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LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK
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STUDIES ON THE FROGS OF THE GENUS *LEPTODACTYLUS* (AMPHIBIA: LEPTODACTYLIDAE). VI. BIOSYSTEMATICS OF THE MELANONOTUS GROUP

By W. RONALD HEYER[1]

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 Brasil.

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 *melanonotus, 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 Capirio, 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 rainfall (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. McDiarmid, 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 Hymen 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),[2] and PAS (Colombia).[2]

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

[2]To be deposited in the herpetological collection of the Los Angeles County Museum of Natural History.

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-vertical 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 coni apicales; tibia especially scattered with coni 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 coni apicales; foot smooth, or outer sole scattered with coni 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 splotches; 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 coni apicales. 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: Pastaza; 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 coni apicales; upper eyelids warty, glandular or smooth, usually lacking coni apicales; rest of back with scattered coni apicales, the coni may be on warts or not; upper femur and tibia scattered with coni apicales; 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 coni apicales; foot smooth, with scattered coni apicales, or coni apicales 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 Farías 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

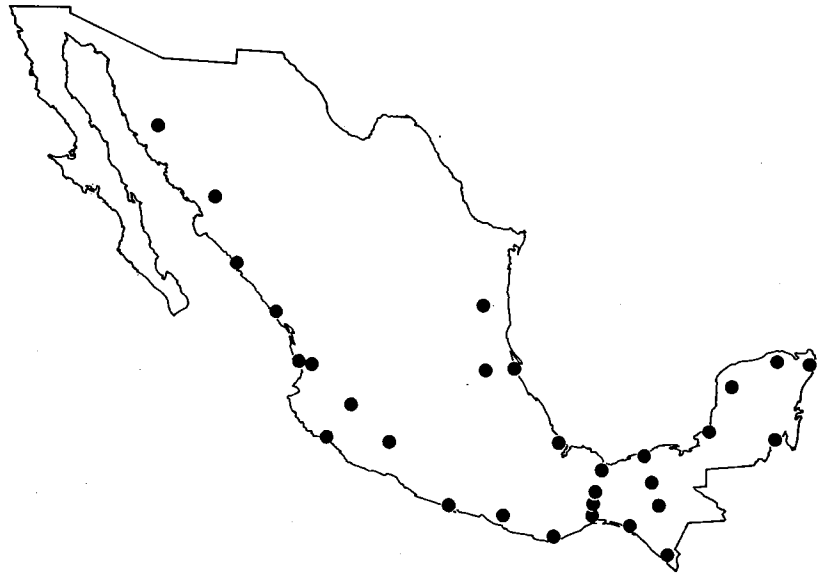

Figure 2. Geographic distribution of *Leptodactylus melanonotus* in Mexico.

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*

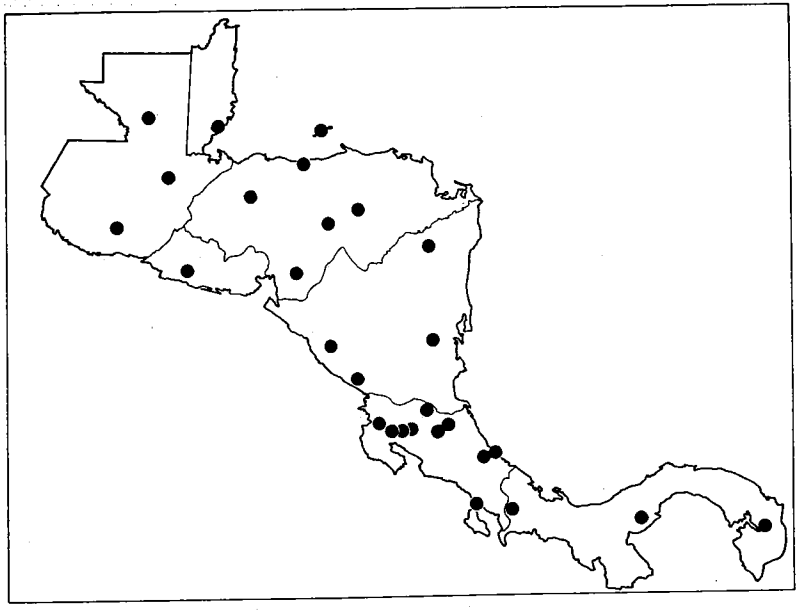

Figure 3. Geographic distribution of *Leptodactylus melanonotus* in Middle America.

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*.

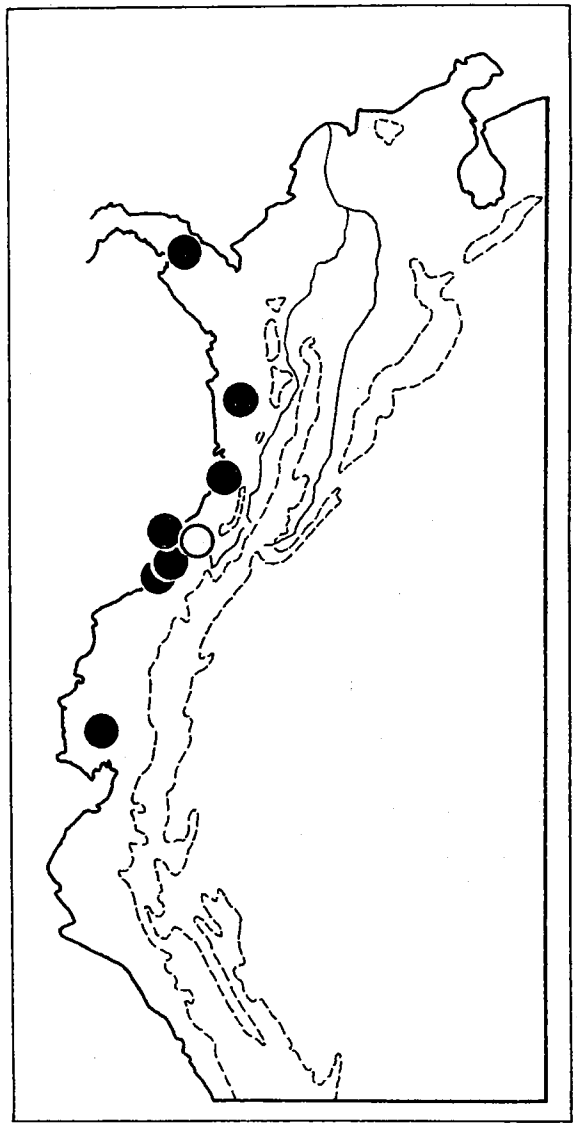

Figure 4. Geographic distribution of *Leptodactylus melanonotus* in South America. Dashed line indicates 2000 meter contour. Open symbol indicates site of sympatry with *wagneri*.

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 Patia 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 Patia 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. Syntypes 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. dantasi* and *L. pustulatus*. *L. dantasi* 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 ½-¾ 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 coni apicales in a row; dorsum smooth, glandular, or warty, scattered with coni apicales, 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 coni apicales; foot smooth or outer sole with scattered coni apicales; 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 Sunsas 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) Philada. 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 Principe 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 coni apicales; 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 ½-¾ tarsus, usually continuous with toe fringe, occasionally weakly continuous; tarsus with scattered coni apicales; foot usually with scattered coni apicales, 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 interorbital 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 Paranaiba, 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 Poti 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 Domingoes, 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 Manaos).

Eleutherodactylus leptodactyloides Andersson, 1945: 43-4, fig. 15 (Type locality, Ecuador: Pastaza; Río 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-vertical in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter ½-¾ eye diameter; male vocal slits elongate, arise lateral 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 coni 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; posttympanic 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 4/7-3/4 tarsus, not continuous with toe fringe; tarsus with scattered coni apicales; foot smooth, with scattered coni apicales, or outer sole with scattered coni 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 Etheridge 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 leptodactyloides* 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: Essequibo; Kartabo. 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 Kartabo 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 *Plectromantis 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*

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

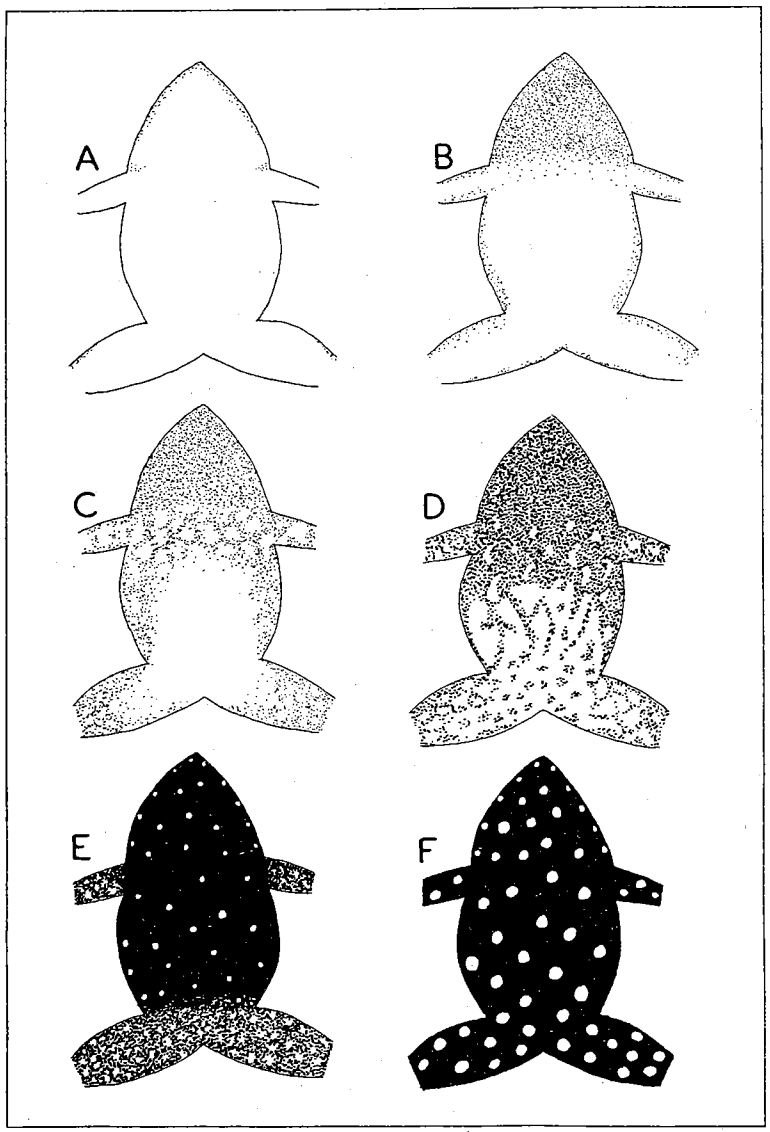

Figure 6. Ventral color pattern standards. Note that pattern F is restricted to *Leptodactylus pustulatus*.

