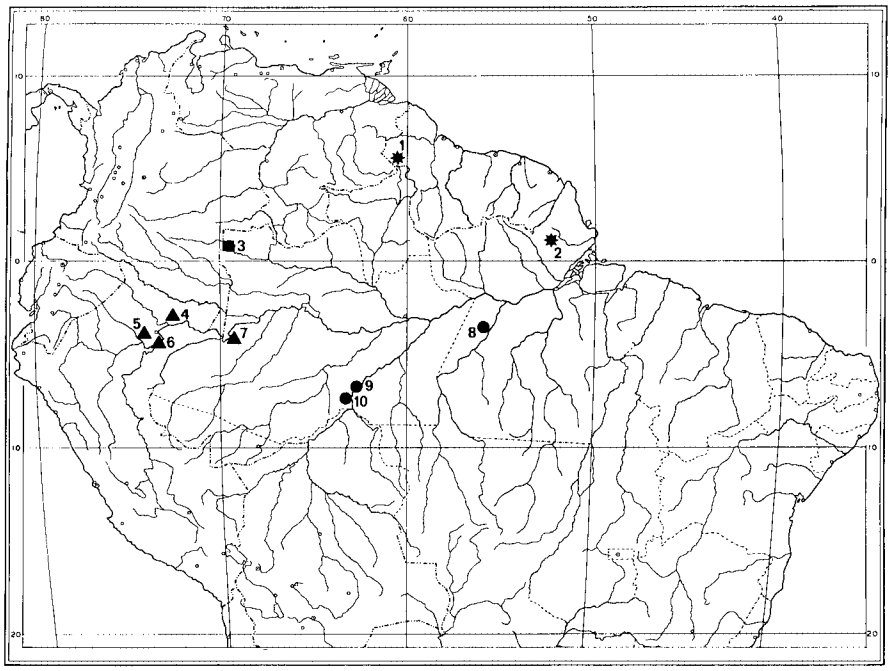


Fig. 11. Map of northern South America, showing the known distribution of four species of small eleutherodactyline frogs here discussed. *Adelophryne gutturosa* (asterisks): 1. Northern slopes of Mount Roraima, 2. Serra do Veado, Serra do Navio; *A. adiastola* (square): 3. Yapima; *Phyllonastes myrmecoides* (triangles): 4. Colonia, 5. Mishana, 6. Centro Union, 7. Igarapé Belem; *Phyzelaphryne miriamae* (dots): 8. Parque Rio Tapajos, SW of Itaituba, 9. Igarapé Puruzinho, 10. Humaita. Localities for *Eleutherodactylus nigrovittatus* are not listed, because they fall completely within the known range of the species (Lynch, 1980a).

## DISCUSSION

The papers by Heyer (1977), Lynch (1976, 1980b), Lynch & Lescure (1980) and the present one, all focus attention on the fact that the Amazonian area still hides a wealth of undescribed small to minute leptodactylid frogs. Some

of these may already have been collected and are waiting in museum collections to be discovered among samples of 'juvenile' frogs. Others will turn up only through specialised fieldwork. These species apparently are largely restricted to leaf litter and possibly also to the superficial soil layer at the base of trees, where the soil is penetrated by roots, or at the base of rocks where cracks and fissures provide good hiding places. These habitats are difficult to sample and this probably explains the paucity of these froglets in older collections, most of which have been made by non-herpetologists. Only when specialised herpetologists started sampling the forest floor herpetozoan communities, some of these species became known to science (*Phyllonastes lochites* due to the work of J. E. Simmons, *P. myrmecoides* due to that of P. Soini and J. R. Dixon, *Phyzelaphryne miriamae* due to that of W. R. Heyer, *Adelophryne adiastola* due to that of W. F. Pyburn and *A. gutturosa* through the efforts of A. N. Warren and P. A. Silverstone). Another source for new species was provided by old collections (e.g. *Barycholos savagei* Lynch was found misidentified as *Eleutherodactylus binotatus* (Spix) and *E. conspicillatus* (Günther)) when studied by specialists (Lynch, 1980b).

