Reproduction and larval morphology of *Adenomera diptyx* (Anura: Leptodactylidae) from the Argentinean humid Chaco and Brazilian Pantanal

VÍCTOR HUGO ZARACHO¹ & MARCELO NOGUEIRA DE CARVALHO KOKUBUM²

¹⁾ Laboratorio de Herpetología, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Av. Libertad 5470, (3400) Corrientes, Argentina

²⁾ Laboratório de Herpetologia, Unidade Acadêmica de Ciências Biológicas e Programa de Pós-graduação em Ciências Florestais, Centro de Saúde e Tecnologia Rural, Universidade Federal de Campina Grande, Brazil, Rodovia Patos/Teixeira, CEP 58708–110, Patos, Paraíba, Brazil

Corresponding author: Víctor Hugo Zaracho, e-mail: victorzaracho@yahoo.com.ar

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Abstract. Whereas the external larval morphology of some species of *Adenomera* has been described, their internal morphology remains poorly studied. In this work, we provide information on the reproductive features and larval morphology of populations of Adenomera from northeastern Argentina and southwestern Brazil, including the first description of the chondrocranium and hybranchial apparatus for a member of the genus Adenomera. We found that, morphologically, the buccal cavity of A. diptyx is more similar to that of the species of the Leptodactylus fuscus group than to that of A. marmorata, the only species of Adenomera whose buccal cavity is known. Adenomera diptyx shares with the species of the L. fuscus group a semicircular crest in the prenarial region, two pairs of infralabial papillae, four lingual papillae, and few papillae on the roof and the floor of the cavity. The chondrocranial morphology of A. diptyx exhibits all the characters that characterise all members of the genus Leptodactylus and several characters that are shared with the L. fuscus group: wide suprarostrals with U-shaped corpora in frontal view, long and narrow cornua, long and finger-like processi anterolaterali on the otic capsules, a posterior curvature of the palaquadrate at the level of the point of attachment of the processus ascendens of the orbital cartilage, a processus ascendens that is almost perpendicular to the main axis of the body, a connection between the processus ascendens and the orbital cartilage just posterior to the oculomotor foramen, and a processus branchialis that is open between ceratobranchials II and III. Considering that the phylogenetic relationships between Adenomera and Leptodactylus are still discussed and that information on the larval morphology of Adenomera species is scarce, new studies are necessary for a more exhaustive analysis, including further data about the internal larval morphology of Adenomera species.

Key words. Underground chamber, foam nest, tadpole, chondrocranium, oral cavity.

Introduction

Currently, the genus *Adenomera* Steindachner, 1867 includes 18 species of small leaf litter frogs distributed in South America, east of the Andes (Frost 2014). The genus was resurrected by Heyer (1974) to include species of the former *Leptodactylus marmoratus* group (Heyer 1969), and different taxonomic arrangements have since been suggested (Frost et al. 2006, Giaretta et al. 2011). Recent phylogenetic analyses, using mainly molecular data, have proposed that *Adenomera* is a valid monophyletic genus, with *Lithodytes* as its sister group, and both are closely related to *Leptodactylus* and *Hydrolaetare* (Pyron & Wiens 2011, Fouquet et al. 2013, and de Sá et al. 2014).

Besides these taxonomic problems, the ecology and reproductive biology of *Adenomera* species are barely known (Kokubum & Giaretta 2005, Menin et al. 2010). Available information indicates that *Adenomera* presents at least two reproductive modes.

Most species exhibit a terrestrial mode of reproduction where endotrophic tadpoles with a rudimentary oral apparatus complete metamorphosis in a foam nest, without an aquatic feeding phase (Mode 22 as per Duellman & Trueb 1994; Mode 32 as per Haddad & Prado 2005; A. Lutz 1930, B. Lutz 1947, Heyer & Silverstone 1969, Heyer et al. 1990, Kwet & Angulo 2002, Kokubum & Giaretta 2005, Lima et al. 2006, Kokubum & Souza 2008, Menin et al. 2010). However, *A. diptyx, A. bokermanni*, and *A. thomei* have exotrophic larvae with a func-

tional oral apparatus and observe an obligate aquatic phase (Mode 21 as per Duellman & Trueb 1994, Mode 30 as per Haddad & Prado 2005; Heyer 1973, de la Riva 1995, Almeida & Angulo 2006).

