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## A new microhylid frog, genus *Rhombophryne*, from northeastern Madagascar, and a re-description of *R. serratopalpebrosa* using micro-computed tomography

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### Abstract

The rainforests of the Marojejy massif in northern Madagascar are a well-known hotspot of amphibian species diversity and endemism. In the present paper, we re-describe *Rhombophryne serratopalpebrosa* (Guibé 1975), a cophyline microhylid frog from high altitude on this massif, based on a re-examination of its holotype, and describe *Rhombophryne vaventy* **sp. nov.** using characters of external morphology and osteology, illustrated by pdf-embedded comparative 3D models of their skeletons. *Rhombophryne serratopalpebrosa* differs from *R. vaventy* **sp. nov.** by smaller size (28 mm snout-vent length vs. 52.9 mm), skin texture (granular vs. rough and tubercular skin respectively), supratympanic fold shape (strong, long and straight reaching the eye vs. curved and not extending anteriorly beyond the tympanum), relative tympanum diameter (78% vs. 41% of eye diameter), shape of the postchoanal prevomerine palate, shape of the footplate of the columella, length of prepollex, and by other subtle osteological features. Morphological comparisons suggest that a specimen from Ambolokopatrika assigned to *R. serratopalpebrosa* in previous genetic studies might belong to yet another undescribed species, closely related to *R. vaventy* **sp. nov.**, whereas DNA sequences of the topotypic *R. serratopalpebrosa* remain unknown. We therefore emphasise the need for collecting additional material from high altitudes of the Marojejy massif to understand the systematics, as well as the natural history, of this poorly known species. For the new species described herein, we propose a Red List threat status of Vulnerable, in line with other Marojejy endemics from a similar altitude.

**Key words:** Amphibia, Anura, Microhylidae, *Rhombophryne vaventy* **sp. nov.**, Madagascar, micro-computed tomography

### Introduction

Microhylid frogs are one of the most successful anuran lineages, consisting of more than 500 species distributed broadly across tropical and subtropical regions of the planet (Köhler & Günther 2008; de Sá *et al.* 2012; Frost 2014). Their diversity is unevenly distributed, however; more than half of all known microhylid species are endemic to just two large islands: New Guinea and Madagascar. Three of the eleven currently recognised microhylid subfamilies are endemic to Madagascar: Cophylinae, Dyscophinae, and Scaphiophryninae (Blommers-Schlösser & Blanc 1991). Of these three subfamilies, the Cophylinae are by far the most diverse, consisting of around 50 described species in seven genera (in contrast to the 3 and 11 species of Dyscophinae and Scaphiophryninae respectively, see Raselimanana *et al.* 2014). Several additional candidate species of cophylines have been identified by recent molecular studies (Andreone *et al.* 2005; Wollenberg *et al.* 2008; Vieites *et al.* 2009; Perl *et al.* 2014), and await formal description.

The centre of diversity of the Cophylinae is in the moist north of Madagascar (Wollenberg *et al.* 2008). While several species of cophyline frogs have recently been discovered from arid parts of western Madagascar (Glaw *et al.* 2007; Andreone & Randrianirina 2008; Raselimanana 2013), the majority of species are restricted to rainforests or moist high-altitude areas along the east coast. These frogs exhibit a wide range of habits, from entirely arboreal frogs possessing terminal discs on the phalanges, to terrestrial and fossorial frogs lacking these terminal discs. This

morphological diversity misled early morphological and osteological studies on the systematics of these frogs (e.g., Guibé 1978; Blommers-Schlösser & Blanc 1991), due to the extent of ecomorphological homoplasy (Wollenberg *et al.* 2008). The currently accepted hypotheses on the phylogeny of these frogs are largely derived from analysis of DNA sequences: A cluster of fossorial, leaf-litter dwelling robustly built cophylines, all but one of which were previously included in *Plethodontohyla*, were found to constitute two distinct clades that have apparently converged on the same ecomorphology. This finding resulted in the rearrangement of these two clades between *Plethodontohyla* and *Rhombophryne*, which are not sister taxa, according to their genetic affinities (Andreone *et al.* 2005; Frost *et al.* 2006; Wollenberg *et al.* 2008; Vieites *et al.* 2009).

The diversity of the cophyline frogs has in part been attributed to their breeding mode: As far as is known, all cophyline frogs have endotrophic (non-feeding) tadpoles (Glaw & Vences 2003; Andreone *et al.* 2005), and exhibit some degree of parental care. This may have been a key innovation freeing these frogs from large water bodies, allowing them to inhabit a wider area, adapt to new niches, and diversify.

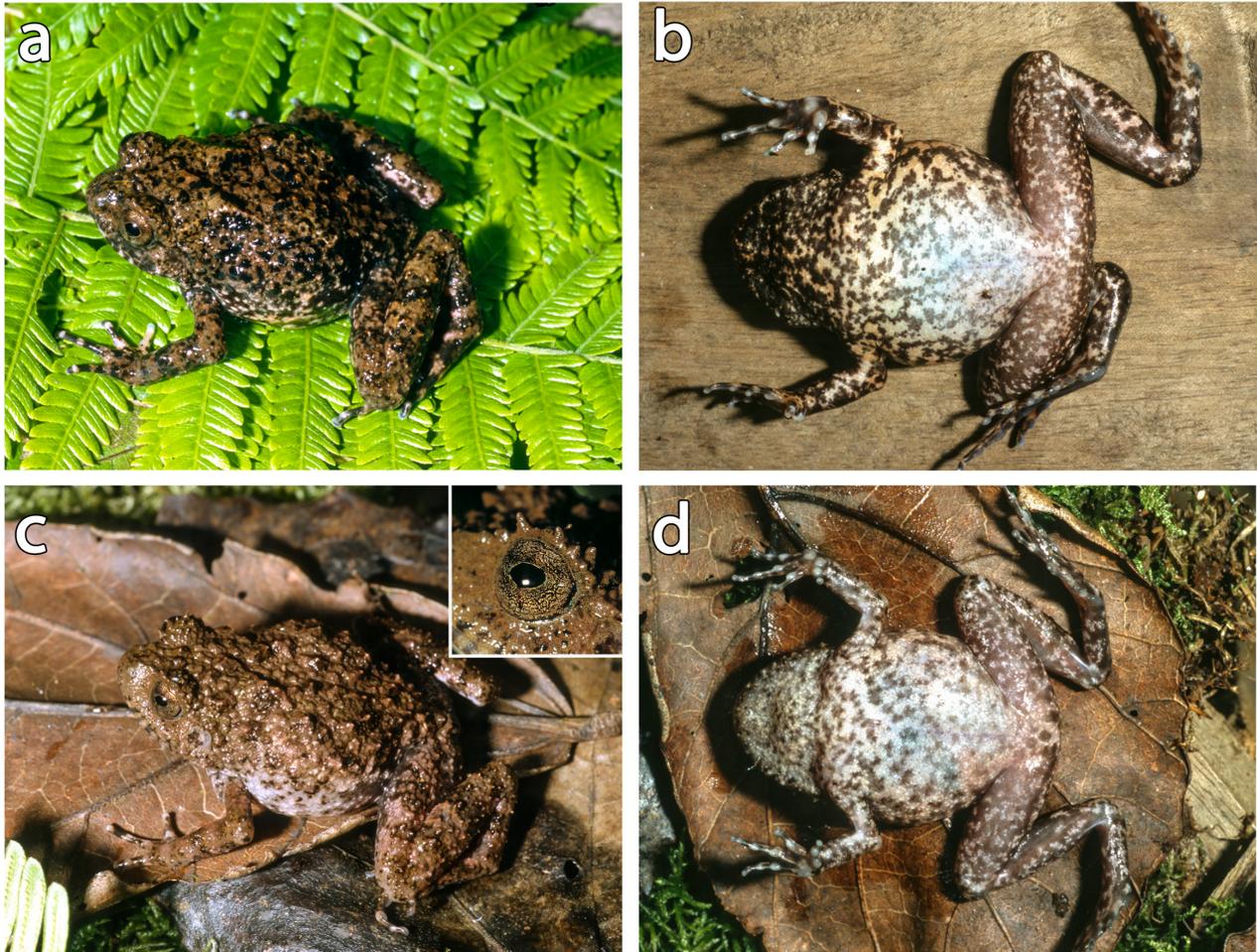
The genus *Rhombophryne* currently consists of 10 nominal terrestrial and fossorial species (Glaw *et al.* 2010; D'Cruze *et al.* 2010): *Rhombophryne alluaudi* (Mocquard), *R. coronata* (Vences & Glaw), *R. coudreau* (Angel), *R. guentherpetersi* (Guibé), *R. laevipes* (Mocquard), *R. mangabensis* Glaw, Köhler & Vences, *R. matavy* D'Cruze, Köhler, Vences & Glaw, *R. minuta* (Guibé), *R. serratopalpebrosa* (Guibé) and *R. testudo* Boettger. Several members of this genus are morphologically quite similar, and differentiation among them based on external characters can be difficult. At least three species, however, differ from all the rest by the possession of soft dermal spines above the eyelids (hereafter termed 'superciliary spines'): *R. coronata* from eastern Madagascar, and two species from the Marojejy massif in northeastern Madagascar (*R. serratopalpebrosa* and the new species described below). Several additional confirmed and suspected candidate species belonging to this complex have been identified (e.g. Perl *et al.* 2014). It was shown by Wollenberg *et al.* (2008) and Vieites *et al.* (2009) that *R. coronata*, *R. vaventy* **sp. nov.**, and a specimen from Ambolokopatrika possibly incorrectly assigned to *R. serratopalpebrosa* (discussed below), probably form a monophyletic group. Unfortunately, no tissue samples or DNA sequences unambiguously assignable to *R. serratopalpebrosa* are yet available and the monophyly of all species possessing superciliary spines still awaits confirmation.

