New Species of the *Boophis tephraeomystax* Group (Anura: Ranidae: Rhacophorinae) from Arid Western Madagascar

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A new species of rhacophorine frog, Boophis xerophilus sp. nov., is described from deciduous dry forest of western Madagascar. The new species is the only known representative of Boophis that is probably restricted to arid habitats. Males are characterized by a silvery back with distinct dark markings, a blackish throat, and advertisement calls. Lectotypes of Polypedates tephraeomystax Duméril, 1853, and Rhacophorus doulioti Angel, 1934, are designated.

PROGS in the genus Boophis Tschudi, 1838, are endemic to Madagascar. Boophis was divided into seven phenetic species groups by Blommers-Schlösser and Blanc (1991). The Boophis tephraeomystax group currently includes seven predominantly brownish species (Glaw and Vences, 1994; Ohler, 1996): B. tephraeomystax (Duméril, 1853), B. idae (Steindachner, 1867), B. hillenii Blommers-Schlösser, 1979, B. guibei (McCarthy, 1978), B. pauliani (Guibé, 1953), B. opisthodon (Boulenger, 1888), and B. microtis (Guibé, 1974). The latter species may actually belong to the genus Mantidactylus (Glaw and Vences, 1994). Members of the B. tephraeomystax group are distinguished from other Boophis by the combination of very reduced or absent webbing between fingers (Blommers-Schlösser and Blanc, 1991), breeding in shallow, often temporary pools (Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994), small eggs with a blackish animal pole, and a golden or copper iris (except B. guibei) with an indistinct grayish periphery (pers. obs.).

Most Boophis species occur in the eastern rain forest belt. The highest species density was recorded around Andasibe (= Perinet), where 30 Boophis species have been found (pers. obs.). Only B. tephraeomystax was known to occur in the arid parts of western Madagascar (Blommers-Schlösser and Blanc, 1991), but this species is also abundant in the humid east. Herein, we describe a new species of the B. tephraeomystax group which occurs syntopically with B. tephraeo mystax in the extremely dry areas of western and southern Madagascar. The new species is currently the only representative of its genus restricted to this habitat.

MATERIALS AND METHODS

Vocalizations were recorded with a portable Tensai tape recorder (model RCR-3222) and an external microphone (Vivanco EM 238). Tapes

(TDK SA 90) were analyzed with the MEDAV sound analyzing system Spektro 3.2. We took the following morphological measurements with a calliper to the nearest 0.1 mm: SVL (snout-vent length), HW (head width), ED (horizontal eye diameter), END (cyc-nostril distance), NSD (nostril-snout distance), TD (tympanum diameter), TBL (tibia length), FL (foot length). Institutional abbreviations are as listed in Leviton et al. (1985). Webbing formula follows Savage and Heyer (1967) as modified by Myers and Duellman (1982). To facilitate comparisons with other species of Boophis, we also give the formula used by Blommers-Schlösser (1979) and most subsequent authors who published accounts on Madagascan anurans.

Boophis xerophilus sp. nov. Figures 1-2

Holotype.—ZFMK 59987, adult male, collected in the Kirindy forest (20°03'S, 44°39'E; below 100 m above sea level), about 60 km north of Morondava, western Madagascar, on 21 January 1995 by F. Glaw.

Paratypes.—ZFMK 59986, 59988 and 59989, adult males, same locality, date and collector as holotype.

Additional specimens.—Several uncataloged male specimens (same locality, date and collector as holotype) were deposited in the herpetological collection of the University of Antananarivo, Madagascar.

Diagnosis and comparison with other species.—A medium-sized species (males 34.5–38.7 mm SVL) characterized by relatively short hind limbs (tibiotarsal articulation reaches the eye), a rounded snout, distinct brown markings on the dorsum and a black throat (in males). Boophis xerophilus is included in the B. tephraeomystax.



Fig. 1. Boophis xerophilus sp. nov. holotype, dorsolateral view.

