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A REVIEW OF THE LEPTODACTYLID FROG GENUS,  
*ODONTOPHRYNUS*

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The frogs of the neotropical genus *Odontophrynus* form a distinctive and phyletically compact group of warty toadlike burrowers, readily distinguished from other members of the family Leptodactylidae. One wide-ranging species, *Odontophrynus americanus*, is among the commonest amphibians in the drier subtropical regions of Argentina and adjacent portions of Bolivia, Brazil, Paraguay, and Uruguay. A second well-differentiated species, *Odontophrynus cultripes*, of southeastern Brazil and Argentina, is characterized by enormous dorsal poison glands. A third nominal form, *Odontophrynus occidentalis*, originally described from Territorio de Neuquén, Argentina, has been of questionable status.

The present study was initiated by the rediscovery of *Odontophrynus occidentalis* from a number of localities along the eastern foothills of the Argentina Andes. Subsequently, in the course of investigations to establish the systematic position of the three known members of the genus, an undescribed species from northeast Brazil was discovered.

The principal aims of this report are to review briefly the systematics and distribution of the four valid species of *Odontophrynus*, provide diagnoses for identification, describe the larvae of three of the forms, and describe the new Brazilian species. Detailed analysis of geographic variation and the ecology of *O. americanus* and *O. occidentalis* is reserved for a future paper by Ceí. Barrio (1964) has recently discussed breeding calls and ecological characters in these two species.

MATERIALS, METHODS, AND ACKNOWLEDGMENTS

Specimens of *Odontophrynus* have been examined through the courtesy of the following individuals; abbreviations in parentheses will be used to indicate specimens in these collections throughout this paper: Antenor L. Carvalho, Museu Nacional do Brasil (MN); Doris M. Cochran, United States National Museum (USNM); Robert F. Inger, Chicago Natural History Museum (CNHM); Osvaldo A. Reig, Universidad de Tucumán, (T), now at Universidad Nacional Buenos Aires; Charles F. Walker, Museum of Zoology, University of Michigan (UMMZ); and Ernest E. Williams, Museum of Comparative Zoology, Harvard University (MCZ). IB indicates specimens in the Instituto de Biología, Universidad Nacional de Cuyo, Mendoza, Argentina.

Measurements for adult specimens were made following the

methods outlined in Savage (1954). For tadpoles, measurements were taken according to the methods given in Savage (1960). Measurements for standard length are in millimeters; all others are given as percentages of standard length. Notation in the following form, 33 (34—44.6—59), indicates the number of individuals, lower limit of range, mean, and upper limit of the range, respectively.

Electrophoretic analysis of blood serum proteins was based upon samples from seven male *O. americanus*, one male and one female *O. cultripes*, and four male and one female *O. occidentalis*. Methods followed those described by Cei and Bertini (1961:336).

We wish to thank especially Dr. F. A. Saez of the Universidad de Montevideo, for his reports on the chromosome numbers and Dr. C. E. Limeses de Ikonikoff of the Universidad Nacional Buenos Aires, who pointed out the muscle differences among the several species to us. The illustrations of larvae were prepared by Mrs. Priscilla H. Starrett and of the new species by Anthony J. Gaudin.

#### *Odontophrynus* Reinhardt and Lütken

1862. *Odontophrynus* Reinhardt and Lütken, p. 159; monotype, *O. cultripes*, Reinhardt and Lütken, 1862.

*Definition*.—Pupil of eye horizontally elliptical; tongue elongate, weakly notched posteriorly, free; very small ostia pharyngea. Skin of head not fused to cranium; no tympanum. Short prominent tarsal fold; single greatly enlarged inner metatarsal tubercle modified for burrowing; first subarticular tubercle on first toe also enlarged. No disks on fingers or toes.

Maxillary and premaxillary teeth; vomerine teeth in two patches between choanae. No toothlike processes on mandible. Palatines thin, not touching one another or vomers. Quadratojugal contacts maxillary. Eight presacral vertebrae; sacral diapophyses narrow, cylindrical. Coccyx with biconcave articulations to sacrum, unexpanded but with a high median dorsal ridge. Sternum enlarged, calcified, no omosternum. Phalangeal formulae, hand: 2-2-3-3, foot: 2-2-3-4-3. Terminal phalanges claw shaped. Greatly enlarged axillary wing on humerus. Outer metatarsals united. Enlarged metatarsal tubercle supported by a large sesamoid element.

Larva with sinistral spiracle, median anus, complex mouth parts; labial papillae well-developed laterally and along lower labium, absent on median portion of upper labium; labia enfolded laterally or not; denticle rows 2/3, second upper row and first lower row in two segments, interrupted medially; beaks weakly serrate.

*General description* (characteristics common to all known species of the genus).—Head, viewed from above, rounded, broader than long, about two-thirds as broad as body. Snout blunt, truncate. Area between nostrils slightly depressed. Upper eyelid much longer than wide; length about one-third mean width, almost twice interorbital width.

