Reproductive ecology and behaviour of a species of *Adenomera* (Anura, Leptodactylineae) with endotrophic tadpoles: Systematic implications

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Abstract

The species of the *Leptodactylus fuscus* group and those of the genus *Adenomera* lay their eggs in underground chambers. According to current systematic arrangement of these genera, this behaviour is convergent. Here we describe reproduction, courtship, tadpole morphology, calls, chamber structure, and populational phenology of an *Adenomera* species, and compare some of these features with those of other species of the genus and with species of *Leptodactylus* of the *fuscus* and *pentadactylus* groups. We tested the tadpoles of the *Adenomera* sp. and those of *Leptodactylus labyrinthicus* (*pentadactylus* group) for their foam-making abilities. There was sexual dimorphism in size; males averaged 22.0 mm and females 24.3 mm in snout–vent length. Males called from late September to late February; calling often began about 2–3 h before sunset. Males called exclusively in open (non-forest) areas. Egg clutches were found around male calling sites. Males excavated spherical chambers which had a direct entrance. During mating, the male led the female towards a previously excavated chamber. Territorial interactions (aggressive calls and fights) occurred when an intruder male approached a calling male. Late-stage tadpoles and newly metamorphosed juveniles were found within underground chambers. Clutch size averaged 10.6; eggs averaged 3.7 mm in diameter and were cream coloured. Tadpoles had horny beaks, but no labial tooth; spiracle was present. All tested groups of tadpoles generated foam within 10 h. As we report for *Adenomera* sp., the males of *Leptodactylus* species of the *fuscus* group lead the female to a previously excavated chamber. Tadpole foam-making behaviour was reported in *Leptodactylus* of the *fuscus* group and was previously unknown for any species of *Adenomera* or for *Leptodactylus* of the *pentadactylus* group. The way in which the tadpoles of *Adenomera* sp., *Leptodactylus* spp. (of the *fuscus* group) and *L. labyrinthicus* made foam was quite similar. The foam-making behaviour of the studied tadpoles may act to avoid compaction of the tadpoles at the bottom of the basin or underground chamber, avoiding overcrowding and increasing respiratory and excretory efficiency. As presently recognized, the phylogenetic position of *Adenomera* suggests that reproductive major behavioural features are convergent with some *Leptodactylus* species. Alternatively, our data point to close phylogenetic relationships between *Adenomera* and *Leptodactylus* of the *fuscus* and *pentadactylus* groups, reinforcing the paraphyletic nature of the genus *Leptodactylus*.

Keywords: Adenomera, Anura, Leptodactylineae, Leptodactylus, phenology, reproduction, systematics
Introduction

Leptodactyline frogs are distributed throughout the Neotropics and most species lay their eggs in foam nests. The precariousness of the current systematic arrangement of the leptodactylids was discussed by Heyer (1998), who presented evidence that *Adenomera* is nested within *Leptodactylus*, and by Larson and de Sá (1998). The species of the *Leptodactylus fuscus* (Schneider, 1799) group and those of *Adenomera* lay their eggs in underground chambers (Heyer 1975; Martins 1988) which, according to the present systematic arrangement of leptodactylid frogs (Frost 2004), implies that this behaviour is convergent in these groups. Species of *Leptodactylus* of the *fuscus* group (*sensu* Heyer, 1978) have exotrophic tadpoles (Philibosian et al. 1974; Heyer 1978; Martins 1988; Arzabe and Almeida 1996; Giaretta and Kokubum 2004) and most of the known *Adenomera* species have endotrophic tadpoles (Lutz 1947; Heyer 1969; Heyer et al. 1990), but some complete their development in water (De La Riva 1995; Almeida and Angulo 2002). Early tadpoles of species of *Leptodactylus* of the *fuscus* group are able to generate foam (Caldwell and Lopez 1989; Downie 1989; Giaretta and Kokubum 2004).

Despite recent recognition of new *Adenomera* species (Kwet and Angulo 2002), the taxonomy of the genus is still unsatisfactory, with a number of species awaiting a formal description (Angulo et al. 2003).