*Rhombophryne serratopalpebrosa* (Guibé, 1975) is a poorly known species, being reliably known only from its holotype. Glaw & Vences (2007) figured two frogs assigned to *R. serratopalpebrosa* and suggested that the larger form might be a new species. In the present work, we re-describe *Rhombophryne serratopalpebrosa* based on a careful re-examination of the holotype, adding additional information pertaining to its skeletal features based on micro-computed tomography (micro-CT) scans, and describe the aforementioned large-sized frog as *R. vaventy* **sp. nov.** (Fig. 1), based on morphological and skeletal differences. We further conclude that it is probable that neither of the individuals figured under the name *R. serratopalpebrosa* in Glaw & Vences (2007) belongs to this species, and emphasise the need to collect additional specimens from the Marojejy massif.

## Material and methods

Specimens were euthanized in a chlorobutanol solution, fixed in 90% ethanol, preserved in 70% ethanol, and deposited in the Zoologische Staatssammlung, München (ZSM) or the Université d'Antananarivo, Département de Biologie Animale, Madagascar (UADBA). The holotype of *Rhombophryne serratopalpebrosa* was loaned from the Muséum Nationale d'Histoire Naturelle, Paris (MNHN). FGZC and ZCMV refer to field numbers of Frank Glaw and Miguel Vences, respectively. MRSN refers to the Museo Regionale di Scienze Naturali, Torino.

Measurements of external morphology were taken with a calliper to the nearest 0.1 mm: SVL (snout-vent length), HW (maximum head width), HL (head length, from the maxillary commissure to the snout tip), ED (horizontal eye diameter), END (eye-nostril distance), NSD (nostril-snout tip distance), NND (internarial distance), TDH (horizontal tympanum diameter), TDV (vertical tympanum diameter), HAL (hand length, from the carpal-metacarpal articulations to the tip of the longest finger), FORL (forelimb length, from the axilla to the tip of the longest finger), HIL (hindlimb length, from the cloaca to the tip of the longest toe), FOL (foot length, from the tarsal-metatarsal articulations to the tip of the longest toe), FOTL (foot length including tarsus, from the tibiotarsal articulation to the tip of the longest toe), TIBL (tibia length), IMCL (maximum length of inner metacarpal tubercle), IMTL (maximum length of the inner metatarsal tubercle).



**FIGURE 1.** Holotype ZSM 357/2005 (FGZC 2876) (a–b) and paratype UADBA uncatalogued (FGZC 2842) (c–d) of *Rhombophryne vaventy* sp. nov. in dorsolateral and ventral views. Inset in c depicts the superciliary spines of the paratype. Note the variance in length of these spines.

For micro-CT scanning the specimens were wrapped in ethanol soaked paper to stabilize them inside the plastic vessels. Scanning was performed with a Nanotom m (phoenix|x-ray, Wunstorf, Germany) cone beam CT scanner at a voltage of 130 kV and a current of 110 mA for 25 (*Rhombophryne vaventy* sp. nov., 2999 projections) and 12 (*R. serratopalpebrosa*, 1440 projections) minutes respectively. Surface meshes of the skeleton were generated using the threshold tool in the segmentation editor of the software Amira 5.4.5 (FEI Visualization Sciences Group, Burlington MA, USA). For varying intensities in the volume data, the threshold was locally adjusted. First the region to be treated separately was transferred into a separate material. After specific adjustment of the threshold for this region, the option “Current material only” was applied for selection.

The PDF 3D models were prepared essentially following the procedures outlined by Ruthensteiner & Heß (2008). These models were examined in Adobe® Reader® XI, and comparative measures of osteological characters were taken using the built-in measurement tool. Osteological terminology follows Duellman & Trueb (1986) and Coloma (2002). Features of the palate are described following Parker (1934). Particular comments are made on the morphology of the columellae (the middle ear bone, also called the stapes), which appear to have diagnostic value in these frogs. These are thin, rod-shaped bones that lie perpendicular to the anteroposterior axis of the body, forming the ossified internal portion of the plectrum, which carries sound waves from the tympanum to the inner ear. They have at their mesial end a footplate, or pars interna, which fills the fenestra ovalis (Duellman & Trueb 1986; Mason & Narins 2002).

## Results

### Species identities and diagnostic differences

Upon examination of ZSM 357/2005 (FGZC 2876), a specimen ascribed to the ‘large form’ of *Rhombophryne serratopalpebroso* by Glaw & Vences (2007), and MNHN 1975.24, the holotype of *R. serratopalpebroso*, we noted differences in body size, the shape of the supratympanic fold, relative tympanum diameter, skin texture, and colouration. Osteological examination of both of these specimens using micro-computed tomography revealed further differences in the shape of the postchoanal prevomerine palate, columella, and nasals, length of the prepollex, breadth order of the transverse processes of the spinal column, and the angle of the medial process of the pterygoid. We therefore consider these two forms to constitute different species.