In profile, the rounded canthus rostralis slopes slightly forward from eye

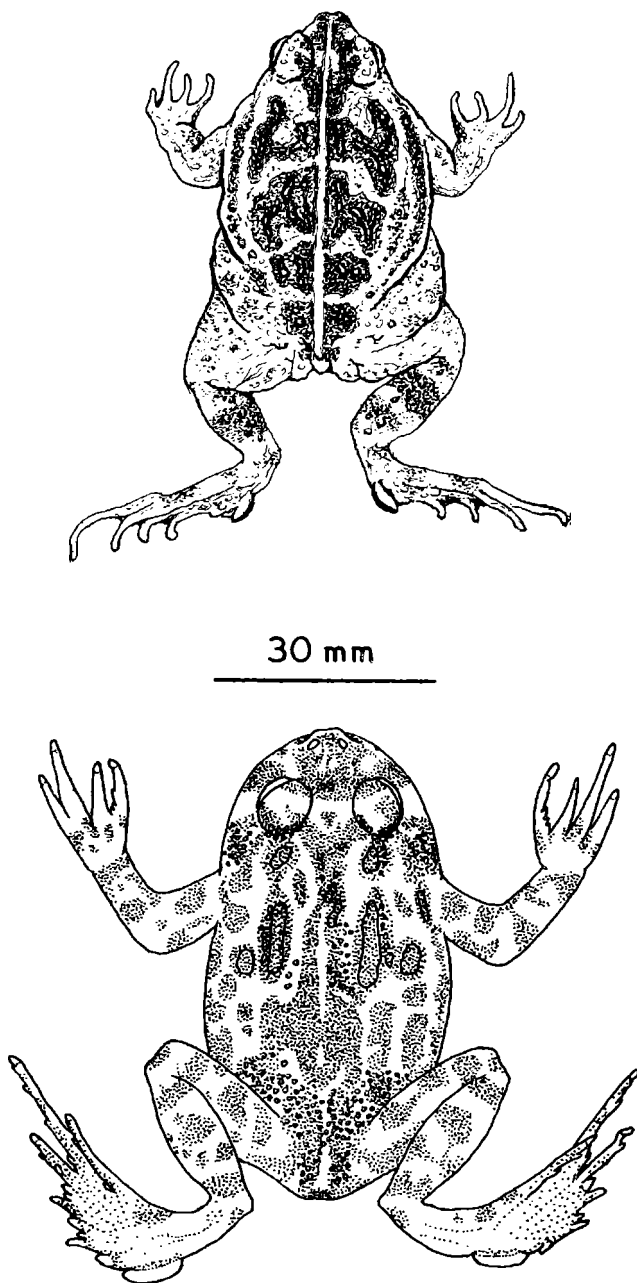


FIG. 1.—Upper, *Odontophrynus americanus*, Provincia de Santa Fe, Argentina (IB 1182); lower, *Odontophrynus carvalhoi*, holotype, Estado do Pernambuco, Brazil (MN 313).

TABLE 1.—Variation in measurements in *Odontophrynus*, as percentage of standard length.

N	<i>americanus</i>	<i>carvalhoi</i>	<i>cultripes</i>	<i>occidentalis</i>
	10	1	6	7
Head Length	31–36.8–41	34.5	28–34.0–38	35–36.3–39
Head Width	36–42.4–48	44.0	36–39.0–42	38–42.9–47
Diameter of Eye	12–12.9–16	12.3	7.9–11.6–15	12–13.3–16
Eye to Nostril	6.5–8.6–10.8	7.9	7.9–8.6–9.8	5.9–9.1–10.8
Interorbital Width	6.7–8.3–10.3	9.5	8.6–9.7–11	5.3–7.7–9.5
Length of Eyelid	11.8–13.4–15	14.0	11–12.0–13	12–14.5–17
Length of Arm	51–55.0–61	55.0	43–53.5–69	49–52.9–56
Length of Third Finger	14–16.6–20	19.0	14–15.5–17	10–16.4–21
Length of Hind Leg	106–115.8–129	126.0	93–107.6–118	112–123.0–130
Length of Tibia	23–26.3–28.3	31.0	24–28.3–48.5	27–29.5–31
Length of Foot	42.5–49.9–55	60.0	41–48.5–56	46–56.3–56

to nostril, snout blunt anteriorly with outline abruptly descending from nostril at a slightly oblique angle forward to upper lip. Nostrils in slightly raised area, elliptical, directed obliquely backwards and laterally. Orbit longer than high, greatest diameter about one-third head width. Eye covered by two membranous eyelids, the upper (tunic) attached to warty portion of eyelid. Distance from eye to tip of snout less than diameter of orbit. Throat granular, males with a single median vocal pouch; paired lateral vocal slits.

Dorsum covered with ridges and rounded warts. Belly granular.

Axillary fleshy wing envelops most of upper arm; length of arm approximately 50 percent of standard length. Upper surface of fingers smooth. First, second, and fourth fingers nearly equal in length, third finger longest. Thenar tubercle large; a large palmar tubercle, divided distally, inner portion smaller, outer portion larger than thenar tubercle; both longer than broad; numerous palmar warts and well-developed single subarticular tubercles. Legs somewhat longer than standard length. Foot smooth above. Toes with membranous margins; fourth toes one-third webbed; toes in order of decreasing length: 4-3-5-2-1. A well-developed short glandular inner tarsal fold. A greatly enlarged elongate inner metatarsal tubercle, raised and free at margins, elliptical. Subarticular tubercles single; tubercle under first toe large, raised and pointed, as large as subarticular tubercles under fingers.

A summary of variation in measurements is provided in Table 1.

*Remarks.*—Cochran (1955:336) has referred two examples of *Bufo variegatus* (USNM 15123–24) from Patagonia to this genus. She further suggests that the species is not a *Bufo* but should be regarded as an *Odontophrynus*. Examination of her material proves it to be representative of typical *B. variegatus* and in no way similar to *Odontophrynus*.

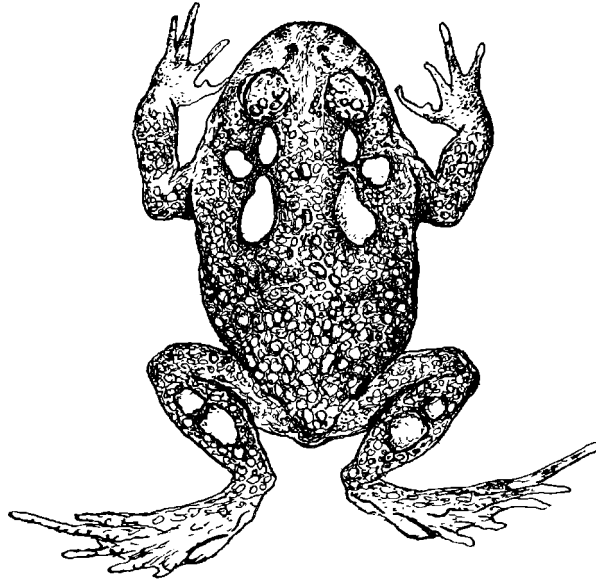
### *Odontophrynus americanus* (Duméril and Bibron)

Figs. 1, 3

1841. *Ptychocheilus americanus* Duméril and Bibron, p. 446.