In this paper, we describe features of the reproduction, ecology and behaviour of an undescribed species of *Adenomera* (*Adenomera* sp.), including reproductive mode, tadpole morphology, season and sites of reproduction, advertisement and aggressive calls, courtship behaviour, chamber structure, and populational phenology. We tested the tadpoles of *Adenomera* sp. and those of *Leptodactylus labyrinthicus* (Spix, 1824) (*pentadactylus* group) for their foam-making abilities, and discuss the possible function of this behaviour. The taxonomic status of the studied population is discussed. We also summarize published data on habitat and egg number/size of all known *Adenomera* species. Details of the reproductive mode of *Adenomera* species are compared with those of species of the *Leptodactylus fuscus* group. The ecological/behavioural data point to possible shared derived features between *Adenomera* and *Leptodactylus* of the *fuscus* and *pentadactylus* groups, reinforcing the evidence for the paraphyletic nature of *Leptodactylus*.

Methods

The present study was carried out in two municipalities in the region of the Triângulo Mineiro, Uberlândia (18°55′S, 48°17′W) and Perdizes (19°13′47″S, 47°08′43″W, 700–1000 m; ca 100 km east of Uberlândia), State of Minas Gerais, south-eastern Brazil. The study period was September 1999 to February 2004. In Uberlândia, the original vegetation was Cerrado (Araújo et al. 1997), which can still be found in some countryside areas. In Perdizes, observations were carried out in the Estação de Pesquisa e Desenvolvimento Ambiental Galheiro (CEMIG), where typical Cerrado vegetation occurs, including semi-deciduous forest (Oliveira-Filho and Fontes 2000). The regional climate has two well-defined seasons, a rainy/hot summer (September to March) and a dry/mild winter (April to August) (Figure 1), with occasional frosts (Rosa et al. 1991). The annual mean precipitation is around 1550 mm, ranging from 750 to 2000 mm.

Reproductive parameters (sex ratio, adult size, clutch size, and sexual dimorphism) were based on pitfall-trapped specimens from Uberlândia. Frogs were trapped at the Clube Caça e Pesca (CP) during the period October 1999 to December 2000 and at the Estação
Ecológica do Panga (EEP), from September 2000 to October 2001. Sampling effort was similar in both localities; details of pitfall sampling techniques and efforts are in Menin and Giaretta (2003) and Giaretta and Kokubum (2004). The CP is a locality that is more affected by human disturbance than Panga, with greater areas covered by exotic grasses, such as *Brachiaria decumbens* Stapf. The meteorological data we used were collected at the campus Santa Mônica of the Universidade Federal de Uberlândia, about 10 km north of Caça e Pesca and 30 km north of Panga.

To determine the age structure, all individuals were sexed and grouped as males, females and juveniles. The size of the smallest male caught during vocalization was used to set the lower limit to mature males; with regards to females, it was the smallest individual bearing mature ovarian eggs and hypertrophied/convoluted oviducts. Clutch size was determined on egg clutches collected in the field and estimated from mature ovarian eggs (>2.5 mm diameter). Frogs, eggs and nests were measured to the nearest 0.1 mm using calipers. Foam nests were searched for by clearing the ground around places where males were found calling. Tadpole staging followed Gosner (1960); morphology nomenclature followed Altig and McDiarmid (1999).

The reproductive season was estimated by weekly (summer months) or quarterly (winter) visits to reproductive sites. The daily pattern of calling activity was determined several times over the 24 h period. Mating behaviour and male fights were observed in the field through continuous records of the most relevant events (Martin and Bateson 1986).