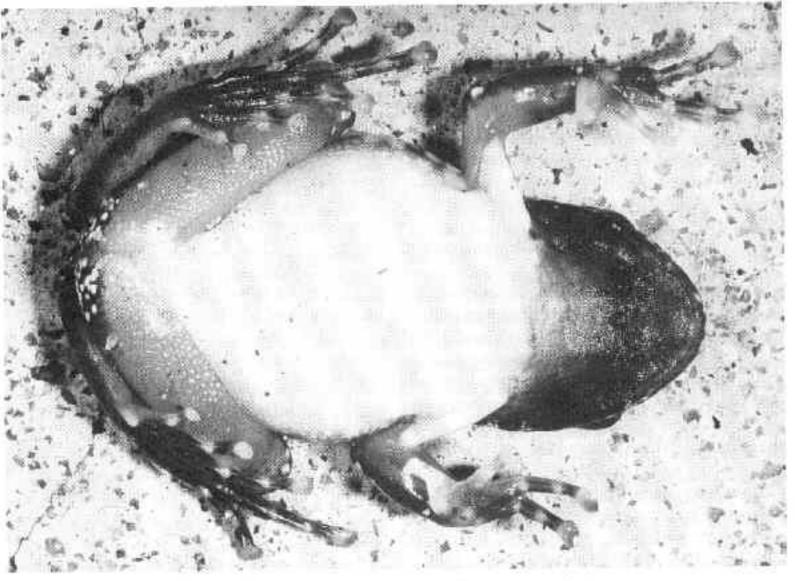


Fig. 2. Boophis xerophilus sp. nov. holotype, ventral view.

group because of the reduced webbing between the fingers, golden iris with indistinct grayish periphery, and breeding habitat. It is distinguished from the other species of the B. tephraeomystax group as follows: from B. opisthodon (SVL of males 52-57 mm) by its smaller size; from B. pauliani (SVL of males 20-23 mm) by its larger size; from B. tephraeomystax by the rounded snout (nostril equidistant from tip of snout and eye in xerophilus, nostrils clearly nearer to tip of snout than to eye in tephraeomystax) and advertisement calls; from B. guibei by less webbing, smoother back, and iris coloration; from B. hillenii by shorter hind limbs and from B. idae by slightly larger SVL and advertisement calls. It differs from all species of the tephraeomystax group by its distinct markings on the back. Boophis idae, B. hillenii, and B. guibei, which are phenetically most similar to B. xerophilus, are only known from the eastern rain forest belt between 800 and 1100 m above sea level (Glaw and Vences, 1994).

Description of holotype.—Body slender, head not broader than body; snout rounded in dorsal and lateral view; nostrils directed laterally, slightly protuberant, equidistant from tip of snout and eye; canthus rostralis weak, slightly concave; loreal region weakly concave; tympanum distinct, medium-sized, rounded, its diameter about half of eye diameter; distinct supratympanic fold; well-developed single subgular vocal sac; tongue ovoid, distinctly bifid posteriorly; vomerine teeth small but distinct; choanae medium-sized, slightly ovoid. Arms slender; subarticular tubercles single; outer metacarpal tubercle rounded, inner metacarpal mbercle elliptical, both weakly developed; fingers with a trace of webbing between second and third finger; finger length 1 < 2 < 4 < 3, finger 4 distinctly longer than 2; well-developed terminal finger disks. Legs moderately robust; tibiotarsal articulation reaches eye; feet with an elliptical inner metatarsal tubercle, no outer metatarsal tubercle; subarticular tubercles single, rounded; toe disks well-developed. Webbing formula of the foot: I 1^+ – 2 II 1^- – 3– III $\bar{2}$ - 3 IV 3- = 1+ V. Webbing formula according to the notation of Blommers-Schlösser (1979): 1(0.5), 2i(1), 2e(0.5), 3i(1.75), 3e(1), 4i(2),4c(1.75), 5(0.5). Lateral metatarsalia not completely separated; toe length 1 < 2 < 3 < 5 <4, toc 5 only slightly longer than 3. Skin on the upper surface smooth, throat and chest smooth, venter and ventral surface of femur granular.

Color of holotype in life.—Dorsum silvery-white with distinct gray-brown markings bordered by

a fine dark line; the markings can be classified in three main figures, which are partly connected and roughly symmetrical on both sides of the vertebral column: one triangle-shaped marking between the eyes, one butterfly-shaped marking in the middle of the back and one irregular marking on the lower back. Tympanum brown; white spots along upper lip; upper surfaces of thigh, tibia and feet silvery-white with dark bars; forcarm silvery-white with dark spots; pupil black, iris golden; belly pure white, throat black, ventral surface of femur pink, ventral sides of the two inner finger tips and the three inner toe tips orange; webbing unpigmented (transparent).