In this work, we provide information on some reproductive features (underground chamber structure, clutches, and fecundity) and the larval morphology (including the original description of the buccal and pharyngeal cavities, chondrocranium, and visceral skeleton) of populations of *Adenomera* from northeastern Argentina and southwestern Brazil, whose reproductive characteristics agree with those of *Adenomera diptyx* reported by DE LA RIVA (1996).

Adenomera diptyx (BOETTGER, 1885) was resurrected to include populations of Adenomera with exotrophic larvae from southeastern Bolivia, Mato Grosso (Brazil), Paraguay, and northeastern Argentina (DE LA RIVA 1996). Nevertheless, the reproductive mode of these Argentinean and Brazilian populations has not been confirmed so far. Additionally, Adenomera diptyx might represent a species complex (V. Zaracho unpubl. data, Fouquet et al. 2013).

Material and methods

This study was carried out at a single locality in Brazil: Base de Estudos do Pantanal (BEP) / Universidade Federal do Mato Grosso do Sul (19°34′ S, 57°00′ W) (Corumbá Municipality, Mato Grosso do Sul State), and at two localities in Argentina: Corrientes (19°34′ S, 57°00′ W) (Corrientes Province) and Laguna Naick Neck (19°34′ S, 57°00′ W) (Formosa Province). The Brazilian population inhabits the Pantanal ecoregion, while the two Argentinean populations occur in the Humid Chaco ecoregion (DINERSTEIN et al. 1995).

Searches for underground chambers and foam nests were carried out at sites where males were calling. Moulds of underground chambers were obtained injecting liquid plaster through the entrance of the chamber and left to cure for 24 hours. The moulds were then removed from the soil, washed with water, and measured with digital callipers to the nearest 0.05 mm. Foam nests containing eggs or tadpoles were collected and fixed in 5% formalin. Some nests were taken to the laboratory to obtain advanced developmental stages. The numbers of eggs and tadpoles per nest were quantified and egg diameters measured. Tadpole staging follows Gosner (1960), and measurements and morphological terminologies follow LAVILLA & SCROCCHI (1986) and ALTIG & McDIARMID (1999). All measurements were taken with the ocular micrometer of a stereomicroscope to the nearest 0.01 mm.

The oral apparatus and internal oral features were examined in four larvae (stage 36) using scanning electron microscopy (SEM). All specimens prepared for SEM had previously been fixed in 10% neutral-buffered formalin. Specimens were dehydrated in a graded ethanol series, dried in a critical point dryer and gold-coated. The terminology of internal oral features follows Wassersug (1976a). The descriptions of the chondrocranium and hyobranchial ap-

paratus are based on 13 tadpoles (stages 31–41) that were cleared and double-stained for bone and cartilage by using the technique introduced by Wassersug (1976b). Our chondrocranial terminology follows Larson & DE SÁ (1998).

Our voucher specimens are stored in the Coleção AAG-UFU of the Museu de Biodiversidade do Cerrado at the Universidade Federal de Uberlândia, Minas Gerais, Brazil: AAG-UFU 4240–4253 (underground chamber moulds), and 4261–4266 (tadpoles), and in the herpetological collection of the Universidad Nacional del Nordeste in Corrientes, Argentina: UNNEC 8368 and 9861 (tadpoles).

