ZOOTAXA

1927

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(*Zootaxa* 1927)

66 pp.; 30 cm.

7 Nov. 2008

ISBN 978-1-86977-273-4 (paperback)

ISBN 978-1-86977-274-1 (Online edition)

FIRST PUBLISHED IN 2008 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

http://www.mapress.com/zootaxa/

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ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)





Comparative larval morphology of eight species of *Hypsiboas* Wagler (Amphibia, Anura, Hylidae) from Argentina and Uruguay, with a review of the larvae of this genus

FRANCISCO KOLENC^{1,8}, CLAUDIO BORTEIRO², LEANDRO ALCALDE^{3,7}, DIEGO BALDO^{4,7}, DARIO CARDOZO^{5,7} & JULIÁN FAIVOVICH^{6,7}

Table of contents

Abstract	1
Introduction	1
Materials and methods	5
Results	3
Tadpole descriptions	3
Hypsiboas andinus (Müller)	3
Hypsiboas caingua (Carrizo)10)
Hypsiboas cordobae (Barrio)1	1
Hypsiboas faber (Wied-Neuwied)	3
Hypsiboas pulchellus (Duméril & Bibron)1	1
Hypsiboas punctatus rubrolineatus (B. Lutz)10	5
Hypsiboas raniceps Cope1)
Hypsiboas riojanus (Koslowsky)2	5
Remarks30)
Discussion3	1
A review of <i>Hypsiboas</i> tadpoles	5
Concluding remarks39)
Acknowledgments4)
References4)
Appendix 14	5
Appendix 26	1
Appendix 36.	5

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Abstract

We studied the external and oral cavity morphology of the tadpoles of eight species of *Hypsiboas* in the *H. albopunctatus*, *H. faber*, *H. punctatus* and *H. pulchellus* species groups. After a review of the available information about larval external and oral cavity morphology, no character state seems to be synapomorphic for *Hypsiboas*. The presence of a fleshy projection in the inner margin of the nostrils and rounded vacuities of the anteromedial surface of the choanae (pending the confirmation of the latter in *Hyloscirtus* and *Myersiohyla*) seems to be synapomorphic for the tribe Cophomantini, as previously noticed by other authors. Some putative synapomorphies are suggested for some species groups of *Hypsiboas*, but a denser sampling is needed to study the taxonomic distribution of these character states, in order to determine which clades they may support. The presence of lateral flaps with labial teeth in the oral disc is a variable feature of many species in the *H. faber* and *H. pulchellus* groups. A spiracular tube free from the body wall is present in some species, mostly in the *H. albopunctatus* group, but also in the *H. rufitelus*, *H. faber* and *H. pulchellus* groups. Unique ventrolateral cumules of neuromasts are present in *H. faber*, and also in some species of other groups of *Hypsiboas* and of the sister genus *Aplastodiscus*. Our results highlight the importance of studying the taxonomic distribution of many character states that were sometimes overlooked in tadpole descriptions but seem relevant to test phylogenetic hypothesis.

Key words: Cophomantini, Hylinae, *Hypsiboas andinus, Hypsiboas caingua, Hypsiboas cordobae, Hypsiboas faber, Hypsiboas pulchellus, Hypsiboas punctatus rubrolineatus, Hypsiboas raniceps, Hypsiboas riojanus,* larval external morphology, oral papillation, neuromasts

Introduction

The tree frogs of the recently resurrected hylid genus *Hypsiboas* Wagler (Faivovich *et al.* 2005) are common components of Neotropical herpetofauna. The 79 species currently assigned to this genus are distributed in Central and South America, from Nicaragua to central Argentina and the islands of Trinidad and Tobago (Duellman 1970; Cei 1980; Frost 2007). No morphological synapomorphy is known for this genus, which comprises seven species groups: the *H. albopunctatus*, the *H. benitezi*, the *H. faber*, the *H. pellucens*, the *H. pulchellus*, the *H. punctatus* and the *H. semilineatus* groups (Faivovich *et al.* 2005).

Although external morphology information about tadpoles of 49 species of *Hypsiboas* is available from the literature (Appendix 1), we are still lacking accurate descriptions of the external morphology of some of these, and tadpoles of many species are still unknown. The information relative to oral cavity morphology is scarce compared with external morphology descriptions. There are oral cavity descriptions available for the tadpoles of only 14 species of *Hypsiboas* (for a list see Appendix 2—Wassersug 1980; Lavilla & Fabrezi 1987; Spirandeli Cruz 1991; d'Heursel & de Sá 1999; Both *et al.* 2007; Vera Candioti 2007; d'Heursel & Haddad 2007).

Within the *Hypsiboas pulchellus* group, some confusion exists in the literature because six currently recognized species were previously considered subspecies of *H. pulchellus*. The earliest description of tadpoles assigned to this species (as *Hyla raddiana*) by Fernández (1927), was based on samples collected at Sierras de Córdoba and in La Plata, Argentina, which are currently assigned to two different species: *H. cordobae* and *H. pulchellus*, respectively. Gallardo (1961) made a very brief description of the tadpole of *H. pulchellus* (as *Hyla raddiana*) based on samples collected in Buenos Aires, Argentina. Later, B. Lutz (1973) described tadpoles of *H. pulchellus* (as *Hyla pulchella* "Platine form") apparently from La Plata, Buenos Aires Province, Argentina, without illustrations. Echeverría (1992) reported variations in oral structures of tadpoles of *H. pulchellus* collected in La Plata, Argentina. Cei (1980) published an illustration of a lateral view of a tadpole attributed to *H. cordobae* (as *Hyla pulchella cordobae*) without further description, and he also presented an illustration and briefly described the tadpole of *H. andinus* (as *Hyla pulchella andina*). Then, Lavilla (1984) redescribed the latter, together with an analysis of intra and inter population variability of this species in Argentina. Duellman *et al.* (1997) made a thorough redescription of the tadpoles of this species based on

Bolivian samples, but without illustrations. Within the *H. faber* group, the tadpole of *H. faber* was first described by Lutz (1973) without illustrations. Later, Cei (1980) gave a brief description and illustration and Spirandeli Cruz (1991) reported some aspects of external morphology of this species. The examination of various lots of tadpoles recently collected of these species revealed variation of morphological characters not previously reported. Furthermore, considering the briefness of the above mentioned descriptions and the uncertain origin of the samples used in some of them, we believe that a redescription of the tadpoles of *H. andinus*, *H. cordobae*, *H. faber* and *H. pulchellus* in a context of synthesis is needed to aid comparison and identification, and to clarify some character states in light of recent phylogenetic hypotheses (Faivovich *et al.* 2004; Faivovich *et al.* 2005). No information is available about the external morphology of the tadpoles of *H. caingua* and *H. riojanus*, other than a brief description of the former in an unpublished dissertation (Spirandeli Cruz 1991, as *Hyla* sp. aff. *pulchella*). Within the *H. punctatus* group, larvae of *H. punctatus* were described from northern South America (Kenny 1969; Duellman 1978; Hoogmoed 1979; Duellman 2005). The tadpole of the southern subspecies, *H. punctatus rubrolineatus*, is unknown. In order to provide information towards clarifying the taxonomic status of this frog, the description of its larval morphology is desirable.

The goals of this study are to describe the larval external morphology of *Hypsiboas caingua*, *H. cordobae*, *H. punctatus rubrolineatus* and *H. riojanus*, redescribe the external morphology of tadpoles of *H. andinus*, *H. faber* and *H. pulchellus* (the latter from its type locality Montevideo, Uruguay), redescribe the oral cavity of tadpoles of *H. andinus*, *H. caingua* and *H. faber*, provide the description of the oral cavity of tadpoles of *H. cordobae*, *H. pulchellus*, *H. punctatus rubrolineatus*, *H. raniceps* and *H. riojanus*, and to review current knowledge about the tadpoles of the genus *Hypsiboas*.

Materials and methods

Specimens used in the descriptions or examined for comparison are deposited in MACN (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina), MLP (Museo de La Plata, La Plata, Argentina), MLP DB (Diego Baldo Collection, Museo de La Plata,), and ZVCB (Vertebrate Zoology Collection, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay).

The following samples were used for tadpole descriptions: Hypsiboas andinus (MLP DB 4806), N = 10, stages 28-37, collected at Laguna Rodeo, Provincial Park Lagunas de Yala, Departamento Doctor Manuel Belgrano, Jujuy Province, Argentina (24°06'15"S; 65°28'49.3"W), on 26 January 2006 by D. Baldo and J. Faivovich; Hypsiboas caingua (MLP DB 4258), N = 10, stages 31–35, collected at the intersection of Ruta Nacional Nº 12 and Ruta Provincial Nº 3, Departamento Candelaria, Misiones Province, Argentina (27°27'46"S; 55°40'55"W), on 18 October 2005 by D. Baldo, D. Cardozo, C. Borteiro and F. Kolenc; *Hypsi*boas cordobae (MLP DB 4722), N = 10, stages 30-35, collected at Río Toro Muerto, Flor Serrana, Tanti, Departamento Punilla, Córdoba Province, Argentina (31°23'00"S; 64°36'20"W), on 25 December 2005 by D. Baldo, S. Rosset, J. Boeris and J. Lescano; Hypsiboas faber (MACN 35116), N = 10, stages 27–37, collected at Campo Anexo INTA "Cuartel Río Victoria", San Vicente, Departamento Guaraní, Misiones Province, Argentina (26°55'S; 54°25'W), by J. Faivovich; Hypsiboas pulchellus (ZVCB 16147), N = 10, stages 31–35, collected at the intersection of Camino Tomkinson and Camino O'Higgins, Montevideo, Departamento de Montevideo, Uruguay, on 19 August 2005 by C. Borteiro and M. Nava; Hypsiboas punctatus rubrolineatus (MLP DB 4548), N = 4, stages 28–36, collected at Antequera, Camino a Isla Cerrito, outskirts of Resistencia, Departamento San Fernando, Chaco Province, Argentina (27°25'43"S; 58°52'11"W), on 25 November 2005 by D. Baldo, C. Borteiro, D. Ferraro, F. Kolenc, E. Kubisch and M. Tedros and Hypsiboas riojanus (MLP DB 2440), N = 10, stages 27-35, collected at km 527, Ruta Nacional N° 40, near to El Siciliano, Sierras de Famatina, Departamento Famatina, La Rioja Province, Argentina, on 26 October 2003 by D. Baldo, B. Blotto and S. Cairo. Additional specimens in earlier or later stages of development studied to address ontogenetic variation and specimens of other species used for comparison are listed in Appendix 3.

Additionally, one or two specimens per species were prepared for the scanning electron microscope (SEM) examination of the features of the oral cavity morphology and keratinized structures of the oral disc following the protocol by Alcalde and Blotto (2006).

The vouchers for the material used for SEM observations are the following: *Hypsiboas andinus* (MLP 3336), N = 2, stages 31 and 38, collected at La Caldera, Salta Province, Argentina, on November 2001 by L. Alcalde and G. Finarelli; *Hypsiboas caingua* (MLP DB 4258), N = 1, stage 36; *Hypsiboas cordobae* (MLP 3337), N = 2, stages 26 and 35, collected at Tanti Stream, Tanti, Córdoba Province, Argentina, on February 2002 by L. Alcalde and G. Finarelli; *Hypsiboas faber* (MACN 35116), N = 1, stage 36; *Hypsiboas pulchellus* (MLP 3339), N = 1, stage 30, collected at Punta Lara, La Plata, Buenos Aires Province, Argentina by L. Alcalde; *Hypsiboas pulchellus* (ZVCB 16147), N = 1, stage 30; *Hypsiboas punctatus rubrolineatus* (MLP DB 4548), N = 1, stage 28; *Hypsiboas raniceps* (MLP 3493), N = 1, stage 26, collected at Ituzaingó, Corrientes Province, Argentina, by L. Alcalde; *Hypsiboas riojanus* (MLP DB 3303), N = 1, stage 26.

Morphological terminology follows that of Altig and McDiarmid (1999a). Lateral line system nomenclature follows that of Lannoo (1987). We use the term "flap" in the sense of Duellman et al. (1997) to refer to the oral structures which resemble broad papillae, usually laterally on the oral disc, which possess labial teeth. Oral cavity morphology terms follow those proposed by Wassersug (1980), and the following abbreviations were used: buccal roof arena (BRA) and buccal floor arena (BFA). Tadpole developmental stages follow Gosner (1960) staging table. Tadpoles were measured to the nearest 0.1 millimeter using an ocular micrometer in a stereoscopic microscope Nikon SMZ-10 or Leica MZ6, except for total length which was measured with calipers. Six measurements were recorded according to Altig and McDiarmid (1999a): total length (TL), body length (BL), tail length (TaL), maximum tail height (MTH), internarial distance (IND, modified from Altig & McDiarmid 1999a: measured between the internal edges of narial apertures), and tail muscle height (TMH). Fourteen additional measures were recorded according to 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-ocular distance (EO, measured between the external edges of pupils), intraocular distance (IO, distance between interior edges of eyes), extranasal distance (EN, distance between external edges of nares), oral disc width (OD) and dorsal gap length (DG). Measurements are given in Table 1. The oral disc was stained with a 1% methylene blue solution to observe the papillation with a stereomicroscope. Additionally, at least one oral disc of every studied species was observed with SEM following the protocol and employing the specimens cited above for SEM observations of the oral cavity morphology. Drawings were made with the help of a drawing tube attached to the stereomicroscope. Identification of the larvae was based on some specimens reared in captivity to metamorphosis.

Throughout this paper we followed the taxonomic arrangement of Hylidae proposed by Faivovich *et al.* (2005). More recently Wiens *et al.* (2006) published as supplementary information, and without any substantial discussion pertaining hylid relationships, the reanalysis of the data employed by Faivovich *et al.* (2005) plus that published by Wiens *et al.* (2005). While the results are overall quite congruent, there are some differences in the relationships within *Hypsiboas*. Unfortunately, the results of Faivovich *et al.* (2005) and Wiens *et al.* (2006) are not directly comparable as both were obtained using different methods and under very different analytic assumptions. Here we follow the group arrangements of Faivovich *et al.* (2005), but comment when appropriate differences emerge with the results of Wiens *et al.* (2006). Except for the eight species whose tadpoles are described herein, species authorships are not mentioned in the text, but are given in Appendices 1 and 2.

Table 1. Measurements (in millimeters) of the tadpoles of seven species of Hypsiboas (mean ± standard deviation, range given in parenthesis). variables are defined in the text.

	Hypsiboas andinus	Hypsiboas caingua	Hypsiboas cordobae	Hypsiboas faber	Hypsiboas	Hypsiboas punctatus	Hypsiboas riojanus
Variable	N = 9, stages 33-37	N = 10, stages 31-35	N = 10, stages 30-35	N = 5, stages 33-37	pulchellus $N = 10$, stages 31-35	rubrolineatus $N = 4$, stages 28-36	N = 9, stages 31-35
TI	$49.5 \pm 5.9 (42.1 -$	$42.0 \pm 3.6 (36.3 -$	$56.5 \pm 4.7 (49.0 -$	$79.6 \pm 4.1 \ (75.3 - 1)$	$53.1 \pm 4.3 (48.0 -$	$34.1 \pm 5.4 (26.7$ -	$58.5 \pm 5.5 (44.5 -$
	61.5)	48.2)	62.8)	86.0)	62.0)	38.4)	63.7)
BL	$17.0 \pm 1.9 (15.3 - 20.9)$	$13.6 \pm 1.1 (11.9 - 15.6)$	$17.8 \pm 1.7 (15.0 - 20.0)$	$25.1 \pm 1.9 (23.4 - 7.79)$	$16.2 \pm 0.8 (14.9 - 18.1)$	$11.8 \pm 1.8 \ (9.4-13.6)$	$20.2 \pm 1.7 (15.7 - 21.8)$
F	$32.6 \pm 4.1 (26.8 -$	$28.4 \pm 2.5 (24.4 - 1)$	$38.7 \pm 3.3 (34.0 -$	$54.5 \pm 3.0 (51.0$	$36.9 \pm 3.7 (31.9 -$	$22.3 \pm 3.6 (17.3 - 19.3)$	$38.3 \pm 4.0 (28.8 -$
IaL	40.6)	32.6)	42.8)	58.1)	43.9)	25.2)	42.1)
MTH 1	$11.3 \pm 1.4 \ (9.7 - 13.7)$	$9.1 \pm 0.7 \ (8.0 - 10.0)$	$12.2 \pm 0.9 (10.9 - 13.2)$	$15.9 \pm 1.3 (14.8 - 17.4)$	$11.1 \pm 0.6 (10.3 - 12.4)$	$7.0 \pm 1.0 \ (5.7-7.9)$	$12.3 \pm 0.9 (10.8 - 13.7)$
IND	$2.9 \pm 0.2 (2.5 - 3.3)$	$2.4 \pm 0.2 (2.2 - 2.7)$	$2.9 \pm 0.2 (2.7 - 3.3)$	$3.9 \pm 0.2 (3.8-4.1)$	$2.6 \pm 0.2 (2.2 - 2.9)$	$2.4 \pm 0.5 (1.7-2.7)$	$3.3 \pm 0.4 (2.2 - 3.8)$
TMH	$5.6 \pm 0.9 \ (4.8-7.3)$	$3.9 \pm 0.4 (3.2 - 4.5)$	$6.0 \pm 0.6 \ (4.7 - 6.8)$	$9.3 \pm 1.2 (11.4 - 9.3)$	$5.9 \pm 0.4 (5.4 - 7.0)$	$3.5 \pm 0.7 (2.5 - 4.1)$	$6.9 \pm 0.9 (5.4 - 8.3)$
BMW	$12.2 \pm 1.4 (10.6 - 15.1)$	$9.1 \pm 0.8 \ (7.6 - 10.3)$	$12.0 \pm 1.3 \ (9.8-14.4)$	$16.5 \pm 2.4 (14.2 - 19.6)$	$9.5 \pm 0.4 \ (9.0 - 10.1)$	$7.8 \pm 1.2 \ (6.0-8.6)$	$14.7 \pm 1.3 (11.6 - 16.2)$
BWN	$6.8 \pm 0.5 (6.2 - 7.9)$	$5.2 \pm 0.5 (4.6 - 6.3)$	$8.3 \pm 0.8 \ (6.8-9.1)$	$9.3 \pm 1.0 (8.3-11.1)$	$6.4 \pm 0.4 (6.1-7.0)$	$5.5 \pm 1.0 \ (4.0 - 6.3)$	$8.2 \pm 0.6 (7.1 - 8.7)$
BWE	9.3 ±1.0 (8.1–11.4)	$7.3 \pm 0.6 (6.3 - 8.3)$	$10.5 \pm 1.1 \ (8.6-12.4)$	$12.8 \pm 1.2 (11.8 - 14.8)$	$8.3 \pm 0.4 (7.7-9.0)$	$7.2 \pm 1.3 (5.3-8.2)$	$11.2 \pm 0.9 \ (9.0 - 11.9)$
BMH 1	$10.5 \pm 1.3 \ (8.7 - 12.7)$	$8.3 \pm 0.9 \ (7.1-9.7)$	$11.3 \pm 1.5 \ (9.1-13.6)$	$13.9 \pm 1.7 (12.4 - 16.2)$	$8.9 \pm 0.5 \ (8.3 - 10.0)$	$6.3 \pm 0.8 \ (5.1-7.0)$	$12.6 \pm 1.1 \ (10.2 - 14.3)$
RSD 1	$10.8 \pm 0.9 \ (9.8 - 12.7)$	$10.3 \pm 0.6 \ (9.5-11.2)$	$13.4 \pm 1.0 (11.8 - 14.4)$	$19.1 \pm 1.1 (18.0 - 21.0)$	$11.9 \pm 0.5 (11.1 - 12.9)$	$8.4 \pm 1.1 \ (6.8-9.5)$	$13.0 \pm 1.2 (10.5 - 14.3)$
FN	$2.1 \pm 0.3 (1.9 - 2.7)$	$1.4 \pm 0.2 (1.1-1.9)$	$2.3 \pm 0.3 \ (1.9 - 2.6)$	$2.6 \pm 0.4 (2.3-3.3)$	$1.7 \pm 0.2 (1.2 - 2.0)$	$1.4 \pm 0.4 (1.0 - 1.8)$	$2.7 \pm 0.3 (2.4 - 3.2)$
END	$1.5 \pm 0.2 (1.3 - 1.7)$	$1.0 \pm 0.1 \ (0.9 - 1.1)$	$2.1 \pm 0.2 \ (1.7 - 2.5)$	$2.2 \pm 0.2 (2.0-2.3)$	$1.5 \pm 0.1 \ (1.2 - 1.6)$	$1.1 \pm 0.2 \ (0.8 - 1.3)$	$2.0 \pm 0.3 (1.6 - 2.4)$
Z	$0.8 \pm 0.1 \ (0.6 - 1.0)$	$0.8 \pm 0.1 \ (0.6 - 0.9)$	$0.8 \pm 0.1 \ (0.7 - 1.0)$	$1.4 \pm 0.1 (1.2 \text{-} 1.5)$	$0.8 \pm 0.1 \ (0.7 - 0.9)$	$0.5 \pm 0.1 \ (0.5 - 0.6)$	$0.7 \pm 0.1 \ (0.6 - 0.8)$
A	$2.3 \pm 0.3 (1.9 - 2.7)$	$2.0 \pm 0.2 \ (1.8 - 2.2)$	$2.4 \pm 0.1 \ (2.2-2.6)$	$2.6 \pm 0.2 (2.3-2.9)$	$2.3 \pm 0.1 \ (2.1-2.5)$	$1.7 \pm 0.3 (1.4 - 2.1)$	$2.4 \pm 0.2 (1.9 - 2.7)$
EO	$6.8 \pm 0.8 (5.7 - 8.3)$	$6.6 \pm 0.5 (5.8 - 7.6)$	$8.7 \pm 0.6 \ (7.4-9.5)$	$10.1 \pm 0.6 (9.7 - 11.2)$	$7.2 \pm 0.3 (6.6 - 7.8)$	$5.0 \pm 0.7 \ (4.0 - 5.7)$	$8.3 \pm 0.5 (7.0 - 8.7)$
01	$3.5 \pm 0.5 (2.7 - 4.3)$	$3.9 \pm 0.4 (3.4 - 4.5)$	$5.5 \pm 0.4 \ (4.8 - 5.9)$	$6.6 \pm 0.4 (6.1-7.1)$	$4.3 \pm 0.2 (3.8 - 4.6)$	$2.8 \pm 0.4 (2.3-3.1)$	$5.0 \pm 0.4 (4.3-5.4)$
EN	$3.9 \pm 0.5 (3.5 - 5.1)$	$3.5 \pm 0.2 (3.1 - 4.0)$	$4.2 \pm 0.2 \ (3.8 - 4.6)$	$6.1 \pm 0.3 (5.6 - 6.4)$	$3.8 \pm 0.2 (3.5 - 4.1)$	$3.1 \pm 0.5 (2.4-3.5)$	$4.4 \pm 0.4 (3.7 - 4.8)$
OD	$4.3 \pm 0.7 (3.5 - 5.9)$	$3.2 \pm 0.6 (2.6 - 4.7)$	$4.7 \pm 0.6 (3.9 - 6.0)$	$6.1 \pm 0.1 \ (6.0 - 6.2)$	$4.1 \pm 0.3 (3.7 - 4.6)$	$3.6 \pm 0.6 (2.6 - 4.0)$	$4.9 \pm 0.5 (3.9 - 5.6)$
DG	$1.3 \pm 0.3 (1.0 - 2.1)$	$0.6 \pm 0.1 \ (0.4-0.8)$	$1.3\pm0.3\ (1.0-1.9)$	$1.5 \pm 0.2 (1.3-1.7)$	$1.2 \pm 0.3 \ (0.8 - 1.8)$	$1.0 \pm 0.4 \ (0.7 - 1.5)$	$1.9\pm0.4\ (1.3-2.5)$

Results

Tadpole descriptions

Hypsiboas andinus (Müller)

Figs. 1A, 1B and 3A.

