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A NEW SPECIES OF *TELMATOBIOUS* (ANURA: LEPTODACTYLIDAE) FROM NORTHERN CHILE

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ABSTRACT: We describe a new species, *Telmatobius fronteriensis*, from the Puna region of La Cordillera de los Andes, northern Chile. This new species is characterized by the combination of the following characters: premaxillary and maxillary teeth present, tympanum absent, stapes absent, vomerine teeth vestigial, skin of dorsum granular, flanks with spicules, and nuptial spines on the chest and inner forearm of males. This new species also is characterized by its small size (maximum SVL = 43.20 mm), by the extreme environmental conditions of its type locality, and by diagnostic morphometric and allozyme evidence presented in an earlier study.

Key words: Amphibia; Anura; Leptodactylidae; *Telmatobius fronteriensis* new species; Osteology; Ollague; Chile

TELMATOBIINE leptodactylid frogs of the genus *Telmatobius* are a particularly speciose component of the High Andean Province. The genus currently is represented by 48 species, mainly restricted to habitats >2000 m (Cei, 1986; Lynch, 1986) throughout the Andean Range from the Equator (02° 05' S; *T. niger* Barbour

and Noble, 1920) to 29° 35' S (*T. contrerasi* Cei, 1977) along the southeastern slopes of the Andes, to 22° 51' 432" S (*Telmatobius affinis halli*, previously confused with *T. halli* Noble, 1938; personal observation) along the southwestern slopes. Although the genus recently has been moderately studied (Benavides et al., 2002; De

la Riva, 1994a,b; Lavilla, 1985; Lavilla and Ergueta, 1995a,b; Salas and Sinsch, 1996; Sinsch and Juraske, 1995; Trueb, 1979; Wiens, 1993), the southwestern limits of its distribution have been barely revisited (Ceï, 1962; Veloso and Trueb, 1976; Veloso et al., 1982), and until the recent discovery of *Telmatobius dankoi* by Formas et al. (1999), only *T. halli* Noble, 1938 was reported for the northern region of Antofagasta, Chile. Here, we describe a new species, sympatric with *T. halli*, from Puquios 15 km north of Ollague on the Chile-Bolivian border.

MATERIALS AND METHODS

Frogs were collected on 17 December 1998, and at the time of capture, photographs, notes on the habitat, and color in life were taken in the field. Geographic coordinates were obtained using a Trimble Global Positioning System (GPS). Measurements were taken from preserved animals to the nearest 0.1 mm with digital calipers. All specimens were preserved as vouchers and were deposited in the following collections: Museo de Zoología de la Universidad de Concepción (MZUC), Colección Boliviana de Fauna (CBF), and Instituto de Zoología, Universidad Austral de Chile (IZUA). Abbreviations used throughout are SVL (snout-vent length); TIBL (tibia length); FOOT (foot length); HLEN (head length); HWID (head width); IOD (interorbital distance); ENOS (eye-nostril distance); IND (internarial distance); EYE (eye diameter); HNDL (hand length); RDL (radioulnar length, elbow to proximal edge of outer palmar tubercle); FEML (femur length, from vent to knee); HUML (humerus length, from the body central axis to the elbow); NMD (narine mouth distance); WEBL (web length, proximal edge of the inner metatarsal tubercle to distal edge of the III-IV toe web). Sexual maturity was assessed by presence of eggs in females (or relative size) and development of nuptial excrescences in males. Osteological observations were made on two stained paratypes (MZUC-25095; MZUC-25103), and cleared and stained skeletons were prepared according to Hollister (1934). Spec-

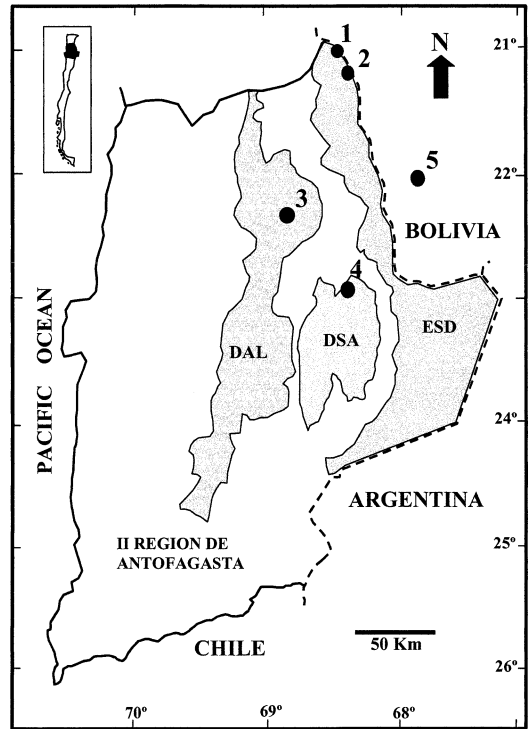


FIG. 1.—Antofagasta Region of Chile (see inset shaded area), showing collecting localities for *Telmatobius fronteriensis* (1, Puquios) and congeners *T. halli* (2, Ollague), *T. dankoi* (3, Calama), *T. affinis halli* (4, San Pedro de Atacama), and *T. huayra* (5, Laguna Colorada). The shaded areas are from Gajardo (1994) and show from right to left the subdesertic steppe of the Puna (ESD: 4000–4500 m), the Atacama desert salt flat (DSA: 2600 m), and the Atacama alluvial desert (DAL: 2200 m).

imens of other species of *Telmatobius* used for comparisons are listed in Appendix I.

