



The tadpoles and advertisement calls of *Pleurodema bibroni* Tschudi and *Pleurodema kriegi* (Müller), with notes on their geographic distribution and conservation status (Amphibia, Anura, Leiuperidae)

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Abstract

Pleurodema bibroni and *P. kriegi* are poorly known species with a troublesome taxonomic history. They are cryptic taxa, currently considered as valid species on the grounds of biogeographic and ecological differences. The first is known from much of southern Uruguay and from the northeastern region of the State of Rio Grande do Sul, Brazil (from sea level to 900 m a.s.l.); the latter is restricted to high grasslands of the Sierras Grandes in central Argentina, between 800–2000 m a.s.l. Herein, we compare their tadpoles and advertisement call and provide some notes on their conservation status and natural history. The tadpoles of both species are very similar, belonging to the benthic ecomorphological guild, and are characterized by: total length about 35 mm at stages 33–36; globose body; short lateral sinister spiracle posterodorsally directed; pineal end organ visible between the eyes; medial vent tube, with its opening aligned with the ventral fin, directed to the left or to the right; vent tube enclosed in a transparent saccular structure underlying the limb buds; tail length about 60% of the total length, with bluntly rounded tip; oral disc anteroventral, laterally emarginated, with very robust jaw sheaths and marginal papillae arranged in a single or double row with a large dorsal gap; labial tooth row formula 2(2)/3(1); gap in A2 wide with the upper jaw sheath partially placed within it; P3 about half the length of the other rows. The advertisement call exhibits the same temporal and spectral structure in both species. It consists of long trills (up to about 45–70 s) that are emitted sporadically; notes are about 0.044–0.062 s, separated by gaps of 0.024–0.058 s (note repetition rate 8.9–13.2/s) and have three pulses. Dominant frequency ranges between 1729 and 2162 Hz. Reproductive season of both species differed, autumn and winter for Uruguayan populations of *P. bibroni* and spring and summer for *P. kriegi*. Defensive encounter behavior (deimatic behavior) consisting in exhibition of the eye-like lumbar glands was documented in *P. bibroni* and *P. kriegi* (along with exposure of reddish flash coloration), and also in *P. borellii*, *P. bufoninum* and *P. thaul*. Similar behavior previously unreported for a *Pleurodema* species lacking noticeable lumbar glands was observed in *P. tucumanum*. The analysis of the literature, material in collections and fieldwork done by the authors over the last decade in Uruguay suggests that *P. bibroni* is undergoing severe decline. It was a common species up to the early 1970's, but few populations close to each other in southeastern Uruguay are the only ones currently known. The conservation status of *P. bibroni* is of major concern as most known remnant populations are located in coastal areas with an increasing impact of urbanization. In contrast, *P. kriegi* seem to have stable populations, many of them within protected areas.

Key words: amphibian decline, biogeography, defensive behavior, deimatic behavior, larval morphology, *Pleurodema borellii*, *Pleurodema bufoninum*, *Pleurodema thaul*, *Pleurodema tucumanum*

Introduction

The genus *Pleurodema* Tschudi, 1838, is currently composed of 13 species (Frost 2008), distributed in the Neotropical region mostly in areas with dry or arid climates (Barrio 1964a; Lynch 1971; Duellman & Veloso 1977; Cei 1980). Fossorial habits are known for most of them (Fernández & Fernández 1921; Fernández 1927; Carvalho & Bailey 1948; Barrio 1964a; Duellman & Veloso 1977) and many species have explosive reproductive strategies related to rainfall (Fernández & Fernández 1921; Barrio 1964a; León-Ochoa & Donoso-Barros 1969–1970; Hulse 1979; Cei 1980; Peixoto 1982; Hödl 1992; Cardoso & Arzabe 1993). Their reproductive modes include foam nests, submerged egg strings, floating egg strings, and floating egg masses (Cei 1962; Duellman & Veloso 1977; Barrio 1977; Cei 1980; Hödl 1992; Martori *et al.* 1994; Weigandt *et al.* 2004). Conspicuous lumbar glands are present in eight species, and deimatic behavior was reported for some of them (Cei 1962; Vaz Ferreira 1984; Martins 1989). At least a brief description of the external morphology of tadpoles is available for most species of *Pleurodema*, except for *Pleurodema bibroni* Tschudi and *Pleurodema fuscomaculatum* (Steindachner); the characters of those known larvae were summarized consecutively by Duellman and Veloso (1977), Cei (1980), Altig and Johnston (1986), and Altig and McDiarmid (1999b).

Pleurodema bibroni (Fig. 1A) and *Pleurodema kriegi* (Müller) (Fig. 1B) have troublesome taxonomic histories. *Pleurodema bibroni*, the type species of the genus, was described from Montevideo, Uruguay (Tschudi 1838) but this name was applied for a long time to specimens of Argentinean and Chilean populations currently known under the name *Pleurodema thaul* (Lesson) (Donoso-Barros 1969). On the other hand, *P. kriegi*

was considered a junior synonym of *Pleurodema cinereum* Cope or of *P. bibroni* (as *Pleurodema darwini* Bell) (Parker 1927; Gallardo 1968; see Barrio 1977 for a more detailed taxonomic history of both species). Barrio (1977) considered *P. bibroni* and *P. kriegi* as distinct species based mostly on biogeographic and ecological arguments; currently, this arrangement remains unchanged (Frost 2008). Both species are very similar morphologically (Laurent 1975; Barrio 1977), their advertisement calls and reproductive modes are noticeably similar (Barrio 1977) and they are also the only known tetraploid species of the genus ($2n=4x=44$; Barrio & Rinaldi de Chieri 1970). Due to these similarities, a common origin was postulated for both species, by allopolyploidy (Barrio & Rinaldi de Chieri 1970; Barrio 1977) or by autopolyploidy and posterior diploidization (Duellman & Veloso 1977). *Pleurodema bibroni* is known from Uruguay and from the State of Rio Grande do Sul, Brazil (Braun 1973; Barrio 1977; Núñez *et al.* 2004), while *P. kriegi* is restricted to the “Sier-ras Grandes” mountains, in the Province of Córdoba, Argentina. The tadpole of *P. kriegi* was briefly described by Ceï (1980), but that of *P. bibroni* is still unknown.

Most species of *Pleurodema* are common components of the anurofaunas of different biomes, and can be seen in large aggregations during reproductive episodes (Fernández & Fernández 1921; Fernández 1927; Ceï 1962; Ceï 1980; Hödl 1992). Although *P. bibroni* was once a common species in southern and southeastern Uruguay (e.g.: Bell 1843; Cordero 1933; Barrio 1977; Gudynas 1989), as suggested by many historical records in museum collections (Núñez *et al.* 2004), it has become a rare frog in this country since the middle 1970's. It was considered a “Threatened” species in Uruguay by Maneyro and Langone (2001), and “Near threatened (NT)” by the Global Amphibian Assessment (IUCN 2008). On the other hand, *P. kriegi* was considered “Vulnerable” by di Tada *et al.* (1996) and Lavilla *et al.* (2000) and “Near threatened (NT)” by the Global Amphibian Assessment (IUCN 2008).

In this paper, we describe the tadpole of *Pleurodema bibroni* based on samples recently collected in south-eastern Uruguay and redescribe the tadpole of *P. kriegi* and their advertisement calls to allow a proper comparison between these closely related species. We also review the geographic distribution and conservation status of both species, and provide some notes on natural history of these and other species of *Pleurodema*.

Material and methods

Specimens used in the descriptions, examined for comparison or otherwise referred in this study are deposited in the following institutions: MACN (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina); CENAI (Centro Nacional de Investigaciones Iológicas, deposited at MACN); MCN (Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, State of Rio Grande do Sul, Brazil); MCNM (Museo de Ciencias Naturales, Madrid, España); MLP A. (Colección de Anfibios, Museo de La Plata, La Plata, Argentina); MLP DB. (Diego Baldo Collection, deposited at Museo de La Plata); MNHN (Museo Nacional de Historia Natural de Montevideo, Uruguay; currently Museo Nacional de Historia Natural y Antropología); and ZVCB (Colección de Batracios, Sección Zoología Vertebrados, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay).

The following samples were used for tadpole descriptions: *Pleurodema bibroni* (MNHN 7167), $N = 10$, stages 33–36, collected at Barra de Valizas, Department of Rocha, Uruguay ($34^{\circ}20'S$; $53^{\circ}48'W$; 2 m a.s.l.), on 3 June 2007; *Pleurodema kriegi* (MLP DB 5059), $N = 9$, stages 30–36, collected at Parador El Cóndor, Pampa de Achala, Province of Córdoba, Argentina ($31^{\circ}37'47''S$; $64^{\circ}42'50''W$; 1850 m a.s.l.), on 27 December 2005. Species identity was confirmed with some individuals reared through metamorphosis (*P. bibroni*: MNHN 7168; *P. kriegi*: juveniles not preserved).

Morphological terminology follows Altig and McDiarmid (1999a). Tadpole developmental stages follow Gosner (1960) staging table. The oral disc was stained with a 1% methyl blue solution for proper visualization of the marginal papillae. Drawings were made using a stereoscopic microscope Nikon SMZ–10 with camera

lucida. Tadpoles were measured to the nearest 0.1 millimeter using an ocular micrometer in the stereoscopic microscope, except for total length, which was measured with calipers. Twenty three morphometric variables were registered, eight of them according to Altig and McDiarmid (1999a): total length (TL), body length (BL), tail length (TAL), maximum tail height (MTH), tail muscle height (TMH), tail muscle width (TMW), internarial distance (IND, modified from Altig & McDiarmid 1999a: measured between the internal edges of narial apertures), and interorbital distance (IOD, modified from Altig & McDiarmid 1999a: measured between the external edges of pupils). Other measurements follow Lavilla and Scrocchi (1986): body maximum width (BMW), body width at nostrils (BWN), body width at eye level (BWE), body maximum height (BMH), rostro-spiracular distance (RSD, measured horizontally from the tip of the snout to the posterior edge of the spiracular tube), fronto-nasal distance (FN, from the tip of the snout to the anterior edge of nostrils), eye-nostril distance (END, from the posterior edge of nares to the anterior edge of eyes), nostril major axis (N), eye diameter (E), extra nasal distance (EN, distance between external edges of nares), intraocular distance (IO, distance between interior edges of eyes), oral disc width (OD), and dorsal gap length (DG). Additionally, dorsal fin height (DFH) and ventral fin height (VFH) were measured at a position coincident with MTH.

We analyzed 31 advertisement calls of *Pleurodema bibroni* from three males and 10 calls of *P. kriegi* from four males (Table 1). The calls were recorded with a Sony TCM 5000 tape recorder and Sure microphone in the case of *P. bibroni*, and with Panasonic RQ-L309 tape recorder equipped with a GBR EM-2000A unidirectional microphone in *P. kriegi*. We also included the recording of *P. kriegi* available in Straneck *et al.* (1993). Recordings were digitized with a Roland UA-100 analogical-digital converter at a sample-rate of 44.1 kHz (16 bit) and analyzed with the software Sound Forge 8.0 (Sony Pictures Digital Inc.). We measured the following temporal parameters from the waveform: call duration, number of notes per call, note duration, inter-note interval, number of pulses per note, and pulse duration. We also calculated the note rate (ratio between number of notes and call duration) and the pulse rate (ratio between number of pulses and call duration). We measured the parameters defining the structure of a single note on a selected sample of 10 notes per call, from three calls of each recorded individual. Mean power spectra of those selected notes were calculated with a FFT of 512 points, overlap 93%, Hamming's sampling window and sonogram resolution of 10000 samplings. From the spectra we measured the dominant frequency. Terminology for advertisement call descriptions follows Heyer *et al.* (1990).

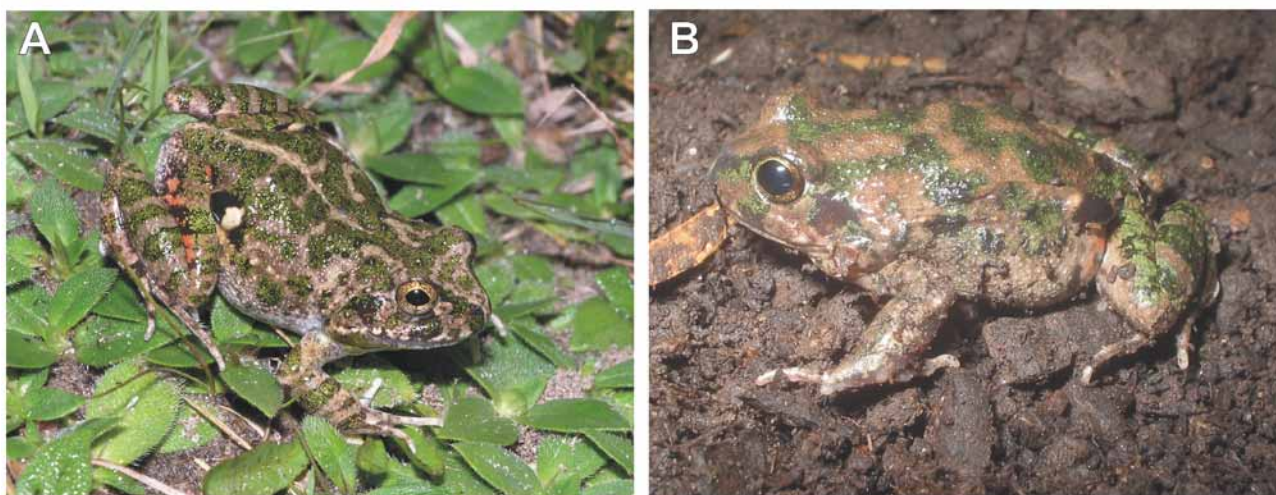


FIGURE 1. (A) *Pleurodema bibroni*, Barra de Valizas, Department of Rocha, Uruguay. (B) *Pleurodema kriegi* (MLP. A 3528), Pampa de Achala, Province of Córdoba, Argentina.

TABLE 1. Advertisement calls of *Pleurodema bibroni* and *P. kriegi* analyzed in this study.

Species	Voucher specimen	Record site location (coordinates, altitude)	Date	Hour	Air T (°C)	Water T (°C)
<i>P. bibroni</i>	MNHN 7169	Barra de Valizas, Rocha, Uruguay (34°20'S; 53°48'W; 2 m a.s.l.)	6 May 2007	20:30	14	16
<i>P. bibroni</i>	MNHN 7170	Barra de Valizas, Rocha, Uruguay	6 May 2007	21:50	12	15
<i>P. bibroni</i>	MNHN 7352	Cerro Verde, Rocha, Uruguay (33°56'S; 53°32'W; 25 m a.s.l.)	22 June 2008	18:45	6	12
<i>P. kriegi</i>	MLP A. 3526	Pampa de Achala, San Alberto, Córdoba, Argentina	11 March 2003	22:15	8.5	11
<i>P. kriegi</i>	MLP A. 4760	Parque Nacional Quebrada del Condorito, Córdoba, Argentina (31°38'S; 64°42'W; 1861 m a.s.l.)	9 February 2006	22:13	14	20
<i>P. kriegi</i>	MACN 33441 (Straneck <i>et al.</i> , 1993)	Pampa de Achala, San Alberto, Córdoba, Argentina (2200 m a.s.l.)	16 October 1984	20:10	17	—
<i>P. kriegi</i>	Not vouchered (Straneck <i>et al.</i> , 1993)	Pampa de Achala, San Alberto, Córdoba, Argentina	16 October 1984	20:10	17	—

Results

Tadpole descriptions

Pleurodema bibroni Tschudi

(Fig. 2A, 2B)

At stages 33–36 mean total length is 35.4 ± 3.1 mm, the body is globose, slightly depressed (mean BMH/BMW = 0.94 ± 0.05). The body length is about 40% of total length (mean BL/TL = 0.42 ± 0.05), body shape is oval in dorsal view with a constriction behind the cephalic region, and the maximum width is placed at the posterior portion of the head or sometimes at the abdominal region. The ventral contour is slightly convex in lateral view; the dorsal contour slopes from the anterior edge of the oral disc to the posterior border of the eyes, and straight from the eyes to the origin of the dorsal fin. The snout is rounded in dorsal view and truncated in lateral view. The nostrils are rounded and placed in a depression; they are dorsolaterally positioned (mean EN/BWN = 0.38 ± 0.04), slightly closer to the eyes than to the tip of snout (mean FN/END = 1.12 ± 0.15) and more visible dorsally than laterally. Their openings are directed dorsally and slightly to the front and present a slightly elevated marginal fleshy rim. The eyes are small (mean E/BWE = 0.18 ± 0.02), dorsally located (mean IOD/BWE = 0.61 ± 0.04), dorsolaterally oriented, and not visible in ventral view. The pineal end organ is visible as a less pigmented spot between the anterior edges of the eyes. The spiracle is single, lateral, sinistral, short, posterodorsally directed, and placed in the second third of the body (mean RSD/BL = 0.58 ± 0.06). The spiracle inner wall is fused to body wall except for the very distal end which folds to delimit the spiracle opening. Spiracle opening is oval, placed below body midline, being its diameter smaller than the tube diameter; it is visible laterally and sometimes also ventrally. The intestinal ansa was observed displaced to the left behind the spiracle opening in most specimens, or approximately at the center of the abdominal ventral surface in the others. The vent tube is medial; it starts at midline but opens to the left in 70% of the examined specimens or to the right in the others, due to a variable folding of the ventral fin at its origin. A medium sized saccular structure underlies the limb buds and encloses the vent tube. The tail is medium-sized (mean TAL/TL = 0.58 ± 0.05), and both fins are as high as the body height (mean MTH/BMH = 0.99 ± 0.10). The

dorsal fin originates on the body-tail junction and its free margin is regularly curved, convex, with the maximum height at the middle length of the tail. It is slightly higher than the ventral fin (mean DFH/VFH = 1.1 ± 0.1). Ventral fin originates from the saccular structure and presents a smoothly convex free margin. The tail axis is straight, and the tail smoothly stretches towards the tip in its last half, ending bluntly rounded. The tail