The ability of *Adenomera* sp. tadpoles to generate foam was tested in the laboratory; tadpoles from three different egg clutches were used. Tadpoles were all about the same size (about 13–15 mm total length), and were at stages 36–42. The three experimental groups contained five, six and 11 tadpoles each. As the species of *Leptodactylus* of the *pentadactylus*
species group (Heyer 1975) also spend a long time within the nest (e.g. *L. fallax* Müller, 1926 (Lescure and Letellier 1983); *L. stenodema* Jiménes de la Espada, 1875 (Hero and Galatti 1990; Silva et al. forthcoming)); we also tested the tadpoles of a species of this group, *L. labyrinthicus*, for foam-making behaviour. Two groups of *L. labyrinthicus* tadpoles were used, one totalling 191 and the other 25 tadpoles (21–25 mm, stage 25). Two groups (27 and 57 individuals; 10.5–12.0 mm TL) of tadpoles of *Leptodactylus fuscus* (a species whose tadpoles are known to make foam) at stage 25 were used as a control for the experimental conditions. For the experiments, all tadpoles were removed from their original foam by carefully rinsing them in dechlorinated tap water; experiments were started within 3 h after the tadpoles were collected in the field. Each tadpole group was kept in a concave-bottomed plastic tube (30 mm diameter) with a film of water not deep enough for the tadpoles to swim in. The experiment was carried out in the shade, with natural illumination (temperature during this time period ranged from 23 to 30°C). Tadpoles were observed for about 60 h, at intervals of 3–8 h. Tadpole behaviour was observed while generating foam. The test was considered positive if tadpoles produced enough foam to freely move around in.

For description and measurements, plaster moulds of the underground chambers of *Adenomera* sp. were made. The liquid plaster was carefully injected with the aid of a tube through the entrance of the chambers and left to dry.

Differences in size between sexes were tested through analysis of variance (ANOVA); correlation between female size and egg number was evaluated through the Spearman test (Wilkinson 1990; Zar 1999). Sex ratio was evaluated through a $\chi^2$ test with Yates correction (Zar 1999).

Calls were recorded with a Nagra E tape recorder (19 cm s$^{-1}$) and with a Sennheiser MKH816T microphone. All records were made from distances less than 1 m from the calling male. The call was digitized with, and the audiospectrogram derived from, the Spectrogram software (Horne 2001). Sample rate was set at 22,050 Hz, with 16 bit resolution. For analysis, a Fast Fourier Transformation (FFT) length of 256 was used.

Voucher specimens are deposited in the collection of frogs of the Museu de Biodiversidade do Cerrado, Universidade Federal de Uberlândia (adults: AAG-UFU 4175, 4182, 4190–91, 4194; tadpoles: AAG-UFU 2632).

**Results**

The reproductive season of *Adenomera* sp., as indicated by calling males, lasted from late September to late February. Males started calling about 1 month after the onset of rains and stopped about 1–2 months prior to the beginning of the dry season. The calling period often began about 2–3 h before sunset; during the peak of the hot/rainy season (December/January) males called throughout the 24 h period.

Males called exclusively in open areas, amidst grasses, bushes or scattered debris. Even when available (i.e. at Perdizes), forest or forest border sites were never used for calling. At the beginning of the reproductive season, males started calling from sites close to (<20 m) permanent water bodies (i.e. wet grass-fields (Veredas) and river banks) but later, when rainfall accumulated, they called from more distant (>500 m) places. Males called on the ground ($N=25$) or perched on elevated ($\leq 30$ cm height) sites ($N=11$), such as leaves, fallen trunks and termite mounds. They called from protected places, such as under dense (<100 cm height) tufts of grass, or from exposed areas, such as recently burned ground or short (<10 cm) grass in gardens.
Egg-bearing females \((N=21)\) were found between November and January. Egg clutches averaged 10.6 (SD=2.13; range=6–13; \(N=9\)). Eggs (yolk portion) averaged 3.7 mm diameter (SD=0.06; \(N=19\) eggs; \(N=2\) egg clutches) and were cream coloured. The egg number, estimated from ovarian eggs, varied between 7 and 13 (mean=10.0; SD=1.7; \(N=21\)) and there was no significant correlation between female size and number of eggs \((r_s=0.05; \(N=21\); \(P>0.10\)). Mature ovarian eggs measured 2.6–3.7 mm (mean=3.1; SD=0.24; \(N=105\); \(N=21\) females) and were cream coloured. Egg clutches were found within underground chambers \((N=5)\), embedded in a white foam; late stage tadpoles (stage >40, \(N=8\) nests) and newly metamorphosed juveniles \((N=1\) nest) were also found within chambers.