SPECIES DESCRIPTION

Telmatobius fronteriensis sp. nov.

Holotype.—Museo de Zoología Universidad de Concepción (MZUC-25094), adult male from Puquios, 21° 00' 42" S–68° 23' 256" W, 15 km NW of Ollague (on the Bolivian border) Provincia El Loa, II Region de Antofagasta, Chile; approximately 4150 m elevation (Fig. 1). Collected on 17 December 1998 by Edgar Benavides, Helen Diaz, Martha B. Hengst, and Juan Carlos Ortiz.

Paratypes.—CBF 3557–59, MZUC 25095–103, and MZUC 25261–78. All adults except juveniles MZUC 25262,



FIG. 2.—Adult male of *Telmatobius fronteriensis* sp. nov., from Puquios, Chile.

MZUC 25265, and MZUC 25268. All specimens collected along with the holotype; MZUC-25095 and MZUC-25103 are cleared and stained skeletons of adult females.

Diagnosis.—*Telmatobius fronteriensis* (Fig. 2) can be distinguished from other members of the genus by a combination of features including (1) mean SVL = 39.28 ± 2.56 mm; (2) premaxillary and maxillary teeth present; (3) tympanum absent; (4) vomerine teeth vestigial; (5) skin of dorsum granular, flanks with spicules; (6) nuptial spines in the chest and inner forearm; (7) dorsum (in life) brownish spotted with black blotches; (8) venter (in life) grayish without marbled pattern; (9) stapes absent.

Telmatobius fronteriensis is geographically, morphologically, and genetically divergent from other high Andean species of *Telmatobius* (Benavides, 1999). In addition, *T. fronteriensis* occurs at an elevation higher than the three species from the eastern slope of the Andes previously re-

ported for the northernmost part of Chile (*T. peruvianus* Wiegmann, 1834, *T. pefauri* Veloso and Trueb, 1976, and *T. zapahuirensis* Veloso et al., 1982). A fourth and larger species, *T. marmoratus* (Dumeril and Bibron, 1841), also has been reported from the Andean Plateau and occurs at an even higher elevation (Veloso et al., 1982).

Telmatobius fronteriensis can be distinguished from *T. marmoratus* (characteristics in parentheses) by its smaller size (\bar{x} = 57.5 mm, see Vellard, 1953); absence of tympanum (Fig. 3A) (rudimentary); absence of supratympanic fold (thick); presence of minute nuptial spines on chest (absent); Toes III and V equal in length (Fig. 3D) (Toe III longer than V); absence of fringes on distal phalanges (present).

Telmatobius fronteriensis can be distinguished from the sympatric *T. halli* (characteristics in parentheses) by its smaller size (up to 57 mm); lean body shape (corpulent in *halli*); rounded snout in lateral and dorsal profile (Fig. 3A,B) (flat); subrectangular tongue (oval), indistinct inner