As a result of our examination of the type material of *R. serratopalpebroso*, the following differences were also noted between this specimen and a photograph of a specimen from Ambolokopatrika (MRSN A4602) which was originally ascribed to *R. serratopalpebroso* (hereafter referred to as *R. sp.* ‘Ambolokopatrika’): the Ambolokopatrika specimen has tubercular dorsal skin, while *R. serratopalpebroso* has roughly granular skin. Additionally, the Ambolokopatrika specimen is dorsally light reddish-brown with two dark dorsal chevrons bordered by yellowish colouration, and, while the holotype of *R. serratopalpebroso* has lost any trace of its natural colour, the colour description by Guibé (1975) suggests a homogeneous brownish dorsal colouration with yellowish lateral speckling, which is absent from *R. sp.* ‘Ambolokopatrika’. However, we were unable to examine the *R. sp.* ‘Ambolokopatrika’ specimen in the present study, so additional work will be required to resolve this issue. Nonetheless, it is important to note that DNA sequences from *R. sp.* ‘Ambolokopatrika’ were used as *R. serratopalpebroso* in the phylogenetic reconstructions of Wollenberg *et al.* (2008), Vieites *et al.* (2009), D’Cruze *et al.* (2010), and Pyron & Wiens (2011), and no topotypic DNA sequences of *R. serratopalpebroso* are known.

Two additional frogs of the genus *Rhombophryne* with superciliary spines occur syntopically on the Tsaratanana massif (Perl *et al.* 2014). These constitute another pair of undescribed species, one, *R. Ca11*, possessing reddish legs with strong dark crossbands and large dark markings on its dorsum and sides (figured in Glaw & Vences 2007, p.118, uppermost fig. ‘5?’), and the other, *R. Ca12* being uniformly brownish. They will be described in an upcoming publication (Scherz *et al.* unpublished manuscript).

### *Rhombophryne serratopalpebroso* (Guibé, 1975)

(Figs. 2–3)

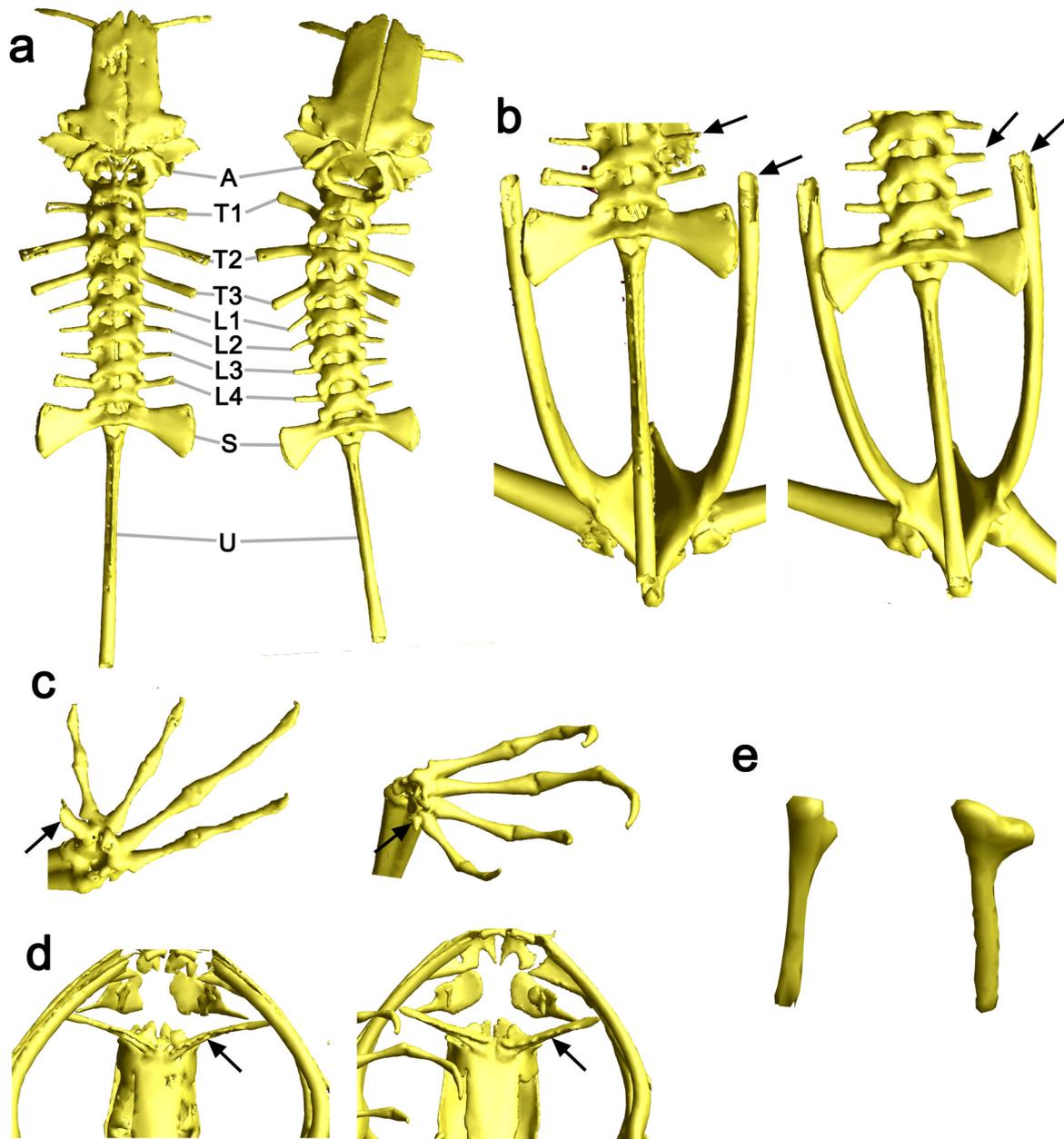
**Remark.** This species was originally described by Guibé (1975) as *Mantipus serratopalpebroso*. This description was reiterated verbatim by Guibé (1978). It was then re-described as *Plethodontohyla serratopalpebroso* based on the holotype by Blommers-Schlösser & Blanc (1991), and then again briefly in Vences & Glaw (2003), and was transferred to *Rhombophryne* by Glaw & Vences (2007).

**Holotype.** MNHN 1975.24, an adult female containing ca. 14 oocytes (as confirmed by soft-tissue micro-CT scan) collected in the scrub at the summit of Marojejy [“dans les fourrés au sommet du Marojézy”] by Charles P. Blanc, 29 November 1972 according to Guibé (1975). The principle peak of the Marojejy massif is at 2132 m above sea level (Goodman 2000). However, according to the catalogue of the Paris museum, the holotype was collected at Massif du Marojezy (1400 m) dans les fourres (Vences & Glaw 2003), indicating substantial uncertainty about the actual altitude of the type locality.

**Diagnosis.** A microhylid frog assigned to the genus *Rhombophryne* on the basis of its lack of enlarged finger discs (vs. presence in several *Plethodontohyla* species), and morphological similarity to *R. coronata* and *R. vaventy sp. nov.*, which have been assigned to *Rhombophryne* on the basis of genetic data (see below). Currently, no diagnostic characters are known in external or internal morphology for the distinction of these two genera (Andreone *et al.* 2005; Wollenberg *et al.* 2008; Glaw *et al.* 2010).