Results Reproduction

In northeastern Argentina and southwestern Brazil, males of *Adenomera diptyx* engage in reproductive activity from September through April, mainly prior to rainfalls. Males call amidst grasses, and occasionally perch on dense vegetation (< 50 cm). In Corumbá (Brazil), males were found in a flooded open area with grass or bare soil (only fallen leaves) near human constructions (stilt houses) (C. P. A. Prado pers. comm., M. N. Kokubum pers. obs.). The study area is situated near a riverbank and will become completely inundated when the level of the river rises. In Argentina, calling males were abundant on roadsides and in gardens, and some populations were found in a banana plantation and inside small forests.

In Corumbá (01-03 November 2006), 14 underground chambers and six foam nests with eggs and/or tadpoles were found. Most chambers presented an almost spherical shape, while a few others (n = 3) were semi-spherical in shape (Figs 1A-B). Leaves or vegetation remains and/ or soil constituted the roof. The height of the underground chambers ranged between 16.5 and 37.6 mm (27.7 \pm 5.7) and the width between 31.2 and 39.2 mm (35.04 \pm 2.3). The entrance widths of two underground chambers were measured and found to be 13.0 and 15.5 mm, respectively. The number of eggs/tadpoles per nest ranged between 26 and 146 (54.3 \pm 45.5, n = 6). Two nests contained only eggs (33) eggs each), three contained only tadpoles (n = 26, 41 and 146), and one nest contained both eggs and tadpoles (n = 16 eggs and 31 tadpoles). The egg diameters varied between 2.4 and 3.0 mm (2.7 \pm 0.2). The smallest distance measured between two underground chambers was ca 10 cm.

In Corrientes City (18 January 2005), a foam nest housing eight tadpoles (stage 30-31) inside an underground chamber was found in the wet soil under a brick in a garden. The tadpoles with vitellic remnants had a total length of approximately 10 mm (body length: 3.3, tail length: 6.7 mm, n=1). This nest was taken to the laboratory and maintained in a block of wet soil, but the tadpoles died during the following days. On 15 April 2005, three days after copious rains flooded the site, 14 tadpoles (eight at stage 31 and six at stage 36) were found in a plastic bottle (3,000 cm³) that had previously set up as a pit fall trap. They were taken

to the laboratory and samples were fixed every three days. Three individuals at stage 36 were maintained in an aquarium until metamorphosis, which occurred 25 days later.

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Figure 1. Underground chambers and foam nest of *Adenomera diptyx*. (A–B) moulds with almost spherical and semi-spherical shapes (Corumbá, Mato Grosso do Sul State, Brazil) (scale bar = 1 cm); (C) foam nest inside a partially opened underground chamber (Laguna Naick Neck, Formosa Province, Argentina).

At that point of time, the snout–vent length (SVL) of the metamorphs varied from 7.4 to 8 mm (n = 3).

In Laguna Naick Neck (29 February 2011), a foam nest containing 61 tadpoles at stage 31 and still with vitellic reserves was collected (Fig. 1C). The foam nest was placed in a small aquarium, causing the tadpoles to emerge immediately and begin to swim freely. Samples of these tadpoles were then fixed every three days for morphological studies.

External larval morphology

The external morphology of a tadpole at stage 29 from Corumbá is illustrated in Figs 2A-B. Here we describe tadpoles at advanced stages, since younger larvae have been described previously (DE LA RIVA, 1996). Tadpoles of Adenomera diptyx from Corrientes (stage 36, n = 3, UN-NEC 8368) present oval, small, external nares (equivalent to 7.5% of the eye diameter), positioned closer to the eyes than to the tip of the snout (external nares-snout distance/external nares-eye distance = 1.53). Snout rounded in dorsal and lateral views. Eyes of medium size (diameter = 25% body width at eye level) and positioned dorsolaterally. Oral apparatus sub-terminal, ventral and mediumsized (oral apparatus width/body maximum width = 0.47); conical oral papillae in a single row; dorsal gap equivalent to 58.6% of oral apparatus width. Jaw sheaths well developed. Upper jaw sheath wider than high, lower jaw sheath V-shaped; both with serrations on margins; labial teeth well developed, with 10-12 cusps on the head; labial tooth row formula: 2(1)/3(1) (Figs 2C-D). Spiracle tube sinistral, simple, short, and posterolaterally directed. Body oval in dorsal and lateral views with the abdominal region being slightly narrower than the head region. Tail length greater than body length; tail length nearly 67% of total length; tail height approximately equal to body height, origin of dorsal fin at tail-body junction; vent tube and vent tube's opening medial in relation to the ventral fin; vent tube opening circular. Dorsal fin slightly higher than ventral fin; tail tip elongate, acuminate. Measurements of tadpoles at stages 33/34 and 36 are shown in Table 1.