r = .38, $P = <.01$, females r = .42, $P = <.01$). The elevational effects producing size differences in these frogs are probably associated with rainfall differences also.

Character displacement apparently occurs in the narrow bands of sympatry between *L. melanonotus, podicipinus*, and *wagneri*. At La Guayacana in Colombia, a female *melanonotus* (mature) measures 38 mm, and a female *wagneri* measures 59 mm. Two instances of sympatry are known for *wagneri* and *podicipinus*. At Buenavista, Bolivia, a female *podicipinus* measures 40 mm, and a female *wagneri* 46 mm. At Forte Principe da Beira, Brasil, a female *podicipinus* measures 34 mm, a female *wagneri* 43 mm, and a male *podicipinus* 29 mm, and a male *wagneri* 38 mm.

Ventral pattern: Five categories were used in scoring the ventral pattern. These ranged from A, in which the throat and belly do not have any melanophores, to E, in which the throat and belly are heavily covered with melanophores, leaving light spots (Fig. 6).

The distribution of ventral pattern is variable throughout most of the geographic range of *L. melanonotus*. In many localities, conditions ranging from B to D, encompassing the variation encountered in this species, are found. The populations at the northern and southern extremes of the geographic range lack much of the variability as in other populations, and are lighter in ventral coloration. Northwestern Mexican and South American populations are average in pattern density. There is a weak trend of darker pattern in Atlantic lowland populations.

No clear geographic trend in ventral pattern in *L. wagneri* is evident. The usual range for the species is B to D, with a few populations having an intermediate condition between D and E. Most adequate samples (10 or more individuals) show a variation through only two categories, either B-C or C-D. The occurrence of individuals with pattern B seems to be random with perhaps more B category individuals throughout the northern part of the species range, including the populations of islands off northern South America.

There is no geographic trend of ventral color pattern in *L. podicipinus*. Almost all populations fall in the E category, with a few individuals in D or between D and E.

A correlation between a darker ventral color pattern and greater annual rainfall is present in *L. melanonotus* (r = .17, $P = .05$). There is no correlation between ventral pattern and glandular extent, number of dry months, or elevation in *melanonotus*. No correlations between ventral color pattern and glandular extent, annual rainfall, number of dry months, or elevation are present in *podicipinus*. A correlation is found between a lighter ventral color pattern and greater ventrolateral gland extent in *wagneri* (r = −.14, $P = .05$). This is most certainly not a cause-effect relationship, but it may indicate that the genes responsible for these two characters are on the same chromosome or are co-functional in some other way. No correlations between ventral color

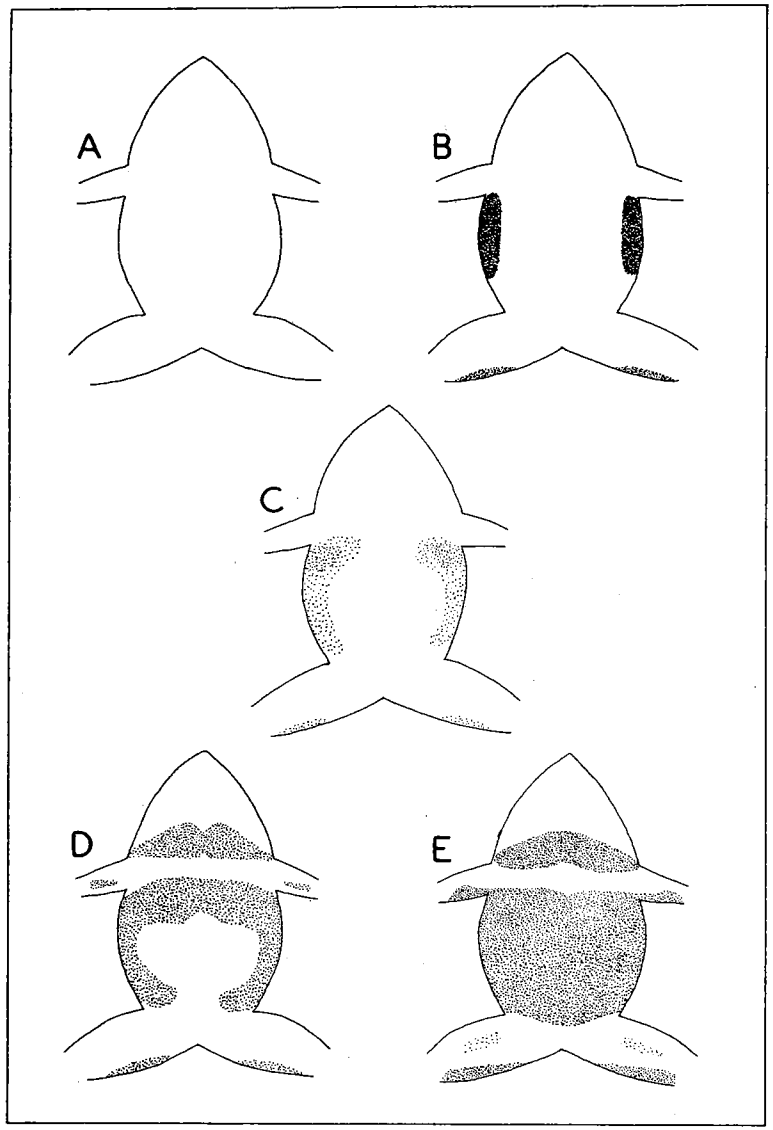

Figure 7. Ventrolateral gland standards.

pattern and annual rainfall, number of dry months, or elevation are found for *wagneri*.

Ventral color pattern is a character that has apparently undergone character displacement in the area of sympatry between *L. podicipinus* and *wagneri*. Certain individuals of *wagneri* closely approach the pattern of *podicipinus*. In the two known instances of sympatry of *podicipinus* and *wagneri*, the ventral color patterns are clearly distinct; *wagneri* individuals have a light belly; *podicipinus* individuals have a dark, light spotted belly. *Leptodactylus discodactylus* and *wagneri* have basically the same ventral color patterns. *Leptodactylus pustulatus* is very distinct from *wagneri* with respect to ventral pattern. *Leptodactylus pustulatus* has a distribution allopatric to those of *dantasi* and *podicipinus*, the species it most closely resembles in ventral color pattern.

Ventrolateral glands: Five categories of ventrolateral gland extent were established, ranging from no glands, A, to the entire belly, and most other ventral surfaces covered with glands, E (Fig. 7). In addition, five categories of gland color were noted in preserved animals: 1—brown; 2—gray; 3—black; 4—orange-brown; and 5—yellow-orange.

The geographic distribution of ventrolateral gland extent and coloration in *L. melanonotus* is a mosaic. The ventrolateral glands are very compact and brownish to orange-brown (B—1,4) in populations from northwest Mexico and Panama. The greater degree of glandular extent is found in populations from the Isthmus of Tehuantepec, Yucatan Peninsula, Atlantic coastal British Honduras and Honduras, and the Arenal pass region in Costa Rica. These generalities are complicated in that individuals from a single locality 1) have or lack glands and 2) demonstrate a range of variation of glandular extent which encompasses the range of the entire species.

Most populations of *L. wagneri* either have no ventrolateral glands or have orange-brown diffuse glands of moderate extent (C—4). A few *wagneri* specimens from the southern part of their geographic range have more extensive glandular extent. Where moderate samples (10 or more individuals) are available, the specimens at any single locality demonstrate categories A and C—4. There is no geographic trend.

Many individuals of *L. podicipinus* lack ventrolateral glands. When ventrolateral glands are present, they are of moderate extent and orange-brown in preservative (C—4, D—4). Individuals from a single locality usually encompass the range of variation found within the species. No clear geographic trend is evident.