This species is distinguished from all other *Rhombophryne* species and also all *Plethodontohyla* species by the possession of the combination of the following characters: rather small size (female SVL 28 mm), granular dorsal skin, smooth ventral skin, fingers and toes without enlarged terminal discs, second and fourth fingers almost equal in size, fifth toe of nearly equal length to third toe, tibia 47% of SVL, prevomers and vomerine teeth straight, nearly

meeting medially, four (the posterior-most indistinct) evenly-spaced superciliary spines, a strong, almost straight supratympanic fold extending forward to the supraocular region, tympanum 78% of eye diameter, the absence of dorsolateral folds, flanks and thighs brownish with yellow spots, domed columellar footplates (Fig. 2e), and nasals with an anterior and posterior lateral process.



**FIGURE 2.** Comparative osteology of *Rhombophryne vaventy* sp. nov. (ZSM 357/2005, left in all pairs), and *Rhombophryne serratopalpebrosa* (MNHN 1975.24, right in all pairs), scaled to be equal in size; see Supplementary Figure S1 for manipulable model and scale. a: spinal columns in dorsal view (A = Atlas, T = Thoracic Vertebra, L = Lumbar Vertebra, S = Sacrum, U = Urostyle); b: ilia in dorsal view, with arrows indicating the third lumbar vertebrae and anterior-most end of the ilia; c: hands in ventral view, with arrows indicating the prepollex; d: head in ventral view, with arrows indicating the postchoanal prevomerine palate; e: columellae in dorsal view.

Within the genus *Rhombophryne*, *R. serratopalpebrosa* may be distinguished from its congeners by the following characters: from *R. mangabensis* by larger size (28 mm SVL vs. 20–24 mm), and presence of four superciliary spines (vs. absence); from *R. alluaudi* by its smaller size (28 mm vs. 40–60 mm), and presence of four superciliary spines (vs. absence); from *R. testudo* by smaller size (28 mm vs. 33–45 mm), absence of barbels on the lower lip (vs. presence), and presence of four superciliary spines (vs. absence); from *R. coudreaui* by the absence of

webbing between digits (vs. traces of webbing), and presence of four superciliary spines (vs. absence); from *R. guentherpetersi* by absence of porous glandular formation in the latero-dorsal region (vs. presence), and presence of four superciliary spines (vs. absence); from *R. laevipes* by smaller size (28 mm vs. 45–47 mm), granular dorsal skin (vs. smooth), and presence of four superciliary spines (vs. absence); from *R. minuta* by larger size (28 mm vs. 16–22 mm), and presence of four superciliary spines (vs. absence); from *R. matavy* by smaller size (28 mm vs. 39–49 mm), and presence of four superciliary spines (vs. absence); and from *R. coronata* by slightly larger size (28 mm vs. 21–23 mm), presence of a strong, almost straight supratympanic fold extending to the supraocular region (vs. indistinct supratympanic fold), larger relative tympanum size (TDH/ED 78% vs. 59%), and longer relative tibia length (TIBL/SVL 47% vs. 39–41%). For distinction from *R. vaventy* **sp. nov.**, see its diagnosis below.

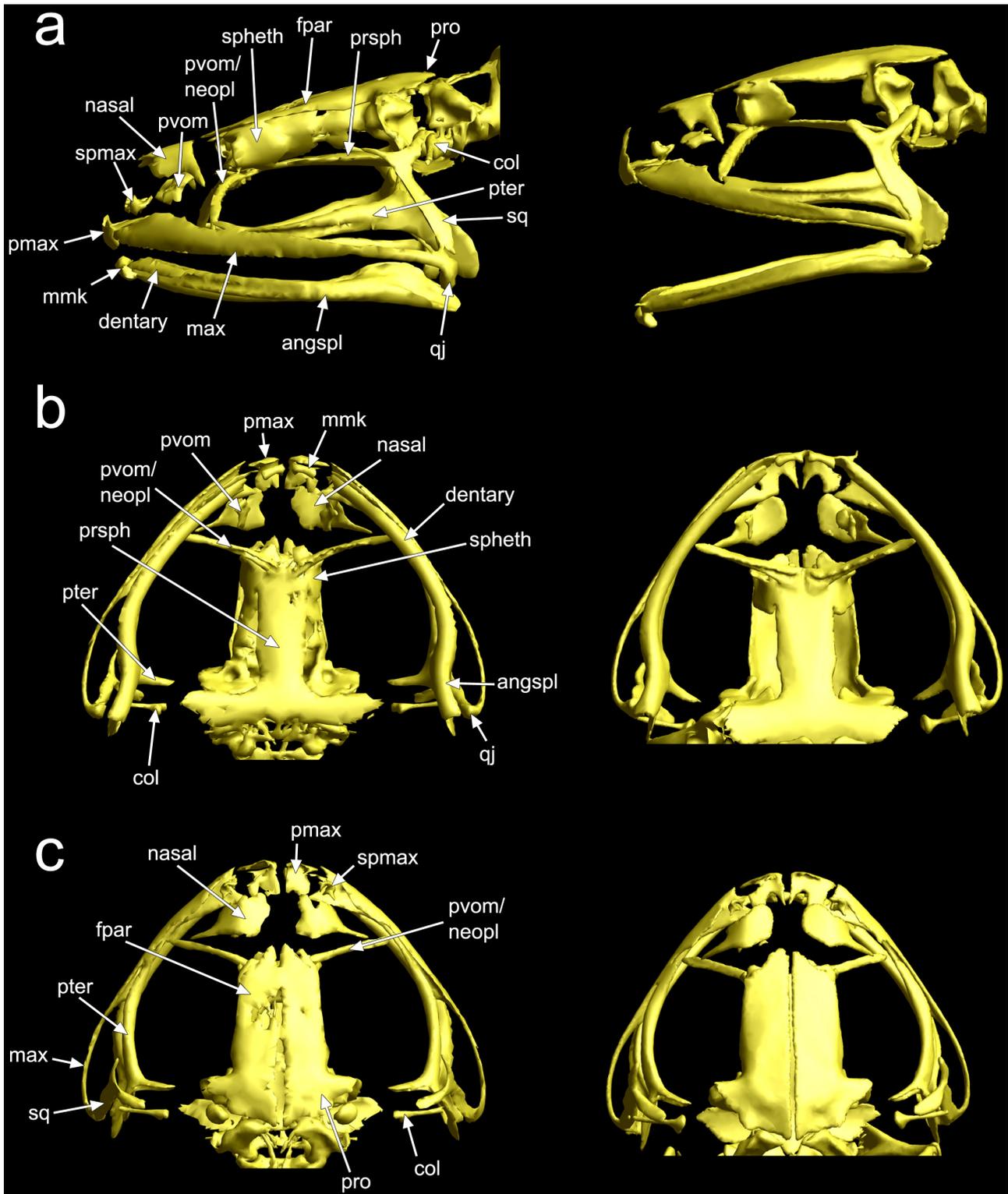
Additionally, due to the morphological similarity of *Plethodontohyla* to *Rhombophryne* we provide differentiation between *R. serratopalpebrosa* and all of the nominal *Plethodontohyla* species: *R. serratopalpebrosa* may be distinguished from all *Plethodontohyla* species by the presence of superciliary spines (vs. absence). Additionally, it may be distinguished from *P. notosticta*, *P. guentheri*, *P. mihanika*, and *P. inguinalis* by the lack of enlarged terminal discs on its digits (vs. presence) and the lack of a sharp border between the dorsal and lateral colouration (vs. presence); from *P. tuberata* by smaller size (28 mm vs. 35–45 mm), and lack of dark dorsal markings (vs. presence); from *P. ocellata* by absence of large black spots bordered with white in the inguinal region (vs. presence); from *P. bipunctata* by absence of dark circular spots in the inguinal region (vs. presence); and from *P. brevipes* by smaller size (28 mm vs. 36 mm).