The fact that these small species here are mentioned in one breath does not imply close relationship, on the contrary, we strongly suspect that a number of leptodactyline and eleutherodactyline frogs independently evolved small body size and adapted to life in leaf litter and in fissures and cracks in the soil, into which they probably slide, as they donot seem to be built for digging and might lack the strength for it. We are more inclined to consider them to belong to the interstitial soil macrofauna, rather than just another group of leaf litter dwelling species. Their capture in leaf litter (apparently always during rainy seasons when there is a lot of water around) may have been due to accidental circumstances, like high groundwater table, flooding, or heavy rainfall. In general habitus they do resemble some of the smaller microhylids that can be found in the same general habitat, though these have a specialised diet of ants and termites. There are no indications that a comparable specialisation for prey evolved in these small leptodactylids and it therefore remains open to debate whether they compete with (micro)sympatric small microhylids. The find of a harvest-man in the stomach of one *Adelophryne adiastola* seems to indicate that they either specialised in a different direction, or have a much broader food-spectrum, a.o. harvest-men, ants, termites and other micro-invertebrates. It is remarkable, though, that they all evolved pointed discs on the toes and pointed fingertips, which are or are not expanded into small discs. The digit tips in all genera concerned are different and seem to have evolved independently. *Eleutherodactylus nigrovittatus* e.g. has small, swollen, subtriangular discs on the toes with deep, uninterrupted circumferential

grooves, while on the fingers the discs are small, not swollen, circumferentially grooved and pointed (III) or bluntly pointed. *Phyllonastes* on the toes has elongate, distinctly swollen, circumferentially grooved discs with a protracted papilla, placed slightly asymmetrically below the groove, while the fingers do not bear discs and the tips are slightly swollen, rounded to bluntly pointed (asymmetrically). *Phyzelaphryne,* on the toes, has enlarged, swollen, laterally grooved (interrupted at the tip) discs which are bluntly pointed, the tip slightly asymmetrical, while on the fingers the discs are small, swollen, laterally grooved (interrupted at the tip), bluntly pointed with the tip slightly asymmetrical. *Adelophryne*, on the toes, has very narrow discs, with a distinctly asymmetrical tip, formed by a papilla and with a horizontal groove that passes through the tip and is interrupted there, while the fingers are strongly asymmetrically pointed, without discs.

The situation found in *Phyzelaphryne* and *Adelophryne*, where the toe discs show lateral grooves which are not connected with each other because of an interruption at the tip is very similar and might reflect true phylogenetic relationship. The situation found in *Phyllonastes* is completely different and must have been attained along quite a different route. It seems unlikely that the situation of two separated lateral grooves evolved from that in *Eleutherodactylus*, which has a transverse groove across the tip of the digital pad (Lynch, 1971). It seems more likely that the situation, as found in *Phyzelaphryne* and *Adelophryne*, evolved from species with swollen digit tips, such as are found, for instance, in some species of *Adenomera* (Heyer, 1973), in *Barycholos* (Heyer, 1969; Lynch, 1980b) and in *Vanzolinius* (Heyer, 1974). This comparison does not imply direct relationship, two of the three genera mentioned (*Adenomera, Vanzolinius*) being considered to belong to another subfamily, the Leptodactylinae (purportedly characterised by the possession of a bony element in the sternum (Lynch, 1971, 1980b)), than *Phyzelaphryne* and *Adelophryne*. Until recently *Barycholos* was also considered to belong to the Leptodactylinae because of its bony mesosternum, but Lynch (1980b) reached the conclusion that its pectoral girdle with the short, wide, posteriorly bifurcate, calcified mesosternum and paired xiphisterna probably is a derived state, quite unlike that seen in the "leptodactylines *sensu stricto* (*Adenomera, Leptodactylus, Lithodytes,* and *Vanzolinius*)", which all have a long, thin, osseous mesosternum with a spade-like xiphisternum, unique in the Leptodactylidae. Lynch (1980b) finally stated that "*Barycholos* seems most closely related to frogs of the *discoidalis* group of *Eleutherodactylus*". Apparently his reasoning was accepted by Laurent (in press), who considers *Barycholos* to belong to his Eleutherodactylinae. We concur with this view. However, this should not be construed as a statement that *Phyzelaphryne* and *Adelophryne* are derived

from *Barycholos*, as we still lack sufficient data and did not complete a detailed study of character states in the genera concerned.