Color of holotype in preservative.—Similar to that in life but grayer and with less contrast; ventral surface of femur faded to yellowish.

Measurements of holotype.—SVL 35.1; HW 13.0; ED 4.1; END 2.7; NSD 3.0; TD 2.3; TBL 16.6; FL 16.0.

Variation.—The distinct markings on the back are present in all four type specimens and were seen in many other specimens from the type locality. In a male specimen from the Berenty park (Glaw and Vences, 1994, fig. 254), the burterfly-shaped marking is broken in the middle of the dorsum and is not connected with other markings. Ventral coloration is very similar to the type specimens from Kirindy. Measurements (range, followed by mean ± standard deviation in parentheses) of the four male types are as follows: SVL 34.5-38.7 (36.6 ± 2.1); HW 12.6-13.9 (13.1 \pm 0.6); ED 3.9-4.3 (4.1 \pm 0.2); END 2.6-3.0 (2.8 ± 0.2); NSD 2.5-3.0 (2.8 ± 0.2); TD 1.7-2.3 (2.0 \pm 0.3); TBL 16.6-17.3 (17.0 \pm 0.4); FL 15.4-16.2 (15.8 ± 0.4). Webbing formula of the foot: I $(1^{-} - 1^{-}) - 2$ II $(1^{-} - 1^{-})$ - 3- III (1 - 2) - (2 - 3) IV 3- - 1- V. Webbing formula according to the notation of Blommers-Schlösser (1979): 1(0-1), 2i(1), 2e(0-0.5), 3i(1.25-1.75), 3e(0.5-1), 4i(1.75-2). 4c(1.5-1.75), 5(0.5-0.75). Tibiotarsal articulation reaches the eye.

Advertisement call.—Vocalizations were recorded on 21 January 1995 at 25 C air temperature. Sonagram and oscillogram of one call are shown in Figure 3. The following data are summarized from calls of several individuals which were separately recorded at the same date and locality. Calls are arranged in series, each call consisting of 1–4 melodious notes. Both short one-note calls and long three- or four-note calls are produced during a single expiration. Usu-

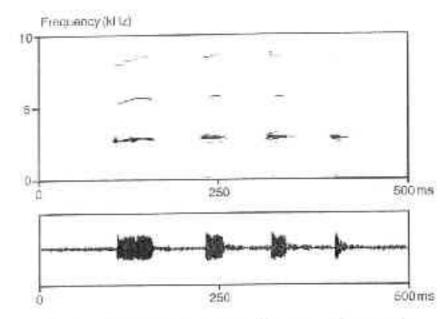


Fig. 3. Sonagram and oscillogram of one advertisement call (with four notes) of *Boophis xerophilus* sp. nov. from Kirindy.

ally calling activity of an individual male starts with series of single-note calls. During the climax of calling, series of three- and four-note calls are emitted. The repetition rate between series of one-note calls (about 2/sec) is much higher than between series of multinote calls (about 1/sec). In 9 of 10 analyzed multinote calls, note duration decreased continuously from the first to the third or fourth note. This decrease is especially evident between the first note (here called the primary note) and the following notes (here called secondary notes). However, the intervals between secondary notes showed no consistent tendency to increase or decrease within a call. Temporal call parameters (in milliseconds) given as range followed by mean ± standard deviation in parentheses are as follows: call duration of one-note calls 26-39 $(33.6 \pm 4.9, n = 16)$; call duration of three-note calls 216-229 (221.8 \pm 5.6, n = 5); call duration of four-note calls 304-316 (308.6 ± 4.7 , n = 5); intervals between one-note calls 365-525 (454.5 \pm 39.1, n = 15); intervals between three- or four-note calls 646-881 (732.4 \pm 79.7, n = 7); duration of primary notes 30-51 (42.2 \pm 6.5, n = 10); duration of secondary notes 13–30 (23.2) \pm 4.2, n = 25); intervals between primary and secondary notes 66-82 (73.2 ± 4.8, n = 10); intervals between secondary notes 57-71 (61.3) \pm 3.7, n = 15). The fundamental and dominant frequency ranged from 2.5-2.9 kHz, two harmonics between 5.5-5.7 and 8.2-8.5 kHz. Calls of B. xerophilus differ from those of B. ûlae and B. tephraeomystax as they were described in Glaw and Vences (1994). Pulsed trills which are known from these two species were not recorded in B. xerophilus. However, the general structure of call series is similar to B. opisthodon (see data in Glaw and Vences, 1994).

