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STUDIES ON THE GENUS *LEPTODACTYLUS* (AMPHIBIA,
LEPTODACTYLIDAE) III. A REDEFINITION OF THE GENUS
LEPTODACTYLUS AND A DESCRIPTION OF
A NEW GENUS OF LEPTODACTYLID FROGS

By W. RONALD HEYER

LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY • EXPOSITION PARK
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STUDIES ON THE GENUS *LEPTODACTYLUS* (AMPHIBIA,
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A NEW GENUS OF LEPTODACTYLID FROGS

By W. RONALD HEYER¹

ABSTRACT: Identification and subsequent study of *Leptodactylus pulcher* Boulenger indicates that *pulcher* does not belong to the genus *Leptodactylus*, nor can it be allocated to any described leptodactylid genus.

The genus *Leptodactylus* is composed of approximately 30 species distributed in the lowlands and intermediate elevations of Latin America. The genus is distinguished from all other New World leptodactylids by the following combination of characteristics: tympanum distinct; toes without web, or with a web vestige only; maxillary and vomerine teeth present; no posterior projection of the vomer; mesosternum a bony style; terminal phalanges claw-shaped. The genus is redefined using characters of external morphology of adults and larvae; osteology; myology; breeding call; egg morphology, placement, and development; and chromosomes.

A new genus, *Barycholos*, is described for *Leptodactylus pulcher* Boulenger. *Barycholos* is distinguished from all other New World leptodactylids by the following combination of characteristics: tympanum distinct; tarsal tubercle present; toe disks present and lacking a groove on the outer circumference; mesosternum a calcified style. The genus is defined using characters of external morphology, osteology, and myology. It is presently known from the single species *pulcher*, which is found along the coastal lowlands of Ecuador. *Barycholos* is most nearly related to *Eleutherodactylus*, but the relationship is not close. *Barycholos pulcher* is redescribed on the basis of external morphology, and a lectotype is designated from the type series.

INTRODUCTION

The determination of the limits of the genus *Leptodactylus* based on re-examination of the named species is critical to a thorough biosystematic knowledge of the genus. A series of frogs made available by Dr. James A. Peters from Ecuador including representatives of *Leptodactylus pulcher* Boulenger raised special questions regarding the limits of the genus. Subsequent study indicated that *pulcher* is not a *Leptodactylus*. In addition, the species cannot be allocated to any described leptodactylid genus. The purpose

¹Research Associate in Herpetology, Los Angeles County Museum of Natural History. Present address Division of Amphibians and Reptiles, Field Museum of Natural History, Chicago, Illinois 60605.

of this paper is 1) to redefine the genus *Leptodactylus*; 2) to establish a new genus for *L. pulcher*; and 3) to redescribe the species *pulcher*.

Leptodactylus Fitzinger, 1826.

Type species: *Rana fusca* Schneider, 1799.

Diagnosis: The following combination of characteristics distinguishes the genus *Leptodactylus* from all other New World leptodactylid genera: tympanum distinct; toes without webs, or a web vestige only; maxillary and vomerine teeth present; no posterior projection of the vomer; mesosternum a bony style; terminal phalanges claw-shaped.

Description: External Morphology—Adult: Pupil rounded; tongue free behind; tympanum distinct; vomerine teeth in transverse, arched, or curved series, partly between or posterior to choanae; vocal slits present in male; thumb spines present or absent in male; chest spines present or absent in male; dorsolateral folds present or absent; parotoid glands distinct, diffuse, or absent; ventrolateral glands present or absent; lumbar (inguinal) glands present or absent; belly with discoidal fold not extending onto legs; toes fringed or free; tarsal fold present or absent; usually no finger disks; toe disks present or (usually) absent, if present, not creased on the anterior border; upper surfaces of terminal phalanges usually not divided; antibrachial tubercle absent; first finger about equal to or much longer than second; toe webbing vestigial or absent; outer metatarsals contained in flesh as sole of foot.

Larvae: Tadpoles generalized; mouth subterminal to almost terminal; oral disk usually entire; oral papillae continuous except for an anterior gap;

denticle row formulae $\frac{2}{3}, \frac{1-1}{3}$, or $\frac{1-1}{1-1}$; beak well developed; spiracle sinistral;

anal tube median; pattern almost uniform to blotched. (Larvae known for 10 species. See Fernandez and Fernandez, 1921, for example illustrations.)

