A new species of *Heterixalus* (Amphibia: Hyperoliidae) from western Madagascar

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Received 10 January 2000. Accepted 26 April 2000

A new species of hyperoliid frog, *Heterixalus carbonei* n.sp., is described from the Antsingy forest in western Madagascar. It is characterized by an advertisement call consisting of long and regular note series. The only other *Heterixalus* with a similar call structure, *H. betsileo* from higher altitudes in eastern Madagascar, has distinctly shorter notes. After recent discoveries of the occurrence of *H. luteostriatus* and *H. tricolor* in western Madagascar, the new species brings the number of *Heterixalus* known from western Madagascar to three.

Key words: **Amphibia: Hyperoliidae: *Heterixalus carbonei* n.sp., Tsingy de Bemaraha, biogeography.**

INTRODUCTION

Frogs of the family Hyperoliidae are currently classified in 19 genera. Seventeen of these are endemic to sub-Saharan Africa (Schiøtz 1999). In addition, the monotypic genus *Tachycnemis* occurs on the Seychelles Islands, and the genus *Heterixalus* (currently 10 species) is endemic to Madagascar (Drewes 1984; Richards & Moore 1996).

Except for the highland species *H. rutenbergi,* all *Heterixalus* are uniform in morphology (Glaw & Vences 1994). Colour patterns, on the other hand, are variable within and among populations of single *Heterixalus* species (Glaw & Vences 1993, 1994). This situation is also typical for other hyperoliids (Schiøtz 1999). On the other hand, many *Heterixalus* species are bioacoustically well differentiated (except the closely related and possibly conspecific *H. boettgeri, H. alboguttatus,* and *H. madagascariensis,* as well as *H. tricolor, H. variabilis,* and *H. andrakata;* Blommers-Schlösser 1982; Glaw & Vences 1991, 1993, 1994; Andreone *et al.* 1994); advertisement calls are therefore the most useful tool to distinguish different species of the genus in the field.

In the present paper a new species of *Heterixalus* is described from the 'Tsingy de Bemaraha' massif in western Madagascar. In recent years several surveys (Emanueli & Jesu 1995; Schimmenti & Jesu 1996, 1997; Jesu *et al.* 1999) of the unique habitats within this massif have led to the discovery of new species of reptiles, some of which may be endemic to the area.

STUDY AREA

Situated in the centre of western Madagascar (18°15′–19°20′S; 44°15′–45°05′E), the World Heritage Site 'Tsingy de Bemaraha' consists of 500 000 ha, most of which are covered with secondary vegetation. The Plateau of Bemaraha (covered by the primary deciduous Antsingy forest at its western slopes) as well as the grasslands, the patches of forest and the mangroves situated between the plateau and the Mozambique Channel, are all included in this poorly known area. The limits of the Strict Nature Reserve N 9 'Tsingy de Bemaraha', established in 1927, coincide almost perfectly with the ones of the Antsingy forest.

The climate is characterized by a marked contrast between the warm dry season (from May to October) and the hot rainy season (from November to April). In the Antsingy forest, which represents the wetter part of the area, annual rainfall is 1000–1500 mm and the mean annual temperature ranges between 25 and 28 °C (Bousquet & Rabetaliana 1992).

The eastern territories of the area, which are part of the sedimentary region of Madagascar, are mainly formed by a massif (Tsingy de Bemaraha) consisting of Upper Jurassic limestone. This massif extends north–south for more than 80 km with an average width of 20 km and a maximum altitude of

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934 m above sea level (a.s.l.). The dissected relief is markedly karstic and shows typical erosion shapes consisting of limestone blocks with sharp tips at the top (locally named 'tsingy') and extensive cave systems.

The abundance of springs and streams allows the presence of a flourishing vegetation, which has never been affected by deforestation due to the impenetrability of the karstic habitat (Bousquet & Rabetaliana 1992). The Antsingy forest, which represents at least 5 % of total western Madagascar deciduous forest cover, shows an extraordinary variety of *facies* in relation to substratum nature, hydrography and exposition. Extensive descriptions of these habitats are given by Bousquet & Rabetaliana (1992) and Emanueli & Jesu (1995).