Opinions about relationships of the minute frogs here discussed fluctuated considerably (see above for *Barycholos*), e.g. Lynch (1976) described two new species of the genus *Euparkerella*, for which Heyer (1977) erected the new genus *Phyllonastes*, whereas at the same time he described the new taxon *Phyzelaphryne miriamae*. Lynch (1980b) in his turn synonymised *P. miriamae* with *Eleutherodactylus nigrovittatus*, simultaneously noting that the Vaupés River specimens referred to *P. miriamae* by Heyer (1977), belonged to a different species. The two species here described a.o. share a peculair character, the distinctly reduced fourth finger, containing only two phalanges in *Adelophryne adiastola* and three in *A. gutturosa*. It should be stressed here that the second phalange of the fourth finger in *A. gutturosa* is peculiar, in that it is cubic (♀, LACM 44277) or at the most forms a short rectangle (♂, BM 1983. 1139), whereas in species with three phalanges in the fourth finger this second phalange usually forms a long rectangle. It is not clear yet whether this intraspecific variation is sex-linked or not. We interpret the shape of the second phalange in the fourth finger of *A. gutturosa* as being an intermediate stage towards losing this phalange completely, as already happened in *A. adiastola*. On the basis of the aforementioned skeletal character, the similarities in external morphology, in brief, the unique combination of characters presented in the generic diagnosis, we consider the two species described here to constitute a new genus, which fits well into the tribe Eleutherodactylini of the subfamily Telmatobiinae (Lynch, 1971; Dowling & Duellman, 1974-1978) or the subfamily Eleutherodactylinae in Laurent's (in press) terminology. At present we refrain from further speculations about the relationships because of the paucity of data and specimens available.

It seems useful to present a key to the small eleutherodactyline frogs with pointed or papillate toe discs and reduced fourth finger, recently described from Amazonian South America, including *Eleutherodactylus nigrovittatus* which has lately been confused with one of the other species.

1. Tarsal tubercle present, no vomerine teeth ..... (*Phyllonastes*) — 2
— Tarsal tubercle absent, vomerine teeth present ..... 3
2. Toe pads rounded, papillate; no supernumerary plantar tubercles ..... *Phyllonastes myrmecoides*
— Toe pads pointed, not papillate; obscure supernumerary plantar tubercles present ..... *Phyllonastes lochites*
3. Fourth finger with two subarticular tubercles, of which the distal one may be rather indistinct; males with a fleshy ridge on the snout .....

..... *Eleutherodactylus nigrovittatus*

— Fourth finger with one subarticular tubercle only; males without a fleshy ridge on the snout, but having a distinct subgular vocal sac ..... 4

4. Digits round in cross-section, with well developed, salient subarticular tubercles, fourth finger without reduction in number or size of the phalanges; males with small subgular vocal sacs .....*Phyzelaphryne miriamae*

— Digits flattened, with indistinct, flat subarticular tubercles, fourth finger either with reduced number of phalanges or with the second phalange distinctly shortened; males with very large subgular vocal sacs ..... ..... (*Adelophryne*) — 5

5. Fourth finger with two phalanges only, free part of fourth finger less than half the length of the free part of the third finger; skin of back shagreened to granular ..... *Adelophryne adiastola*

— Fourth finger with three phalanges of which the second is cubic or forms a short rectangle, free part of fourth finger more than half the length of the free part of the third finger; skin of back smooth ..... ..... *Adelophryne gutturosa*

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| Character | *P. miriamae* | *E. nigrovittatus* |
|---|---|---|
| 1. subarticular tubercles fingers | 1-1-2-1 | 1-1-2-2 |
| 2. subarticular tubercles toes | 1-1-2-3-2 | 1-1-2-3-2 |
| 3. shape subarticular tubercles fingers | salient | flat |
| 4. palmar tubercles | 3 | 4–5 |
| 5. solar tubercles | 0 | 0–1 |
| 6. cross-section fingers/toes | round | depressed, oval |
| 7. relative length fingers/arms | longer | shorter |
| 8. outer metatarsal tubercle | very much smaller than inner metatarsal tubercle | only slightly smaller than inner metatarsal tubercle |
| 9. shape of snout | truncate (dorsal view), truncate (profile) | pointed (dorsal view) acuminate (profile) (♂ with shovel-shaped ridge) |
| 10. lateral surface head | vertical | sloping |
| 11. subtympanic glandular ridge | separated from tympanum | in contact with tympanum |
| 12. vomerine teeth | long transverse series, ca. 9 teeth | short transverse series, 5–7 teeth |
| 13. dorsal skin | shagreened | pustulous – smooth |
| 14. upper eyelid | no tubercles | row of low, flat tubercles |
| 15. inguinal black spot | absent | present |

Table 1. Differences between *Phyzelaphryne miriamae* and *Eleutherodactylus nigrovittatus*.