Osteology: Dorsal process of premaxilla bifid; premaxilla toothed; maxilla toothed; quadratojugal contacting maxilla; nasals in contact or not; sphenethmoid complex lightly to heavily calcified or ossified, region between and anterior to nasals and vomers calcified or not; sphenethmoid contacting optic foramen or not; frontoparietals in contact at least in part; usually lacking a fontanelle (a very small one present in a few species); frontoparietal with or without posterolateral processes; prootic with distinct dorsal ridge, absent in largest specimens of largest species; crista parotica partially to entirely ossified; posterior portion of squamosal spur not contacting, contacting, or overlapping crista parotica; anterior portion of squamosal spur not contacting maxilla; vomer with three distinct spines, anterior spine spikelike or broadened; vomer toothed; vomers in contact or not; vomerine teeth overlapping palatine or not; vomer without distinct posterior process; palatine spearlike to broadened laterally, with or without a raised ridge ventrally; orbitosphenoid calcified or

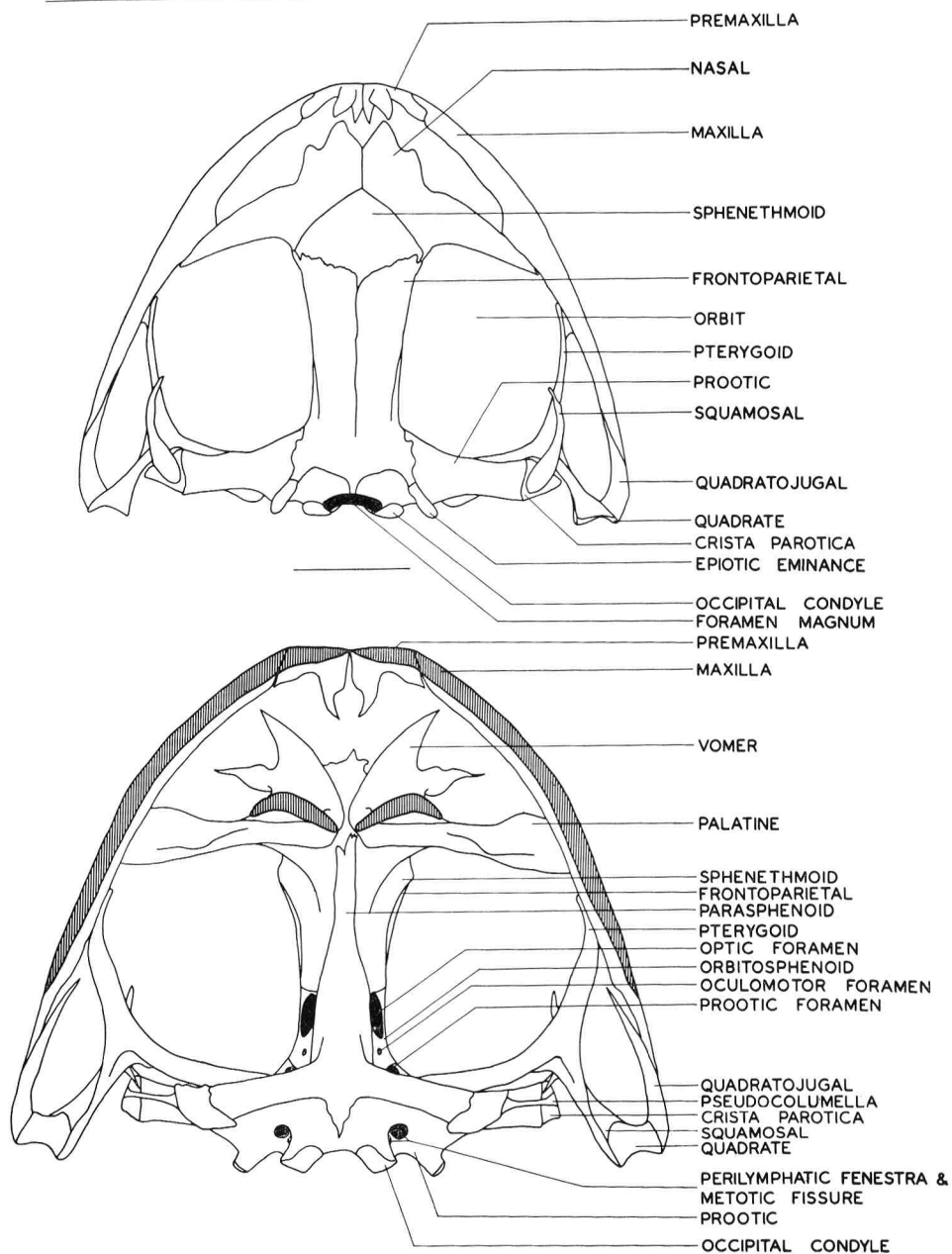


Figure 1. Dorsal and ventral views of the skull of *Leptodactylus pentadactylus*. Dorsal view based on specimen number 435 in the osteological collection of Jay M. Savage (JMS). Ventral view based on JMS 277. Hatching indicates dentigerous zones, dark areas indicate foramina in the skull. Line equals 10 mm.