Natural history.—Calling males were found only after dusk on 21 January 1995, after heavy rain in the afternoon. They were sitting on the ground several meters from the edges of temporary pools. In contrast to B. tephraeomystax and most other Boophis species, the vocal sac of calling males was always largely inflated during the calls and also during the silent intervals between calls. A photograph, made by T. Hafen in the Kirindy forest, shows a couple in axillary amplexus in water, indicating that the new species may lay its eggs directly in the water, as do all other known species of Boophis. The specimen from the Berenty park (found on 25 February 1991 and originally considered a colormorph of B. tephraeomystax) was observed active at night in dry forest despite extreme aridity (Glaw and Vences, 1992).

We also found the following anuran species in the Kirindy forest: Aglyptodactylus madagascariensis, Aglyptodactylus sp., B. tephraeomystax, Dyscophus insularis, Heterixalus luteostriatus, Mantella betsileo, Ptychadena mascareniensis, Scaphiophryne brevis, S. calcarata, and Tomopterna labrosa. Except for Mantella betsileo, which was only found along a small river, all the other species were observed in close syntopy with B. xerophilus.

Distribution.—The new species is known from Kirindy in western Madagascar (the type locality) and from the Berenty park near Amboasary in southeastern Madagascar, indicating that it is not a local endemic. Both localities are in deciduous dry forest in coastal lowland about 20 km from the sea. For climatic and biogeographical reasons, the Berenty locality probably is not far from the southeastern edge of distribution, whereas the distribution in western Madagascar could reach far north of the Kirindy forest.

Etymology.—Xeros (Greek) = dry, philos (Greek) = friend. The species name refers to the distribution in dry areas.

Designation of lectotypes.—Most available names in the B. tephraeomystax group are represented by holotypes or lectotypes. However, Polypedates tephraeomystax Duméril, 1853, and Rhaeophorus doulioti Angel, 1934, are represented by syntypes. To stabilize the names, we hereby designate lectotypes of both taxa.

In the original description of P. tephraeomystax, Diméril (1853) mentioned three specimens in the Paris collection originating from Madagascar. This seemingly was in agreement with Guibé (1978) and Blommers-Schlösser and Blanc (1991), who indicated MNHN 1660 A and B and 4584 as types. However, Blommers-Schlös-

ser and Blanc (1991) mentioned "Madagascar and Nosy Be" as the type locality, whereas Guibé (1978) mentioned only "Madagascar."

According to the "catalogue des entrées" of the MNHN, three specimens originally had the number 4584. Two of these specimens are still present in the MNHN collection and have the numbers MNHN 4584 and 1994,1040 (formerly 4584A). According to A. Ohler (pers. comm.), MNHN 1660 originally included 4 specimens (origin "Nossibé," collected by Boivin). Three of the four specimens are still held in the MNHN collection. These are MNIIN 1660, MNHN 1994.1041 (formerly 1660A), and MNHN 1994.1042 (formerly 1660B). The fourth specimen of this series is obviously held in the NMW, since Häupl et al. (1994) indicated the existence of one syntype with the comment "NMW 22880 Nossi Bc, Madagaskar; 1870. IV., vom Museum Paris" in the "Naturhistorisches Museum Wien."

According to A. Ohler (pers. comm.), only the two remaining specimens, MNHN 4584 (female) and 1994.1040 (male), can be considered as syntypes. We hereby designate MNHN 1994.1040 as the lectotype of *B. tephraeomystax*. Both lectotype and paralectotype are in a poor condition.

Rhacophorus doulioti is represented by the two syntypes MNHN 1891-356 and -357. Specimen MNHN 1891-356 is hereby designated as lectotype of R. doulioti. The lectotype is in relatively good condition, which allows us to confirm its synonymy with B. tephraeomystax.