1843. *Tomopterna americana* Fitzinger, p. 32

1882. *Ceratophrys americana* Boulenger, p. 266



30 mm

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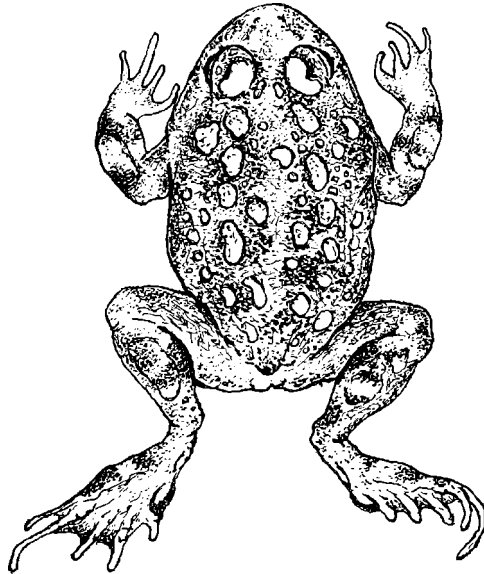


FIG. 2.—Upper, *Odontophrynus cultripes*, Estado do Minas Gerais, Brazil (IB 1015); Lower, *Odontophrynus occidentalis*, Provincia de San Luis, Argentina (IB 230).

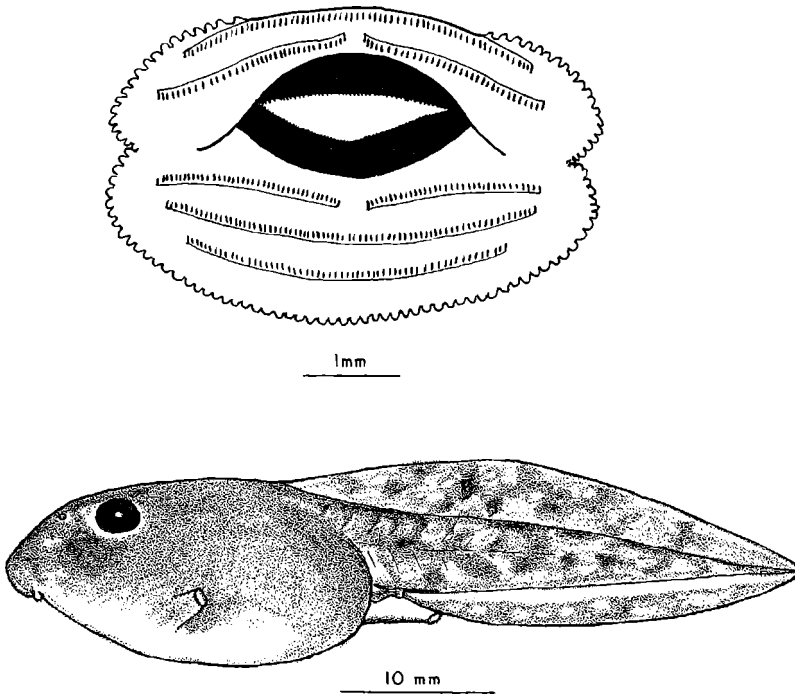


FIG. 3.—Larva of *Odontophrynus americanus*; upper, mouthparts; lower, lateral view.

1920. *Odontophrynus americanus* Miranda-Ribeiro, p. 299

*Holotype*.—Paris Museum 4530.

*Type-locality*.—Argentina: Provincia de Buenos Aires, Buenos Aires.

*Diagnosis*.—Distinguished from other members of the genus by the following combination of characters: Adults—1) warts on the upper eyelid moderate, all about same size; 2) warts on back and sides moderate and numerous, evenly distributed; 3) no distinctly enlarged postorbital gland, although an elongate ridge sometimes present in postorbital area; 4) no distinctly enlarged temporal gland; 5) no enlarged parotoid gland or warts although an elongate ridge sometimes present; 6) a single moderate glandular ridge on posterior surface of forearm; 7) no tibial gland; 8) a series of large well-defined dark blotches on lighter ground color; 9) no *m. tensor fascia lata*; 10) chromosomes,  $N = 21-22$ ; Larvae—11) labia in-folded laterally; 12) labial papillae not heavily pigmented with black.

*Measurements*.—Standard length: males, 80 (31—42.2—58), females 33 (34—44.6—59). Hind limb length 122 (100—115.2—146).

*Coloration*.—Upper surface of head, body and limbs a rich brown, with

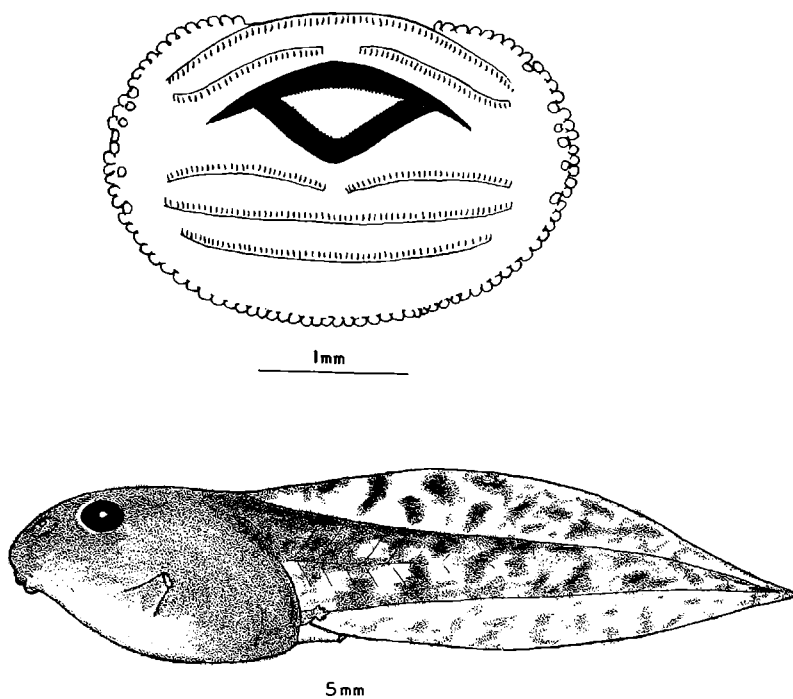


FIG. 4.—Larva of *Odontophrynus cultripes*; upper, mouthparts; lower, lateral view.

dark brown blotches, usually outlined by black. Blotches frequently with a reddish tinge in life. Ground color of sides of body light beige. A slight greenish cast to dorsal coloration in life. Several large rectangular dark blotches alternating with light areas on side of head and upper lip. Blotches on dorsal surfaces of limbs subdued.

Under surfaces dirty white, with some dark brown mottling. Throat of adult males dark gray.

*Larvae*.—The following description is based on a series of nine tadpoles from Argentina: Provincia de San Luis: near San Luis, collected October 2, 1962. The specimens agree in all essentials with the description of Fernández and Fernández (1921:36). The San Luis examples correspond to stages 38–39 of Limbaugh and Volpe (1957).