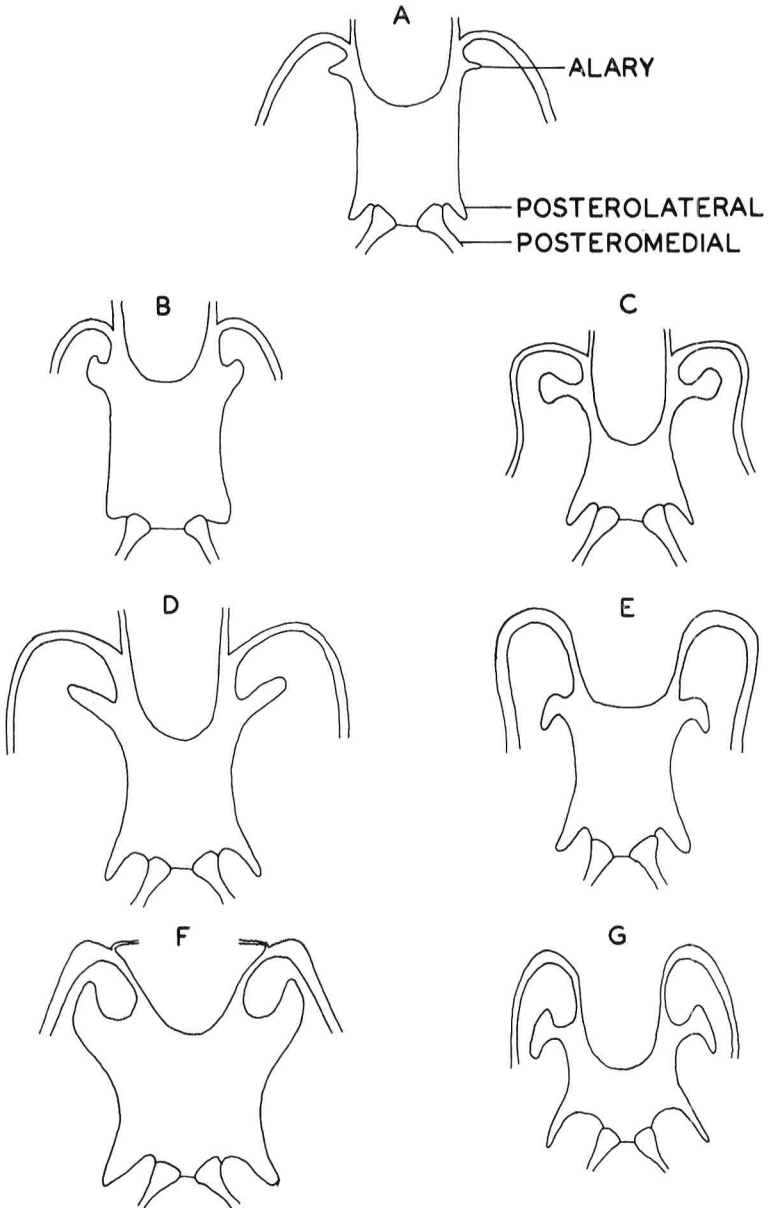


Figure 2. Diagrammatic representations of the hyoids of four leptodactylid genera. A=*Barycholos pulcher*, B=*Eleutherodactylus bransfordii*, C=*Eleutherodactylus fitzingeri*, D=*Eleutherodactylus fleischmanni*, E=*Lithodytes lineatus*, F=*Leptodactylus marmoratus*, G=*Leptodactylus ocellatus*. Processes mentioned in text labelled on the hyoid of *B. pulcher*. Not drawn to scale.

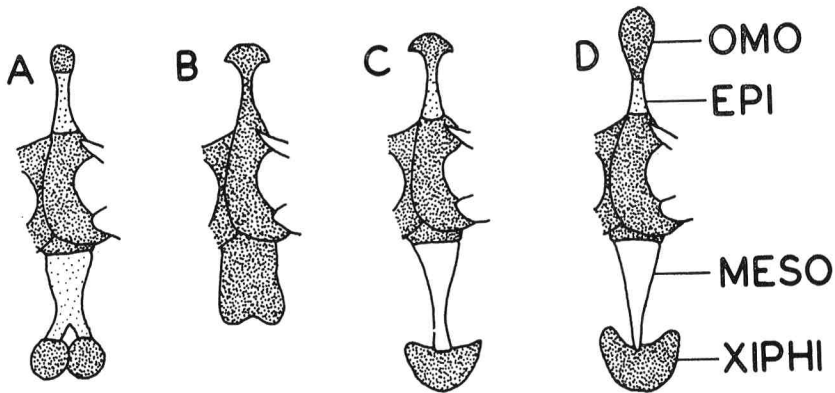


Figure 3. Diagrammatic representations of the sternal apparatus of four leptodactylid genera. A=*Barycholos*, B=*Eleutherodactylus*, C=*Lithodytes*, D=*Leptodactylus*. Sternal components labelled for *Leptodactylus*. Not drawn to scale.

cartilaginous, bordering to completely enclosing optic foramen; parasphenoid dagger-shaped; posterior spur of parasphenoid extending to posterior portion of skull or not; no odontoids on lower jaw (Fig. 1).