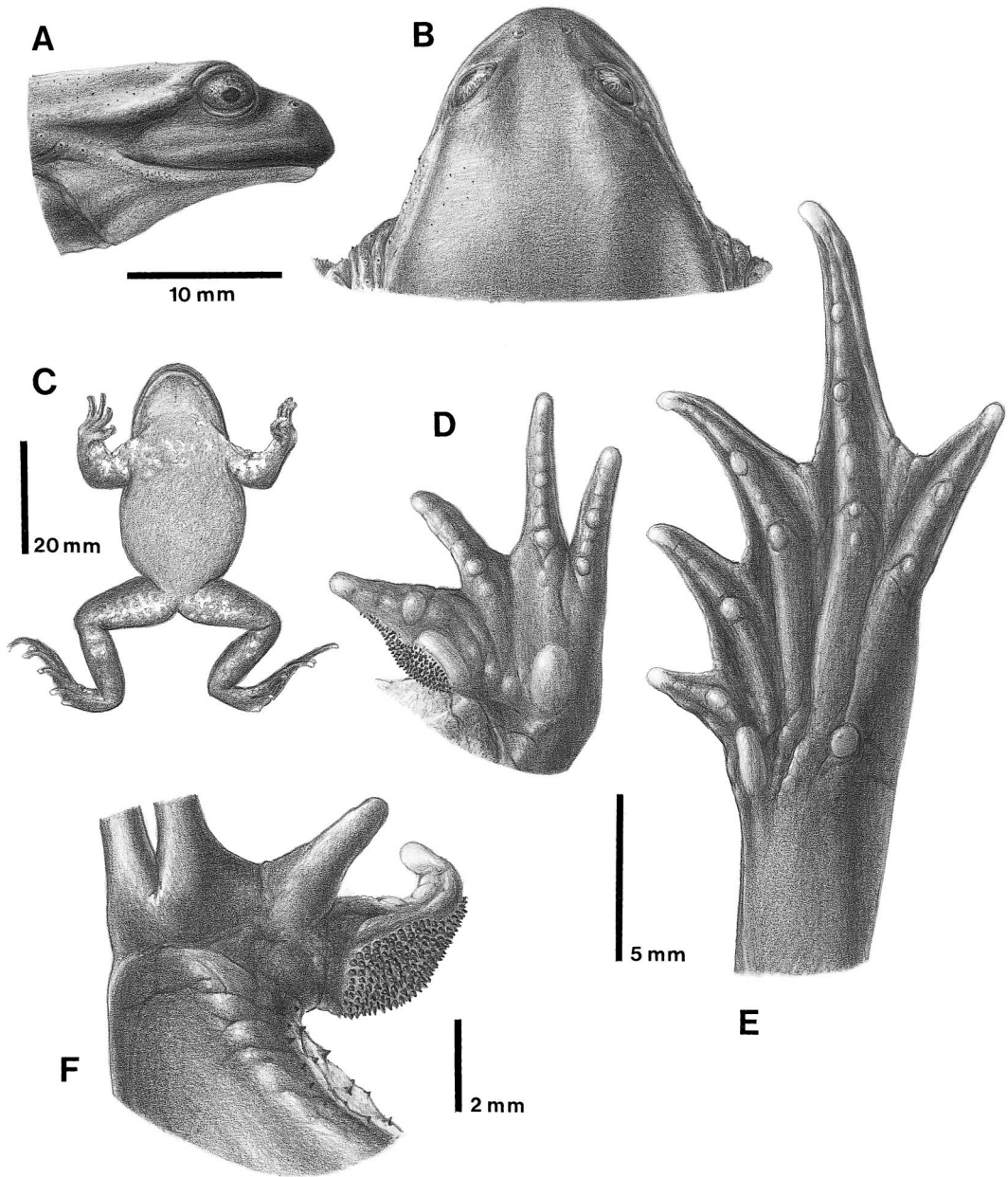


FIG. 3.—*Telmatobius fronteriensis* sp. nov. (MZUC 025261, adult male, SVL = 45.7; collected at Puquios, type locality). (A) Lateral view of the head. (B) Dorsal view of the head. (C) Ventral view. (D) Palmar view of the left hand. (E) Plantar view of the left foot. (F) Nuptial asperities on the dorsal surface of the left thumb.

and outer palmar tubercles (conspicuous); lack of supernumerary palmar tubercles (Fig. 3D) (present); Toes III and V equal in length (Toe III larger than V); partial webbing (Fig. 3E) (fully webbed); indis-

tinct subarticular plantar tubercles (prominent); and granular dorsum skin (smooth).

Differences between *T. fronteriensis* and *T. huayra* Lavilla and Ergueta (characteristics in parentheses) are the smaller

size (45.4–51.2 mm); body shape (subcylindrical); protruding eyes (non-protruded); presence of vomerine teeth (absent); absence of a postocular dermal fold (present); and granular dorsal skin (warty skin).

Telmatobius frontieriensis differs from *T. affinis halli* (characteristics in parentheses) from San Pedro de Atacama (2436 m) by its smaller size (38.36–50.81 mm); snout rounded in dorsal view and bluntly rounded in lateral profile (acuminate and projected distally); premaxillary and maxillary teeth (absent); protruding eyes (non-protruded); presence of internal forearm spines (Fig. 3F) (absent); partial webbing (wide fringes); absence of supernumerary tubercles (present); and granular skin (smooth).

Telmatobius frontieriensis further differs from *T. dankoi* (characteristics in parentheses) from Calama (2260 m) by its smaller size (49.7–51.7 mm); presence of rudimentary premaxillary and maxillary teeth (absent); vomer present (absent); and absence of a postfemoral fold (present).

Description of holotype.—Adult male, very small (38.62 mm snout–vent length). Head slightly narrower than body; head wider than long; HLEN 86.4% of HWID; head length 32.3% SVL; head width 38.11% SVL; snout short, slightly flattened in dorsal view; almost horizontal in frontonasal region and sloping distally; nostrils barely protuberant, oriented dorsolaterally; internarial distance 13.0% head width; internarial region convex; nostrils situated nearer to tip of snout than to eye; canthus rostralis distinct in dorsal profile. Eyes moderately large, protuberant, situated on top of head, oriented dorsoanterolaterally; eye diameter 33.8% of head length; supratympanic fold absent; tympanum and tympanic annulus absent; lips thin; maxillary and premaxillary teeth present and embedded within labial mucosa, so that only tips are noticeable. Vomerine teeth not evident externally; choanae, large, well separated, sub-rectangular in shape, situated perpendicular to antero–posterior axis of skull; tongue subrectangular; slightly longer (6.30 mm) than width (5.37 mm); posterior edge plain, unnotched; attached anteriorly through approximately two-thirds

to three-fourths its length; posterior border free; vocal slits absent.