Body globose, greatest depth half standard length. Eyes and nostrils dorsal, eyes directed laterally. Dorsal and lateral surface of body uniform brown; venter transparent. Tail musculature and fins heavily pigmented with evidence of light spots and a light line along length of base of ventral fin.

Standard length 13–22; tail length 130–196.

*Remarks*.—Several populations of *americanus*, particularly from Bolivia and Choya, Provincia de Santiago del Estero, Argentina, differ markedly from samples from elsewhere. Male Bolivian specimens from Departamento de Cochabamba: Pocona, are much smaller than examples from the central portion of the species



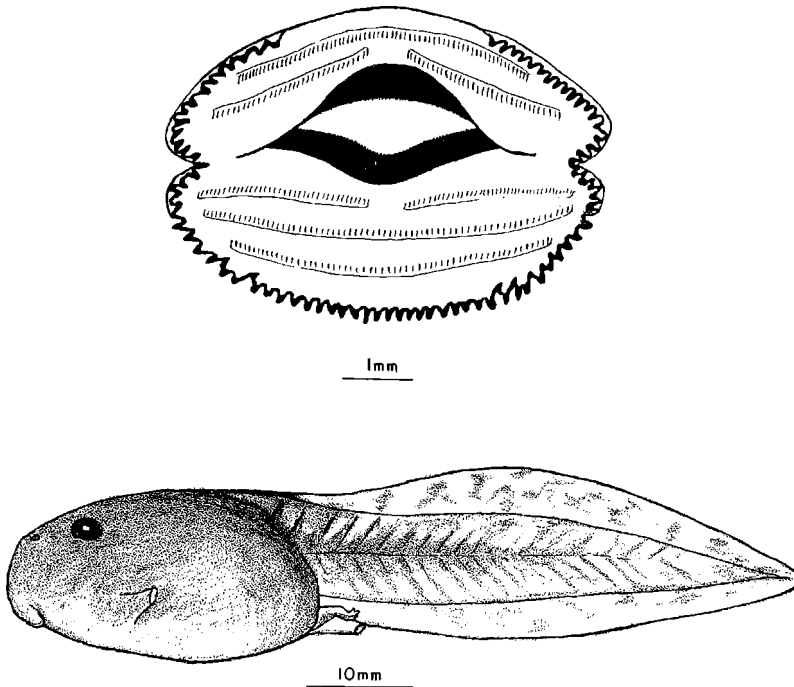


FIG. 5.—Larva of *Odontophrynus occidentalis*; upper, mouthparts; lower, lateral view.

range, standard length 12 (35—37.9—42). The Choyan population differs in coloration from typical *americanus*, in being heavily spotted with discrete bright yellow and black markings.

*O. americanus* occurs sympatrically with *O. occidentalis* in the Sierra de Córdoba of Argentina, without any indication of genetic exchange. Elsewhere it approaches the range of *O. cultripes* in Estado do São Paulo, Brazil, but the two forms have not been taken together at any locality and their ranges are essentially allopatric.

*Distribution.*—The following list of localities includes all material examined in this study and literature records clearly based on this species. ARGENTINA: *Buenos Aires*: Azul, Bahía Blanca, Buenos Aires, Chascomús, Colón (Arroyo Ojo de Buey), between Juárez and Chillan, Mar de Plata, between Tres Arroyos and Juárez; *Chaco*: Ciervo Petiso, Gral Vedia (Río de Oro), Resistencia; *Córdoba*: Ciudad de América, Santa Rosa de Calamuchita, La Serranita (near Anisacate), Sierra de Córdoba; *Formosa*: Ing. Juárez, Mission Tacuagle, Monte Lindo, San José de Pilcomayo, la Urbana; *Jujuy*: El Carmen, Jujuy, San Salvador; *Salta*: Hickman, Metán; *San Luis*: Punta de la Sierra (5 km. from San Luis) near San Luis, *Santa Fe*: Bañados de Rincón, Wheel Wright; *Santiago del Estero*: Choya; *Tucumán*: San Miguel, San Pedro, Tucumán. BOLIVIA: Chochabambo: Pocona; BRAZIL: *Paraná*: Curitiba; *Rio Grande do Sul*: Bela Vista, Morro do Coco (50 km. SE Porto

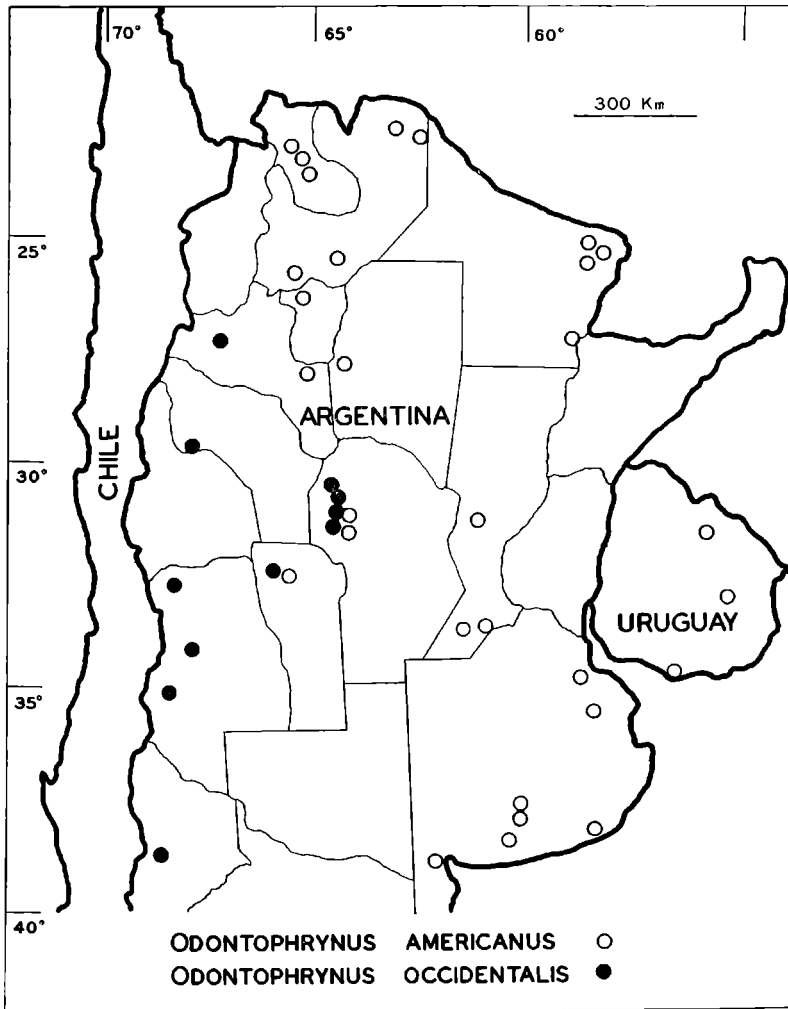


FIG. 6.—Distribution of *Odontophrynus* in southern South America.