Alary process of hyoid expanded distally or not, narrowly or broadly stalked proximally; posterolateral process slender to moderately broad; posteromedial process a slender bony shaft, expanding posteriorly to end in a short cartilaginous epiphysis (Fig. 2). Eight presacral vertebrae; transverse process of sacrum directed laterally or posteriorly, slightly expanded. Ilium with thick crest, usually high; vastus prominence ovaloid, prominent or not. Omosternum cartilaginous; episternum with a style, at least partly calcified; mesosternum a bony style; xiphisternum cartilaginous (Fig. 3a). Phalangeal formula of hand 2-2-3-3, of foot 2-2-3-4-3; terminal phalanges claw-shaped.

Myology: Depressor mandibularis broadly originating from the dorsal fascia, a small slip originating from the squamosal bone, and a few fibers sometimes originating from the tympanic ring; adductor mandibularis externus superficialis absent; adductor mandibularis posteriori subexternus present.

Tendons of the gracilis minor and gracilis major passing dorsad to the tendon of the semitendinosus and adjoining to the posterodorsal tendon of the sartorius muscle, or similar except for the tendon of the gracilis minor piercing the tendon of the sartorius, or the tendons of the sartorius, gracilis minor and major fused together in the same plane; tensor fasciae latae originating as far anterior as the iliacus externus muscle on the iliac bone, or not extending as far anterior as the iliacus externus; tensor fasciae latae wide, inserting on cruralis only, cruralis and gluteus, cruralis and adductor longus, or cruralis, gluteus, and adductor longus muscles; adductor longus small, about 1/5

volume of sartorius to a moderately thick muscle, about equal in volume to the sartorius; adductor longus always visible in superficial dissection; adductor longus always inserting on knee.

Breeding Call: Call of single tone, but usually with distinct harmonics; dominant harmonic being the fundamental (first) or the second harmonic; frequency shift in dominant present or absent; difference between adjacent harmonics equalling or not equalling the fundamental. (See Barrio, 1965, 1966, and Fouquette, 1960, for sonagrams.)

Egg Morphology, Placement, and Development: Eggs with or without melanophores; eggs laid in foam nest; nest floating on water, nest placed in potholes, or nest formed in holes or burrows (incubating chambers); development usually involving an aquatic larval stage, but in at least one species, the larvae metamorphosing within the incubating chamber.

Chromosomes: Haploid number 11; diploid number 22. (Based on four species, see Barbieri, 1950.)

Content: The genus is composed of approximately 30 species allocated to five species groups arranged into two subgenera (Heyer, 1968). The subgenus *Leptodactylus* is composed of the *Fuscus*, *Melanonotus*, *Ocellatus*, and *Pentadactylus* species groups. The subgenus *Adenomera* is composed solely of the *Marmoratus* species group.

Distribution: Extreme southern United States (Texas) and northwestern Mexico through Middle America and South America; South America west of the Andes south to northwestern Peru, east of the Andes south to central Argentina, southern Bolivia, Paraguay, and Uruguay; Dominican Republic, Puerto Rico, various Lesser Antillean islands, San Andres, Providencia, Tobago, and Trinidad.

Barycholos n. gen.

Type species: *Leptodactylus pulcher* Boulenger, 1898.

Diagnosis: The only leptodactylid genera in the New World having a bony or calcified style for the mesosternum are *Barycholos*, *Hydrolaetare*, *Leptodactylus*, *Lithodytes*, *Paratelmatoobius*, *Physalaemus*, and *Pleurodema*. *Barycholos* has a tarsal tubercle, distinguishing it from *Leptodactylus* and *Lithodytes*, which have cutaneous folds on the tarsus. *Barycholos* has a distinct tympanum, distinguishing it from *Paratelmatoobius*, which lacks a tympanum. *Barycholos* has distinct toe disks, distinguishing it from *Hydrolaetare*, *Physalaemus*, and *Pleurodema*, which lack toe disks. Superficially, *Barycholos* closely resembles some of the small species of *Eleutherodactylus*, but it does not have a groove on the outer circumference of the toe disk; *Eleutherodactylus* does.