Dorsal colouration of the body pale brown (at stage 36 and conserved in 10% formalin), gradually lighter towards the lateral region of the body; a light Y-shaped mark between the eyes and the snout; nasal capsules darker than the rest of the body; dorsal gap with some scattered melanophores. Ventral body region translucent, internal organs partly visible through the transparent skin; scattered melanophores in the anterior region; pigmentation on the muscular tail region more diffuse than on the lateral region of the body; dorsal fin similar in colouration to the muscular tail region, both lighter than the ventral fin; spiracle and vent tube not pigmented. In life, light brown dorsally with numerous iridophores; a ring of iridophores on the dark brown iris; yellowish Y-shaped area (Figs 3A-B) that, at advanced stages, assumes a triangular form and will become indistinct near stage 42; ventral colouration similar to that of conserved specimens; vitellum well visible

across the skin until stage 31. The colourations at metamorphic and postmetamorphic stages are shown in Figures 3C and E, respectively.

Internal larval morphology (Figs 4-5)

Buccal floor wider than long. Two pairs of infralabial papillae, the anterior pair small and medial, and the posterior pair larger and lateral. Four conical and single lingual papillae, orientated transversally. Buccal floor arena V-shaped, defined by a row of 4–5 papillae on either side, tall, single or forked; about 20 pustulations distributed in the central region, and 5–6 medial and anterior to the buccal pocket; 2–3 pustulations in the posterior and lateral region

of the buccal floor on the outer side of the papilla rows. Buccal pockets narrow, orientated at 45° from the transverse plane. Perforations not identified. Free velar surface ¼ the length of the rest of the buccal floor; posterior margin with four marginal projections on either side; glandular zone on the margin of the velum. Branchial basket with three filter plates; both full and partial filter rows present; main, secondary and tertiary folds. Glottis exposed.

Buccal roof longer than wide. Wide prenarial ridge with pustulate margin. Choanae about 25% distant from oral apparatus to oesophagus and transversally orientated; anterior narial wall with small prenarial papillae, posterior wall smooth and valve-like. A pair of wide and tall postnarial papillae with pustulate margins are positioned behind each choana. Median ridge semicircular with pustulations