There was sexual dimorphism in size \((F_{51,42}=151, \text{df}=91; P<0.001)\); males averaged 22.0 mm snout–vent length (SD=0.8; \(N=51\)) and females 24.3 mm (SD=1.0; \(N=42\)); males also differ from females by having a more projected, round shovel-shaped snout and a slightly distended subgular vocal sac.

Typical tadpoles at stages 35–40 \((N=2\) nests) (Figure 2) had no labial tooth, the last posterior row can be regarded as vestigial; oral apparatus anteroventral; marginal papillae with a broad anterior and a narrower posterior gap; submarginal papillae absent; disc emargination absent; nares frontally positioned, closer to snout than to eyes (dorsal view); vent tube short, opened to the right, with a short free border; eyes laterally positioned; spiracle sinistral, without a free tube, slightly before the mid-length of body and below the mid-line of height; upper jaw sheath horny, wide-arched, with serrated edge; lower jaw sheath horny, narrowly arched with serrated edge; dorsal fin arched, inserted at the body/tail junction, less deep than the muscular portion and as deep as the ventral at mid-tail; ventral fin almost straight; tail round tipped; body oval-shaped (dorsal and lateral view); body brown on back and sides; fins whitish translucent; tail whitish with small black spots; belly translucent (whitish or yellowish); total length 13.1–14.1 mm, body comprising 35–37% of the total length.

Pitfall traps captured 130 individuals. The sex ratio of the trapped specimens was not significantly different from 1:1 (49 males, 36 females) \((\chi^2=1.99, P>0.10)\); 45 of the individuals captured were juveniles. Most of the individuals were captured between October and December (full rainy season) (Figure 3); no capture was registered during the

![Figure 2. The tadpole of Adenomera sp. Above: lateral view of the left side (scale bar: 4.0 mm). Below: detail of the oral apparatus (scale bar: 0.5 mm). Specimen from Uberlândia (MG, Brazil).]
peak of the dry/cold seasons (July to August). No pattern of emergence/recruitment was observed in juveniles, as they were found in small numbers almost all through the September to June period. Four times more individuals were collected at CP than at Panga (Figure 3).

All tested groups of tadpoles (of all three species) generated foam within 10 h. In all cases, the newly produced foam was consistent enough for the tadpoles to move freely within it. Tadpoles produced foam by releasing bubbles through the mouth. When foam accumulated, the tadpoles often moved to the surface (one or two at a time) and spent 2–5 s releasing bubbles, after which they dived into the foam again.

The nest chambers of Adenomera sp. were built in wet soils, but never had free water on the bottom. They were spherical or slightly elliptical, with an average diameter of 35.1 mm (SD=2.7, N=5); had a direct (no tunnel) entrance (about 6 × 9 mm), on the top or slightly
lateral to the chamber. Close examination revealed shallow markings on the internal wall, which fitted the snout shape of males. On one occasion a male was observed pressing his snout repeatedly against the inner wall of an almost completed chamber.

We observed seven partial mating events. A female approaches a calling male and touches him with her snout on his side. After the contact, the male starts moving towards a previously excavated chamber, about 20–50 cm from the calling site. Along the way the male emits contact calls (not recorded) even after entering the chamber. When the pair arrives at the chamber, the male enters first and is followed by the female. After the female enters, the male sometimes ($N=1$), sometimes not ($N=5$), turns and blocks the entrance, keeping his head out. Egg clutches were found around male calling sites. Behaviours presumably performed within the underground chamber, such as amplexus and foam beating, were never observed directly.

Territorial interactions ($N=4$ events) occurred when an intruder male approached a calling male ($<30$ cm). Resident males changed from emitting advertisement calls (Figure 4) to territorial calls (Figure 5). If the intruder approached even closer ($<20$ cm), physical combat was initiated. The longest observed combat lasted about half an hour. During fights, males hit one another with the tip of their snout and tried to raise the opponent with the snout. Grasping was not observed. Wrestling was performed within a 20 cm diameter area. Both males could emit aggressive calls during wrestling.