External morphology.— Lot MLP DB 4806, Figs. 4A and 4B. Body depressed (BMH/BMW = 0.86 ± 0.04); body length little longer than one third of total length (BL/TL = 0.34 ± 0.01); body shape ovoid in dorsal view; widest at posterior third of body, behind spiracle. In lateral view, ventral contour of body flat in gular and branchial regions, convex in abdominal region. Dorsal contour of body slightly convex from eyes to origin of dorsal fin. Snout semicircular in dorsal view, rounded in lateral view. Nostrils oval, with thin pigmented marginal rim, with a small subtriangular fleshy projection in medial margin (Fig. 18A); nostrils dorsolaterally located (EN/BWN = 0.58 ± 0.04), placed in a depression and closer to eyes than to the tip of the snout (FN/ END = 1.45 ± 0.18), more visible in dorsal than in lateral view. Eyes large (E/BWE = 0.24 ± 0.02), dorsally positioned (EO/BWE = 0.73 ± 0.03), dorsolaterally directed, not visible in ventral view. Spiracle single, lateral and sinistral; its inner wall fused to body except for its distal end (Fig. 17A); its opening oval, slightly elevated, with a diameter smaller than tube diameter, located between second and posterior thirds of body (RSD/ BL = 0.64 ± 0.02), posterodorsally directed, visible in lateral and dorsal views. Lateral line system visible. Intestinal assa located at centre of abdominal region. Vent tube starts at midline, at posterior end of body, reaching free margin of lower fin, opening dextral. Tail large (TaL/TL = 0.66 ± 0.01), with both fins a little higher than body height (MTH/BMH = 1.07 ± 0.07). Dorsal fin originates at tail-body junction. Edge of dorsal fin slightly convex, free margin of ventral fin almost flat. Tail axis straight, tail tip pointed; tail musculature reaching tail tip. Oral disc (Fig. 8A) anteroventral, small (OD/BMW = 0.35 ± 0.02 , disc measured folded), with a well marked infra-angular constriction at each side (also a less marked supra-angular constriction in two specimens). Marginal papillae simple, longer than wide, with rounded or pointed tip. Dorsal gap present, medium-sized (DG/OD = 0.31 ± 0.05). Row of marginal papillae single or double; some infraangular submarginal papillae present. Upper jaw sheath widely arch-shaped, with a slightly convex medial region in one specimen. Lower jaw sheath with free margin U-shaped. Both jaw sheaths well developed, serrated and heavily pigmented in the distal half (upper one) or third (lower one). Labial tooth row formula 2(2)/4(1). A1 bent with an angle directed to the front. Length of P4 about half to one third of P3. In four specimens, P4 appears fragmented. Some lateral flaps or submarginal papillae with labial teeth are present. Tooth of all rows with spatulate and convex heads bearing 6–8 well-marked cusps (Fig. 10A).

Coloration in preservative.— Body light brown, with dark brown spots on dorsal and dorsolateral regions of body. A dark brown, triangular interocular spot, with the base directed backwards. Perinasal region dark brown. Ventral region transparent. Caudal musculature brown in dorsal view, whitish in lateral view with small dark blotches that coalesce forming a reticulation. A black horizontal band runs between epi- and hypaxial musculature for first third of the tail's length. Fins opalescent with few dark flecks, more abundant in dorsal fin.

Variation.— Lot MLP DB 5520. In two specimens (stages 33 and 36) the A1 and A2 tooth row are abnormally arranged.

Oral cavity morphology.— (Figs. 11A and 13A). Buccal roof: Prenarial arena presents a low transversal crest and some pustules surrounding it. Choanae transversely oriented, with anteromedial and rounded vacuities, posterior margins forming the narial valves, and both margins undulated by the presence of small prenarial pustules, in particular the anterior one. Postnarial arena presents 8 conical papillae forming an arch between the lateral ridges. There are some pustules arranged among the postnarial papillae. The low, rounded and wide median ridge presents short undulations on its free margin. Each square-shaped lateral ridge papilla

possess about 4–5 projections on the free margin, none of them predominant in size. There are approximately 160 pustules and 40 long and conical papillae on the buccal roof arena (BRA). The pustules are mainly on the central region and the papillae on the posterior and most lateral areas of the arena placed in a "V" arrangement. Posterior area of the roof with secretory pits and medially interrupted dorsal velum with lobated margins.

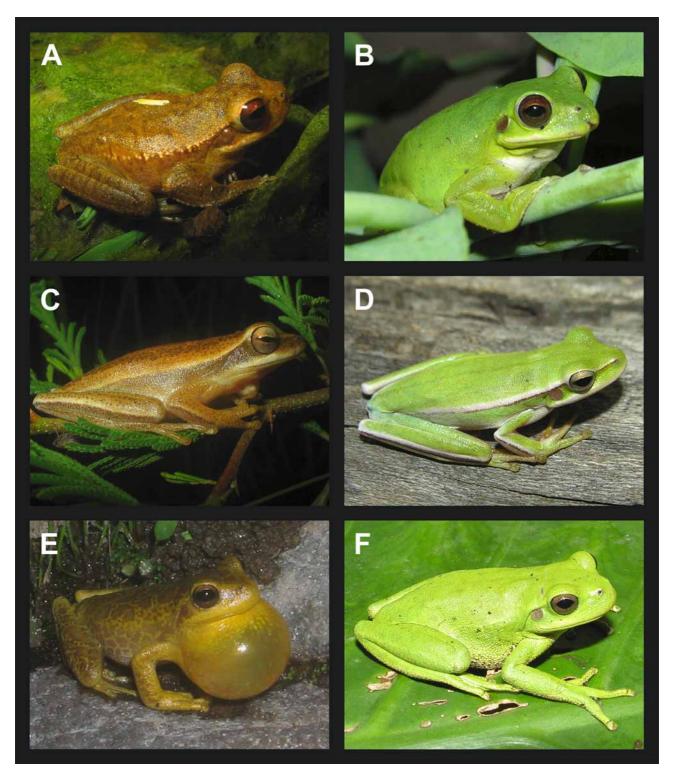


FIGURE 1. Adult specimens of species of *Hypsiboas* studied in this paper. (A) *H. andinus*, Encón Grande, Province of Salta, Argentina. (B) *H. andinus*, Sierra de Metán, Province of Salta, Argentina. (C) and (D) *H. caingua*, Departamento Candelaria, Province of Misiones, Argentina. (E) *H. cordobae*, Inti Huasi, Province of San Luis, Argentina. (F) *H. cordobae*, El Cóndor, Province of Córdoba, Argentina.

Buccal floor: Infralabial papillae on infrarostral cartilages absent. There are two long and digitiform infralabial papillae placed at the level of cartilago meckeli. The lingual anlage bears 2 long and conical lingual papillae placed very close to each other and practically fused at the midline in some specimens. Buccal pockets mostly transversal to the axial axis. Prepocket area with 4 long and 14 short conical papillae and about 80 pustules. There are 20 long and conical papillae (two of them bifid), 26 short and conical papillae and about 190 pustules on the buccal floor arena (BFA). The papillae arrange in one anterior and other posterior V-shaped patterns. The ventral velum has a weakly-marked median notch, three poorly-developed marginal projections at each side of the posterior margin and many secretory pits.

Hypsiboas caingua (Carrizo)

Figs. 1C and 1D

External morphology. — Lot MLP DB 4258, Figs. 4C and 4D. Body slightly depressed (BMH/BMW = $0.90 \pm$ 0.04); body length little less than one third of total length (BL/TL = 0.32 ± 0.01); body ovoid in dorsal view; widest at posterior third of body. In lateral view, ventral contour of body flat or slightly concave in gular and branchial regions, convex in abdominal region. Dorsal contour of body convex. Snout acutely rounded in dorsal view, rounded in lateral view. Nostrils oval, with a subtriangular or rounded elevated projection in medial margin (Fig. 18B); nostrils dorsolaterally located (EN/BWN = 0.68 ± 0.04), placed in a depression, closer to eyes than to the tip of snout (FN/END = 1.38 ± 0.24), more visible in dorsal than in lateral view. Eyes large $(E/BWE = 0.27 \pm 0.01)$, dorsally positioned $(EO/BWE = 0.91 \pm 0.02)$, laterally oriented, external edge of corneas visible in ventral view. Spiracle single, lateral and sinistral; it projects a tube posterodorsally directed, with its internal wall free from body; its opening oval, with a diameter smaller than or equal to tube diameter, located in posterior third of body (RSD/BL = 0.76 ± 0.05), visible in dorsal and lateral views. Lateral line system visible. Infraorbital line runs in a groove which is evident from anterior edge of nostrils to behind posterior edge of eyes (Fig. 19A). Intestinal assa located at centre of abdominal region. Vent tube starts at midline, at the posterior end of body, reaches margin of the lower fin and opens dextrally. Tail large (TaL/TL = $0.68 \pm$ 0.01), with both fins higher than body height (MTH/BMH = 1.10 ± 0.06). Dorsal fin originates at the end of body; its origin is abrupt in some specimens. Ventral fin origin concealed by vent tube. Tail axis straight, tail tapering markedly in last half; end acute; tail musculature reaching tail tip. Oral disc (Figs. 8B and 9A) anteroventral, small (OD/BMW = 0.35 ± 0.05 , disc measured folded) with a well marked infraangular constriction on each side. Marginal papillae simple, longer than wide, subconical, with rounded tip. Dorsal gap present, but small (DG/OD = 0.20 ± 0.03). Row of marginal papillae single on both sides of the dorsal gap, double at angular regions and simple or double at posterior margin of oral disc; some infraangular submarginal papillae present. Upper jaw sheath widely arch-shaped. Lower jaw sheath with free margin V-shaped. Both jaw sheaths well developed, serrated but sparsely pigmented distally. Labial tooth row formula 2(1,2)/ 3(1) (six specimens), 2(1,2)/3 (two specimens), 2(1,2)/3(1,2) (one specimen) or 2(1,2)/0 (one specimen, posterior rows likely lost). Length of P3 about one third the length of other rows of labial teeth.

Coloration in life.— Body yellowish brown in dorsal view, with small dark blotches that coalesce forming a reticulation which is more noticeable laterally. A dark brown, triangular interocular spot, with the base directed backwards. Nostrils surrounded by a dark brown region. Lateral sides of body, head and proximal third of caudal musculature with golden, copper and silver spots and blotches. Gular region transparent. Branchial region with white spots. Abdominal surface white. Caudal musculature yellowish brown, with a black horizontal line between hypaxial and epaxial musculature, that runs for about one third of its length. Distal third of caudal epaxial musculature with dark blotches. Tail fins translucent, with rounded dark brown spots. Iris golden, with four dark zones at the edges of the eye, at the end of imaginary horizontal and vertical rays arising from the pupil.

Coloration in preservative.—Body dark brown with unpigmented regions. Small dark spots on dorsal and dorsolateral regions of body. Ventral region transparent. Caudal musculature with dark irregular bands in lateral and dorsal views. Fins opalescent with irregular dark blotches.

Variation.— Lot MLP DB 5052. LTRF 2(1,2)/3(1) in all specimens. Submarginal papillae absent in two specimens (stages 27 and 34), present in the other two (stages 35 and 38). Some labial teeth between upper jaw sheath and A2 on one side of the oral disc in one individual (stage 34).

Oral cavity morphology.— (Fig. 11B and 13B).

Buccal roof: There are 8 blunt pustules irregularly distributed on the prenarial arena. These pustules do not form a clear prenarial transversal crest, however there are 3–4 of them arranged in the same position that the crest of the previous species. Choanae transversely oriented, with anteromedial and rounded vacuities, posterior margins forming the narial valves, and both margins undulated by the presence of small prenarial pustules, in particular the anterior one. On the postnarial arena, there are 16 pustules and 6 short and blunt papillae. The low, rounded and wide median ridge presents 17 short undulations on its free margin. Each square-shaped lateral ridge papilla possess about 5–6 projections on the free margin, one of them very large. The BRA is not defined, because of the absence of papillae. There are approximately 180 pustules and a few short and conical papillae on the buccal floor; the pustules are mostly on the central region, but there are some in the lateral region forming a continuum with the former. Posterior area of the roof with secretory pits, and dorsal velum bearing lobated margins.

Buccal floor: Infralabial papillae on infrarostral cartilages absent. There are two long and digitiform infralabial papillae placed at the level of cartilago meckeli (not figured). The lingual anlage bears 2 long and conical lingual papillae placed very close to each other. Buccal pockets mostly transversal to the axial axis. Prepocket area scattered with 42 pustules and 24 conical papillae, four of them long. There are 5 long and 7 short conical papillae, and about 160 pustules on the BFA. The papillae are arranged in two V-shaped patterns, one anterior and other posterior. The ventral velum has a weakly-marked median notch, three poorly-developed marginal projections at each side of the posterior margin and many secretory pits.

Hypsiboas cordobae (Barrio)

Figs. 1E, 1F, 3B and 3C

External morphology. — Lot MLP DB 4722, Figs. 5A and 5B. Body slightly depressed (BMH/BMW = $0.94 \pm$ 0.03); body length little less than one third of total length (BL/TL = 0.31 \pm 0.01); body oval in dorsal view, widest at middle or posterior thirds of body. In lateral view, ventral contour of body flat in gular and branchial regions, slightly convex in abdominal region. Dorsal contour of body almost flat and sloping from nostrils to origin of dorsal fin. Snout semicircular in dorsal view and rounded in lateral view. Nostrils oval, with a thin marginal rim, with a small rounded fleshy projection in medial margin; nostrils dorsolaterally located (EN/ BWN = 0.51 ± 0.03), placed in a depression and closer to eyes than to the tip of snout (FN/END = $1.10 \pm$ 0.17), more visible in dorsal than in lateral view. Eyes large (E/BWE = 0.23 ± 0.02), dorsally positioned (EO/ BWE = 0.83 ± 0.03), laterally directed, not visible in ventral view. Spiracle single, lateral and sinistral; its inner wall fused to body except for its very distal end; its opening oval, slightly elevated, with a diameter smaller than tube diameter, located in posterior third of body (RSD/BL = 0.76 ± 0.05), posterodorsally directed and visible in lateral and dorsal views. Lateral line system visible. Intestinal assa located at centre of abdominal region. Vent tube starts at midline, at posterior end of body, reaching free margin of lower fin, opening dextral. Tail large (TaL/TL = 0.69 ± 0.01), with both fins higher than body height (MTH/BMH = 1.09± 0.08). Dorsal fin originates on end of body. Ventral fin origin concealed by vent tube. Edges of both fins subparallel for first and second thirds, convergent in last third. Tail axis straight, tail tip acute or slightly rounded; tail musculature reaching tail tip. Oral disc (Fig. 8C) anteroventral, small (OD/BMW = 0.39 ± 0.04 ,

disc measured folded), with a well marked infraangular and a less evident supraangular constriction. Marginal papillae simple, longer than wide, subconical, with rounded tip. Dorsal gap present, but small (DG/OD = 0.29 ± 0.06). Row of marginal papillae single on both sides of dorsal gap, double at angular regions and double or single at posterior margin of oral disc; some infraangular submarginal papillae usually present. Upper jaw sheath widely arch-shaped. Lower jaw sheath with V-shaped free margin. Both jaw sheaths well developed, but upper one appears smooth and sparsely pigmented distally, while inferior one is finely serrated. Labial tooth row formula 2(2)/3(1). A1 bent at the middle with an angle directed to the front. Length of P3 about half the length of P2. Most specimens have short flaps with labial teeth at angular regions, unconnected with main rows. Tooth of all rows with spatulate, convex heads bearing 8–10 well marked cusps (Fig. 10B).

Coloration in life.— Body light brown with small dark dots, more abundant in central region, a dark triangle between the eyes. Perinasal region dark brown. Gular region with small dark dots. Abdominal region whitish. Caudal musculature dark brown in dorsal view, orange-brown in lateral view, with a black horizontal band between epi- and hypaxial musculature running for first third of the tail's length. Small golden flecks on dorsal and lateral sides of body and tail musculature. Fins translucid with golden dots. Iris gold, with three radial black dots arising from the pupil (a fourth dorsal dot is not evident).

Coloration in preservative.— Body dark brown in dorsal and lateral views with barely evident small dots. Abdominal region whitish. Caudal musculature in dorsal view dark brown; yellowish brown in lateral view, with rounded unpigmented regions and distal third entirely dark brown. A black horizontal band runs between epi- and hypaxial musculature for first third of the tail's length. Fins opalescent with few dark flecks, more abundant in dorsal fin.

Variation.— Lot MLP DB 3280. Supraangular constrictions on both sides of oral disc are more evident than in lot MLP DB 4722. Perioral region pigmented. Some specimens lack submarginal papillae. Jaw sheaths smooth and almost lacking pigmentation. All specimens lacking lateral flaps with labial teeth.

Oral cavity morphology.— (Fig. 11C and 13C).

Buccal roof: Prenarial arena with a low and wide transversal crest and some pustules surrounding it. Choanae transversely oriented, with anteromedial and rounded vacuities, posterior margins forming the narial valves, and both margins undulated by the presence of small prenarial pustules, in particular the anterior one (Fig. 16 A, B). There are about 16 pustules and 8 short papillae on the postnarial arena. The set of postnarial papillae are arranged transversely. The most lateral papilla of each side is bifid. Each square-shaped lateral ridge papilla possesses 4–5 digitiform projections on the free margin, any of them predominant in size. The low, rounded and wide median ridge presents 17 undulations on its free margin. There are about 96 pustules and 44 short and conical papillae placed in the central region of the BRA. Almost all papillae are placed in the lateral regions and on the posterior margin of the arena. Posterior area of the roof with secretory pits and dorsal velum bearing lobated margins.

Buccal floor: Infralabial papillae on the infrarostral cartilages absent. There are two long and digitiform infralabial papillae placed at the level of cartilago meckeli (not figured). The lingual anlage bears 2 long and conical lingual papillae. Buccal pockets mostly transversal to the axial axis. Prepocket area bears 40 pustules and 44 conical papillae, two of them longer and bifid. There are 25 conical papilla of moderate size (6 of them longer than the rest), and about 50 pustules on the BFA. The papillae arranged in two V-shaped patterns but not as clear as in other species. There is a flap (that resembles the lateral ridges of the roof), bearing 5 projections on its free end, and placed posterior to the medial flange of each pocket. The ventral velum has a well-marked median notch, three poorly-developed marginal projections at each side of the posterior margin and many secretory pits.

External morphology. — Lot MACN 35116, (Figs. 5C–E). Body depressed (BMH/BMW = 0.86 ± 0.03); body length little less than one third of total length (BL/TL = 0.31 ± 0.01); body shape oval in dorsal view, widest behind the eyes. In lateral view, ventral contour of body slightly concave in gular and branchial regions, convex in abdominal region. Snout rounded in dorsal and lateral views. Dorsal contour of body almost flat from eyes to origin of dorsal fin. Nostrils oval, rimmed, with triangular elevated projection in the medial margin (Fig. 18C); nostrils dorsolaterally located (EN/BWN = 0.67 ± 0.05), placed in a depression, closer to eyes than to the tip of snout (FN/END = 1.20 ± 0.17), more visible in dorsal than in lateral view. Eyes large (E/BWE = 0.19 ± 0.02), dorsally positioned (EO/BWE = 0.79 ± 0.03), dorsolaterally directed, not visible in ventral view. Spiracle single, lateral, sinistral and short; its inner wall fused to body except for a variable length at its distal end; its opening oval, elevated, with diameter slightly smaller than tube diameter, located in posterior third of body (RSD/BL = 0.74 ± 0.03), posterodorsally directed, visible in lateral and posterior views. Lateral line system visible with a unique pattern of ventrolateral aggregations of neuromasts at each side of the body, near the body-tail junction (Figs. 15 A–E and 20A). Intestinal assa located approximately at centre of abdominal region. Vent tube starts at midline, at the posterior end of the body, reaches free margin of lower fin, opening dextral. Tail large (TAL/TL = 0.69 ± 0.01), with both fins higher than body height (MTH/BMH = 1.12 ± 0.05). Dorsal fin originates at tail-body junction. Ventral fin origin concealed by vent tube. Tail axis straight, edges of both fins subparallel, converging at posterior third, end acutely rounded; tail musculature reaching tail tip. Oral disc (Figs. 8D and 9B) anteroventral, not visible dorsally, small (OD/BMW = 0.39 ± 0.04), ventrolateral folds present, well marked infraangular constriction at each side of the oral disc. Marginal papillae simple, longer than wide, subconical, with rounded tip. Dorsal gap present, but small (DG/OD = 0.23 ± 0.03). Row of marginal papillae single or alternate on both sides of the dorsal gap, usually double at the angular regions and double or single in the posterior margin of the oral disc except at midline where they are sparse and separated in most specimens, very short ventral gap present in two specimens (stages 28 and 33); some infraangular submarginal papillae are usually present. Upper jaw sheath widely arch-shaped. Lower jaw sheath with V-shaped free margin. Jaw sheaths well developed, serrated and heavily pigmented distally. Labial tooth row formula 2(2)/4(1). Length of P4 one quarter to half the length of P2, usually fragmented. Most of the specimens have short flaps with labial teeth at the angular regions, unconnected with main rows. Tooth of all rows spatulate and slightly concave bearing 5–10 poorly-marked distal cusps (Fig. 10C).

Coloration in preservative. — Tadpoles at stages 25–27 body brown, venter translucent, tail and fins black, specially the distal half (Fig. 5E). Tadpoles at later stages (33–37) body dark brown with inconspicuous dark dots in head and snout, tail light brown, with scattered dark blotches in proximal third, with dark reticulation in distal third (tail light brown with rounded dark blotches in some specimens). Belly dark. All specimens have an unpigmented spot ventrolaterally on each side of the abdomen representing aggregations of neuromasts randomly distributed.

Variation.— Lot MLP DB 5410, N = 8, stages 25–27; and MLP DB 3890, N = 3, stages 28–34. All tadpoles LTRF 2(2)/4(1) —except for one tadpole stage 33 in which oral structures are destroyed. P4 very short. Row of marginal papillae single or double, usually double in angular regions, dorsal gap present in all specimens, very short ventral gap in three specimens (with one papilla in the middle in two of them, stages 26 and 28), papillae sparse in the middle of the posterior border of the oral disc in all other specimens, usually with submarginal papillae laterally. Lateral flaps with labial teeth in 7 specimens.

Oral cavity morphology.— (Figs. 11D and 13D).