Available names in the B. tephraeomystax group.— Several available names in the B. tephraeomystax group are currently considered as junior synonyms of valid species names (Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994). These names need to be considered as possible earlier names for B. xerophilus. Polypedates crossleyi Peters, 1874 (type locality Nosy Vola), Polypedates dispar Boettger, 1879 (type locality Nosy Be), P. disparvar. leucopleura Boettger, 1881 (type locality Nosy Be), Rhacophorus hildrbrandti Ahl, 1925 (type locality NW-Madagascar), and R. doulioti Angel, 1934 (type locality Morondava), are considered to be junior synonyms of B. tephraeomystax (see Blommers-Schlösser and Blanc, 1991; Glaw and Vences, 1994). The holotype of Polypedates crossleyi (ZMB 8216) and the lectotype of P. dispar (SMF 6766), both described from humid localities, are clearly referable to B. tephraeomystax morphologically. The holotype of Polypedates dispar var. leucopleura (UMB, without number) was rediscovered by us in the "Uberseemuseum" at Bremen. The specimen was completely desiccated and could not be positively identified. Our intense surveys at Nosy Be revealed only B. tephraeomystax, confirming that both P. dispar and the variant leucopleura are synonyms of tephraeomystax. The holotype of R. hildebrandti (ZMB 10472) and the types of R. doulioti (MNHN 1891-356 and -357), both described from western Madagascar, were also found to be morphologically referable to B. tephraeomystax.

Three junior synonyms, all described from higher altitudes of eastern Madagascar, also exist for B. idae (Glaw and Vences, 1994): The syntypes of Rhacophorus boulengerii Peracca, 1892 (MZUT AN 90; type locality Andrangoloaka) show distinct white spots on the flanks, typical for B. idae but largely lacking in B. xerophilus. Such spots have also been described by Boulenger (1882) in the original description of Rhacophorus femoralis (type locality East Betsileo). However, examination of the holotype (BMNH 1947.2.27.60) has shown that all characteristic coloration is lost, making a definite attribution to any species uncertain. The white spots on the flanks, the small size of the holotype (27 mm SVL), and the eastern type locality may indicate its synonymy with B. idae. We did not examine the holotype of Rhacophorus catalai (type locality "Ruisscau d'Iorantjatsy," 1000 m altitude, district Fianarantsoa), but according to the original description (Angel, 1934), this taxon has, in comparison with B. xerophilus, shorter hind limbs (tibiotarsal articulation reaching tympanum), more webbing between toes (fully webbed except one phalanx of the fourth toe). and distinct white spots on the flanks, suggesting its synonymy with B. idae.

Guibé (1978) considered Rhacophorus difficilis Boettger, 1892, as junior synonym of B. tephraeomystax (as R. tephraeomystax). Blommers-Schlösser (1979) assigned specimens from Andasibe (central-eastern Madagascar) to B. difficilis. We will discuss the status of this taxon in a forth-coming paper. Here we only state that the holotype of R. difficilis clearly differs from B. xemphilus by smaller size (SVI, 28.7 mm) and head shape (snout not rounded; nostrils nearer to tip of snout than to eye).

DISCUSSION

Species of Madagascan rhacophorine arboreal frogs currently included in the genus *Boophis* were long referred to the genus *Rhacophorus*. Guibé (1978) mainly used external characters of preserved specimens for his classification. He included in *Rhacophorus* oriental species as well as Madagascan species currently assigned to *Boo-*

phis and Mantidactylus. Blommers-Schlösser (1979) first recognized Boophis as a natural unit. mainly using characters related to reproduction. She distinguished Boophis from the oriental Rhacophorus by the lack of foam nests and from Mantidactylus by the presence of nuptial pads in males, amplexus during mating, aquatic egg deposition, and absence of femoral glands. However, the definition of Boophis species groups is still largely based on phenetic external characters. In the meantime, many new species have been discovered, and Boophis is today among the most speciose anuran genera in Madagascar (35 named valid species according to Glaw and Vences, 1994). Our observations indicate that the species inventory is far from complete, and the actual number of species may be double the number currently named. Most (including many undescribed) species can be assigned to existing species groups (Claw and Vences, 1994). They may represent monophyletic units, but thus far no one has attempted a phylogenetic analysis of Boophis.