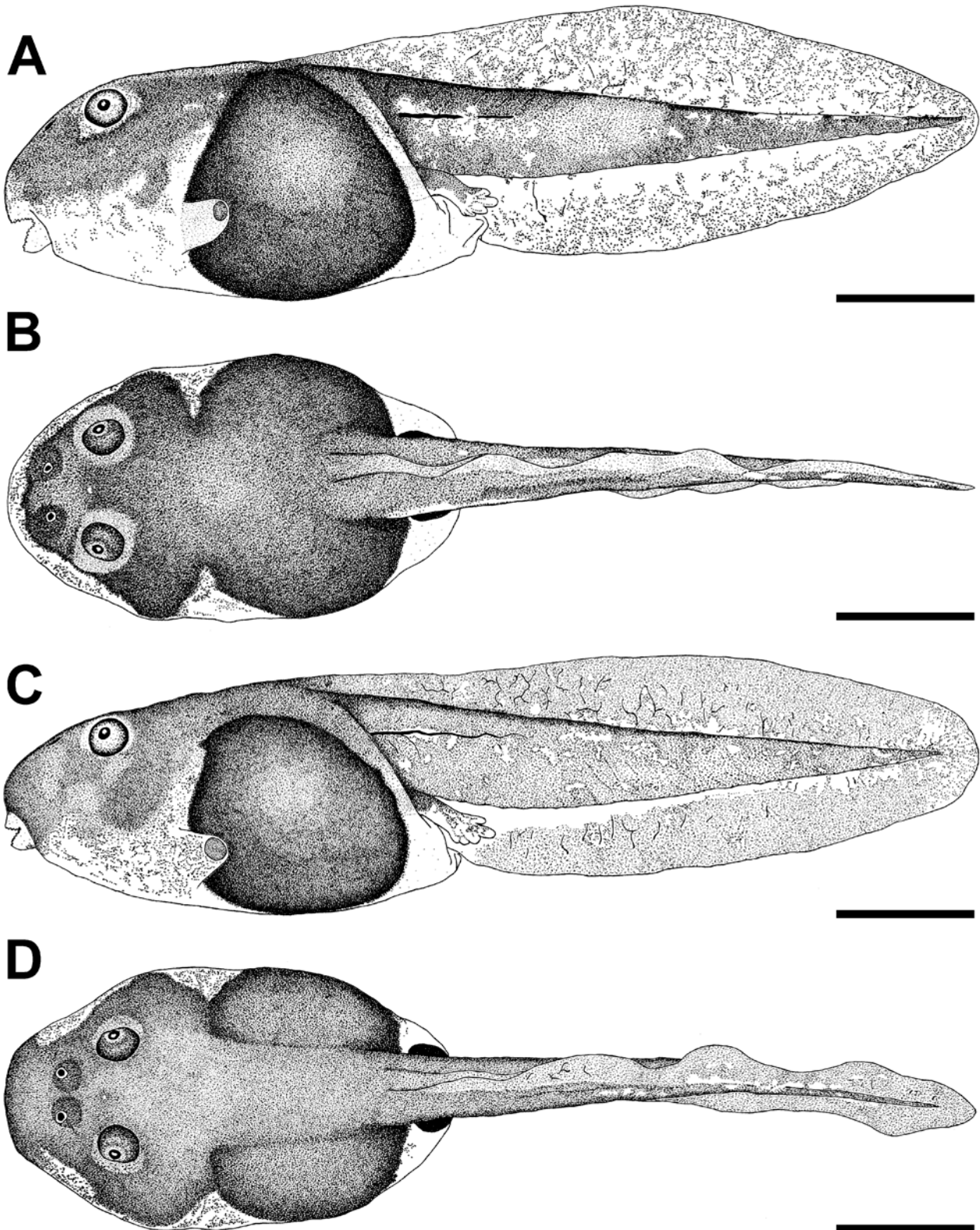


FIGURE 2. Tadpole of *Pleurodema bibroni* (stage 35) from Barra de Valizas, Department of Rocha, Uruguay (MNHN 7167), in lateral (A) and dorsal (B) views, and tadpole of *Pleurodema kriegi* (stage 36) from Parador El Cóndor, Pampa de Achala, Province of Córdoba, Argentina (MLP DB 5059), in lateral (C) and dorsal (D) views. Scale bars = 5 mm.

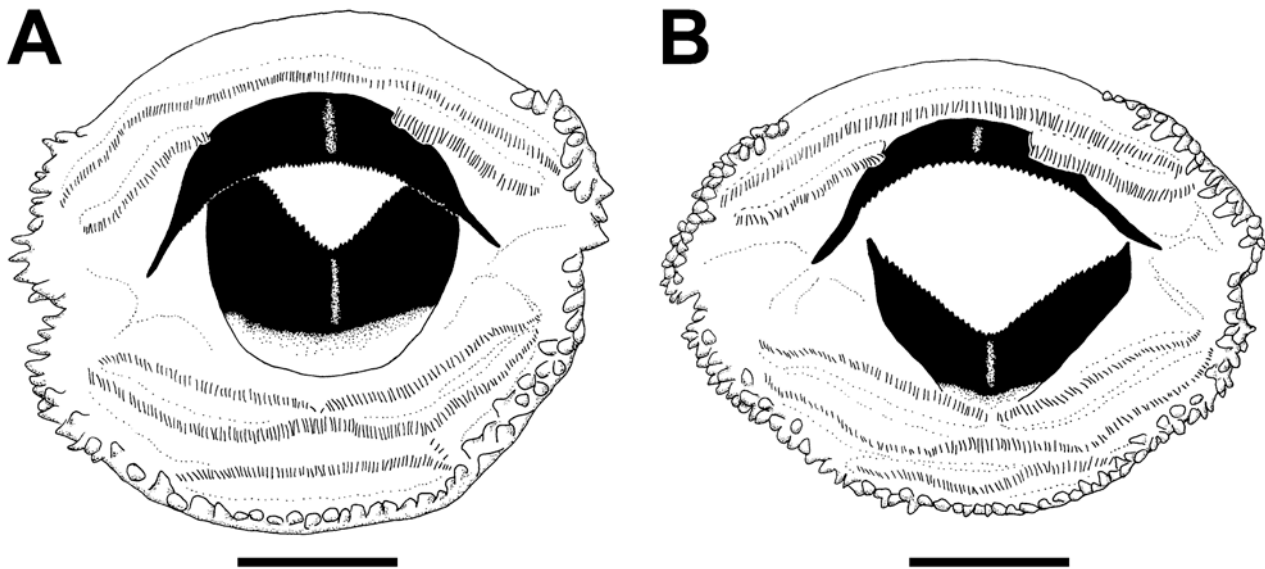


FIGURE 3. (A) Oral disc of a tadpole of *Pleurodema bibroni* (stage 35) from Barra de Valizas, Department of Rocha, Uruguay (MNHN 7167). (B) Oral disc of a tadpole of *Pleurodema kriegi* (stage 36) from Parador El Cóndor, Pampa de Achala, Province of Córdoba, Argentina (MLP DB 5059). Scale bars = 1 mm.

musculature does not reach the end of the tail, and myomeres are more visible in the proximal half. Neuro-masts are very small and hardly visible, even with the help of magnification and after staining the tegument with methylene blue. The oral disc (Fig. 3A) is anteroventral, medium sized (mean OD/BMW = 0.43 ± 0.01), laterally emarginated, and has a large dorsal gap (DG/OD = 0.63 ± 0.04). Marginal papillae are arranged in a single alternated or double row, except in the ventral region in which the row is single for approximately the length of P3. Papillae are simple, small and longer than wide, sub-conical. Sub-marginal papillae are usually absent, but one specimen presents one papilla in the supra-angular region. Jaw sheaths very robust, finely serrated, heavily pigmented distally for about 2/3 to 1/2 their length. The free margin of the upper jaw sheath is widely arch shaped, whereas that of the lower jaw sheath is V-shaped. Labial tooth row formula (LTRF) is 2(2)/3(1). The gap in A2 is wide, almost one third the length of the row, and the anterior edge of the upper jaw sheath is placed within it. The gap in P1 is narrow. The length of P3 is about half the length of the other rows. In two specimens there is a small non medial gap in P2; another specimen presents P2 with a branch fused to P3. The tadpole of *P. bibroni* belongs to the benthic ecomorphological guild (section II: A: 1) of McDiarmid and Altig (1999) as revised from Altig and Johnston (1989). In tadpoles of *P. bibroni* the developing lumbar gland can be observed up from stage 41 as a small dark spot (Fig. 5C).

Measurements (in mm): Mean and Standard Deviation (range given in parentheses): TL = 35.4 ± 3.1 (30.0–40.2); BL = 14.8 ± 1.8 (12.6–19.3); TAL = 20.5 ± 3.0 (14.5–24.4); MTH = 8.6 ± 0.6 (7.6–9.4); TMH = 3.1 ± 0.3 (2.7–3.6); TMW = 2.9 ± 0.5 (2.3–3.8); IND = 1.3 ± 0.1 (1.3–1.5); IOD = 4.9 ± 0.3 (4.2–5.8); BMW = 9.3 ± 0.7 (7.9–10.5); BWN = 5.6 ± 0.7 (4.4–6.7); BWE = 8.0 ± 0.7 (6.8–9.2); BMH = 8.7 ± 0.7 (7.6–9.8); RSD = 8.6 ± 0.6 (7.9–10.0); FN = 1.7 ± 0.3 (1.3–2.1); END = 1.5 ± 0.1 (1.3–1.7); N = 0.3 ± 0.1 (0.2–0.5); E = 1.4 ± 0.1 (1.3–1.6); EN = 2.1 ± 0.1 (1.9–2.2); IO = 2.7 ± 0.2 (2.3–3.0); OD = 4.0 ± 0.2 (3.5–4.3); DG = 2.5 ± 0.2 (2.3–2.8); DFH = 2.1 ± 0.1 (1.9–2.3); VFH = 2.0 ± 0.2 (1.6–2.2).

Coloration in life: The body, cephalic region and snout are brownish in dorsal view, with a more intensely pigmented area around the nostrils and a less pigmented one around the eyes. Green and yellowish shines are noticeable with magnification. The pineal end organ is visible between the anterior edges of the orbits as a less pigmented spot. The cephalic region, body and upper half of the abdomen are brownish in lateral view, also with green and yellowish shines. The ventral region is silver with copper shines, the gut is not visible. The gular and branchial regions are transparent, allowing the visualization of the branchial apparatus,

heart and head musculature. The dorsal surface of the caudal musculature is brownish along its first third but fades distally; the rest of the tail is light brown with scarce small blotches of melanophores; the caudal musculature in ventral view is pale. Fins are almost transparent, with a fine dark reticulation. Abdominal saccular structure transparent.

Coloration in preservative: Body dark brown in dorsal view, with some less pigmented regions around the eyes. Perinasal regions heavily pigmented. Pineal end organ visible. In lateral view, body dark brown, with the abdomen almost black. Gular and branchial regions and saccular structure transparent. Caudal musculature dark brown, less pigmented at midline for the proximal third. Fins irregularly pigmented, except close to the insertion in the caudal musculature. Caudal blood vessels dark.

Pleurodema kriegi (Müller)

(Fig. 2C, 2D)

At stage 36 mean total length is 36.4 ± 1.3 mm, body is globose, depressed (mean BMH/BMW = 0.85 ± 0.04). The body length is about 40% of total length (mean BL/TL = 0.42 ± 0.01), body shape is oval in dorsal view with a constriction behind the cephalic region and the maximum width is placed at the posterior portion of the head, behind the eyes. Ventral contour is slightly convex in lateral view and dorsal contour is rounded, uniformly convex from the anterior edge of the oral disc to the eyes, and then slightly convex to the beginning of the dorsal fin. The snout is truncated, trapezoidal in dorsal view, and rounded in lateral view. The nostrils are rounded and placed in a depression; they are dorsolaterally located (mean EN/BWN = 0.33 ± 0.02), slightly closer to the eyes than to the tip of the snout (mean FN/END = 1.03 ± 0.07), more visible dorsally than laterally. Their openings are directed dorsally and slightly to the front and present a slightly elevated marginal fleshy rim. The eyes are small (E/BWE = 0.17 ± 0.01) and dorsally located (mean IOD/BWE = 0.56 ± 0.03), dorsolaterally oriented, and not visible in ventral view. The pineal end organ is visible as a less pigmented spot between the anterior edges of the eyes. The spiracle is single, lateral, sinistral, short, posterodorsally directed, and placed in the second third of the body (mean RSD/BL = 0.61 ± 0.05). The spiracle inner wall is fused to the body wall except for the very distal end, which folds to delimit the spiracle opening. Spiracle opening is oval, placed below body midline, being its diameter smaller than the tube diameter; it is visible laterally and ventrally. The intestinal ansa was observed approximately at the center of the abdominal ventral surface or displaced to the left behind the spiracle opening. The vent tube is medial; it starts at midline but opens to the right in 60% of the examined specimens or to the left in the others, due to a variable folding of the ventral fin at its origin. A medium-sized saccular structure underlies the limb buds and encloses the vent tube. The tail is medium-sized (mean TAL/TL = 0.58 ± 0.01), and both fins are slightly shallower than body height (mean MTH/BMH = 0.94 ± 0.06). The dorsal fin originates on the body-tail junction and its free margin is regularly curved, convex, with the maximum height at the middle length of the tail. It is as high as the ventral fin (mean DFH/VFH = 1.0 ± 0.05), which originates from the saccular structure, and presents a smoothly convex free margin. The tail axis is straight, and the tail smoothly stretches towards the tip in its last half, ending bluntly rounded. The tail musculature does not reach the tail end, and myomeres are more visible in the proximal half. Neuromasts are very small and hardly visible, even with the help of magnification and after staining the tegument with methylene blue. The oral disc (Fig. 3B) is anteroventral, medium-sized (mean OD/BMW = 0.41 ± 0.02), laterally emarginated, and has a large dorsal gap (mean DG/OD = 0.56 ± 0.04). Marginal papillae are arranged in a single alternated or double row, except in the ventral region in which the row is single for approximately the length of P3. Papillae are simple, small and longer than wide, sub-conical. Sub-marginal papillae are absent. Jaw sheaths very robust, finely serrated, heavily pigmented distally for about 2/3 to 1/2 their length. The free margin of the upper jaw sheath is widely arch shaped, whereas that of the lower jaw sheath is V-shaped. Labial tooth row formula is 2(2)/3(1). The gap in A2 is wide, almost one third the length

of the row, and the anterior edge of the upper jaw sheath is placed within it. The gap in P1 is narrow. The length of P3 is about half the length of the other rows. The tadpole of *P. kriegi* belongs to the benthic ecomorphological guild (section II: A: 1) of McDiarmid and Altig (1999) as revised from Altig and Johnston (1989).

Variation: Four additional specimens from the same lot, stages 30–31, showed no remarkable variation. The vent tube opened to the left or to the right in equal numbers. One specimen at stage 30 showed a very small ventral gap in the marginal row of papillae. Tadpoles from lot MLP A. 4729 (stages 32–38) differed from those of MLP DB 5059 by having a more rounded snout in dorsal view and by lacking an evident pineal organ. The vent tube opens to the right in seven specimens, while it opens to the left and medially in one specimen each. LTRF 2(2)/3(1) in eight specimens (four of them show non-medial small gaps in P2 and P3) and 2(2)/3 in one specimen at stage 34.

Measurements (in mm): Mean and Standard Deviation (range given in parentheses): TL = 36.4 ± 1.3 (35.4–38.2); BL = 15.1 ± 0.5 (14.6–15.8); TAL = 21.3 ± 1.1 (20.0–22.4); MTH = 8.0 ± 0.4 (7.6–8.5); TMH = 3.2 ± 0.1 (3.0–3.3); TMW = 2.8 ± 0.1 (2.6–2.9); IND = 1.2 ± 0.1 (1.2–1.3); IOD = 4.9 ± 0.1 (4.7–5.0); BMW = 10.0 ± 0.3 (9.6–10.5); BWN = 6.2 ± 0.2 (5.9–6.4); BWE = 8.7 ± 0.3 (8.2–9.1); BMH = 8.5 ± 0.5 (7.9–9.2); RSD = 9.2 ± 0.5 (8.6–9.7); FN = 1.8 ± 0.2 (1.5–2.0); END = 1.7 ± 0.2 (1.5–2.0); N = 0.3 ± 0.1 (0.2–0.3); E = 1.5 ± 0.1 (1.4–1.5); EN = 2.0 ± 0.1 (1.9–2.2); IO = 2.6 ± 0.1 (2.6–2.7); OD = 4.1 ± 0.1 (4.0–4.3); DG = 2.3 ± 0.1 (2.2–2.5); DFH = 1.7 ± 0.2 (1.4–1.9); VFH = 1.7 ± 0.2 (1.5–1.9).

Coloration in preservative: Body dark brown in dorsal view, with some less pigmented regions around the eyes. Perinasal regions heavily pigmented. In lateral view, body dark brown and abdomen almost black. Branchial region almost transparent. Gular region and saccular structure transparent. Caudal musculature is dark brown and fins are finely reticulated, except for the region of ventral fin insertion at caudal musculature. Caudal blood vessels dark.