Buccal roof: Prenarial arena scattered with at least 5 blunt pustules and a clear transversal crest. Choanae transversely oriented, with anteromedial and rounded vacuities, posterior margins forming the narial valves, and both margins undulated by the presence of small prenarial pustules, in particular the anterior one. There

are about 48 pustules, 9 short and 10 long conical postnarial papillae between the lateral ridge papillae. The postnarial pustules are scattered among the papillae and also near the posterior margins of the choana. Each square-shaped lateral ridge papilla possesses 5 projections on the free margin, none predominant in size. The low, rounded and wide median ridge presents 9 undulations on its free margin. BRA is not defined; there are approximately 330 pustules and only 10 lateral short and bifid papillae on the buccal roof. Posterior area of the roof with secretory pits and dorsal velum bearing lobated margins.

Buccal floor: There are 3–5 pairs of short and digitated infralabial papillae at the level of the infrarostral cartilages (not figured). There are two long and digitiform infralabial papillae placed at the level of cartilago meckeli (not figured). The lingual anlage bears 2 long and ramified lingual papillae placed very close to each other and with a pustule near their basis. Buccal pockets mostly transversal to the axial axis. Prepocket area with 18 short and conical papillae and about 100 pustules. There are 22 long and conical papillae (4 of them bifid), 16 short and conical papillae and about 260 pustules on the BFA. The papillae are arranged in clear two V-shaped patterns, one anterior and other posterior. The ventral velum has a well-marked median notch, three weakly-marked undulations at each side of the posterior margin and many secretory pits.

Hypsiboas pulchellus (Duméril & Bibron)

Figs. 2C, 2D and 3E

External morphology. – Lot ZVCB 16147, Fig. 6A and 6B. Body slightly depressed (BMH/BMW = 0.93 ± 0.07); body length little less than one third of total length (BL/TL = 0.31 \pm 0.02); body oval in dorsal view, widest at middle third of body. In lateral view, ventral contour of body flat in gular and branchial regions, slightly convex in abdominal region. Dorsal contour of body smoothly convex. Snout semicircular in dorsal view, rounded in lateral view. Nostrils oval, with thin marginal rim, with a subtriangular or rounded elevated fleshy projection in medial margin; nostrils dorsolaterally located (EN/BWN = 0.59 ± 0.04), placed in a depression, closer to eyes than to the tip of snout (FN/END = 1.11 ± 0.13), more visible in dorsal than in lateral view. Eyes large (E/BWE = 0.27 ± 0.01), laterally positioned (EO/BWE = 0.87 ± 0.01), laterally directed, corneas visible in ventral view. Spiracle single, lateral and sinistral; its inner wall fused to body except for its distal end; its opening oval, elevated, with a diameter smaller than tube diameter, located in posterior third of body (RSD/BL = 0.73 ± 0.02), posterodorsally directed, visible in lateral and dorsal views. Lateral line system visible. Intestinal assa located at centre of abdominal region. Vent tube starts at midline, reaching free margin of lower fin, opening dextral. Tail large (TaL/TL = 0.69 ± 0.02), with both fins higher than body height (MTH/ BMH = 1.25 ± 0.06). Dorsal fin originates on end of body. Ventral fin origin concealed by vent tube. Tail axis straight, dorsal fin edge slightly convex and ventral fin edge almost straight, tail tapering markedly in last third, end acute; tail musculature reaching tail tip. Oral disc (Figs. 8E and 9C) anteroventral, small (OD/BMW $= 0.43 \pm 0.04$, disc measured folded), with a well marked infraangular constriction on each side. Marginal papillae simple, longer than wide, with rounded tip. Dorsal gap present, small (DG/OD = 0.29 ± 0.06). Row of marginal papillae single except for angular regions on which it is double; some wider and shorter lateral submarginal papillae present. Upper jaw sheath widely arch shaped with a convex central portion. Lower jaw sheath with V-shaped free margin. Jaw sheaths well developed, serrated and pigmented on their distal third. Labial tooth row formula 2(2)/3(1). A1 bent with an angle directed to the front. Length of P3 about half the length of P2. Tooth of all rows spatulated and concave bearing 8–10 well-marked distal cusps (Fig. 10D).

Coloration in preservative.— Body yellowish-brown in dorsal view, dark brown on head and next to inner margins of nostrils, with small dark spots on head and body. Dark brown laterally. Venter translucent. Caudal musculature yellowish tan, with irregular darker regions that in some specimens made an alternating dark and light transversal pattern in dorsal view. Fins opalescent, with dark blotches.

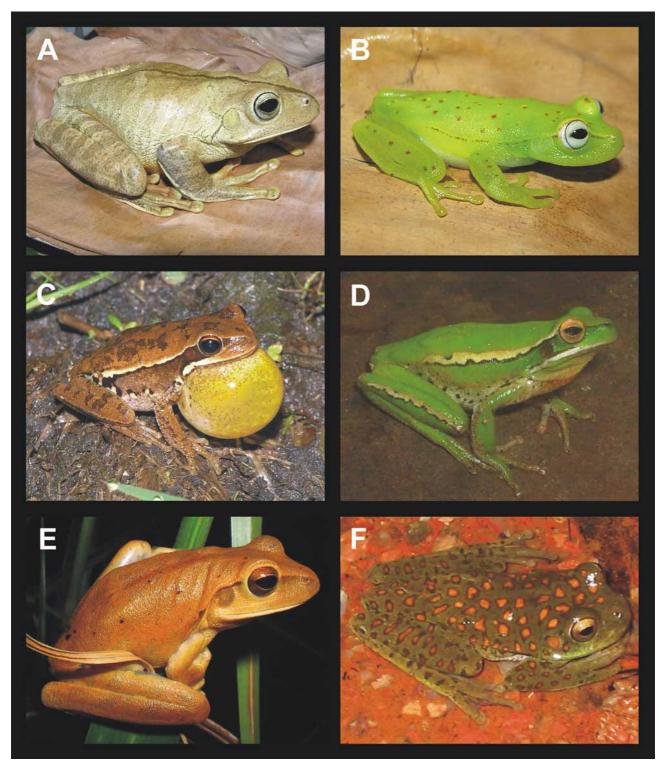


FIGURE 2. Adult specimens of species of *Hypsiboas* studied in this paper. (A) *H. faber*, San Sebastián de la Selva, Province of Misiones, Argentina. (B) *H. punctatus rubrolineatus*, Antequera, Province of Chaco, Argentina. (C) *H. pulchellus*, Department of Rivera, Uruguay. (D) *H. pulchellus*, La Plata, Province of Buenos Aires, Argentina. (E) *H. raniceps*, Ituzaingó, Province of Corrientes, Argentina. (F) *H. riojanus*, Sierras de Famatina, Province of La Rioja, Argentina.

Variation.— MLP DB 7144: LTRF 2(2)/3(1), except for one example 2(2)/3 and another one 2(1,2)/3(1). Three specimens with labial teeth placed on lateral submarginal papillae, on a infraangular lateral flap, or on the anterior labium on both sides of the dorsal gap. MLP DB 5051: Body ovoid in dorsal view, widest on last

third of body. Two specimens (stages 30 and 31) with scarcely evident supraangular constrictions on both sides of oral disc. LTRF 2(2)/3(1). MLP DB 4257: In two specimens (stage 31) LTRF 2(1,2)/3(1), being 2(2)/4(1) in another one (stage 33), which has a short and fragmented P4. Row of marginal papillae double on posterior margin of oral disc in some specimens. P2 has a medial angulation (but is not divided) in six specimens. MLP DB 5306: Row of marginal papillae single, sparse submarginal papillae laterally. LTRF 2(2)/3(2). P3 about 1/3 the length of P2.

Oral cavity morphology.— (Figs. 12A and 14A).

Buccal roof: Prenarial arena with a compact group of 3 short and blunt transversely oriented pustules, not fused forming a crest. Choanae transversely oriented, with anteromedial and rounded vacuities, posterior margins forming the narial valves, and both margins undulated by the presence of small prenarial pustules, in particular the anterior one. There are about 16 pustules, and 6 short papillae on the postnarial arena. The postnarial papillae are transversely oriented between the two lateral ridge papillae. The most lateral papilla of each side is bifid. Each square-shaped lateral ridge papilla possesses 4–5 digitiform projections on the free margin, none of them predominant in size. The low, rounded and wide median ridge presents 9–11 undulations on its free margin. There are approximately 140 pustules and only 10–12 short and conical papillae on the BRA. Most of them are uniformly distributed on the central region of the arena, posterior to the median ridge and anterior to the secretory pits. However, 10 pustules and 2–3 papillae are placed in each lateral area of the arena, separated from the main group by an area without papillation. Some of the lateral papillae are bifid. The longest papillae of the arena form a V-shaped pattern on the posterior margin of the central region. Posterior area of the roof with secretory pits and dorsal velum bearing lobated margin.

Buccal floor: Infralabial papillae on infrarostral cartilages absent. There are two long and digitiform infralabial papillae placed at the level of cartilago meckeli (not figured). The lingual anlage bears 2 long and conical lingual papillae and some pustules. Buccal pockets mostly transversal to the axial axis. Prepocket area scattered with 20 pustules and 16 short and conical papillae. There are 18 long and conical papillae, 4 short and conical papillae and about 100 pustules on the BFA. There is a flap (that resembles the lateral ridges of the roof) bearing 3 projections on its free end and placed posterior to the medial ridge of the pocket. The papillae are arranged in two V-shaped patterns, one anterior and other posterior. The ventral velum has a well-marked median notch, three weakly-marked projections at each side on the posterior margin and many secretory pits.

Hypsiboas punctatus rubrolineatus (**B. Lutz**) Figs. 2B and 3F

External morphology.— Lot MLP DB 4548, Figs. 6C and 6D. Body depressed (BMH/BMW = 0.81 ± 0.03); little longer than one third of total length (BL/TL = 0.35 ± 0.01); body shape oval in dorsal view, widest at spiracle level. In lateral view, ventral contour of body flat in gular and concave in branchial regions, slightly convex in abdominal region. Dorsal contour of body slightly convex from the nostrils to beginning of dorsal fin. Snout rounded in dorsal and lateral views. Nostrils oval, with slightly elevated marginal rim and a rounded projection in medial margin; nostrils dorsolaterally located (EN/BWN = 0.57 ± 0.03), placed in a depression, closer to eyes than to the tip of snout (FN/END = 1.37 ± 0.30), visible in dorsal and lateral views. Eyes large (E/BWE = 0.23 ± 0.03), dorsally positioned (EO/BWE = 0.70 ± 0.04) and dorsolaterally directed, not visible in ventral view. Spiracle single, lateral and sinistral, its inner wall fused to body except for its distal end; its opening oval, elevated, with diameter smaller than or equal to tube diameter, located in posterior third of body (RSD/BL = 0.71 ± 0.03), visible in dorsal and lateral views. Lateral line system visible. Intestinal assa located at the centre of abdominal region. Vent tube starts at midline, at posterior end of body, reaching free margin of lower fin, opening dextral. Tail large (TaL/TL = 0.65 ± 0.01), with both fins higher than body height (MTH/BMH = 1.12 ± 0.03). Dorsal fin originates at tail-body junction. Ventral fin origin concealed by vent tube.

Dorsal fin contour slightly convex; ventral fin contour almost flat, both fins tapering to tip of tail in last third. Tail axis straight, end acute; tail musculature reaching tail tip. Oral disc (Figs. 8F and 9D) ventral, small (OD/BMW = 0.46 ± 0.02 , disc measured folded) with a well marked infraangular constriction on each side. Marginal papillae simple; those at anterior lip short and blunt, while the ones at posterior lip longer and thinner, with pointed tip. Dorsal gap present, small (DG/OD = 0.29 ± 0.11). Row of marginal papillae single or biserially disposed in angular and infraangular regions; some infraangular submarginal papillae present, shorter and wider than marginal ones. Upper jaw sheath slightly convex in the middle and concave laterally, pigmented in distal third and finely serrated. Lower jaw sheath with V-shaped free margin, pigmented in distal 14 , finely serrated. Labial tooth row formula 2 (2)/4(1). A1 bent with an angle directed to the front. P4 located very close to papillae of posterior border of oral disc, with its labial teeth smaller than other ones. Tooth of all rows spatulate and concave, bearing 8–10 well-marked distal cusps (Fig. 10E).

Variation.— One tadpole (stage 28) has one submarginal papilla on each side of oral disc, bearing labial teeth; P4 fragmented. Another one (stage 29) with some short and conical papillae making a double row in anterior lip, row of marginal papillae double at angular and infraangular regions, while row is single and discontinuous at posterior margin of oral disc. P4 well developed and continuous, with labial teeth smaller than the other ones. At the infraangular regions there are some submarginal papillae and some flaps with labial teeth. In another specimen (stage 36) there is a double fold with papillae on both sides of the rostral gap, and P4 has multiple interruptions. One premetamorph (stage 41) has double or multiple rows of papillae in the infraangular regions and some submarginal papillae, one bearing labial teeth. Row of papillae in the posterior lip discontinuous and most of P4 is lost due to the metamorphosis.

Coloration in preservative.— Body light brown in dorsal and lateral views, with fine melanophores. Inner margin of nostrils dark brown. Abdomen dark brown. Caudal musculature little pigmented with a marbled pattern, darker in dorsal view, unpigmented in ventral view. Dorsal fin translucent with dark flecks. Ventral fin translucent, with some melanophores in the last third.

Oral cavity morphology. - (Fig. 12B and 14B).

Buccal roof: Prenarial arena with 20 blunt pustules and a clear transversal crest. The pustules are arranged surrounding the crest. Choanae transversely oriented, with anteromedial and rounded vacuities, posterior margins forming the narial valves, and both margins undulated by the presence of small prenarial pustules, in particular the anterior one. There are about up to 20 pustules, 11 short and simple papillae, and 8 long and bifid papillae on the postnarial arena. The series of longest papillae are arranged forming an arch between the lateral ridge papillae. Each square-shaped lateral ridge papilla possesses 7 projections, some of them longer, on the free margin. The tall, distally narrow but proximally wide square-shaped median ridge presents 8 short undulations on its free margin, lateral borders free of undulations and one short papilla at each side of the base. BRA not defined; there are approximately 264 pustules, and no more than 2 very short and conical papillae on central region of the buccal roof. Posterior area of the roof with secretory pits and dorsal velum bearing lobated margin.

Buccal floor: Infralabial papillae on infrarostral cartilages absent. There are two long and digitiform infralabial papillae placed at the level of cartilago meckeli (not figured). The lingual anlage bears 2 long and conical lingual papillae. Buccal pockets mostly transversal. Prepocket area with 22 long and ramified papillae, 10 short conical papillae and 48 pustules. There are 12 long and conical papillae, 32 short and conical papillae and about 120 pustules on the BFA. The papillae are not arranged in a V-shaped pattern. There is a flap (that resembles the lateral ridges of the roof) bearing 3 long projections on its free end and placed posterior to the medial flange of the pocket. The ventral velum has a well-marked median notch, three few-marked projections at each side on the posterior margin and many secretory pits.

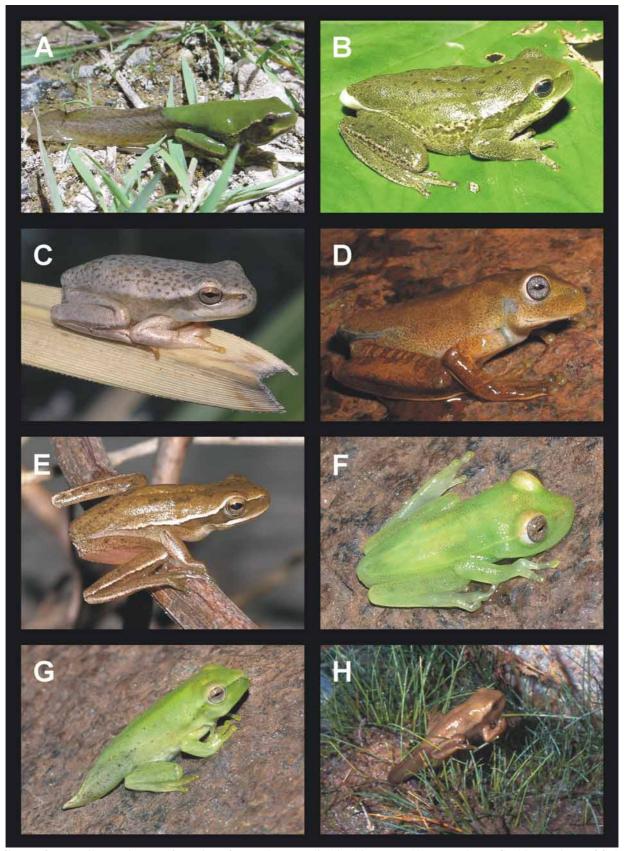


FIGURE 3. Juvenile specimens of species of *Hypsiboas* studied in this paper. (A) *H. andinus*, Cachi, Province of Salta, Argentina. (B) *H. cordobae*, El Condor, Province of Córdoba, Argentina. (C) *H. cordobae*, Río Toro Muerto, Province of Córdoba, Argentina. (D) *H. faber*, Eldorado, Province of Misiones, Argentina. (E) *H. pulchellus*, Department of Montevideo, Uruguay. (F) *H. punctatus rubrolineatus*, Antequera, Province of Chaco, Argentina. (G) *H. raniceps*, Antequera, Province of Chaco, Argentina. (H) *H. riojanus*, Sierras de Famatina, Province of La Rioja, Argentina.

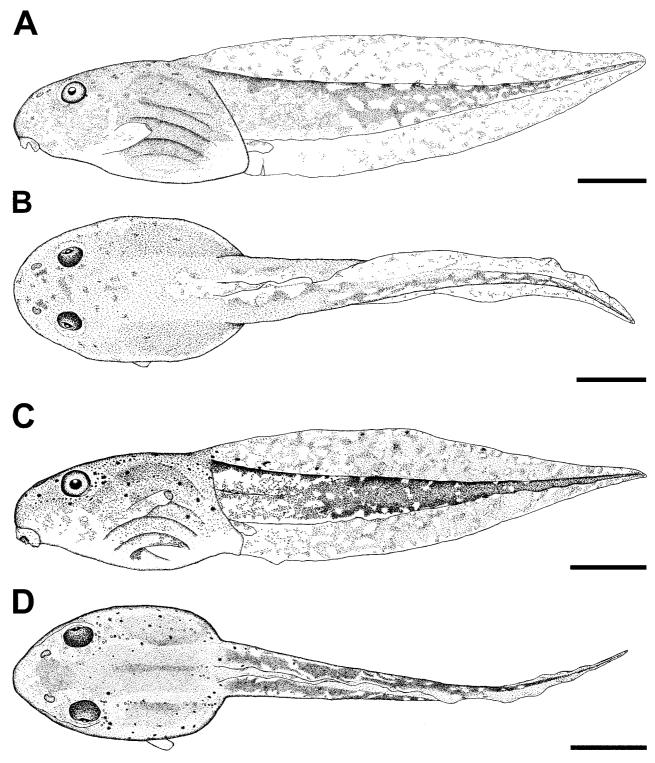


FIGURE 4. Lateral and dorsal views of the tadpoles of: (A) and (B) *Hypsiboas andinus* (MLP DB 4806, stage 34); (C) and (D) *H. caingua* (MLP DB 4258, stage 33). Scale bars = 5 mm.

Hypsiboas raniceps Cope

Figs. 2E and 3G

External morphology.— Lot MLP DB 5303, Figs. 7A, 7B and 18D. The external morphology of the studied specimens is in agreement with the detailed description presented by Rossa-Feres & Nomura (2006), except

that we observed a very short ventral gap in one specimen, and a short P4 row in another one (Figs. 8G and 9E). We provide a SEM photograph of the oral disc (Fig. 9E) and a description of the oral cavity morphology.

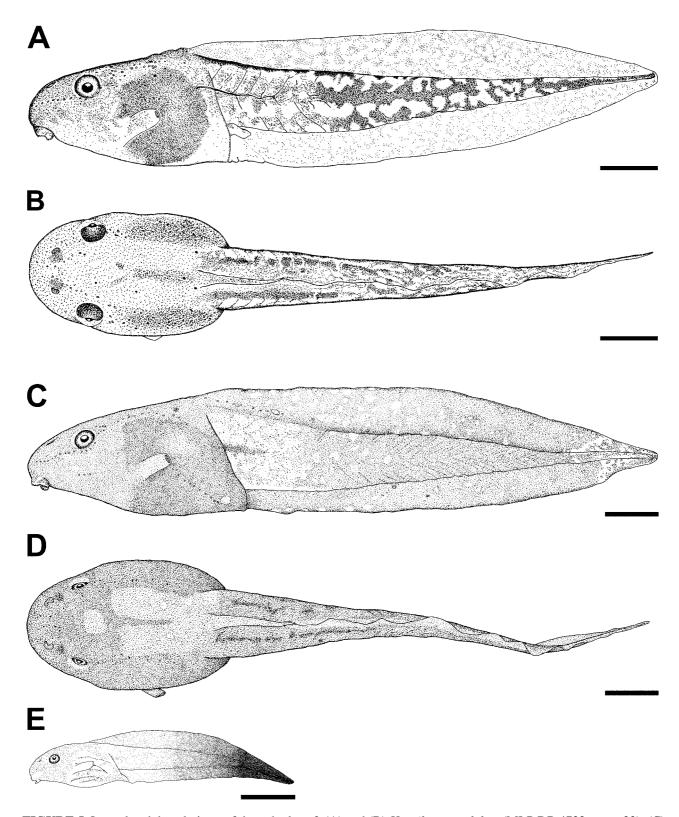


FIGURE 5. Lateral and dorsal views of the tadpoles of: (A) and (B) *Hypsiboas cordobae* (MLP DB 4722, stage 33); (C) and (D) *H. faber* (MACN 35116, stage 28); (E) *H. faber* (MLP DB 5410, stage 25). Scale bars = 5 mm.

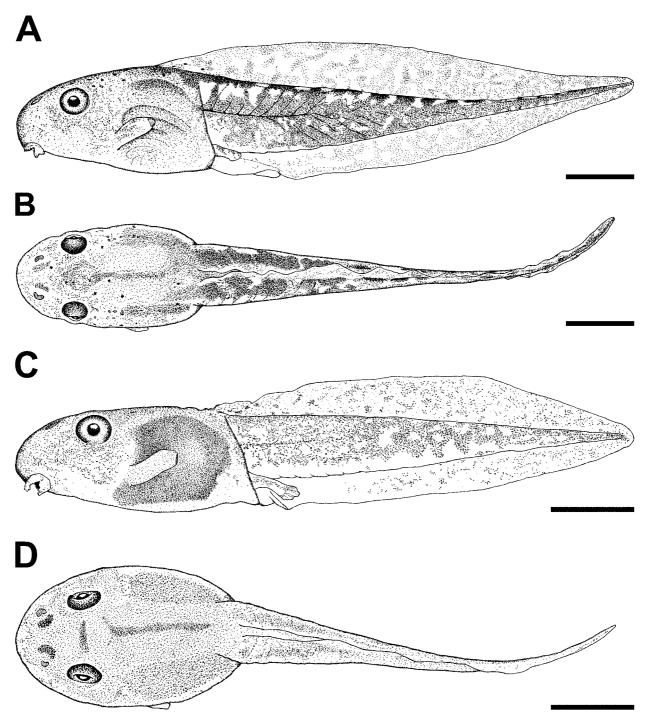


FIGURE 6. Lateral and dorsal views of the tadpoles of: (A) and (B) *Hypsiboas pulchellus* (ZVCB 16147, stage 31); (C) and (D) *H. punctatus rubrolineatus* (MLP DB 4548, stage 36). Scale bars = 5 mm.

Oral cavity morphology.— (Fig. 12C and 14C).