Forelimbs moderately robust; dermal wrist fold absent; relative length of digits III > II = IV > I; webbing absent; lateral fringes present along inner margin of Finger II only; tips of fingers spherical, approximately equal in size to fingertips; inner palmar tubercle indistinct; outer metacarpal tubercle ovoid, barely visible; distal edge raised; one subcircular, distinct, subarticular tubercle proximally positioned on each finger; distal subarticular tubercle present on Fingers III and IV; Fingers II and III each bearing small, indistinct proximal subarticular tubercle; supernumerary palmar tubercles absent; nuptial spines moderately small, conical, keratinized on ventral and lateral surface of thumb. Hind limb length (foot plus tibia) 110.6% SVL; relative length of toes IV > III = V > II > I; webbing formula: $\text{II}-2\frac{2}{3}\text{III}1\frac{1}{2}-3\frac{1}{3}\text{III}2\frac{1}{2}-3\frac{2}{3}\text{IV}3\frac{2}{3}-2\text{V}$; webbing diminishing distally to form narrow fringes along lateral margins of toes; lateral fringes absent on distalmost two phalanges on Toes III and IV and absent from distalmost phalanges only on Toes I, II, V; tarsal fold extending approximately two-thirds length of tarsus, confluent distally with narrow fringe along inner margin of toe I; tips of toes rounded, roughly equal in size to fingertips; inner metatarsal tubercle raised, narrow, ellipsoid; external tubercle subcircular, indistinct, approximately one-third length of inner tubercle; subarticular tubercles round, indistinct, distributed on toes as follows: I(2), II(2), III(2), IV(3), V(2); row of 2–3 indistinct supernumerary tubercles present proximally on Toes III and IV.

Skin of dorsum granular with small pustules on back and dorsal side of limbs; small spiculate pustules along flanks; ventral skin smooth, with minute horny spicules on chest and inner surface of forearms; skin having loose folds, “bagginess” absent; cloacal opening directed posteriorly at dorsal level of thighs; opening round and unornamented.

Color in preservative.—Dorsum, dorsal surface of head and limbs dull brown-grayish, extensively spotted with irregular

darker blotches; whitish mottling along forearms, legs and flanks; throat cream; venter cream with diffuse brownish mottling increasing peripherally; ventral surface of thighs brownish except for a cream irregular preanal blotch (Fig. 3C); palmar and plantar surfaces of extremities darker than other ventral surfaces; ventral tarsal and plantar surfaces mottled uniformly with white spots; all digital tips pale tan dorsally and ventrally.

Color in life.—Dorsal ground color light brown or greenish brown, profusely spotted with irregular black blotches; skin of belly gray without marmorations.

Measurements of holotype (in mm).—SVL 38.62, TIBL 16.74, FOOT 25.98, HLEN 12.36, HWID 14.72, IOD 4.96, ENOS 2.58, IND 2.06, EYE 4.19, HNDL 9.63, RDL 9.95, FEML 18.32, HUML 15.58, NMD 3.23, WEBL 9.69.

Osteology

Cranium.—The skull (Fig. 4A,C) is slightly wider than long; frontoparietals wider posteriorly than anteriorly; sphenethmoid large, as long as the frontoparietal fenestra, overlapped by frontoparietals posterolaterally; frontoparietals clearly identifiable investing fused prootic and exoccipital; frontoparietal fenestra elongate, small, nearly $\frac{1}{4}$ of the skull length; nasals small, almost triangular in form, medially separated, reaching sphenethmoid but not pars facialis of maxillary arch; maxillary arch complete; premaxilla and maxilla in close contact; alary process of premaxilla rectangular, sloping posteriorly, pars palatina reduced; 4–5 premaxillary teeth; each maxilla bearing 22–23 teeth; pars facialis of maxilla moderately deep, inclined medially, low preorbital process; fused prootics and exoccipitals well ossified; occipital condyles not stalked, with wide medial separation; stapes absent; otic process of squamosal short, in contact with otic shelf of prootic; zygomatic process of squamosal slender, acuminate; squamosal–maxilla angle approximately 45° ; parasphenoid cruciform, with cultriform process not reaching levels of neopalatines; anterior ramus of pterygoid in contact with the palatal shelf of the maxilla; neopalatines slender,

straight, making contact with sphenethmoids and maxillae; vomers moderate in size, thin, separate medially, bearing 2–3 minute teeth in interchoanal position.

Pectoral girdle.—Pectoral girdle arciferal (Fig. 4D). Clavicles arched, not in contact medially; distal end extremely dilated and fused with the proximal border of the scapula; suprascapula ossified on lateral halves and across anterior margins; coracoids straight, dilated at distal and proximal ends; epicoracoid cartilages free and partially mineralized; omosternum moderate in size with manubrial portion well defined; sternum robust with bony style; xiphisternum cartilaginous expanded.

Hyoid.—Hyoid plate (Fig. 4E) cartilaginous, as long as wide; hyoglossal sinus U-shaped, deeper than wide; anterolateral processes with narrow base and distal expansion; posterolateral process acuminate, slender; posteromedial process, ossified except for distal cartilaginous tips; hyale proximal expansion slender, long and curved.

Vertebral column.—Vertebral column (Fig. 5A,B) with eight procoelus presacral vertebrae, Vertebral Centra II and III fused; cervical cotyles moderately separated; neural archs nonimbricate, lacking neural spines; Vertebrae II–IX bearing transverse processes, lacking ribs; transverse processes of II–IV larger (wider) than those of V–VIII; processes of Vertebrae II and III deflected anteriorly, V and VI deflected posteriorly, and IV, VII, and VIII oriented perpendicular to longitudinal axis; centra of sacrum and VIII Vertebra fused; sacrococcygeal articulation bicondylar; sacral diapophysis weakly dilated; anterodorsal urostyle with a dorsal prominence from which arises a low, thin plate that disappears at midlength of urostyle.

