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SYSTEMATICS OF THE MARMORATUS GROUP OF THE FROG GENUS *LEPTODACTYLUS* (AMPHIBIA, LEPTODACTYLIDAE)

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SYSTEMATICS OF THE MARMORATUS GROUP OF THE FROG GENUS *LEPTODACTYLUS* (AMPHIBIA, LEPTODACTYLIDAE)[1]

By W. RONALD HEYER[2]

ABSTRACT: The geographic distribution patterns of eight characters of size, shape, texture, and color pattern were examined for members of the Marmoratus species group of the frog genus *Leptodactylus*. Analysis of the geographic distribution of character states indicates that the group is composed of five species. *Leptodactylus bokermanni,* new species, has nonexpanded toe tips and occurs in the forests of southeast Brasil. *Leptodactylus hylaedactylus* has nonexpanded or slightly expanded toe tips and inhabits the forests of greater Amazonia and southwestern Brasil. *Leptodactylus andreae* has toe disks and occurs in the Orinocan and greater Amazonian forests. *Leptodactylus marmoratus* has toe disks and occurs in the forests of southeastern Brasil. *Leptodactylus martinezi* has nonexpanded toe tips and inhabits the dry forests of central Brasil. Each species is diagnosed and described, and a key is provided.

It is hypothesized that the foam nest in the Marmoratus group and that of the other species groups in the genus *Leptodactylus* evolved in response to different selective forces. In the case of the other species groups, the foam nest has evolved in reponse to arid conditions with sporadic heavy rain. In these situations, rainfall can be used in a predictive manner to ensure reproductive success. In the Marmoratus group, rainfall may not be a good predictor of reproductive success. Terrestrial organisms have a relatively stable reproductive environment in wet tropical forests, however. The foam nest in the Marmoratus group apparently has developed as a response to selection for terrestriality.

INTRODUCTION

This paper is the second of a projected series on the systematics of the species groups of the genus *Leptodactylus*. The first treated the Melanonotus group (Heyer, 1970a); the present paper treats members of the Marmoratus group as previously defined by Heyer (1968). The members of this group have been poorly understood, both with respect to how many species comprise the group and to what the relationships of the Marmoratus group are to the other species groups within the genus. This paper is addressed to the first problem.

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The reviewers of this paper do not all concur that the methods of analysis used are the most appropriate. That decision, as well as all interpretations, remains solely mine.

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METHODS AND MATERIALS

Over 1300 preserved specimens form the basis of this analysis. Early in the study, it became clear that the problem could best be treated in the manner used by Gans (1959, 1966). The analysis was done in three stages; in the first, the following were recorded:

1) Sex. Individuals were determined to be either male, female, or juvenile. Males were determined by the presence of vocal slits. Females were determined by presence of eggs visible through the ventral body wall, or by size if males were present from the same locality. If there was any question, the individual was scored as a juvenile.

2) Size. The snout-vent length was measured to the nearest 0.1 mm with vernier calipers.

3) Snout shape. A ratio was determined which in selected samples reflects the differences between blunt and pointed snout shapes. A specimen was lined up under a grid-type ocular micrometer in a dissecting microscope so that one line traversed the distance between the anterior corners of the eyes. This distance was read and used as the denominator. The numerator was determined by reading the distance at right angles from the grid line connecting the anterior eye corners to the tip of the snout. The larger the value of the ratio, the longer the snout.

4) Toe tip shape. Four categories of toe tip shape were recognized, ranging from

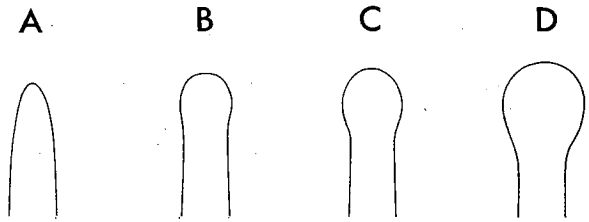

FIGURE 1. Toe tip character states, see text.

state A, the tips pointed, to state D, the tips with large, distinct disks (Fig. 1). In this character only, intermediate categories were used, such as B–C or C–D.

5) Dorsal texture. Four character states were recognized: A, dorsum smooth; B, Dorsum with white tipped tubercles; C, dorsum with ridges or warts; D, dorsum with dorsolateral folds and white tipped tubercles. The method of preservation affects this character. Many of the specimens scored as having state A certainly had one of the other states in life. Because of this, the variation of dorsal texture was not analyzed in detail, but the range of variation is described in the individual species accounts in a later section.