Buccal roof: There are four blunt pustules on the central region of the prenarial arena; three of them are transversely arranged forming a crest. Choanae transversely oriented, with anteromedial and rounded vacuities, posterior margins forming the narial valves, and both margins undulated by the presence of small prenarial pustules, in particular the anterior one. There are about 12 short conical papillae on the postnarial arena forming a transversal line between the lateral ridge papillae. Each square-shaped lateral ridge papilla possesses 4 digitiform projections on the free margin. The low, rounded and wide median ridge presents 11 undulations on its free margin. BFA not defined; there are approximately 130 pustules lying throughout the central

area of the buccal roof. The lateral regions possess two pustules per side. Posterior area of the roof with secretory pits and dorsal velum bearing lobated margin.

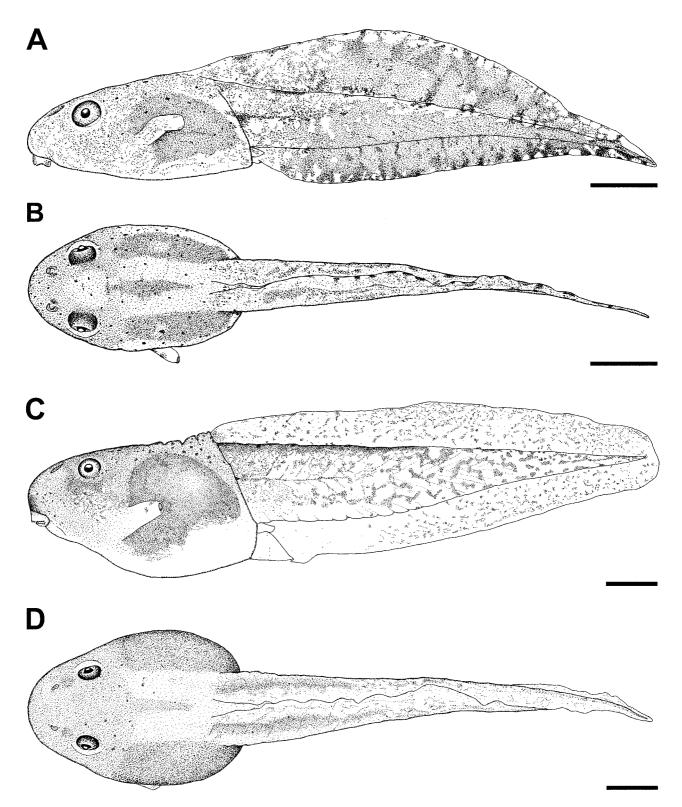


FIGURE 7. Lateral and dorsal views of the tadpoles of: (A) and (B) *Hypsiboas raniceps* (MLP DB 5303, stage 31); (C) and (D) *H. riojanus* (MLP DB 2440, stage 31). Scale bars = 5 mm.

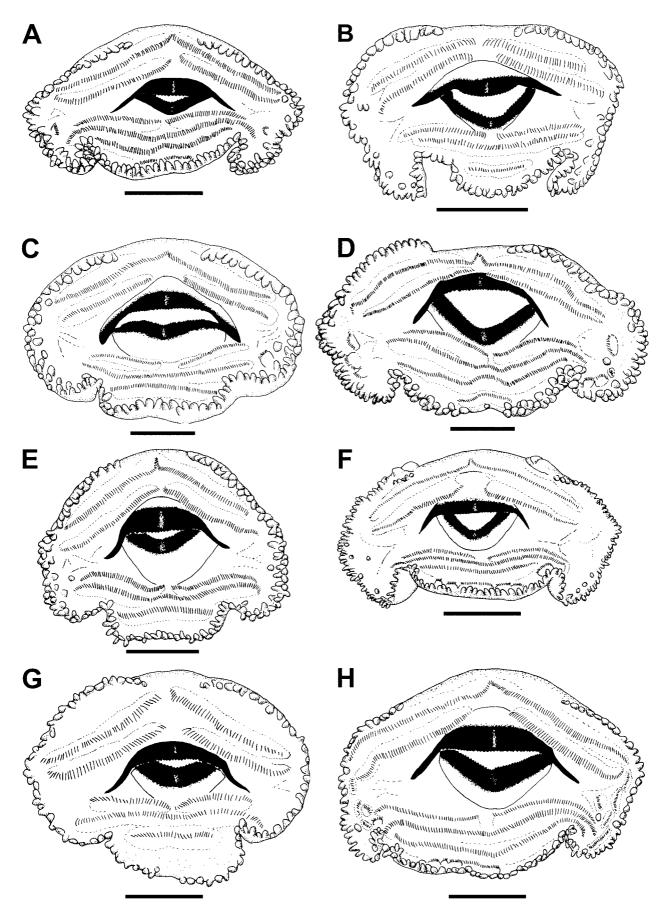


FIGURE 8. Oral discs of the tadpoles of: (A) *Hypsiboas andinus*; (B) *H. caingua*; (C) *H. cordobae*; (D) *H. faber*; (E) *H. pulchellus*; (F) *H. punctatus rubrolineatus*; (G) *H. raniceps*; (H) *H. riojanus*. Scale bars = 1 mm.

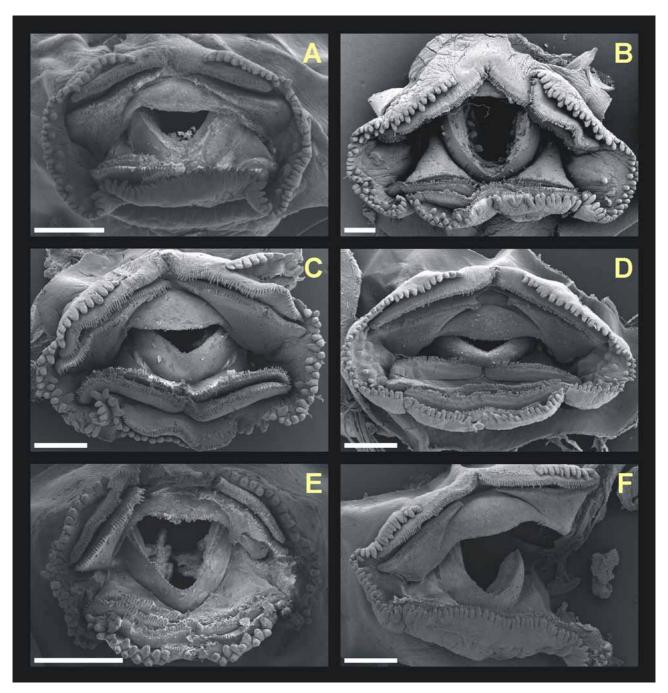


FIGURE 9. SEM micrographs of the oral discs of (A) *Hypsiboas caingua*; (B) *H. faber*; (C) *H. pulchellus*; (D) *H. punctatus rubrolineatus*; (E) *H. raniceps*; (F) *H. riojanus*. Scale bars = 500 µm.

Buccal floor: Infralabial papillae on infrarostral cartilages absent. There are 2 pairs of digitiform infralabial papillae, both placed on the cartilago meckeli. The anterior pair is shorter than the posterior one which is twofold higher. The lingual anlage bears 2 long and conical lingual papillae on each side of the midline, and some pustules and short papillae on the margins of the anlage. Buccal pockets mostly transversal to the axial axis. Prepocket area with about 20 short papillae. There are 24 long and conical papillae and about 34 pustules on the BFA. The papillae are arranged in two V-shaped patterns. The papillae of the anterior V are forming 2 ridges. The ventral velum lacks the median notch, shows 2–3 marginal projections (the medial ones less evident) on each side, and many secretory pits.

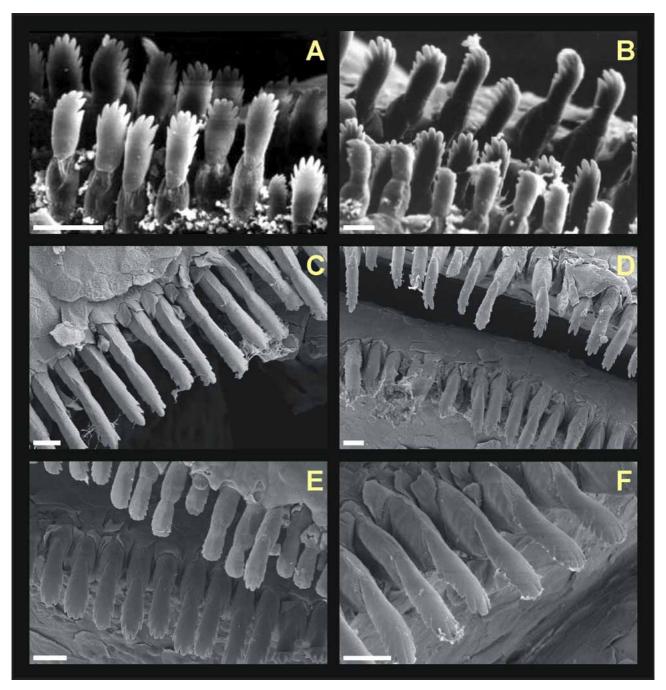


FIGURE 10. SEM micrographs of keratodonts (labial teeth) from the P rows of (A) *Hypsiboas andinus*; (B) *H. cordobae*; and from the A rows of (C) *H. faber*; (D) *H. pulchellus*; (E) *H. punctatus rubrolineatus*; and (F) *H. riojanus*. Scale bars = $20 \, \mu m$.

Hypsiboas riojanus (Koslowsky)

Figs. 2F and 3H

External morphology.— Lot MLP DB 2440, Figs. 7C and 7D. Body depressed (BMH/BMW = 0.86 ± 0.02); body length little longer than one third of total length (BL/TL = 0.35 ± 0.02); body shape ovoid in dorsal view with a constriction behind eyes; widest at posterior third of body, behind spiracle. In lateral view, ventral contour of body flat in gular and branchial regions, convex in abdominal region. Dorsal contour of body almost flat from eyes to origin of dorsal fin. Snout semicircular in dorsal view and rounded in lateral view. Nostrils

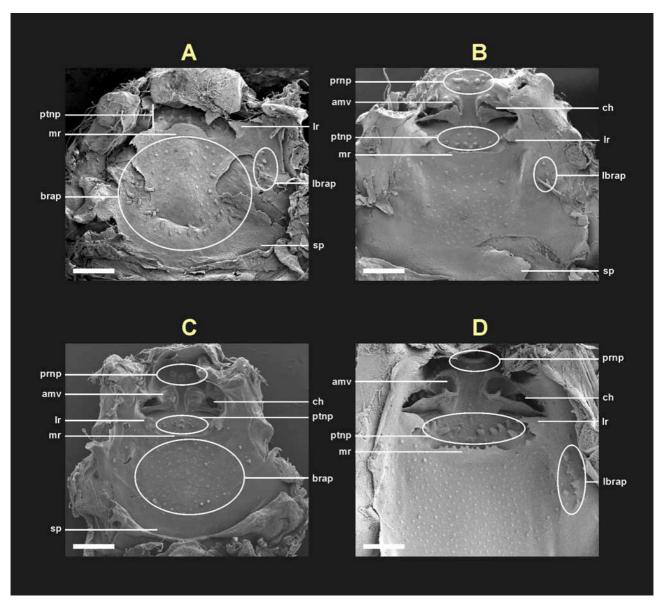


FIGURE 11. SEM micrographs of oral roofs of (A) *Hypsiboas andinus*; (B) *H. caingua*; (C) *H.cordobae*; (D) *H. faber*. References: amv: anteromedial vacuity of the choana, brap: buccal roof arena papillae, ch: choana, lbrap: lateral buccal roof papillae, lr: lateral ridge papilla, mr: median ridge, prnp: prenarial arena papillae, ptnp: postnarial papillae, sp: secretory pits. Scale bars = 1 mm.

oval, with thin marginal rim, with a small rounded or subtriangular fleshy projection in medial margin; nostrils dorsolaterally located (EN/BWN = 0.54 ± 0.06), placed in a depression, closer to eyes than to the tip of snout (FN/END = 1.32 ± 0.15), more visible in dorsal than in lateral view. Eyes large (E/BWE = 0.21 ± 0.01), dorsally positioned (EO/BWE = 0.75 ± 0.03), dorsolaterally directed, not visible in ventral view. Spiracle single, lateral and sinistral; its inner wall fused to body except for its distal end; its opening oval, slightly elevated, with a diameter smaller than tube diameter, located between second and posterior thirds of body (RSD/BL = 0.65 ± 0.03), posterodorsally directed, visible in lateral and dorsal views. Lateral line system visible. Intestinal assa located at centre of abdominal region. Vent tube starting at midline, at posterior end of body, reaching margin of lower fin, opening dextral. Tail large (TaL/TL = 0.65 ± 0.02), with both fins slightly lower than body height (MTH/BMH = 0.98 ± 0.04). Dorsal fin originates at tail-body junction. Ventral fin origin concealed by vent tube. Edges of both fins sub-parallel for first and second thirds, convergent in last one. Tail axis straight, tail tip rounded; tail musculature not reaching tail tip. Oral disc (Figs. 8H and 9F) anteroventral,

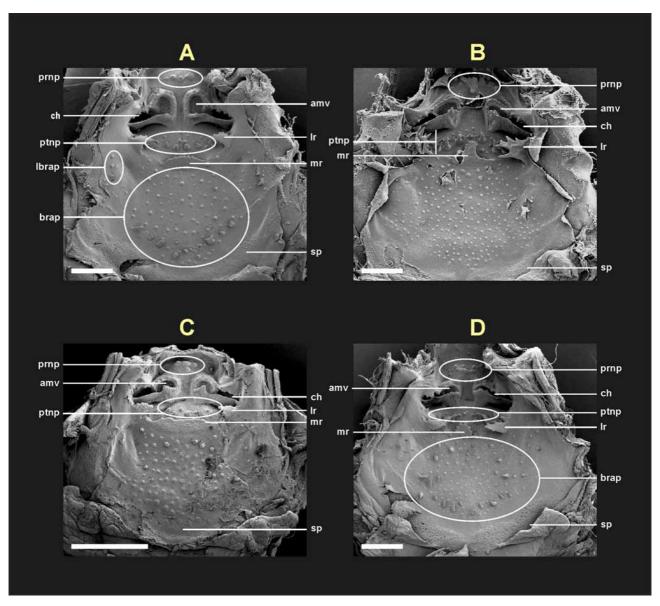


FIGURE 12. SEM micrographs of oral roofs of: (A) *Hypsiboas pulchellus*; (B) *H. punctatus rubrolineatus*; (C) *H. raniceps*; (D) *H. riojanus*. Same references as in Fig. 11. Scale bars = 1 mm.

small (OD/BMW = 0.33 ± 0.02 , disc measured folded), with a well marked infraangular constriction on each side of oral disc (also a less marked supraangular constriction in one example). Marginal papillae simple, longer than wide, with rounded or pointed tip. Dorsal gap present, medium-sized (DG/OD = 0.39 ± 0.09). Row of marginal papillae single or double; some infraangular submarginal papillae present. Upper jaw sheath widely arch-shaped. Lower jaw sheath with U-shaped free margin. Jaw sheaths well developed, but appear smooth and sparsely pigmented distally. Labial tooth row formula 2(2)/3(1). P3 almost as long as P2. Tooth of all rows spatulated and concave bearing 8–10 well-marked distal cusps (Fig. 10F).

Coloration in preservative.— Body dark brown in dorsal view, even darker next to the inner margins of nostrils, with small dark spots on the head and body. Almost black laterally. Venter translucent. Caudal musculature in dorsal view dark brown, except at the insertion of the dorsal fin; in lateral view yellowish, with a dark brown marbled pattern. Fins translucent, delicately marbled in dark brown.

Variation.— MLP DB 2440. Three specimens (stages 28 and 31) exhibited some labial teeth anterior to A1, at one or both sides of the dorsal gap. In many specimens, labial teeth are partially lost from some rows.

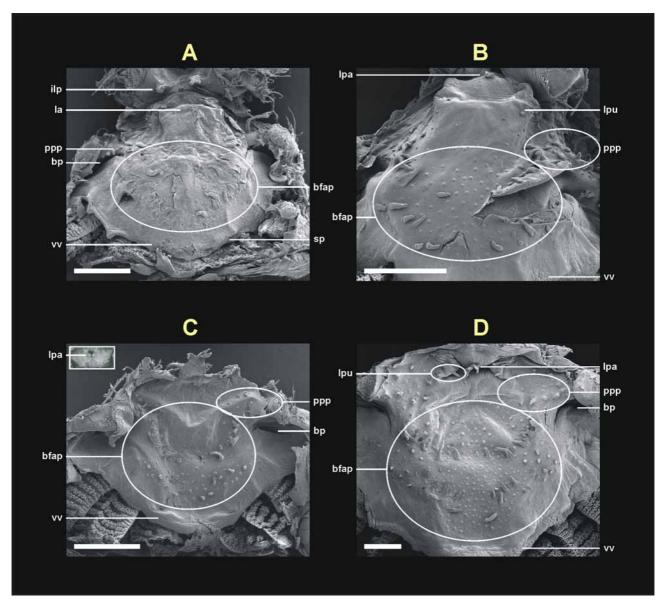


FIGURE 13. SEM micrographs of oral floors of (A) *Hypsiboas andinus*; (B) *H. caingua*; (C) *H. cordobae*, with detail of the lingual anlage of a specimen at stage 35 showing the lingual papillae; (D) *H. faber*. References: bfap: buccal floor arena papillae, bp: buccal pocket, ilp: infralabial papillae, la: lingual anlage, lpa: lingual papillae, lpu: lingual pustules, ppp: prepocket papillae, sp: secretory pits, vv: ventral velum. Scale bars = 1 mm.

One specimen (stage 35) with some labial teeth arranged as a short P4, and another one (stage 28) with one lateral submarginal flap with labial teeth. Two additional specimens at later developmental stages (37 and 40) with LTRF 2(2)/3(1), without extra labial teeth. Lot MLP DB 3303. LTRF 2(2)/3(1) in four specimens (stages 26–37), 2(2)/4(1) in another three (stages 35–39). When present, P4 appears irregularly fragmented. A1 is bent at the middle, with an angle directed to the front. Some lateral submarginal flaps with labial teeth are present in five specimens (stages 26–37), absent in another two (stages 27 and 39).

Oral cavity morphology.— (Figs. 12D and 14D).

Buccal roof: There are about 11 blunt pustules on the central region of the prenarial arena. Three of them are transversely arranged, tending to but not forming a crest. Choanae transversely oriented, with anteromedial and rounded vacuities, posterior margins forming the narial valves, and both margins undulated by the presence of small prenarial pustules, in particular the anterior one. There are about 12 pustules, 2 short and 6 long conical papillae on the postnarial arena. The six longest postnarial papillae are placed anteriorly and

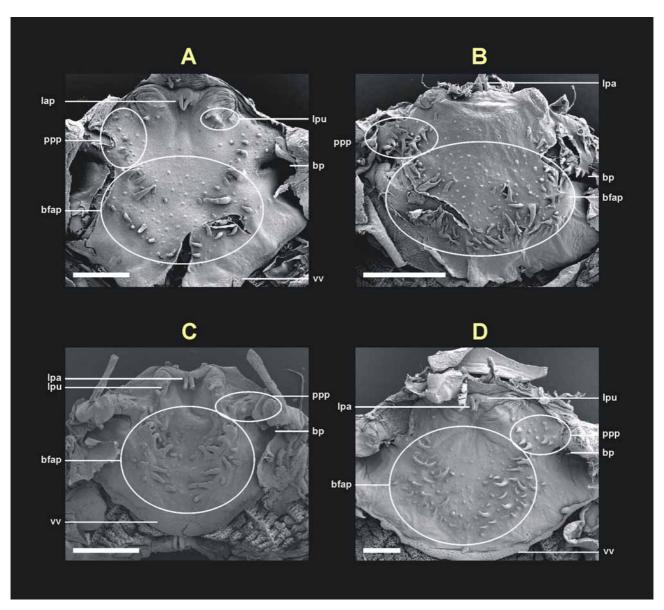


FIGURE 14. SEM micrographs of oral floors of: (A) *Hypsiboas pulchellus*; (B) *H. punctatus rubrolineatus*; (C) *H. raniceps*; (D) *H. riojanus*. Same references as in Fig. 13. Scale bars = 1 mm.

between the two lateral ridge papillae, forming a discontinuous arch. None of these papillae seems to be bifid. Each square-shaped lateral ridge papilla possesses 6 digitiform projections on the free margin. The high, rounded and narrow median ridge presents 6 undulations distributed in all the free margin and one short papillae per side. There are approximately 200 pustules and 25 conical papillae on the BFA. The pustules are occupying all the area of the arena. The papillae are mostly arranged in a V-shaped pattern on the posterior margin of the arena, but some of them are scattered among the central pustules. The lateral regions of the arena possess few pustules. Posterior area of the roof with secretory pits and dorsal velum bearing lobated margin.

Buccal floor: Infralabial papillae on infrarostral cartilages absent. There are 2 long and digitiform infralabial papillae placed at the level of cartilago meckeli (not figured). The lingual anlage bears 2 long and conical lingual papillae very near to each other, and some pustules surrounding them. Buccal pockets mostly transversal to the axial axis. Prepocket area with 14 conical papillae of moderate size and 48 pustules. There are 40 long and conical papillae, 24 short and conical papillae and about 100 pustules on the BFA. The papillae are not arranged in two V-shaped patterns. The ventral velum has a well-marked median notch, three weakly-marked serrations on each side on the posterior margin and many secretory pits.

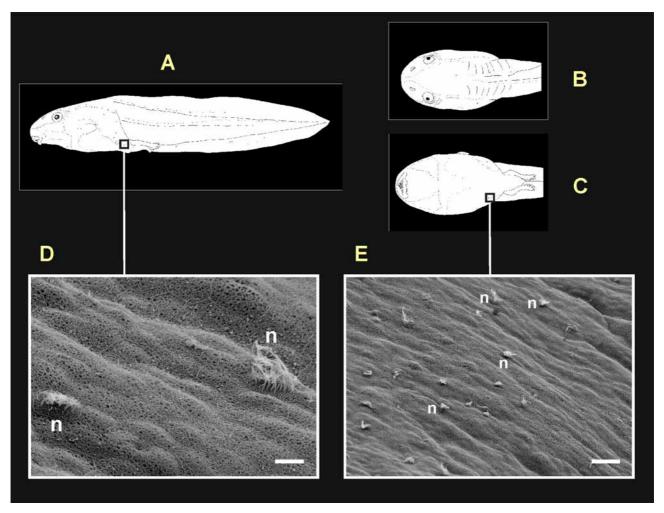


FIGURE 15. (A), (B) and (C) Pattern of lateral line system of *Hypsiboas faber*. (D) Two neuromasts (n) from the ventral line. (E) Concentration of neuromasts (n) associated to the ventral line near the body-tail junction. Scale bars: (D) = $10 \mu m$, (E) = $20 \mu m$.

Remarks

The lateral line system is present in the eight species, but it is not equally evident in all of them. It is most noticeable in *Hypsiboas faber* tadpoles, in which the following lines are present (Figs. 15 A–D): preorbital, supraorbital, infraorbital, angular, longitudinal oral, oral, dorsal, medial and ventral. In the other species, neuromasts from preorbital, supraorbital, infraorbital, dorsal and medial lines are more evident than the others. In *H. caingua*, the infraorbital line runs in a groove. Neuromasts are hardly noticeable in *H. riojanus*.