The B. tephraeomystax group is one of the most heterogeneous species groups within Boophis in external morphology. It includes species as large as 85 mm (B. opisthodon) and as small as 23 mm (B. pauliant). One unidentified species (Boophis sp. c. in Glaw and Vences, 1994) has small dermal flaps on the heels which were previously thought to be found only in the B. goudoti group (Blommers-Schlösser and Blanc, 1991). Nevertheless, the species of the B. tephraeomystax group, except for B. microtis, share a set of morphological characters (iris and iris periphery coloration, reduced webbing between fingers) and a preference for stagnant water bodies as breeding habitat that may indicate close phylogenetic relationships. This character combination was also observed in the new species B. xerophilus.

However, the occurrence of the new species in dry areas of Madagascar is exceptional. Using the classification of reproductive modes by Duellman and Trueb (1986), the genus Boophis displays only the two most generalized ones: mode 1 (eggs and feeding tadpoles in lentic water) is obligatory for the B. tephraromystax group, whereas mode 2 (eggs and feeding tadpoles in lotic water) is found in nearly all other species of Boophis. Judging from observations on calling and breeding activity in and around temporary pools, mode 1 probably occurs in 10 of the 11 anuran species (all except Mantella betsileo) found at Kirindy (91%), suggesting a selective advantage for this mode in arid areas. On the other hand, mode I is less frequent in anuran communities from humid eastern Madagascar,

generally not exceeding 25% (pers. obs.). This suggests that the preference of most *Boophis* for lotic water may reduce their ability to colonize dry areas.

Until now, only *B. tephraeomystax* was known to occur in dry areas. Another species occurring in wetter patches of western Madagascar is *B. erythrodactylus*. The adaptation of this species to running water can be seen in the specialization of the tadpoles (large, adhesive oral disk with three to six rows of papillae and numerous denticle rows) as asserted by Lamotte and Lescure (1989) and Blommers-Schlösser and Blanc (1993). *Boophis erythrodactylus* may be a remnant of a more humid period, when climatic conditions favored wet forest in western Madagascar.

It is remarkable that B. xerophilus and other western anuran and reptile species were not discovered earlier. The anuran community at Kirindy contains two species of Aglyptodactylus and one species of the hyperoliid genus Heterixalus. Heterixalus luteostriatus is even common in cultivated areas (e.g., around pools in the western town of Morondava). Both genera are easy to identify; however, Heterixalus (and therefore the whole family Hyperoliidae) was considered to be absent from most of western Madagascar until a few years ago (see maps in Duellman and Trueb, 1986 and Blommers-Schlösser and Blanc, 1991). The same is true for the genus Aglyptodactylus (see map in Blommers-Schlösser and Blanc, 1991). Recent herpetological discoveries in the Kirindy forest further include two new species of the snake genus Stenophis, one of which (S. citrinus) shows a very striking aposematic pattern of black and yellow bands (Domergue, 1994). Primatologists rediscovered the mouse lemur Microcebus myoximus, which is the smallest primate species in the world (Schmid and Kappeler, 1994). All these recent data show how much still remains to be discovered in Madagascar's western dry deciduous forests, a vegetation type that is even more dramatically endangered than the eastern rain forest (Ganzhorn, 1992).