MATERIALS & METHODS

Fieldwork was carried out by R.J. and G.S. during the rainy season (25–29 January 1995 and 2–14 March 1997) at two sites along the western slopes of the Antsingy forest: Trano Passage (18°43′S, 47°07′E; 70 m a.s.l.) and Ambodyreana (18°41′S, 47°07′E; 120–150 m a.s.l.). The specimens of the new species described in this paper were observed and collected only at the former site. The search for frogs was carried out after sunset when males could be easily located while emitting their advertisement calls, which were recorded using a SONY TCM-77V tape recorder with external microphone; at the same time air temperature and relative humidity were recorded. After exposure to acetic ether, the sacrificed specimens were fixed and preserved in 70 % ethanol.

Calls were analysed with the MEDAV sound analysing system Spektro 3.2. Morphological measurements were taken by the same person (M.V.) with a calliper to the nearest 0.1 mm. Specimens were deposited in the Museo di Storia Naturale di Genova (MSNG). Webbing formula is given according to Blommers-Schlösser (1979).

To ascertain the genetic differentiation of the new species to other *Heterixalus,* we sequenced a fragment (555 bp) of the mitochondrial 16S rRNA gene homologous to the base pair positions 4006–4543 of the *Xenopus laevis* mt genome (Roe *et al.* 1985), using the primers and cycling protocols given in Vences *et al.* (2000). Sequences were submitted to Genbank (accession numbers AF215433–AF215437 and AF215502–AF215503). More detailed information on the genetic analyses will be published in a forthcoming paper.

***Heterixalus carbonei* n.sp.**, Figs 1–5

Etymology. Dedicated to the memory of Ermanno Carbone, last Honorary Consul of Madagascar in Genova, this new tree frog species will always remind us of his enthusiastic willingness to help and his endless pleasantness.

Diagnosis. A species of the genus *Heterixalus* as indicated by a vertical pupil, presence of a gular gland, connected lateral metatarsalia, and absence of spinulous skin in males which is typical in *Afrixalus* (Drewes 1984). Distinguished from all *Heterixalus* except *H. betsileo* by the general structure of the advertisement call which consists of a single unharmonious note type repeated after regular intervals. Distinguished from *H. betsileo* by the distinctly longer note duration of advertisement calls. Further distinguished from *H. rutenbergi* by the lack of black pigment on the gular gland and lack of a medial dorsal stripe; from *H. madagascariensis, H. boettgeri, H. alboguttatus,* and *H. punctatus* by the presence of light dorsolateral bands in adults; and from *H. andrakata* by the lack of dark dorsal marbling and vermiculations.

Holotype. Adult male (MSNG 49090; Figs 1, 2), collected 13 March 1997 at Trano Passage, Strict Nature Reserve N 9 'Tsingy de Bemaraha', 18°42′S, 44°43′E, 70 m a.s.l., Antsalova Fivondronana, Mahajanga Province, Madagascar, by Riccardo Jesu, Giovanni Schimmenti, Herinjato M. Rakotondrasoa, Paolo Bistagnino and Giacomo Berichilli.

Other types. None.

Description of the holotype. Body slender; head wider than long, slightly broader than body; snout rounded in dorsal and lateral views; nostrils directed laterally, not protuberant; canthus rostralis indistinct, concave; loreal region more or less even; tympanum indistinct, rounded, very close to eye; its diameter almost half of eye diameter; supratympanic fold absent; tongue ovoid, distinctly bifid posteriorly; vomerine teeth absent, choanae small, rounded; maxillary teeth present. Arms slender; subarticular tubercles single; no visible outer or inner metacarpal tubercles; comparative finger length 1<2<4<3; well-developed terminal finger disks; webbing formula of hand 1 (1.5), 2i (2), 2e(1), 3i (2), 3e (2), 4 (1.5). Legs slender; tibiotarsal articulation reaches anterior corner of eye when the limbs are adpressed along body; feet with a small elliptical inner metatarsal tubercle and without recognizable outer metatarsal tubercle; subarticular tubercles single; toe disks