Alegre), 10 km. SE Osorio, 39 km. W Río Pardo, Santa María, Serrara, Teresopolis, Torres; *Santa Catarina*: Ouro Verde, Tres Barros; *São Paulo*: Bertioga, Campos de Jordoa, São Paulo; *PARAGUAY*: Asunción, Río Apa, San Luis de la Sierra, Trinidad; *URUGUAY*: Arroyo Carpintería, Limar, Montevideo, Quebrada de los Cuervos. (Figs. 6-7)

*Odontophrynus americanus* is a wide-ranging form that occurs from sea level to 900 m. In general it inhabits subhumid to semi-arid areas in subtropical Argentina, Bolivia, Paraguay, Uruguay, and Brazil. Peripheral to the central portion of its range *americanus* is found in wetter situations in coastal southeastern Brazil. It is a

common species of the Chaco, Pampa, and Campo dry forest formations and penetrates the humid forest possibly through savanna islands in Bolivia and from Estado Rio Grande do Sul to Estado do São Paulo, Brazil.

*Odontophrynus carvalhoi* sp. nov.

Fig. 1

1937. *Odontophrynus americanus*, Miranda-Ribeiro, p. 56.

*Holotype*.—MN 313, an adult female, collected in 1936 by Antenor L. de Carvalho.

*Type-locality*.—Brazil: Estado do Pernambuco: Poção (1,035 m.).

*Diagnosis*.—A distinctive new form geographically isolated from other members of the genus and distinguished from them in: Adults—1) warts on upper eyelid relatively small, all about the same size; 2) a few scattered enlarged warts on back and sides; 3) a distinctly enlarged smooth postorbital gland; 4) no temporal gland; 5) two enlarged smooth parotoid glands, a greatly attenuated dorsal gland and an ovoid lateral gland; 6) a single moderate glandular ridge on posterior surface of forearm; 7) no tibial gland; 8) an irregular mottling of dark brown on a lighter ground color; presence of *m. tensor fascia* not determined, number of chromosomes and larval characteristics unknown.

*Measurements*.—Summarized in Table 1.

*Coloration*.—Upper surfaces of head, body, and limbs light brown, heavily mottled with dark brown; dorsal blotches not well defined. Side of head and upper lip marked with definite dark blotches and alternating light areas. Under surfaces yellowish white with considerable brown mottling especially on throat.

*Distribution*.—The new form is known from a single locality in the *Borborema*, an ancient hilly upland that reaches 1,100 m. in altitude, in northeastern Brazil. The environment of this tropical region resembles that of the subtropical Chaco 1,500 miles to the southwest, although the situation in the *Borborema* is moister than in the surrounding caatinga covered plains. Nearest records for the genus are of *O. cultripes* 900 miles to the south in central Estado do Minas Gerais (Fig. 7).

*Odontophrynus cultripes* Reinhardt and Lütken

Figs. 2, 4

1862. *Odontophrynus cultripes* Reinhardt and Lütken, p. 159, pl. 3, fig. 1.

1863. *Pyxicephalus cultripes* Cope, p. 51

1882. *Ceratophrys cultripes* Boulenger, p. 226

*Syntypes*.—Presumably in the Copenhagen Museum.

*Type-localities*.—Brazil: Estado do Minas Gerais: Lagôa Santa and Taboleiro Grande.

*Diagnosis.*—A species readily separated from *americanus*, *carvalhoi*, and *occidentalis* by: Adults—1) warts on eyelid variable in size, but usually one or two moderate sized and several distinctly smaller ones; 2) warts on back and sides moderate sized and numerous, evenly distributed; 3) an obvious and greatly enlarged smooth post-orbital gland; 4) a markedly enlarged, smooth temporal gland; 5) a greatly developed smooth, kidney-shaped parotoid gland; 6) a single moderate glandular ridge on posterior surface of forearm; 7) a greatly enlarged tibial gland; 8) mostly dark above with a lateral light stripe; 9) *m. tensor fascia lata* present; 10) chromosomes,  $N = 11$ ; Larvae—11) labia not infolded laterally; 12) labial papillae not heavily pigmented with black.

*Measurements.*—Standard length: males 7 (51—54.4—57), females 6 (46—58.6—70). Hind limb length, 13 (92—108.5—128).

*Coloration.*—Dorsal surfaces of head, back and limbs a rich rusty brown, with faint lighter beige areas on head and some faint black markings on back and limbs. Enlarged warts uniform brown except for some black edging. A distinct yellow streak along side running obliquely downward from level of parotoid gland toward groin. Side of head and upper lip with regular dark blotches on lighter ground color. Undersides dirty yellow with some brown pigment. Throat of males dark chocolate brown.

*Larvae.*—A series of five larvae from Brazil: Estado do Minas Gerais: Belo Horizonte, collected January 11, 1962, form the basis for the following description. These examples are at stage 37 in the system of Limbaugh and Volpe (1957).

Body globose, slightly flattened below. Eyes and nostrils dorsal, eyes directed laterally. Dorsal and lateral body surfaces dark brown, with several small dark blotches dorsally; venter finely pigmented with black but transparent. Tail musculature and fins heavily pigmented with a sharp contrast between light and dark areas.

Standard length 11–14; tail length 145–174.

*Distribution.*—All localities listed are supported by specimens examined in the course of the present study or are based on literature records with verified identification. BRAZIL: Minas Gerais: Araxá, Barro Alto, Belo Horizonte, Congonhas, Lagôa Santa, Taboleira Grande, Tres Pontes; Rio de Janeiro: Alta Itatiaia; Rio Grande do Sul: Passo Fundo; São Paulo: Santa Silvéria (Fig. 7).