Pelvic girdle.—Iliac shaft absent (Fig. 5C). Dorsal prominence low, oriented laterally; dorsal acetabular expansion prominent (Fig. 5C); ventral acetabular expansion well developed relative to dorsal expansion, preacetabular angle about 90° ; acetabulum rounded; dorsal border interrupted; ischium prominent; pubis well mineralized.

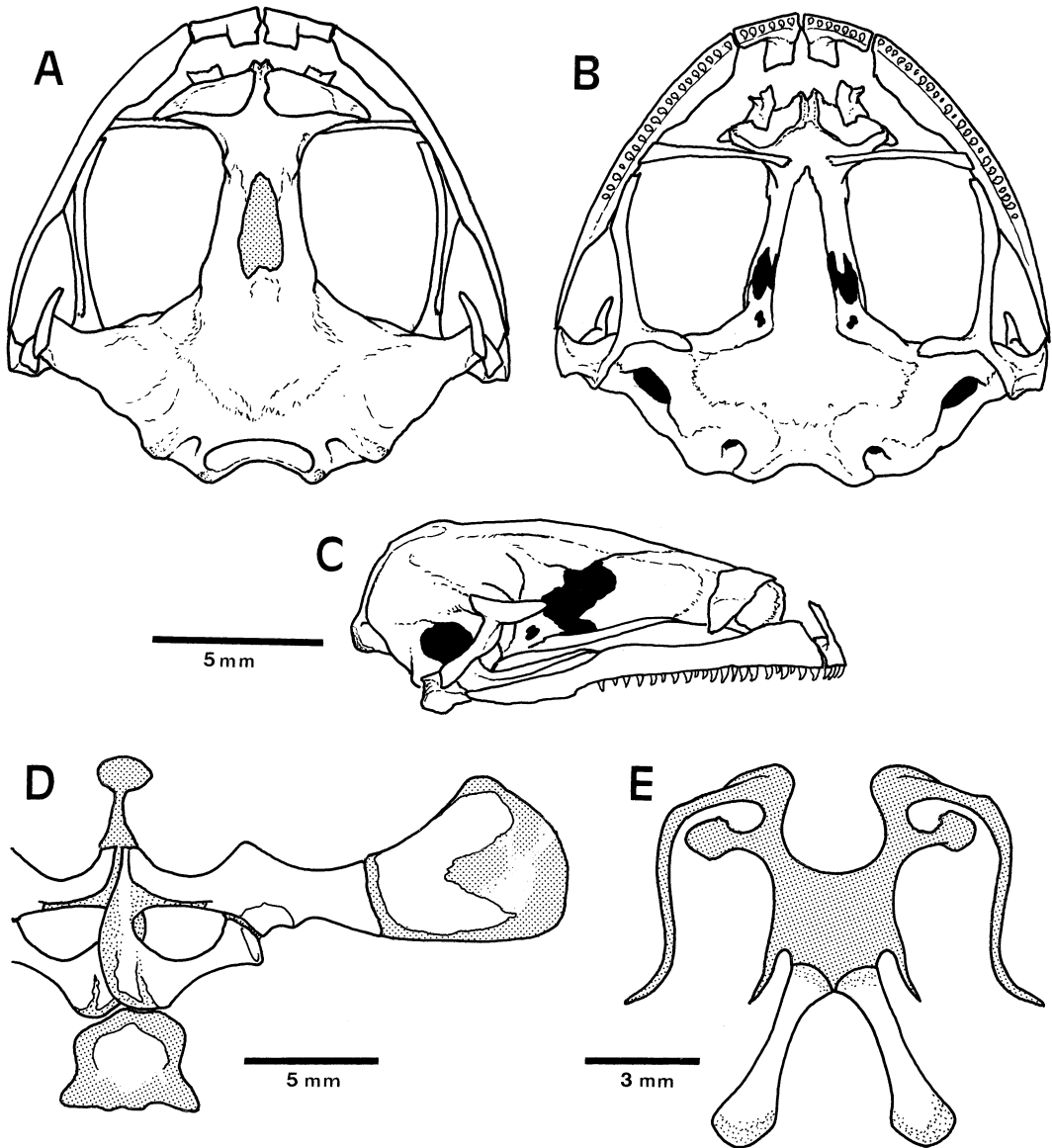


FIG. 4.—(A) dorsal, (B) ventral, and (C) lateral views of the skull of the paratype (MZUC 25095). Ventral views of the (D) hyoid and (E) pectoral girdle of the paratype (MZUC 25103) of *Telmatobius fronteriensis*.

Appendages.—Humerus longer and more robust than radioulna; humeral crests well developed, specially the crista ventralis; phalangeal formula for manus: 2-2-3-3; terminal phalanges rounded; outer border of first metacarpal with tubercle at midpoint; prepollex with two elements (Fig. 5D), similar in length; radiale and ulnare and intermedium separated; centrale 2, Distal Carpal 2 and Distal Carpal 3 in-

dependent; femur and tibiofibula similar in length; tibiae and fibulae fused proximally and distally, half length of femur; phalangeal formula of foot: 2-2-4-3, terminal phalanges moderately pointed; prehallux with two elements (Fig. 5E), distal one more laterally extended than proximal; additionally, two metatarsal bones present, whose homology is unresolved.