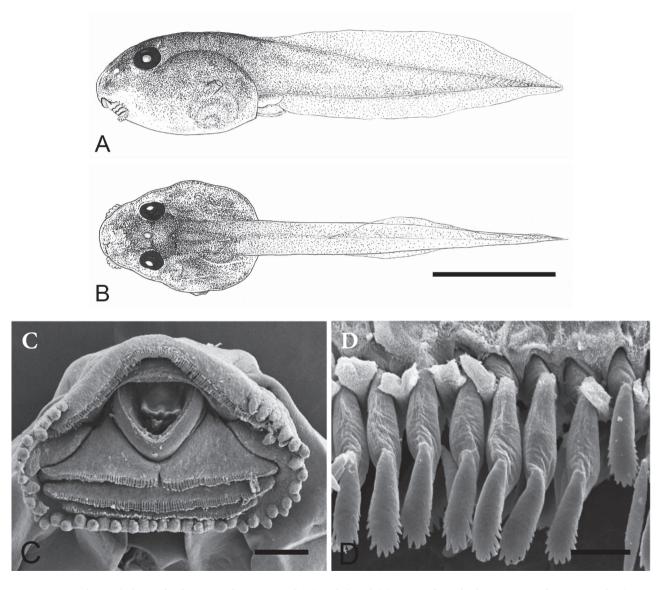


Figure 2. Larval morphology of *Adenomera diptyx*. Lateral (A) and dorsal (B) views of a tadpole at stage 29 from Corumbá (Mato Grosso do Sul, Brazil) (scale bar = 5 mm); (C) oral apparatus of a tadpole at stage 36 from Laguna Naick Neck (Formosa, Argentina) (scale bar = 0.2 mm); (D) detail of labial teeth (scale bar: 15 um).

Table 1. Measurements (in mm) of Adenomera diptyx tadpoles from Corrientes (Corrientes Province, Argentina). Mean \pm standard deviation (range).

	Stage 33/34 (n=6)	Stage 36 (n=3)
Body length	6.19±0.26 (5.9-6.6)	5.91 ±0.40 (5.62-6.37)
Tail length	10.37±0.40 (9.75-10.75)	11.79±0.62 (11.37-12.5)
Total length	16.56±0.53 (15.9–17.4)	17.70 ±1.01 (18.87–17.12)
Maximum tail height	3.17±0.10 (3-3.25)	3.08±0.40 (3.37-2.62)
Tail muscle width	$1.08\pm0.06(1-1.12)$	1.41±0.18 (1.6-1.25)
Internarial distance	0.72±0.05 (0.65-0.8)	0.66±0.01 (0.67-0.65)
Interorbital distance	1.33±0.04 (1.25-1.37)	1.26±0.08 (1.35-1.22)
Eye diameter	0.89±0.06 (0.77-0.94)	0.80±0.09 (0.9-0.75)
External nares diameter	$0.10\pm0.01~(0.09-0.11)$	0.06±0.01 (0.07-0.05
Tail muscle height	1.27±0.05 (1.25-1.37	1.50±0.13 (1.62-1.37
Snout-spiracle distance	2.08±0.05 (2.05-2.17	2.11±0.04 (2.15-2.07
Snout-external nares distance	3.91±0.23 (3.62-4.25)	3.67±0.38 (4-3.25
External nares-eye distance	0.96±0.11 (0.87-1.12)	1.01±0.08 (1.1-0.95
Oral apparatus width	1.67±0.05 (1.6-1.72)	1.74±0.12 (1.62-1.85)
Rostral gap width	0.96±0.01 (0.95-0.97)	1.02± 0.05 (0.97-1.07)

on free margin. Lateral ridge papillae on each side of median ridge similar in size and shape to postnarial papillae. Buccal roof arena with a row of 3–4 papillae on either side and approximately 30 pustulations randomly distributed. Glandular zone conspicuous. Dorsal velum distinct with irregular margin.

Chondrocranium longer than wide. Width approximately 80–85% of the total length. Height about ½ the total length and approximately 40% the total width (stage 33–34).