*Odontophrynus cultripes* is restricted to the Campo (Savanna) region of southeast Brazil. It occurs at elevations between 500 to 900 m. in the hilly subtropical uplands interior to the Great Escarpment that separates the narrow coastal plain and hills belt (the Baixada Fluminense) from the Planalto Central. In suitable situations along the coast *O. americanus* is found as far north as São Paulo.

A single specimen (USNM 121327) of *O. cultripipes* from Estado do Rio Grande do Sul, is also from a Campo area at a moderate elevation (684 m.). This record at Passo Fundo is widely separated from the major segment of the species range by the Paraná pine (*Araucaria*) woodlands of Estados do Santa Catarina and Paraná. It is to be anticipated that *cultripipes* from this apparent gap (450 miles in extent) will be discovered in appropriate savanna islands throughout the pine forests.

Vellard's (1948) specimen from Argentina: Territorio de Formosa: Espinillo, referred to this species, has not been available for study. It seems unlikely that *cultripipes* will be found in Argentina, and we regard the record as based on a misidentification.

*Odontophrynus occidentalis* Berg

Figs. 2, 5

1898. *Odontophrynus occidentalis* Berg. p. 168

*Holotype*.—Presumed to be in the Museo Nacional de Historia Natural, Buenos Aires.

*Type-locality*.—Argentina: Territorio de Neuquén: Arroyo Agrio.

*Diagnosis*.—Distinguished from *americanus*, *carvalhoi*, and *cultripipes* by the following combination of characteristics:

Adults—1) warts on upper eyelid consist of a few greatly enlarged warts and several smaller ones; 2) numerous enlarged glands on back and sides; scattered and widely spaced; 3) a distinctly enlarged postorbital gland; 4) an enlarged temporal gland; 5) a group of large parotoid glands; 6) enlarged glands on anterior and posterior surfaces of forearm; 7) a greatly enlarged tibial gland; 8) uniform gray above; 9) *m. tensor fascia lata* present; 10) chromosomes,  $N = 11$ ; Larvae—11) labia infolded laterally; 12) labial papillae heavily pigmented with black.

*Measurements*.—Standard length: males 11 (37—49.3—62), females 7 (37—48.3—57); hind leg 18 (112—117.1—130).

*Coloration*.—Uniform gray above, except for a few dirty white areas, contrasting slightly dark gray-brown glands. In poorly preserved specimens dark glands and warts produce a pattern of dark blotches on lighter ground color. Undersurfaces dirty-white. Throat deep gray in males.

*Larvae*.—A series of nine tadpoles at stage 37 following the system of Limbaugh and Volpe (1957) are available from Argentina: Provincia de San Luis: El Volcán, collected April 9, 1956.

Body relatively short and deep, somewhat depressed; greatest depth half of standard length. Eyes and nostrils located dorsally and directed upwards. Dorsal surface of body and tail covered by an evenly distributed brown pigment; sides of body uniform brown; ventral area with light pigment, transparent. Tail musculature cov-

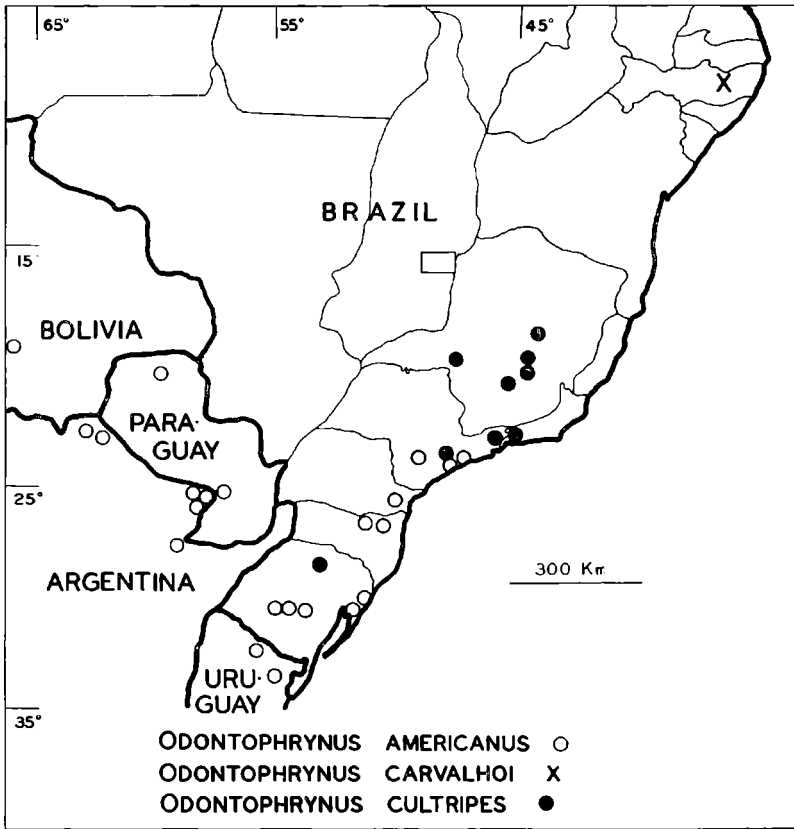


FIG. 7.—Distribution of *Odontophrynus* in eastern South America.

ered by brown pigment with only a suggestion of pattern; tail fins with obscure dark blotches.

Standard length 21—27; tail length 143—215.

*Distribution.*—Specimens have been examined from all the listed localities except the type locality. ARGENTINA: *Catamarca*: Carrizal de Belem; *Córdoba*: Río Ceballos (Sierra de Córdoba), Ciudad de América (Sierra de Córdoba), Santa Rosa de Calamuchita, La Serranita (Sierra de Córdoba), Valle Hermoso (Sierra de Córdoba); *Mendoza*: Río Atuel, Mendoza (Parque San Martín), San Rafael, El Sosneado, Tunuyán; *Neuquén*: Arroyo Agrio; *San Juan*: San Agustín del Valle Fértil, Ischigualasto (Aguada la Pina); *San Luis*: El Volcán (Sierra San Felipe); (Fig. 6).

*Odontophrynus occidentalis* is known only from the lower montane xeric regions of the eastern Andean foothills and the Sierras de Córdoba and San Felipe. Specimens have been collected from streams running through the typical desert scrub (Monte Occidental) of these regions from 800 to 2,000 m. in altitude.