There are no correlations between ventrolateral gland extent and annual rainfall, number of dry months, or altitude in *L. melanonotus* and *podicipinus*. A correlation is present between greater ventrolateral gland extent and greater annual rainfall in *wagneri* ($r = .13$, $P = .05$). Such a correlation is more suggestive of a causal relationship than the correlation between ventral color pattern and ventrolateral gland extent in *wagneri*. There are no correlations

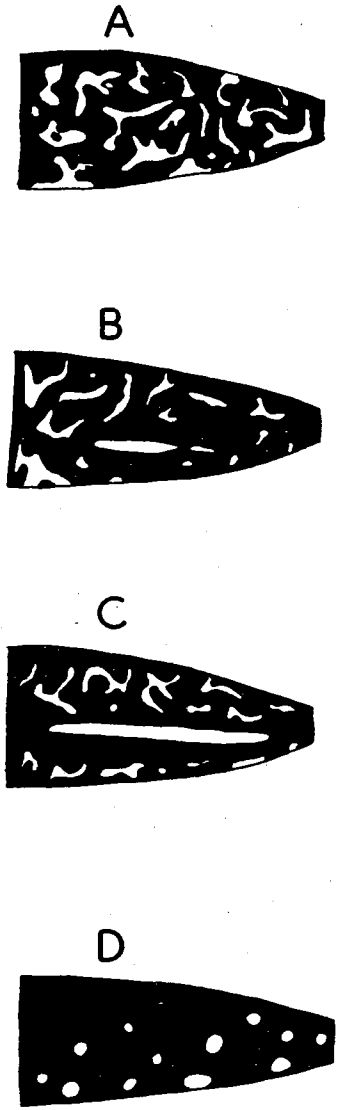

Figure 8. Posterior surface of thigh color pattern standards. Note that pattern D is restricted to *Leptodactylus pustulatus*.

between ventrolateral gland extent and number of dry months or elevation in *wagneri*.

Changes of extent of ventrolateral glands may occur seasonally, but there are no collections made at all seasons from a single locality. In the summer of 1967 when breeding was just beginning, Dr. James R. Dixon and I collected several series of *L. melanonotus* from western Mexico. We noticed that no glands were evident on living animals. After a few days in preservative, however, the ventrolateral glands on the animals were dark brown in color and distinct. The function of ventrolateral glands is not known.

Color pattern of posterior surface of thigh: Four categories were distinguished: A) mottled; C) with a light longitudinal stripe; B) intermediate between A and C; D) with distinct light spots on a dark background (Fig. 8).

Almost all *L. melanonotus* have a mottled posterior thigh, although a few individuals from scattered localities show some indication of a light stripe (category B).

In large series of *L. wagneri* from one locality, character states A, B, and C are represented. This is true throughout the geographic range of *wagneri*, with the exception of the Cauca Valley (Colombia) population.

Few large samples from *L. podicipinus* demes were available for this study, but, on the basis of the series available, the distribution of the thigh pattern appears to parallel the situation in *wagneri*. That is, categories A, B, and C are represented within any deme.

There is no correlation between the posterior thigh pattern and the climatic and elevational parameters used. It appears likely that the light stripe in *L. wagneri* and *podicipinus* is genetically controlled by very few genes, perhaps one. The scattered B categories in *melanonotus* populations indicate that the gene potential for a posterior thigh light stripe is present. The D category is found only in *pustulatus*.

The light stripe on the posterior thigh is another feature that shows character displacement in the instances of sympatry between *L. podicipinus* and *wagneri*. At both sites of known sympatry, *wagneri* individuals have well developed stripes. The *podicipinus* at the sites of sympatry either have a mottled thigh (Buenavista, Bolivia), or only an indication of a light stripe (Forte Principe da Beira, Brasil). At this latter locality, the differences in thigh pattern are very striking. The light stripe in *wagneri* individuals is completely bordered with black and is very distinct from the thigh pattern of sympatric *podicipinus*.

Toe-disk size: Three categories were used (Fig. 9): A) toe tips not expanded at all; C) Toe tips expanded into definite disks; B) intermediate condition.

There is a gradient of toe-tip size in *L. melanonotus*. In the northern part of the range, Mexico to Costa Rica, most are in category A, only 3 demes among those examined within this area had individuals with B condition. Many

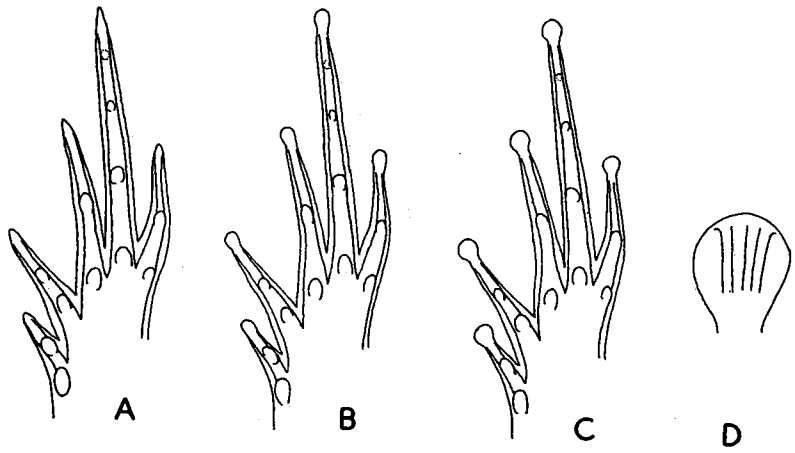

Figure 9. Toe tip standards. Pattern D is the upper disk surface of *Leptodactylus discodactylus* showing longitudinal grooves.

individuals from Costa Rica have intermediate disks, B. In the South, from Panama through Ecuador, all populations have B disks. In no case is the toe tip expansion developed into a distinct disk as found in *L. discodactylus*.

A distinct geographic gradient in toe tip expansion is also seen in *L. wagneri*. The Cauca Valley (Colombia) population is marked by non-expanded toe tips. The rest of the Andean slope and upper Amazonian populations of Colombia, Ecuador, Peru, and Bolivia have categories A and B, with B predominant. The frogs associated with the rivers draining northward, those upon the islands, and probably those of the eastern Amazon region are either B or C; that is, many individuals from these areas have distinct toe disks such as are found in *L. discodactylus*.

No distinct geographic gradient in toe tip expansion is evident in *L. podicipinus*. Most specimens lack expanded toe tips, A, but a few individuals from scattered demes have slightly expanded toe disks, B.

The possible role of character displacement in toe-tip expansion is evident at the two sites of sympatry between *L. podicipinus* and *wagneri*. At both sites, the toe tips of *podicipinus* are not expanded, A, and the toe tips of *wagneri* are slightly, but noticeably, expanded, B.

Mating call: Mating call samples were chosen to answer the specific status concerning *L. occidentalis*. Demes were sampled in lowlands throughout the latitudinal geographic range of *occidentalis* from Sonora through Nayarit. Lowland samples of *melanonotus* from Jalisco, Colima, and Michoacán were

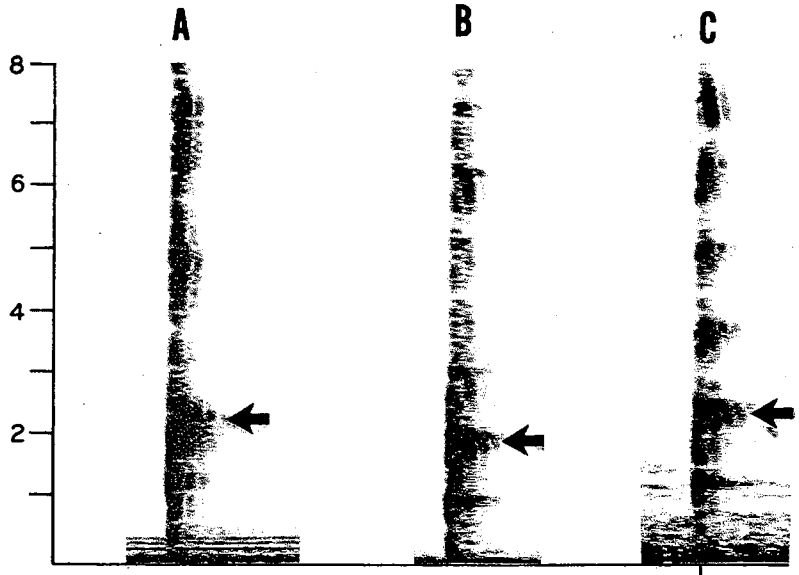

Figure 10. Mating calls of *Leptodactylus melanonotus* in western Mexico. Vertical scale in kilocycles per second, horizontal scale in seconds. Arrows indicate dominant frequency band. A—Call specimen from Sinaloa, 36 km S Los Mochis turnoff on Mexico Highway 15. B—Call specimen from Jalisco, 0.5 km NE Tonila. C—Call specimen from Jalisco, 7.7 km E La Huerta.

also taken. Demes along elevational transects were sampled in the states of Jalisco and Nayarit.

All of the calls have a basic similarity when heard and when viewed on sonagrams. All calls consist of quite short notes, with a very wide frequency range. The call components are difficult to compare with calls of other species in which the components are very distinct. I consider the dominant frequency the darkest, widest portion of the sonagram of the call, as substantiated in sections, measuring the call duration at that point (Fig. 10A). Any other noticeably prominent frequency below the dominant is taken as the fundamental frequency (Fig. 10B). Any periodic emphasized frequencies above the dominant are considered harmonics, even though they may not be sharply differentiated (Fig. 10C). The duration of the call is from .04 to .09 seconds, the range .05 to .08 seconds being common in the call of a single individual. Call duration does not correlate with temperature in the samples at hand. The most striking differences among the calls are: 1) one or two notes per call group; 2) the fundamental frequency is dominant or not; 3) the dominant frequency values; 4) whether harmonics above the dominant are distinct or

not; 5) whether the note is straight on the paper, or components are displaced to the right.