Advertisement calls

The advertisement call of both species (Fig. 4) is a relatively long trill of pulsed notes. Each note is composed of three pulses, the second one having the highest amplitude. Calls are not frequency modulated. Amplitude of calls rises gradually in the first 0.9–5.0 s and then remains constant up to the end of the call. The end is always abrupt. Calls are emitted sporadically, and the inter-call interval is highly variable, sometimes lasting several minutes. The parameters used to describe the temporal and spectral structures of the call strongly overlap between species and are shown in Table 2.

Natural history

Study sites of *Pleurodema bibroni* in the Department of Rocha were surveyed by the authors during February and March 2007 (during the Austral summer), but this species was not detected. Choruses formed by hundreds of individuals were first heard in the autumn, during visits on 1 and 6 May 2007. Calling activity started right after sunset. Males called with their bodies submerged in areas with low grass at the shallow flooded margins of ponds (Fig. 5A). Other species vocalizing in the same ponds were *Hypsiboas pulchellus* (Duméril & Bibron), *Odontophrynus maisuma* Rosset and *Physalaemus henselii* (Peters). Two amplexant pairs of *P. bibroni* were observed at night on 6 May 2007, floating in the deepest part of large ponds (Fig. 5B). Amplexus was axilar. Tadpoles of *P. bibroni* at different developmental stages were collected on 3 June 2007 and 23 September 2007 in scarcely vegetated temporary ponds with clear and standing water, about 20 to 40 cm deep (Fig. 6A and 6B). They were collected along with tadpoles of *H. pulchellus*, *P. henselii*, *O. maisuma*, *Pseudis minuta* Günther and *Scinax squalirostris* (Lutz). In a survey carried out on 21 and 22 June 2008, we detected

calling activity of *P. bibroni* at night, on a strip of flooded grasslands approximately 25 km long, between the Atlantic shoreline and the wetlands of Laguna de Castillos in the Department of Rocha, including localities close to Cabo Polonio, Barra de Valizas and Aguas Dulces. In addition, calling males were heard and observed near Cerro Verde, Department of Rocha, on the same dates.

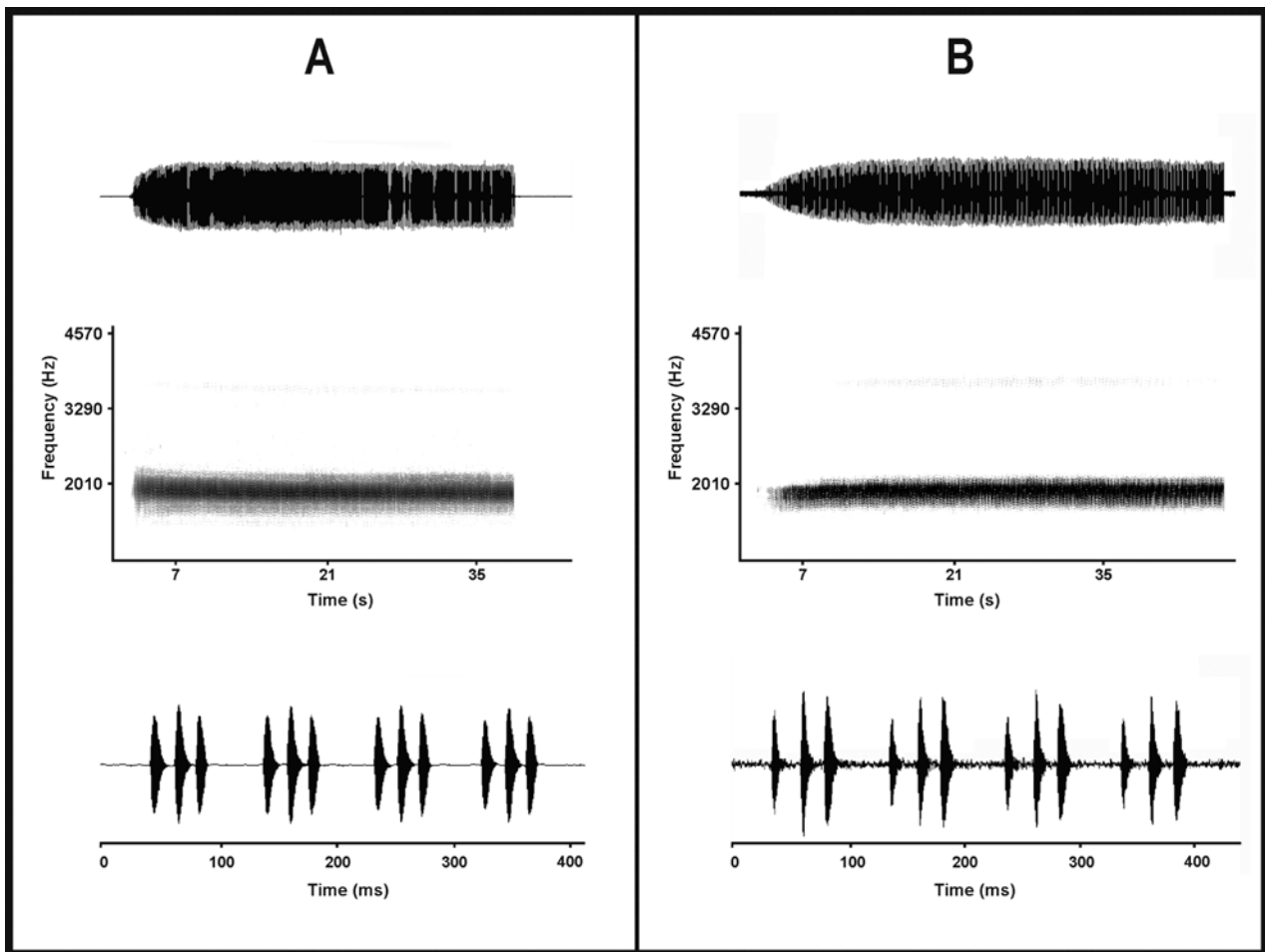


FIGURE 4. Advertisement call of *Pleurodema bibroni* (A) from Barra de Valizas, Department of Rocha, Uruguay (MNHN 7169, water temperature 16°C, air temperature 14°C), and *Pleurodema kriegi* (B) from Pampa de Achala, Province of Córdoba, Argentina (MLP. A 3526, water temperature 11°C, air temperature 8.5°C). Oscillogram (top) and sonogram (center) of a single call, and oscillogram of four notes (bottom).

We found *Pleurodema kriegi* in the high grassland of Pampa de Achala, Province of Córdoba, Argentina (Fig. 6C), an area described by Cei (1972) and Barrio (1977). On 11 March 2003 and 9 February 2007 we heard some males calling from temporary ponds starting in the evening. Males were hidden among herbaceous vegetation and were hard to find; they stopped calling when we came close to the ponds. One male was calling from a hidden position into a small natural depression at the edge of a pond and another one was calling floating in the water, under an emerging bush of herbaceous vegetation. Several adults and juveniles were found during day surveys under medium to large sized stones. Tadpoles were collected or observed on 27 December 2005, 10 February 2006 and 17 November 2007 in temporary ponds about 30 cm deep, formed on a granitic rock outcrop, surrounded by herbaceous vegetation (Fig. 6D); tadpoles of no other species were found in the same ponds. Other sympatric anurans were *Hypsiboas cordobae* (Barrio) and *Odontophrynus achalensis* Di Tada, Barla, Martori and Cei at Parque Nacional Quebrada del Condorito and “Parador El Cóndor” (both in Pampa de Achala), while *Leptodactylus gracilis* (Duméril & Bibron) and *Rhinella achalensis* (Cei) are sympatric in “Pampa de San Luis” (Y. Arzamendia & J. Baldo, pers. comm. to D. Baldo).

TABLE 2. Characteristics of the advertisement calls of *Pleurodema bibroni* (Department of Rocha, Uruguay) and *P. kriegi* (Province of Córdoba, Argentina). Values are mean \pm SD, range given in parentheses.

	Species	
	<i>Pleurodema bibroni</i>	<i>Pleurodema kriegi</i>
Number of specimens	3	4
Calls analyzed	31	10
Temporal structure		
Call duration (s)	18.67 \pm 15.04 (1.59–67.82)	20.49 \pm 15.71 (4.04–44.76)
Notes per call	188 \pm 149 (17–649)	215 \pm 157 (41–431)
Note duration (s)	0.049 \pm 0.004 (0.044–0.058)	0.054 \pm 0.006 (0.042–0.062)
Internote interval (s)	0.048 \pm 0.005 (0.041–0.058)	0.036 \pm 0.008 (0.024–0.051)
Pulses per note	3	3
First pulse duration (s)	0.011 \pm 0.001 (0.008–0.013)	0.009 \pm 0.001 (0.007–0.013)
Second pulse duration (s)	0.011 \pm 0.001 (0.009–0.013)	0.010 \pm 0.001 (0.007–0.012)
Third pulse duration (s)	0.008 \pm 0.001 (0.006–0.011)	0.011 \pm 0.001 (0.008–0.013)
Note rate (notes/s)	10.4 \pm 0.7 (8.9–11.8)	10.6 \pm 1.3 (9.4–13.2)
Pulse rate (pulses/s)	31.3 \pm 2.0 (26.7–35.3)	31.7 \pm 3.9 (28.2–39.7)
Spectral structure		
Dominant frequency (Hz)	1960 \pm 105 (1816–2162)	1801 \pm 42 (1729–1877)

Calling males of *Pleurodema bibroni* are particularly wary. Once approached they usually stop calling and submerge remaining immobile among the vegetation, being thus very hard to detect. During day time some adult and subadult specimens were found at retreat sites under dead boles close to breeding ponds (up to five at the same site). Most of them were partially buried in sandy and scarcely humid soil, with their eyes above the ground. Once found, they remained immobile and the sand cover on their skin gave them great visual resemblance to the background. When forced to move or gently manipulated, a thin layer of sand particles remained stuck to their skin, maintaining the cryptic background-matching (Fig. 7A). Specimens found hidden among leaf litter and/or unburied by us, usually made quick attempts to bury into the sandy soil. Burrowing behavior was displayed by moving backwards into the ground, excavating with hind limbs. A few specimens found in retreat sites tried to escape by consecutive short leaps. Defensive encounter behavior was observed in some specimens. Death feigning was displayed by two specimens, who remained flaccid, immobile, with their limbs extended (Fig. 7B). A presumably intimidating encounter behavior (deimatic behavior) was displayed by specimens that were thoroughly manipulated: it consisted in elevating the pelvic region from the ground, arching the dorsum while keeping the head downwards, and puffing up the body. This posture resulted in exhibition of the eye-like lumbar glands and the orange-reddish flash coloration of the inguinal and hidden surfaces of the thighs towards the source of disturbance (Fig. 7C). When tactile stimuli were

applied by the observer from one side, the defensive posture was displayed tilting the body laterally to the same side (Fig. 7D). Similar intimidating exhibition of the prominent lumbar glands was also observed in specimens of *P. borellii* (Peracca), *P. bufoninum* Bell (Fig. 7E; note the white secretion of the lumbar glands), *P. kriegi* (Fig. 7F; with exhibition of flash orange coloration) and *P. thaul* (Fig. 7G). Although less evident, a similar behavior was observed in *P. tucumanum* Parker, a species which lacks externally visible lumbar glands (Fig. 7H).

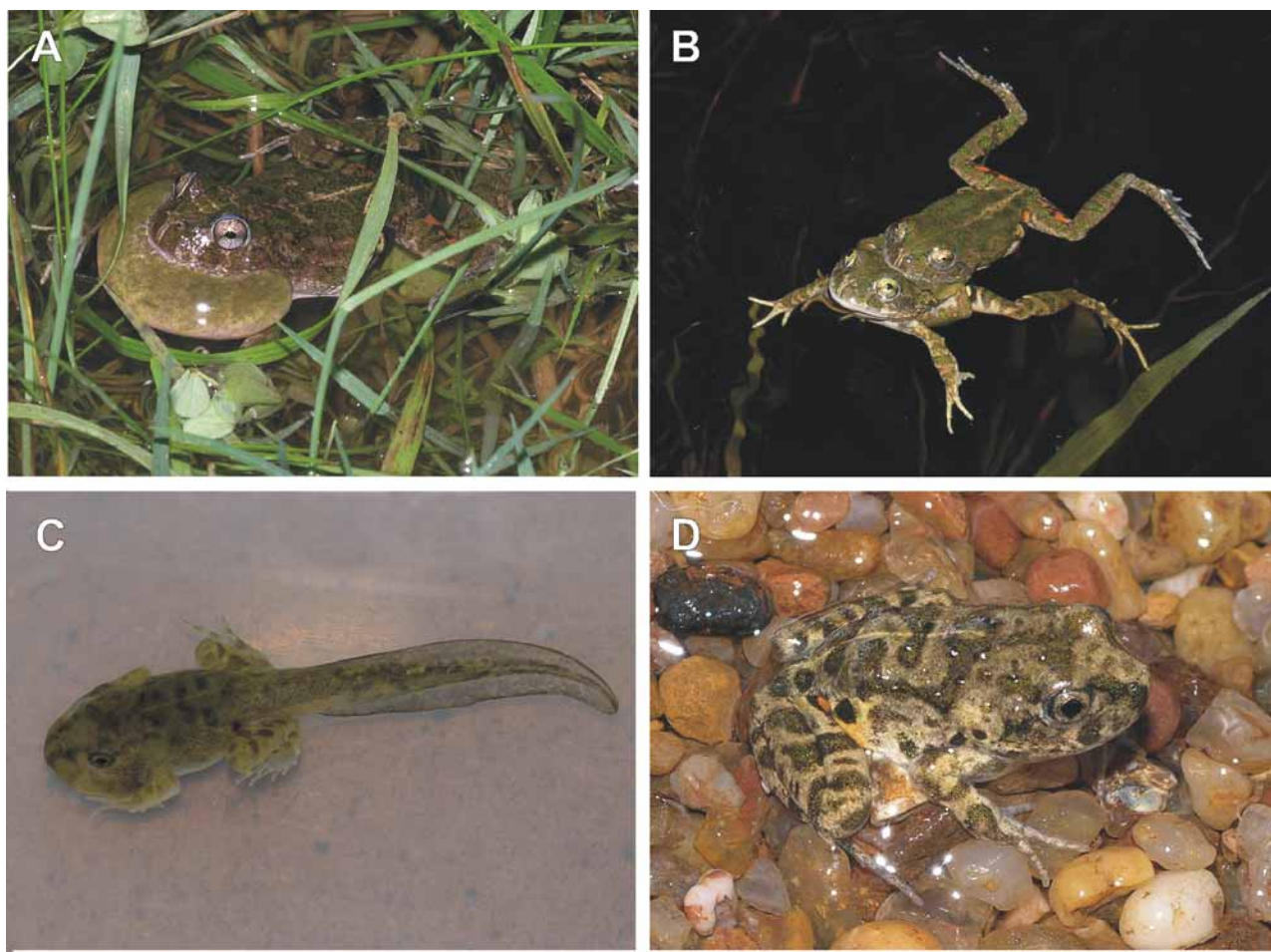


FIGURE 5. (A) *Pleurodema bibroni* male calling at the edge of a shallow pond, (B) couple in amplexus, floating on a pond, (C) metamorph *circa* stage 43, showing the developing lumbar gland, and (D) juvenile about one week after the end of metamorphosis.

Geographic distribution and habitat

The historical geographic range of *Pleurodema bibroni* shows an interesting disjunct distribution pattern (Fig. 8A). Most records are located in southern Uruguay, in the northeastern region of the State of Rio Grande do Sul, Brazil, and apparently also in the State of Santa Catarina, Brazil (Barrio 1977). Records of this species are spread through different ecoregions (WWF 2008). The Uruguayan populations of *P. bibroni* occur in the Uruguayan Savanna ecoregion, a biome characterized by a mosaic of savannas and submontane forests. Historical records in this country include three landscape units according to Evia and Gudynas (2000): “Praderas”, composed by inland grasslands that occupy much part of the country; “Serranías”, which consist of hilly landscapes of no more than 500 m altitude with rocky floors covered with grasslands and native forests; and “Arenales costeros del sur”, a narrow band of sandy habitats with psammophytic communities along the La

Plata River and the Atlantic coast. On the other hand, northernmost populations of *P. bibroni* occur in two different ecoregions, the Atlantic Coast Restingas (locality of Praia da Cidreira) and Araucaria Moist Forests. The former is characterized mainly by sandy dune habitats with shrubs, mangroves, small swamps, grasslands, and also inland forests. The second is mainly a subtropical montane forest landscape of coniferous and broad-leaved trees from around 500 m altitude to about 1600 m a.s.l. at Serra da Mantiqueira, with mean annual precipitation ranging from 1300 to 3000 mm (WWF 2008).

Populations of *Pleurodema bibroni* studied in this work inhabit psammophytic communities in coastal Uruguay located on cattle and sheep grazing lands that are close to the Atlantic Ocean (Fig. 6B). The habitats consisted of fixed sand dunes and the contiguous grasslands of sandy soils, or temporarily flooded grasslands with associations of palm trees [*Butia capitata* (Martins)] (Fig. 6A). Mean annual temperature and precipitation are about 16°C and 1000 mm respectively (PROBIDES 2000). The vegetation is predominantly herbaceous with exotic crops of *Pinus* spp. and *Eucalyptus* spp. in the surroundings; remnant areas with psammophytic coastal forest are present at the locality of Barra de Valizas.

