A new yellow-toed Platypelis species (Anura, Microhylidae, Cophylinae) from the Maroantsetra region, northeastern Madagascar

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Abstract

We describe a new species of arboreal narrow-mouthed frog, genus Platypelis, from Ambodivoangy near Maroantsetra in northeastern Madagascar. The new species, Platypelis ando sp. nov., is characterised by small body size (under 19 mm), a generally rather slender body, yellowish finger and toe tips, and a dark brown dorsal chevron. Its advertisement call is a single, moderately long, high-pitched whistle repeated at regular intervals. It is the sister species of P. ravus from Marojejy National Park, but differs from that species by considerable pairwise genetic distances (7.9%) in a fragment of the mitochondrial 16S rRNA gene, and also in bioacoustic and morphological features, especially the absence of yellow on the posterior abdomen. It is also surprisingly similar in external appearance to Cophyla occultans and C. maharipeo, to which it is not, however, closely related; these species are most easily discerned based on their calls. Platypelis ando sp. nov. joins the ranks of several species recently described from Ambodivoangy with close affiliations to species in the nearby Marojejy National Park, that are still divergent at species level. The species qualifies as Critically Endangered according to the IUCN Red List criteria, in line with other species recently assessed from this area, but we urge that more research be conducted in the nearby forests to extend the range of this and other species known only from Ambodivoangy.

Key Words

Amphibia
bioacoustics
systematics
taxonomy
morphology
molecular genetics

Introduction

Platypelis Boulenger, 1882 is a genus of arboreal microhylid frogs endemic to Madagascar. They are characterised by expanded terminal discs on the toes and especially the fingers, with T- or Y-shaped terminal phalanges (Guibé 1978, Blommers-Schlösser and Blanc 1991, Scherz et al. 2016, 2017). The taxonomy of the genus has been discussed recently by Scherz et al. (2016, 2017, 2019), Pelo so et al. (2016, 2017), and Tu et al. (2018). While a final resolution of the genus-level taxonomy of this group has not yet been finally achieved, we here tentatively adopt the taxonomy of Scherz et al. (2016, 2017, 2019), supported also by Tu et al. (2018), and consider Platypelis a separate genus from the generally similar but osteologically distinct Cophyla Boettger, 1880 (Rakotoarison et al. 2015, Scherz et al. 2016). As such, we currently consider Platypelis to include 13 described species: P. gran dis (Boulenger, 1889), P. tuberifera (Methuen, 1920), P. cowanii Boulenger, 1882, P. tsaratananaensis Guibé, 1974, P. pollicaris (Boulenger, 1889), P. tetra Andreone, Fenolio & Walvoord, 2003, P. karenae Riahi, Crottini, Noël, Rabibisoa, Raxworthy & Andreone, 2014, P. alticola (Guibé, 1974), P. milloti Guibé, 1950, P. ravus Glaw, Köhler & Vences, 2012, P. mavomavo Andreone, Fenolio & Walvoord, 2003, P. barbouri Noble, 1940, and P. olgae

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A considerable amount of the diversity of *Platypelis* is currently undescribed: Vieites et al. (2009) recognised 10 candidate species within the genus, only two of which have been subsequently described and formally named (Glaw et al. 2012, Rosa et al. 2014). Several additional lineages have subsequently been discovered as well (Rosa et al. 2012, Scherz et al. 2016). Indeed, species discovery within this genus is considerably outstripping the rate of description, which has been low compared to other cophyline genera, e.g. *Stumpfiella* (Köhler et al. 2010, Klages et al. 2013, Ndriantsoa et al. 2013, Glaw et al. 2015, Rakotoarison et al. 2017). In this paper, we describe a new *Platypelis* species from Ambodivoanjo in northeastern Madagascar, known for other recent discoveries of new anuran species (Köhler et al. 2011, 2015, Pabijan et al. 2015, Rakotoarison et al. 2017). This new *Platypelis* species has not been included in any molecular studies, so it has not previously been given a candidate species number.

**Material and methods**

Frog specimens were collected at night by opportunistic searching, using torches and head lamps. Specimens were euthanized by immersion in a solution of chlorobutanol, fixed in 95% ethanol, and preserved in 70% ethanol. Locality information was recorded with GPS receivers (WGS 84 datum). Specimens were deposited in the collection of the Zoologische Staatsammlung München (ZSM) and of the University of Antananarivo, Zoologie et Biodiversité Animale, Madagascar (UADBA), but only ZSM specimens were available for this study. FGZC refers to F. Glaw field numbers, ZFMK is the Zoologisches Forschungsmuseum A. Koenig, Bonn, Germany.