Most of the calls are characterized by having a single note per call group. Only in the state of Nayarit did individuals have calls consisting of two notes per call group. One of the calls recorded at Tepic has a call consisting of both one and two notes, as does the individual recorded from near San Blas. The specimen recorded from Santa Cruz has a call consisting of two notes.

The calls recorded from near Acatlán, Jalisco, Tepic, Nayarit, and Hermosillo, Sonora, show the fundamental to be the same as the dominant. One call from near Los Mochis, Sinaloa, has a fundamental distinct from the dominant; another call has the fundamental equal to the dominant. All other calls have fundamentals distinct from the dominant. Where fundamental frequencies are present, they approximate one half the frequency of the dominant.

The dominant frequencies usually range from 2000 to 2500 cycles per second. A range of 2000 to 2400 cycles per second is recorded in the deme from Tepic, Nayarit. The only dominant differing from the range is from a call recorded from Santa Cruz, Nayarit, which has a dominant of 3000 cycles per second. The higher frequency can not be accounted for by differences in temperature or elevation.

Three categories are used to distinguish whether harmonics above the dominant are evident: 1) not present; 2) some indication of presence; 3) present. Calls from Colima, Michoacán, and near La Huerta and Tecalitlan, Jalisco, have harmonics. The call from near Tonila, Jalisco, has some indication of harmonics. The calls from near Acatlán, Jalisco, show all three states. The calls from Tepic, Nayarit, either lack harmonics, or show some indications of harmonics. The calls from Santa Cruz, Nayarit, show harmonics present or absent. All calls recorded north of Santa Cruz lack harmonics above the dominant frequency.

Notes with certain components displaced to the right on the sonagram are found in calls from localities that also have straight notes on the sonagram. These localities demonstrating both types of notes are near Los Mochis, Sinaloa, Santa Cruz, Nayarit, and near Acatlán, Jalisco.

Two of the call characteristics are gradually clinal in nature; the relation of the fundamental to the dominant, and the presence or absence of harmonics above the dominant. Two of the call characteristics are largely variable within demes, and not constant on any geographic basis: number of notes per call group; and whether the call is displaced to the right on the sonagram or not. A call from a single deme shows a higher dominant frequency than the others.

Discussion: Physical size appears to be a major, pre-mating isolating mechanism between *L. melanonotus* and *wagneri*. Additional collecting around the northern end of the Andes in Colombia is necessary to determine the interactions or lack of interactions between these two species.

Character displacement is most noticeable in sympatric demes of *L. podicipinus* and *wagneri*, where respective adult sizes, ventral color patterns, posterior thigh color patterns, and toe tip expansions are very distinct. Expression of certain of these characters are similar in other populations of *podicipinus* and *wagneri*. Ventral color pattern in particular shows the effects of character displacement. Certain demes along the slopes of the Andes in Bolivia and southern Peru have ventral color patterns that closely approach the pattern of some *podicipinus*. The ventral patterns of *wagneri* and *podicipinus* are distinct at points of sympatry; the specimens do not exhibit gradation of ventral pattern D to E.

The status of the population of frogs in northwest Mexico (*L. occidentalis* Taylor) has been particularly uncertain. The main characters used to distinguish the population are adult size and extent and color of the ventrolateral glands. The size of the population fits into a larger pattern discussed above and is not peculiar to a series of demes in northwest Mexico. The ventrolateral gland condition (B) is characteristic of the population in northwest Mexico, but the same condition is found in certain demes in Panama. The mating call data indicate that the extreme northwestern demes are differentiated from the lowland demes in Colima and Michoacán, but that the differences are connected by a series of demes demonstrating intermediate call types. The lowland demes in Colima and Michoacán are separated geographically from the highland demes of Jalisco and Nayarit by terrain with virtually no standing water; water is either cascading or nonexistent. The population from northwest Mexico appears to be isolated at present from the coastal demes of Colima and southward. Morphological differentiation of the northwest Mexican population is slight, and the same differentiation is repeated in other demes of *L. melanonotus* throughout its geographic range.

The island demes of *L. wagneri* are in no way distinguishable from mainland *wagneri*; in fact, the presence of expanded toe disks and the adult size indicate that the demes originated from the population found in northern Venezuela and Guyana.

I follow an earlier statement on the value of the subspecies concept (Savage and Heyer, 1967). I believe the methods treating variation within a species, as here presented, reveal more of the populational trends than does the arbitrary practice of designating subspecies. It is nearly impossible to fragment the three widespread species on the basis of any combination of characters.

It is appropriate to interject a comment on my evaluation of the taxonomic decisions at this point. Most of the study was based on morphology; I did not have the benefit of any biological data for most of the specimens; I regard the taxonomic decisions as conservative. With the evidence available for this study, my best judgment is that the Melanonotus species group is composed of six species.

Relationships: Four characters shared by members of the Melanonotus

group are useful in determining the degree of evolutionary advancement of the species. More adequate justification for determining primitive and advanced character states is presented elsewhere (Heyer, 1968). The presence of toe disks is considered an advanced condition, and the presence of grooves on the upper disk surfaces is considered a further advancement. Absence of thumb spines in males, a striped or distinctly spotted pattern on the posterior thigh surface, and a ventral pattern of light spots on a dark background are considered advanced conditions.

Certain trends among the species are clear. *Leptodactylus melanonotus* is primitive in all four characters, and is probably most like the ancestral Melanonotus group stock which gave rise to the six extant species. *Leptodactylus discodactylus* and *pustulatus* are the most specialized. *Leptodactylus discodactylus* has the most advanced disks, and the males lack thumb spines. *Leptodactylus pustulatus* has an advanced ventral and thigh pattern, and the males also lack thumb spines. *Leptodactylus dantasi, podicipinus,* and *wagneri* are intermediate. *Leptodactylus dantasi* has the advanced ventral pattern. The male is unknown for this species. *Leptodactylus podicipinus* and *wagneri* have individuals with the advanced thigh stripe. *Leptodactylus podicipinus* has a spotted belly and *wagneri* has individuals with toe disks. Based on only these four characters, a graphic representation is very difficult as evolution appears to have produced a mosaic pattern. *Leptodactylus melanonotus, podicipinus,* and *wagneri* are the most closely related. I think *dantasi* and *pustulatus* are more closely related to these three species than they are to *discodactylus*. *Leptodactylus dantasi, pustulatus,* and *podicipinus* resemble each other in general appearance, and the distinctive patterns of *dantasi* and *pustulatus* could have been derived from a species very much like that of *podicipinus*. For the present, I regard the loss of thumb spines to be a case of parallel loss in *discodactylus* and *pustulatus*. The relationships are presented as a dendrogram (Fig. 11).

DISTRIBUTIONAL ANALYSIS

Although some areas of Latin America have been studied moderately intensively, the geology, climate, soil types, and vegetation of many parts of Middle and South America are known poorly or not at all. Savage (1966) has recently given an excellent synthesis on the origins and history of the Central American herpetofauna, but no such synthesis has been attempted for South America. Only the broadest generalizations can be made with respect to the distribution of the components of the Latin American herpetofauna and the following remarks must be considered as provisional.

To discuss the distribution of the Melanonotus group, it is necessary to review briefly the broad geographic, paleogeographic, climatic, and vegetational patterns of Latin America.

Geography: The great American Cordillera forms a distributional barrier

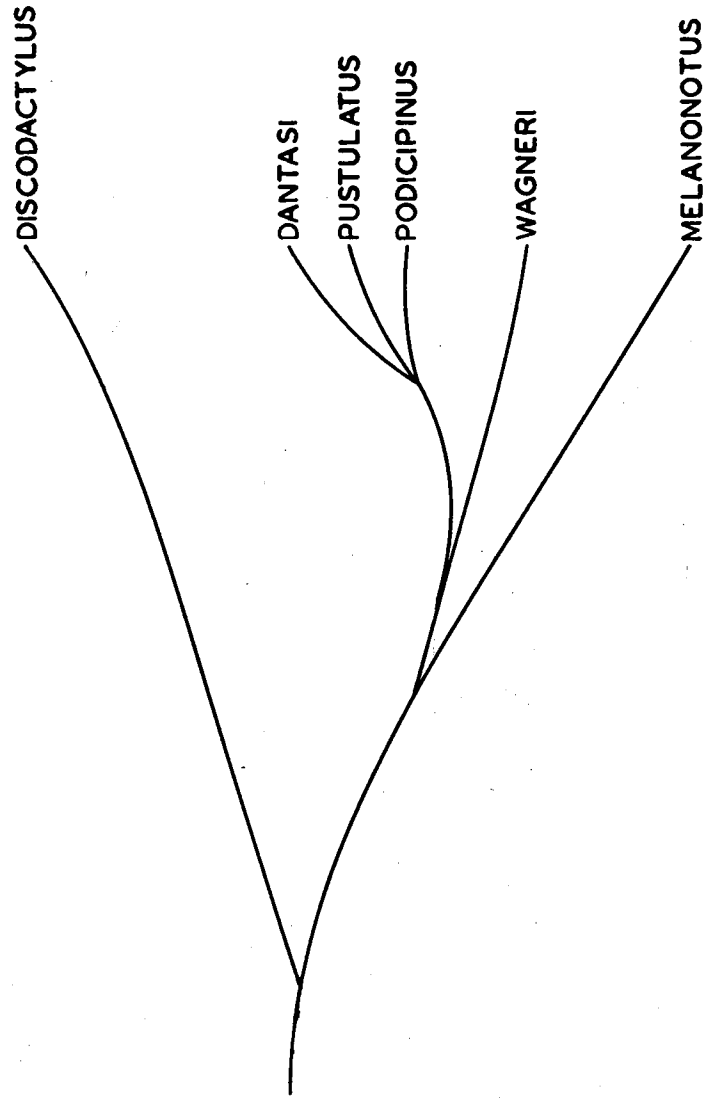

Figure 11. Proposed phylogeny of members of the Melanonotus group.

to frogs of the Melanonotus species group; the upper elevational limit for any species is about 1800 meters. Breaks in the montane chain where faunal interchange occurs are: the Isthmus of Tehuantepec in Mexico; the region around Lake Managua in Nicaragua; the Arenal pass in Costa Rica; and an extensive area including most of Panama and northernmost Colombia. The Andes of South America pass along the western outline of the continent, abut against the sea, or leave a very narrow lowland coastal strip to the west.