Variation.—Adults of *Telmatobius fron-*

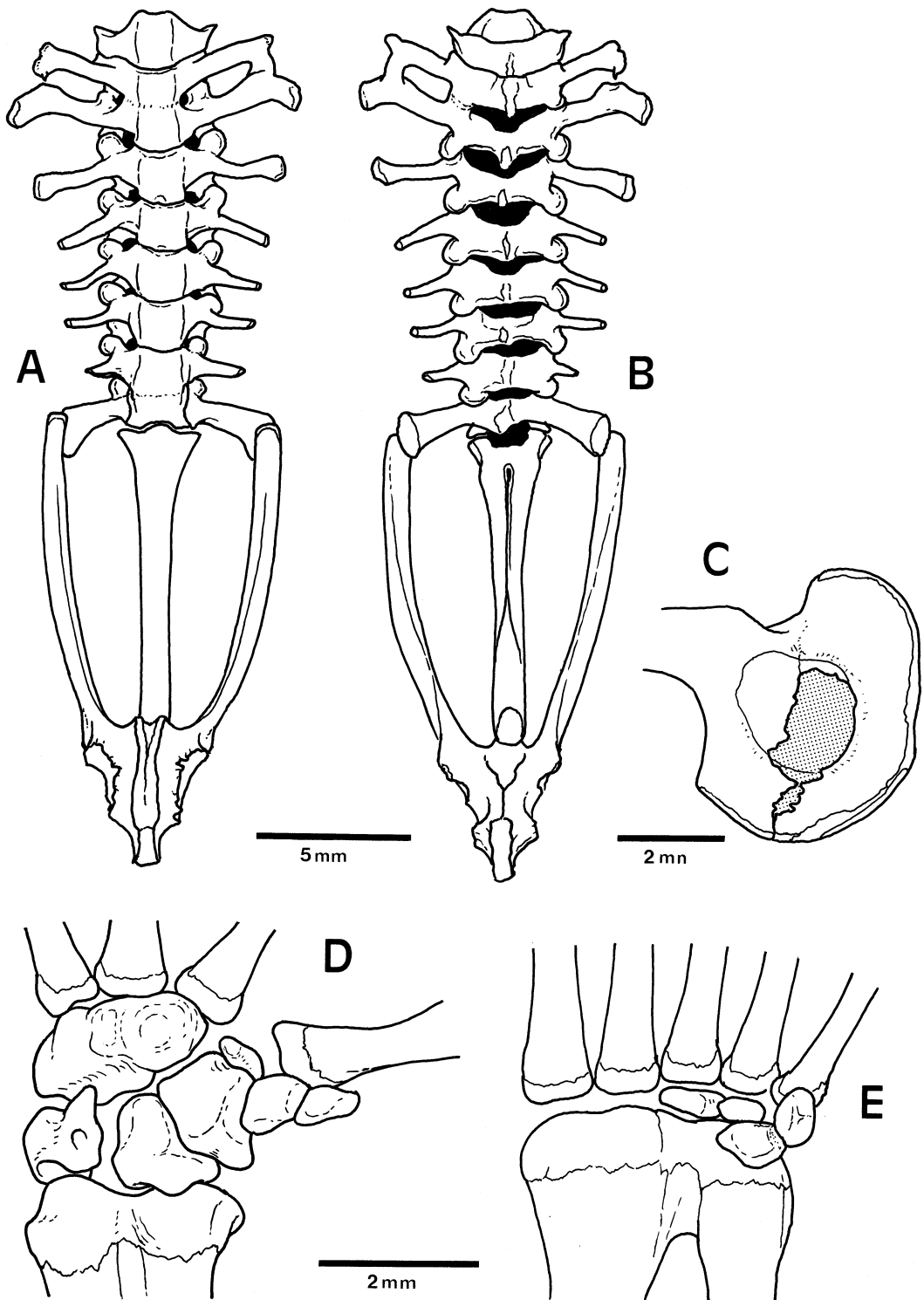


FIG. 5.—(A) ventral and (B) dorsal views of the vertebral column and pelvic girdle, (C) lateral view of the left acetabulum, (D) ventral view of the right carpus, and (E) ventral view of right tarsus of the paratype MZUC 25103 of *Telmatobius fronteriensis*.

TABLE 1.—Variation in morphometric characters of males, females, and juveniles of *T. fronteriensis*. Measurements are in millimeters, and numbers for each variable indicate mean \pm standard deviation and range in parentheses.