6) Dorsal pattern. Six different character states were recognized (Fig. 2). Here,

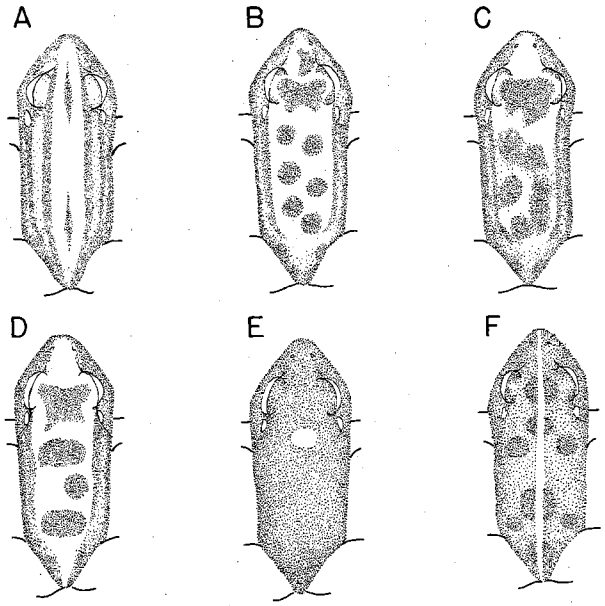

FIGURE 2. Dorsal pattern character states, see text.

as in the other characters which were broken down into arbitrary states (with the exception of toe disks), a specimen with an intermediate category was placed into the category it most resembled.

7) Dorsolateral stripes. Three states were recognized: A, no dorsolateral stripes; B, light, narrow, dorsolateral stripes from the eye to the inguinal region; C, light, broad, conspicuous dorsolateral stripes from the eye to the inguinal region.

8) Light mid-dorsal stripe. Seven states were recognized: A, no mid-dorsal stripe; B, a mid-dorsal pin stripe from above the vent to about midbody; C, a pin stripe from above the vent to the snout; D, a stripe wider above the vent, tapering to a point not beyond the sacrum; E, a broad stripe from above the vent to the tip of the snout; F, a pin stripe from above the vent not extending beyond the sacrum; G, a wide stripe in the sacral region only.

The specimens were examined locality by locality. As the first stage of analysis was being done, the specimens from each locality were examined to determine if there were one or more distinctive forms; that is, specimens exhibiting consistent discontinuous variation in two or more characters. Localities of presumed instances of sympatry of two distinctive types were noted. Detailed comparison of the specimens from the presumed sites of sympatry formed part of the second stage of analysis. This part of the analysis, termed "the recognition of non-dimensional species" by Gans (1966), centers about study of sympatric occurrences. Distinctive specimens from the same locality are examined in detail. Samples from surrounding localities are then compared with and determined to be one or the other distinctive forms from the site of sympatry. This was done separately for each of seven large areas.

The third stage of analysis, termed, "the recognition of species in space" by Gans (1966), involves detailed analyses of similar forms over the entire geographic range. Decisions are made as to how many species are represented based on this third stage of analysis.

This methodology is nothing more than standardized common sense as historically used in systematics. It is not a phenetic analysis in the numerical taxonomy sense, but rather a "classical" taxonomic approach. The reason for utilizing the methods outlined by Gans (1959, 1966) is that it allows one to keep track of variability when large numbers of specimens over wide geographic areas are being studied.

THE RECOGNITION OF "NON-DIMENSIONAL" SPECIES

Seven large areas were delineated to form the study units for the recognition of "non-dimensional" species. Each area was determined on the basis of at least one locality where two forms occurred together, proximity of other localities from which specimens originated, amount of material, and intuition. The situation for each area follows.

