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(AMPHIBIA: LEPTODACTYLIDAE). VI.  
BIOSYSTEMATICS OF THE MELANONOTUS GROUP

By W. RONALD HEYER

LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK  
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STUDIES ON THE FROGS OF THE GENUS *LEPTODACTYLUS*  
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By W. RONALD HEYER<sup>1</sup>

ABSTRACT: Six species are recognized in the Melanonotus group: *dantasi*, *discodactylus*, *melanonotus*, *podicipinus*, *pustulatus*, and *wagneri*. A synonymy, diagnosis, summary of characteristics, and distributional summary are presented for each species. Series of *Leptodactylus* were analyzed from broad geographic and ecologic areas and situations for standard length, ventral pattern, ventrolateral gland development, posterior thigh pattern, and toe disk development. Correlations are evident between 1) larger size and more mesic habitats in *wagneri*, 2) darker ventral pattern and greater annual rainfall in *melanonotus*, 3) lighter ventral pattern and greater ventrolateral-gland extent in *wagneri*, and 4) greater ventrolateral-gland extent and greater annual rainfall in *wagneri*. The hypothesis is presented that character displacement is involved in the sharp differences in size and pattern between populations of *melanonotus* and *wagneri* as well as *podicipinus* and *wagneri* in sympatry. *Leptodactylus melanonotus* is the most primitive of the species, while *discodactylus* and *pustulatus* are the most advanced.

*Leptodactylus melanonotus*, *podicipinus*, and *wagneri* are associated with old land masses and are species adapted for xeric conditions. *Leptodactylus dantasi* and *discodactylus* are limited to the Tropical Rainforest of the western Amazonian Basin. *Leptodactylus pustulatus* is distributed in the xeric regions of eastern Brazil.

INTRODUCTION

Since the frog genus *Leptodactylus* was proposed by Fitzinger in 1826, it has had an unstable systematic history. No one since Boulenger, in 1882, has treated the group as an entity. The present paper is the first of a projected series attempting to elucidate the biosystematics of each of the species groups within the genus. In the Melanonotus species group, characters of gross morphology and distribution are used to analyze the interspecific relationships, ecological distribution patterns, and geographical distribution patterns of the species.

METHODS

All adult specimens of the Melanonotus species group were examined for size, sex, ventral color pattern, ventrolateral gland development, posterior

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thigh pattern, and degree of toe-tip expansion. Analysis of these characters is the basis for the taxonomic conclusions. For convenience, taxonomic conclusions are presented first before discussing the variation of characters analyzed in detail.

All available adult individuals of *L. dantasi*, *discodactylus* and *pustulatus* were studied for variation in 34 characters. The same 34 characters were examined in a series of 15 males and 15 females for each of the other three species. Thirty specimens of *melanotus*, *podicipinus*, and *wagneri* were chosen to represent the extremes in geographic origin and morphological variation. Details of the methods of examining individuals are the same as used previously (Heyer, in press). Percentages of standard length (SL) are presented as follows, 5-6-1-7, where the first number is the minimum, the second the mean, and the third the maximum percentage. The terminology follows Peters (1964) and Elias and Shapiro (1957). A dissecting microscope was used to examine the pattern of melanophore distribution on the ventral surfaces since melanophores in a contracted state are difficult to distinguish with the naked eye.

Prior to this study, five characters appeared adequate to define populations of the *Melanonotus* species group. Male and female sizes were recorded, and standardized forms were drawn which encompassed the range of variation for the ventral pattern, ventrolateral gland development, posterior thigh pattern, and toe-disk development. If a selected character appeared intermediate in any single frog, it was arbitrarily placed in the category it more closely resembled.

One to 100 individuals have been collected from each of 454 localities in Mexico and Middle America. As the status of the frogs in this geographic area was reasonably clear, samples for analysis were selected every 100 km along both coasts and in any inland area. In regions where faunal changes might be expected on the basis of other anuran distribution patterns more samples were analyzed. The samples, usually 10 frogs per locality, from 56 localities from Mexico through Panama and all available South American specimens of the *Melanonotus* species group were analyzed. The frogs were examined to determine how many distinctive morphotypes were present. Examples demonstrating the range of variation for individuals from each population were then recorded. Analyses of only the largest specimens of each distinct morphotype from each locality were recorded. Thus in the following analysis, size refers to the maximum for males and females for a given locality.

A series of mating call recordings were made in western Mexico in July 1967 on an Uher 4000 L portable tape recorder at 7.5 ips. The tapes were analyzed on a Kay Sonagraph 6061 B. Information on number of notes per call group, dominant frequency, harmonics, and frequency shifts was recorded from the sonagrams. The tapes are deposited at the University of Southern California, Department of Biological Sciences. Localities, tapes

(one individual per tape), and specimens on deposit at the Los Angeles County Museum of Natural History, respectively, are: COLIMA, Colima, WRH 67-12, LACM 37037; JALISCO, 5 km W Acatlán, 1400 m, WRH 67-20, LACM 37038, WRH 67-21, WRH 67-22, WRH 67-23, LACM 37039, WRH 67-24, WRH 67-25, LACM 37040; 7.7 km E La Huerta, 340 m, WRH 67-26, LACM 37041; 37.5 km SW Tecalitlan, 910 m, WRH 67-15, WRH 67-16, WRH 67-17; 0.5 km NE Tonila, 1300 m, WRH 67-18, LACM 37428; MICHOACÁN, 2.6 km N Capitío, 300 m, WRH 67-13, LACM 37427; NAYARIT, 13.2 km NE San Blas, WRH 67-31; Santa Cruz, 15 m, WRH 67-30, LACM 37043; Tepic, 950 m, WRH 67-27, LACM 37042, WRH 67-28; SINALOA, 36 km S Los Mochis turnoff on Mexican Highway 15, 10 m, WRH 67-2, LACM 37426, WRH 67-3, LACM 37036; SONORA, 3.1 km E Hermosillo, WRH 67-32.

Certain environmental parameters were chosen to evaluate as possible correlates with SL, gland development, ventral pattern, and posterior thigh pattern.

Total annual rainfall, number of months with less than 100 mm of rain-fall (dry months), and elevation were recorded for each locality. The climatic data were taken from Espinal and Montenegro (1963) for Colombia; Holdridge (1964) for Middle America; Tosi (1960) for Peru; Vivo Escoto (1964) for Mexico; Walter and Lieth (1960-67) for South America and Lesser Antillean Islands. Elevational data were taken from museum catalogues or from the Millionth Map series (American Geographical Society).

The correlation coefficient used to compare categories was the product moment method for ungrouped data, as presented by Arkin and Colton (1966, pp. 80-82). Mary Nafpaktitis wrote a Fortran program for this formula suited to my data. Robert J. Lavenberg wrote a Basic program for a *t*-test, as presented by Fisher (1948, pp. 193-196). The correlation coefficients and *t*-tests were run on a General Electric Time Share Computer terminal, provided by the Los Angeles County Museum of Natural History. The *t* values were located on a table (Fisher, 1948, p. 174) to determine the level of statistical significance (*P* value) of the correlation coefficients. A *P* value of .05 or less was considered statistically significant.

#### ACKNOWLEDGMENTS

This report is a modified section from my doctoral dissertation on file at the University of Southern California. My dissertation committee has been a constant source of encouragement—Jay M. Savage, Chairman, Robert M. Chew, John S. Garth, John L. Mohr, Basil G. Nafpaktitis, and John D. Soule. My fellow graduate students have aided me considerably in helping to define my ideas through stimulating discussions. Of particular help have been John R. Meyer, Roy W. McDiamid, Norman J. Scott, Jr., Philip A. Silverstone and David B. Wake.

My studies of the genus *Leptodactylus* would have been lessened without the help of the following field companions: James R. Dixon, Miriam Heyer, Roy W. McDiarmid, Marco Tulio Pacheco, Norman J. Scott, Jr., and Charles F. Walker.