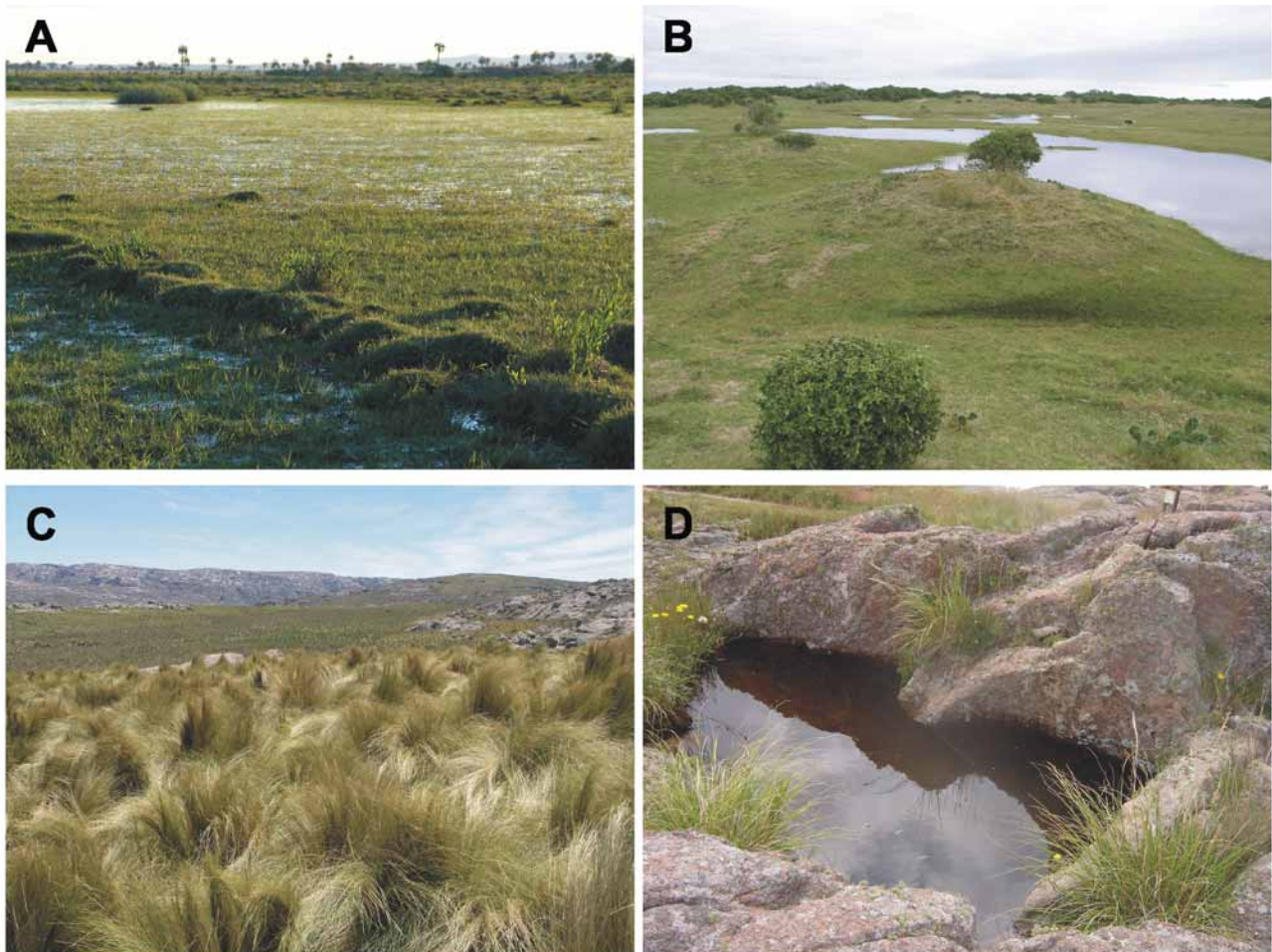


FIGURE 6. Habitat of *Pleurodema bibroni* at the Department of Rocha, Uruguay: (A) flooded grassland with palm trees (*Butia capitata*) and (B) sandy coastal grassland close to the Atlantic shoreline, where tadpoles were found. Habitat of *Pleurodema kriegii* at Pampa de Achala, Province of Córdoba, Argentina (C) and pond inhabited by tadpoles of this species (D).



FIGURE 7. Defensive behavior of some species of *Pleurodema*. *Pleurodema bibroni* (A) emerging from the ground covered with sand, (B) death feigning with limbs outstretched, (C) deimatic behavior, with exposition of lumbar glands and flash coloration and (D) body tilting towards a disturbing stimulus. Deimatic behavior in (E) *Pleurodema bufoninum* (note the white secretion of the prominent lumbar glands), (F) *Pleurodema kriegii*, and (G) *Pleurodema thaul*. (H) Defensive display in *Pleurodema tucumanum*, with elevation of the pelvic region.

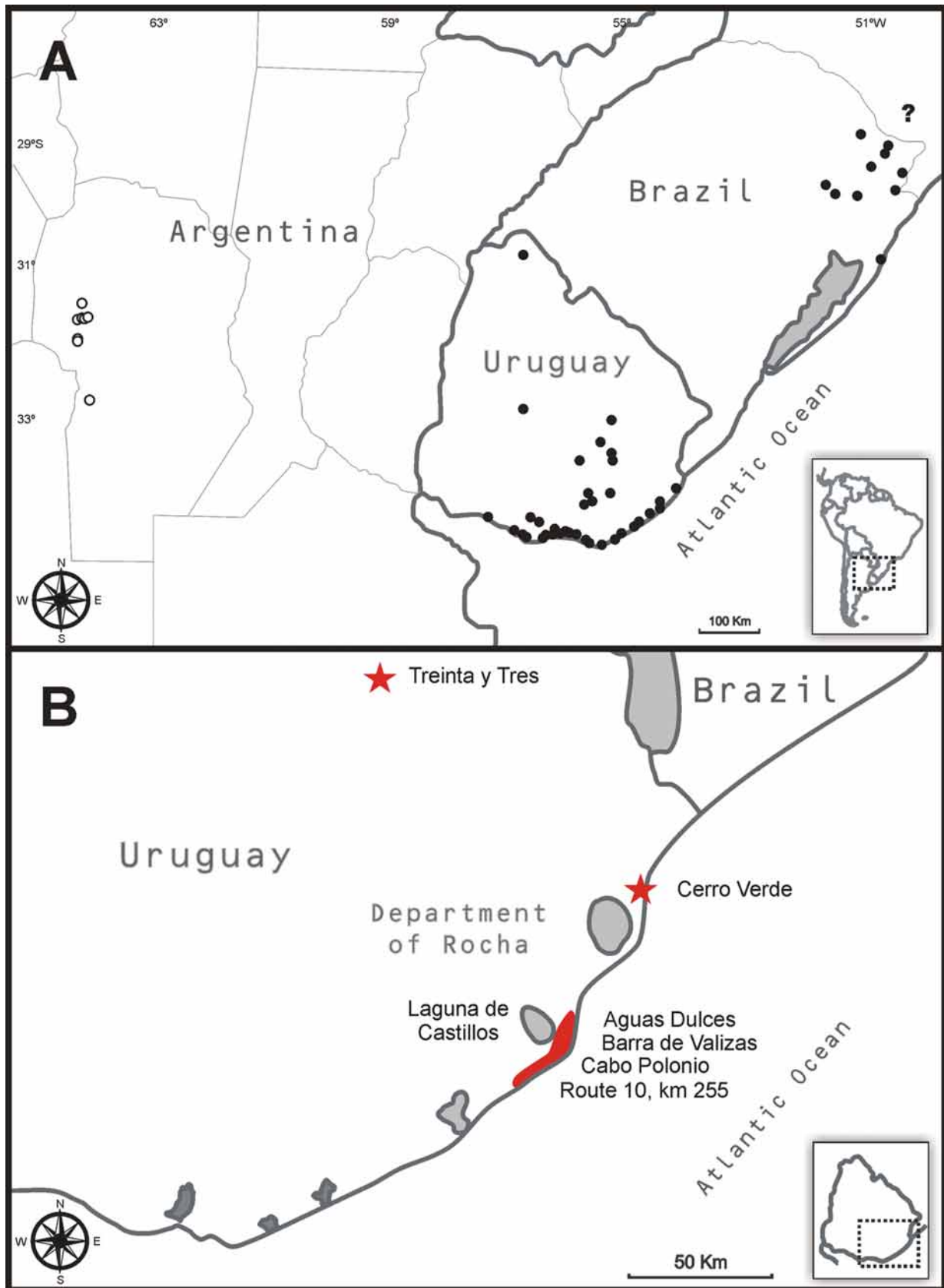


FIGURE 8. (A) Historical geographic distribution of *Pleurodema bibroni* (closed circles) and *Pleurodema kriegi* (open circles), based on specimens deposited in collections (see Appendix 1) and literature data (see text). (B) Current known distribution of *P. bibroni* in Uruguay, based on specimens collected in the last ten years deposited in collections (MNHN 7167–71, 7352–3, ZVCB 16137) and field work of the authors.

Pleurodema kriegi exclusively inhabits highlands in the mountain landscapes of the “Sierras Grandes” system, in the central-west part of the Province of Córdoba, Argentina. These mountains of precambrian origin are part of the Sierras Pampeanas orographic system, and occupy a band about 50–60 km wide with mountain chains oriented in a north-south direction over approximately 300 km (Ceí 1972; Miró 1999). *Pleurodema kriegi* was historically known only from a few localities in the highland grasslands of one of these chains, “Pampa de Achala”, between 1800 and 2500 m a.s.l. (Barrio 1977; Bridaroli & Di Tada 1994). This species was also found in other close systems of the Sierras Grandes, “Sierras de Comechingones” (Ávila & Priotto 1995; Ávila et al. 1999) and “Pampa de San Luis” (Y. Arzamendia and J. Baldo pers. comm.), at approximately 800 and between 1800 and 1900 m a.s.l. respectively. The climate in the region is cold-temperate with winter snowfall, a mean annual temperature of 8°C and an annual precipitation of about 800–900 mm distributed mainly in spring and summer, between October and April (Capitanelli 1979).

Discussion

Tadpole morphology

The striking similarity between the adults of *Pleurodema bibroni* and *P. kriegi* is also present between the tadpoles of both species. They are very similar, but subtle differences can be observed in the shape of the snout in dorsal view, which appears truncated and trapezoidal in profile in most *P. kriegi*, but rounded in *P. bibroni*. Nevertheless, the variation we observed between the studied samples of *P. kriegi* does not allow relying on this character to tell both species apart. Some interesting features are shared by the tadpoles of both species, as the presence of a medium-sized transparent saccular structure that underlies the hind limb buds and which covers them ventrally and encloses the vent tube. This structure was not reported previously for other species of *Pleurodema*, and is present in the tadpoles of stream dwelling larvae of some anurans (Lötters *et al.* 2005; and references therein). In those species, it is supposed to protect the hind limb buds from abrasion, but the tadpoles of all species of *Pleurodema* are pond dwelling. Its possible function and its presence in other species of the genus should be investigated. The presence of the pineal end organ, which is noticeable in the tadpoles of both species of *Pleurodema* described herein, has never been reported for any tadpole of the family Leiuperidae, as far as we are aware. Although not mentioned in the description, it seems to be present in the tadpole of *P. brachyops* (Cope), based on the illustration provided by Rada (1981). It was also observed in tadpoles of some species of the Bufonidae genera *Melanophryniscus* and *Rhinella* (Baldo & Basso 2004; Borteiro *et al.* 2006), and its presence has probably been overlooked in many taxa. The vent tube with a medial configuration, but with an opening variably directed to the right or to the left was also reported for *P. diplolister* (Peters) (Peixoto 1982). A similar case would be that of *P. thaul*, for which a sinistral vent tube was reported by Fernández (1927), Ceí (1962), and Ceí (1980), but it was reported as medial by Úbeda (1998). Within the oral disc features, an LTRF 2(2)/3(1) is present, in addition to *P. bibroni* and *P. kriegi*, in *P. brachyops* (although variable, 2(2)/3 is also present; León-Ochoa & Donoso-Barros 1969–1970; Rada 1981), *P. bufoninum* (Úbeda 1998; Weigandt *et al.* 2004), *P. diplolister* (Peixoto 1982) and *P. thaul* (Ceí 1980; Úbeda 1998). In all of these species, the gap in A2 is wide, and sometimes the anterior border of the upper jaw sheath is positioned between the divided ridge of this row, as it is remarkably noticeable in *P. bibroni*, *P. diplolister*, and *P. kriegi* (Peixoto 1982; present study). Conversely, the P1 medial gap is always very narrow, when present. An LTRF 2(2)/3 was reported for *P. brachyops* (León-Ochoa & Donoso-Barros 1969–1970; Rada 1981), *P. bufoninum* (Fernández 1927), *P. cinereum* (Fernández & Fernández 1921; Ceí 1980), *P. marmoratum* (Ceí 1980) and *P. thaul* (Fernández 1927; Ceí 1962). The length of P3 is usually equal to that of the other rows, but is reduced to about a half in *P. bibroni*, *P. diplolister* and *P. kriegi* (Ceí 1980; Peixoto 1982; present study). The tadpoles of *P. guayanae* Barrio, *P. nebulosum* (Burmeister) and *P. tucumanum* are unique in having an LTRF 2(2)/2. This feature and the almost ventrally positioned spiracle opening characterize the tadpoles of

these three related species (Cei 1980). We observed a very short ventral gap in the row of marginal papillae of one specimen of *P. kriegi*, which was also observed as an occasional feature in *P. bufoninum* and *P. thaul* (Fernández 1927). Additionally, Cei (1980) described a ventral gap in tadpoles of *P. marmoratum*, but Duellman and Veloso (1977) did not report it for tadpoles of any of the several species studied by them, which included *P. marmoratum*. The presence of a short ventral gap in the marginal row of papillae seems to be an alternative state of a polymorphic character rarely present in some species of *Pleurodema*, which is interesting due to its presence in some other species of Leiuperid frogs of the genera *Physalaemus*, *Pseudopaludicola* (see Kolenc *et al.* 2006; and references therein) and *Somuncuria* (Cei 1980). Outside Leiuperidae, it is considered a synapomorphy of Bufonidae (Frost *et al.* 2006), the basal family of Agastorophrynia, the sister group of Leiuperidae (Grant *et al.* 2006). A laterally emarginated oral disc and the presence of a wide dorsal gap in the row of marginal papillae is a common feature to all tadpoles of *Pleurodema* and also to the other genera included in Leiuperidae. Selected external morphological characters of *Pleurodema* larvae known to date are summarized in Table 3.

Advertisement calls

The advertisement calls of *Pleurodema bibroni* and *P. kriegi* are indistinguishable to the human ear and very similar in structure, temporal, and spectral parameters, as already noticed by Barrio (1977). Even in the laboratory, males of *P. bibroni* recently caught during reproductive activity started calling in response to recorded calls of *P. kriegi*. In our analysis, the spectral components of the notes of *P. kriegi* have slightly lower frequencies than those of *P. bibroni* (ranges of dominant frequencies overlap) and the internote interval is shorter in *P. kriegi* (although ranges also overlap). Selected parameters describing the advertisement calls of both species are shown in Table 4 and compared with information published about the other species of the genus. *Pleurodema bufoninum* Bell was not included because this species probably does not call (Cei 1980), and neither was *P. fuscomaculatum* because its vocalization is unknown.

Natural history

Our observations about reproduction in *Pleurodema bibroni* and *P. kriegi* are coincident with those of Barrio (1977). In addition to Uruguayan populations of *P. bibroni*, which breed mainly in autumn and winter, reproductive season of *P. thaul* was registered starting in July and August in Chile (local winter; Cei 1962) and from October to December in Argentina (local spring; Úbeda 1998). Cei (1980) suggested that *P. thaul* breeds irregularly all year round, while Díaz-Páez and Ortiz (2001) demonstrated the occurrence of a partially continuous reproductive cycle in females and a continuous one in males. *Pleurodema brachyops* also seem to have a continuous reproductive pattern through most of the year (León-Ochoa & Donoso-Barros 1969–1970). Other species of *Pleurodema*, including *P. kriegi*, are mostly spring and summer breeders (Barrio 1964a; Barrio 1977; Cei 1980; Peixoto 1982; Hödl 1992; Cardoso & Arzabe 1993; Straneck *et al.* 1993; Weigandt *et al.* 2004).

Burrowing behavior in *Pleurodema* was previously reported for *P. diplolister*, which excavates almost vertical burrows in sandy soil (Carvalho & Bailey 1948). Our observations in *P. bibroni* and *P. kriegi* are quite similar, and fall into the backward sliding burrowing mode (Davies & Withers 1993). Barrio (1977) mentioned the finding of Uruguayan specimens of *P. bibroni* under stones and sometimes buried in sand. This author also reported the observation of specimens of *P. kriegi* hidden under stones, sometimes several individuals together at the same retreat site similarly to our observations on *P. bibroni*. The cryptic appearance of the specimens of *P. bibroni* covered with sand after emerging from their underground retreats was also described for *P. brachyops* (Staton & Dixon 1977).

TABLE 3. Main morphological features of the known tadpoles of *Pleurodema*. Abbreviations: AV (anteroventral), BH (body height), BL (body length), BF (dorsal fin), DG (dorsal gap), DL (dorsolateral), OD (oral disc width), E (eye), FH (fin height), L (in life), LJS (lower jaw sheath), LTRF (labial tooth row formula, max. (maximum), MP (marginal papillae), P (in preservative), PD (posterodorsally), S (sinistral), SMP (Sub-marginal papillae), TBJ (tail-body junction), TL (total length), TAL (tail length), TM (tail musculature), TOS (tip of snout), TOT (tip of tail), UJS (upper jaw sheath), unk. (unknown), VF (ventral fin) VG (ventral gap), VL (ventrolateral), w/ (with).