Suprarostral cartilage with corpora fused ventromedially, delimiting a U-shaped space; each corpus dorsolaterally continuous with the ala through a relatively narrow strip of cartilage. Lateral alae flat, wide, and ventrally rounded; posterodorsal margin of each ala with a well developed processus posterior dorsalis. Lamina orbitonasalis as a small triangular expansion of the planum ethmoidale, just dorsal to the attachment of the commissura quadratocranialis anterior. Cornua trabeculae about 25% of the total length of the chondrocranium, distally expanded and diverging in V-shape. Processus lateralis trabeculae indistinct. In the orbitotemporal region, fenestra basicranialis large and rectangular, foramina carotica primaria visibly surrounded by cartilage in the posterior portion of the cranial floor, foramina craniopalatina not visible. Orbital cartilages poorly developed, lower in the anterior region and posterodorsally attached to the optic capsules by a narrow strip of cartilage. Large and elongated foramen prooticum, and foramen opticum smaller than foramen oculomotorium, these latter two located in the posteroventral region of the orbital cartilage. Frontoparietal fontanel undivided. In the oto-occipital region, otic capsules ovoid, dorsally connected by a narrow tectum synoticum. Crista parotica poorly distinct. Long and finger-like processus anterolateralis. Processus posterolateralis absent. Fenestra ovalis ventrolaterally on otic capsule (about 1/3 the otic capsule length). Foramen perilymphaticum in the ventromedial region of the otic capsule, lateral to the foramen jugulare. Palatoquadrate narrow anteriorly and rounded posteriorly; lateral and posterior margins slightly curved dorsally; posterior curvature at the level of the point of attachment of the processus ascendens to the orbital cartilage. Processus ascendens attached just posterior to the oculomotor foramen ("intermediate" condition according to SOKOL 1981), and almost perpendicular to the main axis of the chondrocranium. Processus muscularis quadrati triangular. Processus hyoquadratis small and triangular in lateral view. Facies articularis hyalis distinct. Short and wide pars articularis quadrati. Wide commissura quadratocranialis anterior with a triangular processus quadratoethmoidalis on anterior margin; processus pseudopterygoideus absent. Commissura quadratoorbitalis rod-like, in contact with dorsal margin of the processus muscularis quadrati. Meckel's cartilages stout, sigmoid-shape; rounded processus retroarticularis. Infrarostral cartilages slender and wedge-shaped, connected ventromedially by connective tissue forming a V-shape structure.

Hyobranchial apparatus with ceratohyalia wide and flat; anterior margin of each ceratohyal with a processus anterior hyalis, and processus anterolateralis well-developed, triangular in shape; processus posterior hyalis distinct on the posterior margin. Pars reuniens poorly chondrified. Copula posterior with a small processus urobranchialis. Hypobranchial plates wide, in contact medially along most of their length. In the branchial baskets, ceratobranchials I and IV are attached to the hypobranchial plate by a wider strip of cartilage than in ceratobranchials II and III. Ceratobranchial I with a distinct processus branchialis. Processi branchiale on ceratobranchials II and III as two opposing, ventrally projecting cartilages ("open" processus branchialis). Ceratobranchials I, II, and III with a dorsally projecting spiculum near their point of attachment to the hypobranchial plate.

Discussion

A historical review of the knowledge of the terrestrial reproductive mode (including endotrophic tadpoles) in *Adenomera* species was summarized by DE LA RIVA (1995).

Later, this same reproductive mode was reported for other populations of the genus (Kokubum & Giaretta 2005, Kokubum & Souza 2008, Menin et al. 2010). The endotrophic tadpoles of this genus have keratinised upper and lower jaw sheaths, but lack labial teeth and a spiracle (Hey-

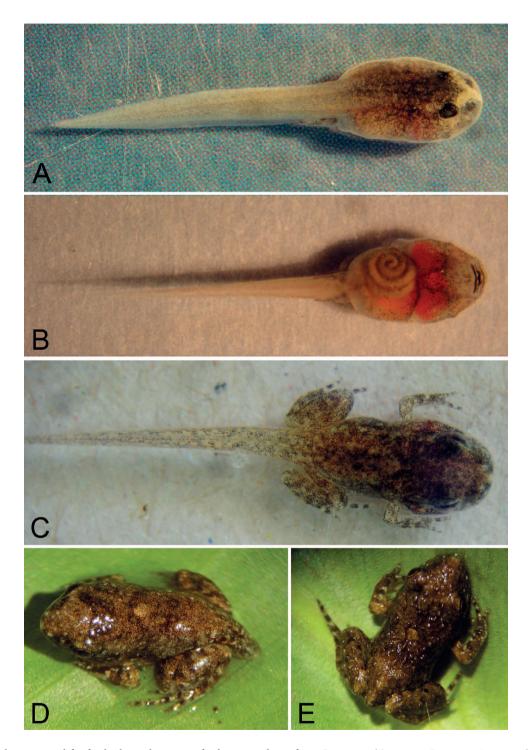


Figure 3. Colouration in life of tadpoles and a young of *Adenomera diptyx* from Corrientes (Corrientes Province, Argentina). (A) dorsolateral view at stage 36; (B) ventral view at stage 36; (C) dorsal view t stage 42; (D) dorsal view t stage 45; (E) recently metamorphosed individual.