Fig. 1. Holotype of *Heterixalus carbonei* n.sp. (MSNG 49090) from Trano Passage, Antsingy forest (diurnal markings).

moderately expanded; webbing formula of foot 1 (0.5), 2i(1), 2e(0.5), 3i(1), 3e(0.5), 4i(1), 4e(1.5), 5(0.5). Lateral metatarsalia connected; comparative toe length 1<2<3<5<4. Finger and toe pads with continuous circummarginal groove. Skin on the upper surface smooth; ventral surface of legs and chest smooth, venter slightly granular. A large, ovoid gular gland on throat, wider than long (width 6.0 mm, length *c.* 4.7 mm), not heart-shaped, without clear posterior border. First finger with a distinct whitish nuptial pad.

Colour in life (at night) dorsally dirty brownish (Fig. 1). A single yellow-brown dorsolateral band on each side. Shanks and foot also partly yellow-brown. Inguinal region and lateral parts of limbs yellow. Venter white, slightly translucent. Throat yellow, gular gland less brightly coloured than surrounding portion of throat. Fingers and toes ventrally yellow, webbing yellowish. In preservative, back and dorsal surface of legs brown. Dorsolateral stripes faintly recognizable as light brown areas. Ventrally uniformly whitish.

Measurements of holotype. Snout-vent length 26.4 mm; maximum head width 8.5 mm; head

Fig. 2. Holotype of *Heterixalus carbonei* n.sp. (MSNG 49090) from Trano Passage, Antsingy forest.

length measured from snout tip to maxillary commissure 8.0 mm; horizontal tympanum diameter 1.7 mm; horizontal eye diameter 3.7 mm; eye-nostril distance 2.0 mm; nostril-snout tip distance 1.9 mm; forelimb length 17.1 mm; hand length 8.1 mm; hind-limb length 41.3 mm; foot length including tarsus 19.2 mm; foot length 11.0 mm.

Variation. Data on diurnal live colouration are available for a second specimen which was found in 1995 (Fig. 3). This specimen was not preserved, but its calls were recorded (call descriptions herein thus refer to this specimen). Dorsum and flanks were brown. The broad dorsolateral bands were white. The same white colour was also present as a triangular patch on the anterior head, and on fore- and hind limbs. The iris was silvery. Fingers and toes were orange-yellow.

Distribution. Known only from the type locality.

Natural history. The type specimen was collected during the night in subhumid forest while calling on a bush (250 cm above the ground) in dense vegetation close to an exposed pond (surface about 3000 m^2). Calling specimens had already been observed at the same spot in January 1995. No females were observed. At the same pond, calling males of *Heterixalus luteostriatus* were also observed. During the study period, rain was mainly recorded in the late afternoon each day. Air temperature range was 22.7–29.3 °C in 1995 and 22.4–26.2 °C in 1997; relative air humidity was 75–98 % in 1995 and 84–98 % in 1997.

Calls. Recorded 28 January 1995 at the type locality (description referring to calls of the specimen shown in Fig. 3, which was not preserved). Single notes (Fig. 4) that are repeated after regular intervals as a monotonous note series. A second note type was not recorded (but is likely to occur as in other *Heterixalus*). Temporal and spectral call patterns are summarized in Table 1.

Genetic differentiation. DNA sequences of the analysed fragment of the 16S rRNA gene were available for eight *Heterixalus* species: *H. alboguttatus, H. betsileo, H. boettgeri, H. luteostriatus, H. madagascariensis, H. punctatus, H. tricolor* and *H. carbonei.* In a phylogenetic reconstruction of the data (which will be published in more detail elsewhere), *H. carbonei* clustered with *H. betsileo* which can thus most probably be regarded as its sister species. Differences between these two taxa were found at 13 base pairs (2.5 %) which is a similar level of differentiation as found between other *Heterixalus* species: 16–26 bp (3.1–4.8 %) difference between well-differentiated species (*H. betsileo, H. punctatus, H. tricolor*), 2–8 bp (0.4–1.5 %) between the closely related *H. madagascariensis, H. alboguttatus* and *H. boettgeri.*