Area A—This area consists of lands of north draining rivers. A single instance of sympatry was found (Surinam; Nickerie, Sipaliwini, Fig. 3, number 1). The forms are distinctive when closely compared (Fig. 4). The forms are designated as I and II and differ as follows. Form I (11 specimens) is more robust than form II (4 specimens); form I has either a uniform dorsum or wide saddlelike dark blotches, form II has more or less distinct small spots dorsally; 1 specimen of form I has type C dorsolateral

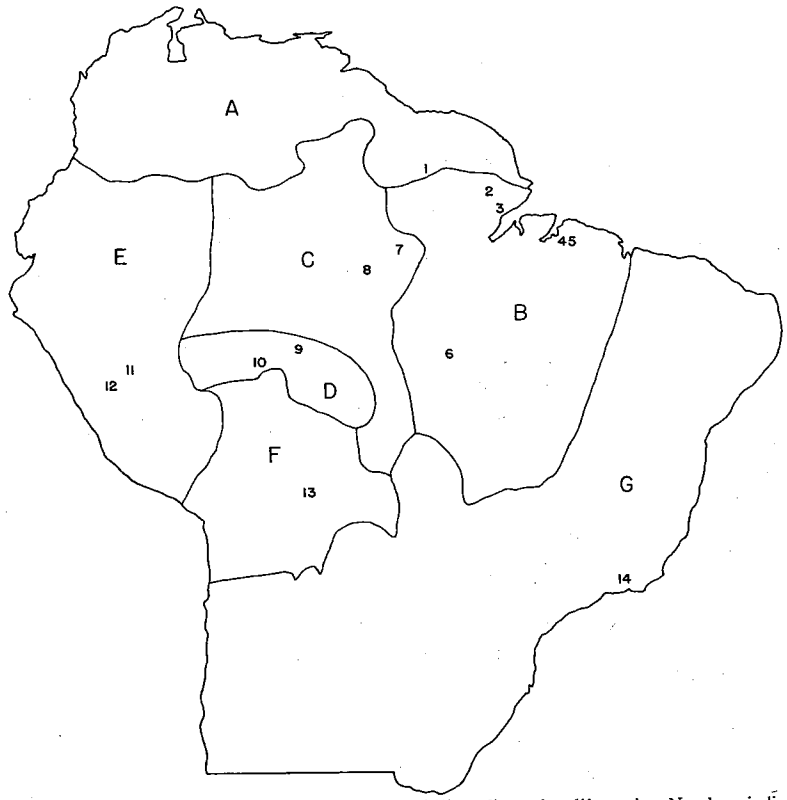

FIGURE 3. The seven study areas for recognition of "non-dimensional" species. Numbers indicate localities where more than one form is represented in collections.

stripes, none of the form II specimens has dorsolateral stripes; the snout of form I males is sharply pointed in profile, the snout of form II males is rounded in profile; the toe tips of form I specimens are either type C or D, the toe tips of form II specimens are type B, or type B almost type C; the dorsum is smooth in all form I specimens, the dorsum in a single form II specimen is warty. Specimens from all localities within Area A were readily allocated as either form I or II using the Sipaliwini specimens as standards.

Area B—This area covers the Brasilian territory and states of Amapá, Mato Grosso, Pará, and Goiás which are drained by the Amazon or Tocantins river systems. Instances of sympatry are at Amapá; Serra do Navio 220–300 m, Serra do Veado, 290–310 m (Fig. 3, number 2), Mazagão (Fig. 3, number 3); Pará; Belém (Fig. 3, number 4), IPEAN, 3 km E Belém (Fig. 3, number 5), and Cachimbo (Fig. 3,

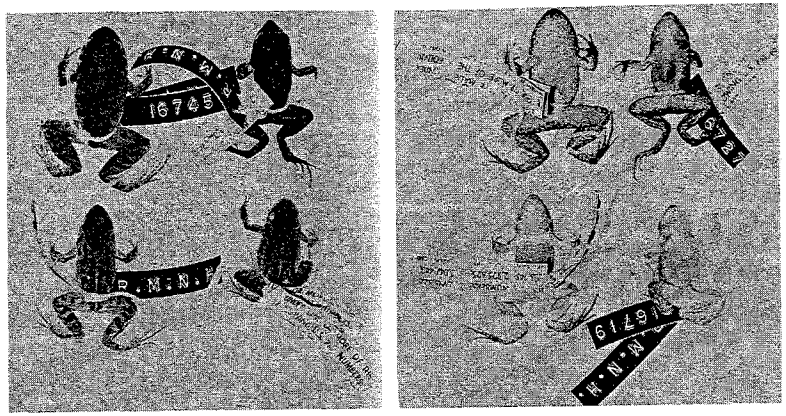

FIGURE 4. Frogs from locality one of Fig. 3. Left—dorsal views; upper two specimens are form I individuals, lower two form II. Right—ventral views; upper two specimens are form I individuals, lower two form II.