| Character | *Adelophryne adiastola* | | | | *Adelophryne gutturosa* | | | *Phyzelaphryne miriamae* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | UTACV | | | | BM | LACM | LACM | MZUSP | | USNM | | |
| Reg. no. | 4940 | 4941 | 4942 | 4943 | 1983.1139 | 44277 | 44278 | 49894 | 49895 | 202607 | 202608 | 239363 |
| sex | ♂ | ♂ | ♀ | ♂ | ♂ | ♀ | hgr. | ♀ | ♂ | ♀ | ♀ | ♂ |
| s-v length | 13.0 | 13.3 | 13.9 | 13.7 | 14.5 | 13.0 | 8.3 | 20.0 | 15.1 | 20.0 | 19.4 | 14.6 |
| head length | 4.7 | 5.3 | 5.3 | 5.4 | 5.1 | 4.9 | 3.4 | 7.3 | 5.8 | 7.1 | 7.0 | 5.5 |
| head width | 4.5 | 4.4 | 4.5 | 4.6 | 5.0 | 4.5 | 3.0 | 6.4 | 5.0 | 6.3 | 6.0 | 4.8 |
| tibia length | 6.0–? | 6.4–6.1 | 6.6–? | 6.3–? | 7.1–7.1 | 5.9–6.1 | 4.4–4.3 | 8.8–8.9 | 7.6–7.5 | 8.5–8.5 | 8.5–8.7 | 6.5– |
| IOD | 1.4 | 1.4 | 1.7 | 1.4 | 1.6 | 1.8 | 1.3 | ? | ? | 2.1 | 2.1 | 1.8 |
| width eyelid | 0.9–0.9 | 1.0–1.1 | 1.0–? | 1.0–1.1 | 1.0–1.2 | 0.9–0.9 | 0.7–0.8 | ? | ? | 1.4–1.5 | 1.4–1.6 | 1.3–? |
| eye length | 1.8–1.7 | 1.9–1.7 | 1.8–1.7 | 1.8–1.9 | 2.0–1.8 | 1.6–1.6 | 1.2–1.3 | 2.7–2.6 | 2.2–2.4 | 2.3–2.5 | 2.4–2.5 | 2.2–? |
| tymp. length | 0.6–0.5 | 0.6–0.7 | 0.8–0.8 | 0.7–0.7 | 0.6–0.6 | 0.7–0.7 | 0.4–0.4 | 1.2–1.1 | 0.8–0.8 | 1.0–1.1 | 1.1–1.1 | 0.8–? |
| eye-tip snout | 1.8–1.9 | 1.9–2.1 | 1.9–2.1 | 2.1–2.1 | 2.1–2.1 | 1.7–1.8 | 1.3–1.3 | 3.1–2.9 | 2.7–2.4 | 2.5–2.8 | 2.9–3.0 | 2.3–? |
| vomerine teeth | 2–3? | 7–8 | 3–3? | 5–5? | 5–3 | 3–2 | ? | ? | ? | 9–9(?) | 9–9 (?) | ? |
| vocal sac | – | large | – | large | large | – | – | – | small | – | – | small |
| vocal slits | + | + | – | + | + | – | – | – | + | – | – | + |
| oviducts | – | – | large | – | – | large | – | ? | – | large | ? | – |

Table 2. Morphometric and secondary sexual characters of *Adelophryne adiastola*, *A. gutturosa* and *Phyzelaphryne miriamae*. Under vomerine teeth the question-mark indicates that these counts are not exact, but they indicate the range. Elsewhere a question-mark means that the value either could not be obtained because of technical problems, or was not recorded. + = present, – = absent, IOD = interorbital distance. All measurements are in mm. The DZUB specimen of *P. miriamae* was not measured, only identified.

| character | *Euparkerella brasiliensis* | *Adelophryne adiastola* | *Adelophryne gutturosa* | *Phyzelaphryne miriamae* | *Phyllonastes myrmecoides* | *Eleutherodactylus nigrovittatus* |
|---|---|---|---|---|---|---|
| discs circumferentially grooved | – | – | – | – | + | + |
| | | | | | – | – |
| discs laterally grooved | – | + | + | + | – | – |
| tarsal tubercle | – | – | – | – | + | – |
| vomerine teeth | – | + | + | + | – | + |
| subarticular tubercles fourth finger | 1 | 1 | 1 | 1 | 1 | 2 |
| phalangeal formula hand | 2-2-3-2 | 2-2-3-2 | 2-2-3-3 | 2-2-3-3 | 2-2-3-2 | 2-2-3-3 |
| second finger compared to fourth | much $2 > 4$ | $4 < 2$ | $4 \leqslant 2$ | $2 = 4$ | slightly $2 > 4$ | much $2 > 4$ |
| skin | slightly shagreened | rugose | smooth | shagreened | finely rugose | smooth |
| fingers | extremely short | short | short | long | moderately long | moderately long |
| subarticular tubercles fingers | flat, distinct | flat, indistinct | flat, indistinct | salient, rounded | flat, indistinct | flat, distinct |

Table 3. Comparison of small eleutherodactyline genera from the Amazonian area and SE Brazil with reduced fourth finger and pointed digit tips.