**Redescription of the holotype.** A specimen in a poor state of preservation. The ventral dermis has been cut open, probably to study character states of the shoulder girdle, and the left lateral region has been cut open, probably to check the sex.

Body robust. Head wider than long. Snout rounded in dorsal view and truncated in lateral view. Canthus rostralis slightly concave. Loreal region weakly concave, with an anterior fold projecting in an S-shape above the nostril. Nostrils not protuberant, directed laterally, equidistant between eye and tip of snout; eye-nostril distance smaller than the internarial distance. Tympanum distinct; oval in shape, width 78% of eye diameter ( $\frac{3}{4}$  according to Blommers-Schlösser & Blanc 1991). A series of four, evenly spaced superciliary spines present above each eye, the posterior-most of which is indistinct and was not noted in any previous description (Guibé 1975, 1978; Blommers-Schlösser & Blanc 1991; Vences & Glaw 2003), and the anterior three of which are distinct. Supratympanic fold strong, almost straight, extending forward to the supraocular region. Vomerine teeth present in two long straight series, almost meeting at the median line. Tongue not notched, but in poor condition.

Arms slender. Fingers without webbing, relative lengths  $1 < 2 \leq 4 < 3$  (2 and 4 are very similar in size, and were described by Guibé [1975, 1978] as being equal in size); without trace of finger-tip enlargement; nuptial pads absent; prepollex not externally visible; inner metacarpal tubercle indistinct; outer metacarpal tubercle indiscernible, although described by Guibé (1975, 1978) as ‘peu marqués’ (weakly evident)—this may be obscured due to the staining of the specimen (see Colouration of the Holotype). Hindlimbs slender; tibiotarsal articulation of the right leg reaches the snout tip, while the left tibiotarsal articulation reaches between the tympanum and the eye. This difference may be due to the bent profile of the specimen, and the incision made on the left side, or the fracture in the left femur, as both legs are equal in length. Nonetheless, which of these tibiotarsal articulations reflects the natural level of articulation is unclear, and this character does not, therefore, feature in the diagnosis above (Note: this feature was described as reaching the snout tip by Guibé 1975, 1978, but as reaching the eye in Blommers-Schlösser & Blanc 1991, Vences & Glaw 2003, and Glaw & Vences 2007). Inner metatarsal tubercle indistinct, outer metatarsal tubercle absent; no webbing between toes; relative toe lengths  $1 < 2 < 5 \leq 3 < 4$  (5 and 3 are very similar in size, and were described by Guibé [1975, 1978] and Blommers-Schlösser & Blanc [1991] as being equal in size). Dorsal skin finely granular, however described by Guibé (1975, 1978) as ‘roughly granular’; texture presumably lost as a consequence of preservation. Dorsolateral folds absent. According to Guibé (1975, 1978), a medio-dorsal fold was present from the tip of the snout to the vent, but this appears to be an artificial character, probably due to strong fixation. Ventral skin completely smooth.

*Measurements:* The holotype measurements (in mm) are: SVL 28.5, HW 12.8, HL 8.6, ED 3.2, END 2.3, NSD 2.4, NND 3.6, TDH 2.5, TDV 2.0, HAL 9.5, FORL 20.3, HIL 50.5, FOL 15.8, FOTL 24.3, TIBL 13.3, IMCL 1.1, IMTL 1.4.



**FIGURE 3.** Comparative skull osteology of *Rhombophryne serratopalpebrosa* (MNHN 1975.24, right in all pairs) and *Rhombophryne vaventy* sp. nov. (ZSM 357/2005, left in all pairs), scaled to be equal in size. a: lateral view; b: ventral view; c: dorsal view. Abbreviations: angspl = angulosplenial, col = columella, fpar = frontoparietal, max = maxillary, mmk = mentomeckelian bone, pmax = premaxilla, pro = prootic, prsph = parasphenoid, pter = pterygoid, pvom = prevomer, pvom/neopl = prevomer/neopalatine (either fused or replaced), qj = quadratojugal, spheth = sphenethmoid, spmax = septomaxilla, sq = squamosal.

*Osteology of the holotype (Figs. 2, 3 and Supplementary Fig. S1):* Skull triangular in dorsal view. Prevomer divided; post-choanal portion long and straight, extending anteroventrolaterally from the sphenethmoid where it nearly meets medially; postchoanal prevomers overlapping, fused with, or replacing the palatine, possessing a serrated ridge along the ventral surface that is here referred to as being ‘vomerine teeth’, although the true dental nature of these teeth is uncertain. Teeth present on maxilla and premaxilla. Premaxilla L-shaped in anterior view, U-shaped in dorsal view; a thick lateral ramus and tapering, pointed medial ramus extend posteriorly from the anterior bone plate. Septomaxilla U-shaped in dorsal view, consisting of a flat anterior plate with one posterior-jutting ramus on its ventromedial edge, and one on its ventrolateral edge; the lateral ramus possesses one medial and one lateral apophysis; the medial apophysis extending medioventrally, almost to the level of the medial ramus in dorsal view. Squamosal broad and Y-shaped. Nasal broad and fairly elliptical, with two lateral projections from its lateral edge, the posterior of which is much longer than the anterior. Columella slender with a slightly domed footplate, reminiscent of a red blood cell (Fig. 2e).

Humerus with just one humeral crista (crista ventralis), beginning 15% from the proximal end of the humerus, and extending to its midpoint. Caput humeri with a distinct, knob-like postero-dorsal apophysis on its distal edge, and a ventral ridge in line with the humeral crista, but not as high (46% of crista ventralis height). Ulna and radius fused. Finger phalangeal formula: 2,2,3,3. Terminal phalanges of fingers 2 and 3 with distal knobs. Prepollex present but small (28% of first metacarpal). Clavicles slim and curved anteriorly, approximately in parallel to the anterior curve of the coracoid. Sternal features not apparent from the scan, and probably not ossified.

The left femur has been fractured 33% of the length from its distal end. Toe phalangeal formula: 2,2,3,4,3. Terminal phalanges of toes 2, 3, 4, and 5 with distal knobs. Iliac long, extending beyond the sacrum, nearly to the level of the transverse processes of the seventh presacral vertebra; iliac shafts almost cylindrical, with a subtle dorsal crest extending most of their length; posteriorly fused synostotically with the ischia and pubes, which are ossified. Ten vertebrae are present: the atlas, three thoracic vertebrae (T), four lumbar vertebrae (L), the sacrum and the urostyle. Urostyle with a dorsal ridge running along its anterior half. Transverse process breadths relative to the breadth of the sacral processes are T1 (99.7%), T2 (116.8%), T3 (94.1%), L1 (72.9%), L2 (68.3%), L3 (69.1%), and L4 (73.0%). Posterior articular processes round.