Species	Reference	Body shape	Oral disc & Papillae	LTRF	Jaw sheaths	Spiracle	Vent tube opening	Nostrils	Dorsal Fin	Tail	Eyes	Pattern	Total length (mm) (stages)
<i>P. bibroni</i>	Present study	Oval, globose, slightly depressed, saccular structure at posterior end of abdomen	AV, OD = 43% BW, laterally emarginated, large DG = 63% OD, single or double row of MP	2(2)/3(1), A2 gap wide, P1 gap narrow, P3 about 1/2 the length of the other rows	Well developed and pigmented, finely serrated, UJS arch shaped, LJS V-shaped	Single, lateral, S, placed at 58% BL, below body midline	Medial, opening directed to the left or to the right	Small, rounded, DL, closer to E than to TOS, w/ marginal fleshy rim	DF as high as VF, origin on TBJ	TAL = 58% TL, TM not reaching TOT, end bluntly rounded	Dorsal, small	Dark brown, perinasal region heavily pigmented, gular and branchial regions transparent, abdomen golden	$\bar{X} = 35.4$ (33–36)
<i>P. borellii</i>	Fabrezi and Vera 1997	Ovoid	Wide DG, laterally emarginated	2(2)/3(1)	—	Lateral	—	—	DF as high as VF, origin on body	TAL \leq 2/3 TL, TOT acute	Dorsal	—	—
<i>P. brachyops</i>	León-Ochoa and Donoso-Barros 1969–1970	Sub-ovoid, depressed	AV, single row of MP, DG present	2(2)/3(1), sometimes 2(2)/3	Well developed, finely serrated	S	—	Between TOS and E	—	TOT rounded	—	—	35 (unk.)
<i>P. brachyops</i>	Rada 1981	Sub-ovoid, depressed	AV, OD < 50% BW, laterally emarginated, single row of MP, DG = 64% OD	2(2)/3, sometimes 2(2)/3(1)	Well developed, finely serrated	S, placed at 50% BL, on body midline	Medial	Dorsal, pigmented, between TOS and E, or closer to E than to TOS	DF as high as VF, not extending onto body	TAL shorter than 2/3 TL, TM not reaching TOT, end acutely rounded	DL	Yellowish, w/small dark flecks on dorsum, gular and branchial regions transparent, abdomen golden, tail scarcely pigmented	26.2 (36)
<i>P. bufoninum</i> ¹	Fernández 1927, Later reproduced by Cei 1962	Depressed	Laterally emarginated, single row of MP, some angular SMP, DG present, sometimes very short VG	2(2)/3, sometimes 2(2)/3(1) in late stages	—	S, slightly anterior to body mid-length	Medial, longer than free margin of VF	—	—	TAL = 50–60% TL, TOT rounded	—	P: uniformly pale gray-brown, tail almost unpigmented	Max. 58 (unk.)

TABLE 3. (continued)

Species	Reference	Body shape	Oral disc & Papillae	LTRF	Jaw sheaths	Spiracle	Vent tube opening	Nostrils	Dorsal Fin	Tail	Eyes	Pattern	Total length (mm) (stages)
<i>P. bufoninum</i>	Úbeda 1998	Elliptic, depressed, BL = 36-42% TL	AV, single or double row of MP, DG, sometimes some lateral SMP	2(2)/3(1), A2 gap wide	Well developed, finely serrated, LJS V-shaped	S, below body midline, at 55% BL	Medial, wider at opening	Rounded, rimmed, closer to E than to TOS	Origin at TBJ	TAL = 58-64% TL, TM not reaching TOT, TOT rounded	Almost lateral	Dark brown w/ golden shines. Ventrally brown, sometimes silvery. Fins less pigmented	Max. 58
<i>P. bufoninum</i>	Weigandt et al. 2004	Ovoid, elliptic in dorsal view, BH = BW	AV, laterally emarginated, OD = 41% BW, DG = 61% OD, single or double row of MP, SMP absent or scarce at angular regions	2(2)/3(1), A2 gap wide, P1 gap narrow	Well developed, w/ fine sharp serrations, UJS slightly curved, LJS angled	S, at 58% BL, on lower half of body	Medial, may widen toward opening	Circular, slightly rimmed, DL, closer to E than to TOS	Originates at fleshy crest at posterior part of trunk, DF height = VF one	61% TL, FH similar to BH, TM not reaching TOT, TOT rounded	DL, almost lateral	Dark brown w/ golden patches, ventrally brown w/ silver and gold patches. Fins translucent and less pigmented	63.7 (39)
<i>P. cinereum</i> ²	Fernández and Fernández 1921	Depressed	MP in single row, laterally emarginated, DG present	2(2)/3	UJS arched, LJS V-shaped	S	Medial	—	—	50-60% TL	—	—	Max. 38
<i>P. cinereum</i>	Cei 1980	Oval, slightly depressed	Laterally emarginated, single row of MP, DG present	2(2)/3	UJS widely arched, LJS U-shaped	S, latero-dorsally positioned	Medial	—	—	Relatively short tail w/ high fins	—	Body dark, fins transparent speckled w/ dark	—
<i>P. dipolister</i>	Peixoto 1982	Oval	AV, laterally emarginated, single row of MP, wide DG present	2(2)/3(1), P1 gap wide or narrow, P3 = 1/3-1/2 P2	UJS arch-shaped, LJS V-shaped, serrated	S, opening positioned at 2/3 BL	May open to the left, right or medially	Circular, closer to E than to TOS	Originates at TBJ, DF higher than VF	2/3 TL, slightly lower than BH, TOT acutely rounded	DL	V: olive, w/ gold and black dots, gular region unpigmented, abdomen white w/ golden shines. Fins scarcely pigmented	25 (36)
<i>P. guayanae</i>	Cei 1980	Oval, wide, somewhat depressed	Laterally emarginated, single row of MP, DG present,	2(2)/2	—	S, almost ventrally positioned	Medial	—	—	TAL less than 2/3 TL	—	Dorsum and TM speckled w/ dark spots and points	—

TABLE 3. (continued)

Species	Reference	Body shape	Oral disc & Papillae	LTRF	Jaw sheaths	Spiracle	Vent tube opening	Nostrils	Dorsal Fin	Tail	Eyes	Pattern	Total length (mm) (stages)
<i>P. kriegi</i>	Cei 1980	Oval, somewhat depressed	Laterally emarginated single row of MP, DG present	2(2)/3(1), P3 half the length of other rows	—	S, opening 70% BL	Medial	Closer to the E than to TOS	—	TAL Almost 2/3 of TL, TOT rounded	Large and dorsal	Dorsally brownish, belly light, darker blotches on fins and TM	—
<i>P. kriegi</i>	Present study	Oval, globose, slightly depressed, saccular structure at posterior end of abdomen	AV, OD = 41% BW, laterally emarginated, large DG = 56% OD, single or double row of MP	2(2)/3(1), A2 gap wide, P1 gap narrow, P3 about 1/2 the length of the other rows	Well developed and pigmented, finely serrated, UJS arch shaped, LJS V-shaped	Single, lateral, S, 61% BL, below body midline	Medial, opening directed to the right or to the left	Small, rounded, DL, slightly closer to E than to TOS, marginal fleshy rim	DF as high as VF, origin on TBJ	TAL = 58% TL, TM not reaching TOT, TOT bluntly rounded	Dorsal, small	P: Dark brown, perinasal region heavily pigmented, tail and branchial regions transparent, abdomen golden	$\bar{x} = 36.4$ (36)
<i>P. marmoratum</i>	Cei 1980	Ovoid, slightly depressed	Laterally emarginated, single row of MP, DG and VG present	2(2)/3	—	S, opening laterally on posterior half of body	Medial	Closer to the E than to TOS	—	TAL almost 2/3 TL, pointed tip	Large, latero-dorsally located	Dark grey, fins transparent, speckled w/ dark, ventrally paler	27-30 (38)
<i>P. nebulosum</i>	Fernández 1927	Depressed	Single row of big MP, DG present	2(2)/2	Serrated	S, on first half of body, ventrally visible	Medial, opening at level of VF free edge	—	Origin on body	TAL = 1/2 TL	—	—	31 (max. length)
<i>P. nebulosum</i>	Cei 1980	High and elongate	Single row of MP, DG present	2(2)/2, tooth rows weak and reduced	—	S, almost ventrally positioned	Medial	—	—	TAL less than 2/3 TL	—	Dorsum and TM pale	—
<i>P. thaul</i>	Fernández 1927	Depressed	Laterally emarginated, single or multiple rows of MP, SMP laterally. DG present, sometimes short VG	2(2)3; 2(2)/2 in late stages of development, last lower row as long as the others	Both serrated, those of LJS bigger than those of UJS	S, opens before body midlength	Opening slightly to the left, at level of VF free margin	—	—	TAL 1/2 or slightly longer than TL	—	—	37 (max. length)

TABLE 3. (continued)

Species	Reference	Body shape	Oral disc & Papillae	LTRF	Jaw sheaths	Spiracle	Vent tube opening	Nostrils	Dorsal Fin	Tail	Eyes	Pattern	Total length (mm) (stages)
<i>P. thaul</i>	Cei 1962	Ovoid, depressed	—	2(2)3; 2(2)2	—	S	S	—	—	—	—	Grey-brown, fins scarcely pigmented	—
<i>P. thaul</i>	Cei 1980	Wide and rounded	Laterally emarginated, variable series of MP, DG present, AV, laterally emarginated, double row of MP, DG present, some SMP sometimes	2(2)3(1) [medial gap in AI is seen in the illustration]	Strong and wide	S, latero-ventrally positioned	Almost S	—	—	Very short tail	—	Grayish, scantily spotted above	—
<i>P. thaul</i>	Úbeda 1998	Elliptic, almost as tall as wide	AV, laterally emarginated, double row of MP, DG present, some SMP sometimes	2(2)3(1)	Well developed, serrated, LJS V-shaped	S, opening below body midline, at 52-58% BL	Medial	Circular, rimmed, DL, closer to E than to TOS	Origin on body	TAL as tall as body, 58-62% TL, TM almost reached TOT	Almost lateral	L: Greyish brown w/ golden shines, ventrally black w/ gold and copper shines, fins translucent, scarcely pigmented	60 (max. length)
<i>P. tucumanum</i>	Cei 1980	Oval, wide, somewhat depressed	Several rows of MP	2(2)2	—	S, latero-ventrally positioned	Medial	Almost protruding	—	TAL almost twice BL	—	Dorsum and TM speckled w/ dark spots and points	—
<i>P. tucumanum</i>	Fabrezi and Vera 1997	Ovoid	Laterally emarginated wide DG,	2(2)2	—	Lateral	—	—	DF as high as VF, DF origin on body	TAL \leq 2/3 TL, TOT acute	Dorsal	—	—

Notes: ¹ Cei (1980) presented a drawing of the tadpole of *P. bufoninum* from the Province of Santa Cruz, Argentina, which in general agrees with the description of Fernández (1927). ² We follow Cei (1980) in considering this description as of *P. cinereum* due to the geographic origin of the samples, *contra* Fernández (1927), which referred it to *P. borellii*.

TABLE 4. Advertisement call parameters of 11 species of *Pleurodema*. Values are mean \pm SD, range given in parentheses (pulse and note rate data from the literature were scaled to seconds to easier comparisons).

Species	Reference	Call duration (s)	Number of notes per call	Note duration (s)	Internote interval (s)	Note rate (notes/s)	Pulse rate (pulses/s)	Pulses/note	Dominant frequency (Hz)
<i>P. bibroni</i>	Present study	18.67 \pm 15.04 (1.59–67.82)	188 \pm 149 (17–649)	0.049 \pm 0.004 (0.044–0.058)	0.048 \pm 0.005 (0.041–0.058)	10.4 \pm 0.7 (8.9–11.8)	31.3 \pm 2.0 (26.7–35.3)	3	1960 \pm 105 (1816–2162)
<i>P. bibroni</i>	Barrio 1977	---	---	0.04	0.07	10	70	3	1500–2400
<i>P. borellii</i>	McLister <i>et al.</i> 1991	0.13–0.15	---	---	---	---	96.2–105.8	---	1600
<i>P. brachyops</i>	Duellman and Veloso 1977	---	---	1.0 (0.5–1.5)	---	0.63 (0.60–0.66)	60	---	700 (650–750)
<i>P. cinereum</i>	Duellman and Veloso 1977	---	---	0.17 (0.14–0.20)	---	-	59.9 (50–60)	---	1600
<i>P. cinereum</i>	Márquez <i>et al.</i> 1995	---	1	0.120–0.183 (\bar{x} = 0.157)	---	3.69 (3.05–4.26)	77.5 (67.4–92.7)	10–18	1530 (1292–1635)
<i>P. diplolister</i>	Hödl 1992	11.4 (3–33)	---	61 (0.052–0.082)	---	8.93 (7.52–9.73)	---	---	875 (832–912)
<i>P. diplolister</i>	Cardoso and Arzabe 1993	---	---	0.045	0.094	3.26	---	---	1365
<i>P. guayanae</i>	Barrio 1964	---	---	0.20	0.35–0.40	1.8	---	---	700–800
<i>P. kriegi</i>	Present study	20.49 \pm 15.71 (4.04–44.76)	215 \pm 157 (41–431)	0.054 \pm 0.006 (0.042–0.062)	0.036 \pm 0.008 (0.024–0.051)	10.6 \pm 1.3 (9.4–13.2)	31.7 \pm 3.9 (28.2–39.7)	3	1801 \pm 42 (1729–1877)
<i>P. kriegi</i>	Barrio 1977	---	---	0.05	0.05	11	53	3	1500–2400 1716 at the beginning, rising to 1958 at end of note (1600–1900)
<i>P. marmoratum</i>	Duellman and Veloso 1977	---	---	0.34 (0.24–0.48)	---	65 (50–80)	---	---	---

TABLE 4. (continued)

Species	Reference	Call duration (s)	Number of notes per call	Note duration (s)	Internote interval (s)	Note rate (notes/s)	Pulse rate (pulses/s)	Pulses/note	Dominant frequency (Hz)
<i>P. nebulosum</i>	Barrio 1964	---	---	0.12–0.14	0.13–0.20	3.33	---	---	2600–3800
<i>P. thaul</i>	Duellman and Veloso 1977	0.2–9.0 (\bar{x} = 2.54), extends to nearly 60 in choruses	---	---	---	---	---	---	2047 (1500–2300)
<i>P. thaul</i>	Barrio 1977	---	---	0.03	0.03	16	90	6	1800–2300
<i>P. tucumanum</i>	McLister <i>et al.</i> 1991	0.29	---	---	---	---	120.6	---	2700
<i>P. tucumanum</i>	Barrio 1964	---	---	0.28–0.33	0.37–0.40	1.46	---	---	2600–3200

Deimatic behavior with exhibition of lumbar glands in species of *Pleurodema* as a defensive encounter behavior was already mentioned in *P. brachyops*, *P. bufoninum*, and *P. thaul* (Ceï 1962; Ceï 1980; Martins 1989). It was first described in *P. bibroni* by Vaz-Ferreira (1984) but without illustrations. Tilting the body towards the potential predator and death feigning in this species were previously not documented, as well as the exhibition of lumbar glands in *P. borellii* and *P. kriegi*. These glands are concentrations of tubular granular glands, with presumably toxic secretion (Adam 1954; Ceï *et al.* 1967; Toledo *et al.* 1996; Mangione & Lavilla 2004). The release of this secretion after an external disturbing stimulus is reported here for *P. bufoninum*. The elevation of the pelvic region as part of an encounter behavior in a species of *Pleurodema* lacking externally noticeable lumbar glands is reported here for the first time in *P. tucumanum*. Although protruding lumbar glands are absent in this species, it has a dark-brown contrasting pattern in this region. It was recently demonstrated that the skin of the lumbar region of this and other species of *Pleurodema* lacking externally visible glands presents patches of granular and mucous glands (Mangione & Lavilla 2004). Presentation of this presumably unpalatable part of the body to predators may be an effective dissuasive encounter behavior. The exhibition of lumbar glands seems to be a behavior phylogenetically conserved among the species of the genus, which is also present in some species of the related Leiuperid genera *Eupemphix* and *Physalaemus* (Sazima & Caramaschi 1986; Borteiro & Kolenc 2007).

Biogeographic and taxonomic remarks

The apparent allopatry of the two known population clusters of *Pleurodema bibroni* lead some authors to propose that this form is probably a complex of more than one species (IUCN 2008). However, there is currently no published evidence supporting this hypothesis. Most records of *P. bibroni* in the State of Rio Grande do Sul, Brazil, correspond to forested highland habitats, except for the coastal locality of Praia da Cidreira in the northeast (Braun 1973; Braun & Braun 1980). The habitat at the latter is similar to that at coastal localities inhabited by *P. bibroni* in Uruguay, about 600 km southwards. It is uncertain whether the distributional gap of *P. bibroni* in coastal Rio Grande do Sul is due to the scarce fieldwork historically done in this region, to recent putative decline of the populations (see below) or to real disjunct distribution of this species in recent times. As there is a continuum of coastal sandy habitats (where *P. bibroni* is probably present) along the Atlantic coast between eastern Uruguay and northern Rio Grande do Sul, further survey effort is needed to study this region.