The curators of collections with which I worked were particularly gracious in providing information, lending large amounts of material and allowing dissections and skeletal preparations in certain cases (Museum abbreviations as used in the text in parentheses): James E. Böhlke, Academy of Natural Sciences, Philadelphia (ANSP); Werner C. A. Bokermann, São Paulo (WCAB); Antenor Leitao de Carvalho, Museu Nacional, Rio de Janeiro; Javier Castroviejo, Museo Nacional de Ciencias Naturales, Madrid; Doris M. Cochran and James A. Peters, United States National Museum (USNM) and field series GOV and JAP); James R. Dixon, Texas A. & M. University (TCWC); William E. Duellman, Museum of Natural History, University of Kansas (KU); Josef Eiselt, Naturhistorisches Museum, Vienna; Alice G. C. Grandison, British Museum (Natural History) (BMNH); W. Hellmich, Zoologische Sammlung des Bayerischen Staates, Munich; B. Hubendick, Naturhistoriska Museet, Göteborg; Robert F. Inger and Hyman Marx, Field Museum of Natural History (FMNH); Alan E. Leviton, California Academy of Sciences (CAS); Clarence J. McCoy, Carnegie Museum (CM); Günther Peters, Institut für Spezielle Zoologie und Zoologisches Museum, Berlin; Hobart M. Smith, formerly of Museum of Natural History, University of Illinois (UIMNH); Robert C. Stebbins, Museum of Vertebrate Zoology, University of California at Berkeley (MVZ); Paulo E. Vanzolini, Departamento de Zoologia, São Paulo (DZ); Greta Vestergren, Naturhistoriska Riksmuseet, Stockholm; Charles F. Walker, Museum of Zoology, University of Michigan (UMMZ); Ernest E. Williams, Museum of Comparative Zoology, Harvard University (MCZ); John W. Wright, Los Angeles County Museum of Natural History (LACM); Richard G. Zweifel, American Museum of Natural History (AMNH). Field series from the University of Southern California collections are designated CRE (Costa Rica), JRM (Honduras),<sup>2</sup> and PAS (Colombia).<sup>2</sup>

Robert J. Lavenberg and Mary Nafpaktitis facilitated my use of the General Electric Time Share Computer service provided by the Los Angeles County Museum of Natural History.

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<sup>2</sup>To be deposited in the herpetological collection of the Los Angeles County Museum of Natural History.

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For her constant encouragement and secretarial help, I thank my wife, Miriam.

#### SPECIES ACCOUNTS

Adult members of the *Melanonotus* species group may be confused only with those of the *Ocellatus* species group because members of both groups have extensive toe fringes as adults. The *Ocellatus* group members always have smooth dorsolateral folds, while members of the *Melanonotus* group usually do not have any indication of a dorsolateral fold, or, if such are present, they are weak and warty, never smooth.

Only brief synonymies are presented, including synonyms and generic reallocations of the valid species, as Gorham (1966) has recently published a bibliographic synonymy of the genus *Leptodactylus*.

#### *Leptodactylus dantasi* Bokermann

*Leptodactylus dantasi* Bokermann, 1959: 5-8, figs. 1-5 (Type locality, Brasil: Acre; Feijó. Holotype WCAB 1240, female).

**Diagnostic characters:** The only other species in the *Melanonotus* group with dark bellies with discrete light spots are *podicipinus* and *pustulatus*. *L. dantasi* has large light spots on the belly and lacks a metatarsal fold; *podicipinus* has small light spots on the belly and has a well developed metatarsal fold. *Leptodactylus dantasi* lacks light spots on the posterior face of the thigh, *pustulatus* has large, well defined light spots on the posterior face of the thigh.

**Summary of characteristics:** Snout rounded from above, rounded acute in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter 0.5 eye diameter; vomerine teeth in slightly arched series, posterior to choanae; head length greater than width, 43 per cent SL; head width 39 per cent SL; interorbital distance 6 per cent SL; first finger much longer than second, first just shorter than third, second longer than fourth; no distinct ulnar ridge; back warty-pustulose, tibia with many, pronounced warts; supratympanic fold does not reach shoulder; ventrolateral glands present but not distinct; toe tips very slightly expanded, dorsal surfaces not grooved; toes with well developed lateral fringes; subarticular tubercles moderately well developed; metatarsal fold absent; tarsal fold distinct along distal two-thirds of tarsus, weakly continuous with toe fringe; tarsus and foot with many horny spicules, spicules dark on scattered warts; standard length of female holotype 68 mm; femur shorter than tibia, 37 per cent SL; tibia shorter than foot, 39 per cent SL; foot longer than femur, 48 per cent SL; upper lip barred; light outlined dark band from interorbit to sacrum; rest of back uniform; upper surfaces of limbs faintly barred; venter with large light spots on

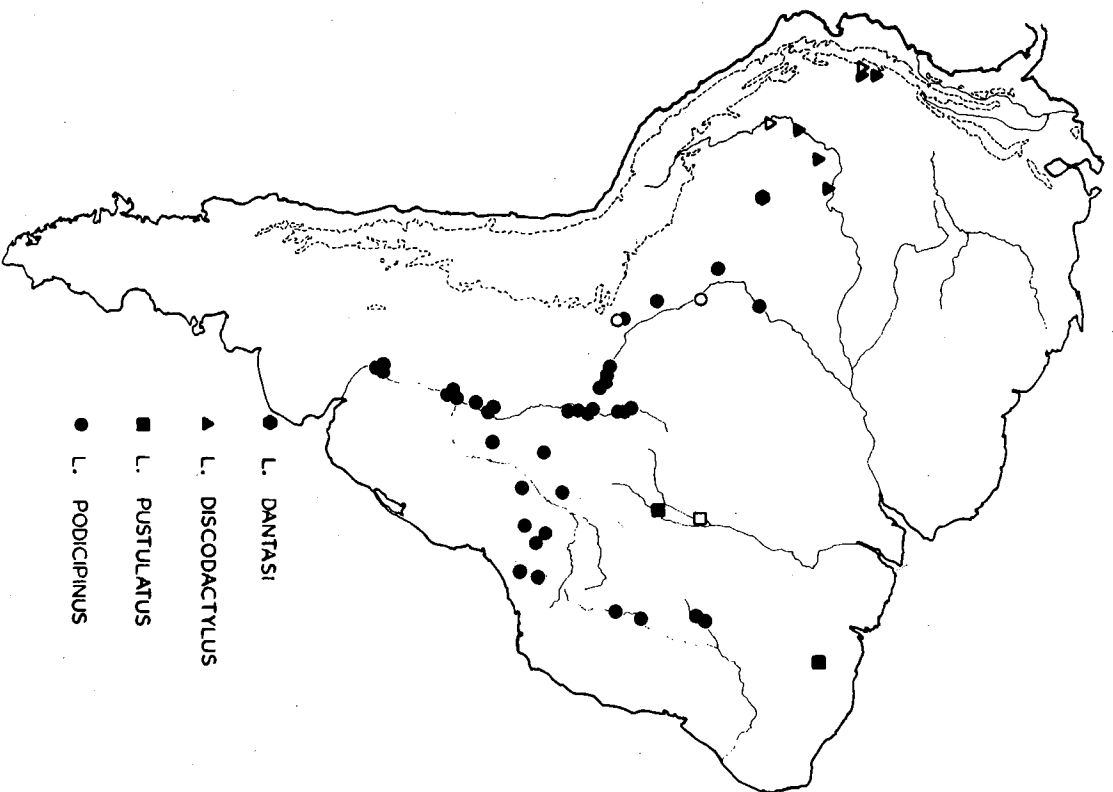


Figure 1. Geographic distribution of *Leptodactylus dantasi*, *discodactylus*, *pustulatus*, and *podicipinus*. Dashed line indicates 2000 meter contour. Open symbols indicate sites of sympatry with *wagneri*.

a dark ground, spots not always regular, spots anastomosing on limbs; posterior thigh uniformly dark.