In South America, there are three major upland regions in addition to the Andes. These are the Guiana shield, the central Brasilian shield, and the coastal Brasilian shield. These upland regions do not form an elevational barrier to the distribution of frogs of the Melanonotus group. The Guiana shield is somewhat continuous from eastern Colombia, extending through central and southern Venezuela, to and including almost all of the Guianas and part of Brasil just below the Guianas. The central Brasilian shield is of irregular outline bordering Bolivia on the west and extending as a band eastward along the southern edge of the Amazon basin. The coastal Brasilian shield extends from the easternmost tip of South America in the state of Rio Grande do Norte along the coast southward to the state of São Paulo.

Paleogeography: The Cordillera of Latin America is geologically young, its present form attained in the very vigorous orogenesis from Mid to Late Tertiary, especially in Miocene and Pliocene times. Orogenesis continues in some parts of the Cordillera. (For a more detailed account and further references, see Childs and Beebe, 1963; Harrington, 1962; and Savage, 1966).

The Guiana, central Brasilian, and coastal Brasilian shields date from the Early Precambrian and have probably been land positive since then (Harrington, 1962). The history of the present land areas amidst the shields is poorly known, particularly since Mid-Tertiary to present, comprising, probably, the whole of the history of the Melanonotus species group. The Amazon basin has had a recurrent history of continental sediment deposition and marine embayment. Continental deposition has definitely occurred in the Late Tertiary, but whether any marine embayment alternated with continental deposition during or following this time is not known (Harrington, 1962). No precise information on the isolation or continuity of the shields with relation to each other exists, and it is impossible to comment on the isolation of the ancestral stocks of the frogs of the Melanonotus species group.

Climate: Comments are limited to climates affecting the distribution of members of the Melanonotus group. The coasts of Mexico and Middle America are characterized by seasonal rainfall patterns. A very pronounced hot and dry season is found along the western Mexican coast southward to the middle of Costa Rica. Similar conditions are found along the east coast of Mexico south to Nicaragua. The Atlantic coastal area of Costa Rica is wet the year around, but a seasonality in rainfall occurs. The only place in Middle America with a nearly continuously wet tropical rainforest is the Osa peninsula region

of Pacific Costa Rica. A wet climate with no cool season and basically no dry season occurs in four restricted areas in South America. The first such area is the Chocó region along the western coast of Colombia extending into northwest coastal Ecuador. The second and largest region is amidst the upper tributaries of the Amazon in southern Colombia, eastern Ecuador, most of eastern Peru, and northwestern Brasil. The third extends from coastal Guianas to the Brasilian coast just south of the mouths of the Amazon. The fourth area extends along a sometimes very narrow coastal strip of eastern Brasil from the states of Bahia south to Rio de Janeiro. All the other regions in South America occupied by the Melanonotus group have a pronounced dry season from one to nine months in duration. The driest regions in South America, also four, appear to limit the distribution of the Melanonotus group. The first runs along the western lowlands of middle Ecuador southward the length of the western lowlands of South America. The second lies along the north coast of Colombia and Venezuela, penetrating inland various distances. The third is in northeastern Brasil including the states of Maranhão, Piauí, and Ceará. The fourth is the Gran Chaco of northern Argentina, southeastern Bolivia, and southwestern Brasil (James, 1959; see also Walter and Lieth, 1960-1967).

Vegetation: The vegetation of Latin America is very complex and very inadequately studied. Many different systems have been used to define and describe the vegetation of Latin America. For the present I use the broad vegetational maps found in James (1959) and Wagner (1964) as the basis for discussion.

True tropical rainforests are found in the Osa peninsula region of Costa Rica; along western coastal Colombia and northwestern coastal Ecuador; along upper drainages of the Amazon characterized by high, continuous rainfall; and along the narrow coastal strip of Brasil from the states of Rio Grande do Norte to Rio de Janeiro. Tropical and subtropical rainforests which have a definite seasonal rainfall distribution are found in a continuous belt along the east coast of Mexico through Panama. Coastal patches of deciduous forest are found within the tropical and subtropical rainforests along the Carribean coast of Mexico, the tip of the Yucatán peninsula, easternmost British Honduras, easternmost Honduras and northeastern Nicaragua. Seasonal tropical rainforest is continuous with the tropical rainforest of the upper Amazon and covers almost all of the Amazon basin not covered by the tropical rainforest. Tropical deciduous forests are found along the west coast of Mexico from the state of Jalisco southeast to the middle of the Pacific coast of Costa Rica; along the periphery of the Guiana shield; in eastern Brasil from the north coast of the state of Rio Grande do Norte to middle Bahia, excluding the narrow eastern coastal strip; and in the Gran Chaco. Thorn forests are found along the northern coasts of northeast Colombia and Venezuela. Savannas cover the Guianan and central Brasilian shields, and most of the coasts ad-

jacent to the Brasilian shields. A palm forest is found in northeast Brasil in the states of Piauí and Maranhão.

Distribution of the Melanonotus Species Group: Most of the species are known from scattered localities. *Leptodactylus melanonotus* has been most thoroughly sampled, and moderately accurate distributional data are available for at least Mexico and Costa Rica. Records for *dantasi, discodactylus,* and *pustulatus* are very spotty, and more distributional data are needed to define the geographic limits of the species. *Leptodactylus podicipinus* has been moderately well collected in Argentina, but inadequate distributional data are available for the rest of its geographic range. Distributional data of *wagneri* are most adequate for Ecuador, parts of Colombia and Guyana. Throughout the rest of the geographic range of *wagneri,* records are so spotty that it is impossible to determine whether it has a broadly continuous range or if it is composed of many isolated populations.

The limited information gives the following patterns of occurrence:

Leptodactylus melanonotus, wagneri, and *podicipinus* form a series of closely related, basically allopatric species ranging throughout low and moderate elevations of tropical Latin America. All three species are found in areas having a definite dry season. Judged by collections, *melanonotus* is not common along the continuously wet lowlands of Colombia and Ecuador. Only *wagneri* is commonly associated with the tropical rainforests of eastern Colombia, Ecuador, and Peru. The foam nest formed by these species appears to be an adaptation to a definite dry season.

In some more xeric portions of its range (southern Sonora and northern Sinaloa, Mexico), *melanonotus* is found only in association with permanent bodies of water, such as persisting springs or irrigation water. The northernmost locality for *melanonotus* on the west coast of Mexico is a dam seepage by Hermosillo, Sonora. In more mesic areas, it is often associated with temporary bodies of water, such as rain filled ditches along roadsides.

Leptodactylus melanonotus, podicipinus, and *wagneri* are found in regions with old land masses in South America: *melanonotus* with an old land mass in western Colombia and Ecuador (land positive at least during Late Mesozoic and Tertiary time, Harrington, 1962:1780); *podicipinus* with the Brasilian shields; and *wagneri* with the Guiana shield. If one assumes that the three species had a common, widespread ancestor, isolation of the land masses in the Cenozoic could account for the fragmentation of the stock that gave rise to *melanonotus, podicipinus,* and *wagneri.*

Individuals of *melanonotus* in the region from the Isthmus of Tehuantepec to the Arenal Pass of Costa Rica are characterized by having a larger size, a more variable ventral pattern, and a greater ventrolateral gland extent than individuals to the north or south. Such character gradients suggest that the major dispersal point of *melanonotus* has been from this land bloc in Middle America. Secondary dispersal in Middle America by a species which had its

evolutionary origin in South America has also been hypothesized for the hylid frog *Phrynohyas venulosa* by McDiarmid (1968). Dispersal into Middle America by a species from western South America is consistent with Savage's (1966) scheme of historical herpetofaunal dispersal. He suggested that an assemblage of species, termed the Western South American Herpetofaunal Complex, evolved during the separation of nuclear Middle America from South America from Eocene through Miocene. When Middle America and South America were joined again at the beginning of the Pliocene, members of the Western South American Complex invaded Middle America.

Leptodactylus wagneri today is found in a variety of climates and associated vegetation types, but is found consistently in more mesic situations than either *melanonotus* or *podicipinus*. Throughout most of its range, *wagneri* is found in tropical or subtropical rainforest with either a short or no dry season. An exception occurs in the northern part of the range, particularly along the extreme north coasts of Colombia and Venezuela. *Leptodactylus wagneri* is not recorded from the palm forest or tropical deciduous forest of eastern Brasil in the states of Maranhão through Rio Grande do Norte. Records are so scattered for eastern Brasil that it is hard to tell whether its absence in any region is a collecting artifact.