DISCUSSION

The new species described herein is easily distinguished from all other *Heterixalus* except *H. betsileo* by its call structure. *H. carbonei* shares with *H.*

Fig. 3. Diurnal markings in a male of *Heterixalus carbonei* n.sp. observed in Trano Passage, Antsingy forest, in 1995. This specimen was not preserved, but its calls were recorded, being the basis of the call description in this paper (Fig. 4).

Table 1. Call parameters in *Heterixalus carbonei*, and in different populations of *H. betsileo.* Data are given as minimum-maximum, followed by mean ± standard deviation and sample size (*n*).

	H. carbonei	*H. betsileo* Andasibe	*H. betsileo* Manjakatompo	*H. betsileo* Ranomafana	*H. betsileo* Andringitra
Recording date and time	28. i.1995	9. ii.1996, 20:30	8. i.1994, 21:20	29. ii.1996, 22:10	19.i.1994, 22:30
Recording temperature	22.7–29.3 °C	23 °C	<16 °C	22 °C	18.5 °C
Note duration (ms)	372–395 385 ± 6 *n* = 11	186–225 199 ± 8 *n* = 38	159–270 208 ± 33 *n* = 10	143–175 160 ± 10 *n* = 11	219–266 236 ± 15 *n* = 10
Interval duration (ms)	669–850 756±58 *n* = 9	1092–2226 1380 ± 256 *n* = 36	1914–2319 2075 ± 173 *n* = 4	1100–4022 2237 ± 975 *n* = 9	1212–2940 2155 ± 517 *n* = 9
Note repetition rate (1/s)	0.8/s	0.6	0.5	0.4	0.4
Pulses per note	63–73 70.4 ± 4.2 *n* = 5	36–38 36.9 ± 0.7 *n* = 11	26–48 32.6 ± 6.6 *n* = 11	29–35 32.5 ± 2.2 *n* = 11	40–51 45.8 ± 3.0 *n* = 10
Pulse repetition rate (1/s)	169–190 183 ± 8 n = 5	182	178	197	200
Frequency (Hz)	2300–3750	2700–4000	2550–3800	2700–4550	2500–3500
Dominant frequency (Hz)	2950–3450	3400–3700	—	3000–3200	—

betsileo an advertisement call consisting of single notes arranged in regular series (Glaw & Vences 1993, 1994). A second, longer note type is known in *H. betsileo* (Glaw & Vences 1994) but it is rarely heard and generally not produced in the context of normal advertisement calls. Such a second note type, which may have territorial function in *H. betsileo,* has so far not been recorded in *H. carbonei* but is likely to occur also in this species. All other *Heterixalus* have at least two different note types and (excluding the largely divergent *H. rutenbergi*) are known to combine different note types in their advertisement calls.