*Distribution:* Known only from the type locality (Fig. 1), 249 m.

*Remarks:* *L. dantasi* is at present known only from the holotype.

*Leptodactylus discodactylus* Boulenger

*Leptodactylus discodactylus* Boulenger, 1883: 637, pl. 58, fig. 3 (Type locality, Peru: Loreto; Yurimaguas. Holotype BMNH 84.2.18.44, female). Gorham, 1966: 128 (Literature list, synonymy).

*Leptodactylus nigrescens* Andersson, 1945: 57-58 (Type locality, Ecuador: Río Pastaza and Río Napo, Watershed. Type series, Naturhistoriska Riksmuseet, Stockholm, unnumbered. Gorham, 1966: 132 (Literature list, synonymy)).

*Diagnostic characters:* The only other species in the *Melanonotus* species group that has disk-like swellings of the toe tips is *wagneri*. The upper disk surfaces of *discodactylus* have longitudinal grooves; if disks are present in *wagneri*, the upper surfaces are never grooved.

*Summary of characteristics:* Snout rounded, subovoid, or subelliptical from above, usually rounded or rounded-ventral in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter 0.5-0.66 eye diameter; male vocal slits elongate, arise lateral to posterior 0.25-0.33 tongue and parallel jaw almost to the angle of the jaw; single internal vocal sac in males; vomerine teeth in transverse or very slightly arched series, posterior to choanae; head length greater than width, 37-39.1-43 per cent SL; head width 32-35.2-39 per cent SL; interorbital distance 8-9.5-11 per cent SL; finger tips swollen or not; first finger longer than second, first shorter than third, second longer than or rarely equal to fourth; no spines on thumb of male; arm of male not hypertrophied; no distinct ulnar ridge; back rarely smooth to scattered with conical apicales; tibia especially scattered with conical apicales; supratympanic fold extends to shoulder; gland present at corner of mouth or not; post-tympanic gland present or absent; ventrolateral glands if present, not extensive; glands usually not present on posterior face of thigh; no chest spines on males; toe tips expanded into disks, dorsal disk surfaces grooved; toes with well developed lateral fringes; subarticular tubercles well developed; metatarsal fold present, weakly to strongly developed; tarsal fold distinct along distal 0.5-0.66 tarsus, not continuous with toe fringe; tarsus scattered with conical apicales; foot smooth, or outer sole scattered with conical apicales; standard length of males to 35 mm, females to 35 mm; femur shorter than tibia, 38-43.6-48 per cent SL; tibia shorter than foot, 43-45.8-49 per cent SL; foot longer than femur, 48-52.0-56 per cent SL; upper lip uniform or barred; interorbital region usually with a light stripe bordered behind by a dark

triangle, the dark triangle may extend to the sacral region, or uniformly dark; rest of back usually uniform, may have faint large blotches; upper surfaces of limbs barred to uniform; venter with a profusion of melanophores anteriorly only, to profuse over the entire venter; posterior thigh mottled.

*Distribution*: Known elevational range: 150-1000 m.

Known from a few localities of the upper Amazonian drainage in Ecuador and Peru (Fig. 1).

*Nomenclature*: Boulenger described *L. discodactylus* from Peru in 1883. The subsequent use of the name in the literature has been only a citation of the original description. Dr. James A. Peters allowed me to send one of his specimens, JAP 6197, to the British Museum for comparison with the holotype of *L. discodactylus*. Specimen 6197 is from the upper known elevational range of the species, and its characteristics agree with those of other high elevation populations discussed in the remarks section. Dr. Alice G. C. Grandison of the British Museum (Natural History) compared specimen 6197 with the holotype of *L. discodactylus*. She noted the departures from the holotype characters associated with elevation (see remarks section, below), but concluded that in all other aspects, including the diagnostic toe fringe, toe disks, and upper toe disk surface grooves, the specimens were identical.

Andersson described *Leptodactylus nigrescens* on the basis of three specimens from east Ecuador in 1945. His description is based upon the largest specimen. I was able to examine the largest syntype of *L. nigrescens* at the United States National Museum where Dr. Peters' private collection was available for comparison. Mr. Werner C. A. Bokermann had previously borrowed the two smaller specimens and allowed me to examine them at the National Museum. The type series is composite. The largest syntype of *L. nigrescens* possesses the diagnostic combination of toe fringe and toe disks with grooved upper surfaces of *L. discodactylus*. The other two specimens have well developed toe disks, no finger disks, no toe fringe, no tarsal fold, and two rows (1 pair) of dorsolaterally arranged conical apicalia. I consider the smaller two syntypes of *L. discodactylus* to represent *Eleutherodactylus nigrovittatus* Andersson, described in the same paper as *L. nigrescens*. In a cursory literature review, I was unable to find a senior synonym for this distinct little frog, but one may exist. To avoid future confusion, I hereby designate the largest (35 mm) specimen (the specimen has no museum number) the lectotype of *L. nigrescens*. *Leptodactylus nigrescens* Andersson is a junior synonym of *L. discodactylus* Boulenger.

*Remarks*: The few individuals available have certain differences which correlate with elevation.

Contrasting the highland samples from Ecuador (1000 m) with the lowland samples from Ecuador and Peru (150-300 m), one finds the following consistent differences (lowland population characteristics in parentheses): 1) the finger tips are not swollen (finger tips swollen, forming small disks);

2) the tarsal fold is usually distinct along the distal 0.66 of the tarsus (tarsal fold usually distinct on distal 0.5 of tarsus); and 3) smaller adult size, males to 30 mm, females to 32 mm (both males and females to 35 mm). I assume that the differences noted are responses to different climatic parameters associated with differences in elevation.

*Leptodactylus discodactylus* has been taken in sympatry with *L. wagneri* at two localities, Ecuador: Pasaza; Puyo, 1000 m and Peru: Loreto; Río Tamaya, Sobral, 150 m.

*Leptodactylus melanonotus* (Hallowell)

*Cystignathus melanonotus* Hallowell, 1860: 485 (Type locality, Nicaragua. Type apparently lost).

*Cystignathus echinatus* Brocchi, 1877: 181-2 (Type locality, Guatemala: Río-madre Nieja. Syntypes Paris Museum 6322-3).

*Cystignathus microtis* Cope, 1879: 265 (Type locality, Mexico: Guanajuato; Guanajuato. Syntypes USNM 9906, 9908, 9909).

*Cystignathus perlaevis* Cope, 1879: 269-270 (Type locality, Mexico: Oaxaca; Japana. Holotype USNM 10041, female).

*Leptodactylus melanonotus*, Brocchi, 1881: 20 (Cites Hallowell's record). Gorham, 1966: 131 (Literature list, synonymy).

*Leptodactylus occidentalis* Taylor, 1937: 349-52, pl. 1, figs. 1, 2, 7 (Type locality, Mexico: Nayarit; Tepic. Holotype FMNH 100015, female). Gorham, 1966: 133 (Literature list, synonymy).

*Diagnostic characters*: There is no one character that immediately distinguishes *L. melanonotus* from the other members of the *Melanonotus* species group. The toe disks of *L. discodactylus* distinguish it from *L. melanonotus* (toe tips not expanded into disks). *Leptodactylus dantasi*, *L. podicipinus*, and *L. pustulatus* have dark bellies with discrete light spots; *L. melanonotus* may have a dark belly, but it is mottled and never distinctly spotted. Certain few individuals of *L. melanonotus* are difficult to distinguish consistently from *L. wagneri* (*L. melanonotus* characters in parentheses): *L. wagneri* may have the toe tips expanded into distinct disks (toe tips never disk-like); *L. wagneri* may have a light longitudinal stripe on the posterior face of the thigh (no distinct stripe); *L. wagneri* reaches a larger adult size, standard length of males to 63 mm, females to 81 mm (males to 46 mm, females to 50 mm). The only way to distinguish consistently *L. melanonotus* from *L. wagneri* is by geography. *Leptodactylus melanonotus* is distributed from Mexico through Middle America, and west of the Andes in South America. *Leptodactylus wagneri* is found east of the Andes in South America.