The conspicuous ventrolateral unpigmented spots observed in *Hypsiboas faber* (Fig. 20A) appear slightly elevated with respect to the surrounding tissues. They represent a concentration of neuromasts belonging to the ventral line but disposed randomly, as can be seen by SEM (Fig. 15E). Other similar cumuli of neuromasts, although smaller, appear on the lateral sides of the body, close to the origin of the caudal musculature, and also in the dorsal and ventral fins (Fig. 15A and 20A) Similar ventrolateral spots are also present, although less evident, in *H. andinus*, *H. caingua*, *H. cordobae* and *H. punctatus rubrolineatus*. These structures can be evidenced by lightly staining the tadpoles with methylene blue solution: the cumuli remain less stained than the surrounding tissues.

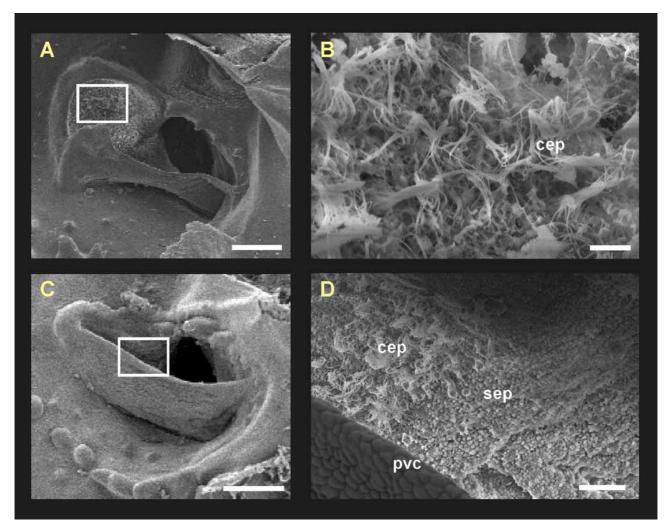


FIGURE 16. (A) Choana of *Hypsiboas cordobae*; (B) detail of the ciliated epithelia of the anteromedial vacuities of the same specimen of *H. cordobae*; (C) choana of *Pseudis platensis*; (D) detail of the ciliated epithelia of the anteromedial concavity of the same specimen of *P. platensis*. References: cep (ciliated epithelia and mucus), pvc: posterior valve of the choana, sep: secretor epithelia (limiting laterally to the vacuity). Scale bars: (A) = 200 μ m, (B) = 5 μ m, (C) = 500 μ m, (D) = 20 μ m.

Discussion

Selected external morphological characters of the tadpoles described in this study are summarized in Appendix 1, together with previous descriptions, if available. It is noticeable that the tadpoles of the *Hypsiboas pulchellus* species group described herein show remarkable interpopulation variability, as well as some intrapopulational variability. For instance, in *H. andinus*, Lavilla (1984) reported a LTRF 2(2)/3(1) and no submarginal papillae in samples from Tucumán and Salta Provinces, Argentina. Duellman *et al.* (1997) observed LTRF 2(2)/4(1) or 2(2)/3(1) and the presence of lateral submarginal papillae in samples from Cochabamba, Bolivia. The tadpoles we studied from Jujuy Province, Argentina have LTRF 2(2)/4(1) and submarginal papillae. Lateral flaps with short rows of labial teeth were present in all samples. The oral cavity of this species was first described by Lavilla and Fabrezi (1987). We found in the specimens examined by us three features that diverge from those described by Lavilla and Fabrezi (1987). These are (character states as observed by Lavilla & Fabrezi [1987] between brackets): prenarial arena with a low transversal crest and some pustules surrounding it (U-shaped crest); presence of 40 long and conical papillae on the buccal roof

arena (14–25 BRA papillae); and 20 long and conical papillae —two of them bifid—, 26 short and conical papillae on the BFA (63–83 papillae in the buccal floor arena, although in their figure no more than 40 are illustrated). These divergences more likely are due to intraspecific variation.

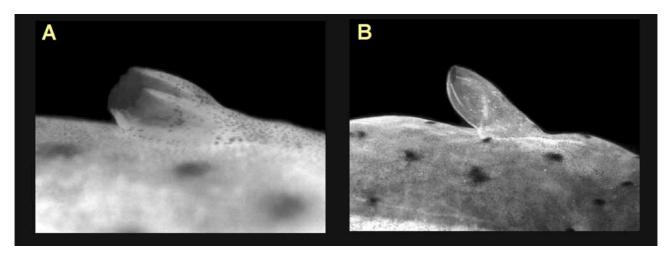


FIGURE 17. Dorsal views of the spiracles of tadpoles of (A) *Hypsiboas andinus* and (B) *H. raniceps*, showing different degrees in the attachment of the medio-distal portion of the internal wall of the spiracle to the body wall. Not to scale.

The tadpoles of *Hypsiboas riojanus* are very similar to those of *H. andinus*, differing mainly in the rounded tip of the tail and in the tail musculature not reaching the tail tip. LTRF is variable in this species also; 2(2)/3(1) is the most common in the population from El Siciliano, La Rioja Province, Argentina, and only one had lateral flaps with teeth. Conversely, in the sample from Guayamba, Catamarca Province, Argentina, formulae 2(2)/3(1) and 2(2)/4(1) were present and most specimens had lateral flaps with teeth. The spiracle opening is located more close to the snout in the tadpoles of *H. andinus* and *H. riojanus* than in the other species studied herein (measurement ratio = 0.64-0.65 vs. 0.71-0.76 in the other species). The sister species *H. andinus* and *H. riojanus* are the species of the *H. pulchellus* group that possess the highest papillation known on the BRA.

Similar variation was also observed in *Hypsiboas pulchellus*: 2(2)/3(1) was the LTRF observed in most samples from Uruguay, while Lutz (1973) and Echeverría (1992) observed 2(2)/3 in samples from La Plata and Buenos Aires, Buenos Aires Province, Argentina, and we also found 2(1,2)/3(1) and 2(2)/4(1) in two specimens from Misiones Province, Argentina. Lateral flaps with teeth were absent in all samples, except for one specimen from Sierras de Carapé, Departamento de Rocha, Uruguay.

Tadpoles of *Hypsiboas cordobae* are similar to those of *H. pulchellus*, with a LTRF 2(2)/3(1), but the eyes are lateral in *H. pulchellus* and dorsolateral in *H. cordobae*, and the tail fins are relatively higher in *H. pulchellus* (FH/BMH = 1.25 ± 0.06 vs. 1.09 ± 0.08 in *H. cordobae*). The tadpoles of both species have a relatively higher body than the other species studied herein: BH/BMW = 0.93-0.94 vs. 0.90 in *H. caingua*, and 0.81-0.86 in the other ones. Most specimens of *H. cordobae* from Río Toro Muerto, Córdoba Province, Argentina, had lateral flaps with teeth, which are absent in the specimens from La Posta, Córdoba Province, Argentina.

The tadpoles of Hypsiboas caingua presented three different LTRF within the same population, the most prevalent one -2(1,2)/3(1)— agrees with that reported by Spirandeli Cruz (1991) from São Paulo, Brazil. The presence of a lateral groove bearing the neuromasts of the infra-naso-orbital line (Fig. 19A) and a spiracular tube free from the body are unique within the H. pulchellus group. A free spiracular tube is also present in some species of the H. albopunctatus, H. faber and H. semilineatus groups (see below). The tadpoles of H. caingua described herein resemble those of H. raniceps (Rossa-Feres & Nomura 2006) in dorsal and lateral profile, papillation of the oral disc, LTRF and in the free spiracular tube (Fig. 17B). However, those of H. raniceps are larger, lack the lateral groove with neuromasts on the sides of the head (Fig. 19B), and have well

marked dark transverse bars on the dorsal caudal musculature (MLP DB 5303, MACN 36892 and 36893). The oral cavity morphology of *H. caingua* was first described by Spirandeli Cruz (1991) as *Hyla* sp. (aff. *pulchellus*). We found in the specimens examined by us six features that diverge from those described by Spirandeli Cruz (1991). These are (character states as observed by Spirandeli Cruz [1991] between brackets): a low, rounded and wide median ridge with 17 short undulations on its free margin (with three-lobated margins); infralabial papillae on infrarostral cartilages absent (4–5 infrarostral papillae); two long and digitiform infralabial papillae (four infralabial papillae); prepocket area scattered with 42 pustules and 24 conical papillae, four of them long (8–10 prepocket papillae, pustules not mentioned); 5 long and 7 short conical papillae, and about 160 pustules on the BFA (8–10 BFA papillae, number of pustules not stated); BFA papillae arranged in two V-shaped patterns, one anterior and other posterior (arranged in parallel to the axial axis). These divergences are most likely explained as intraspecific variation.

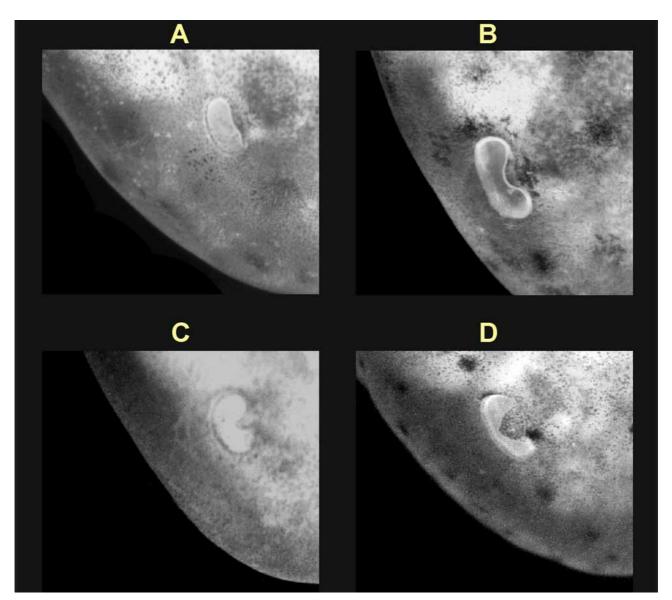


FIGURE 18. Dorsal views of the nares of (A) *Hypsiboas andinus*, (B) *H. caingua*, (C) *H. faber*, and (D) *H. raniceps*; showing the development of the fleshy projection of the internal margin of the nasal rim. Not to scale.

The tadpoles of *Hypsiboas faber* described herein are very similar to those of previous descriptions (Lutz 1973; Cei 1980; Spirandeli Cruz 1991). The LTRF we observed is the same reported by Spirandeli Cruz (1991) for Brazilian populations, but Lutz (1973) observed a divided P2, and Cei (1980) stated that the LTRF

was usually 2(1)/4(1) in tadpoles from Misiones Province, Argentina. A shorter and fragmented distal posterior row (P4 in this case) was observed by Lutz (1973) and by us (present study) and is common in many species of Hypsiboas, especially in the H. faber and H. pulchellus groups (see below). The sparse papillae present around the middle of the posterior border of the oral disc, the small ventral gap observed in some specimens, and the presence of lateral flaps with teeth were not previously reported for this species, but these features are shared with other species belonging to the H. faber group (see below). The ontogenetic shift in the coloration pattern of the tadpoles of this species was previously noticed by Kwet and Di-Bernardo (1999). The ventrolateral unpigmented spots present in this species, and also (but less evident) in other species of Hypsiboas described in this study, were first noticed by Altig and McDiarmid (1999a): "Close examination of certain tadpoles reveals a circular area of slightly contrasting color anterolateral to the base of the vent tube. This slightly raised area appears glandular, but it may be associated with the lateral line system. It is most obvious in darkly pigmented, neotropical, lotic hylids". They are also present in tadpoles of Hypsiboas angelicus and H. jimenezi (Myers & Donnelly 2008), Aplastodiscus perviridis (MLP DB 5413; Fig. 20B) and A. eugenioi (Carvalhoe-Silva & Carvalho-e-Silva 2005). Our SEM study confirms that these structures are cumuli of neuromasts, randomly arranged. Further study is needed to assess the taxonomic distribution of these structures in other tadpoles, and its correlation with their ecomorphological guilds. The tadpoles of H. faber are typical inhabitants of lentic water bodies, so the presence of these structures is not restricted to lotic tadpoles. The oral cavity morphology of H. faber was first described by Spirandeli Cruz (1991). The author observed the oral features using optic microscopy. We found in the specimens examined by us four features that diverge with those described by Spirandeli Cruz (1991). These are (character states as observed by Spirandeli Cruz [1991] between brackets): a low, rounded and wide median ridge with nine undulations on its free margin (high median ridge); presence of 330 pustules and 10 short and bifid papillae on the BRA placed on the lateral regions of the arena (lateral papillae not mentioned, maybe absent); two long and digitiform infralabial papillae (two pairs of infralabial papillae); prepocket area with 18 short and conical papillae and about 100 pustules (no more than 10 prepocket papillae, pustules not mentioned). As in H. caingua, these divergences are most likely caused by intraspecific variation.

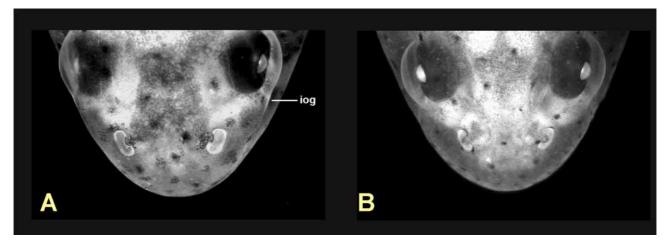


FIGURE 19. Dorsal views of the heads of tadpoles of (A) *Hypsiboas caingua*, and (B) *H. raniceps*, showing the presence in the former of the groove (iog) in which runs the infraorbital line of neuromasts. Not to scale.

The taxonomic status of *Hypsiboas punctatus rubrolineatus* has been controversial for a long time. Lutz (1951) described this subspecies from Buena Vista, Departamento de Santa Cruz, Bolivia, based on subtle morphological differences with the nominal form from northern South America. Later, she stated that this form may not deserve subspecific recognition (Lutz 1973). Duellman (1974) synonymized it with *H. punctatus*, but Cei (1980), Gallardo (1987), Cei (1987) and Lavilla and Cei (2001) among others, recognized the

validity of the taxon. Lavilla and Cei (2001) suggested the possible specific status of this form on the basis of published bioacoustic information. Recently, Napoli and Cruz (2005) suggested that *H. punctatus punctatus*, *H. atlanticus* (which was formerly included in *H. punctatus*) and *H. punctatus rubrolineatus* could be different species based on slight differences in bioacoustic data. The morphology of the tadpoles further supports the specific recognition of *rubrolineatus*, since its LTRF 2(2)/4(1) differs from that of *H. punctatus* from Trinidad, Ecuador and Suriname, which is 2(2)/3 or 2(1,2)/3(1) (Kenny 1969; Duellman 1978; Hoogmoed 1979; Duellman 2005). Within the *H. punctatus* group, other species with four posterior rows of labial teeth are *H. alemani* with 2(1,2)/4, *H. cinerascens* with 2(2)/4(1) and some specimens of *H. jimenezi* with 2/4 and 3/4 (Mijares-Urrutia 1992; Mijares-Urrutia 1993; Myers & Donnelly 2008), while *H. sibleszi* and many specimens of *H. jimenezi* have five, being their LTRF 2(2)/5(1) and 2-3/5 respectively (Hoogmoed 1979; Myers & Donnelly 2008).

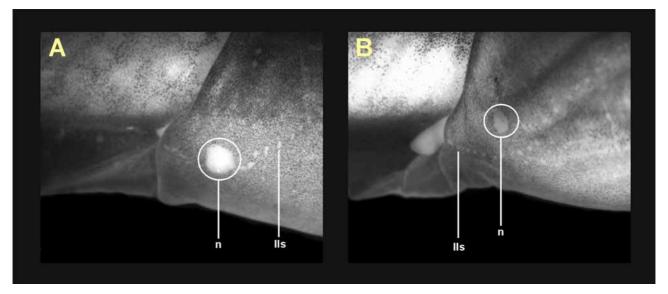


FIGURE 20. Lateral views of tadpoles of (A) *Hypsiboas faber*, and (B) *Aplastodiscus perviridis*, showing the ventral line of neuromasts of the lateral line system (lls) and the associated ventrolateral cumuli of neuromasts (n). Not to scale.

A review of Hypsiboas tadpoles

A descriptive summary of tadpole external morphology at the family and genus level was made by Altig and McDiarmid (1999b). The success of this exhaustive review was hampered to some extent because many taxa were not natural, monophyletic units. This was particularly true for the large and non-monophyletic genus Hyla, as then understood. The wide morphological variation found in the tadpoles of the 289 species placed into approximately 40 species groups which were formerly included in Hyla, made the data summarized for this genus almost uninformative. In a recent systematic review, the former genus Hyla was split into several new or resurrected genera (Hypsiboas among the latter), and larval morphological character states seem to fit nicely into this arrangement (Faivovich $et\ al.\ 2005$). The main external morphological traits of all tadpoles of Hypsiboas known to date are summarized in Appendix 1. External morphological characters that show no or little variation were excluded from this table, but are mentioned in the following summary, together with the oral cavity features of those species of Hypsiboas whose internal oral anatomy was described.

Hypsiboas: Tadpole type IV (Orton 1953), exotroph, from lentic and lotic habitats, benthic (Altig & Johnston 1989; as revised by McDiarmid & Altig 1999). Body ovoid or oval in dorsal view, depressed. Eyes dorsal or dorsolateral (lateral in some species of the *H. pulchellus* group). Nostrils oval, rimmed, with a triangular or rounded projection in the medial margin which gives them a reniform aspect; nostrils located closer to

the eyes than to the tip of the snout (midway in some species). Spiracle sinistral, lateral, placed around midline, posteriorly or posterodorsally directed, opening located at about two thirds of body length (range: 50– 90%), attached to the body for almost its entire length (free from body in some species of the H. albopunctatus, H. faber and H. pulchellus group). Oral disc anteroventral or ventral, surrounded by a single or double row of marginal papillae, with a median dorsal gap (continuous in a few species of the H. benitezi, H. pulchellus and H. semilineatus groups), with ventrolateral folds limited by medial indentations (apparently absent in Hypsiboas benitezi, a species in a basal group), submarginal papillae usually present laterally, lateral flaps with labial teeth in some species of the H. faber and H. pulchellus groups. LTRF usually 2/3–2/4, rarely 3/4, 3/ 5, 4/7 and 5/8. Jaw sheaths pigmented, finely serrated, upper sheath wide arched, sometimes convex in median part, lower sheath U-shaped. Vent tube opening dextral, reaching free margin of ventral fin (reported as median in some species —Heyer et al. 1990; Chacon-Ortiz et al. 2004— deserves revision). Tail axis straight, dorsal fin usually higher than ventral fin, dorsal fin originating at tail-body junction, sometimes extending onto the end of the body, tip of tail pointed (acutely rounded in some species), caudal musculature usually reaches the tip of tail, tail length approximately 60–70% of total length, maximum tail height larger than maximum body height (sometimes equal). Neuromasts reported in some species (maybe widespread, usually overlooked in descriptions). Coloration pattern: usually with dark dots or spots on the dorsal and lateral body surfaces, dark blotches or reticulation on tail musculature and fins, some species with dark transversal bands on dorsal caudal musculature. Buccal roof: prenarial arena with a variable number of pustules, some of them forming a transversal crest in some species (e.g., H. andinus, H. cordobae, H. faber, H. geographicus, H. lundii, H. prasinus, H. punctatus and H. semilineatus). Choanae transversely oriented, with anteromedial and rounded vacuities, posterior margins forming the narial valves, and both anterior and posterior margins undulated by the presence of small prenarial pustules. Postnarial arena with pustules and a variable number of papillae arranged transversely or forming an arch between the lateral ridge papillae. Lateral ridge papilla bearing distal undulations. The low or high median ridge is always undulated on the free margin. Buccal floor always pustulated, bearing a variable number of papillae in several species of the H. pulchellus species group and BRA sometimes poorly or not defined (e.g., H. caingua, H. faber, H. raniceps, H. puntactus rubrolineatus). Posterior area of the roof with secretory pits and lobated margin. Buccal floor: Paired infralabial papillae on infrarostral cartilages present or absent. Paired infralabial papillae on cartilago meckeli always present. Lingual anlage bearing two long and conical papillae paired near the midline, and sometimes with a variable number of pustules. Buccal pockets mostly transversal to the axial axis. Prepocket area always scattered with pustules and a variable number of papillae. BFA papillae always present, sometimes arranged in two V-shaped patterns, with or without a serrated flap near the pocket. Ventral velum with three poorly defined projections at each side on the posterior margin and many secretory pits.

Hypsiboas benitezi group: Within this basal group, two tadpoles were described, although their species assignations are only tentative (Myers & Donnelly 1997; Myers & Donnelly 2008). The main features of the tadpole assigned to H. benitezi are a not emarginated oral disc, completely surrounded by a double row of papillae, with few lateral submarginal papillae and a high number of tooth rows: 5/8 (Myers & Donnelly 1997). A continuous row of papillae and a high LTRF appear as plesiomorphic states in the phylogenetic analysis of Faivovich et al. (2005). Conversely, the tadpole assigned to H. angelicus shows a LTRF 2(1,2)/3 and a ventrolaterally emarginated oral disc (Myers & Donnelly 2008). The oral cavity features remain unknown for the species of this group. Wiens et al. (2006) obtained this group paraphyletic, with the H. semilineatus group nested within it. The larval morphology known to date does not provide any evidence for that grouping either.

Hypsiboas punctatus group: LTRF 2/3, 2/4, 2/5, 3/4 and 3/5 were reported for this group. The last lower row is weak, composed of smaller and more spaced teeth. LTRF 1/2 reported for H. cinerascens (Duellman 1978) seems to be due to the early stage of development (stage 25, see Mijares-Urrutia 1993). The oral cavity features were described for two species of this group: H. cinerascens and H. punctatus rubrolineatus (d' Heursel & Haddad 2007; present study). At the light of the present knowledge, these two species share the

presence of a high square-shaped median ridge with undulations only in the ends, with lateral borders free of serrations and one short papilla at each side of the base. This combination of features relative to the median ridge is unique to these two species within *Hypsiboas* and may be used to diagnose the *H. punctatus* species group (*H. riojanus* is similar but possesses serrations in all the free margins of the ridge). Wiens *et al.* (2006) obtained a paraphyletic *H. punctatus* group, with *H. sibleszi* being the sister taxon of the remaining species of the group included by Faivovich *et al.* (2005) plus the *H. albopunctatus* group. The larval morphology studied here does not provide any evidence for that grouping either.

Hypsiboas semilineatus group: Remarkable ontogenetic changes in LTRF (ranging from 2/3 to 3/5) were reported for some species in this group (Kenny 1969; d'Heursel & de Sá 1999) which may explain the different LTRF attributed to them (e.g., H. boans, H. geographicus; Duellman 1970; Duellman 1978; Kenny 1969; Duellman & Lescure 1973; Pyburn & Hall 1984). Hypsiboas hutchinsi was at first placed into the H. benitezi group, but was later transferred to this group on the basis of some adult morphological traits (Faivovich et al. 2006) although its tadpole has some plesiomorphic character states (continuous row of marginal papillae, high LTRF: 4/7; Pyburn & Hall 1984). The tadpole of this species also has a unique color pattern: pink tail with a conspicuous black spot on the sides (Pyburn & Hall 1984). Schooling behavior is present in the tadpoles of H. geographicus and H. semilineatus, whose tadpoles are entirely black (Bokermann 1963; Kenny 1969; Duellman & Lescure 1973; Caldwell 1989; d'Heursel & Haddad 2002). The oral cavity features were described for two species of this group: H. geographicus and H. semilineatus (d'Heursel & de Sá 1999). At the light of the present knowledge, there are no features shared by these two species that may be used to diagnose the H. semilineatus species group.