The close phylogenetic relationship between the cryptic and currently isolated species *Pleurodema bibroni* and *P. kriegi* was suggested by Barrio and Rinaldi de Chieri (1970) and later by Barrio (1977) and Duellman and Veloso (1977). The allopatric speciation of *P. bibroni* and *P. kriegi* was proposed on the grounds of the similar external morphology of adults, advertisement call, and reproductive biology (Barrio 1977). This is strongly supported by karyologic studies indicating that these species (at least Uruguayan populations in the case of *P. bibroni*) are up to date the only known tetraploid forms of the genus, certainly derived from a formerly more widely distributed, tetraploid ancestor (Barrio & Rinaldi de Chieri 1970). Duellman and Veloso (1977) and Barrio (1977) proposed that the ancestor originated in central-western Argentina and dispersed eastwards to the central part of this country, southern Brazil and Uruguay. The first tended to assume an autopolyploid event prior to the vicariant process, probably from the geographically close species *P. borellii* or from a related form. Conversely, Barrio and Rinaldi de Chieri (1970), based mainly on the meiotic chromosome pairing and differences in the mitotic chromosome quartets, proposed as more plausibly an allopolyploid mechanism. They stated that allopolyploidy would not necessarily have been the result of hybridization between extant species, of which they indicated *P. thaul* as a likely candidate. Barrio (1977), in discrepancy with Duellman and Veloso (1977), added that between the geographically close species of *Pleurodema*, *P. borellii* would not be expected to be a parental lineage of the ancestral hybrid because it builds foam nests and dwells mainly in subtropical forests. He proposed an Andean-patagonic origin of *P. bibroni* and *P. kriegi*, which would derive from species like *P. thaul* and *P. bufoninum*, which share with them the presence of lumbar glands, similar chromosome morphology and reproductive mode (Barrio 1977). This hypothe-

sis is congruent with the presence of other endemic taxa in the Sierras Grandes which are related to groups with mainly Andean-patagonic distribution. Examples of this are the toad *Rhinella achalensis* (closely related to the Andean *R. spinulosa* species group), the lizard *Prystidactylus achalensis* (Gallardo) (Ceí 1972; Barrio 1977), and the canid *Pseudalopex culpaeus smithersi* Thomas (Jiménez & Novaro 2004). Other vertebrates endemic of these mountain environments in central Argentina are the cycloramphid frog *Odontophrynus achalensis*, the ctenomyid rodent *Ctenomys osvaldoreigi* Contreras (Contreras 1995), and some birds (Miatello *et al.* 1999). The mountain landscapes of the Sierras Grandes were traditionally included within the Chaco ecoregion (Ab'Sáber 1977a; Cabrera & Willink 1980). However, their particular dry habitats with endemic flora and fauna merit being considered a distinctive biogeographic unit (Ringuelet 1961; see also Ceí 1972 and Barrio 1977).

The current distribution pattern of *Pleurodema* species was suggested to be strongly related to vicariant events driven by climatic fluctuations that occurred during the Pleistocene and Holocene (see Duellman & Veloso 1977). Barrio (1977) agrees with this approximate dating of vicariation for *P. bibroni* and *P. kriegi*. It is worth noting that there are no records of these species at extensively surveyed intermediate places over the fluvial plain of the Paraná River basin. This fact, in addition to present distributional and ecological data, led us to conclude that extense wetland areas are not suitable for *P. bibroni* and *P. kriegi*. Indeed, as earlier mentioned in this work, most species of *Pleurodema* inhabit regions with strong seasonal dry or arid climates (Barrio, 1964a; Lynch 1971; Duellman & Veloso 1977; Ceí 1980). It is likely that similar environmental conditions would have been a prerequisite for the geographic expansion of the common ancestor of *P. bibroni* and *P. kriegi*. Such a scenario would have allowed its dispersal across the extense plains of the Paraná River, which were established during the last 10 Myr before present (BP), under the influence of marine incursions from the Atlantic (Camacho 1967; Hubert & Renno 2006). An important event that should be considered as an explanatory hypothesis for the expansion of the ancestral form of *P. bibroni* and *P. kriegi* is a significant phase of arid climate reported for South America from the Late Pleistocene, at about 18000 yr BP, that lasted up to the Lower Holocene, around 8500 yr BP (van der Hammen 1974; Ab'Sáber 1977b). This long period of extremely dry climate is well documented for central-eastern Argentina, and was followed by a phase of humid subtropical and tropical climate with development of fluvial belts (Iriondo & Garcia 1993). There is evidence of another semiarid climate period in the region but of lower intensity and relatively short duration during the Late Holocene, from 3500 to 1000 yr BP (Iriondo 1990; Iriondo & Garcia 1993). Holocene changes towards more humid climates would have caused range retraction and fragmentation of Neotropical species that were well adapted to xerophilous habitats (Vanzolini 1992).

Phylogenetic and phylogeographic analysis of the genus and molecular clock dating are needed to test the possible origins of *Pleurodema bibroni* and *P. kriegi*, as well as the biogeographic hypotheses discussed herein.

On the conservation status of *Pleurodema bibroni* and *Pleurodema kriegi*

The literature references about *Pleurodema bibroni* suggest that it was a fairly common species in Uruguay, apparently until the last decades. It was the first amphibian described from Uruguay, based on “several individuals brought from Monte-Video to Paris by Mr. d’Orbigny” (Tschudi 1838; translated from German), of which only the lectotype MNHNP 4501 remains (Ortiz & Lescure 1989). These specimens were most probably collected by d’Orbigny when he traveled through this country in 1826–1827 (d’Orbigny 1835–1847). Later, several naturalists and biologists collected specimens of *Pleurodema* in Uruguay in the 19th and 20th centuries, which sometimes were used for the description of new species that are currently considered as synonyms of *P. bibroni*. Bell (1843) described *P. darwinii* and stated that it was “repeatedly found by Mr. Darwin at Maldonado” where he collected during 1832–1833 (Darwin 1839). Jiménez de la Espada (1875) described his *P. granulosum* based on two specimens [currently MNCN 1685–1686, two syntypes, J.E. González Fernández (curator), pers. comm. to D.P. Ferraro] collected close to Montevideo. There are records that

Arechavaleta, Director of the Museo Nacional de Historia Natural de Montevideo, sent two specimens of this species to Philippi between 1895 and 1896, who worked at the Museo de Santiago, Chile (Klappenbach 1968). In 1926 and 1927, Sanborn collected amphibians in Uruguay which are housed at the Chicago Field Museum of Natural History (Gudynas 1983); according to Gallardo (1968) this collection includes 20 specimens of *P. bibroni* collected in the Departments of Maldonado and Treinta y Tres in 1926. During the early 20th century, Cordero (1919a; 1919b; 1933) described parasites of some anuran species which he commonly found in the outskirts of Montevideo, including many specimens of *P. bibroni*. Legrand (1959) reported it from the psammophytic vegetal communities at Carrasco, in the eastern part of the Department of Montevideo and adjacent coastal Department of Canelones. A few years later, Klappenbach (1969) stated that its distribution was geographically restricted to some Departments of Uruguay and its biology was unknown, but did not consider it uncommon. Barrio and Rinaldi de Chieri (1970) studied the cytogenetics of this species on the basis of 53 specimens collected in the Departments of Montevideo, Canelones and Rocha, in Uruguay. Barrio (1977) addressed the study of the biology of *P. bibroni* on many samples from Uruguay, and he considered this species very tolerant to environmental conditions and able to occur in varied habitats in Uruguay, from the sandy shoreline of the La Plata River and Atlantic Ocean coasts to the hilly environments in the southeastern part of this country. Altuna (1983) found this species inhabiting subterranean galleries of *Ctenomys pearsoni* Lessa and Languth (Mammalia: Rodentia) at Autódromo Nacional, Department of San José, 27.5 Km westwards from Montevideo, in an area still scarcely urbanized at the time. Gudynas and Rudolf (1987) and Gudynas (1989) studied coastal herpetological communities in the Departments of Montevideo and Canelones between 1977 and 1984 and could not find *P. bibroni*, but Gudynas (1989) stated that this species still occurred in the Carrasco area, and was then not considered rare or secretive. There were no published concerns about the conservation status of *P. bibroni* until recently, when it was listed as “Threatened” in an assessment of the conservation status of Uruguayan amphibians (Maneyro & Langone 2001). Núñez *et al.* (2004) summarized all known geographic records in Uruguay based on museum collections, and they considered it a species with wide geographic distribution in this country without further comments. Recent amphibian surveys targeting areas where this species used to occur failed to find it (Gambarotta *et al.* 1999; Langone 1999; González & Gambarotta 2001; Prigioni 2001; da Rosa *et al.* 2006), until the recent record of one individual of this species in Barra de Valizas, Department of Rocha (Natale & Maneyro 2008). The presence of *P. bibroni* in Rio Grande do Sul, Brazil, was first recorded by Jiménez de la Espada (1875), and almost a century later Braun (1973) provided the first documented records for this species in the northern region of this state, between 700 and 900 m a.s.l. Currently, the Global Amphibian Assessment (IUCN 2008) lists this species as “Near threatened” due to widespread habitat loss and intolerance to habitat disturbance.

The examination of the main scientific collections in Argentina and Uruguay where most collected specimens of *Pleurodema bibroni* were historically deposited (MACN, CENAI, MNHN, ZVCB) totalled 633 specimens collected in Uruguay alone until the present study (see Appendix 1). The first one was collected in 1939 and the last one in 2007 (Fig. 9). The dates of collection are scattered throughout the time-line, and most specimens seem to have been collected as a result of occasional findings. Many localities are placed at resorts and other commonly visited points of tourist attraction in coastal Departments (San José, Montevideo, Canelones, Maldonado and Rocha). Between 1969 and 1972, A. Barrio, A.G. Dewailly and J.E. García actively collected individuals of *P. bibroni* in Uruguay for Barrio’s studies. Together, they collected more than 500 specimens from a very few localities close to Montevideo, and García also collected in other places, wherever he could find them. None of them considered the species rare by this time, and García and Barrio found it even at urban and suburban areas like Punta Gorda, in the Department of Montevideo, and the town of Canelones and Carrasco Airport, in the Department of Canelones (A.G. Dewailly, and J.E. García, pers. comm.). However, less than ten specimens were deposited at national scientific collections over the last three decades, although fieldwork in the country has increased over the same period of time. The last specimens of *P. bibroni* collected in

Uruguay until this study were found in the Department of Rocha at the following places and dates: Playa de las Achiras, Santa Teresa National Park in 1984 and Barra de Valizas in 1987 (MNHN 6817 and 6815 respectively, collected by F. Kolenc); La Paloma in 1991 (ZVCB 17127, collected by C. Borteiro), El Potrerillo, coast of Laguna Negra in 1995 (observational record, Maneyro *et al.* 1995) and Barra de Valizas in 2007 (Natale & Maneyro 2008). The collection of MCN houses 23 specimens of *P. bibroni* collected in Rio Grande do Sul, Brazil, between 1955 and 1976 (see Appendix 1). Most of them were collected between 1973 and 1976 by P.C. and C.S. Braun, but no additional records are available for the Brazilian populations.

Since 2000, some of us (CB, FK, CP) thoroughly surveyed large areas of southern and eastern Uruguay searching for *Pleurodema bibroni*, specially at places where the species was previously recorded or close to them, and taking into account the reproductive conditions observed by Barrio (1977). Until recently, all efforts had had negative results. Despite some of these places being heavily altered (for example, some coastal resorts like Carrasco, currently part of Montevideo city, Atlántida, Las Toscas and Punta del Este, and some suburban areas of the Department of Montevideo, like Santiago Vázquez and Barra de Santa Lucía), other places present a notably diverse and conserved anuran fauna. We repeatedly visited the localities of Delta del Tigre, Playa Penino, and the surroundings of Playa Pascual, Department of San José, where A.G. Dewailly and J.E. García used to collect the species in the early 1970's. Presumably suitable habitats are still present at these localities, where large populations of many anurans occur, with the exceptions of *P. bibroni*, *Physalaemus fernandezae* (Müller), *P. henselii* and *Ceratophrys ornata* (Bell), which were found there at least until the early 1970's (Barrio 1964b; García 1972; Barrio 1977). We found a similar situation on the coast of the Department of Canelones: although habitats close to the shoreline are currently very altered due to urbanization, most amphibians known to have occurred there (based on Núñez *et al.* 2004) are still present, with the exception of *Chthonerpeton indistinctum* (Reinhardt & Lütken), *Melanophryniscus montevidensis* (Philippi), *P. henselii* and *P. bibroni*. Only 3–5 km away from the shoreline, urbanization is scattered at many places and suitable habitats for amphibians are common, and although populations of some species are large, the pattern of species presence/absence is the same. Intense field surveys at many localities along Route 8, in the Departments of Canelones, Lavalleja, and Treinta y Tres in all four seasons during the last decade resulted on records of all anuran species historically known to occur there, except again for *P. bibroni* and *P. henselii*. The same happened in the hilly environments of the Departments of Lavalleja, Maldonado, and Treinta y Tres. On the coast of the Department of Rocha, in searches at Laguna de Rocha, La Paloma, and La Pedrera and their respective surroundings we failed to find *P. bibroni* and *P. henselii*, although large populations of *M. montevidensis* and many other amphibians are still present mostly in remnants of unmodified or little modified habitats. Currently, we are aware of the presence of *P. bibroni* only at very few localities mostly in the Department of Rocha. Most of these localities are placed very close to each other, in a strip of land of approximately 25 km long between the Atlantic shoreline and the wetlands of Laguna de Castillos, and at Cerro Verde, another coastal locality distant about 45 km to the northeast (Fig. 8B). Attempts to find it in other places in the Department of Rocha have failed to date (e.g. La Esmeralda, Punta del Diablo, Santa Teresa, La Coronilla, Palmares de La Coronilla, and Barra del Chuy), although two other declining species, *P. henselii* and *M. montevidensis*, still have large populations in many of these places. An advertisement call assignable to *P. bibroni* by its acoustic parameters was recorded in the surroundings of the town Treinta y Tres in 2001 by one of the authors (CP) but the specimen could not be seen or captured. This is the only evidence of the current presence of *P. bibroni* in an inland locality.

In conclusion, from the analysis of the literature, specimens deposited in scientific collections, and the authors' field experience, we state that the populations of *Pleurodema bibroni* in Uruguay are undergoing a severe decline, which apparently started in the middle 1970's or early 1980's. This decline seems to cover

most of its historical geographic range, except for some populations in southeastern Uruguay, mainly in the Department of Rocha. It seems to be associated with that of other species from southern Uruguay, like *Argenteohyla siemersi* (Mertens), *Ceratophrys ornata*, *Physalaemus fernandezae*, *Melanophryniscus montevidensis* (Kolenc 1987; Langone 1995; Maneyro & Langone 2001) and also *P. henselii* (Borteiro & Kolenc, unpublished results). The causes of the decline of *P. bibroni* are only partially understood. Widespread habitat destruction and intolerance to habitat disturbance have been proposed as causative factors (IUCN 2008). Indeed, extensive natural areas on the country coast have experienced rapid urban development. Consequently, most of the coastal habitats previously inhabited by this species were destroyed, and remnant patches are severely altered (Scasso 2002; Alonso-Paz & Bassagoda 2006). However, relatively unaltered habitat remains at other inland localities where the species was previously found, so other factors may have acted on the viability of some populations of this species. Most species of *Pleurodema* are very abundant, adapted to hard environmental conditions. Even *P. bibroni* was considered a very tolerant species, based on the variety of habitats it used to occupy (Barrio 1977). Nevertheless, it seems that population declines have occurred in most of them. The decline of *P. bibroni* seems to occur at a very rapid pace and in a short period of time, similarly to what occurred with many other amphibians (Pounds *et al.* 2006), and besides habitat destruction other factors have been associated to these amphibian declines worldwide (Alford & Richards 1999; Alford *et al.* 1999; Pounds *et al.* 2006). It is likely that a combination of these factors would have negatively affected the persistence of *P. bibroni* in many areas, for which retrospective studies could help clarify. Additionally, further field work should be done to accurately assess the presence of *P. bibroni* throughout its entire historical range, together with monitoring the few remaining populations known at present, in order to develop efforts to preserve this endangered species.

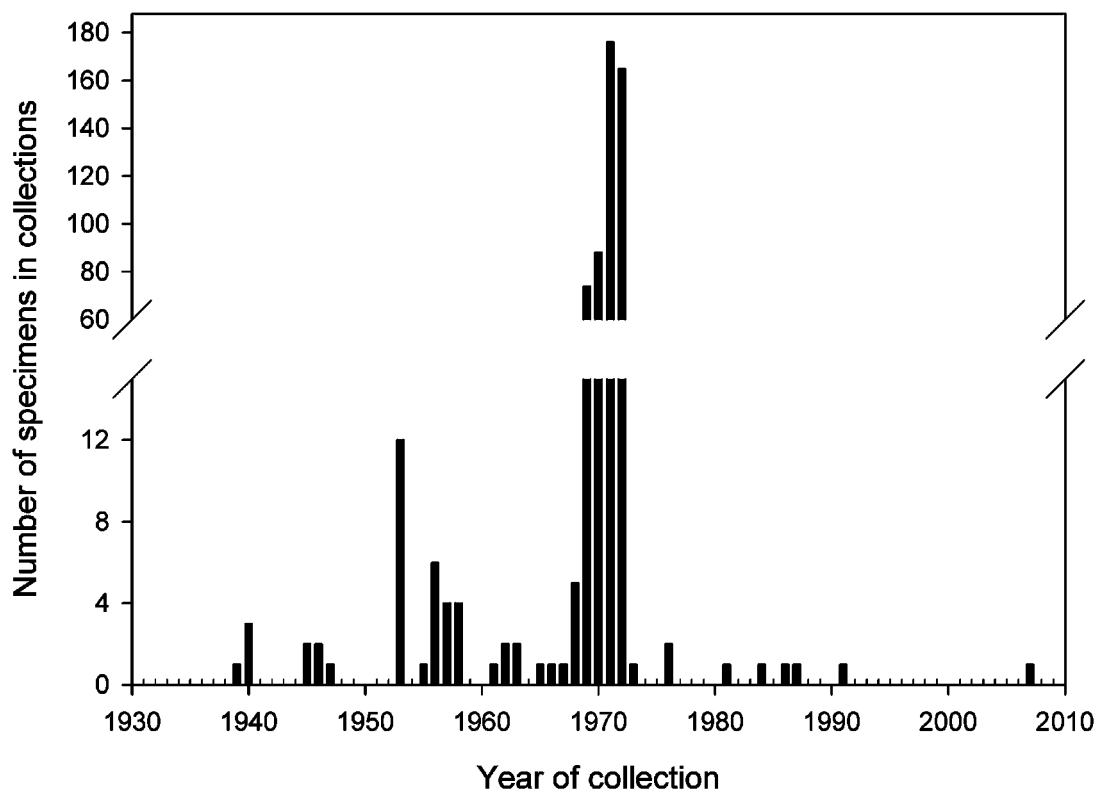


FIGURE 9. Number of specimens of *Pleurodema bibroni* from Uruguay, and deposited in the main herpetological collections of Argentina and Uruguay, sorted by year of collection. Specimens collected in 2007–2008 for this study were not included.