The islands of Trinidad and Tobago are on the continental shelf and were probably connected to the mainland during glacial maxima. The presence of *wagneri* on these islands is to be expected. The islands of Grenada, Bequia, and St. Vincent are not on the continental shelf; they probably have been always isolated from the continent of South America. Grenada and Bequia are on the same bank. Currently, Bequia lies only 10 km from St. Vincent and possibly was separated by no more than 5 km of water during glacial maxima. The distance from the 100 fathom contour outside of Tobago to the 100 fathom line surrounding Grenada is at most 100 km, and these two points are directly connected by westerly surface ocean currents. All island populations are indistinguishable from mainland populations of northeast Venezuela, suggesting either that dispersal to the Lesser Antilles has been a rather recent event or that Lesser Antillean populations have been populated repeatedly from the mainland stock. A single dispersion of *wagneri* from South America (including Trinidad and Tobago) could account for all of the populations on the Lesser Antilles. Other members of the genus *Leptodactylus* are more successful island colonizers, especially *mystaceus* which has apparently hopped from island to island along the Lesser Antilles to as far as Haiti. As judged from the similarity of the island and mainland populations, it is reasoned that *wagneri* dispersed to the Lesser Antilles during the glacial maxima of the Pleistocene.

Leptodactylus podicipinus is associated with the southern river drainages and the São Francisco drainage system. All of the regions, such as the Gran Chaco, where *podicipinus* has been found have a very distinct dry season. *L. podicipinus* is generally adapted to more xeric conditions than *wagneri.*

This may be seen where the two species occur close together, most notably with *wagneri* along the thin mesic coastal strip of east Brasil, and *podicipinus* close by in the dry parts of the São Francisco drainage system.

Leptodactylus dantasi, discodactylus, and *pustulatus* are known from spotty distributional records, which suggest a distribution associated with climatic and vegetational factors. *Leptodactylus dantasi* has been taken only from the tropical rainforest in western Brasil. *Leptodactylus discodactylus* is apparently limited to the tropical rainforest of southeastern Colombia, eastern Ecuador, most of eastern Peru, and western Brasil. *Leptodactylus pustulatus* is apparently limited to the more xeric conditions in the palm forest, tropical deciduous forest, and savannas of eastern Brasil.

The total distribution of members of the Melanonotus species group indicates that three species have broad ecologic tolerances and are distributed in extensive geographic regions and that three of the species have much narrower ecologic tolerances and have restricted geographic distributions.

SPECIMENS EXAMINED

Leptodactylus dantasi (N = 1): BRASIL. TERRITORIO DO ACRE: Feijó, 249 m—WCAB 1240 (Holotype).

Leptodactylus discodactylus (N = 15): ECUADOR. NAPO: Payamino, 304 m—GOV 7238; PASTAZA: Puyo, 1000 m—GOV 2062, JAP 6197-8; 6333; Veracruz, 1000 m—JAP 6151, 6153-6, 6164. PERU. LORETO: Estiron, Río Ampiacu, 200 m—CAS 93316, 7; Río Itaya, 150 m—AMNH 43217; Río Tamaya, Sobral, 150 m—AMNH 42680.

Leptodactylus melanonotus (N = 520): BRITISH HONDURAS. STANN CREEK: Mango Creek, 120 m—MCZ 37884; 4.8 km S Waha Leaf Creek, 120 m—MCZ 37875-6. COLOMBIA. CHOCÓ: Río San Juan, Playa de Oro, 400 m—FMNH 54374; NARIÑO: La Guayacana, 230 m—PAS 44; Río Mataje, 200 m—USNM 147393; Valle de Cauca: Río Raposo Virology Field Station, 20 m—USNM 151463. COSTA RICA. Alajuela: Cariblanco, 800 m—CRE 2928 (10); 0.5 km S Cariblanco, 820 m—CRE 694; Los Chiles, 70 m—AMNH 54638, 54641-3, CRE 7217, 7219; Punta Cortéz, 70 m—CRE 7218; CARTAGO: Cervantes, 1441 m—KU 28189; IICA, Turrialba, 600 m—CRE 575, 2808 (2), 7074 (2), 7079 (7); GUANACASTE: Arenal, 520 m—CRE 6251, 6258 (4), 6259, 6260 (2); 4.8 km NW Arenal—CRE 2901 (3); Bebedero, 6 m—CRE 7162; Cañas, 88 m—CRE 7164; 9.6 km S La Cruz—CRE 8091; Río Lagarto at Inter. Am. Hiway, 100 m—CRE 7122 (2); 2 km W Liberia—CRE 728 (4); 9 km N and 4 km E Liberia on Inter. Am. Hiway on Río Colorado—CRE 714 (2); 14.8 km S Liberia, 90 m—CRE 8168; 45 km SW Liberia, Hwy #21—CRE 8216; Hacienda La Norma, 5 km N and 4.5 km W Liberia on Río Colorado, 150 m—CRE 105 (2), 106 (6), 107, 251 (2); 3-11 km E Playa del Coco, 45 m—CRE 8012 (2); Finca San Bosco de Tilarán, 640 m—CRE 6273, 6278; 3.2 km W Santa Cruz on the

Playa del Tamarindo rd.—CRE 8233; Santa Cruz, 50 m—CRE 7128, 8232 (3); Silencio de Tilarán, 825-850 m—CRE 6217 (8), 6225 (2), 6228 (2); 0.5 km NW Tilarán, 530 m—CRE 520 (7); 3 km NE Tilarán—CRE 524; 5 km NE Tilarán, 600 m—CRE 8021; 5.5 km NE Tilarán, 560 m—CRE 8022; 6 km NE Tilarán, 550 m—CRE 523 (3), 8020 (9); Finca Taboga, 9.6 km S and 8.0 km W Cañas, 4 m—CRE 2902; HEREDIA: Puerto Viejo, 100 m—KU 65683; 6.5 km W Puerto Viejo—KU 91798; 7.5 km W Puerto Viejo—KU 86293; LIMÓN: Batán, 15 m—KU 34146-51; 2.4 km E Los Diamantes, 260 m—CRE 8049; El Tigre, 680 m—CRE 290 (2); PUNTARENAS: 9.6 km ESE Golfito, 10 m—CRE 7105; junction of road and rail line (Base of Peninsula), 5 m—CRE 238 (2), 253-4. ECUADOR. ESMERALDAS: San Javier, 200 m—JAP 9077-82; Cacnauí, 20 m—JAP 2889-9; Río Bogotá, 200 m—GOV 6398; LOS RIOS: Vinces, 150 m—UMMZ 55587 (7). EL SALVADOR. SAN SALVADOR: San Salvador, 620 m—FMNH 65071-86. GUATEMALA. EL PETÉN: N of La Libertad—UMMZ 75367 (12); 5.2 km S La Libertad—MCZ 21454; Toocog, 15 km SE La Libertad, 170-200 m—KU 58959; ESCUINTLA: Río Guacalate, nr. Masagua, 100 m—USNM 125246-51, 125253, 125261-3; ZACAPA: 8 km ENE Río Hondo, 175 m—KU 58960; 23 km NE Zacapa—ANSP 22165-6; 23 km W Zacapa, 240 m—TCWC 16403, 16406. HONDURAS. ATLÁNTIDA: Corozál, 15 km E La Ceiba, 10 m—JRM 2316, 2328-33, 2335, 2337-8, 2341, 2343; CHOLUTECA: 1.5 km NW Choluteca, 170 m—KU 65676; 5 km S Choluteca, 80 m—MCZ 26460-2; CORTÉS: Agua Azul, Laguna Yogoa, 700 m—AMNH 54778; FRANCISCO-MORAZÁN: 31 km S Guaimaca, Santa Clara, 1000 m—AMNH 54884-5, 54887; ISLAS DE LA BAHIA: Isla de Guanaja, SE shore opposite Guanaja, 10 m—JRM 1938, 1961-6; Isla de Roatán, .5-4 km N Roatán, 10-30 m—JRM 1828-9, 1896, 1916; OLANCHO: Escuela Nacional de Agricultura, 4.5 km SE Catacamas, 400 m—JRM 1660-2. MEXICO. CAMPECHE: Chuina, 46 km S Champotón, 50 m—KU 75017-26; CHIAPAS: 4 km NW La Esperanza, 100-300 m—USNM 114372-6, 114381-2, 114385, 114388; Tonala, 55 m—USNM 114338-44; Tuxtla Gutierrez—UMMZ 115530; 9.8 km W Tuxtla Gutierrez, 520 m—UMMZ 119147 (2); COLIMA: 25.9 km N Manzanillo, 10 m—CAS 97111-8, 97155-7; GUERRERO: 12.9 km SW Tierra Colorada, 300 m—TCWC 8323-6, 8333-9; JALISCO: 5.2 km W Acatlán, 1400 m—LACM 37381-408; MICHOACÁN: Apatzingan, 540 m—FMNH 38835, 38837, 38853-5, 38859-60, 38862, 38865-6, 38873; NAYARIT: San Blas, 3 m—UMMZ 110892 (7), 115543 (3); Tepic, 1000 m—LACM 37042-3; OAXACA: Cacahuatepec at river, 150 m—UIMNH 52854-8; 8.3 km N Pochutla, 100 m—UMMZ 123982 (8); 5.2 km N Matías Romero, 150 m—UMMZ 115522 (3); 7.8 km S Matías Romero, 150 m—UMMZ 113804 (4); Tehuantepec, 35 m—FMNH 123248-50, 123253, 123256, 123264, 123267-9; Tolosa, 50 m—AMNH 53610; QUINTANA ROO: 3 km E Caobas, 5-10 m—KU 75033; 4 km WSW Puerto Juarez, 5 m—KU 71117-