Description: External Morphology: Pupil horizontal; tongue free posteriorly; tympanum distinct; vomerine teeth in long curved series, posterior to choanae; vocal slits in males; no thumb adspersities in males; dorsal texture

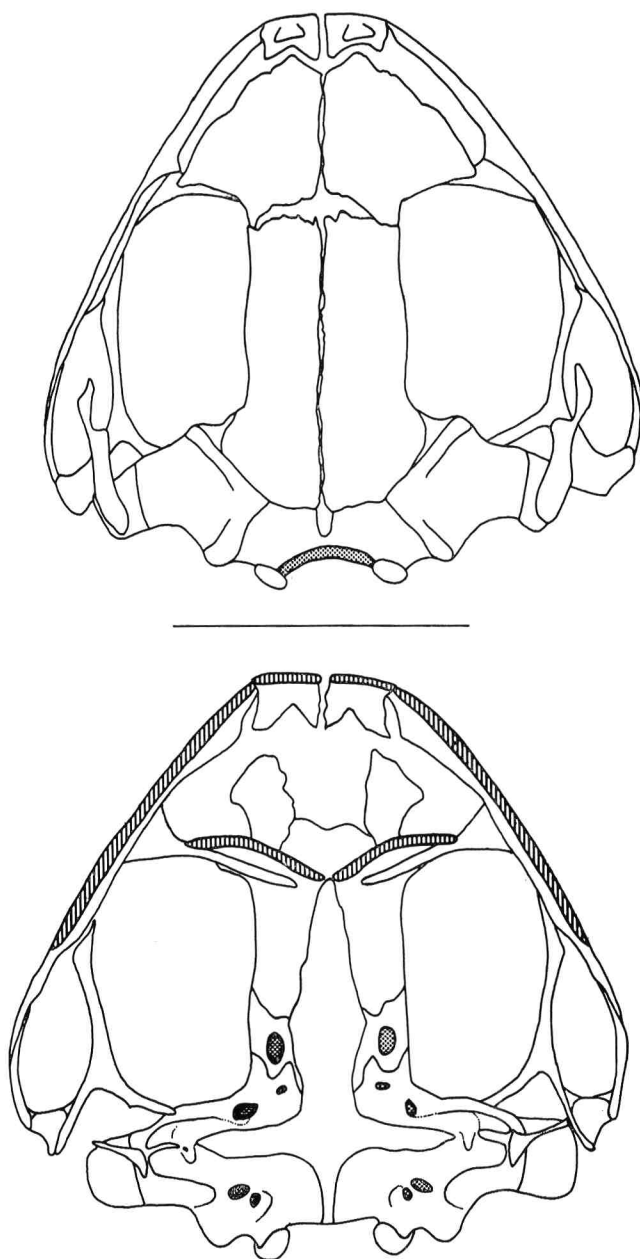


Figure 4. Dorsal and ventral views of the skull of *Barycholos pulcher*. Hatching indicates dentigerous zones, dark areas indicate foramina in the skull. Line equals 5 mm.

smooth; no distinct glands; belly with discoidal fold not extending onto legs; fingers and toes free, not fringed; tarsal tubercle present, no tarsal fold; finger disks small, toe disks larger, no groove on outer circumference of disk; upper disk surface not divided; no antebrachial tubercle; first finger longer than second; no webbing between toes; outer metatarsals contained in flesh as sole of foot. (Based on specimens listed under the redescription of the species.)

Osteology: Dorsal process of premaxilla bifid; premaxilla toothed; maxilla toothed; quadratojugal contacting maxilla; nasals in contact; anterior sphenethmoid complex cartilaginous; sphenethmoid not contacting optic foramen; no frontoparietal fontanelle; frontoparietal without posterolateral processes; prootic with dorsal ridge; crista parotica cartilaginous; posterior portion of squamosal spur overlapping crista parotica; anterior portion of squamosal spur not contacting maxilla; vomer lacking distinct processes; vomer toothed; vomerine teeth overlapping palatine; palatine spearlike; palatine without a raised ridge ventrally; orbitosphenoid a tectum; orbitosphenoid enclosing optic foramen; parasphenoid dagger-shaped; posterior spur of parasphenoid extending to posterior portion of skull; no odontoids on lower jaw (Fig. 4).

Alary process of hyoid rudimentary; posterolateral process small, blunt; posteromedial process a slender bony shaft, expanding posteriorly to end in a short cartilaginous epiphysis (Fig. 2a).

Eight presacral vertebrae; transverse process of sacrum directed posterolaterally, slightly expanded.

Ilium with a high crest; vastus prominence rounded, prominent.

Omosternum cartilaginous; episternum a calcified style; mesosternum a calcified style, bifid posteriorly, each half bearing a cartilaginous xiphisternum (Fig. 3a). Phalangeal formula of hand 2-2-3-3, of foot 2-2-3-4-3; terminal phalanges T-shaped. (Osteological observations based on GOV 8015 and UMMZ 2881.)

Myology: Depressor mandibularis muscle originating in three almost equal slips from the dorsal fascia, squamosal spur, and tympanic ring; adductor mandibularis externus superficialis absent; adductor mandibularis posteriori subexternus present.

Tendons of the gracilis minor and gracilis major passing dorsad to the tendon of the semitendinosus and not adjoining to the tendon of the sartorius; tensor fasciae latae not extending as far anteriorly as the iliacus externus; tensor fasciae latae inserting on cruralis and gluteus; adductor longus thin, straplike, inserting on adductor magnus muscle. (Myological observations based on GOV 8015.)