Character	Juveniles (n = 2)	Females (n = 13)	Males (n = 16)
SVL	33.23 \pm 2.27 (31.62–34.84)	39.94 \pm 2.32 (36.18–42.58)	39.50 \pm 1.78 (37.29–43.20)
TIBL	15.16 \pm 2.22 (13.59–16.73)	16.66 \pm 0.97 (14.99–18.39)	16.85 \pm 1.12 (15.02–19.20)
FOOT	22.87 \pm 1.50 (21.81–23.94)	25.55 \pm 1.67 (23.00–28.74)	25.53 \pm 1.33 (23.93–27.66)
HLEN	10.61 \pm 0.73 (10.09–11.13)	12.96 \pm 1.34 (10.71–15.22)	13.24 \pm 1.24 (11.40–15.18)
HWID	12.98 \pm 1.50 (11.92–14.05)	15.12 \pm 0.77 (13.48–16.15)	15.04 \pm 0.63 (13.35–16.07)
IOD	4.81 \pm 0.50 (4.46–5.17)	4.91 \pm 0.55 (4.34–6.34)	5.07 \pm 0.34 (4.16–5.67)
ENOS	2.53 \pm 0.27 (2.34–2.73)	2.71 \pm 0.22 (2.47–3.12)	2.66 \pm 0.25 (2.35–3.29)
IND	2.36 \pm 0.54 (1.98–2.75)	2.42 \pm 0.25 (2.07–2.82)	2.49 \pm 0.29 (2.16–3.25)
EYE	3.66 \pm 0.07 (3.61–3.72)	4.29 \pm 0.34 (3.65–4.79)	4.21 \pm 0.25 (3.82–4.86)
HNDL	8.22 \pm 0.63 (7.77–8.67)	9.24 \pm 0.41 (8.60–10.12)	9.05 \pm 0.55 (7.93–10.11)
RDL	8.20 \pm 0.61 (7.77–8.64)	9.55 \pm 0.66 (8.57–10.56)	9.52 \pm 0.50 (8.62–10.36)
FEML	16.36 \pm 2.25 (14.77–17.96)	17.35 \pm 1.00 (16.37–19.10)	17.73 \pm 0.97 (15.77–19.67)
HUML	13.76 \pm 0.70 (13.27–14.26)	16.05 \pm 1.42 (13.92–19.08)	15.83 \pm 0.88 (14.20–17.62)
NMD	2.51 \pm 0.57 (2.11–2.92)	3.17 \pm 0.42 (2.30–3.85)	3.21 \pm 0.31 (2.73–3.81)
WEBL	8.15 \pm 0.37 (7.89–8.42)	9.49 \pm 0.71 (8.26–10.65)	9.41 \pm 0.72 (8.05–10.41)

teriensis are particularly homogeneous in coloration. Ventral surface of the body and limbs varies from immaculate in juveniles to diffusely mottled in adults. Creamy blotches in the proximal region of the thighs are present in some adult individuals only (35.7%) (Fig. 3C). Some males and most females show a distinct and larger outer palmar tubercle as well as more conspicuous subarticular tubercles. Palmar supernumerary tubercles are always absent in this species. Tarsal folds and webbing is less developed in juveniles. Variation of mensural characters of males, females and juveniles is summarized in Table 1.

Distribution.—This species is known only from the type locality.

Etymology.—The name of the species, a Latin adjective, refers to the type locality, located at the border between Bolivia and Chile.

Remarks.—*Telmatobius fronteriensis* was found in a small thermal pond without vegetation; water temperature was 22.9 C and environmental temperature was 9.8 C. When handled, both the male and female produced a warning consisting of single grunts given at regular intervals. The type locality is dry and characterized by a rocky substrate covered by “Yareta” (*Azorella*

compacta) and low grasses and bushes (*Festuca ortophylla*, *Stipa nardoides*) typical of the Puna biogeographic province (Fig. 1).

DISCUSSION

Telmatobius fronteriensis is the second of a set of three new species (*T. dankoi* Formas et al., 1999, and another, still undescribed, previously referred to *T. affinis halli*) recently discovered in this section of the western slope of the Andes. Interestingly enough and regardless of the elevation, the entire region is characterized by subdesert conditions (Fig. 1). Moreover, all five species mentioned in this work (including *T. halli* and *T. huayra*) are basically confined to small streams or permanent springs in an area of less than 200 km². Therefore, a high level of endemism and high species diversity has to be noted, and invites consideration of the events that lead to such a remarkable diversification.

Although no phylogenetic statement can be made so far, the pattern of speciation of the five species considered here is undoubtedly related to the uplift of the Andes and the progressive desiccation of its steep southwestern slope. It seems likely that a differentiation along this sharp altitudinal and dryness gradient could be responsible for both isolation and adaptation to particularly stressful environments. Clear-cut differences in body shape but low levels of genetic divergence between *T. fronteriensis* sp. nov. and *T. cf. affinis halli* (Benavides et al., 2002) seem to partially support this hypothesis.

Finally, it is important to stress the point of geographic rarity; all of the above mentioned species are confined to small water bodies within desert habitats, which has important implications for the conservation policies of localized populations.

RESUMEN

Se describe una nueva especie, *Telmatobius fronteriensis*, de la Región de Puna, de la Cordillera de los Andes, en el Norte de Chile. La nueva especie puede ser distinguida de otros miembros del género *Telmatobius* por una combinación de caracteres que incluye: presencia de dientes

maxilares y premaxilares, tímpano ausente, dientes vomerianos vestigiales, piel del dorso granular y flancos con espinas corneas, así como espinas nupciales en el antebrazo de los machos. Esta nueva especie puede también ser diagnosticada en base a su reducida talla (SVL máximo = 43.20 mm) y las condiciones ambientales extremas de la localidad tipo. Finalmente, un trabajo anterior identificó caracteres diagnóstico de tipo morfométrico y aloenzimático.