The advertisement call (Figure 4) was a sequence of regular notes repeated about 55–85 times per minute. The notes were about 105–145 ms in duration, between-note intervals were 580–10,151 ms. To the human ear each note sounded like a short and sharp scream. Pulses (up to 10) were not distinctly defined within notes. Two harmonics were evident, the second (around 4100 Hz) being emphasized. The frequency rose slightly during the call. The aggressive call (Figure 5) was heard when two males were close ($<20$ cm) together ($N=2$). It could be easily distinguished from the regular advertisement call by being quite variable in duration (48–140 ms) and intensity, by being issued at a faster rate (178 per minute), and by having better defined pulses.

Discussion

The recognized number of component species in the genus *Adenomera* appears to be quite conservative. Three *Adenomera* species have been reported from Cerrado environments, *A. hylaedactyla* (Cope, 1868) (Straughan and Heyer 1976), *A. marmorata* Fitzinger, 1867 (Cochran 1955) and *A. martinezi* Bokerman, 1956 (Bokerman 1956). *Adenomera marmorata* appears to be restricted to the Atlantic Forest domain (Heyer et al. 1990); *A. martinezi* is peculiar in possessing four longitudinal symmetrically arranged rows of glands, which are not present in the population we studied (Kokubum, in preparation). Regarding call length and dominant frequency, *Adenomera* sp. is similar to the population called *A. hylaedactyla* by Straughan and Heyer (1976). However, the tadpole of *A. hylaedactyla* described from French Guyana (Heyer and Silverstone 1969) differs markedly from that described here, mainly in not possessing a spiracle. If calls attributed to *A. hylaedactyla* (Angulo et al. 2003, and references therein) for Amazonian populations correspond to the nominal species, the population we studied represents an undescribed species.

The reproductive behaviour of relatively few *Adenomera* species is known; four studies report underground chambers and foam nests (Lutz 1931; Lutz 1947; Heyer and Silverstone 1969; Almeida and Angulo 2002). Males of the *Adenomera* sp. excavate underground chambers using their snout, as do males of species of *Leptodactylus* of the
Figure 4. Oscillogram (first row), audiospectrogram (second and fourth rows) and power spectrum (third row) of the advertisement call of *Adenomera* sp. The first three rows are representations of single notes, the fourth represents a sequence of three notes. Recording files: first column, Adenomspmg2AAGd (17 December 2003, 17:00 h, air 24°C, unvouched recording); second column, AdenomspmgAAGd (10 December 2003, 20:10 h, air 26°C, unvouched recording); fourth row, AdenomspmgAAG21 (5 October 1999, 19:40 h, air 21°C, voucher AAG-UFU 2633).
fuscus group (Martins 1988; Freitas et al. 2001; Reading and Jofre 2003; see Figure 6 in Giaretta and Kokubum 2004). In Adenomera, the degree of development tadpoles undergo within the chamber is variable, some completing development outside the chamber (i.e. aquatic tadpoles; De La Riva 1995) and others completing their development within the chamber (Lutz 1931; Lutz 1947; Duellman 1989, Heyer et al. 1990; Hödl 1990; present study). There is evidence that *A. diptyx* Boettger, 1885 (De La Riva 1996) and *A. cf. marmorata* (Almeida and Angulo 2002) have aquatic tadpoles. The mating behaviour we report for *Adenomera* sp. is the first for a species of the genus. The males of species of Leptodactylus of the *fuscus* group (Martins 1988; Giaretta and Kokubum 2004) and *Adenomera* sp. both lead the female to a previously excavated chamber.

Some *Adenomera* species live within or at the border of forests (Heyer et al. 1990; Rodriguez 1992; Mercolli et al. 1995), and some other species (e.g. *A. martinezi*, *A. bokermannii* (Heyer, 1973), *A. diptyx*, and *A. hylaedactyla*), including the species here reported, are strictly open area dwellers (Table I). Human activities appear to create good conditions for the establishment of dense populations of the *Adenomera* species we studied, especially when resulting in areas covered by exotic grasses. All known *Adenomera* species are both diurnal and nocturnal callers (Pombal 1997; Kwet and Angulo 2002; present study). In Uberlândia, a lower number of individuals was trapped in the dry season, as other terrestrial frogs (Giaretta and Kokubum 2004; Giaretta and Menin 2004) they possibly do not move around during this period (Seebacher and Alford 1999).