Content: One species, *B. pulcher*, with a known range along the coastal lowlands of Ecuador.

Etymology: The name barycholos is from the Greek βαρύχολος meaning savage. The new genus is named in honor of Dr. Jay M. Savage.

Relationships: The relationships among leptodactylid genera are unclear.

John D. Lynch is currently reviewing the generic arrangements of members of the Leptodactylidae. Until this task is completed, the relationships of the distinctive *Barycholos* will remain uncertain.

Boulenger placed the species *pulcher* in the genus *Leptodactylus* on the basis of the following combination of characteristics; vomerine teeth present, toes not webbed, and the sternum with a style. *Barycholos* and *Leptodactylus* are not closely related. The sterna of the two genera are distinctive (Fig. 3a), and they differ in many other aspects of external morphology, osteology, and myology. The two genera may also differ with respect to life histories. The cleared and stained female of *B. pulcher* contained 43 large ova (about 2.8 mm in diameter), indicating the likelihood of direct development.

In addition to the possible character of direct development, *Barycholos* shares many characters with the composite genus *Eleutherodactylus*. The shape of the squamosal spur, T-shaped terminal phalanges, and myological characters are essentially identical in these two genera. *Barycholos* is most closely related to *Eleutherodactylus*, but the relationship is not a close one.

The only other genus with which *Barycholos* might be confused is *Lithodytes*, but this is due, not to a similarity of characters, but to the fact that *Lithodytes* has been treated in the literature as part of *Eleutherodactylus*. *Lithodytes* shares many characteristics with *Leptodactylus*, indicating that the relationships of *Lithodytes* lie with *Leptodactylus* rather than *Barycholos*.

A summary of diagnostic features of *Barycholos*, *Eleutherodactylus*, *Leptodactylus*, and *Lithodytes* are presented in Table 1 and Figures 2 and 3.

***Barycholos pulcher* (Boulenger, 1898)**

Leptodactylus pulcher Boulenger: 1898, 122, Pl xiv, fig. 4 (Type locality—Ecuador: Guayas; Puente del Chimbo, railway terminus about 70 miles from Guayaquil, about 1,000 feet. Syntypes BMNH 1947.2.17.36-38).

Summary of characteristics: Snout rounded, subelliptical, or subovoid from above; snout rounded in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, horizontal diameter $\frac{1}{2}$ diameter of eye; male vocal slits paired, small, parallel to jaw, from posterior attachment of tongue to angle of jaw; male external vocal sac large, single, including chest region; vomerine teeth in long curved series, posterior to choanae; head longer than wide; head length 33-38.2-42 per cent standard length (SL); head width 32-34.7-37 per cent SL; interorbital distance 10-10.9-12 per cent SL; first finger (thumb) longer than second, second longer than fourth, first shorter than third; fingers usually free, rarely finger two with a lateral dermal ridge; finger tips swollen; two very large palmar tubercles at base of hand, three small round palmar tubercles between the large palmar tubercles and thenar tubercles; male without nuptial adspersities; no ulnar ridge; supratympanic to shoulder fold present, rest of dorsum smooth or glandular appearing, only one specimen with indication of five weak dorsolateral folds; well defined gland

posterior to angle of jaw only; venter smooth; toe tips expanded into distinct disks; toes entirely free, no lateral ridges or fringes; toes not webbed; sub-articular tubercles large, globose or pointed; no metatarsal fold; distinct tarsal tubercle, rest of tarsus smooth; foot with white tubercles; standard length to 29 mm; femur shorter than tibia; femur 40-43.8-50 per cent SL; tibia shorter than, equal to, or longer than foot; tibia 44-49.6-56 per cent SL; foot equal to or longer than femur; foot 43-49.0-55 per cent SL; upper lip barred; dark eye stripe present or absent, if present sometimes expanding into broad dark axillary band; dorsum with pattern of end to end hourglasses from interorbital region to sacrum, hourglass pattern sometimes reduced or interrupted medially by a mid-dorsal light stripe extending from the tip of the snout to the anus; upper limb surfaces with dark transverse stripes, stripes sometimes faint; venter scattered with melanophores, usually concentrated under the throat; posterior surface of thigh profused with melanophores interrupted by small dotlike spots.

Distribution: The known altitudinal range is from 30 to 600 m.

The coast of Ecuador has a dramatic climatic change along the North-South axis. The north coastal region is covered with Tropical Rain Forest, the south coastal region with Tropical Dry Forest. *Barycholos pulcher* apparently inhabits the regions along the coastal lowlands intermediate between the extreme climates and associated vegetations (Fig. 5). If the species is restricted to the transition zone between the Tropical Rain and Dry Forests, its geographic range may well be limited to western Ecuador.