H. betsileo, as far as is known, does not occur

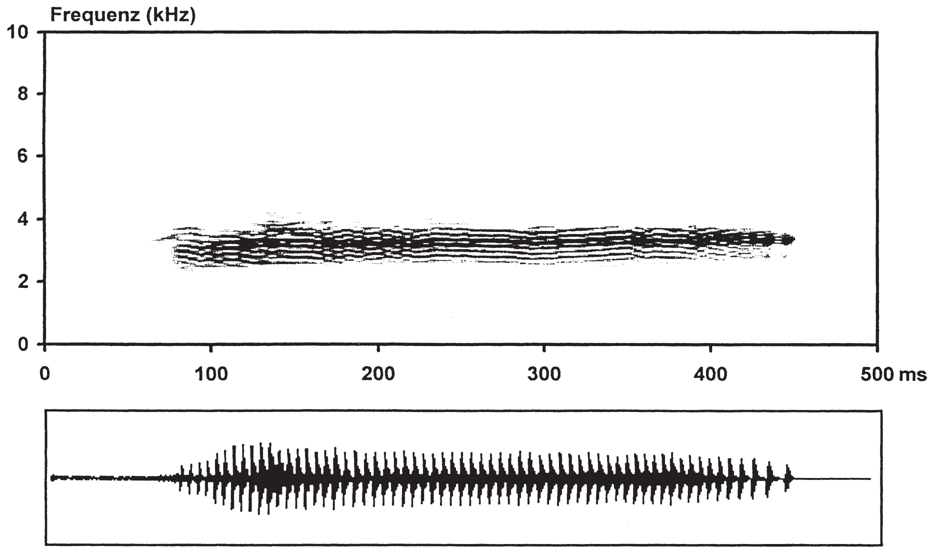

Fig. 4. Sonagram and oscillogram of *Heterixalus carbonei* n.sp. (specimen shown in Fig. 3) from the type locality, recorded on 28 January 1995.

sympatrically with *H. carbonei;* it is distributed in a rather large range in central eastern Madagascar (Blommers-Schlösser & Blanc 1991) and has an isolated population in Montagne d'Ambre in the north (Glaw & Vences 1994); a record from the Marojezy massif (Blommers-Schlösser & Blanc 1991) is in need of confirmation. Calls of *H. betsileo* from six localities were briefly described by Glaw & Vences (1994). We re-analysed recordings from four of these localities; detailed call parameters are summarized in Table 1. Note duration is distinctly lower in all *H. betsileo* calls than in *H. carbonei* (Fig. 5), without range overlap. Differences between both species also exist in the number of pulses per note, interval duration and note repetition rate. The note duration of 500 ms given by Blommers-Schlösser (1982) for *H. betsileo* from Antananarivo was obviously only a rough estimate, measured on the sonagram. In our own recordings from Antananarivo, note duration was 130–165 ms (Glaw & Vences 1994). Calls from the apparently largely isolated population occurring at Montagne d'Ambre in northern Madagascar were also described as having a low note duration of about 230 ms by Glaw & Vences (1994). However, calls from this locality show differences to calls of typical *H. betsileo* as well as to calls of *H. carbonei,* and the taxonomic status of this population therefore requires further study.

In conclusion, populations of *H. betsileo* from central eastern Madagascar (between Andasibe and Andringitra) are remarkably similar in call structure. Beside the mentioned populations, this is also true for the localities Mandraka and Fianarantsoa where we heard very similar calls (Glaw & Vences 1994). The differences between *H. carbonei* and *H. betsileo* can thus not be ascribed to inter- or intrapopulational variation but are clearly indicative of genetically separated species. This is in accordance with the degree of differentiation found in the DNA sequences of the rather conservative 16S rRNA gene of both taxa, which indicates a rather long genetic isolation.

A further difference between *H. carbonei* and *H. betsileo* may regard gular gland shape. According to Blommers-Schlösser (1982) and Glaw & Vences (1994), the gular gland of *H. betsileo* is heart-shaped. This shape is evident in most well-preserved specimens of *H. betsileo* in ZFMK (M. Vences pers. obs.), whereas the gular gland of the *H. carbonei* holotype has a regular ovoid shape. If this difference could be corroborated by further material of *H. carbonei,* it would be a good diagnostic character for the determination of preserved specimens.

Until a few years ago the genus *Heterixalus* (and thus the entire family Hyperoliidae) was thought to be absent from the largest part of western Madagascar (see distribution maps in Duellman & Trueb 1986; Blommers-Schlösser & Blanc 1991). Andreone *et al.* (1994) revalidated *Heterixalus luteostriatus* from the Mahajanga region in the north-