ER & SILVERSTONE 1969, MENIN et al. 2010). Vestigial labial teeth in a posterior row, and a sinistral spiracle without a free tube were reported for a nameless species by Kokubum & Giaretta (2005). In contrast, the exotrophic tadpoles of *Adenomera bokermanni, A. diptyx,* and *A. thomei* have spiracles with a free tube and an oral apparatus with well-developed labial teeth (Heyer 1973, De La Riva 1995, Almeida & Angulo 2006). In these species, as in those of the *Leptodactylus fuscus* group, the eggs are deposited in a foam nest in an almost closed chamber that is constructed near a temporary pond, from which the tadpoles emerge when the nest is flooded and continue their development in the water (Reproductive Mode 21 as per Duellman & Trueb 1994, Mode 30 as per Haddad & Prado 2005).

DE LA RIVA (1995) found that *Adenomera* populations from Buenavista-Amboró (Bolivia) have exotrophic tadpoles and employed this character state to revalidate *Adenomera diptyx* (DE LA RIVA 1996). Additionally, he suggested that populations of *Adenomera* from northeastern Argentina and southwestern Brazil might belong to this taxon, although he examine neither tadpoles nor adult

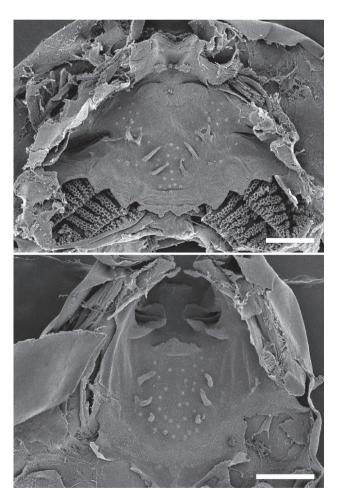


Figure 4. Floor (above) and roof (below) of the oral cavity of an *Adenomera diptyx* tadpole (stage 36) from Laguna Naick Neck, Formosa Province, Argentina. Scale bar = 0.5 mm.

specimens from these countries. In this work, we corroborate the presence of the same reproductive mode for populations from Corumbá (Brazil) and Corrientes and Formosa Provinces (Argentina), which allows us to confirm the presence of *Adenomera diptyx* in both countries. In addition, molecular data have recently confirmed these populations as representing *Adenomera diptyx* and revealed four subclades within this taxon (Fouquet et al. 2013). While the populations from Corumbá and Argentina belong to the same subclade, the Amboró population was included in another subclade. Further studies are needed to evaluate the taxonomic status of these populations.

The external larval morphologies of some species of *Adenomera* are already known (see Tab. 3 in Kokubum & Sousa 2008), whereas internal morphology has been poorly studied. Observations on the internal oral morphology are currently available only for *A. marmorata* (Wassersug & Heyer 1988), while the morphology of the chondrocranium and hyobranchial apparatus has not previously been described for any member of the genus. Therefore, we compared our results with those available for *Leptodactylus* (Larson & De Sá 1998, Sandoval 2004, De Sá et al. 2007, Vera Candioti et al. 2007, Miranda & Ferreira 2009, Miranda et al. 2015).