Hypsiboas albopunctatus group: Most species in this group have a single row of marginal papillae with a few submarginal papillae, and LTRF 2/3, with P3 being much shorter than the other rows. An exception is the rheophilous tadpole of H. heilprini, which has an oral disc completely surrounded by a double row of papillae, the highest number of labial tooth ridges known for the genus (6/9) and many lateral flaps with teeth (Noble 1927). A spiracular tube free from the body wall was reported for H. albopunctatus (Spirandeli Cruz 1991; de Sá 1995; Rossa-Feres & Nomura 2006), H. fasciatus (Wild 1992) and H. raniceps (Rossa-Feres & Nomura 2006, this paper). A pattern with dark transverse bars on the dorsal caudal musculature is present in H. calcaratus, H. fasciatus, H. lanciformis and H. raniceps (Duellman 1978; Wild 1992; Faivovich et al. 2005; also present in some species in the H. faber, H. pulchellus and H. semilineatus groups, see below). The oral cavity features were described for two species of this group: H. albopunctatus and H. raniceps (Spirandeli Cruz 1991; present study). At the light of the present knowledge, there are no features shared by these two species that may be used to diagnose the H. albopunctatus species group.

Hypsiboas pellucens group: LTRF: 2/4. The spiracle of *H. rufitelus* was described as "hose-shaped, notably large" (Hoffmann 2005), although it is not stated whether it is free from the body or not. This state should be revised, due to the sister-group relationship of this group with the *H. albopunctatus* group, in which four species exhibit this character state (see above). The oral cavity was described only for *H. rufitelus* (Wassersug 1980), and this species has not unique features that may be useful to diagnose the group.

Hypsiboas faber group: LTRF: 2/4 (sometimes 2/3 in H. pardalis; Bokermann 1968; Heyer et al. 1990). A short ventral gap in the row of marginal papillae was reported in H. lundii (Rossa-Feres & Nomura 2006), H. pardalis (Heyer et al. 1990) and in some specimens of H. faber (present study), a character state that is unique among Hylidae (this three species form a clade in the study of Faivovich et al. 2005; we also observed it in some specimens of H. raniceps). P4 is usually noticeably shorter than the other rows and fragmented. Lateral submarginal papillae or flaps bearing teeth were reported in H. albomarginatus (Peixoto & Cruz 1983), H. faber (present study) and seem evident from the illustration of H. crepitans in Kenny (1969). This feature is also present in many species of the sister group H. pulchellus (see below). A spiracular tube free from the body is present in H. albomarginatus (Peixoto & Cruz 1983), H. crepitans (Rada 1981; evident from the illustration) and in H. faber (more noticeably in early stages of development; present study). The former

two species also have dark transverse bars on the dorsal caudal musculature (Peixoto & Cruz 1983; Rada 1981). The oral cavity was described for the species H. albomarginatus, H. faber, H. lundii and H. rosenbergi (Spirandeli Cruz 1991; Vera Candioti 2007; d'Heursel & Haddad 2007; present study). Three of these species are unique in having 2 long lingual papillae ramified at the free ends and two pustules placed laterally to them (H. faber, H. lundii and H. rosenbergi). However, d'Heursel & Haddad (2007) did not report the distal ramifications on the lingual papillae of H. albomarginatus. The two lateral pustules were interpreted by Spirandeli Cruz (1991) as a second pair of papillae for the species H. lundii (see text on page 68), but in the respective figure (Fig. 7B, page 67) these two additional papillae are clearly a pair of pustules. On the other hand, Vera Candioti (2007) described for *H. rosenbergi* the presence of two simple lingual papillae (see text on page 60), but in the respective figure (Fig. 33E, page 60) they are clearly ramified. Then, the presence of a pair of long and ramified lingual papillae is a feature that, within Hylinae, is only present in three of the species of the H. faber species group (H. faber, H. lundii and H. rosenbergi), so it is likely a putative synapomorphy of the Hypsiboas faber group or of a less inclusive clade, due to its absence in H. albomarginatus, a basal species in this group. Wiens et al. (2006) obtained this species not as the sister group of the remaining species of the H. faber group, but as the sister group of the H. pellucens group. The larval morphology studied here does not provide any evidence for that grouping either.

Hypsiboas pulchellus group: LTRF: 2/3 in most species. In some species of the Atlantic Forest (H. caipora, H. freicanecae, H. joaquini, H. marginatus and H. semiguttatus) and from the Andean clade (H. andinus, H. balzani, H. marianitae, H. palaestes and some H. riojanus) the LTRF is 2/4 (Duellman et al. 1997; Lötters et al. 1999; Garcia et al. 2001a; Garcia et al. 2003; Carnaval & Peixoto 2004; Garcia et al. 2007; Antunes et al. 2008; present study), in H. poaju is 2/5 (Garcia et al. 2008), and H. curupi presents a LTRF 3/5 and a continuous double or triple row of marginal papillae (Faivovich 1996). These species also have lateral flaps or submarginal papillae bearing labial teeth (same references; also occasionally in some H. cordobae and H. pulchellus, present study). The last posterior row is usually much shorter than the other rows, and P4, when present, is usually fragmented. Hypsiboas balzani, H. marianitae and H. riojanus may have a third and divided upper row of labial teeth close to the marginal papillae (Duellman et al. 1997; Lötters et al. 1999; present study). Hypsiboas caingua has A1 divided and a free spiracular tube (present study). Some species have a coloration pattern with dark transverse bars on the dorsal caudal musculature (H. balzani, H. palaestes, H. polytaenius and H. pulchellus; Lutz 1973; Heyer et al. 1990; Duellman et al. 1997; present study).

The oral cavities were described for Hypsiboas andinus, H. caingua, H. cordobae, H. joaquini, H. leptolineatus, H. pulchellus, H. prasinus, and H. riojanus (Lavilla & Fabrezi 1987; Spirandeli Cruz 1991; Both et al. 2007; d'Heursel & Haddad 2007; present study). The absence of infralabial papillae laying on the infrarostral cartilages within the orobranchial chamber is a feature shared for several species of the H. pulchellus species group: H. andinus, H. caingua, H. cordobae, H. pulchellus, H. prasinus and H. riojanus. D'Heursel & Haddad (2007) did not mention these papillae in *H. joaquini*, so we assume they are absent in this species. Both et al. (2007) did not mention them in H. leptolineatus, but a few of them, although very reduced, can be seen in their micrograph. The infralabial papillae laying on the infrarostral cartilages are present in the sister group of the H. pulchellus species group (H. faber species group), in related groups (H. pellucens group) and in the sister group of Hypsiboas (at least in Aplastodiscus perviridis as described by Spirandeli Cruz 1991). The species of Aplastodiscus and Bokermannohyla described by d'Heursel & Haddad (2007) possess some pairs of papillae anterior to the pair of infralabial papillae, which based on their position they are clearly placed on the infrarostral cartilages. Within *Hypsiboas*, they are known to be absent also in *H. albopunctatus*, H. cinerascens, H. punctatus and H. raniceps (d'Heursel & Haddad 2007; present study). A denser sampling is needed to study the taxonomic distribution of this character state, and determine which clade it may support.

Other putative synapomorphy for at least a clade within the *Hypsiboas pulchellus* group is the presence of long and conical papillae on the central area of the BRA. The species of the group possess BRA with a vari-

able number (8–40) of long and conical papillae arranged forming a V in the posterior limit of the central arena (exception *H. caingua*, *H. cordobae* and *H. joaquini*, where these are absent). These papillae are always absent in the species of the other species groups of *Hypsiboas* (BRA bears very short papillae and pustules), but are present in some species of *Aplastodiscus* (*A. albofrenatus* and *A. eugenioi*, both in the *A. albofrenatus* group), and also in *Bokermannohyla luctuosa* (d'Heursel & Haddad 2007). Moreover, the sister species *H. andinus* and *H. riojanus* are the species of the *H. pulchellus* species group that possess the highest BRA papillation. Again, the taxonomic distribution of this putative synapomorphy deserves additional study.

Concluding remarks

Within the Hylinae the oral cavity morphology was described for 60 species, which are listed in Appendix 2 (Wassersug 1976; Wassersug 1980; Viertel 1982; Lannoo et al. 1986; Lavilla & Fabrezi 1987; Duellman & de Sá 1988; Spirandeli Cruz 1991; Echeverría & Montanelli 1992; Schiesari et al. 1996; de Sá & Lavilla 1997; Echeverría 1997; Fabrezi & Vera 1997; d'Heursel & de Sá 1999; Sandoval 2000; Vera Candioti et al. 2004; Vera Candioti 2004; Vera Candioti 2007; Both et al. 2007; Wogel et al. 2006; Conte et al. 2007; d'Heursel & Haddad 2007; Aguilar et al. 2007). Considering the published descriptions and those made by us, we found that no oral features seem to be synapomorphic for the species of *Hypsiboas*. Nevertheless, there is one trait shared between the species of Hypsiboas, Aplastodiscus and Bokermannohyla. Wassersug (1980), Spirandeli Cruz (1991), Faivovich et al. (2005) and more recently d'Heursel & Haddad (2007) called attention about the rounded vacuities —as huge cul de sac structures— of the anteromedial surface of the choana present in all the species of these three genera, but absent in the other genera of Hylinae studied by them and by other authors. We observed these vacuities in all the species of Hypsiboas studied here. The chemoreceptive function of these structures was first suggested by Wassersug (1980). The epithelia lying on the bottom of the vacuities is ciliated and possess important quantities of mucous (Fig 16B), supporting Wassersug's view about their chemoreceptive function. Most authors have not focused on the presence of anteromedial vacuities of the choanae in the other genera of Hylinae. However, some sort of concavity was described for Scinax catharinae (Conte et al. 2007). These concavities are oval-shaped in this species. We observed oval-shaped concavities also in other species of Scinax (S. berthae) and in Pseudis platensis (Figs. 16C and 16D). Scinax berthae and Pseudis platensis also present ciliated epithelia on the bottom of the concavities. These oval concavities and the round shaped vacuities of the above mentioned Hylinae genera are clearly homologous, considering their relation with the other parts of the choana and also taking into account the presence of the ciliated epithelia. For the time being two states are recognized for the character "anteromedial concavity of the choana": oval and rounded. The second character state, for which we reserve the term "vacuity" following Wasserssug (1980), seems to be exclusive —as previously suggested by Faivovich et al. (2005) and d'Heursel and Haddad (2007)— of a clade composed at least by the genera Aplastodiscus, Bokermannohyla and Hypsiboas, pending on the knowledge of the state in the species of Hyloscirtus and Myersiohyla (the oral cavities of two species of Hyloscirtus were recently illustrated — Aguilar et al. 2007 — but it is not clear from these illustrations whether those vacuities are present or not). Whether this character state optimizes as a synapomorphy of this clade, as suggested by Faivovich et al. (2005) and d'Heursel and Haddad (2007), or it is the plesiomorphic state for Hylinae will only be elucidated with further studies on the taxonomic distribution of these vacuities and its morphological variation within hylinae.

Although no synapomorphy for the genus *Hypsiboas* seems evident from the analysis of external and oral cavity tadpole morphology, the evolution of larval morphology within the tribe Cophomantini follows the pattern already noticed by Faivovich *et al.* (2005), in which the most basal clades have "rheophilous" tadpoles with muscular tails with relatively low fins, ventral and enlarged oral discs completely surrounded by marginal papillae and large numbers of labial tooth rows, while derived clades have most typical "pond tadpoles"

with reduction in size of the oral disc and in the number of tooth rows and with a dorsal gap in the row of marginal papillae. Within the genus *Hypsiboas*, the same evolutive pattern seems to be present, as can be inferred from the review presented above. Tadpoles of *Hypsiboas* are very similar to those of its sister taxon *Aplastodiscus*, whose known tadpoles possess relatively small ventral or subterminal oral discs, with ventrolateral emarginations, a small dorsal gap in the marginal papillae, LTRF 2(2)/4(1) —3(1–3)/6(1,6) in *A. albofrenatus*, Peixoto & Cruz 1983— with the last posterior row shorter than other rows and submarginal papillae usually present (Caramaschi *et al.* 1980; Peixoto & Cruz 1983; Garcia *et al.* 2001b; Gomes & Peixoto 2002; Carvalho-e-Silva & Carvalho-e-Silva 2005). A distinctive feature of *Aplastodiscus* tadpoles seems to be a relatively slender body and long tail (same references). As the tadpoles of many species of Cophomantini, especially from the genera *Aplastodiscus* and *Bokermannohyla* and from the *H. benitezi* species group are still unknown, the picture presented herein is still quite tentative. Future work will fill the gaps in our knowledge of larval morphology of this tribe.

Acknowledgments

We are grateful to the following friends who collected tadpoles with us and were great companions in the field: B. Blotto, D. Ferraro, E. Kubisch, M. Tedros, M. Nava, D. Martí, J.C Fernicola, A. Lopez, M. Pereyra, J. Urdampilleta, F. Burgos, G. Aguilera, R. Moreno, S. Cairo, S. Rosset, J. Boeris, G. Finarelli and J. Lescano. We acknowledge S. Barrionuevo and B. Blotto for the photographs of juvenile specimens of *H. andinus* and *H. riojanus* respectively. The following people kindly shared bibliography with us: J. Langone, T. Gomes dos Santos, C. Martins, V. Orrico, M.F. Vera Candioti, C. Both, C. Aguilar and A. Camargo. Three anonymous reviewers made very helpful suggestions. F. Kolenc and C. Borteiro acknowledge DINARA-MGAP and A. Britos for logistic support and G. Pereira for helping with the English. L. Alcalde (ILPLA Scientific Contribution N°776) acknowledges Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) for Post-doctoral Scholarship (2007). D. Baldo and D. Cardozo acknowledge ANPCyT for Grants PICT (16-35045) and PICT-O (37035) and CONICET. D. Baldo and J. Faivovich thanks ANPCyT for Grants PICT. J. Faivovich thanks FAPESP procs. 05/56756-0 and 06/52088-5, and CONICET.

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APPENDIX 1.

width), DF (dorsal fin), DG (dorsal gap), DL (dorsolateral), OD (oral disc width), E (eye), FH (fin height), L (in life), MP (marginal papillae), P (in illustrations, but not stated in the descriptions by the authors. Abbreviations: AV (anteroventral), BH (body height), BL (body length), BW (body preservative), PD (posterodorsally), S (sinistral), SMP (submarginal papillae), TBJ (tail-body junction), TL (total length), TaL (tail length), TM Table with the main morphological features of the known tadpoles of Hypsiboas. Characters noted as "*" were measured or inferred from the (tail musculature), TOS (tip of snout), TOT (tip of tail), VF (ventral fin) VG (ventral gap), VL (ventrolateral), w/ (with).

Total Total length (stages)	P: Darker brown spots, tail marbled, longitudinal 36.3 (27) medial brown stripe on first third, fins marbled	44.7 (37)	P: dark brown w/ small dark dots, IM pale cream w/ *: 45.4 dorsal edge dark (36) brown, fins w/ brown spots	Yellowish-brown, sometimes w/ 39.5–58. dark dots, tail w/ 2(37–40) translucent fins
Tail Pa	P: Darl TM spo reaches ma TOT, tip long pointed. *: medis 70% TL stripe third, fin	*: slightly higher than body, 65% TL	P: dark TOT acute small c *: FH = TM pal, BH, 65% dorsal TL browr	*: TOT Yellow pointed, some FH > BH, dark do 69% TL translı
Fins	DF origin slightly onto the body, FH >BH, both fins arched. *: DF>VF		DF origin at base of tail, DF>VF, DF curved, VF straight	DF slightly convex, DF origin at TBJ, VF straight.
Nostrils	l, Nearer E than to TOS, reniform	Dorsal, s reniform. *: nearer E than to TOS	Oval, w/ medial triangular dermal flap, dorsal.	Oval w/ large projection on marginal rim, dorsally
Spiracle	S, PD directed opens at 90% BL	Lateral, long, attached to the body only at its base, opening posteriorly directed, *: opens 84% BL	S, lateral, long, tube-like, opening raised	S, long and narrow, posteriorly directed, internal wall free from body wall
LTRF	2(1,2)/3(1)	2(2)/3(1)	G 2(2)/3(1)	y 2(1,2)/3(1), P3=50% P2
Oral disc and Papillae	AV, 34% BW, DG, MP single row. *: VL emarginations	Ventral, < 33% BW, MP single row, DG	AV, VL folds, DG small & medial, MP single row, SMP few in folds	Ventral, ventrally emarginate, MP single row, DG narrow
Reference (name used in publication)	Heyer et al. 1990 (Hyla albopunctata)	Spirandeli Cruz 1991 (Hyla albopunctata)	de Sá 1995 (<i>Hyla</i> albopunctata)	Rossa-Feres & Nomura 2006
Hypsiboas albopunctatus species group	H. albopunctatus (Spix)			

	31.8 (38)	34.4(35), 38.1(38)	25.1 (30)	
Dark brown with tan mottling and tan interorbital bar. Tail with vertical dark bands	L: dark brown w/tan mottling and tan interorbital bar, tail yellowish tan w/vertical brown bare	L: greenish-gray (w/fine black spots at stage 38), dark stripe from mouth to E, tail w/black vertical bands	L: greenish gray, TM pale yellow, w/vertical black marks	
TOT pointed	TOT slender	TOT pointed *: 69% TL	TOT pointed	
DF not extending onto body	DF origin on dorsal TM	DF terminates at TBJ, DF>VF, DF convex, VF straight	DF origin at base of TM, DF higher than VF	
Closer to E than to TOS	Ovoid, dorsal, midway between TOS and E, median narial papillae	Dorsal, closer to E than to TOS, papilla on medial margin	Large, dorsal, closer to E than to TOS, small papilla on median margin of	
Tube long, opening posteriorly directed, at 2/3 BL	S, long, distal third free from body wall, PD directed, at 2/3 BL	S, tube long, free, PD directed *: 90% BL	S, tube long and free from body wall, PD directed	
2(2)/3	2(2)/3, P3 slightly shorter	2(1-2)/3(1), very small and incomplete P4 in stages 35–38	2(2)/3, P3 shorter, sometimes incomplete P4 present	*: 6(1,2,6)/9(1), lateral flaps w/teeth
AV, lateral folds, MP single row, DG Few sub-marginal lateral papillae at	stages 35-36 AV, w/ lateral folds, MP single row, DG	AV, not marginated, MP single row, narrow DG and frequently narrow VG, some SMP laterally and ventrally, VL	AV, MP single row, DG and narrow VG, some SM papillae, VL folds	*: VL folds, MP complete double row, some SMP laterally
Duellman 1978 (Hyla calcarata) Wild 1992 (Hyla calcarata)	Duellman 2005 (<i>Hyla calcarata</i>)	Wild 1992 (Hyla fasciata)	Duellman 2005 (Hyla fasciata)	Noble 1927 (Hyla heilprini)
H. calcaratus (Troschel)		H. fasciatus (Günther)		H. heilprini (Noble)

45 (35)	*: 26.3 (29)	38.2 (34)		52.6–66. 9 (34–37)	Total length (stages)
Dark brow, tail with vertical dark brown bars Tail with vertical dark brown bars	P: Pale brown w/dark reticulations, tail pale w/ dark spots	P: body grayish brown, TM tan w/square middorsal brown blotches and small brown blotches laterally on tail	Yellowish brown, tail marbled with indistinct dark spots	Reddish-brow, w/ small black dots, dark rectangular blotches in dorsal tail muscle	Pattern
70% TL, TOT pointed	TOT slightly flagellifor m	61% TL, TOT acutely rounded	*: TOT pointed, 68% TL	*: TOT pointed, FH higher than body, 69% TL	Tail
Fins shallow, DF not extends onto the body Low DF	DF extends slightly onto the body, DF convex, VF straight, DF>VF	DF origin at TBJ, DF convex, DF>VF	*: DF > VF	DF begins at posterior third of body, DF>VF *: both fins arched	Fins
Midway between TOS and E	Oval, w/small medial triangular dermal flap, dorsal	Moderately small, DL, closer to E than to TOS, papilla on median margin of nostrils	Bean-shaped, with a central operculum	Oval, w/ large projection on marginal rim, dorsally positioned	Nostrils
S, posteriorly directed, opens 75% BL Attached tube	S, lateral, long, tube-like, opening raised, on the posterior third of body *: 73%, BI	S, short and attached to body wall, PD directed, opening below midline and about 50% BL	S, opening laterally and posteriorly directed, 66% BL	S, long and narrow, internal wall not fused to body, posteriorly directed *: 81% BL	Spiracle
2(2)/3, P3 much shorter than other rows	2(2)/3(3), P3 shortest	2(1)/4(1), P4 weak and fragmented * 2(2)/4(1) and lateral flaps w/teeth are seen in the illustration	2/3(0-1) *: 2(1,2)/3(1) seen in the illustration, P3 = 50% P2	2(1,2)/3(1), P2 longer than P1 and P3	LTRF
AV, lateral folds, MP single row, wide DG	AV, VL folds, MP single row, small median DG, few SMP in VL folds	AV, emarginate, VL folds, MP single row, broad median DG, SMP absent	MP single row, short median DG *: VL folds, SMP	Ventrall, ventrally emarginate, MP single row, narrow DG, SMP one or two laterally	Oral disc and Papillae
Duellman 1978 (Hyla lanciformis) Wild 1992 (Hyla lanciformis)	de Sá 1996 (Hyla multifasciata)	Duellman 1997 (Hyla multifasciata)	Cei 1980, after Vizotto 1967 (Hyla raniceps)	Rossa-Feres & Nomura 2006	Reference (name used in publication)
H. lanciformis Cope	H. multifasciatus (Günther)		H. raniceps Cope		Hypsiboas benitezi species group

P: head and body 35.7 (25) uniformly brown, TM pale yellowish brown	P: uniform brown, 42.7 (37) tail tan, dark brown stripe on dorsal edge of TM, fins transparent with blotches and flecks	Total length (stages)	-fi	Olive brown, dark 55 mottled on flanks, (maximu black line from m length) snout to E, tail w/two longitudinal stripes, fins spotted
	_	Pattern	P: brown, interocular dark triangle, TM wit bands in dorsal view	
64.7%TL	TOT rounded, TM J reaches TOT, 63.2% TL *: FH>BH	Tail	*: TH>BH *: TOT pointed, 70% TL	TOT at tapered *: 63% TL
DF>VF	DF>VF *: both fins arched, DF origin at TB.	Fins	DF origin on last third of body, DF arched *: DF > VF, VF slightly arched	
DI	Dorsal, laterally directed	Nostrils	Reniform, w/ projection inner margin, closer to E than to snout	Large, dorsal, with papillae on median margin, pigmented rim
S, tube adhered to body wall	S, tube 2 mm long *: 71% BL, PD directed	Spiracle	S, long, PD directed. *: projects tube free from body wall, 75% BL	S. *; PD directed, 58% BL
2(1,2)/3, P3 shorter	5(1,5)/8(1)	LTRF	2(2)/4(1), P4 shorter than others	2(1,2)/4(1), isolated patches of teeth on papillae in angles
Ventral, not emarginate, MP single row, DG *: VL folds, very narrow DG, SMP absent	Ventral, not emarginate, completely surrounded by double row of MP, few SMP *: 54% BW	Oral disc and Papillae	Ventral, MP single row, DG, VL folds, some SMP with labial teeth	MP single row, much folded laterally *: DG, VL and DL folds, some IMP w/ labial teeth
Myers & Donnelly 2008 (tentative assignation)	Myers & Donnelly 1997 (<i>Hyla benitezi</i> , tentative assignation)	Reference (name used in publication)	Peixoto & Cruz 1983 (Hyla albomarginata)	Kenny 1969 (Hyla crepitans)
H. angelicus Myers & Donnelly	H. benitezi (Rivero)	Hypsiboas faber species group	H. albomarginatus (Spix)	H. crepitans (Wied-Neuwied)