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LITERATURE CITED

- BENAVIDES, E. 1999. Situación taxonómica de *Telmatobius albiventris* (Anura: Leptodactylidae) y complejos relacionados. Un enfoque morfológico y molecular. M.S. Thesis, Universidad de Concepción, Concepción, Chile.
- BENAVIDES, E., J. C. ORTIZ, AND J. W. SITES, JR. 2002. Species boundaries among the *Telmatobius* (Anura: Leptodactylidae) of the Lake Titicaca Basin: allozyme and morphological evidence. *Herpetologica* 58:31–55.
- CEI, J. M. 1962. Batracios de Chile. Editorial Universitaria, Santiago, Chile.
- . 1986. Speciation and adaptive radiation in Andean *Telmatobius* frogs. Pp. 374–386. In F. Vuilleumier and M. Monasterio (Eds.), *High Altitude Tropical Biology*. Oxford University Press, Oxford, U.K.
- DE LA RIVA, I. 1994a. Description of a new *Telmatobius* from Bolivia (Amphibia: Anura: Leptodactylidae). *Graellsia* 50:161–164.
- . 1994b. A new aquatic frog of the genus *Telmatobius* (Anura: Leptodactylidae) from Bolivian cloud forests. *Herpetologica* 50:38–45.
- FORMAS, J. R., I. NORTHLAND, J. CAPETILLO, J. J. NUÑEZ, C. CUEVAS, AND L. BRIEVA. 1999. *Telmatobius dankoi* una nueva especie de rana acuática del norte de Chile (Leptodactylidae). *Revista Chilena de Historia Natural* 72:427–445.
- GAJARDO, R. 1994. La Vegetación Natural de Chile. Clasificación y Distribución Geográfica. Editorial Universitaria, Santiago, Chile.
- HOLLISTER, G. 1934. Clearing and dying fish for bone study. *Zoologica* 12:89–101.
- LAVILLA, E. O. 1985. Diagnosis genérica y agrupación de las especies de *Telmatobius* (Anura: Lep-

- todactylidae) en base a caracteres larvales. *Physis* (Buenos Aires), Sección. B., 43:63–67.
- LAVILLA, E. O., AND P. ERGUETA. 1995a. Una nueva especie de *Telmatobius* (Anura: Leptodactylidae) del Sudoeste de Bolivia. *Ecología en Bolivia* 24:91–101.
- . 1995b. Una nueva especies de *Telmatobius* (Anura, Leptodactylidae) de la ceja de montaña de La Paz (Bolivia). *Alytes* 13:45–51.
- LYNCH, J. D. 1986. Origins of the high Andean herpetological fauna. Pp. 478–499. In F. Vuilleumier and M. Monasterio (Eds.), *High Altitude Tropical Biogeography*. Oxford University Press, Oxford, U.K.
- SALAS, A. W., AND U. SINSCH. 1996. Two new *Telmatobius* species (Leptodactylidae, Telmatobiinae) of Ancash, Peru. *Alytes* 14:1–26.
- SINSCH, U., AND N. JURASKE. 1995. Reassessment of central Peruvian Telmatobiinae (genera *Batrachophrynus* and *Telmatobius*). 2. Allozymes and phylogenetic relationships. *Alytes* 13:45–51.
- TRUEB, L. 1979. Leptodactylid frogs of the genus *Telmatobius* in Ecuador with the description of a new species. *Copeia* 1979:714–733.
- VELOSO, A., AND L. TRUEB. 1976. Description of a new species of Telmatobiine frog, *Telmatobius* (Amphibia: Leptodactylidae), from the Andes on northern Chile. *Occasional Papers of the Museum of Natural History, University of Kansas* 62:1–10.
- VELOSO, A., M. SALABERRY, J. NAVARRO, P. ITURRA, J. VALENCIA, M. PENNA, AND N. DIAZ. 1982. Contribución sistemática al conocimiento de la herpetofauna del extremo norte de Chile. Pp. 135–268. In A. Veloso and E. Bustos (Eds.), *La vegetación y los vertebrados ectotérmicos del transecto Arica-Lago Chungara*. Volumen de síntesis, Proyecto MAB 6-UNEP-UNESCO, Santiago de Chile, Chile.
- VELLARD, J. 1953. Estudios sobre batracios andinos. II. El Grupo *Marmoratus* y formas afines. *Memorias del Museo de Historia Natural*. Javier Prado 2: 1–53 + vi pl.
- WIENS, J. 1993. Systematics of the leptodactylid frog genus *Telmatobius* in the Andes of northern Peru. *Occasional Papers of the Museum of Natural History, University of Kansas* 162:1–76.

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APPENDIX I

Specimens Examined

Telmatobius halli.—CHILE: II REGION de ANTOFAGASTA: Warm springs near Ollague (21° 18' S–68° 12' W), 10000 ft. [3048 m] (AMNH A-44753, holotype; A-44754, paratype).

Telmatobius huayra.—BOLIVIA: POTOSI: SUD LIPEZ: Campamento Khastor, 22° 02'–66° 08' W, 4600 m (CBF 01223, holotype; CBF 01221–22, paratypes).

Telmatobius marmoratus.—BOLIVIA: LA PAZ: PROV MURILLO: (CBF 03244–56, CBF 1009–11, CBF 468–70).

Telmatobius affinis halli.—CHILE: II REGION de ANTOFAGASTA: SAN PEDRO DE ATACAMA: Estero Vilama, 22° 56' S–68° 11' W, 2600 m, (CBF 3760–62; MZUC 25725–38).

Telmatobius dankoi.—CHILE: II REGION de ANTOFAGASTA: 3 km S of Calama, Las Cascadas, 22° 29' 54" S–68° 58' 18" W, 2260 m, (IZUA 2108, holotype; IZUA 2109–10, paratypes).