8; SAN LUIS POTOSÍ: 5.1 km NE Tamazunchale, 150 m—TCWC 7285-91; 5.1 km SW Tamazunchale, 150 m—UIMNH 16802-3; SINALOA: Culiacán, 45 m—AMNH 58382-91; 18.9 km SW Mazatlán, 48 m—KU 78259-61; 5.2 km W Villa Union—KU 29901-7; SONORA: Alamos, 300 m—AMNH 51356-65; Hermosillo, 28 m—AMNH 62737, MVZ 26066; TABASCO: Teapa, 40 m—UMMZ 119148 (2); 20.7 km N Teapa—UMMZ 119901 (2); 33.7 km N Teapa—UMMZ 119903 (6); 57 km N Villahermosa, 30 m—AMNH 69007-8; TAMAULIPAS: Paño Ayuctle, 12.9 km NE Gómez Farías, 100 m—UMMZ 98947 (2), 101185 (5), 102263, 102912; VERACRUZ: 5 km SW Boca del Río—KU 23700; Cuatotolapam, 13 m—UMMZ 41640-3, 41646-7, 41649; 1 km E Mecayucán, 30 m—KU 24084, 24086, 24091-4; 25.9 km WNW Temapache, 50 m—KU 60225-8; YUCATÁN: 31 km N Tizimín, 5 m—CM 40108-10; 16.2 km S Yaxcopoil, Aguada Xcamal, 5 m—CM 45233-43; Yuncu, 25-50 m—UMMZ 73155, 73158 (2). NICARAGUA, MANAGUA: 15.5 km NW Managua, 55 m—KU 43030-39; RIVAS: San Jorge, Shore of Lake Nicaragua, 50 m—MCZ 28980-89; ZELAYA: Bonanza, 260 m—KU 84839-41, 84843-48; 10.4 km SW Bonanza, 300 m—KU 84842; 25.9 km above Recreo, Río Mico, 30 m—UMMZ 79734, 79735 (4). PANAMA. CHIRIQUÍ: Las Lagunas, ± 6 km W El Volcán, ± 1200 m—KU 76522; Finca Palosanto, 6 km WNW El Volcán, 1230 m—KU 76520-1; COCLÉ: El Valle, 560 m—KU 76523-32; DARIÉN: Río Canclón, 60 m—UMMZ 125008, 125009 (10). UNITED STATES, TEXAS: Starr County, 5.1 km SE Rio Grande City—UIMNH 29817.

Leptodactylus podicipinus (N = 154): ARGENTINA. CHACO: Resistencia, 60 m—KU 84732-4; CORRIENTES: 30 km W Itati, 60 m—CAS 100504; Manantiales, 50 m—MCZ 35589-90; FORMOSA: Esteros Laguna Oca, 65 m—MCZ 32775-6; SANTA FÉ: Bañados Monteira, 15 km N Santa Fé, 20 m—CM 38011; Bañados del Rincón, 20 m—CM 37981-3, 38003, 38005; Santa Fé, 18 m—CM 39181, 39194. BOLIVIA. BENI: Ivon, 150-200 m—UMMZ 64099 (7); Puerto Almacén, 260 m—AMNH 72245-53; SANTA CRUZ: Buenavista, 500 m—AMNH 39538; El Carmen, 212 m—CM 36234-7; Naranjal, 5 km from Montero, 350 m—USNM 146551; El Porton, 550 m—CM 36248; Robore, 330 m—MCZ 30032-6; 3 km S Robore, 330 m—CM 36238-41; San José de Chiquitos, 350 m—CM 36164, MCZ 30028-9. BRASIL. BAHIA: Barreiras, 500 m—UMMZ 109986; Rio Grande at São José, 450 m—UMMZ 109989; MATO GROSSO: Agua Clara, 304 m—FMNH 67088; Conceicao, Paraguay River, 150 m—FMNH 9161; Corumbá, 115 m—CM 2429, 36165, UMMZ 104225 (2); 40 km from Corumbá, Urucum Mts., 200-300 m—CM 2430; Descalvados, 142 m—FMNH 9097, 9100-14; 1 day's run below Descalvados, 150 m—USNM 132736-7; Maracajú, 385 m—USNM 107705-8, 107710-11; Pôrto Esperança, 120 m—UMMZ 104232 (11), USNM 133005-8; Salobra, 190 m—UMMZ 104227 (2); MINAS GERAIS: Januaria, 454 m—UMMZ 109984; Pirapora, 472 m—UMMZ

109982 (10), USNM 98535, 99801-3; PARANA: Andira, 480 m—MCZ 32725-6; RONDÔNIA: Forte Principe da Beira, 100-200 m—WCAB 8330, 8982; Pôrto Velho, 60 m—KU 92933-37; SÃO PAULO: Anhembi, 500 m—WCAB 30880-1; Baurú, 499 m—DZ 53-4; Cachoeira de Emas, Pirassununga, 650 m—DZ 4636-42; Lins, 396 m—DZ 9024; Pôrto Marcondes, Paranapanema, 250 m—DZ 19979, 19999 (10 total). PARAGUAY. CAAGUAZJU: Pastorea nr. Caaguazú, 250 m—MCZ 17902-11; CORDILLERA: Villeta, 110 m—AMNH 50654; PRESIDENTE HAYES: Río Pilcomayo, 38.8 km W Río Paraguay, 80 m—MCZ 25827-33.

Leptodactylus pustulatus (N = 7): BRASIL. GOIÁS: Aruaña, 200 m—DZ 4992, 8109; MATO GROSSO: São Domingoes, Rio das Mortes, 200 m—DZ 986-7, 996, 1069; PIAUÍ: Rio Poti—MCZ 373.

Leptodactylus wagneri (N = 711): BOLIVIA. BENI: Cachuela Esperanza, 150 m—UMMZ 64102 (2); nr. Guauará-mirim, Río Marmorí, 160 m—CM 2666; Swamp along Río Guaporé, San Antonio de Guaporé, 150 m—USNM 115973; Huachi, 250 m—UMMZ 64103 (3), 64104; Puerto Almacén, 260 m—AMNH 72251, 72254, 72398-402; Lake Rogoagua, 200 m—UMMZ 64100 (7); Rurrenabaque, 227 m—UMMZ 64097 (3); Villa Bella, 120 m—CM 2659; COCHABAMBA: Puerto Chipiriri, 300 m—AMNH 72242-3; PANDO: in front of Placido de Castro, Acre, Brasil—DZ 6529-31; SANTA CRUZ: Buenavista, 500 m—CM 4331, 4353, UMMZ 64028-29, 64030 (2), USNM 118688-9, 146523-4. BRASIL. ALAGOAS: Fazenda Canoas, Río Largo, 60 m—DZ 9279; Mangabeiras, 50 m—DZ 11982-3; São Miguel, 20 m—DZ 9250; AMAZONAS: Manacapuró, 50 m—USNM 103621-2; BAHIA: Salvador, 15 m—DZ 9131, 9550-1; GOIÁS: km 47 Estrada Goiás-Aruaña, 350 m—DZ 1518; MARANHÃO: Carolina, 168 m—DZ 21664-5; MATO GROSSO: Dumbá, 200 m—DZ 1448; Banks of center of Río Guaporé, 250 m—CM 2508-9; Confluence of Rio Araguaia and Rio Tapirape, 190 m—AMNH 68093; São Domingoes, Rio das Mortes, 200 m—DZ 10891-2, 10894-900, USNM 148677-91; PARÁ: Belem, 20 m—FMNH 83264-5, MCZ 36010-1, USNM 154068; Cachimbo, 500-600 m—DZ 21656-61; Río Mapuera at the Equator, 80 m—AMNH 46181; Santarem, betwn Rio Tapajos and Rio Amazonas, 16 m—CM 2641; RIO DE JANEIRO: km 31 on Estrada Mage-Estrada Río Petropolis, 100 m—DZ 12034-5; RIO GRANDE DO NORTE: Natal, 120 m—AMNH 36261, MCZ 15847, UMMZ 68791; TERRITORIO DO ACRE: Iquiri, 150 m—DZ 6588-92; TERRITORIO DO RIO BRANCO: Rio Urariquera, 100-200 m—WCAB 18792; TERRITORIO DO RONDÔNIA: Forte Principe da Beira, 100-200 m—WCAB 10690, 10703. COLOMBIA. AMAZONAS: Falls of Engano—MCZ 28063; Leticia, 275 m—CM 36081-2, USNM 142179-86, 142187-94, 146252, 147031; ANTIOQUIA: Envigado, 1600 m—AMNH 39265, 39274, 39281; Medellín, 1500 m—AMNH 38785, 38808-15, 39465; Sonsón, 2500 m—AMNH 39631; BOYACÁ: Muzo, 1240 m—FMNH 69744, MCZ 24920;