*Summary of characteristics:* Snout rounded-nearly semicircular, rounded, rounded-subelliptical, or rarely subovoid from above, rounded to rounded-vertical in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter 0.5 to 0.75 eye diameter; male vocal slits elongate, arise lateral to mid-point of tongue to almost the angle of the jaw, usually parallel to jaw, rarely slightly oblique to the jaw; single internal vocal sac in males; vomerine teeth usually in transverse series, rarely very slightly arched, always posterior to the choanae; head usually longer than wide, rarely equal, or rarely head length shorter than wide, head length 30-36.3-41 per cent SL; head width 30-34.1-38 per cent SL; interorbital distance 5-7.2-9 per cent SL; finger tips not noticeably swollen; first finger just longer than or about equal to second, first shorter than third, second longer than fourth; finger ridges present, especially on second and third fingers; 2 spines on male thumb; male arm not hypertrophied; ulnar ridge not developed; head smooth or scattered with conical apical; upper eyelids warty, glandular or smooth, usually lacking conical apical; rest of back with scattered conical apical; the conical may be on warts or not; upper femur and tibia scattered with conical apical; supratympanic fold extends to shoulder, rarely indications of several warty dorsolateral folds; brown to orange ventrolateral glands poorly to extensively developed, same glandular material may or may not be on jaw angle, post-tympanic region, groin, posterior thigh, or inner tibia and along the tarsal fold; no chest spines on male; toe tips usually not expanded, sometimes slightly expanded, never disk-like, never with dorsal surfaces grooved; toes with well developed lateral fringes; subarticular tubercles well developed; metatarsal fold present, weakly to well developed; tarsal fold distinct along distal 2/3-5/6 tarsus, not continuous with toe fringe; tarsus with scattered conical apical; foot smooth, with scattered conical apical; or conical apical on outer sole only; standard length of males to 46 mm, females to 50 mm; femur longer than equal to, or usually shorter than tibia, 36-40.0-45 per cent SL; tibia shorter than foot, 37-42.7-47 per cent SL; foot longer than femur, 43-49.3-53 per cent SL; upper lip barred to uniform; interorbit with dark, light outlined triangle, a light and dark bar, or a light triangle reaching tip of snout anteriorly, bordered posteriorly by a dark triangle; rest of back brown to gray with darker indistinct spots, blotches, bands, stripes, or without pattern; upper limb surfaces barred to uniform; venter with few melanophores, appearing light to many melanophores profused especially anteriorly to rarely heavily profused over entire venter; posterior thigh mottled.

*Distribution:* Elevational range: sea level—1440 m. The species is known from both coasts of Mexico—Hermosillo, Sonora and the Gómez Farias region, Tamaulipas in the north, extending southward throughout Middle America. The species is known only from the western lowlands of South America to mid-Ecuador. (Figs. 2-4.)

*Nomenclature:* The holotype of *Cystignathus melanonotus* Hallowell is

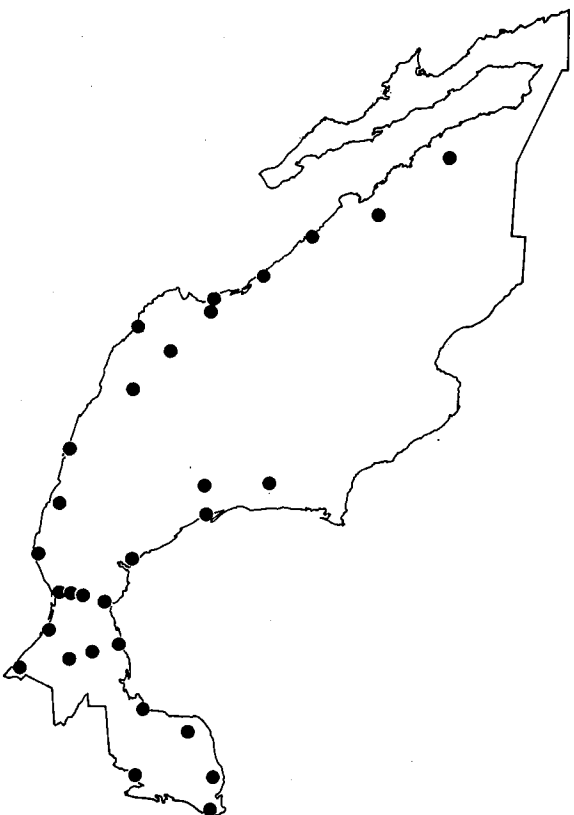


Figure 2. Geographic distribution of *Leptodactylus melanonotus* in Mexico.

apparently lost. The late E. R. Dunn noted (Dr. Dunn's notes presently on deposit in the library of Dr. Jay M. Savage) that the type was originally deposited in the National Museum as specimen number 6264 and that it was missing. The specimen is not listed in the catalog of type specimens of reptiles and amphibians in the U.S. National Museum (Cochran, 1961). In recent visits to the U.S. National Museum, although aided by the late Dr. Cochran and by Dr. Peters, I was unable to locate the type. The evidence indicates that the original holotype is lost.

*Leptodactylus melanonotus* is very closely related to both *L. wagneri* and *L. podicipinus*. *L. melanonotus* is found in Mexico and Middle America, where there is relatively little question as to what the species is. *L. melanonotus* is found west of the Andes and some individuals are very difficult to differentiate consistently from some individuals of *L. wagneri*, an Amazonian species. For nomenclature stability, the name *L. melanonotus* should be applied to a single specimen from the population found in Nicaragua, the type locality of the original, now lost, holotype. I therefore designate specimen number 84848 in the collection at the University of Kansas, an adult male, from Nicaragua, Zelaya, Bonanza, as the neotype of *Cystignathus melanonotus* Hallowell.

I have examined the holotype and two paratypes of *Cystignathus microtis*

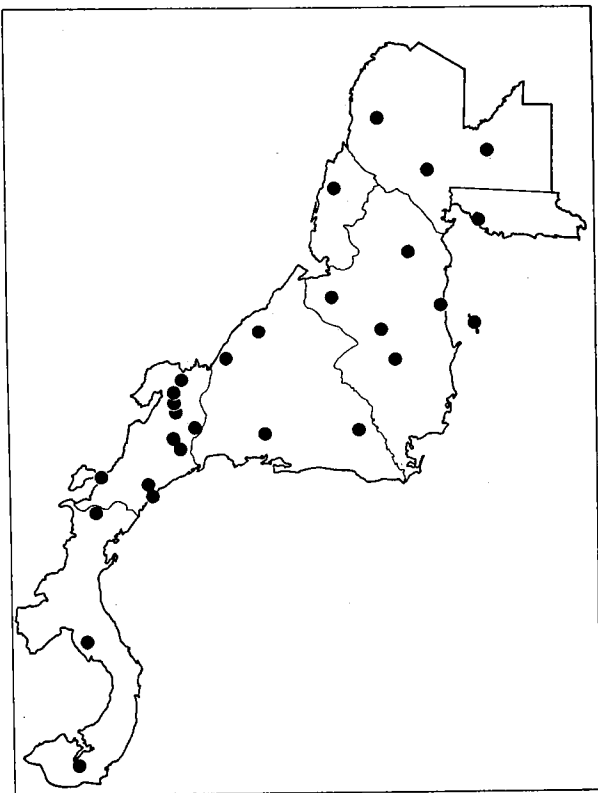


Figure 3. Geographic distribution of *Leptodactylus melanonotus* in Middle America.