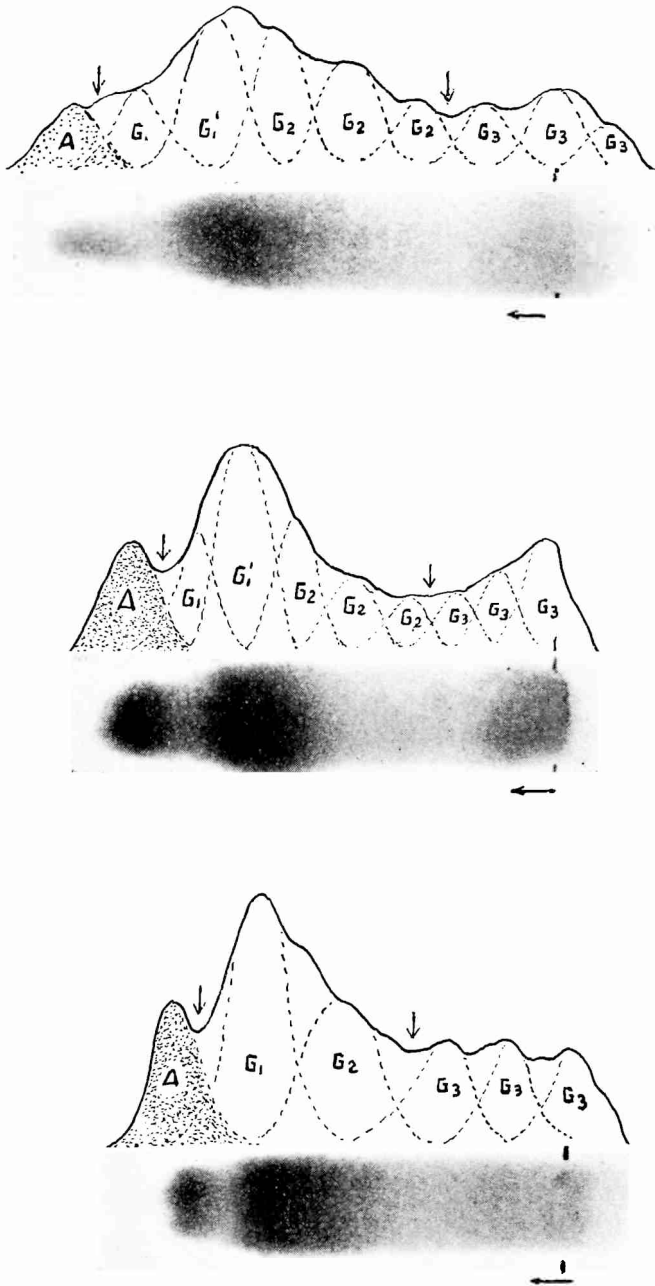


FIG. 8.—Electrophoretic patterns of blood serum proteins in *Odontophrynus*. Upper, *O. americanus*; center, *O. cultripes*; lower, *O. occidentalis*. A = albumin-like fractions, G = globulin fractions.

TABLE 2.—Albumin-like fraction mobility in the same Electrophoretic field.

		mm. from the point of sample application				
<i>americanus</i> ♂	N. 1	Tucumán	59	<i>americanus</i> ♂	N. 2 Tucumán	59
<i>occidentalis</i> ♂	N. 3	Córdoba	49	<i>americanus</i> ♂	N. 3 Tucumán	61
<i>occidentalis</i> ♀		Córdoba	52	<i>occidentalis</i> ♀	Córdoba	52
<i>americanus</i> ♂	N. 2	Tucumán	56	<i>americanus</i> ♂	N. 2 Formosa	65
<i>americanus</i> ♂	N. 3	Tucumán	75	<i>occidentalis</i> ♂	N. 2 Córdoba	60.5
<i>occidentalis</i> ♀		Córdoba	51.5	<i>occidentalis</i> ♂	N. 4 Córdoba	59
<i>americanus</i> ♂	N. 3	Formosa	60	<i>americanus</i> ♂	N. 4 Formosa	63
<i>occidentalis</i> ♂	N. 2	Córdoba	47.5	<i>occidentalis</i> ♂	N. 2 Córdoba	50
<i>occidentalis</i> ♂	N. 4	Córdoba	53.5	<i>occidentalis</i> ♂	N. 4 Córdoba	43
<i>americanus</i> ♂	N. 1	Formosa	40	<i>americanus</i> ♂	N. 1 Formosa	46
<i>occidentalis</i> ♂	N. 1	Córdoba	30	<i>occidentalis</i> ♂	N. 1 Córdoba	34
<i>occidentalis</i> ♂	N. 3	Córdoba	30	<i>occidentalis</i> ♂	N. 3 Córdoba	40
<i>americanus</i> ♂	N. 1	Tucumán	54	<i>americanus</i> ♂	N. 1 Tucumán	56
<i>occidentalis</i> ♂	N. 1	Córdoba	41	<i>occidentalis</i> ♂	N. 1 Córdoba	34
<i>occidentalis</i> ♂	N. 3	Córdoba	44	<i>occidentalis</i> ♂	N. 3 Córdoba	28
<i>americanus</i> ♂	N. 4	Tucumán	71	<i>americanus</i> ♂	N. 4 Tucumán	71
<i>cultripes</i> ♀		Minas Gerais	58	<i>cultripes</i> ♀	Minas Gerais	60
<i>occidentalis</i> ♂	N. 1	Córdoba	48	<i>occidentalis</i> ♂	N. 1 Córdoba	50.5
<i>americanus</i> ♂	N. 4	Tucumán	75	<i>americanus</i> ♂	N. 1 Formosa	56
<i>cultripes</i> ♀		Minas Gerais	64	<i>cultripes</i> ♂	Minas Gerais	51.5
<i>cultripes</i> ♂		Minas Gerais	60	<i>cultripes</i> ♀	Minas Gerais	48
				<i>americanus</i> ♂	N. 1 Formosa	55
				<i>cultripes</i> ♂	Minas Gerais	49
				<i>cultripes</i> ♀	Minas Gerais	49

Albumin/Globulin Ratios—*americanus*, 7(0.04—0.08—0.13); *cultripes*, 2(0.14—0.155—0.17); *occidentalis*, 5(0.16—0.245—0.33)

The species has been taken in sympatry with *O. americanus* in the Sierra de Córdoba at La Serranita, near Anisacate, Ciudad de América, and Santa Clara de Calamuchita. These localities are near the lower altitudinal limit for *occidentalis* at 800 m. The two forms occur in proximity in the Sierra de San Felipe, just north of San Luis, but have not been collected together in these mountains as yet.