CAUCA: Popayán, 1700 m—FMNH 54377-83; CUNDINAMARCA: Anolaima, 1500 m—USNM 147054-5; Bogotá, 2600 m—AMNH 13471; Fusagasugá, 1700 m—AMNH 71581; La Mesa, 1000-1300 m—USNM 144892-3; META: Buenavista, 1200 m—MVZ 63067-73; Menegua, upper Río Meta, 260 m—USNM 147273-4; 46 km S, 22 km W San Martín, 490 m—MVZ 63076; Villavicencio, 500 m—ANSP 25765, FMNH 30571, 81788-9, MCZ 16277, MVZ 63074-5, 63738-9, UMMZ 74811, USNM 144848-66, 147056-62; 7 km NE Villavicencio, 500-700 m—USNM 146382-4; NARIÑO: La Guayacana, 100 m—FMNH 61754; NORTE DE SANTANDER: Astillero, 100-200 m—USNM 147063; E of Cucuta 200-500 m—ANSP 25758; PUTUMAYO: Río Putumayo, 5 km N Puerto Asís, 260 m—PAS 47; Rumiyaco, 1000 m—FMNH 54376; SANTANDER: nr. Lebrija, 1086 m—USNM 144883-8, 146250; San Gil, 1095 m—CM 7938, UMMZ 74799; TOLIMA: Guindio Mtns.—MCZ 8217; VALLE DE CAUCA: Buenaventura—USNM 147076; 2 km S Cali, 950 m—USNM 148800-23; VICHADA: Puerto Carreño—CM 17122. ECUADOR. NAPO: Lagarto Cocha, 200 m—GOV 9208; Loreto, 400 m—GOV 9205, WCAB 36541; Río Napo, Avila, 300 m—UMMZ 92145-6; PASTAZA: Upper Bobonaza—JAP 8732; Canelos, 530 m—MCZ 17950; Cerros de Abitagua, 1100 m—FMNH 25789, 26899, UMMZ 92147; Chichirota, 300 m—GOV 9207; Upper Río Curaray—GOV 9210; Upper Río Oglán, 500 m—GOV 9206; Río Pindo, 190 m—GOV 9195-7; Puyo, 940 m—JAP 1958-71, 1973-2005, 2036, 2038, 6182, 6186-7, 6191-5, 6289-99, 6303-5, 6329-32, 6334, GOV 8021-2; Shell Mira, 1064 m—GOV 8503, JAP 2177; Don Tomás, 340 m—GOV 9209; Río Villano, 300-400 m—GOV 7731-6, JAP 3776; ZAMORA-CHINCHIPE: Copal, 910 m—JAP 6747-8; Limón, 1550 m—JAP 6937, 6964-5; Río Llushin—GOV 9198-201, 9203, JAP 3751; Mendez, 580 m—JAP 2037, 6805, 6870, 6872-5, 6880, 6832-4, 6837, 6845-6, 6855-6, 6936; Plan de Milagro, 1700 m—JAP 7008, 7014-6, 7018-23, 7027, 7057; Plan Grande, 880 m—JAP 6903; NE of Riobamba—FMNH 23509 (8); Sucua—JAP 2186, 2225. FRENCH GUIANA. Sophie, on trail leading S from St. Elie Gold Pits, 200 m—MCZ 44564. GUYANA. DEMARARA: Atkinson, McKenzie Trail, 50 m—USNM 162872-3; Dunoon, Demerara Riv., 20 m—UMMZ 50183-9; Georgetown, 5 m—UMMZ 80497; Wismar, 50 m—AMNH 45750, UMMZ 77517, 80417; ESSEQUIBO: Isheraton, 250 m—AMNH 53435-7; Karanambo, 100 m—AMNH 53438; Kartabo, 10 m—AMNH 10377, 10379-83, 11659, 13518-9, 25233, CM 5443-4, USNM 118059-62; Kuyuwini Landing, 250 m—AMNH 46281, 49352, 49355 (5); Lethem, 100 m—MCZ 50708; Marudi, 250 m—AMNH 46238 (2); Moku Moku, 100-200 m—USNM 146366-7; Oko Mts., 115 m—FMNH 26691; Santa Rosa Is., Moruca Riv., 7 m—UMMZ 55833 (2), 80417; Shudikarwan, 200-300 m—AMNH 46274 (9). PERU. AYACUCHO: Candalosa, ± 1400 m—FMNH 39727-32, 39734-46; La Mar, ± 760 m—FMNH 39725; La Mar, Ayna ± 1900 m—FMNH 39726; HUANUCO; Ganzo Azul, 150 m—FMNH 45144; JUNÍN: Satipo, 500 m—MCZ 24424-8, UMMZ 89476 (7); Tarma, Palmapata, 1200-1400 m—FMNH 36827-30; Tarma, Valley of Vitoc River, 1200-1400 m—FMNH 36817-26; LORETO: Río Marañón, mo. of Río Pastaza, 150 m—AMNH 42221-3, 42225-7; Pampa Hermosa, 176 m—AMNH 42142-4, 42661; Roaboya, 100 m—AMNH 42823-4; Río Tamaya, Sobral, 150 m—AMNH 43238; Río Alto Tapiche, mo. R. Contaya, 200 m—AMNH 42988; Tibi Playa, 150 m—AMNH 42783; Río Ucayali, Pacapa, 150 m—FMNH 56322; Upper Utoquina, 200 m—AMNH 42599; PASCO: Iscozazin Valley, Chontilla, 780 m—LACM 40660-5; Río Pachitea, Monte Alegra, 150 m—AMNH 43013; SAN MARTÍN: Tocache, 450-750 m—AMNH 42627. SURINAM. MAROWIJNE: Kaiserberg airstrip, Zuid R., 200-300 m—FMNH 128925, 128927-8, 128933-7, 128939-40. VENEZUELA. AMAZONAS. Río Pescado—AMNH 23182; ARAGUA: Colonia Tuvar, 1830 m—CM 7729; Cumboto, 150 m—UMMZ 113975 (2); Rancho Grande, nr. Maracay, 450 m—AMNH 70687; BOLÍVAR: Arabopo, 1280 m—UMMZ 85197 (5); Mt. Roraima, Paulo, 1216 m—AMNH 39753, 39758-9; DELTA AMACURO: 140 km NE Barrancas, 5-10 m—LACM 31382-97; DISTRITO FEDERAL: Cotiza, Camino de Calipan, 900 m—USNM 117526, 128837; El Limón, 577 m—CM 7676-7, 7697, 7699, USNM 121146; FALCÓN: Cerro Cosme, 100-200 m—MCZ 26144-6; Lagoon, Palma Sola, 50 m—UMMZ 55551; MÉRIDA: Mérida, 1641 m—MCZ 2640, USNM 118176; Río Albirregas nr. Mérida, 1640 m—AMNH 10517-9; MIRANDA: Petare, 885 m—CM 7769-71, 7791; USNM 121147; MONAGAS: Caripito, ± 50 m—AMNH 70669-86, USNM 117088-9; SUCRE: Cumanocoa, 300 m—CM 9055-76; Latal, Hacienda Mirasol, 975 m—CM 9099, 9101; San Rafael, nr. Cumanocoa, 200-400 m—CM 8972; El Yaque, 800 m—CM 9108-9; TÁCHIRA: La Fría, Rt. Fork Río Oropito, 110 m—UMMZ 55552-3; ZULIA: Chama, 10 m—AMNH 10685-8. WEST INDIES: BEQUIA: north end—USNM 103976-8; GRENADA: Grand Etang—MCZ 2963-71, 2974-6; no specific locality—AMNH 18961, 18970-2, 18992, USNM 67183-4, 67186-94; ST. VINCENT: Botanical Garden—USNM 144246; Brighton—USNM 79068-75; Mt. St. Andrews—USNM 79076-7; TOBAGO: Bacolet River—AMNH 55873; Buccoo Bay—AMNH 55863-5; nr. Speyside, 180 m—MCZ 27788-9; TRINIDAD: Nariva: Brickfield—FMNH 49656-60; Upper Tucker Valley—USNM 119055-60; St. Andrew: Mount Harris—FMNH 49654-5; Sangre Grande—MCZ 3295-8; San Rafael—FMNH 49664-5; St. George: St. Augustine—CM 5466.

RESUMEN

En el grupo Melanonotus se reconocen las siguentes seis especies: *dantasi, discodactylus, melanonotus, podicipinus, pustulatus,* y *wagneri.*

Para cada especie se ofrecen: sinonímia, diagnóstico, sumario de carac-

terísticas y distribución. Series de *Leptodactylus* procedentes de amplias áreas geográficas y ecológicas fueron analizadas para estudiar largo normal, apariencia ventral, desarrollo de las glándulas ventrolaterales, apariencia de las extremidades posteriores, y desarrollo de los discos digitales. Se encontraron correlaciones evidentes entre: tamaño grande y habitates húmedos en *wagneri*, 2) apariencia ventral más oscura y una cantidad mayor de lluvia anual en *melanonotus*, 3) apariencia ventral pálida y una mayor extensión de las glándulas ventrolaterales en *wagneri*, y 4) mayor extensión de las glándulas ventrolaterales y mayor cantidad anual de lluvia en *wagneri*.

Se postula la hipótesis de que existe displazamiento de caracteres en la estricta diferencia en tamaño y apariencia tanto entre poblaciones de *melanonotus* y *wagneri* como entre *podocipinus* y *wagneri* las cuales viven simpátricamente.

Leptodactylus melanonotus es la especie más primitiva, mientras que *discodactylus* y *pustulatus* son más avanzadas.

Leptodactylus melanonotus, podicipinus, y *wagneri* están asociadas con regiones antiguas y son especies adaptadas a condiciones xéricas. *Leptodactylus dantasi* y *discodactylus* están limitados al bosque tropical húmedo del valle al oeste del Amazonas. *Leptodactylus pustulatus* se encuentra en las regiones orientales xéricas de Brasil.

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