The endemic anurans of high grasslands of the “Sierras Grandes” (including *Pleurodema kriegi*) were considered “Vulnerable” by di Tada *et al.* (1996) because of habitat fragmentation and alteration, but unlike others *P. kriegi* was considered a common species. Lavilla *et al.* (2000) listed *P. kriegi* as “Vulnerable”, and the Global Amphibian Assessment considered the species “Near threatened” due to a restricted geographical distribution (less than 5000 km²; IUCN 2008). Other studies about the herpetofauna of the Province of Córdoba made no comments on the abundance or conservation status of *P. kriegi* (di Tada *et al.* 1976; Lavilla *et al.* 1992; Bridarolli & Di Tada 1994; Ávila & Priotto 1995; Martori & Aùn 1995; Ávila *et al.* 1999). Barrio (1977) mentioned that field collection of this species was common during summer, as we observed in recent years at Pampa de Achala. In summary, the populations of *P. kriegi*, although presenting a restricted distribution, seem to be healthier than those of *P. bibroni*. Furthermore, many of them are benefited by the protected areas of the Provincial Hydric Reserve Pampa de Achala, which comprises 146000 hectares, and Parque Nacional Quebrada del Condorito, with *circa* 40000 hectares in Pampa de Achala between 1900 and 2300 m a.s.l., created in 1996.

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References

- Ab’Sáber, A.N. (1977a) Os domínios morfoclimáticos na América do Sul. Primeira aproximação. *Geomorfologia* (São Paulo), 52, 1–21.
- Ab’Sáber, A.N. (1977b) Espaços ocupados pela expansão dos climas secos na América do Sul, por ocasião dos períodos glaciais quaternários. *Paleoclimas* (São Paulo), 3, 1–20.
- Adam, H. (1954) Das lumbalorgan des chilenischen sumpffrosches, *Pleurodema bibroni* Tschudi. *Zeitschrift fuer Morphologie und Ökologie der Tiere*, 43, 154–170.
- Alford, R.A. & Richards, S.J. (1999) Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics*, 30, 133–165.
- Alford, R.A., Bradfield, K.S. & Richards, S.J. (1999) Global warming and amphibian losses. *Nature*, 447, E3–E4.
- Alonso-Paz, E. & Bassagoda, M.J. (2006) Flora y vegetación de la costa platense y atlántica uruguaya. In: Menafrá, R., Rodríguez-Gallego, L., Scarabino, F. & Conde, D. (Eds.), *Bases para la conservación y el manejo de la costa uruguaya*. Vida Silvestre Uruguay, Montevideo, pp. 71–88.

- Altig, R. & Johnston, G.F. (1986) Major characteristics of free-living anuran tadpoles. *Smithsonian Herpetological Information Service*, 67, 1–75.
- Altig, R. & Johnston, G.F. (1989) Guilds of anuran larvae: Relationships among developmental modes, morphologies, and habitats. *Herpetological Monographs*, 3, 81–109.
- Altig, R. & McDiarmid, R.W. (1999a) Body Plan. Development and Morphology. In: McDiarmid, R.W. & Altig R. (Eds.), *Tadpoles: The Biology of Anuran Larvae*, Univ. of Chicago Press, Chicago, pp. 24–51.
- Altig, R. & McDiarmid, R.W. (1999b) Diversity. Familial and Generic Characterizations. In: McDiarmid, R.W. & Altig R. (Eds.), *Tadpoles: The Biology of Anuran Larvae*, Univ. of Chicago Press, Chicago, pp. 295–337.
- Altuna, C.A. (1983) Sobre la estructura de las construcciones de *Ctenomys pearsoni* Lessa y Langguth, 1983 (Rodentia, Octodontidae). *Resúmenes y comunicaciones de las Jornadas de Ciencias Naturales, Montevideo*, 3, 70–72.
- Ávila, L.J. & Priotto, J.W. (1995) Geographic Distribution. *Pleurodema kriegi*. *Herpetological Review*, 26, 106.
- Ávila, L.J., Morando, M. & Priotto, J.W. (1999) Amphibia and Reptilia of the high grasslands of the Sierra de Comechingones, Córdoba, Argentina. *Bulletin of the Maryland Herpetological Society*, 35, 97–114.
- Baldo, D. & Basso, N.G. (2004) A new species of *Melanophryniscus* Gallardo, 1961 (Anura: Bufonidae), with comments on the species of the genus reported for Misiones, northeastern Argentina. *Journal of Herpetology*, 38, 393–403.
- Barrio, A. (1964a) Especies crípticas del género *Pleurodema* que conviven en una misma área, identificadas por el canto nupcial (Anura, Leptodactylidae). *Physis*, 24, 471–489.
- Barrio, A. (1964b) Relaciones morfológicas, eto-ecológicas y zoogeográficas entre *Physalaemus henseli* (Peters) y *P. fernandezae* (Müller) (Anura, Leptodactylidae). *Acta Zoológica Lilloana*, 20, 284–305.
- Barrio, A. (1977) Aportes para la elucidación del “status” taxonómico de *Pleurodema bibroni* Tschudi y *Pleurodema kriegi* (Müller) (Amphibia, Anura, Leptodactylidae). *Physis*, 37, 311–331.
- Barrio, A. & Rinaldi de Chieri, P. (1970) Estudios citogenéticos sobre el género *Pleurodema* y sus consecuencias evolutivas (Amphibia, Anura, Leptodactylidae). *Physis*, 30, 309–319.
- Bell, T. (1843) *Zoology of the voyage of H.M.S. Beagle, under the command of Captain Fitzroy, R.N., during the years 1832 to 1836. Part V. Reptiles*. Smith, Elder & Co., London, 51 pp.
- Borteiro, C. & Kolenc, F. (2007) Redescription of the tadpoles of three species of frogs from Uruguay (Amphibia: Anura: Leiuperidae and Leptodactylidae), with notes on natural history. *Zootaxa*, 1638, 1–20.
- Borteiro, C., Kolenc, F., Tedros, M. & Prigioni, C. (2006) The tadpole of *Chaunus dorbignyi* (Duméril & Bibron) (Anura, Bufonidae). *Zootaxa*, 1308, 49–62.
- Braun, C.A.S. (1973) Sobre a ocorrência de *Pleurodema bibronii* Tschudi, 1828 no estado do Rio Grande do Sul, Brasil (Anura, Leptodactylidae). *Iheringia Sér. Zool.*, 44, 28–31.
- Braun, P.C. & Braun, C.A.S. (1980) Lista prévia dos anfíbios do Estado do Rio Grande do Sul, Brasil. *Iheringia Sér. Zool.*, 56, 121–146.
- Bridarolli, M.E. & di Tada, I.E. (1994) Biogeografía de los anfibios anuros de la región central de la República Argentina. *Cuadernos de Herpetología*, 8, 63–82.
- Cabrera, A.L. & Willink, A. (1980) *Biogeografía de América Latina*. OEA, Serie Biología, Monografía 13, Washington, 117 pp.
- Camacho, H.H. (1967) Las transgresiones del Cretácico Superior y Terciario de la Argentina. *Revista de la Asociación Geológica Argentina*, 22, 4, 253–280.
- Capitanelli R.G. (1979) III Clima. In: Vázquez, J.B., Miatello R.A. & Roqué, M.E. (Eds.), Geografía física de la provincia de Córdoba. Editorial Boldt, Buenos Aires, pp. 45–138.
- Cardoso, A.J. & Arzabe, C. (1993) Corte e desenvolvimento larvário de *Pleurodema diplolistris* (Anura: Leptodactylidae). *Revista Brasileira de Biologia*, 53, 561–570.
- Carvalho, A.L. de & Bailey, J.R. (1948) Sobre os hábitos e ecologia de “*Pleurodema diplolistris*” (Peters) (Amphibia, Anura). *Revista Brasileira de Biologia*, 2, 261–264.
- Cei, J.M. (1962) *Batracios de Chile*. Ed. Universidad de Chile, Santiago de Chile, 128 pp.
- Cei, J.M. (1972) Segregación corológica y procesos de especiación por aislamiento en anfibios de la Pampa de Achala, Córdoba. *Acta Zoológica Lilloana*, 29, 233–244.
- Cei, J. M. (1980) Amphibians of Argentina. *Monitore zoologico italiano, N.S., Monografia*, 2, 1–609.
- Cei, J.M., Erspamer, V. & Roseghini, M. (1967) Taxonomic and evolutionary significance of biogenic amines and polypeptides occurring in amphibian skin. I. Neotropical Leptodactylid frogs. *Systematic Zoology*, 16, 328–342.
- Contreras, J.R. (1995) *Ctenomys osvaldoreigi*, una nueva especie de tuco-tuco procedente de las sierras de Córdoba, República Argentina (Rodentia: Ctenomyidae). *Nótulas Faunísticas (Corrientes)*, 84, 1–3.
- Cordero, E.H. (1919a) *Cystodiscus immersus* Lutz. Mixosporidio de los batracios del Uruguay. *Physis*, 4, 403–409.

- Cordero, E.H. (1919b) “*Opalina antillensis*” Metcalf. Ciliado parásito de los batracios del Uruguay. *Physis*, 4, 531–535.
- Cordero, E.H. (1933) Sur quelques Acanthocéphales de l’Amérique Méridionale. I. *Annales de Parasitologie Humaine et Comparée*, 11, 271–279.
- da Rosa, I., Camargo, A., Canavero, A., Naya, D.E. & Maneyro, R. (2006) Ecología de un ensamble de anuros en un humedal costero del sudeste de Uruguay. In: Menafrá, R., Rodríguez-Gallego, L., Scarabino, F. & Conde, D. (Eds.), *Bases para la conservación y el manejo de la costa uruguaya*. Vida Silvestre Uruguay, Montevideo, pp. 447–456.
- Darwin, C. (1839) Journal and remarks. 1832–1836. In *Narrative of the Surveying Voyages of His Majesty’s Ships Adventure and Beagle between the years 1826 and 1836, describing their examination of the Southern Shores of South America and the Beagle’s circumnavigation of the Globe*, 3: I–XVI, 1–615 pp.
- Davies, M. & Withers, P.C. (1993) Morphology and physiology of the Anura. In: Glasby, C.G., Ross, G.J.B. & Beesley, P.L. (Eds.), *Fauna of Australia 2A Amphibia Reptilia*, 04. Australian Government Publishing Service, Canberra, pp. 1–26.
- Díaz-Páez, H. & Ortiz, J.C. (2001) The reproductive cycle of *Pleurodema thaul* (Anura, Leptodactylidae) in central Chile. *Amphibia-Reptilia*, 22, 431–445.
- di Tada, I.E., Saluso, M.M. & Martori, R. (1976) Lista de los Batracios de Córdoba. *Boletín de la Academia Nacional de Ciencias de Córdoba*, 51, 324–362.
- di Tada, I.E., Zavattieri, M.V., Bridarolli, M.E., Salas, N.E. & Martino, A.L. (1996) Anfibios Anuros de la provincia de Córdoba. In: di Tada, I.E. & Bucher, E.H. (Eds.), *Biodiversidad de la Provincia de Córdoba. Fauna. Vol. I*, Univ. Nac. Río Cuarto y Centro de Zoología Aplicada, Córdoba, pp. 191–213.
- Donoso-Barros, R. (1969) Posición nomenclatural de un leptodactylido Uruguayo (Amphibia-Anura). *Boletín de la Sociedad de Biología de Concepción*, 41, 161–162.
- D’Orbigny, A. 1835–1847. *Voyage dans l’Amérique méridionale (le Brésil, la République Orientale de l’Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivia, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833*. Bertrand, Paris, 9 volumes.
- Duellman, W.E. & Veloso, A. (1977) Phylogeny of *Pleurodema* (Anura, Leptodactylidae). A biogeographic model. *Occasional Papers of the Museum of Natural History*, 64, 1–46.
- Evia, G. & Gudynas, E. (2000) *Ecología del paisaje en Uruguay*. Junta de Andalucía-DINAMA-AECI, Sevilla, 173 pp.
- Fabrezi, M. & Vera, R. (1997) Caracterización morfológica de larvas de anuros del noroeste argentino. *Cuadernos de Herpetología*, 11, 37–49.
- Fernández, K. & Fernández, M. (1921) Sobre la biología y reproducción de algunos batracios argentinos. *Anales de la Sociedad Científica Argentina*, 91, 97–140.
- Fernández, K. (1927) Sobre la biología y reproducción de batracios argentinos (Segunda Parte). *Boletín de la Academia Nacional de Ciencias de la República Argentina*, 29, 271–320.
- Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. (2006) The Amphibian Tree of Life. *Bulletin of the American Museum of Natural History*, 297, 1–370.
- Frost, D.R. (2008) *Amphibian Species of the World: an Online Reference Version 5.1*, American Museum of Natural History, New York, USA. Available from <http://research.amnh.org/herpetology/amphibia/index.php> (accessed April 12, 2008)
- Gallardo, J.M. (1968) Sobre la validez de algunas especies argentinas de *Pleurodema* (Anura, Leptodactylidae). *Physis*, 28, 135–144.
- Gambarotta, J.C., Saralegui, A. & González, E.M. (1999) Vertebrados tetrápodos del refugio de fauna Laguna de Castillos, Departamento de Rocha. *Relevamientos de Biodiversidad*, 3, 1–31.
- García, J.E. (1972) Ampliación de la distribución geográfica de *Ceratophrys ornata* (Bell) (Anura, Ceratophrynidae) y algunas observaciones etoecológicas. *Physis*, 31, 656–658.
- González, E.M. & Gambarotta, J.C. (2001) Anfibios de Aguas Dulces, Departamento de Rocha, Uruguay (Amphibia: Anura). *Relevamientos de Biodiversidad*, 5, 1–7.
- Gosner, K.L. (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16, 183–190.
- Grant, T., Frost, D.R., Caldwell, J.P., Gagliardo, R., Haddad, C.F.B., Kok, P.J.R., Means, B.D., Noonan, B.P.S.W. & Wheeler, W.C. (2006) Phylogenetic systematics of dart-poison frogs and their relatives (Anura: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History*, 299, 1–262.