Specimens Examined: EL ORO: 7 km SE Buenavista, 30 m, JAP 2464-5; Gualtaco, GOV 8012; 2 km S Pasaje, 30 m, JAP 2498; ESMERALDAS: Hacienda Equinox, 38 km NW Santo Domingo de los Colorados, 300 m, JAP 1771-2; Rio Cupa, GOV 8017; Quininde, GOV 8016; GUAYAS: Bucay, GOV 8018-9; 20 km W Guayas, 100 m, JAP 2524; 5.2 km E Milagro, Hacienda San Miguel, 60 m, JAP 2519-20, 2522-23, LACM 42080; MANABI: Cordillera de Balzar, 9 km E San Placido, km 83 on Quevedo-Manta Hiway from Manta, 60 m, JAP 8154, 8159-60; 2 km W Desvio, Quevedo-Manta Hiway, 16 km W Pichincha, in Cordillera de Balzar, 75 m, JAP 8150; PICHINCHA: Puerto de Ila, GOV 8013-5, 3838; Rio Toachi, GOV 6474; 6 km E Santo Domingo de los Colorados, Cmdr. Dyott Farm, JAP 8239, UMMZ 2881; 18 km W Santo Domingo de los Colorados, J. Ramsey Farm, km 19, Chone Rd, 200 m, JAP 4034-6, 4105-7, LACM 42081.

Remarks: Boulenger (1898) described *Leptodactylus pulcher* on the basis of three specimens, but did not designate one of them as a holotype. His description, however, is based upon a single specimen, BMNH 1947.2.17.36. This specimen is in the poorest shape of the three. BMNH 1947.2.17.38 is in good condition, and shows the characteristic dorsal pattern figured by Boulenger. I hereby designate BMNH 1947.2.17.38, an 18.3 mm

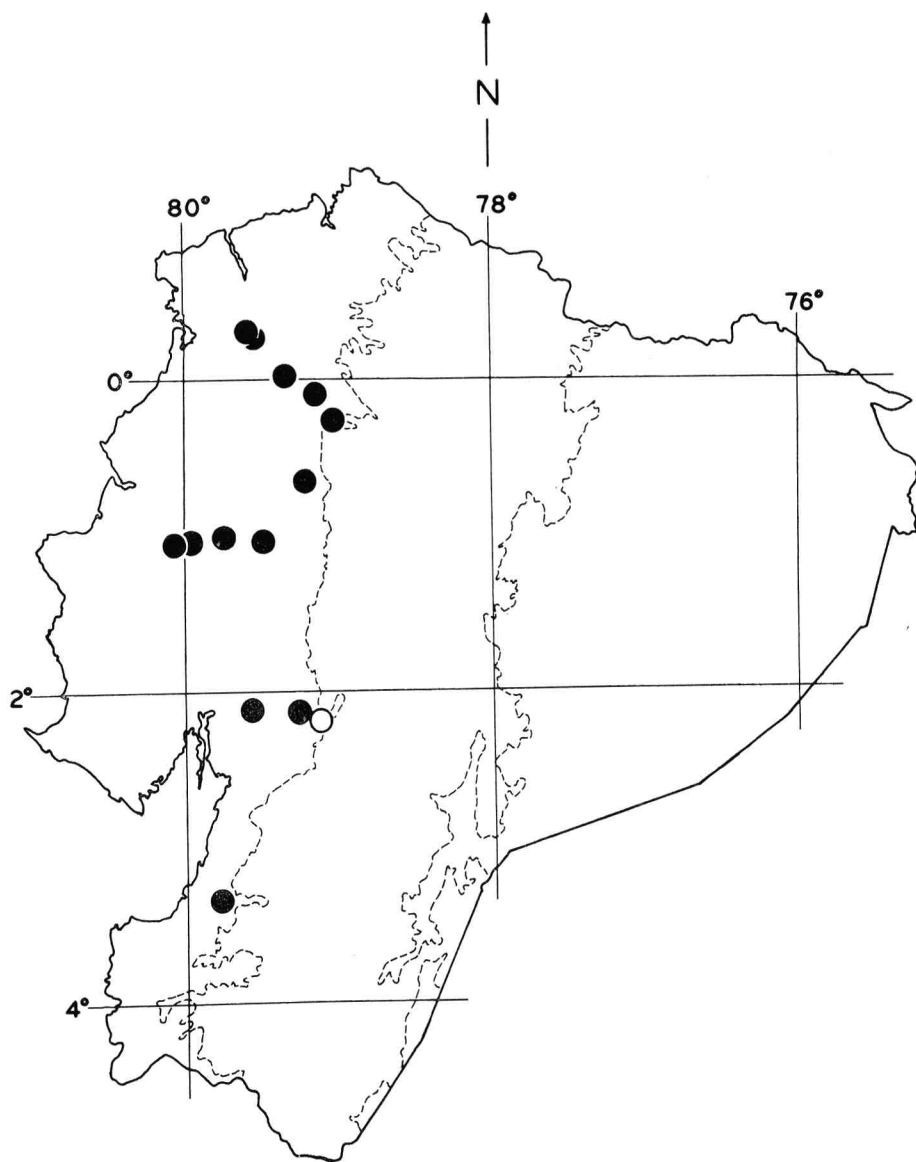


Figure 5. Map of Ecuador showing the distribution of *Barycholos pulcher*. Open circle indicates type locality. Dashed line indicates 1,000 meter contour.

