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Integrative taxonomy of Malagasy treefrogs: combination of molecular genetics, bioacoustics and comparative morphology reveals twelve additional species of *Boophis*

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Abstract

We describe ten new species of treefrogs assigned to the genus *Boophis* (Anura: Mantellidae) and resurrect two species from synonymy, based on materials collected during fieldwork in Madagascar, carried out mainly between 2000 and 2007. Our comparative database assembled over the past years comprises fresh material for molecular analysis from all 58 nominal *Boophis* species, and advertisement call recordings from all except three species. We follow an integrative approach and combine molecular, bioacoustic and morphological evidence to diagnose the new species. In most cases, the new species have uncorrected molecular divergences of over 4–5% in the mitochondrial 16S rRNA gene to their closest relatives. In some cases the divergences are lower (2–2.5%) but are then accompanied by distinct differences in advertisement calls or morphology. *Boophis piperatus* **sp. nov.** from Ranomafana National Park is a small brown species assigned to the *B. majori* group that is similar to *B. miniatus* but differs in morphology and advertisement calls. *Boophis arcanus* **sp. nov.** is assigned to the *B. majori* group as well and is known from only two female specimens from a site close to Ranomafana; it is described mainly based on its strong genetic differentiation (> 7.2% to all other species). *Boophis entingae* **sp. nov.** is a species of the *Boophis goudoti* group occurring in northern Madagascar, similar to and sympatric with *B. brachychir*, but with a strongly different advertisement call. *Boophis roseipalmatus* **sp. nov.** belongs to the *B. goudoti* group, is similar to *B. madagascariensis*, and appears to replace this species in most of northern Madagascar, with possible areas of sympatry in the north east. *Boophis spinophis* **sp. nov.** is an enigmatic, morphologically highly divergent species from Ranomafana National Park that belongs into the *B. goudoti* group but differs from all other spe-

cies in the group by having distinct dermal tubercles along the lateral parts of the shank and around the elbow. *Boophis praedictus* **sp. nov.** is a sibling species of *B. albilabris* in the *B. albilabris* group, diagnosable by its red iris periphery and distributed in rainforest along the east coast. *Boophis sandrae* **sp. nov.** belongs to the *B. luteus* group and is superficially similar to the sympatric *B. elenae*, but has a faster call and smaller body size. *Boophis miadana* **sp. nov.** and *B. haingana* **sp. nov.**, both in the *B. albipunctatus* group and syntopically occurring at Andohahela National Park, are related to *B. ankaratra* and *B. schuboeae* and differ mainly by their advertisement calls. *Boophis luciae* **sp. nov.**, also in the *B. albipunctatus* group, differs from the sympatric *B. albipunctatus* and *B. sibilans* by having slightly smaller body size and different advertisement calls. We furthermore resurrect *Rhacophorus obscurus* Boettger, 1913 (as *Boophis obscurus* in the *B. goudoti* group) from the synonymy of *Boophis goudoti* as well as *Rhacophorus andrangoloaka* Ahl, 1928 (as *Boophis andrangoloaka* in the *B. microtympanum* group) from the synonymy of *Boophis rhodoscelis*, and propose to consider *Rhacophorus brevirostris* Ahl, 1928 as junior synonym of *Boophis andrangoloaka*. We discuss our integrative methodological approach and the different lines of evidence used to delimitate the species described or resurrected herein. By applying IUCN Redlist criteria, we evaluate the threat status of the species considered: six species are classified Data Deficient (*B. arcanus, B. haingana, B. miadana, B. piperatus, B. praedictus, B. spinophis*), four Vulnerable (*B. andrangoloaka, B. entingae, B. roseipalmatus, B. sandrae*), and two Least Concern (*B. luciae, B. obscurus*).

Key words: Amphibia: Anura: Mantellidae; *Boophis*; cryptic species; DNA barcoding; integrative taxonomy; Madagascar

Introduction

The amphibian fauna of Madagascar is characterized by a high species diversity of currently 250 species of frogs and, especially, by a high degree of endemism which amounts to 100% in native species (Glaw & Vences 2007). Most species belong to the family Mantellidae, and one of the largest mantellid genera is *Boophis* Tschudi, with 58 currently recognized species (Cadle 2003; Glaw & Vences 2007; Vallan *et al.* 2010). *Boophis* are usually arboreal frogs, with the exception of a few montane species that can be more terrestrial in areas where no trees or bushes are found. *Boophis* can be divided in two major clades, one with stream-breeding specialists found mainly in rainforest or montane habitats, and a second with species breeding in ponds that occur in rainforests as well as in arid regions of western and southern Madagascar. Early results indicating that the pond-breeding *Boophis* may not be monophyletic (Vences *et al.* 2002) are contradicted by new analyses based on more extensive sampling of taxa and molecular characters (Glaw & Vences 2006; Glaw *et al.* 2006). Consequently, pond breeders are classified in a separate subgenus, *Sahona* Glaw & Vences, 2006, whereas all other (stream-breeding) species of *Boophis* are classified in the nominal subgenus *Boophis*. This latter subgenus is by far more diverse, and is divided in eight species groups (Glaw & Vences 2006; Wollenberg *et al.* 2008; Köhler *et al.* 2008): the *Boophis albilabris* group, *B. albipunctatus* group, *B. goudoti* group, *B. luteus* group, *B. majori* group, *B. mandraka* group, *B. microtympanum* group, and the *B. ulftunni* group. At least the *B. majori* group is known to be non-monophyletic (e.g., Glaw & Vences 2006; Raharivololoniaina *et al.* 2006; Randrianiaina *et al.* 2009); however, after a number of recent changes (e.g., Glaw & Vences 2006) most of these groups probably do represent clades. Independent from the phylogenetic status of these *Boophis* species groups, they are a very useful tool by subdividing this species-rich genus into manageable units that are then more accessible for taxonomic revision. Each of the groups consists of phenetically similar species assigned to the groups on the basis of combining several morphological characters (even if the defining character states of each group do not necessarily represent synapomorphies).

In general, *Boophis* are very vocal frogs that emit their loud advertisement calls almost exclusively at night. Because bioacoustic evidence has been extensively used in the taxonomy of Malagasy frogs (Köhler *et al.* 2005), and the calls of most *Boophis* are known (Vences *et al.* 2006), the taxonomic knowledge of this group can be considered comparatively well assessed. The available data sets also allow a relatively fast recognition of new, undescribed species, and the possibility of basing species records of many *Boophis* on solely their characteristic calls led to a relatively good knowledge of their distribution (Vences *et al.* 2008).