*Colouration of the holotype:* The specimen has been dyed a bright green, possibly in an attempt to stain it for an unknown reason with an unknown chemical. Unfortunately, this dye has obscured any of the original colour. However, the original description (Guibé 1975) includes the following comments on body colour (translated from the original French): “dorsally brown, with fine black vermiculated dots, somewhat lighter on the dorsal surface of the head. The flanks and thighs are dorsally and posteriorly tobacco-brown in colour, riddled with yellow spots. This colour runs into the dorsal pattern in the inguinal region. Tibia and tarsus dorsally coloured as the back. Ventrally, many fine dark spots on the throat and chest, more loosely obvious on the abdomen and thighs, with small white spots anteriorly, wider posteriorly.”

### ***Rhombophryne vaventy* sp. nov.**

(Figs. 1–3)

*Rhombophryne serratopalpebrosa*—Glaw & Vences 2007: pp. 118–119, Fig. 3a. (depicts the paratype, FGZC 2842)

*Rhombophryne* sp. 4—Wollenberg *et al.* 2008

*Rhombophryne* sp. 6—Vieites *et al.* 2009: Suppl. Material

*Rhombophryne* sp. aff. *serratopalpebrosa*—D’Cruze *et al.* 2010

*Rhombophryne* sp. Ca6 Marojejy—Perl *et al.* 2014: Suppl. Material

**Holotype.** ZSM 357/2005 (FGZC 2876), adult male, collected by F. Glaw, M. Vences, R.D. Randrianiaina on 17 February 2005 at Marojejy National Park, “Camp Simpona”, 14°26.199’S, 49°44.601’E, 1326 m above sea level), northeastern Madagascar.

**Paratype.** UADBA uncatalogued (FGZC 2842), probably adult, sex unknown, collected by F. Glaw, M. Vences, R.D. Randrianiaina on 16 February 2005 at Marojejy National Park, “Camp Simpona”, 14°26.199’S, 49°44.601’E, 1326 m above sea level), northeastern Madagascar. GenBank Accessions Numbers: KF611595, EU341107.

**Diagnosis.** A microhylid frog assigned to the genus *Rhombophryne* on the basis of molecular data (see

discussion below). Currently there are no morphological characters to distinguish between *Rhombophryne* and *Plethodontohyla* (Andreone *et al.* 2005; Wollenberg *et al.* 2008; Glaw *et al.* 2010). This species differs from all other *Rhombophryne* species and from all *Plethodontohyla* species by the combination of the following characters: large size, rough and tubercular dorsal skin, smooth ventral skin, fingers and toes without enlarged terminal discs, tibiotarsal articulation reaching beyond snout tip, second finger shorter than fourth, fifth toe shorter than third toe, a series of four soft superciliary spines, anterior-most two being most distinct, absence of dorsolateral folds, dark colouration beneath chin fading to lighter posteriorly, dorsal brown colouration with distinct black spots arranged almost symmetrically, a series of faint but distinct crossbands on the legs, stepped columellar footplates (Fig. 2e), curved prevomers and vomerine teeth (Fig. 2d), and nasals with a posterior but no anterior lateral process (Fig. 3c). It differs from all other sequenced Malagasy microhylid frogs by a pairwise genetic divergence in its 16S rDNA sequence of  $\geq 6.6\%$ , being most closely related to *R. sp.* ‘Ambolokopatrika’ as discussed above (Vieites *et al.* 2009).

Additionally, *R. vaventy* may be distinguished from its congeners by the following characteristics: from *R. mangabensis* by larger size (53 mm vs. 20–24 mm), tibiotarsal articulation reaching beyond the snout tip (vs. reaching the tympanum), and the presence of four superciliary spines (vs. absence); from *R. alluaudi* by tibiotarsal articulation reaching beyond the snout tip (vs. reaching the tympanum), and the presence of four superciliary spines (vs. absence); from *R. testudo* by larger size (53 mm vs. 33–45 mm), absence of barbels on the lower lip (vs. presence), tibiotarsal articulation reaching beyond the snout tip (vs. reaching the tympanum), and the presence of four superciliary spines (vs. absence); from *R. coudreau* by larger size (53 mm vs. 28 mm), absence of webbing between digits (vs. traces of webbing), tibiotarsal articulation reaching beyond the snout tip (vs. reaching the tympanum), and the presence of four superciliary spines (vs. absence); from *R. guentherpetersi* by larger size (53 mm vs. 32–35 mm), absence of porous glandular formation in the latero-dorsal region (vs. presence), tibiotarsal articulation reaching beyond the snout tip (vs. reaching the eye), and the presence of four superciliary spines (vs. absence); from *R. laevipes* by larger size (53 mm vs. 45–47 mm), granular and tubercular dorsal skin (vs. smooth), tibiotarsal articulation reaching beyond the snout tip (vs. reaching the eye or nostril), and the presence of four superciliary spines (vs. absence); from *R. minuta* by larger size (53 mm vs. 16–22 mm), tibiotarsal articulation reaching beyond the snout tip (vs. reaching the eye), and the presence of four superciliary spines (vs. absence); from *R. matavy* by larger size (53 mm vs. 39–49 mm), tibiotarsal articulation reaching beyond the snout tip (vs. not reaching the insertion of the arms), and the presence of four superciliary spines (vs. absence); from *R. coronata* by much larger size (male SVL 53 mm vs. 21–23 mm), coarsely granular and tubercular dorsal skin (vs. slightly granular), presence of a distinct supratympanic fold (vs. indistinct supratympanic fold), smaller relative tympanum diameter (TDH/ED 41% vs. 51%), tibiotarsal articulation reaching beyond the snout tip (vs. reaching the tympanum), and longer relative tibia length (TIBL/SVL 56% vs. 39–41%).

*Rhombophryne vaventy* may be distinguished from *R. serratopalpebroso* by larger size (53 mm vs. 28 mm), distinct supratympanic fold not extending beyond the anterior edge of the tympanum (vs. strong, almost straight supratympanic fold extending to the supraocular region), presence of almost symmetrical dark dorsal spots (vs. absence), and much smaller relative tympanum size (TDH/ED 41% vs. 78%). Furthermore, the following osteological differences were noticed (Figs. 2 and 3): shape of the columellar footplate (stepped vs. domed), relative length of the prepollex (61% vs. 28% of first metacarpal), relative extension of the ilium (reaching the eighth presacral vertebra vs. reaching the seventh presacral vertebra), lateral processes of the nasal bone (just posterior vs. anterior and posterior), postchoanal prevomerine palate (curved vs. straight), the size order of the breadths of the vertebrae, measured from the tips of the transverse processes ( $L3 < L2 < L4 < L1 < T1 < S < T3 < T2$  vs.  $L2 < L3 < L1 < L4 < T3 < T1 < S < T2$ ; S = Sacrum), shape of the posterior vertebral articulations (slender vs. rounded), ossification of the sternum (present vs. absent), and the angle of the medial process of the pterygoid. However, due to the extremely low number of specimens available (one male of *R. vaventy* and one female of *R. serratopalpebroso*), we cannot exclude that some of these apparently diagnostic features are due to sexual dimorphism, individual variation, or differences in resolution of the CT scans.