Cope. Only two species of *Leptodactylus* (*labialis* and *melanonotus*) occur in Mexico; they are quite distinct from each other. Members of the type series of *C. microtis* agree with *L. melanonotus* in having fringed toes and mottled thighs; both characters differentiate *L. melanonotus* from *L. labialis*. There is no morphological reason for retaining *C. microtis*. The status of *C. microtis* has always been questioned, because the type locality was given as Mexico: Guanajuato; Guanajuato. Guanajuato is well above the elevational limits of *L. melanonotus*. No other specimens of *L. melanonotus* have since been taken from Guanajuato. I think the locality data are in error and probably represent the shipping point from which the specimens were sent to the U.S. National Museum rather than the collecting site.

I have examined numerous paratypes of *Leptodactylus occidentalis* Taylor and have collected topotypic specimens which correspond closely with the type series of *L. occidentalis*. As is shown in the character analysis portion, *L. occidentalis* does not differ in any consistent way from *L. melanonotus* and is therefore considered a junior synonym of the latter.

I have examined the holotype of *Cystignathus perlaevis* Cope and concur with the numerous workers who have placed it in synonymy with *L. melanonotus*.

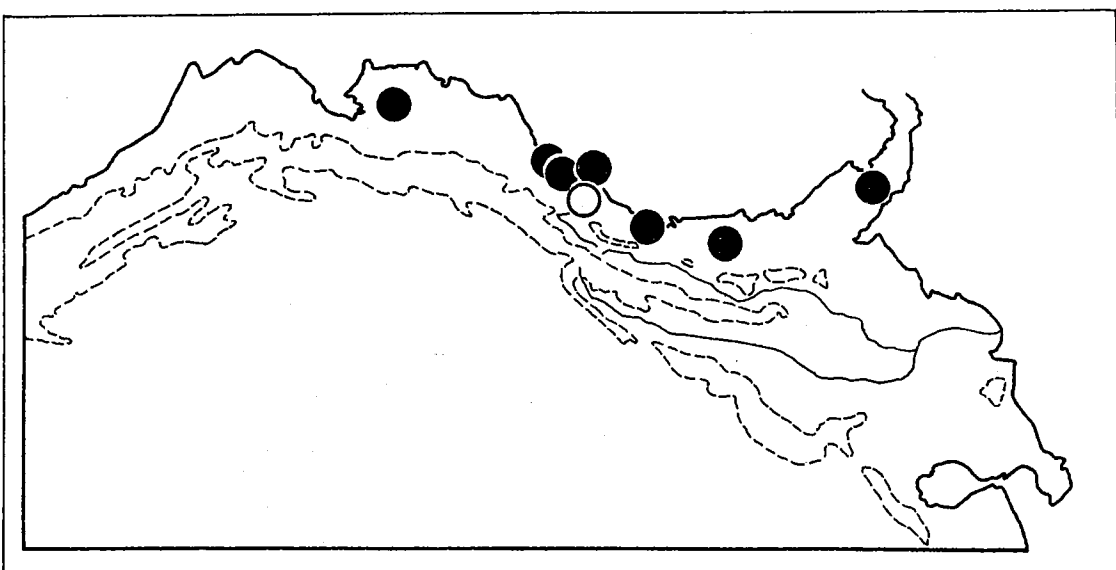


Figure 4. Geographic distribution of *Leptodactylus melanonotus* in South America. Dashed line indicates 2000 meter contour. Open symbol indicates site of sympatry with *wagneri*.



*Remarks:* A single specimen of *L. melanonotus* is recorded from Starr County, Texas, in the United States. I have examined the specimen (UIMNH 29817); it is a juvenile *L. melanonotus*. This single record is about 400 km north of the next recorded locality, from which several samples are known. The locality data for the Texas specimen is possibly in error, and for that reason I have not included the record in the range of *L. melanonotus*.

*Leptodactylus melanonotus* has been taken in sympatry with *L. wagneri* at one locality in western Colombia (Nariño, La Guayacana). This instance of sympatry is not too surprising, as the sources of the rivers Cauca and Patía interdigitate at about 1600-1800 m within the range of *L. wagneri*. *Leptodactylus wagneri* is found throughout the Valle de Cauca. Apparently *L. wagneri* follows the Río Patía into the west-coast lowlands of Colombia.

*Leptodactylus podicipinus* (Cope)

*Cystignathus podicipinus* Cope, 1862: 156 (Type locality, Paraguay. Holotype ANSP 14539).

*Leptodactylus podicipinus*, Boulenger, 1882: 248 (Catalogue, synonymy). Gorham, 1966: 135-6 (Literature list, synonymy).

*Leptodactylus nattereri* Lutz, 1926: 1011-2 (Type locality, Brasil: São Paulo; Itapura, Ilha Seca. Synatypes AL 1314-1315).

*Leptodactylus podicipinus podicipinus*, Gans, 1960: 305-6 (List). Gorham, 1966: 136 (Literature list, synonymy).

*Diagnostic characters:* The only other species in the *Melanonotus* species group with a dark belly with discrete light spots are *L. daniasi* and *L. pustulatus*. *L. daniasi* has large light spots on the belly and lacks a metatarsal fold. *L. podicipinus* has small light spots on the belly and has a well developed metatarsal fold. *L. pustulatus* has large, light discrete spots not only on the belly, but on the entire ventral surface of the leg and on the posterior surface of the thigh. *L. podicipinus* has small spots which, if on the leg, are only on the ventral surface of the thigh. The males of *L. podicipinus* have thumb spines, the males of *L. pustulatus* lack thumb spines.

*Summary of characteristics:* Snout rounded, subelliptical to subovoid from above, rounded in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter  $\frac{1}{2}$ - $\frac{3}{4}$  eye diameter; male vocal slits elongate, arise lateral to middle of tongue, parallel jaw almost to angle of jaw; single internal vocal sac in males; vomerine teeth usually in transverse series, rarely in very slightly arched series, always posterior to choanae; head length greater than width, 34-37.0-41 per cent SL; head width 32-34.6-38 per cent SL; interorbital distance 7-8.2-10 per cent SL; finger tips not swollen; first finger usually longer than second, sometimes

equal, first finger much shorter than, shorter than, or about equal to third, second longer than fourth; finger ridges present, especially on second and third fingers; 2 spines on male thumb; male arm not hypertrophied; ulnar ridge usually not developed, sometimes a glandular ridge or 4 conical apicalles in a row; dorsum smooth, glandular, or warty, scattered with conical apicalles, especially on posterior dorsum and upper leg surfaces; supratympanic fold extends to shoulder, may or may not be faint indication of several warty dorsolateral folds; ventrolateral glands orange-brown, small to large or absent, glands present or absent on angle of jaw, dorsolateral folds, posterior thigh, inner tibia, and along tarsal fold; no chest spines on male; toe tips not expanded; toes with well developed lateral fringes; subarticular tubercles well developed; metatarsal fold well developed; tarsal fold distinct along distal 2/3-5/6 tarsus, usually not continuous with toe fringe, rarely weakly continuous with toe fringe; tarsus scattered with conical apicalles; foot smooth or outer sole with scattered conical apicalles; standard length of males to 38 mm, females to 44 mm; femur usually shorter but sometimes longer than tibia, 35-40.9-48 per cent SL; tibia shorter than foot, 38-42.9-48 per cent SL; foot longer than femur, 44-50.7-56 per cent SL; upper lip barred or uniform; interorbital region with light and dark stripe, or light outlined dark triangle extending to sacrum or not; rest of back uniform or with indistinct darker bands; upper limb surfaces uniform or with indistinct dark bars; throat, chest, belly dark with small light spots, rest of venter dark, but not with distinct light spots, posterior portion of belly occasionally with limb pattern rather than light-spotted; posterior thigh usually mottled, rarely with a moderately distinct light longitudinal line.

*Distribution:* Elevational range: 18-550 m.