Among frogs, territorial behaviour is expected in those species with a prolonged reproductive period, and is frequently related to the defence of suitable sites for
reproduction (Wells 1977). Territorial behaviour has been reported in several species of *Leptodactylus* (Martins 1988; Rossa-Feres et al. 1999; Freitas et al. 2001). The present work is the first to describe aggressive behaviour in an *Adenomera* species.

Egg number varies widely among *Adenomera* species (Table I), from 9–14 in *A. hylaedactyla* to 103 in *Adenomera* sp. (Bolivia) (De La Riva 1995). Egg diameter also varies (Table I), from around 1.8 mm in *Adenomera* sp. (Bolivia) (De La Riva 1995) to ca 3 mm in *A. hylaedactyla* (Aichinger 1985), *A. andreae* Müller, 1923 (Crump 1974; Rodriguez and Duellman 1994), *A. marmorata* (Cochran 1955), *Adenomera* aff. *marmorata* (Almeida and Angulo 2002), and *Adenomera* sp. (present study).

Tadpole foam-making behaviour has been reported in *Leptodactylus* of the *fuscus* group (Caldwell and Lopez 1989; Downie 1989; Giaretta and Kokubum 2004) and in *Adenomera* sp. (present study); evidence for this behaviour in other *Adenomera* species was provided by Almeida and Angulo (2002). Foam-making behaviour has not previously been reported for any *Leptodactylus* of the *pentadactylus* group. The way in which the tadpoles of *Adenomera* sp., *Leptodactylus* spp. (of the *fuscus* group) and *L. labyrinthicus* make foam is quite similar, involving the release of bubbles through the mouth while the tadpoles swim up to the foam surface. In *L. fuscus* tadpoles, foam-making behaviour is restricted to the chamber phase (below stage 28) or shortly after they enter the water (Downie 1984); *Adenomera* sp. tadpoles show a relatively extended foam-making period, being able to generate foam until close to metamorphosis (stage 42).

| Species          | Habitat | SVL (mm) | Egg number | Egg diameter (mm) | Source                          |
|------------------|---------|----------|------------|-------------------|---------------------------------|
| *A. andreae*     | NR      | 27       | 12         | 3.0               | Crump 1974                      |
| *A. andreae*     | F       | NR       | NR         | NR                | Toft and Duellman 1979          |
| *A. andreae*     | F       | NR       | 3–10       | NR                | Moreira and Lima 1991          |
| *A. andreae*     | F       | NR       | 29         | 2.0–3.0           | Rodriguez 1992                  |
| *A. andreae*     | F       | 18–24    | <20        | 3.0               | Rodriguez and Duellman 1994     |
| *A. araucaria*   | F/O     | NR       | NR         | NR                | Bernarde et al. 1999            |
| *A. andreae*     | F       | 18.8–19.9| NR         | NR                | Kwet and Angulo 2002            |
| *A. bockermanni* | O       | NR       | 18         | NR                | Heyer 1973; personal observation|
| *A. hylaedactyla*| F       | NR       | NR         | NR                | Toft and Duellman 1979          |
| *A. hylaedactyla*| NR      | 26       | 9–14       | 3.0               | Aichinger 1985                  |
| *A. hylaedactyla*| O       | 26       | 32         | 3.4               | Rodriguez 1992                  |
| *A. hylaedactyla*| O       | 18–24    | <20        | 3                 | Rodriguez and Duellman 1994     |
| *A. hylaedactyla*| F/O     | 20–28    | NR         | NR                | Mercalli et al. 1995            |
| *A. marmorata*   | NR      | 20.9     | 2–7        | 3.0               | Cochran 1955                    |
| *A. marmorata*   | F/O     | NR       | NR         | NR                | Heyer et al. 1990               |
| *A. aff. marmorata* | F    | 27–29    | 3.0        |                   | Almeida and Angulo 2002         |
| *A. martinezi*   | O       | NR       | 20         | 0.8*              | Bokermann 1956; personal         |
|                  |         |          |            |                   | observation                     |
| *A. diptyx*      | F/O     | 24       | 17–18      | 2.6               | De La Riva 1995                 |
| *Adenomera* sp.  | F/O     | 26       | 103        | 1.8               | De La Riva 1995                 |
| *Adenomera* sp.  | O       | 22–24    | 7–13       | 3.0               | Present study                   |

Habitats: F, forest; F/O, forest and open areas; O, just open areas; NR, not reported.