*Rhombophryne vaventy* may be distinguished from all species of *Plethodontohyla* by the presence of superciliary spines (vs. absence), and from all *Plethodontohyla* except *P. tuberata* by its roughly tubercular skin (vs. smooth to granular skin). Additionally, it may be distinguished from *P. notosticta*, *P. guentheri*, *P. mihanika*, and *P. inguinalis* by the lack of enlarged terminal discs on its digits (vs. presence) and the lack of a sharp border between the dorsal and lateral colouration (vs. presence); from *P. tuberata* by larger size (53 mm vs. 35–45 mm),

tibiotarsal articulation reaching beyond the snout tip (vs. the insertion of the arms); from *P. ocellata* by absence of large black spots bordered with white in the inguinal region (vs. presence), and tibiotarsal articulation reaching beyond the snout tip (vs. reaching the tympanum); from *P. bipunctata* by larger size (53 mm vs. 25–32 mm), and tibiotarsal articulation reaching beyond the snout tip (vs. reaching the insertion of the arm, the tympanum, or the eye); and from *P. brevipes* by larger size (53 mm vs. 36 mm), and tibiotarsal articulation reaching beyond the snout tip (vs. reaching the insertion of the arms).

**Description of the holotype.** Specimen in a very good state of preservation. A piece of muscle was taken from the right thigh as a tissue sample for genetic analyses. An incision was made in the right flank to check the sex and examine the contents of the intestines.

Body robust. Head wider than long. Pupil very small and roundish. Snout rounded in dorsal and lateral view. Canthus rostralis slightly concave. Loreal region slightly concave. Nostrils closer to tip of snout than to eyes; directed laterally; not protuberant. Eye-nostril distance smaller than the internarial distance. Tympanum distinct, rounded, 41% of eye diameter. A series of four short but distinct soft dermal spines present above each eye, not equally spaced; anterior two most distinct, the third almost imperceptible. Distinct supratympanic fold, curved over and behind the tympanum, not extending anteriorly beyond the tympanum. Vomerine teeth present, curving posteriorly toward the medial line of the palate. Tongue broad and disc-like, without distinct lobes.

Arms stout. Fingers without webbing, relative lengths 1<2<4<3. Fourth finger distinctly longer than second. Finger tips distinct but not enlarged; nuptial pads absent; prepollex not externally visible; inner metacarpal tubercle present; outer metacarpal tubercle absent. Hindlimbs long and muscular; tibiotarsal articulation reaches slightly beyond the snout tip; tibial length 56% of SVL. Large inner metatarsal tubercle present, outer metatarsal tubercle absent; no webbing between toes; relative toe lengths 1<2<5<3<4. Dorsal skin very granular and tubercular, with shallow ridges above the shoulders; ventral skin smooth. No dorsolateral folds.

*Measurements.* The holotype measurements (in mm) are: SVL 52.9, HW 25.05, HL 13.5, ED 7.0, END 4.0, NSD 3.3, NND 5.2, TDH 2.9, TDV 2.8, HAL 16.7, FORL 36.9, HIL 94.5, FOL 29.0, FOTL 42.8, TIBL 29.8, IMCL 3.0, IMTL 4.2.

*Osteology of the holotype (Figs. 2, 3 and Supplementary Fig. S1):* Skull triangular in dorsal view. Prevomer divided, the postchoanal portion long, slightly posteriorly curved, nearly meeting medially, extending anteroventrolaterally from the sphenethmoid; overlapping, fused with, or replacing the palatine; possessing a serrated ventral ridge herein referred to as ‘vomerine teeth’. Teeth are present on the maxilla and premaxilla. Premaxilla without a distinct dorsal ramus visible in anterior view, rounded and without deeply separated rami in dorsal view. Septomaxilla U-shaped in dorsal view, consisting of an anterior plate with a small dorsal apophysis and two posterior-jutting rami, one on its ventromedial edge, and one on its ventrolateral edge; the ventrolateral ramus possessing a medial and a lateral apophysis, the medial apophysis extending ventromedially, toward, but not reaching, the medial ramus of the anterior plate. Squamosal broad, straight, and Y-shaped. Nasal broad and fairly rectangular, with a long process extending posterolaterally from the posterior end of its lateral edge. Columellar footplate with a stepped structure, reminiscent of a flush toilet in ventral view (Fig. 2e).

Humerus with one humeral crista (crista ventralis), beginning 17% from the proximal end of the humerus, and extending to 45% of the way along it. Caput humeri with a distinct postero-dorsal apophysis on its distal edge, arcing distally, and a ventral ridge in line with the humeral crista, but not as high (81% of crista ventralis height). Ulna and radius fused. Finger phalangeal formula 2,2,3,3. Terminal phalanges of all fingers with distal knobs. Prepollex present; 61% of first metacarpal. Clavicles slim and curved anteriorly, approximately in parallel to the anterior curve of the coracoid. Sternum ossified anteriorly.

Toe phalangeal formula: 2,2,3,4,3. Terminal phalanges of all toes with distal knobs. Iliia rather short, extending beyond the sacrum to the level of the transverse process of the eighth presacral vertebra; ilial shafts laterally compressed, not cylindrical; fused synostotically with the ischia and pubes, which are ossified. Ten vertebrae are present: atlas, three thoracic vertebrae (T), four lumbar vertebrae (L), the sacrum and the urostyle. Urostyle possessing a dorsal ridge extending two thirds of the way down its length, beginning at its anterior. Transverse process breadths relative to the breadth of the sacral processes are T1 (89.3%), T2 (118.5%), T3 (102.9%), L1 (80.1%), L2 (71.3%), L3 (70.3%), L4 (76.2%). Posterior articular processes slender.

*Colouration of the holotype:* After almost nine years in preservative, dorsum light brown, with strong black mottling in a nearly symmetrical pattern. Each shoulder has on it a pair of dark oblong markings separated by a light brown bar. Venter dark brown beneath the chin, fading posteriorly to cream mottled with light brown.

Tympanic and supralabial regions are a lighter brown. A series of one distinct and two indistinct crossbands are present on the hindlimbs, which, in sitting position, line up across the thighs, shanks, and feet; two crossbands are present on the lower forelimbs. Feet dorsally strongly mottled white and brown. Hands dorsally white on the inner half, but brown as the rest of the dorsum on the outer. Toes of the left foot have light and dark crossbands, while the right foot is marbled light and dark; fingers of both hands banded, but less distinctly than toes; finger and toe tips light brown. No distinct border between dorsal and ventral colouration; white mottling extends up to the lateral regions. Tympanic region slightly lighter, with faint small dark spots.

In life (Fig. 1), dorsally similar in colouration though a darker brown, with blackish markings strongly distinguished from the background colouration. Dark oblong markings in shoulder region distinct. Iris golden-copper with black vermiculation.

**Variation.** The paratype was not available for this study. However, based on colour photographs of it (Fig. 1), its four superciliary spines are more strongly pronounced than those of the holotype, and it has a more strongly tuberculated dorsum. Its colouration is generally similar to the holotype, with the following notable differences: lighter overall colouration; less distinct black mottling of the dorsum; partially faint dark crossbands on the lower legs, and almost indistinct crossbands on the lower forelimbs; less distinct toe banding; ventrally lighter in colour, especially in the chin region.

**Etymology.** The specific epithet is the Malagasy word ‘vaventy’ which translates as ‘huge’ or ‘enormous’, and refers to the rather large size of the new species in comparison to its congeners (the only comparably sized species is *R. alluaudi*). It is used as a noun in apposition.

**Natural history.** The holotype and paratype were collected in the late afternoon close to dusk on the ground around a local campsite (Camp Simpona). The micro-CT scan revealed a millipede in the stomach of the holotype, which was identified as *Zoosphaerium* sp. by Thomas Wesener (pers. comm. 2013). It is recovered with a similar x-ray absorption to the bone of the frog (Fig. 2), probably due to the presence of both chitin and calcium deposits in its exoskeleton, which is typical for millipedes (Blower 1951). The large intestine contained the remains of at least six ants, a spider, a dipteran, and at least three species of beetle (as judged by the presence of their heads).