TABLE 1

Comparison of certain characteristics between four leptodactylid genera. Jaw muscle abbreviations and data for *Eleutherodactylus* from Starrett (1968).

	<i>Barycholos</i>	<i>Eleutherodactylus</i>	<i>Leptodactylus</i>	<i>Lithodytes</i>
Vomer with distinct processes	-	+	+	+
Tarsal decoration	tubercle	tubercle, fold, or none	fold or none	fold
Toe disks, if present, with distinct groove on outer circumference	-	+	-	-
Alary process of hyoid	rudimentary	distinct	distinct	distinct
Type of mesosternum	calcified style, bifid posteriorly	cartilaginous plate	bony style	bony style
Terminal phalanges	T-shaped	T-shaped	Claw shaped	T-shaped
Depressor mandibularis	DFSQAT	DFSQ, DFSQAT, dfsq, dfsqat	DFSq, DFSqat	DFSq, DFSqat
Adductor mandibularis externus superficialis	-	+, -	-	-
Adductor mandibularis posteriori subexternus	+	+, -	+	+
Adductor longus insertion	adductor magnus muscle	adductor magnus muscle	knee	knee

specimen (specimen not dissected to determine sex), as the lectotype of *Leptodactylus pulcher* Boulenger.

The presence or absence of vocal sacs and slits in males may vary within the species. Only one of the specimens at hand (GOV 8017, 24.5 mm) has vocal slits and a sac. Another specimen lacking vocal slits and sac (JAP 1771, 24.3 mm) was dissected and has large, well developed testes.

Dr. Walker (pers. comm.) kindly provided the following observations on freshly preserved specimens; most individuals with a tawny-cinnamon area in groin and another on proximal tibia near the knee.

ACKNOWLEDGMENTS

Dr. Charles F. Walker (Museum of Zoology, University of Michigan, UMMZ) has been generous in sharing his knowledge of leptodactylid genera and commenting on the manuscript. Dr. James A. Peters (United States National Museum, GOV, JAP) kindly made all of his Ecuadorian collections available and allowed me to clear and stain one of the specimens of *B. pulcher*. Dr. Alice G. C. Grandison (British Museum (Natural History), BMNH) graciously loaned the syntypes of *L. pulcher*. Dr. John W. Wright (Los Angeles County Museum of Natural History, LACM) made several helpful comments on the manuscript.

To my major professor, Dr. Jay M. Savage, I owe a debt of thanks.

The research and report were completed while I was a National Science Foundation Graduate Trainee at the University of Southern California.

RESUMEN

La identificación y posterior estudio de *Leptodactylus pulcher* Boulenger indican que *pulcher* no pertenece al género *Leptodactylus* y que además, esta especie no puede ser asignada a ningún género descrito de leptodactilidos.

El género *Leptodactylus* está compuesto aproximadamente de 30 especies distribuidos en las tierras bajas y elevaciones intermedias en Centro y Sur America. El género se distingue de todos los otros leptodactilidos del Nuevo Mundo por la siguiente combinación de características: timpano distinguible; dedos sin membrana o con vestigio de la misma únicamente; dientes maxilar y vomeriano presentes; el vomer carece de proyección posterior; el meso-esternón es un estilo óseo; falanges terminales en forma de garra. El género se define de nuevo haciendo uso de características de morfología externa de adultos y larvas; osteología; miología; canto (entimiento de reproducción); forma de los huevos; lugar en donde son puertos y desarrollo; y cromosomas.

Un nuevo género, *Barycholos*, is descrito para *Leptodactylus pulcher* Boulenger. *Barycholos* se distingue de todos los otros leptodactilidos del Nuevo Mundo por la siguiente combinación de características: timpano distinguible; tubérculo tarsal presente; discos presentes en los dedos, sin una ranura en la circunferencia externa; el meso-esternón es un estilo calcificado. El género es

definido utilizando características de morfología externa; osteología y miología. Al presente el género comprende una sola especie, *pulcher*, la cual ha sido encontrada a lo largo de las tierras bajas costeras en Ecuador. *Barycholos* está relacionado con *Eleutherodactylus*, pero la relación no es muy cercana. *Barycholos pulcher* es descrito en base a la morfología externa y un leptotipo se designa de la serie tipo.

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