*a* Immature ovarian eggs?
The tadpoles of seven Adenomera species have been described (Heyer and Silverstone 1969; Heyer 1973; Hero 1990; Heyer et al. 1990; De La Riva 1995). The presence of a gap in the posterior row of papillae is unknown in Leptodactylus species and in Adenomera bokermanni (Heyer 1973) and may be indicative of close phylogenetic relationships between species in which it occurs, such as A. andreae (Hero 1990), A. marmorata (Heyer et al. 1990) and Adenomera sp. (Amboró National Park, Bolivia) (De La Riva 1995).

In leptodactylid frogs, such as Physalaemus cuvieri Fitzinger, 1826, the foam nests built by the parents while egg laying may play an anti-predatory role (Menin and Giaretta 2003). Downie and Smith (2003) studied the function of the foam generated by L. fuscus tadpoles. They emphasized that the foam may help the tadpoles to obtain moisture from the substratum, but also considered alternative hypotheses such as the foam assisting with respiratory and excretory exchange. The discovery of foam-making behaviour in a species of Leptodactylus of the pentadactylus group may help in this discussion. The reproductive behaviour of L. labyrinthicus was described by Silva et al. (forthcoming). The female of L. labyrinthicus builds a basin at the edge of a water body within which she lays her eggs and the tadpoles may spend several weeks within the basin prior to entering adjacent water bodies. The basin normally retains a certain amount of water at the bottom and short drought periods may not be a serious problem for the tadpoles, which can freely move from the water of the basin to the foam, and vice versa. After 2–3 days without rains, the typical foam covering the basin loses volume and develops a dry crust, even if water is present at the bottom of the basin. On wet days the tadpoles exhibit intense activity at the surface of the foam and the fresh appearance of the foam is restored. These data on L. labyrinthicus suggest that water absorption is not the main function of the foam released by the tadpoles. The foam may, instead, act to avoid compaction of the tadpoles at the bottom of the basin or underground chamber, avoiding overcrowding and increasing respiratory and excretory efficiency.

Currently, the genera Adenomera and Leptodactylus are widely accepted (De La Riva 1995; Heyer 1975; Frost 2004). Before De La Riva’s (1995) publication, the lack of an aquatic larval phase essentially defined the genus; the criteria used by De La Riva to include the species he studied within Adenomera instead of Leptodactylus, is unknown. As presently recognized (Heyer 1969, 1973, 1974, 1975), the phylogenetic position of Adenomera among the leptodactylid frogs suggests that at least three major behavioural features are convergent with some Leptodactylus species. Two characters are shared with Leptodactylus species of the fuscus group, which are (1) laying eggs in dug underground chambers that are (2) excavated by the males using their snouts; and one character is shared with Leptodactylus species of the fuscus group and L. labyrinthicus, which is the foam-making behaviour of tadpoles. Invoking the most parsimonious explanation, this set of behavioural data points to close phylogenetic relationships between Adenomera and Leptodactylus of the fuscus and pentadactylus groups, reinforcing the paraphyletic nature of the genus Leptodactylus (Heyer 1998). A close relationship between Leptodactylus of the fuscus and pentadactylus groups was previously recognized by Larson and de Sá (1998) based on tadpole morphology. The genus Adenomera may not form a monophyletic unity either; the discrepancies in egg number (Table I) and the presence of aquatic tadpoles in some species may be indicative that their typical small size has evolved several times. In our opinion, future phylogenetic studies evaluating the monophyletic nature of Adenomera should include A. martinezi, a relatively common species in central Brazil (unpublished observation). A possible natural history feature of the ancestor of the clade that joins both the L. fuscus group (including Adenomera) and L. pentadactylus group is a relatively large-sized hatchling, which was able
to swim powerfully to generate foam, features not observed in *Leptodactylus* species such as those of the *Leptodactylus podicipinus–wagneri* group (sensu Heyer, 1994).

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