## Discussion

The differentiation in morphology and osteology between *Rhombophryne vaventy* and *R. serratopalpebrosa* support the recognition of *R. vaventy* as a new species. However, despite differences in size and colouration, the morphological characters to distinguish them are subtle. There are several instances of strong sexual size dimorphisms in large cophylines, where males are much larger than females (*Platypelis grandis* and *Plethodontohyla inguinalis*). As the *R. serratopalpebrosa* holotype is a female and the *R. vaventy* holotype is a male, it is conceivable that the differences observed between them are a result of sexual dimorphism within the same species. However, we consider this to be highly unlikely, due to (1) the large difference in relative tympanum size (41% of eye in *R. vaventy* vs. 78% of eye in *R. serratopalpebrosa*); under typical sexual dimorphism scenarios, males have a larger relative tympanum size (e.g. known in many species of the genus *Mantidactylus* but not in cophyline microhylids: Blommers-Schlösser & Blanc 1991), but in the present case, the male individual has a smaller relative tympanum size; (2) the much more pronounced and differently-shaped supratympanic fold of *R. serratopalpebrosa* as compared to that of *R. vaventy*; (3) differences in the shape of the postchoanal prevomerine palate; (4) differences in the shape of the columellae (although this may also be sexually dimorphic); (5) differences in the shape of the nasals; and (6) differences in features of the spinal column (breadth order of transverse processes and the shape of the posterior articular processes).

The genetic distinction between *R. vaventy* and *R. serratopalpebrosa* remains unknown. In a molecular phylogeny of Madagascar’s frogs based on a short fragment of the 16S rRNA gene, Vieites *et al.* (2009) placed *R. vaventy* sister to ‘*R. serratopalpebrosa*’ (i.e. *R. sp.* “Ambolokopatrika”), and this clade was placed sister to *R. coronata*. However, as discussed above, the identity of *R. sp.* “Ambolokopatrika” is uncertain; we think it likely that it is a yet undescribed species. Thus, the phylogenetic relationships and the degree of genetic differentiation of *R. serratopalpebrosa* and *R. vaventy* are uncertain.

While both *R. vaventy* and *R. serratopalpebrosa* are known from higher altitudes of the Marojejy massif, there is an altitudinal difference between the known localities of both species (1326 m vs. 1400 or 2132 m a.s.l.) and it

remains to be studied if both species occur allopatrically or partially in sympatry. Although *R. serratopalpebrosa* has allegedly been found in Marojejy between 1225 and 1875 m a.s.l. (Raselimanana *et al.* 2000), Anjanaharibe and Tsaratanana from 1100 to 1600 m a.s.l. (Raxworthy *et al.* 1998), Andringitra at 1625 m a.s.l. (Raxworthy & Nussbaum 1996), and Ambolokopatrika from 860 to 1250 m a.s.l. (Andreone *et al.* 2000), it is now obvious that several different species, similar in morphology, have been attributed to *R. serratopalpebrosa*. Thus the validity of the mentioned records remains highly questionable without a thorough examination of all of the collected specimens. The only known record that can be assigned with high probability to the true *R. serratopalpebrosa* is represented by a photograph taken by C. J. Raxworthy in 2010 (see: <http://scientistatwork.blogs.nytimes.com/2010/05/14/chameleon-fever-but-no-malaria/>). This specimen was identified as *Plethodontohyla* sp., and was found at high altitudes on the Marojejy Massif, corresponding to the region of the type locality. Unfortunately this frog could not be examined for this study, but it shows the strongest known resemblance to both Guibé's (1975) original description and the re-description presented here: it possesses three distinct superciliary spines, a strong, almost straight supratympanic fold extending to the eye, appears to have rough dorsal skin, not as strongly tubercular as *R. vaventy*, and whitish blotches on its flanks. It is most clearly distinguished from *R. vaventy* by the supratympanic fold (extending to the eye vs. not extending anteriorly beyond the tympanum) and the absence of dark dorsal markings.

Despite considerable herpetological survey efforts on the Marojejy massif, both historically and in recent years, no additional specimens of *R. serratopalpebrosa* are known to have been recovered from its type locality. This may be because no survey has ranged to the summit of the massif (Raselimanana *et al.* 2000). These surveys have, however, yielded numerous new frog species around Camp Simpona, several of which have already been described: *Plethodontohyla guentheri* Glaw & Vences, 2007, *Gephyromantis ranjomavo* Glaw & Vences, 2011, *G. tahotra* Glaw, Köhler & Vences, 2011, *Platypelis ravus* Glaw, Köhler & Vences, 2012, and the herein described *R. vaventy*.

The recent description of numerous new cophyline species (Glaw *et al.* 2007, 2010, 2012; D'Cruze *et al.* 2010; Vences *et al.* 2010; Köhler *et al.* 2010; Rakotoarison *et al.* 2012; Klages *et al.* 2013; Ndriantsoa *et al.* 2013; and the present study), identification of many additional undescribed species (Wollenberg *et al.* 2008; Vieites *et al.* 2009; Perl *et al.* 2014), and continued absence of further specimens of *R. serratopalpebrosa*, point toward an improving, but still fundamentally incomplete, knowledge of the microhylid fauna of Madagascar. The knowledge gap is even more extensive concerning the ecology of these frogs. As far as is known, all cophyline frogs have nidicolous, endotrophic (non-feeding) tadpoles, lay their eggs in small burrows, leaf axils, and tree holes, and exhibit some degree of parental care (nest guarding) (Blommers-Schlösser 1975; Blommers-Schlösser & Blanc 1991; Glaw & Vences 2007). The terrestrial and fossorial *Rhombophryne* frogs are highly secretive, with a simplified vocal repertoire (but see Glaw *et al.* 2010), and these features may be responsible for the relatively large proportion of undescribed diversity, and difficulty finding more individuals.

*Rhombophryne vaventy* is known only from the primary forests around Camp Simpona, on the upper slopes of the Marojejy massif, 1326 metres above sea level. The rainforests of Marojejy are heavily threatened by anthropogenic deforestation. We posit that, like much of the cophyline diversity (Wollenberg *et al.* 2008), *R. vaventy* might constitute a microendemic species, and that it is unlikely to be distributed beyond the Marojejy massif (an area of approximately 555 km<sup>2</sup>). Therefore, due to its expected small range of occurrence (<20,000 km<sup>2</sup>), knowledge from only one location (Camp Simpona), probable restriction to rainforest, and the on-going decline in quality of this forest due to slash and burn agriculture and logging, we propose a conservation status of Vulnerable for this species, under IUCN (2012) criteria VU B1ab(iii)+2ab(iii), in line with other Marojejy endemics from a similar altitude (e.g. Glaw & Vences 2011)

It is hoped that the present addition to our knowledge of the cophyline microhylids of Madagascar will facilitate future work on this enigmatic group of frogs. It is clear that availability of micro-CT scanning for rapid, non-invasive examination of skeletal features will also expedite this process, and the process of osteological descriptions of new and old species in general. The comparative presentation of different skeletons in a single pdf-embedded model as shown in the Supplementary Figure S1 allows for direct comparisons of osteological details at high resolution (as exemplified in the derived Figs. 2 & 3) and is therefore a useful novel tool to improve the presentation of anatomical data.

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