54.5 (39)	35(25?)	47.5–53. 3 (36)	38–47 (25)	30–37 BL, 55–74 TaL (largest tadpoles, stage unknown)	
P: Pale gray with scattered black flecks, TM tan with gray blotches, fins transparent with grayish flecks	Greenish-brown	Light green, sometimes w/dark flecks, dark line from snout to E. Dark dots after stage 41. *: transverse dark bars on dorsal TM	L: dorsum brown w/greenish marks, belly greenish-white, tail tan w/brown marks	Body dark, tail with dark blotches or large round dots.	Dark, tail scattered with large round dots
TM almost reaches TOT, TOT pointed. *: 71% TL	TOT pointed	66% TL, TM does not reaches TOT		TOT pointed, blunt in some specimens	TOT pointed *: 63% TL
DF does not extend onto the body, DF > VF	DF>VF	DF>VF, DF not extends onto body *: DF arched, VF straight		DF slightly > LF, DF not reaching the back	DF > VF, DF not extending towards the back
Anterolaterall y directed, midway between E and TOS		Dorsal, w/medial papilla, closer to E than to TOS		Oblique, reniform, with a valve on inner edge	Dorsal, oblique
S, PD directed, opens 66% BL	S, small	S, long and narrow *: projecting tube free from body		S, directed slightly upwards	S, located at posterior part of the body *: 71% BL
2(2)/4(1), P4 extremely short	1/1(1)	2(2)/4(1), sometimes 2(2)/4, P4 w/few teeth		2(2)/4(1,2), P4 fragmented, last row shorter	2(1)/4(1) *: P4 noticeably shorter
AV, 33% BW, folded laterally, MP single row, median DG		AV, VL folds, MP single row, DG		Dense rows of papillae, median DG, VL and lateral folds	Close rows of papillae, narrow median DG *: SMP, VL and DL folds
Duellman 1970 (Hyla crepitans)	Donoso-Barros and León 1972 (Hyla crenitans)	Rada 1981 (Hyla crepitans)	Duellman 1997 (Hyla crepitans)	Lutz 1973 (Hyla faber)	Cei 1980 (Hyla faber)
				H. faber (Wied-Neuwied)	

78.1 (37)	75.3–86. 1 0 (33–37)	66 (37)	57.5 (36)	1 40.1–52. 4 (35–39)	43 (stage 38 Limbaug h & Volpe 1957)
	Stages 25–27 body brown, tail black; stages 33–37 body brown with dark dots, tail w/dark reticulation distally, or dark blotches	Yellowish, with small black dots *: tail with dark reticulation		Brown, w/ small black dots, fins translucent	Brown, w/dark dots, TM banded in dorsal view, fins hyaline w/ dots
*: FH > BH, 68% TL	TOT acutely rounded, tail 69% TL	*: FH > BH, TOT acutely rounded, 72% TL	*: FH > BH, 66% TL	*: FH = BH, 63% TL	FH = BH, TOT pointed *: 70% TL
	DF origin at TBJ, fins subparallel, converging at distal third	*: DF>VF, both fins convex, DF origin on tail		DF convex, DF origin at TBJ, VF straight *: DF > VF	*: DF > VF, DF origin at the end of the body
Dorsal, elliptic. *: Closer to E than to TOS	Oval, rimmed, triangular projection inner margin, dorsolaterally located, closer to E than to TOS	Dorsal	Dorsal, elliptic. *: Closer to E than to TOS	Oval, w/ large projection on marginal rim, dorsally positioned	Dorsal * reniform, closer to E than to TOS
S, free opening PD directed. *: opening 72% BL	S, PD directed, 74% BL	*: S, 83% BL, posteriorly directed	Short and wide, with free ending posteriorly directed. *: 64%	S, lateroventral, long and wide, PD directed, internal wall not fused to body wall *: 76% BL	Protruding. *: S, 77% BL, PD directed
2(2)/4(1)	2(2)/4(1), P4 shorter and fragmented, lateral flaps with teeth	2(2)/3(1) *: 2(2)/4(1)	2(2)/4(1)	2(2)/4(1)	2(2)/3(1)
Ventral, OD > 1/3 BW, MP single row, DG	AV, DG, MP single or double row, SMP laterally, sparse papillae in middle of ventral lip, short VG sometimes	Ventral, MP double row, DG *: VL folds	Ventral, OD > 33% BW, MP double row, DG	Ventral, MP double row, DG, VG, few SMP laterally, ventrally emarginated	VL folds, MP single row *: wide DG
Spirandeli Cruz 1991 (Hyla faber)	Present study	Bokermann & Sazima 1973 (Hyla biobeba)	Spirandeli Cruz 1991 (Hyla biobeba)	Rossa-Feres & Nomura 2006	Bokermann 1968 (<i>Hyla pardalis</i>)
		H. lundii (Burmeister)			H. pardalis (Spix)

39.2 (35)	39.1 ± 0.2 (35)		27.0 (27)	54.8 (37)	
P: Brown, transverse dark bands on dorsum of TM	P: grey w/dark dots		P: Dark brown, dark blotches in tail, dorsal surface of TM with transverse bars	P: Mottled tan, tend to form transverse dark bands on dorsal TM	
FH = BH, TM reaches TOT, TOT pointed. *: 69% TL	TM reaches TOT, TOT acute	*: TM reaches TOT, TOT pointed. 65% TL	TM reaches TOT, TOT pointed. *: 62% TL	TM almost reaches TOT, TOT pointed.	
DF origin slightly onto the body, DF arched, VF straight. * DF > VF	DF > VF	*: DF does not extend onto the body, DF > VF	DF does not extend onto the body, DF > VF. *: both fins almost straight	DF does not extend onto the body, DF > VF. *: DF curved, VF straight	
Closer to E than to TOS, reniform	Antero-dorsal, halfway between E and TOS, rounded w/ triangular fold		Anterolaterall y directed, midway between E and TOS	Anterolaterall y directed, midway between E and TOS	
S, PD directed, opens 69% BL	S, lateral, PD directed, slightly tubular	*: S, lateral, posteriorly directed, 70% BL	S, PD directed, opens slightly posterior to 50% BL	S, PD directed, opens 66% BL	
2(2)/3-4(1)	2(2)/4(1), P4 noticeably shorter	*: 2(1,2)/3 (in error, fide Duellman, 1970, who studied the same sample)	2(2)/4(0-1), P4 noticeably shorter and fragmented	2(2)/4, P4 noticeably shorter	2(2)/4(1), P4 shorter, sometimes fragmented
AV, 44% BW, MP single row, DG, small VG. * VL emarginations	AV, w/ lateral folds, MP single row	*: VL folds, completely bordered by double row of MP	AV, OD = 1/3 BW, completely bordered by single or double row of MP, deeply folded laterally. *: median DG shown in the illustration	Ventral, OD = 1/3 BW, MP single row, DG, deeply folded laterally	AV, 30 % BL, single or double row, narrow DG. *: VL emarginations
Heyer et al. 1990 (Hyla pardalis)	Chacon-Ortiz et al. 2004 (Hyla pugnax)	Breder 1946 (Hyla rosenbergi)	Duellman 1970 (<i>Hyla</i> rosenbergi)	Duellman 1970 (Hyla rufitela, fide Savage, 2002)	Vera Candioti 2007
	H. pugnax (Schmidt)	H. rosenbergi (Boulenger)			

used in an publication) Hoffmann 2005	Olai disc	_	מוממות	TACSULIES	ciii i	ıaıı	I attenti	Local
500	and Papillae		.					length (stages)
	Ventral, MP in	2(2)/4, A1	S, hose-shaped,	Midway	DF origin on	TL %69	Dark marbled,	33.2 ±
(<i>Hyla rufitela</i>) sii ro	single or double row	double rowed *: 2(2)/4(1)	notably large *: 70% BL, PD	between E and TOS	body end, DF > VF	*: TOT pointed.	blackish-brown pattern	2.9 (32–36).
**	*: VL folds		directed	*: oval, with		both fins	1	38.1 ±
				medial		arched		2.6 (37)
				subtriangular projection				
ice (name	Oral disc	LTRF	Spiracle	Nostrils	Fins	Tail	Pattern	Total
used in an publication)	and Papillae							length (stages)
	MP single row,	2(1,2)/3(1)	S, 66% BL	Closer to E		*: DF >	Dark gray, with	
(Hyla pulchella na andina)	narrow DG		*:PD directed	than to TOS, slightly		BH, 62% TL	dilute spots on the tail	
				protruding, with a folded				
	Ventral, VL	2(2)/3(1),	S, lateral, 65%	moutn Oval, rimmed,	Both fins	FH > BH,	Olive, tail w/ dark	51.9–58.
(Hyla pulchella co andina) = .	constrictions, OD = 43% BW, MP	labial teeth in supernumerary	BL	medial projection,	curved, DF origin at TBJ	TOT acute	olive blotches	5 (stages unknown
	single or double	short rows		DL, closer to E)			<u> </u>
0.	row, DG	*; P3 noticeably shorter		than to 10S				
man et al.	Ventral, VL	2(2)/4(1),	S, PD directed,	Oval, weakly	DF	Pointed	P: uniformly	57.4 (37)
	emarginated, DG,	sometimes	attached to the	rimmed, rim	terminating at	TOT, TM	brown w/ dark	
(Hyla andina) fe	few SMP, lateral	2(2)/3(1)	body for most of	medially	dorsal TBJ,	reaches	brown spots, fins	
IIS	ılaps		its length	raised	DF > VF	101	transparent w/	
			*: 59% BL	*: closer to E		*: 00%	small blotches	

5 (33–37)	41.7 (38)	41.0 (26)	38.4 (36)	36.3-48.
P: light brown w/dark brown spots, dark brown interocular triangular spot, fins opalescent w/dark flecks	P: uniformly pigmented, tail w/ pale brown blotches, mainly in DF L: TM w/ dark brown bars	Black, with scattered white flecks		P: dark brown w/ unpigmented regions, w/ small dark dots. TM w/ dark irregular bands, fins opalescent w/ dark blotches
Pointed TOT, TM reaches TOT, 66% TL, TH >BH	Pointed TOT, sometimes rounded *: 65% TL	FH = BH, TM reaches TOT, TOT pointed. *: 70% TL	*: FH > BH, 62% TL	Pointed TOT, TM reaches TOT, 68% TL, TH > BH
DF origin at TBJ, DF > VF, DF arched, VF straight	DF terminating at dorsal TBJ, DF > VF on posterior half	Origin slightly onto the body, DF slightly arched, VF straight. *: DF > VF		DF origin onto end of body, DF > VF, DF arched, VF straight
Oval, DL, weakly rimmed, medial subtriangular projection, closer to E than to TOS.	Oval, weakly rimmed, rim medially raised *: closer to E than to TOS	Midway between E and TOS, reniform	Dorsal, reniform. *: Closer to E than to TOS	Oval, weakly rimmed, medial subtriangular projection, closer to E than to TOS, DL
S, PD directed, attached to the body for most of its length, 64% BL	S, posteriorly directed, attached to the body for most of its length *: 57% BL	S, PD directed, opens 75% BL	Moderately long, protruding, free ending DL directed *: 73% BL	S, PD directed, projecting tube free from body, 76% BL
2(2)/4(1); P4 about one half-one third P3, P4 fragmented sometimes	3(1,3)/4(1) stage 38; 2(2)/3(1) stage 25, 2(2)/4(1) stage 30	2(2)/3(1)	2(1,2)/3(1)	2(1,2)/3(1); 2(1,2)/3; 2(1,2)/3(1,2); P3 about one third of P2
AV, emarginated VL, MP single or double row, DG, some SMP and flaps w/ teeth	Ventral, posterolaterally emarginated, DG, many SMP, lateral flaps w/ teeth	AV, OD = 45% BW, MP single row, brief DG. *: VL emarginations, one IMP on each	Ventral, OD less than 1/3 BW, MP single row, small DG	AV, VL emarginations, MP single or double row, DG, some SMP laterally
Present study	Duellman et al. 1997 (Hyla balzani)	Heyer <i>et al.</i> 1990 (Hyla multilineata)	Spirandeli Cruz 1991 (<i>Hyla</i> sp. aff. pulchella)	Present study
	H. balzani (Boulenger)	H. bischoffi (Boulenger)	H. caingua (Carrizo)	

34.1 (28)	42.1 (26)	71 (maximu m length)		49.0–62. 8 (30–35)
L: brownish w/ dark brown, gray and reddish blotches	L: grayish to brownish, w/ blackish spots, posterior part of tail darkly pigmented) -		P: dark brown w/small dots, fins opalescent w/dark flecks
*: 61% TL, tip rounded	Tip rounded *: FH > BH, 70% TL	60–70% TL, tip pointed	*: FH > BH, TOT acutely rounded, 64% TL	TOT acute or slightly rounded, TM reaches TOT, 69% TL, FH >BH
DF origin on body, DF > VF	Fins convex, DF > VF, origin DF slightly anterior to base of tail	DF not extending onto the body	*: DF > VF, both fins arched	DF origin on end of body, DF > VF, both fins subparallel, converging at the end
Oval w/ small elliptic projection on inner margin	Dorsal, reniform, closer to E than to TOS			Oval, weakly rimmed, medial rounded projection, closer to E than to TOS, DL
Medium sized, wide, S, PD directed	S, attached to body, posteriorly directed *: 71% BL	S, posteriorly directed, 66% BL	* S, posteriorly directed, 59% BL	S, PD directed, attached to the body for most of its length, 76% BL
2(2)/4(1), P4 shorter, lateral flaps w/teeth	2(2)/3(1)	2(2)/3; 2(2)/3(1-2) at stages close to metamorphosi s *: P3 noticeably shorter		2(2)/3(1), P3 = 1/2 P2
Ventral, subterminal, OD = ½ BW, DG. *: MP double row, IMP present laterally, VL emarginations	Ventral, w/lateral folds, MP single row, DG, SMP laterally	MP single or double row, DG *: VL folds and lateral emarginations		AV, VL emarginations, MP single or double row, DG, some SMP, flaps w/ teeth laterally
Antunes <i>et al.</i> 2008	Eterovick et al. 2002 (Hyla cipoensis)	Fernández, 1927 (Hyla raddiana)	Cei 1980 (Hyla pulchella cordobae)	Present study
H. caipora Antunes, Faivovich & Haddad	H. cipoensis (B. Lutz)	H. cordobae-pulchell us?	H. cordobae (Barrio)	

<i>H. curupi</i> Garcia, Faivovich & Haddad	Faivovich 1996 (Hyla semiguttata)	AV, OD = 56% BW, VL folds, MP continuous, double or triple row	3(1,3)/5(1), short rows of teeth laterally placed	S, lateral, PD directed *: 64% BL	Oval, reniform, w/medial projection, weakly rimmed *: closer to E than to TOS	DF origin at TBJ *: DF > VF, both fins arched	FH > BH *: TOT pointed, TM reaches TOT, 68% TL	P: dark brown, tail pale yellow, w/dark blotches	38.3-45. 3 (31–34)
H. freicanecae (Camaval & Peixoto)	Carnaval & Peixoto 2004 (Hyla freicanecae)	Ventral, 31% BW, MP single or double row, DG, slight VG, some SMP laterally, lateral flaps w/ teeth, VL emarginations	2(2)/4[3](1), P4 if present shorter and fragmented	S *: PD directed, 64% BL	Reniform, closer to E than to TOS	DF > VF, both fins slightly arched, DF reaching body	TH > BH, TOT rounded *: 65% TL	P: Dark brown to black, w/ big dark spots on tail	52.0 (29)
H. goianus (B. Lutz)	Eterovick et al. 2002 (Hyla goiana)	Ventral, w/ lateral folds, MP single row, DG	2(1,2)/3(1)	S, attached, posteriorly directed *: 78% BL	Dorsal, reniform, closer to E than to TOS	Fins convex, DF > VF, origin DF on body *: tip pointed	*: FH > BH, 73% TL	L: pale brown w/darker patches, tail pale brownish	43.6 (33)
H. joaquini (B. Lutz)	Garcia et al. 2003 (Hyla joaquini)	AV, VL emarginations, DG, SMP laterally, small lateral flaps w/teeth	2(2)/3-4(1), P4 when present shorter or fragmented	S, short and wide, PD directed, distally free *: 60% BL	Reniform, closer to E than to TOS	DF > VF	FH = BH, TOT pointed *: 66% TL	P: dark brown w/small darker dots, TM white w/brown dots	54.4 ± 0.66 (34)
H. latistriatus (Caramaschi & Cruz)	Orrico et al. 2007	AV, DG, MP single or double row, some SMP on lower lip	2(1,2)/3(1); 2(1,2)/3; 2(2)/2	S, lateroventral, posteriorly directed, inner wall free from body, 63% BL	Reniform, DL, closer to E than to TOS	Fins slightly convex, DF > VF, DF origin at end of body	FH > BH, TM reaching TOT, TOT pointed	P: dark brown, TM lighter, DF dark brown, VF lighter except last third. Spotted pattern in earlier stages.	55.8 (30); 53.9 (35)

45.4-49. 8 (34-37)	42.2 (35)	39.7–46. 7 (36)	55.2 (37)	42.0 ± 1.8 (34–35)
P: Body grayish to brownish, w/small dark dots. Tail yellowish w/dark longitudinal line.	rins transparent	P: Uniformly pigmented grayish brown, fins transparent w/ diffuse pale brown blotches	P: uniformly pigmented, tail w/ pale brown blotches, mainly in DF L: TM w/dark brown bars	L: body black w/transversal golden or silver stripes, iris reddish copper, tail whitish yellow w/large dark brown blotches, venter black
TL %89	FH = BH *: TOT acutely rounded, 68% TL	Tip pointed *: 69% TL, FH > BH	Pointed TOT *: 64% TL	Rounded TOT *: 62% TL
Fins convex, TOT pointed, DF origin anterior to base of TM	DF > VF *: DF origin on end of body, both fins arched	DF terminating at dorsal TBJ, DF > VF	DF terminating at dorsal TBJ, DF > VF	DF > VF *: DF origin on end of body, DF arched
Dorsal, reniform, closer to E than to TOS	Reniform, closer to E than to TOS	Oval, slightly rimmed, medial edge weakly raised *: closer to E	Oval, weakly rimmed, rim medially raised *: closer to E than to TOS	Small, reniform, closer to E than to TOS
S, attached to body wall *: posteriorly directed, 76% BL	S, short, PD directed, completely attached to body *: 63% BL	S, attached to body for almost entire length, PD directed *: 54% BL	S, PD directed, attached to the body for its entire length *: 53% BL	S, short and wide, PD directed, distally free, opening 50% BL
2(2)/3(1) *: P3 half the length of P2	2(2)/3-4(1), P4 if present, shorter and fragmented. Labial teeth laterally placed in short	2(2)/4; 3(1,3)/4 in one individual *: labial teeth laterally in short rows	2(2)/4(1); some w/gaps in A1, P2 or P3	2(2)/5(1), P5 shorter or fragmented
Ventral, w/ VL folds, DG, MP single or double row	AV, VL emarginations, MP single or double row, small DG, many VL SMP	Ventral, DG, sometimes short VG, VL emarginations, several SMP and flans	Ventral, VL emarginations, DG, sparse SMP laterally, lateral flaps w/ teeth	AV, VL emarginations, narrow DG, SMP laterally, small flaps w/teeth laterally on the posterior labium,
Both et al. 2007 (Hyla leptolineata)	Garcia et al. 2001a (Hyla marginata)	Lötters et al. 1999 (Hyla marianitae)	Duellman et al. 1997 (Hyla palaestes)	Garcia, Peixoto & Haddad 2008
H. leptolineatus (Braun and Braun)	H. marginatus (Boulenger)	H. marianitae (Carrizo)	H. palaestes (Duellman, de la Riva & Wild)	<i>H. poaju</i> Garcia, Peixoto & Haddad

13–18 BL, 32–44 TaL (before metamor phosis)	38.0 (37)	40.8 (35)	47–52 (stage unknown)	71 (maximu m length, stage unknown)
Olive, tail with alternate light and dark olive bars above	Brown, tail marbled, transverse bars on dorsum of TM, longitudinal median dark stripe on first third. *:dark spots on bodv	·	Brown, w/ dark spots	L: clay-colored or light greenish, olive tail
TOT blunt	FH > BH, TM reaches TOT, TOT pointed. *: 67% TL	*: FH > BH, 61% TL		66 % TL, pointed TOT
DF origin on body, VF straight	DF origin at end of body, DF and VF slightly arched. *: DF > VF			DF extending onto body
	Closer to E than to TOS, reniform	Dorsal, reniform, with valve medial projections. *: closer to E than to TOS	*: DL, reniform	
S, nearer to the vent tube than to the TOS	S, PD directed, opens 80% BL	Long, attached to the body almost to the end, dorsally directed. *: opens 59% BL		S, 66% BL, posteriorly directed
2/3	2(2)/3(1,2)	2(2?)/3(1)	1(1)/2 in tadpoles 12–14 mm, stage unknown; 2(2)/3(1) in tadpoles 52 mm, stage unknown	2(2)/3, variable. 2(2)/3(1) at metamorphosi s
	AV, OD = 37% BW, MP single row, DG. *: VL emarginations	Ventral, OD > 1/3 BW, MP single or double row, small DG		Ventral, MP single row, DG, VL folds
Lutz 1973 (Hyla polytaenia) (Dubious identification, may be H. latistriatus, see Orrico et al.	Heyer et al. 1990 (Hyla polytaenia)	Spirandeli Cruz 1991 (Hyla prasina)	Gallardo 1961 (Hyla raddiana)	Lutz 1973 (Hyla pulchella pulchella)
H. polytaenius (Cope)		H. prasinus (Burmeister)	H. pulchellus (Duméril & Bibron)	