The specimen (USNM 64133) from Provincia de Mendoza: Tunuyán, referred to as *americanus* by Cochran (1955:337) is a poorly preserved example of *O. occidentalis*. There are no authenticated records for *americanus* in the desert area of Argentina, where the species is characteristic of the subtropical dry forests of the Chaco and Pampa.

#### ELECTROPHORETIC ANALYSIS OF BLOOD SERUM PROTEINS IN *ODONTOPHRYNUS*

Significant differences among *americanus*, *cultripes*, and *occidentalis* are indicated by the comparative mobilities of their fastest



moving albumin-like fractions (A). *O. americanus* samples always superate the corresponding runs for *cultripes* and *occidentalis* (Table 2). The ratios of albumin/globulin fractions are markedly lower for *americanus* than for the other two species. *O. occidentalis* ratios are the highest, with *cultripes* intermediate to the others.

The several globulin fractions exhibit some differences as indicated by electrophoretic strips analyzed densitometrically (Fig. 8). *O. cultripes* and *O. occidentalis* are rather different from *americanus* as indicated by these analyses, particularly in the faster moving globulin fraction densities. The former two forms differ from one another in the mobility of the slowest moving globulin fractions, in which *occidentalis* resembles *americanus* more closely than it does *cultripes*.

#### RELATIONSHIPS

The characteristics analyzed in the present study form a mosaic pattern that makes determination of interspecific relationships difficult. Each species is a well-defined unit amply set off from the other members of the genus by a combination of dorsal gland, larval, musculature, and chromosomal features.

*Odontophrynus americanus* is the most distinctive species in lacking the enlarged and complex system of dorsal glands and the *m. tensor fascia lata*, and in having a higher number of chromosomes than *cultripes* or *occidentalis*. Although information is not available on the muscle, chromosome, or larval characteristics of *O. carvalhoi*, adult morphology links this form to *americanus*. In *carvalhoi* only the postorbital and parotoid glands are developed and it lacks the enlarged tibial gland.

*O. cultripes* and *O. occidentalis* are strikingly different from one another, particularly in details of glandular development and larvae, but they share the characters of a full complement of dorsal glands (postorbital-temporal-parotoid), tibial glands, *m. tensor fascia lata*, and chromosome numbers ( $N = 11$ ). In comparison with *americanus* their electrophoretic patterns are similar and differ significantly from the latter species.

The general phyletic trend in the group appears to be in the direction of greater poison gland development. In this regard *americanus* appears to be the least advanced in having no well defined or enlarged poison glands. In addition the larvae of this species are typical of the family Leptodactylidae in basic characteristics (infolded labia, denticle rows 2/3). *O. carvalhoi* represents an evolutionary advance over *americanus* in gland development and is somewhat intermediate between the latter species and the other two forms.

*O. occidentalis* exhibits maximum expression of gland development in terms of the considerable number of enlarged glands on the

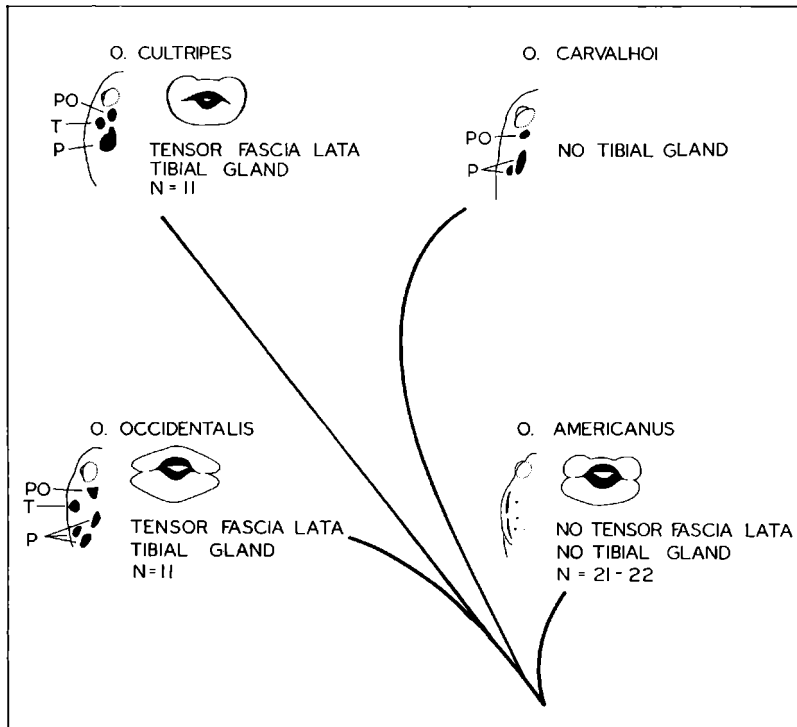


FIG. 9.—Phylogenetic diagram of relationships within the genus *Odontophrynus*, indicating poison glands, larvae, musculature, and chromosome characteristics. Terminology of poison glands, P = parotoid, PO = postorbital, T = temporal.

body and limbs. *O. cultripes* appears to have evolved in the direction of enlargement through fusion of the parotoid glands into a single unit. Although more closely related to one another than to *americanus* and *carvalhoi*, *cultripes* and *occidentalis* have undergone extensive divergence and their ancestral stocks must have evolved from any suggested precursor well back in Tertiary times.

A summary of proposed relationships among the four species, significant characteristics, and an indication of the general evolutionary pattern within the genus are presented in pictorial form (Fig. 9).

#### A KEY TO THE ADULTS OF THE GENUS *ODONTOPHRYNUS*

- 1a. No tibial or temporal glands.
  - 2a. No well-developed dorsal glands in postorbital and parotoid regions, although glandular ridges sometimes indicated ..... *O. americanus*
  - 2b. Well developed postorbital and parotoid glands ..... *O. carvalhoi*
- 1b. Tibial and temporal glands present.

- 3a. Several moderate sized parotoid glands; numerous enlarged glands scattered over back and sides; enlarged glands on anterior and posterior surface of forearm ..... *O. occidentalis*
- 3b. A single greatly developed, smooth kidney-shaped parotoid gland; no enlarged glands present on back and sides, except postorbital-temporal-parotoid series; glandular fold on posterior surface of forearm ..... *O. cultripes*

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