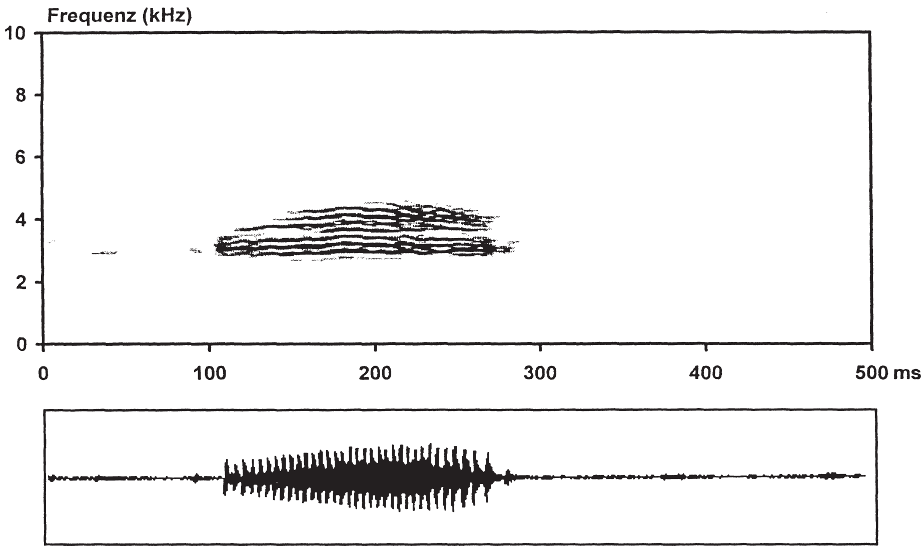

Fig. 5. Sonagram and oscillogram of *Heterixalus betsileo* from Ranomafana, recorded on February 1996 (22:10), at 22 °C air temperature.

west. Glaw & Vences (1994) recorded the species from two western localities (Ranohira and Kirindy). Recently, K. Schmidt and S. Wanke (unpubl. data) discovered a population of a second *Heterixalus* species in the Kirindy forest which can be tentatively assigned to *H. tricolor* by its call structure and the presence of black dots above the eyes. Together with *H. carbonei,* three distinct species of the genus are currently known in arid western Madagascar. These three species are probably endemic to western Madagascar (including the Sanbirano region). This indicates that the importance of this biogeographical region as a centre of diversity and endemism for *Heterixalus* has so far been clearly underestimated, as may be the case in other amphibian genera and groups (e.g. Glaw & Vences 1997).

ACKNOWLEDGEMENTS

We are indebted to Costa Aquarium S.p.A. for the financial support of the expeditions, in particular to Giovanni Battisti Costa, the Director of Acquario di Genova and the staff of the Fish, Reptile and Invertebrate Department, and to Marlène Rakotomalala and Daniel Rakotondravony (Département de Biologie Animale de l'Université d'Antananarivo) for their help in the framework of the Scientific Cooperation Agreement between D.B.A. and Acquario di Genova. We are particularly grateful to Guido Nicosia, Ambassador of Italy in Madagascar, to Pina Alivernini and the entire staff of the Embassy. It would not have been possible to carry out the survey of the Antsingy forest without the invaluable help and advice of Father Arthur Luc (Catholic Mission of Antsalova). The fieldwork was shared with our cameramen Paolo Bistagnino and Giacomo Berichilli, and with Denis Vallan, Herinjato Rakotondrasoa, Felix and William. We also wish to express our gratitude to Kathrin Schmidt and Stefan Wanke (Bonn) who shared with us their observations and call recordings of *Heterixalus tricolor* at Kirindy; to Christian Schäfer, Joachim Kosuch and Michael Veith (Mainz) who contributed to the genetic analyses; to Jaspert Rahajaharison and Celestine Ravaoarinoromanga (Eaux et Forêts, Antananarivo) for their assistance; to Noëline H. Raondry (UNESCO-PNUD, Antananarivo) and Vonjisoa Rasoloarison (Project Bemaraha) for the logistic support in the field; to Roberto Poggi and Giuliano Doria (Museo Civico di Storia Naturale 'Giacomo Doria' of Genoa) and Franco Andreone (Museo Regionale di Scienze Naturali, Torino) who provided the materials for fixing and preserving the specimens; and to Renato Alaimo and Paolo Murri for their support and help. Many thanks also to our sponsors: Telecom Italia, Kodak, Distal ITR, Ferrino, Invicta.

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