Morphologically, the buccal cavity of Adenomera diptyx is more similar to that of the species of the Leptodactylus fuscus group than to that of Adenomera marmorata. However, this is not unexpected since A. marmorata have endotrophic tadpoles with drastic reductions in their oral and buccal parts (Wassersug & Heyer 1988). Adenomera diptyx shares with the L. fuscus group the presence of a semicircular crest in the prenarial region (absent in A. marmorata), two pairs of infralabial papillae (but the first one

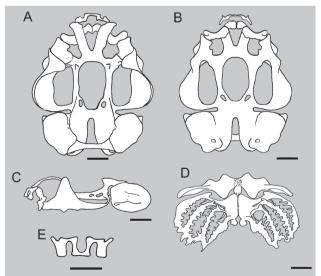


Figure 5. Chondrocranium of *Adenomera diptyx* (stage 34) from Laguna Naick Neck, Formosa Province, Argentina. (A) dorsal view; (B) ventral view; (C) lateral view; (D) ventral view of hyobranchial apparatus; (E) suprarostral cartilages. Scale bars = 5 mm.

basally fused in the *Leptodactylus fuscus* group), four lingual papillae (two in *A. marmorata*), and few papillae on the roof and floor of the cavity. Additionally, *A. diptyx* is differentiated from *A. marmorata* by the presence of tall lingual papillae (pustules in *A. marmorata*), presence of papillae on the floor and roof (only pustulations in *A. marmorata*), and presence of a glandular zone and dorsal velum (absent in *A. marmorata*).

The chondrocranial morphology of Adenomera diptyx contains all characters that LARSON & DE SÁ (1998) and MI-RANDA et al. (2015) suggested as characterising all members of the genus Leptodactylus. Additionally, we observed several characters that are shared with the L. fuscus group and were pointed out by LARSON & DE SÁ (1998): 1) wide suprarostrals with a U-shaped corpora in frontal view (also in L. rhodomystax); 2) long and narrow cornua; 3) long and finger-like processi anterolaterale on otic capsules; 4) posterior curvature of the palaquadrate at the level of the point of attachment of the processus ascendens (also in L. albilabris and L. labrosus); 5) processus ascendens almost perpendicular to the main axis of the body; 6) connection between the processus ascendens and the orbital cartilage just posterior to the oculomotor foramen ("intermediate" condition according to SOKOL, 1981) (also in the pentadactylus group, L. ocellatus, and L. chaquensis), and 7) processus branchialis open between ceratobranchials II and III (also in the *pentadactylus* group).

Recently, two major clades within *Leptodactylus* were defined using larval characters of internal oral anatomy and cranium (MIRANDA et al. 2015). The larval morphology of *Adenomera diptyx* agrees with that of the clade composed by the *Leptodactylus fuscus*, *L. latrans*, and *L. melanonotus* species groups, differing from the clade of the *L. pentadactylus* species group. Until a comprehensive study of all species of *Adenomera* is conducted, discussions about phylogenetic implications will remain poorly supported.

Adenomera spp. also share with the *Leptodactylus fuscus* species group the habit of constructing underground chambers for oviposition, but theirs have no entrance tunnel as is the case in most of species of *L. fuscus* group except *L. furnarius* (Cei 1949, Giaretta & Kokubum 2004, Kokubum & Giaretta 2005, Toledo et al 2005, Oliveira Filho & Giaretta 2008, Kokubum et al 2009).

The reproductive mode and larval morphology of *Adenomera diptyx* are similar to those of the species of *Leptodactylus*, mainly to species of the *L. fuscus* group. Considering that the phylogenetic relationships between *Adenomera* and *Leptodactylus* are still debated, and that information on the larval morphology of *Adenomera* species is scarce, further studies, including more data about the internal larval morphology of *Adenomera* species, are necessary for a more exhaustive analysis. This will facilitate comparisons between species with endotrophic and exotrophic tadpoles within this genus and may help reveal whether the character states shared with *Leptodactylus* represent conserved features in phylogenetically close species or a case of convergence associated with the feeding ecology of the larvae.

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