*Leptodactylus podicipinus* is found south of the Amazonian drainage region in the following river drainages: São Francisco, Parana, Paraguay. The species is absent from the narrow coastal lowland strip along eastern Brazil from the States of Rio Grande do Norte to Rio de Janeiro. The species follows the Serras de San José, Santiago, and Sunnas in Bolivia, and the Serras dos Parecis and Pacaás Novos in western Brasil. (Fig. 1).

*Nomenclature:* In his description of *Cystignathus podicipinus*, Cope designated as type(s) "Mus. Smithsonian, (No. 5831) Phlada. Acad." Dr. James A. Peters informed me that in the catalog under 5831 is a later remark stating that the specimen had been sent to the Academy of Natural Sciences in Philadelphia. Apparently there was only one specimen upon which Cope based *C. podicipinus*. I have examined the holotype of *C. podicipinus* from the Academy of Natural Sciences. The specimens I have examined from Paraguay are morphologically similar to the holotype in all diagnostic features.

Lutz described *Leptodactylus nattereri* on the basis of specimens collected in the state of São Paulo, Brasil, and included the specimens figured by Steindachner (1864) from the collection of Natterer. The figures in Steindachner

(Plate XI, figs. 1 a-d) show the two spines per thumb and dark belly with small light spots characteristic of *L. podicipinus*.

*Remarks:* *Leptodactylus podicipinus* has been taken in sympatry with *L. wagneri* at two localities: Bolivia (Santa Cruz: Buenavista, 500 m) and Brasil (Rondônia: Forte Príncipe da Beira, 100-200 m). At both localities the species are very distinct, markedly differing in size, belly pattern, and posterior thigh pattern. There is apparently a narrow band of sympatry between *L. podicipinus* and *L. wagneri*, with character displacement occurring in the band of sympatry.

*Leptodactylus pustulatus* (Peters)

*Entomoglossus pustulatus* W. Peters, 1870: 647, Pl. 2, fig. 1 (Type locality, Brasil: Ceará. Type apparently lost).

*Leptodactylus pustulatus*, Boulenger, 1882: 239 (Catalogue, synonymy); Gorham, 1966: 137 (Literature list, synonymy).

*Diagnostic characters:* The only other species in the Melanonotus species group with a dark belly with discrete light spots are *L. dantasi* and *L. podicipinus*. *Leptodactylus pustulatus* has large, light discrete spots on the posterior surface of the thigh. *Leptodactylus dantasi* and *L. podicipinus* do not have spots on posterior surface of the thigh. The males of *L. pustulatus* lack thumb spines, the males of *L. podicipinus* have thumb spines.

*Summary of characteristics:* Snout rounded to subovoid from above, rounded to rounded-obtuse in profile; canthus rostralis indistinct; loreal slightly concave in profile; tympanum distinct, horizontal diameter 2/3 eye diameter; male vocal slits elongate, parallel to jaw, extend from mid-tongue almost to angle of jaw; single internal vocal sac in male; vomerine teeth usually in transverse series, rarely very slightly arched, always posterior to choanae; head length greater than width, 35-36.4-38 per cent SL; head width 33-34.0-35 per cent SL; interorbital distance 5.6-7.8 per cent SL; finger tips not expanded; first finger longer than second, first shorter than third; second greater than fourth; finger ridges present, especially on fingers two and three; no spines on male thumb; male arm not hypertrophied; ulnar ridge not developed; dorsal texture pustulose, with scattered conical apical; supratympanic fold extends to shoulder, may or may not be indications of 6-8 warty dorsolateral folds; brown ventrolateral glands extend onto belly, or entire frog appears glandular; no chest spines on males; toe tips not expanded; toes with well developed lateral fringes; subarticular tubercles well developed; metatarsal fold present; tarsal fold distinct along distal 1/2-3/4 tarsus, usually continuous with toe fringe, occasionally weakly continuous; tarsus with scattered conical apical; foot usually with scattered conical apical, rarely smooth; standard length of males to 38 mm, females to 51 mm; femur shorter than tibia, 37-39.0-41 per cent SL; tibia shorter than foot, 39-41.8-44 per cent SL; foot longer than femur, 45-

51.3-55 per cent SL; dorsum uniform or patterned, if patterned, a light inter-orbital triangle originating at tip of snout bordered behind by a dark triangle, rest of back with darker longitudinal lines; upper limb surfaces faintly barred to uniform; venter dark with large light spots extending onto lower leg surfaces and groin; posterior thigh with light spots as on venter.

*Distribution:* Known elevational range: 100-200 m.

The few localities from which *L. pustulatus* have been collected are all low Amazonian. The major river drainages for which accurate locality data are available include the Paranaíba, Araguaia, and Tocantins. (Fig. 1).

*Nomenclature:* *Entomoglossus pustulatus* was described by W. Peters on the basis of a single female from Ceará, Brasil, in the collection of the Royal Zoological Museum, Berlin. Dr. Peter Beurton of the Berlin Museum states that he was unable to locate the type in the collections there. Dr. Hellmich of the Munich Museum informed me that the type of *Entomoglossus pustulatus* is not and has never been in the Munich collection, the likely alternative depository for the type. This suggests that the type is lost. The identity of *L. pustulatus* has been very unclear because of the rarity of specimens in collections. Because of this confusion and because there appears to be no other Ceará (topotypic) material in collections, I have selected an individual representative of the population that I consider to be *L. pustulatus*. The nearest locality to the type locality is the Rio Poi in Piauí. The specimen from this locality is only in a fair state of preservation, but it still retains the pattern diagnostic of *L. pustulatus*. I designate this specimen, MCZ 373, from the collection of the Museum of Comparative Zoology, Harvard University, as the neotype of *Entomoglossus pustulatus* Peters.

*Remarks:* *L. pustulatus* has been taken in sympatry with *L. wagneri* at one locality (Brasil: Mato Grosso: São Domingos, Rio das Mortes, 200 m).

*Leptodactylus wagneri* (Peters)

*Plectromantis wagneri* W. Peters, 1862: 232-3 (Type locality, Ecuador, west side of the Andes. Type formerly at Munich Museum, destroyed in World War II).

*Platymantis petersii* Steindachner, 1864: 254-6, Pl. 16, fig. 2, 2 a-c (Type locality, Brasil: Amazonas; Marabitanas. Type lost).

*Leptodactylus brevipes* Cope, 1887: 51-2 (Type locality, Brasil: Mato Grosso, Chupada, 30 mi. NE of Cuyata, near the headwaters of the Xingu. Holotype ANSP 11270, female).

*Leptodactylus validus* Garman, 1887: 14 (Type locality, West Indies: St. Vincent; Kingston. Syntypes ANSP 26108, MCZ 2185).

*Leptodactylus wagneri* Nieden, 1923: 479 (Literature list, synonymy). Gorham, 1966: 140 (Literature list, synonymy).

*Leptodactylus pallidirostris* A. Lutz, 1930: 25-6, Pl. 1, fig. 3 (Type locality, British Guiana; Essequibo; Kartabo).

*Leptodactylus natalensis* A. Lutz, 1930: 26-7, Pl. 1, figs. 7-7a, Pl. 3, figs. 1-2 (Type locality, Brasil: Rio Grande do Norte; Rio Bahu. Syntype USNM 81130, male).

*Leptodactylus intermedius* A. Lutz, 1930: 27-8, Pl. 3, fig. 6 (Type locality, Brasil: Amazonas; Manacapuri near Manaus).

*Eleutherodactylus leptodactyloides* Andersson, 1945: 43-4, fig. 15 (Type locality, Ecuador: Pastaza; Rio Pastaza. Holotype Stockholm Royal Museum, male).

*Leptodactylus podicipinus petersii*, Rivero, 1961: 47 (Redescription, synonymy). Gorham, 1966: 136 (Literature list, synonymy).