- Gudynas, E. (1983) Comentarios sobre anuros (Amphibia) del Uruguay: la expedición Sanborn y breves notas sistemáticas. *Resúmenes y comunicaciones de las Jornadas de Ciencias Naturales, Montevideo*, 3, 92–93.
- Gudynas, E. (1989) Amphibians and reptiles of a coastal periurban ecosystem (Solymar, Uruguay): list, preliminary analysis of community structure, and conservation. *Bulletin of the Maryland Herpetological Society*, 25, 85–123.
- Gudynas, E. & Rudolf, J.C. (1987) La herpetofauna de la localidad costera de “Pajas Blancas” (Uruguay): Lista sistemática comentada y estructura ecológica de la comunidad. *Comunicações do Museu de Ciências da PUCRS*, 46, 173–194.
- Heyer, W.R., Rand, A.S., Gonçalves da Cruz, C.A., Peixoto, O.L. & Nelson, C.E. (1990) Frogs of Boracéia. *Arquivos de Zoologia*, 31, 237–410.
- Hödl, W. (1992) Reproductive behaviour in the neotropical foam-nesting frog *Pleurodema diplolistris* (Leptodactylidae). *Amphibia-Reptilia*, 13, 263–274.
- Hubbert, N. & Renno, J.F. (2006) Historical biogeography of South American freshwater fishes. *Journal of Biogeography*, 33, 1414–1436.
- Hulse, A.C. (1979) Notes on the biology of *Pleurodema cinerea* (Amphibia, Anura, Leptodactylidae) in northwestern Argentina. *Journal of Herpetology*, 13, 153–156.
- Iriondo, M. (1990) A Late Holocene dry period in the Argentine plains. *Quaternary of South America and Antarctic Peninsula*, 7, 197–218.
- Iriondo, M. & Garcia, N. (1993) Climatic variations in the Argentine plains during the last 18,000 years. *Paleogeography, Paleoclimatology, Palaeoecology*, 101, 209–220.
- IUCN, Conservation International, and NatureServe (2008) *Global Amphibian Assessment*. Available from www.globalamphibians.org (accessed April 12, 2008).
- Jiménez, J.E. & Novaro, A.J. (2004) Culpeo *Pseudalopex culpaeus* (Molina, 1872). In: Sillero-Zubiri, C., Hoffmann, M. & McDonald, D.W. (Eds.), *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan*. IUCN/SSC Canid Specialist Group, Gland, Switzerland and Cambridge, pp. 44–49.
- Jiménez de la Espada, M. (1875) *Vertebrados del viaje al Pacífico verificado de 1862 a 1865 por una comisión de naturalistas enviada por el gobierno español*. *Batracios*, Imprenta Miguel Ginesta, Madrid, 208 pp.
- Klappenbach, M.A. (1968) Notas herpetológicas, III. Identificación de las especies uruguayas descritas por Philippi en el “Suplemento a los batraquios chilenos”. *Investigaciones Zoológicas Chilenas*, 13, 147–151.
- Klappenbach, M.A. (1969) Anfíbios. In: Klappenbach, M.A. & Orejas-Miranda, B., *Anfíbios y Reptiles*, Nuestra Tierra, Montevideo, 11, pp 1–36.
- Kolenc, F. (1987) Anuros del género *Melanophryniscus* en la República Oriental del Uruguay. *Aquamar*, 30, 16–21.
- Kolenc, F., Borteiro, C., Tedros, M., Núñez, D. & Maneyro, R. (2006) The tadpole of *Physalaemus henselii* (Peters) (Anura: Leiuperidae). *Zootaxa*, 1360, 41–50.
- Langone, J.A. (1995) *Ranas y sapos del Uruguay (Reconocimiento y aspectos biológicos)*. Museo Dámaso Antonio Larrañaga, Montevideo, (Divulgación) 5, 123 pp.
- Langone, J.A. (1999) Anfíbios de Aguas Corrientes, Departamento de Canelones, Uruguay (Amphibia). *Relevamientos de Biodiversidad*, 4, 1–6.
- Laurent, R.F. (1975) Diferencias biométricas entre dos poblaciones similares de *Pleurodema*. *Acta Zoológica Lilloana*, 31, 99–106.
- Lavilla, E.O. & Scrocchi, G.J. (1986) Morfometría larval de los géneros de Telmatobiinae (Anura: Leptodactylidae) de Argentina y Chile. *Physis*, 44, 39–43.
- Lavilla, E.O., Scrocchi, G.J. & Ávila, L.J. (1992) Clave para la identificación de los anfíbios de la Provincia de Córdoba (Argentina). *Serie de divulgación de la Asociación Herpetológica Argentina*, 7, 1–18.
- Lavilla, E.O., Ponssa, M.L., Baldo, D., Basso, N., Bosso, A., Céspedes, J., Chebez J.C., Faivovich J., Ferrari, L., Lajmanovich, R., Langone, J.A., Peltzer, P., Úbeda C., Vaira, M. & Vera Candioti, F. (2000) Categorización de los Anfíbios de Argentina. In: Lavilla, E.O., Richard, E. & Scrocchi, G.J. (Eds.), *Categorización de los Anfíbios y Reptiles de la República Argentina*, Asociación Herpetológica Argentina, Tucumán, pp. 11–34.
- Legrand, C.D. (1959) Comunidades psamófilas de la región de Carrasco (Uruguay). *Anales del Museo Nacional de Historia Natural, Montevideo* (2ª Ser.), 6, 1–65.
- León-Ochoa, J. & Donoso-Barros, R. (1969–1970) Desarrollo embrionario y metamorfosis de *Pleurodema brachyops* (Cope) (Salientia-Leptodactylidae). *Boletín de la Sociedad Biológica de Concepción*, 42, 355–379.
- Lötters, S., Reichle, S., Faivovich, J. & Bain, R. (2005) The stream-dwelling tadpole of *Hyloscirtus charazani* (Anura: Hylidae) from Andean Bolivia. *Studies on Neotropical Fauna and Environment*, 40, 181–185.

- Lynch, J.D. (1971) Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. *Miscellaneous Publications of the Museum of Natural History of the University of Kansas*, 53, 1–238.
- Maneyro, R., Forni, F. & Santos, M. (1995) Anfibios del Departamento de Rocha. *PROBIDES, Serie Divulgación Técnica*, 1, 1–24.
- Maneyro, R. & Langone, J.A. (2001) Categorización de los Anfibios del Uruguay. *Cuadernos de Herpetología*, 15, 107–118.
- Mangione, S. & Lavilla, E.O. (2004) Histología de la piel de la región lumbar de las especies sin glándula lumbar del género *Pleurodema* (Anura: Leptodactylidae). *Acta Zoológica Lilloana*, 48, 37–56.
- Márquez, R., de la Riva, I. & Bosch, J. (1995) Advertisement calls of Bolivian Leptodactylidae (Amphibia, Anura). *Journal of Zoology*, 237, 313–336.
- Martins, M. (1989) Deimatic behavior in *Pleurodema brachyops*. *Journal of Herpetology*, 23, 305–307.
- Martori, R., Aùn, L. & Vignolo, P.E. (1994) Aporte al conocimiento de la biología y distribución de *Pleurodema tucumana* (Anura, Leptodactylidae). *Boletín de la Asociación Herpetológica Argentina*, 10, 18–19.
- Martori, R. & Aùn, L. (1995) Relevamiento de la herpetofauna de las Sierras Pampeanas del este en la Provincia de Córdoba (Argentina) (registro de taxa comentarios taxonómicos). *Acta Zoológica Lilloana*, 43, 1, 87–97.
- McDiarmid, R.W. & Altig, R. (1999) Research: Materials and techniques. In: McDiarmid, R.W. & Altig, R. (Eds.), *Tadpoles: The Biology of Anuran Larvae*, Univ. of Chicago Press, Chicago, pp. 7–23.
- McLister, J.D., Loughheed, S.C. & Bogart, J.P. (1991) Electrophoretic and vocalization comparisons among three leptodactylid frogs (*Pleurodema* spp.) from northwestern Argentina. *Canadian Journal of Zoology*, 69, 2397–2403.
- Miatello, R., Baldo, J., Ordano, M., Rosacher, C. & Biancucci, L. (1999) *Avifauna del Parque Nacional Quebrada del Condorito y Reserva Hídrica Provincial Pampa de Achala, Córdoba, Argentina. Una lista comentada*. Secretaría de Agricultura, Ganadería y Recursos Renovables, Córdoba, 193 pp.
- Miró, R.C. (1999) El basamento Precámbrico-Paleozoico inferior de las Sierras Pampeanas, Famatina, Cordillera Oriental y Puna. *Geología Argentina. Anales*, 29, 6, 133–167.
- Natale, G.S. & Maneyro, R. (2008) Notes on Geographic Distribution. Amphibia, Anura, Leiuperidae, *Pleurodema bibroni*: Rediscovery. *Check List*, 4, 47–49.
- Núñez, D., Maneyro, R., Langone, J. & de Sá, R.O. (2004) Distribución geográfica de la fauna de anfibios del Uruguay. *Smithsonian Herpetological Information Service*, 134, 1–36.
- Ortiz, J.C. & Lescure, J. (1989) Les types d'amphibiens anoures du Chili dans les collections du Museum National d'Histoire naturelle. Catalogue critique. *Bulletin du Muséum National d'Histoire Naturelle*, 3, 113–122.
- Parker, H.W. (1927) A revision of the frogs of the genera *Pseudopaludicola*, *Physalaemus*, and *Pleurodema*. *Annals and Magazine of Natural History*, 9, 450–478.
- Peixoto, O.L. (1982) Observações sobre a larva de *Pleurodema diplolistris* (Peters, 1870) (Amphibia, Anura, Leptodactylidae). *Revista Brasileira de Biologia*, 42, 631–633.
- Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, 439, 161–167.
- Prigioni, C. (2001) Herpetofauna. In: Rodríguez-Mazzini, R. (Ed.), *Evaluaciones ecológicas rápidas aplicadas a la Reserva de Biosfera Bañados del Este*. PROBIDES, Serie Documentos de Trabajo N° 36, Rocha, 145 pp.
- PROBIDES (Programa de Conservación de la Biodiversidad y Desarrollo Sustentable en los Humedales del Este, Uruguay) (2000) *Plan Director. Reserva de Biosfera Bañados del Este. Uruguay*. PROBIDES, Rocha, 159 pp.
- Rada, D. (1981) Renacuajos de algunos anfibios de Clarines (Edo. Anzoátegui, Venezuela). *Memorias de la Sociedad de Ciencias Naturales La Salle*, 41, 57–76.
- Ringuelet, R.A. (1961) Rasgos fundamentales de la Zoogeografía argentina. *Physis*, 22, 151–170.
- Sazima, I. & Caramaschi, U. (1986) Descrição de *Physalaemus deimaticus*, sp. n., e observações sobre comportamento deimático em *P. nattereri* (Steindn.) – Anura, Leptodactylidae. *Revista Brasileira de Biologia*, 13, 91–101.
- Scasso, F. (2002) *Ambientes acuáticos de la zona costera de los Humedales del Este. Estado actual y estrategias de gestión*. PROBIDES, Serie Documentos de Trabajo N° 43, Rocha, 44 pp.
- Staton, M.A. & Dixon, J.R. (1977) The Herpetofauna of the Central Llanos of Venezuela: noteworthy records, a tentative checklist and ecological notes. *Journal of Herpetology*, 11, 1, 17–24.
- Straneck R., de Olmedo, E.V. & Carrizo, G.R. (1993) *Catálogo de Voces de Anfibios Argentinos. Parte I*. Editorial L.O.L.A., Buenos Aires, 131 pp.
- Toledo, R.C.D., Jared, C. & Brunner, Jr. (1996) The lumbar glands of the frog *Pleurodema thaul* (Amphibia, Anura, Leptodactylidae): an ultrastructural study. *Revista Brasileira de Biologia*, 56, 451–457.

- Tschudi, J.J. (1838) Classification der Batrachier, mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien. *Mémoires de la Société des Sciences Naturelles de Neuchâtel*, 2, 1–99.
- Úbeda, C.A. (1998) *Batracofauna de los bosques templados patagónicos: un enfoque ecobiogeográfico*. PhD Thesis (unpublished), Fac. Ciencias Exactas y Naturales, Univ. Buenos Aires, 354 pp.
- van der Hammen, T. (1974) The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography*, 1, 3–26.
- Vanzolini, P.E. (1992) Paleoclimas e especiação em animais da América do Sul tropical. *Estudos Avançados* (São Paulo), 6, 41–65.
- Vaz-Ferreira, R. (1984) *Etología: el estudio biológico del comportamiento animal*. OEA, Serie Biología, Monografía 29, Washington, 150 pp.
- Weigandt, M., Úbeda, C.A. & Díaz, M. (2004) The larva of *Pleurodema bufoninum* Bell, 1843, with comments on its biology and on the egg strings (Anura, Leptodactylidae). *Amphibia-Reptilia*, 25, 429–437.
- WWF (World Wildlife Fund) (2008) *Ecoregions. Neotropic*. Available from: <http://www.worldwildlife.org/science/ecoregions/neotropic.cfm> (accessed April 12, 2008).

Appendix 1. Specimens examined

Pleurodema bibroni.—**BRAZIL**: Rio Grande do Sul State: São Francisco de Paula, Boca da Serra, MCN 54; São Francisco de Paula, Veraneio Hampel, MCN 55; Tainhas River, close to Cipó River, MCN 1333; Cambará do Sul, Itaim-bezinho, MCN 2428; São Francisco de Paula, Cazuzza Ferreira, MCN 5533–4, 55367; Nova Petrópolis, Linha Imperial, MCN 7401; Vacaria, MCN 6616–22; Bom Jesus, Fazenda de Ari Velho (34 km from the city), MCN 9847–52; Farroupilha, MCN 5574. **URUGUAY**: Unknown locality, ZVCB 3132; Department of Artigas: Arroyo Tres Cruces, ZVCB 1093; Department of Canelones: Sauce Stream, Pueblo Solís, CENAI 10856; Tropa Vieja Stream, CENAI 4951–64; Atlántida, ZVCB 185; La Tuna Resort, CENAI 4938; Bañados de Carrasco, ZVCB 186; Canelones, CENAI 4236, 4968–70; Canelones City, ZVCB 685; Las Toscas, ZVCB 47–48, 11082–3; Route Interbalnearia, in front of International Airport, CENAI 8057–8; Salinas, MNHN 942; Sauce, MNHN 2102; Department of Durazno: del Estado Stream, CENAI 7483; Department of Florida: Est. San Lorenzo, Reboledo, MNHN 946; Department of Lavalleja: Aiguá, MNHN 2499; Arequita, ZVCB 563, 1791; Minas Viejas Stream, ZVCB 605; Tapes de Godoy Stream, MNHN 945, ZVCB 11096; 15 Km SW Arroyo Tapes Godoy Stream, ZVCB 368, 919; Cañada de los Troncos, Route 8, Km 162, close to Marmarajá Stream, ZVCB 1403; Arequita Hill, MNHN 441; Estancia Bella Vista, Nico Pérez, MNHN 601; Estancia Bella Vista, Nico Pérez, MNHN 706; Estancia La Salvaje, Route 81, 13 Km from intersection with Route 8, MNHN 5522; Cebollatí River, Barra de los Tapes, ZVCB 38; Tapes, ZVCB 803, 11080; Department of Maldonado: unknown locality, MNHN 309 (three specimens); San Antonio Hill, Piriápolis, MNHN 359; Pan de Azúcar, CENAI 11005, MNHN 2063, 2103; Punta del Este, intersection of 11th and 12th streets, ZVCB 3159; Punta José Ignacio, ZVCB 679; headwaters of San Carlos Stream, MNHN 478; Department of Montevideo: Intersection of Gral. Osvaldo Rodríguez avenue and Mendoza street, CENAI 8056; Bañados de Carrasco, ZVCB 184, 548, 11077–8; Barra de Santa Lucía: CENAI 3280, 3309, 3341–4, 3576, 3974, 4173–5, 4216–35, 4237–52, 4926–8, 4966–7, 5043–78, 5103–59, 5203–311, 5330–69, 5407–36, 6155–63, 6170–5, 6184, 6187, 6202–19, 6245–7, 6249–71, 6286, 6313, 6321–2, 6328, 6330, 6332–4, 6339–52, 6357–77, 6379, 6381–2, 6385–6, 6391–400, 6402–3, 6408–17, 6433–7, 6442–6, 6480–7, 6884, 8059–66; Carrasco Street, ZVCB 2025; ZVCB 479, 11064–73, 11079; Carrasco, MNHN 311, 355, 414, 3491; Malvín, ZVCB 377, 684, MNHN 435; Carrasco National Park, ZVCB 380; Bridge over Carrasco Stream, MNHN 1575; Santiago Vázquez, MNHN 6816, CENAI 4934–4937, 5018–42; Department of Rocha: Barra de Valizas, MNHN 6815, 7167 (lot of tadpoles), 7168–7170, ZVCB 1004, 16137; Cerro Verde, MNHN 7352; La Coronilla, MNHN 944; Laguna Garzón, MNHN 329; La Paloma, MNHN 302, 361, ZVCB 17127; La Pedrera, CENAI 8054–5; La Pedrera, CENAI 4939–41; Refugio de Fauna Laguna de Castillos, MNHN 7353; Rocha: MNHN 486; Route 10 Km 255, MNHN 7171; Santa Teresa, Las Achiras Beach, MNHN 6817. Department of San José: Arazatí, MNHN 2612; Autódromo Nacional, Route 1 Km 27.5, ZVCB 3946; Delta del Tigre, MNHN 943; Playa Pascual, CENAI 4176–8; Playa Pascual, 10 Km NW from Santiago Vázquez, ZVCB 2431; Department of Treinta y Tres: Santa Clara de Olimar, ZVCB 413, 11081.

Pleurodema borellii.—**ARGENTINA**: Province of Tucumán: Capital Department: Yerba Buena, MLP A. 3909–10.

Pleurodema bufoninum.—**ARGENTINA**: Province of Chubut: Futaleufú Department: Esquel, MLP DB 2914, 2917.

Pleurodema kriegi.—**ARGENTINA**: Province of Córdoba: Pampa de Achala, FML 02781, MACN 28112–3, 31498–9, 31510–7, 32177–83, 32407–12, 33441–4, MACN 38738, 38740–1, CENAI 02886, 03278, 03289–93, 03556, 04183–215, 04254, 04529–42, 04573–4, 04929–33, 04943–7, 04971–94, 04996–5017, 05079–102, 05160–202, 05312–29, 06150–4, 06176–8, 06182–3, 06197–201, 06224–34, 06275–85, 06287, 06299, 06311–2, 06368, 06378, 06380, 06383, 06401, 06407, 06418–9, 06429–31, 06438–9, 06450–2, 06454, 06459–60, 06501, 06518–20, 06534, 06536–7, 06630, 06659–62, 06698, 06748, 06798–800, 06885–7, 07119, 07127, 07858–60, 08018–30, 08073–4, 08764–72, 08926, 11008, MLP A. 0316–7, MLP A. 3526–9; Pampa de Achala, Cerro La Desgracia, CENAI 06324–5; San Alberto Department: Pampa de Achala, Hotel El Cóndor, CENAI 04925; Pampa de Achala, Monolito, CENAI 04552–60; Pampa de Achala, National Route N° 34, near to La Posta, MLP A. 4762–4; Pampa de Achala, near to Pampilla, MACN 38739; Pampa de Achala, La Posta, CENAI 04942, 04948–50; Parque Nacional Quebrada del Condorito, Pampa de Achala, MLP A 4728, 4729 (lot of tadpoles), 4759–61; Punilla Department: near Río Huastos, Pampa de San Luis, MLP DB 6733; San Agustín Department: Champaquí, CENAI 06192; Rosa de Champaquí, CENAI 05901.

Pleurodema thaul.—**ARGENTINA**: Province of Chubut: Cushamén Department: Lago Puelo: MLP DB 2915

Pleurodema tucumanum.—**ARGENTINA**: Province of La Rioja: Independencia Department: Establecimiento Santa Rosa, National Route 150, km 11, near to Patquía, MLP A 3858, 3863, 3898, 3901.