number 6). At each site except Cachimbo, there are two forms, which are again designated as I and II. Here and in the other major areas, designation of I forms indicates that the I form of Area A is most similar to the I form of Area B, but relationships among all the I forms from all areas constitutes the analysis of the species in space of the next section. The sympatric I forms of Area B (143 specimens) differ from the II forms of Area B (17 specimens) as follows: the body shape of form I specimens is slightly more robust than in form II specimens, but the differences are not as pronounced as in Area A; the dorsal patterns of form I specimens are more uniform, the dorsal patterns of form II specimens are more mottled with a tendency toward spotting; the venters of form I specimens are darker than in form II specimens; some form I individuals have broad, light dorsolateral stripes, no form II individuals have such stripes; no form I specimens have B or C category light mid-dorsal stripes, while some form II individuals do; the toe tips of form I individuals are C or D category (Fig. 1), the toe tips of form II individuals are either B or C category (Fig. 1)—in the C cases of both forms the disks are distinctive in that the C category disk of form I is flattened while the C category disk of form II is rounded (Fig. 5). At Cachimbo, two distinctive forms were recognized. The first corresponds to the II form of Area B. The second corresponds to the F dorsal pattern of Figure 2 and is designated form III. This is the only site where more than one distinctive form is known to occur in which both forms have no disk development of the toes. The specimens from all other localities from within Area B. were readily designated as being either form I, II or III. The form I specimens from Pará, Jacareacanga have notably large toe disks.

Area C—This area includes samples from the Brasilian state of Amazonas. Instances of sympatry were found at Itapiranga (Fig. 3, number 7) and Ducke Reserve, near Manaus (Fig. 3, number 8). At both sites, the different forms consisted of forms I and II. The differences between form I (7 specimens) and form II

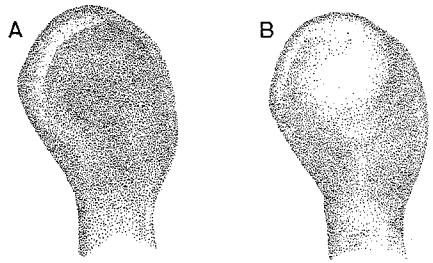

FIGURE 5. A, C category of toe disk of form I individuals. B, C category of toe disk of form II individuals.

(5 specimens) at the two sites of sympatry are: some form I individuals have light, broad dorsolateral stripes, no form II individuals have such stripes; no form I specimens have B or E category mid-dorsal light stripes, some form II specimens do; form I individuals have C or D category toe tips, form II individuals have B category toe tips. Individuals from all other localities within Area C were readily distinguished as either I or II forms using the specimens from localities 7 and 8 (Fig. 3) as standards with the exception of the specimens available from Manaus. These 4 particular individuals are so desiccated that proper allocation is not possible.

Area D—This area includes samples from the Brasilian state and territory of Acre and Rondônia. Two sites of sympatry were identified: Rondônia, Pôrto Velho (Fig. 3, number 9) and Igarapé Marmelo (Fig. 3, number 10). At Pôrto Velho, two forms were present, I (4 specimens) and II (9 specimens) which differ as follows: two form I individuals have broad, light, dorsolateral stripes, no form II individuals have such stripes; no form I individual has an E category light mid-dorsal stripe, one form II individual does; form I individuals have C or D category toe tips with flattened disks (Fig. 5A), form II individuals have category B or C toe tips, if category C, the disks are rounded (Fig. 5B). Specimens from other localities within Area D were readily identified as either form I or form II using the Pôrto Velho specimens as standards with the exception of the specimens from Igarapé Marmelo. Igarapé Marmelo is the only locality where intermediate individuals between form I and form II types were identified for any of the areas. Three individuals are clearly the same as form I individuals from the other localities within Area D with respect to toe disk development. Seven individuals are clearly the same as form II individuals from other Area D localities in toe tip development and in some individuals having B, C, and E categories of mid-dorsal stripe development (Fig. 6). Two individuals are intermediate with respect to toe tip development. In addition, the dorsal patterns are complex and not easily described in the total sample, but the form I specimens tend towards uniformity, the form II specimens tend toward spotting, while the two individuals intermediate in toe disk development appear to be a combination of both form I and II patterns (Fig. 6).

Area E—This area includes Amazonian localities from Colombia, Ecuador, and Peru. Two instances of sympatry were noted: Peru; Loreto, Iparia (Fig. 3, number 11) and Peru; Pasco, Iscozazin Valley, Pan de Azucar (Fig. 3, number 12). Seven form I