**Diagnostic characters:** *Leptodactylus wagneri* may have expanded toe tips, but the upper surface of the toe tip is never with longitudinal grooves, distinguishing *wagneri* from *discodactylus*, which has well developed toe disks with the upper disk surfaces grooved. *Leptodactylus wagneri* may have a dark belly, but it is mottled, and not with distinct light spots, distinguishing it from the dark-bellied, light-spotted *dantasi*, *podicipinus*, and *pustulatus*. Some individuals of *wagneri* are difficult to distinguish consistently from *melanonotus* (*melanonotus* characters in parentheses); *wagneri* may have the toe tips expanded into distinct disks (toe tips never disk-like); *wagneri* may have a light longitudinal stripe on the posterior face of the thigh (no distinct stripe); *wagneri* reaches a larger adult size, standard length of males to 63 mm, females to 81 mm (males to 46 mm, females to 50 mm). The only consistent way to distinguish *melanonotus* from *wagneri* is by geography. *Leptodactylus melanonotus* is distributed from Mexico through Middle America, and west of the Andes in South America. *Leptodactylus wagneri* is found east of the Andes in South America.

**Summary of characteristics:** Snout usually rounded, rarely subelliptical or subovoid from above, rounded to rounded-ventral in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter  $\frac{1}{2}$ - $\frac{3}{4}$  eye diameter; male vocal slits elongate, arise laterally to tongue, parallel jaw and extend almost to the angle of the jaw or slightly oblique to jaw; single internal vocal sac in male; vomerine teeth in transverse to arched series, posterior to choanae; head length greater than, equal to, or less than width; head length 33-36.8-42 per cent SL; head width 32-34.9-39 per cent SL; interorbital diameter 6-7-8.9 per cent SL; finger tips not noticeably swollen; first finger longer than second, first shorter than or equal to third, second longer than or equal to fourth; fingers with lateral ridges, especially on second and third fingers; two spines on male thumb; male arm

slightly hypertrophied only in largest specimens; no ulnar ridge; dorsal texture smooth to glandular, posterior portion of back and legs with scattered conical apicales; supratympanic fold extends to shoulder, may or may not be indication of 2-4 faint dorsolateral folds; orange-brown ventrolateral glands moderately developed or absent; gland at angle of jaw developed or not; post-tympanic gland developed or not; posterior thigh gland present or absent; no chest spines on male; toe tips not expanded to moderately expanded and disk-like, never with longitudinal grooves on dorsal surface; toes with well developed lateral fringes; subarticular tubercles well developed; metatarsal fold present; tarsal fold distinct along distal  $\frac{4}{7}$ - $\frac{3}{4}$  tarsus; not continuous with toe fringe; tarsus with scattered conical apicales; foot smooth, with scattered conical apicales, or outer sole with scattered conical apicales; standard length of males to 63 mm, females to 81 mm; femur shorter than tibia, 35-42.4-48 per cent SL; tibia shorter than foot, 41-46.9-51 per cent SL; foot longer than femur, 49-52.4-57 per cent SL; upper lip usually barred, sometimes uniformly patterned; light and dark interorbital bar, dark bar may extend posteriorly as a triangle or band as far as sacrum; rest of back uniformly patterned or indistinctly spotted or striped, warts on sides may be darker than ground color; upper limb surfaces barred to uniform; ventral pattern of scattered melanophores, melanophores may be profuse anteriorly only, or profuse over entire venter; posterior thigh with distinct light longitudinal stripe to mottled.

**Distribution:** Elevational range: sea level—1900 m.

The species is widely distributed throughout northern and central South America east of the Andes. There is a single record west of the Andes in Colombia. The species occurs in the Cauca and Magdalena valleys of west-central Colombia, and throughout the greater Amazonian Basin; the species is also distributed along the narrow eastern coastal strip of Brasil from the States of Rio Grande do Norte to Rio de Janeiro. The species occurs on the islands of Bequia, Granada, St. Vincent, Tobago, and Trinidad. (Fig. 5).

**Nomenclature:** Wilhelm Peters (1862) described *Plectromantis wagneri* from Ecuador on the basis of a single male specimen. Peters listed the type as "von Dr. Moritz Wagner an den Westseite der Anden in Ecuador . . . im zoologischen Cabinet du München." Dr. Richard Eberidge kindly looked for the type when he was at the Munich museum. He writes (personal communication), ". . . the old museum had one specimen, No. 1080/0, from 'Pastassa' collected by Wagner. This may or may not have been the type, there is no indication in the record that it was, but in any event the specimen was destroyed during World War II." It is likely that specimen number 1080/0 was the unique type of *Plectromantis wagneri*. Pastassa is a geographically more reasonable locality than the west side of the Andes. Peters' description is quite good, and the secondary sexual characteristics of spines on the thumb of the male leave no doubt as to the identity of the frog described by Peters. It is the population herein called *L. wagneri*. The only *Leptodactylus* west of the

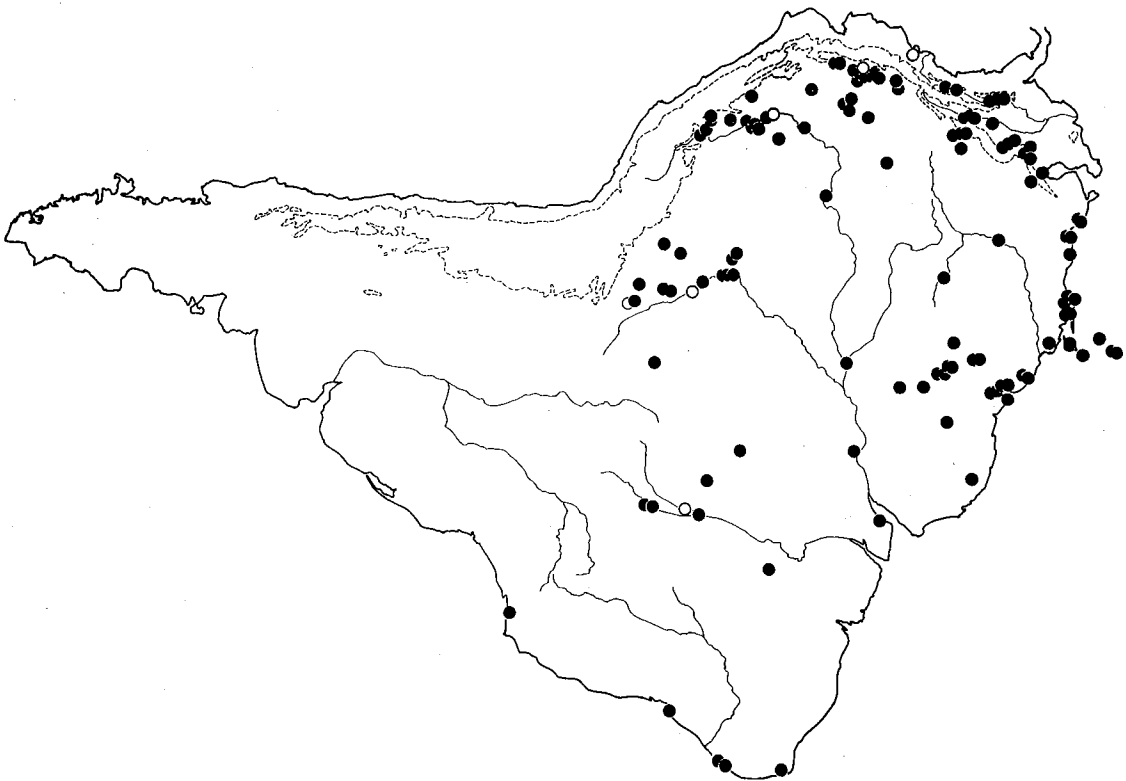


Figure 5. Geographic distribution of *Leptodactylus wagneri*. Dashed line indicates 2000 meter contour. Open symbols indicate sites of sympatry with other species of the *Melanonotus* group.