	Echeverría 1992 (Hyla pulchella nulchella)	MP single row, DG	2(2)/3(1); 2(2)/3; P3 shorter						
	Present study	AV, VL emarginations, MP single or	2(2)/3(1), P3 50% P2	S, PD directed, attached to the body for most of	Oval, weakly rimmed,	DF origin on end of body,	TOT acute, TM reaches	P: Yellowish brown w/small dark dots TM	48.0–62. 0 (31–35)
		double row, DG, some SMP		its length, 73%	subtriangular or rounded	convex, VF straight	TOT, 69% TL, TH >	w/irregular dark regions,	
		laterally			projection, closer to E		ВН	sometimes transverse dark	
					than to TOS, DL			bands dorsally, fins w/ dark blotches	
H. riojanus	Present study	AV, VL	2(2)/3(1);	S, PD directed,	Oval, weakly	DF origin at	TOT	P: Dark brown,	44.5–63.
(Koslowsky)		emarginations, MP single or	2(2)/4(1); P3 almost as long	attached to the hody for most of	rimmed, medial	TBJ, DF >VF, both fins	rounded, TM does	w/small dark dots, tail vellowish	7 (27–35)
		double row, DG,	as P2; P4	its length, 65%	rounded or	subparallel,	not reaches	marbled in dark	
		some SMP, flaps	fragmented	BL	subtriangular	converging at	TOT, 65%	brown	
		w/ teeth laterally	when present		projection,	the end	TL, FH =		
		In some specimens			closer to E than to TOS.		ВН		
		1			DL				
H. semiguttatus	Garcia et al.	AV, VL	2(2)/4(1), P4	S, wide and	Small, ovoid,	DF > VF,	FH > BH	L: yellowish	47.5 (35)
(A. Lutz)	2007.	emarginations,	shorter and	long, PD	w/medial			brown w/small	
		DG, SMP	sometimes	directed, distally	internal			dark brown spots,	
		laterally, latereal flaps w/ teeth	fragmented	free	projection, closer to E			venter transparent, fins vellowish and	
		 			than to TOS			transparent w/	
								dark blotches	
Hypsiboas	Reference (name	Oral disc	LTRF	Spiracle	Nostrils	Fins	Tail	Pattern	Total
punctatus	used in	and Papillae							length
species group	publication)								(stages)

42.7 (34); 52.1 (38)	22.5 (25)	28.1 (37)	42.4 (35)	28.8 (38)	
Dark grey w/small black dots, fins translucent	Dull pale green, fins transparent	Transparent olive brown w/scattered white chromatophores, tail transparent	P: brownish cream w/dark brown rounded spots, TM minute dots, fins semitransparent w/ minute dots	P: brown, venter gray, fins translucent w/small brown spots	L: dark brown spots on dorsum (about stage 37), bright red iris
TOT pointed, TM does not reaches TOT *: 67% TL	67% TL, pointed TOT	*: 66% TL, TM does not reaches TOT	TM does not reach tail TOT, TOT acute *: 66% TL, TM reaches TOT	TOT narrow pointed	*: TOT rounded
DF origin at TBJ, DF > VF *: DF arched, VF straight	Fins shallow, DF does not extends onto the body	*: DF origin on TBJ, DF > VF	DF origin on TBJ, DF > VF	DF origin on TM, DF higher than VF	*:DF origin on TBJ, both fins arched, DF > VF
Rounded, rimmed, w/triangular medial fold, closer to E than to TOS	Midway between TOS and eyes	*: reniform	Reniform, edge slightly protuberant, directed DL, closer to E than to TOS	DL, ovoid, closer to eyes than to TOS, narial papillae absent	
S, lateral, PD directed, 70% BL	S, PD directed, opens at 50% BL	*: S, PD directed, opens 74% BL	S, forming a very short tube, 71% BL, posteriorly directed	S, short, completely attached to body wall, PD directed, about midlength of body	
2(1,2)/4, P2-P4 multiserial *: short rows of teeth laterally?	1(1)/2	2(1,2)/3-4(1)[2]	2(2)/4(1), labial teeth of P4 weaker than the others	2(2)/3(1)	2/4, 3/4, 2/5, 3/5; A1, A2, A3, P1 and P5 may have median gaps * A1 bent w/an angle to the front
Ventral, MP single row, DG *: VL folds	AV, lateral folds, MP single row, DG	*: MP single row, DG, small VG, P4 noticeably short	Ventral, OD = ½ BW, MP double row, DG, VL folds	Ventral, small, large DG, MP single or double row	VL folds, median fold in posterior labium, MP double row, DG, few blunt SMP on lower labium
Mijares-Urrutia 1992 (<i>Hyla alemani</i>)	Duellman 1978 (<i>Hyla granosa</i>)	Hero 1990 (<i>Hyla</i> granosa)	Mijares-Urrutia 1993 (Hyla granosa)	Duellman 2005 (Hyla granosa)	Myers and Donnelly 2008
H. alemani (Rivero)	H. cinerascens (Spix)				H. jimenezi Señaris and Ayarzagüena, 2006

40 (maximu m length)	37.5 (36)	13.5 (25), 31.5 (36)	34.3 (38)	26.7–38. 4 (28–36)	33–36 (26), 46–51 (36–41)
Dark greenish brown, tail translucent cream to pale orange. Pineal organ faintly visible.	Dark green with black flecks, tail olive green	P: Brown, w/few dark spots on back, base of tail dorsally w/dark spots	L: Dark green w/black flecks, belly dark gray, tail olive green	P: uniformly brown, TM little pigmented, darker in dorsal view; fins translucent, DF w/darker dots	Grey, w/dark spots on back and belly. MT creamish, fins opaque grey, proximal part of tail w/dark spots
Tapered *: 67% TL	70% TL, pointed TOT	Tip pointed *: 67% TL	TOT	TOT acute, TM reaches TOT, 65% TL, FH > BH	TOT pointed *: 68% TL
DF originating from tail, DF > VF	DF not extends onto the body	Fins low, DF > VF, DF starting at base of muscular part of tail	DF origin on proximal TM, DF = VF	DF origin at TBJ, DF >VF, DF convex, VF straight	DF > VF, DF starting at base of muscular part of tail
w/prominent rim and flap	Midway between TOS and E	w/large rounded flap, closer to E than to TOS	Large, DL, midway between TOS and E, narial papillae	oval, weakly rimmed, medial rounded projection, closer to E than to TOS, dorsal	w/ small pointed triangular flap, closer to E than to TOS
S *: 62% BL, PD directed	S, PD directed, at 66% BL	S *: 76% BL, PD directed	S, completely attached to body wall, PD directed, about 2/3 BL	S, PD directed, attached to the body for most of its length, 71% BL	S *: 62% BL, PD directed
2(2)/3	2(2)/3	2(1,2)/3(1) *: P3 noticeably shorter than others	2(2)/3, P3 much shorter	2(2)/4(1), P4 w/ smaller teeth	2(2)/5(1), P1 w/ spur dorsally directed, P5 not well developed, fragmented, w/ small labial teeth
MP single row *: VL folds, DG	AV, lateral folds, MP single row, DG	MP single row, VL emarginations *: DG	AV, lateral folds, OD about 1/3 BW, MP single row, DG	Ventral, VL emarginations, MP single row, DG, some SMP laterally	Single row, VL emarginations *: narrow DG
Kenny 1969 (Hyla punctata)	Duellman 1978 (Hyla punctata)	Hoogmoed 1979 (Hyla punctata)	Duellman 2005 (Hyla punctata)	Present study	Hoogmoed 1979 (Hyla sibleszi)
H. punctatus punctatus (Schneider)				H. punctatus rubrolineatus (B. Lutz)	H. sibleszi (Rivero)

BL 10.5, TL 30.0 (25)	Total length (stages)	42 (maximu m length)	40.0 (36)	43 (37)	30.7 (34)
L: Body and tail yellowish tan w/golden sheen on tail, iris pale bronze	Pattern	P: cream or pale pink w/brown saddle on back and flanks, dark spots. Tail marbled. Pineal organ visible	P: Mottled dark brown and creamy tan. Blotches tend to form transverse bars across dorsal part of TM	Reddish tan with dark markings, tail cream with reddish-tan reticulations	Body transparent olive brown, tail transparent
	Tail	Tapered *: 68% TL	TM almost reaches TOT, TOT pointed. *: 64% TL	65% TL, TOT acutely rounded	*: 69% TL
	Fins	DF originating from tail, DF > VF	DF deeper, does not extends onto the body *: DF > VF, DF curved, VF slightly curved	DF does not extends onto the body	*: DF does not extends onto the body, DF > VF
	Nostrils	Opens laterally, mesial projection *: closer to E than to TOS	Directed anterolaterally , midway between E and TOS	Closer to E than to TOS	
	Spiracle	S *: PD directed, 57% BL	S, PD directed, opens 66% BL	S, PD directed, opens 50% BL	*; S, PD directed, opens 71% BL
	LTRF	2(2)/3(1), P4 occasionally present in later stages	2(2)/4, P4 noticeably shorter than others. *: IMP and a fragmented and almost equally long P4 are visible in the illustration	2(2)/4, P4 much shorter than others	2(2)/3-4(1)
	Oral disc and Papillae	MP double row in lower lip, supernumerary rows laterally	AV, OD about ½ BW, MP single row, DG, deep lateral folds	Ventral, folded laterally, MP single row, DG	*: VL folds, DG, MP single row, double laterally
Duellman 1997 (<i>Hyla sibleszi</i>)	Reference (name used in publication)	Kenny 1969 (Hyla maxima)	Duellman 1970 (Hyla boans)	Duellman 1978 (Hyla boans)	Hero 1990 (<i>Hyla</i> boans)
	Hypsiboas semilineatus species group	H. boans (Linnaeus)			

15.5–16. 5 BL, 43–45 TaL (36)	41.8 (36)	75 (maximu m lenghth)	48.5 (37)	52 (33)	30.7 (34)
L: Brown w/green flecks, venter silvery white, tail tan w/reddish-brown marks	L: Reddish tan w/dark olive brown markings, belly white, fins translucent w/brown reticulations	Uniformly black. Pineal organ visible, particularly in smaller specimens	Entirely black	Black, caudal fins opaque gray	Black
	TOT acutely rounded	Tapered *: 60% TL	Narrowly rounded tail, TM almost reaches TOT ** 63%, TL	62% TL, acutely rounded terminally	*: TOT acutely rounded, 63% TL
	DF origin at TBJ, DF twice as high as VF	DF originating from back, DF = VF *: both fins arched	DF does not extend onto the body, DF = VF *: both fins arched	DF does not extend onto the body	*: DF does not extend onto body, DF=VF, both arched
	DL, about 3/5 the distance between TOS and E	Simple, open laterally	Midway between TOS and E	Midway between TOS and E	
	S, completely attached to body wall, PD directed	S *: posteriorly directed, opens 60% BL	S, PD directed *: 60% BL	S, PD directed, opens 60% BL	*: S, lateral, PD directed, opens 56% BL
2(1)/3-4(1), a short and fragmented P5 occasionally present	2(2)/4, P2 sometimes medially interrupted, P4 fragmented	2(2)/4, P4 appears later in larval life	3(1,3)/5	2(2)/4 2/4, 2/5, 3/5	2-3[1](3)/3-5[
	AV, OD about 50% BW, lateral folds, DG, MP single row	MP double row *: DG, VL folds	Ventral, MP double row, DG, VL folds	AV, lateral folds, MP single row, DG	*: MP double row, DG, VL folds, many SMP laterally
Duellman 1997 (Hyla boans)	Duellman 2005 (Hyla boans)	Kenny 1969 (Hyla geographica geographica)	Duellman & Lescure 1973 (Osteocephalus taurinus, fide Caldwell, 1989)	Duellman 1978 (Hyla geographica) Pyburn and Hall 1984 (Hyla	geographica) Recognaphica)
		H. geographicus (Spix)			

		54.8 (38)	44.0 (36)	65 (stage unknown)		34.7 (37)
		L: black, fins dull gray	P: black, tail cream-white (pink in life), conspicuous black spot on side of tail	P: black, fins dark brown		P: brownish tan w/darker reticulation, tail cream w/ brown reticulation
Less than 66% TL, TOT pointed		TOT pointed	*: TOT acutely rounded, 66% TL	TOT acute *: 62% TL		TOT rounded *: FH > BH, 65% TL
DF does not extend onto the body, DF = VF		DF origin at TBJ	*: FH > BH, both fins arched, DF > VF, DF origin at TBJ	FH > BH *: both fins arched, DF>VF, DF origin not extending onto body		DF origin on body *: both fins arched
Closer to E than to TOS		DL, closer to E than to TOS, narial rim present, narial papillae absent		Dorsal, nasolacrimal groove		
S, lateral		Short, conical, S, completely attached to body wall, PD directed, about midlength of body	S *: PD directed, 67% BL	s *: 58% BL, posteriorly directed		S *: 69% BL, posteriorly directed
2(2)/4, 2(2)/4(1)	2(2)/3 stage 25, 2(2)/4 and 2(2)/5 stage 28, 3(1,3)/5 stages 27-30, after stage 31 3-4 lower rows	2(1)/4, P4 slightly shorter	4(1,4)/7, P5-7 progresively shortened	2(2)/4	2(2)/3 stage 25, 2(2)/4 and 2(2)/5 stage 28, 3(1,3)/5 stages 27-30, after stage 31 3-4 lower rows	2(2)/3
AV, MP double row, DG	Ventral, MP double row, small DG, lateral folds	AV, OD = 1/3 BW, lateral folds, DG, MP single row	MP complete double or triple row *: VL folds	Ventral, MP double row, VL folds *: DG	Ventral, MP double row, small DG, lateral folds	AV, MP single row, VL folds *: short medial DG
Rada de Martínez 1990–1991 (Hyla geographica)	D'Heursel & de Sá 1999 (Hyla geographica)	Duellman 2005 (<i>Hyla</i> geographica)	Pyburn & Hall 1984 (Hyla hutchinsi)	Bokermann 1963 (<i>Hyla</i> geographica)	D'Heursel & de Sá 1999 (Hyla semilineata)	Martins & Moreira 1991 (Hyla wavrini)
			H. hutchinsi (Pyburn and Hall)	H. semilineatus (Spix)		H. wavrini (Parker)

Appendix 2

List of published descriptions of oral cavity morphology of tadpoles of Hylinae.

Tribe Cophomantini

Aplastodiscus albofrenatus (A. Lutz). — d'Heursel & Haddad 2007

Aplastodiscus callipygius (Cruz and Peixoto). — d'Heursel & Haddad 2007

Aplastodiscus cochranae (Mertens). — d'Heursel & Haddad 2007

Aplastodiscus eugenioi (Carvalho e Silva and de Carvalho e Silva). — d'Heursel & Haddad 2007

Aplastodiscus perviridis A. Lutz in B. Lutz. — Spirandeli Cruz 1991

Bokermannohyla alvarengai (Bokermann). — d'Heursel & Haddad 2007

Bokermannohyla itapoty Lugli and Haddad. — d'Heursel & Haddad 2007

Bokermannohyla luctuosa (Pombal and Haddad). — d'Heursel & Haddad 2007

Bokermannohyla nanuzae (Bokermann and Sazima). — d'Heursel & Haddad 2007

Bokermannohyla saxicola (Bokermann).— d'Heursel & Haddad 2007

Hyloscirtus armatus (Boulenger). — Aguilar et al. 2007

Hyloscirtus phyllognathus (Melin). — Aguilar et al. 2007

Hypsiboas albomarginatus (Spix). — d'Heursel & Haddad 2007

Hypsiboas albopunctatus (Spix). — Spirandeli Cruz 1991

Hypsiboas andinus (Müller). - Lavilla & Fabrezi 1987; present study

Hypsiboas caingua (Carrizo). — Spirandeli Cruz 1991; present study

Hypsiboas cinerascens (Spix). — d'Heursel & Haddad 2007

Hypsiboas cordobae (Barrio). — present study

Hypsiboas faber (Wied-Neuwied). — Spirandeli Cruz 1991; present study

Hypsiboas geographicus (Spix). – d'Heursel & de Sá 1999

Hypsiboas joaquini (B. Lutz).— d'Heursel & Haddad 2007

Hypsiboas leptolineatus (Braun and Braun). — Both et al. 2007

Hypsiboas lundii (Burmeister).— Spirandeli Cruz 1991

Hypsiboas pulchellus (Duméril and Bibron). — present study

Hypsiboas punctatus rubrolineatus (B. Lutz). — present study

Hypsiboas prasinus (Burmeister). — Spirandeli Cruz 1991

Hypsiboas raniceps Cope. - present study

Hypsiboas riojanus (Barrio). — present study

Hypsiboas rosenbergi (Boulenger). — Vera Candioti 2007

Hypsiboas rufitelus (Fouquette). — Wassersug 1980

Hypsiboas semilineatus (Spix). — d'Heursel & de Sá 1999

Tribe Dendropsophini

Dendropsophus ebraccatus (Cope). — Wassersug 1980

Dendropsophus minutus (Peters). — Spirandeli Cruz 1991; Echeverría 1997

Dendropsophus microcephalus (Cope). — Vera Candioti 2007

Dendropsophus nanus (Boulenger). - Spirandeli Cruz 1991; Vera Candioti et al. 2004; Vera Candioti 2007

Dendropsophus phlebodes (Stejneger). — Wassersug 1980

Dendropsophus sanborni (Schmidt). - Spirandeli Cruz 1991

Dendropsophus sarayacuensis (Shreve). — Wassersug 1980

Pseudis limellum (Cope). — Vera Candioti 2004; Vera Candioti 2007

Pseudis minuta Günther. — de Sá & Lavilla 1997

Pseudis platensis Gallardo. — Vera Candioti 2007

Scarthyla goinorum (Bokermann). — Duellman & de Sá 1988

Scinax acuminatus (Cope). — Sandoval 2000

Scinax berthae (Barrio). — Spirandeli Cruz 1991

Scinax boulengeri (Cope). — Vera Candioti 2007

Scinax catharinae (Boulenger). — Conte et al. 2007

Scinax cf. catharinae (Boulenger).—Spirandeli Cruz 1991

Scinax sp. gr. catharinae (Boulenger).—Spirandeli Cruz 1991

Scinax fuscovarius (A. Lutz). — Spirandeli Cruz 1991; Echeverría & Montanelli 1992; Fabrezi & Vera 1997

Scinax nasicus (Cope). – Fabrezi & Vera 1997; Vera Candioti et al. 2004; Vera Candioti 2007

Scinax similis (Cochran). — Spirandeli Cruz 1991

Tribe Hylini

Acris crepitans Baird. — Wassersug 1980
Anotheca spinosa (Steindachner). — Wassersug 1980
Bromeliohyla dendroscarta (Taylor). — Wassersug 1980
Duellmanohyla schmidtorum (Stuart). — Wassersug 1980
Hyla arborea (Linnaeus). — Viertel 1982
Hyla femoralis Bosc in Daudin. — Wassersug 1980
Megastomatohyla mixe (Duellman). — Wassersug 1980
Pseudacris regilla (Baird and Girard). — Wassersug 1976
Ptychohyla leonhardschultzei (Ahl). — Wassersug 1980
Smilisca sordida (Peters). — Wassersug 1980

Tribe Lophiohylini

Aparasphenodon brunoi Miranda-Ribeiro. — Wogel et al. 2006
Osteocephalus oophagus Jungfer and Schiesari. — Schiesari et al. 1996
Osteocephalus taurinus (Steindachner). — Schiesari et al. 1996
Osteopilus brunneus (Gosse). — Lannoo et al. 1986
Trachycephalus resinifictrix (Goeldi). — Schiesari et al. 1996
Trachycephalus venulosus (Laurenti). — Schiesari et al. 1996; Fabrezi & Vera 1997

Appendix 3

Additional material examined.

- Aplastodiscus perviridis.—ARGENTINA: MISIONES: Departamento Iguazú: Parque Provincial Urugua-í, Ruta Provincial Nº 19 (25°53'52.4"S; 54°13'02.5"W): MLP DB 5413, collected on 6 December 2006 by D. Baldo, C. Borteiro, F. Kolenc and D. Martí, lot of tadpoles.
- *Hypsiboas andinus*.—ARGENTINA: SALTA: Departamento Metán: Arroyo Cacharí, Campamento León (27°26′12″S; 55°53′24″W): MLP DB 5520; collected on 03 January 2007 by D. Baldo, F. Burgos, G. Aguilera and R. Moreno, *N* = 9, stages 28–42.
- *Hypsiboas caingua*.—ARGENTINA: MISIONES: Departamento Capital: Villa Lanús, Campus UNaM (27°26′12″S; 55°53′24″W): MLP DB 5052, tadpoles rose from couple (included in lot MLP DB 0139–0147); collected on 11 May 1998 by D. Baldo and J. Urdampilleta, *N* = 4, stages 27–38.
- *Hypsiboas cordobae.*—ARGENTINA: Córdoba, Departamento San Alberto, Ruta Provincial 34, 1 km from La Posta (31°36'48.9"S; 64°53'10.2"W): MLP DB 3280, collected on 2 October 2004 by D. Baldo, D. Cardozo, D. Ferraro and M. Pereyra, *N* = 7, stages 28–38.
- *Hypsiboas faber.*—ARGENTINA: MISIONES: Departamento Iguazú: Parque Provincial Urugua-í, Ruta Provincial N° 19 (25°53'53.4"S; 54°13'02.5"W): MLP DB 5410, collected on 6 December 2006 by D. Baldo, C. Borteiro, F. Kolenc and D. Martí, *N* = 8, stages 25–27. Departamento Gral. San Martín: Garuhapé (26°54'5.6"S; 54°55'0.3"W): MLP DB 3890, collected on September 2004 by D. Aichino and D. Méndez, N = 3, stages 28–34.
- Hypsiboas pulchellus.—ARGENTINA: CORRIENTES: Departamento Curuzú Cuatiá: Perugorría, Estancia "El Oscuro" (29°11'37"S; 58°30'36"W): MLP DB 5306, collected on 17–20 November 2006 by D. Baldo, N=1, stage 40. MISIONES: Departamento Candelaria: Puerto San Juan, Reserva Privada Campo San Juan (27°22'47"S; 55°38'22.2"W): MLP DB 4257, collected on 18 October 2005 by D. Baldo, D. Cardozo, C. Borteiro and F. Kolenc, N=10, stages 31–34. URUGUAY: LAVALLEJA: Camino al Salto del Penitente (34°21'S; 55°05'W): MLP DB 5051, collected on 28 August 2005 by C. Borteiro and F. Kolenc, N=8, stages 27–33. ROCHA: Sierra de Carapé, Ruta 109: MLP DB 7144, collected on 8 October 2006 by C. Borteiro, F. Kolenc and M. Tedros, N=13, Stages 33–40.
- Hypsiboas raniceps.—ARGENTINA: CHACO: Departamento Libertador General San Martín: 6 Km north of General San Martín, by Ruta Provincial N° 90: MACN 36892, collected on 06 January 1997 by J. Faivovich, J.C Fernicola and A. Lopez. CORRIENTES: Departamento Curuzú Cuatiá: Estancia el Oscuro (29° 11'S; 58°30'W): MLP DB 5303, col-

- lected on 18 November 2006 by D. Baldo, N = 2, stages 31 and 35. SANTA FE: Departamento Vera: Vera, Estancia "Las Gamas": MACN 36893, collected on 03 January 1998 by J. Faivovich, J.C Fernicola and A. Lopez.
- *Hypsiboas riojanus*.—ARGENTINA: CATAMARCA: Departamento El Alto: Guayamba, Río Guayamba (28°21'19"S; 62°22'30"W): MLP DB 3303, collected on 22 October 2004 by D. Baldo, D. Cardozo and M. Pereyra, *N* = 7, stages 26–39.
- Pseudis platensis.—ARGENTINA: CHACO: north-eastern Chaco Province ($26^{\circ}53'27.5"S 59^{\circ}01'06.1"W$): MLP 3839. No other collection data, N = 1, stage 37.
- Scinax berthae.—ARGENTINA: BUENOS AIRES: Partido de Magdalena, $(35^{\circ}01'54"S~57^{\circ}29'59"W)$: MLP 4993. Collected on February 2007 by L. Alcalde, N = 1, stage 38.