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LITERATURE CITED

- AHI., E. 1925, Herpetologische Notizen, Zool. Anz. 75:18–20.
- ANGEL, M. F. 1934. Reptiles et batraciens de Madagascar et description d'une espèce nouvelle du genre Rhacophorus, Bull. Mus. Nat. Hist. Nat., Ser. 2, 6: 247-249.
- BLOMMERS-SCHLÖSSER, R. M. A. 1979. Biosystematics of the Malagasy frogs II. The genus *Boophis* (Rhacophoridae). Bijdr. Dierk. 49:261–312.
- ———, AND C. P. BLANC. 1991. Amphibiens (première partie). Faune Madagascar 75:1–379.
- BOETTGER, O. 1879. Die Reptilien und Amphibien von Madagascar. Zweiter Nachtrag. Abh. Senckenb. Nat. Ges. 11:457–497.
- BOUTENGER, G. A. 1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum. British Museum, London.
- ———. 1888. Descriptions of new reptiles and batrachians from Madagascar, Ann. Mag. Nat. Hist., Ser. 6, 1:101–107.
- DOMERGUE, C. A. 1994. Serpents de Madagascar: note liminaire sur des espèces nouvelles du genre Stenophis Boulenger, 1896 (Colubridae-Boiginae). Arch. Inst. Pasteur Madagascar 61:121–122.
- DUELLMAN, W. E., AND L. TRUEB. 1986. Biology of amphibians. McGraw-Hill, New York.
- DUMÉRIL, A. 1853. Mémoire sur les batraciens anoures de la famille des Hylaeformes ou rainettes, comprenant la description d'un genre nouveau et de onze espèces nouvelles. Ann. Sci. Nat. (3, Zool.) 19: 135–179.
- GANZHORN, J. U. 1992. Fallstudie zur integrierten Nutzung von Trockenwäldern, p. 183–190. *In:* Madagaskar—Mensch und Natur im Konflikt. A. Bittner (cd.), Birkhäuser, Basel, Switzerland.
- GLAW, F., AND M. VENCES. 1992. Zur Kenntnis der Gattungen Boophis, Aglyptodactylus und Mantidactylus (Amphibia: Anura) aus Madagaskar, mit Beschreibung einer neuen Art. Bonner Zool, Beitr. 43:45–77.

- GUBÉ, J. 1953. Deux Hyperolius nouveaux pour la fanne malgache (batraciens). Nat. Malgache 5:101–103.
- Bull, Mus. Nat. Hist. Nat., Ser 3, 171:1169–1192.
- ———. 1975. Batraciens nouveaux de Madagascar. Ibid. 323:1081–1089.
- ———. 1978. Les batraciens de Madagascar. Bonn. Zool. Monogr. 11:1–140.
- HÄLPL, M., E. TIEDEMANN, AND H. GRILLITSCH. 1994.
 Katalog der Typen der Herpetologischen Sammlung nach dem Stand vom 1. Jänner 1994. Teil I: Amphibia. Kataloge der wissenschaftlichen Sammlungen des Naturhistorischen Museums in Wien, Vertebrata. Selbstverlag Naturhistorisches Museum 9:1–102.
- LAMOTTE, M., AND J. LESCURE. 1989. Les tétards rhéophiles et hygropétriques de l'ancien et du nouveau monde. Ann. Sci. Nat. Zool. 10:111-122,125-144.
- LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology. Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.
- McCarthy, C. J. 1978. Un nouveau nom pour remplacer Rhacopharus granulosus Guibé, 1975 (Anura, Rhacophoridae). Bull. Mus. Nat. Hist, Nat., Ser. 3, 514:305.
- MYERS, C. W., AND W. E. DUELLMAN. 1982. A new species of Hyla from Cerro Colorado, and other tree frog records and geographical notes from western Panama. Am. Mus. Novit. 2752:1–32.
- OHLER, A. 1996. Valid name and holotype of the Malagasy frog currently known as *Boophis granulusus* (Guibé, 1975) (Amphibia, Anura). Copeia 1996: 1010–1012.
- Peracca, M. G. 1892. Descrizione di nuove specie di Rettili e Anfibi di Madagascar. Boll. Mus. Zool. Anat. Comp. 7:1-5.
- PETERS, W. C., H. 1874. Ueber neue Amphibien. Gesammtsitzung (15. October 1874). Monatsber. Akad. Wiss. Berlin 1874:616–624.
- SAVAGE, J. M., AND W. R. HEMER. 1967. Variation and distribution in the tree frog genus *Phyllomedusa* in Costa Rica, Central America, Beitr. Neotrop. Fauna 5:111–131.
- SCHMID, J., AND P. M. KAPPELER. 1994. Sympatric mouse lemurs (*Microcebus* spp.) in western Madagascar. Folia Primatol. 63:162–170.
- STEINDACHNER, E. 1867. Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859, unter den Befehlen des Commodore B. von Wüllerstorf-Urbair. Zoologischer Theil. Amphibien. Staatsdruckerei, Wien, Austria.
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