Andes in Ecuador with thumb spines on the male is *L. melanonotus*. The males of *L. melanonotus* reach 40 mm SL in Ecuador; the type of *P. wagneri* was 68 mm SL. I consider that Peters' locality is probably incorrect, and the data as recorded for Munich specimen 1080/0 are correct. The name *L. wagneri* has never been used in association with a *Leptodactylus* population in the literature since the original description. The status of the northern South American population of the *Melanonotus* group has always been uncertain. To stabilize the nomenclature I hereby designate the holotype of *Eleutherodactylus leptodactylodes* Andersson in the Stockholm Royal Museum of Natural History (no number), an adult male, from the Río Pastaza, as the neotype of *Plectromantis wagneri* Peters.

Steindachner described *Platymantis petersii* on the basis of a single male specimen from Marabitanas, Amazonas, Brasil. Dr. Josef Eiselt of the Vienna Museum has been unable to find the unique type of *Platymantis petersii*. The type has been searched for several times and is most likely lost. *Leptodactylus petersii* has been used in various combinations for various populations of frogs of the *Melanonotus* species group. I consider *P. petersii* to be a junior synonym of *L. wagneri*, and that nomenclatural stability would be served by designating a neotype which conforms with my analysis. I have not examined any material from Marabitanas, nor do I know of any material from there. The closest record that I know of to Marabitanas is in Venezuela. This specimen, AMNH 23182, is in very good condition. The locality is Venezuela: Amazonas; Río Pescado, approximately 150 m. The specimen is a female. I hereby designate AMNH 23182 as neotype of *Platymantis petersii* Steindachner.

Cope described *Leptodactylus brevipes* on the basis of a single specimen from Chupada, Mato Grosso, Brasil. The name has been cited in literature lists based upon the original description but not upon the basis of recent material. I have examined the type, and find it the same as *wagneri*. The belly has very few melanophores, so that no confusion is possible with either *podicipinus* or *pustulatus*, the only other members of the *Melanonotus* species group with which it could possibly occur or be confused. *Leptodactylus brevipes* is regarded as a junior synonym of *L. wagneri*.

*Leptodactylus validus* was described by Garman from a series of specimens from the island of St. Vincent. I have found no differences between any of the island populations and the mainland population of *wagneri*, as shown below in the character analysis section. No holotype was designated by Garman. I hereby designate MCZ 71920, an adult male, from Kingston, St. Vincent, as the lectotype of *Leptodactylus validus* Garman.

Lutz described three species of *Leptodactylus* of the *Melanonotus* group in the same paper in 1930. The first, *pallidirostris*, was described from British Guiana: Essequebo; Kartaibo. I have not been able to examine the type, but have examined numerous examples of the *Melanonotus* group from the type locality. All specimens represent a single species and conform with the type

description of *pallidirostris*. The specimens from Karabo are not distinct from *wagneri*. Thus, *L. pallidirostris* is considered a junior synonym of *L. wagneri*.

*Leptodactylus natalensis* is the second species described by Lutz. I have examined one syntype of the type series and find it the same as other specimens examined in this study from the type locality (vicinity of Natal). The syntype has a lightly pigmented venter and marbled posterior thigh surfaces. I consider *L. natalensis* Lutz to be a junior synonym of *L. wagneri*. No holotype was designated. I designate the specimen I have examined, USNM 81130, a male, as the lectotype of *Leptodactylus natalensis* Lutz.

The third species of the Melanonotus group described by Lutz is *L. intermedius*. As in the case of *pallidirostris*, I have not seen the types, but have examined material from the type locality. The topotypic material I have examined from Manaus agrees with the description of *intermedius*. I consider the material from Manaus to be *wagneri*; hence *intermedius* is a junior synonym of *L. wagneri*.

Andersson described *Eleutherodactylus leptodactyloides* on the basis of a single specimen from Ecuador. I have been able to examine the type specimen. It is a *Leptodactylus* as suggested by the specific name, rather than an *Eleutherodactylus*. I have designated this specimen, above, as the neotype of *Plectronotus wagneri*, thereby making *Eleutherodactylus leptodactyloides* a junior synonym of *L. wagneri*.

*Remarks:* *Leptodactylus wagneri* has been taken in sympatry with *discodactylus*, *melanonotus*, *podicipinus*, and *pustulatus*.

#### KEY TO ADULT MEMBERS OF THE MELANONOTUS SPECIES GROUP

- 1a. Toe tips expanded into disks, dorsal surfaces with longitudinal grooves ..... *discodactylus* 2
- 1b. Toe tips usually not expanded into distinct disks, dorsal surfaces never grooved ..... 2
- 2a. Ventral surfaces of legs and posterior surface of thigh with large, light, distinct spots ..... *pustulatus*
- 2b. Ventral surfaces of legs light or dark, if large spots present, spots not distinct; posterior surface of thigh light or dark, never with large, light, distinct spots ..... 3
- 3a. Belly dark with distinct, light spots, spots usually distinct over entire belly, but sometimes anastomosing on posterior belly ..... 4
- 3b. Belly light or dark; if dark, no distinct light spots ..... 5
- 4a. Belly with large light spots; no metatarsal fold ..... *dantasi*
- 4b. Belly with small light spots; well developed metatarsal fold ..... *podicipinus*
- 5a. Moderate sized frogs, males to 46 mm SL, females to 50 mm; posterior thigh never with light longitudinal stripe; toe tips never noticeably expanded; Mexico, Middle America, South America west of the Andes to Ecuador ..... *melanonotus*

- 5b. Moderate to large frogs, males to 63 mm SL, females to 81 mm; posterior thigh may have a light longitudinal stripe; toe tips often noticeably expanded; South America east of the Andes ..... *wagneri*

#### CHARACTER ANALYSIS

*Standard length:* Two broad geographic patterns are evident in male *L. melanonotus*. The coastal populations vary between 30 and 40 mm. Modal sized individuals (36 mm Hermosillo, Sonora, Mexico) or smaller specimens (34 mm Gómez Farías region, Tamaulipas, Mexico; 33 mm Ecuador) are associated with the extreme northern and southern geographic range. The largest specimens are associated with two lowland pass regions in the montane backbone of the Americas: the lowland pass at Tehuantepec, Mexico; and the Arenal pass in Costa Rica. The geographic pattern of female *L. melanonotus* size parallels the male geographic pattern, but the trends are not as pronounced. In addition to the Tehuantepec and Arenal passes harboring the largest females (47-50 mm), the Yucatan Peninsula and eastern lowlands of Costa Rica also have females of large size (46-48 mm). The range of adult female size is approximately 35-50 mm.

*Leptodactylus wagneri* males attain greatest size along the eastern slopes of the Andes in Colombia, Ecuador, and Peru, ranging from about 40-60 mm. Along the northern coast of South America, on the islands, and in the Amazonian basin, the sizes range from 30-40 mm. The geographic pattern of *L. wagneri* female size exactly parallels the male adult size with the exception of the ranges. The east Andean slope populations most frequently range in size from 50-80 mm; the north coast, island, and Amazonian populations usually range from 40-60 mm.

Adult male *L. podicipinus* range from about 28-38 mm in length, with a trend towards smaller size at the southern end of the geographic range. Adult female *L. podicipinus* range in size from 36-44 mm also with a trend towards smaller size at the southern end of the geographic range.

The geographic pattern of size variation is basically the same in males and females, the only difference being that the females average larger than the males.

The relationship between size and rainfall, number of dry months, and elevation are statistically significant only in the case of *L. wagneri*. In *L. wagneri* males, a statistically significant correlation is present between greatest size of adults and mesic habitats ( $r = .28$ ,  $P < .01$ ). This correlation appears to be biologically valid for both males and females, as a statistically significant correlation was found with smaller size in more xeric habitats as measured by number of dry months (males  $r = -.50$ ,  $P < .01$ , females  $r = -.27$ ,  $P < .01$ ). A statistically significant correlation was found for greatest size and increasing elevation for both males and females in *L. wagneri* (males