Measurements were taken with a digital calliper to the nearest 0.1 mm by MV. Abbreviations are as follows: SVL, snout-vent length; HW, head width at widest point; HL, head length, measured as the diagonal from the rictus to the anterior-most point of the head; TD, horizontal tympanum diameter; ED, horizontal eye diameter; END, eye-nostril distance (anterior corner of eye to centre of nostril); NSD, nostril-snout tip distance (centre of nostril); NND, nostril-nostril distance (from the centres of the nostrils); FOL, foot length, measured from the axilla to the tip of the longest (third) toe with the forelimb extended; HAL, hand length, measured from the base of the hand to the tip of the third finger; HIL, hindlimb length, measured from the cloaca to the tip of the longest (fourth) toe with the foot extended laterally outward from the body; FOTL, foot and tarsus length, measured from the tibiotarsal articulation to the tip of the longest toe; FOL, foot length, measured from the tarsal-metatarsal articulation to the tip of the longest toe; TBL, tibia length, from the tibiotarsal articulation to the knee.

Vocalizations were recorded in the field using a Tascam DR-07 digital recorder with built-in microphone and saved as uncompressed files at a sampling rate of 44.1 kHz. Recordings were re-sampled at 44.1 kHz and 32-bit resolution and computer-analysed using ADOBE AUDITION 1.5. Frequency information was obtained through Fast Fourier Transformation (FFT; width 1024 points). Spectrograms were obtained at Hanning window function with 256 bands resolution. Temporal measurements are given as mean ± standard deviation with range in parentheses. Terminology in call descriptions follows Köhler et al. (2017).

Tissue samples (tongue or leg muscle) were taken from the euthanized animals before fixation, and preserved in 99% ethanol. We extracted genomic DNA using a standard salt extraction protocol (Bruford et al. 1992). We sequenced a fragment of the 5′ end of the mitochondrial 16S rRNA gene (16S) after amplification with primers 16S3L (AGCAAGAHYWACCTGGATACCTTGTGGCAT) and 16SAH (ATGTTTCTGATAAACAGGGCG) from Vences et al. (2003). Polymerase Chain Reaction (PCR) was as follows: 90 s at 94 °C followed by 33 cycles of 45 s at 94 °C, 45 s at 52 °C, 90 s at 72 °C, and a final extension step of 300 s at 72 °C. PCR products were purified with 0.15 units of Shrimp Alkaline Phosphatase (SAP) together with 1 unit of Exonuclease I (New England Biolabs, Frankfurt am Main, Germany), incubating first for 15 min at 37 °C and subsequently for 15 min at 80 °C. Sequencing was performed on automated DNA sequencers at LGC Genomics (Berlin). We checked and edited chromatograms with CODONCODE ALIGNER 3.7.1 (Codon Code Corporation, Dedham, MA, USA) and submitted newly determined sequences to GenBank (accession numbers MK452342–MK452345).

Sequences were combined with those from previous studies, and alignment performed using the Clustal algorithm in MEGA7 (Kumar et al. 2016). Total alignment length was 633 bp, although due to a multi-C repeat in the middle of the sequences only 301 bp could be sequenced for the focal lineage. For tree-building, the full alignment of 633 bp was used. We calculated a maximum likelihood (ML) tree under a GTR+G+I model (as determined by model testing in MEGA7 based on the Akaike Information Criterion), with 500 full heuristic bootstrap replicates to assess node support. Pairwise distances between sequences (uncorrected p-distances) were calculated in MEGA7, including only sites present in all species (251 positions after full deletion). We compare the genetic divergences of the new species to its closest relatives to other divergences among well-established *Platypelis* species as a measure of its genetic differentiation. The phylogeny we present is intended to be a visual representation...
of genetic divergence of the new species, broadly indicative of genetic distinction of lineages; interpretation of inter-species relationships is tentative, and will need to be reinforced with multi-locus phylogenies in future.

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Results

The phylogenetic tree obtained under the ML optimality criterion (Fig. 1) places the specimens of our focal lineage from Ambodivoaony sister to Platypelis ravus, a species from elevations above 1000 m in the Marojejy Massif in the North East region of Madagascar, with 80% bootstrap support. The clade of the Ambodivoaony lineage and P. ravus is sister to P. milloti, a conspicuous red-bellied species from the North West of the island, and the clade of these three species received 90% bootstrap support. Although the Ambodivoaony specimens morphologically resemble Cophyla occultans, the molecular tree clearly refutes relationships with this species, which is confidently placed in the Cophyla clade (99% bootstrap support).

Genetic divergences of the Ambodivoaony lineage to other Platypelis and Cophyla were high; in the 251 bp available for all species studied here for the fragment of the 5′ end of the 16S rRNA mitochondrial gene studied there was an uncorrected pairwise distance (p-distance) of 7.2% to P. ravus, of 11.2% to P. milloti, and 10.8–25.2% to all other Platypelis and Cophyla species. The lowest divergence of the Ambodivoaony lineage (7.2% to P. ravus) was at similar levels as between pairs of other well-established and morphologically highly distinct species of Platypelis, such as between P. alticola and P. olgae (6.0%), P. alticola and P. tsaratanaaenasenis (4.4%), or Platypelis sp. aff. tetra and P. pollicaris (8.8%). Given its strong genetic distinction and presence of morphological and/or bioacoustic differences from related and similar-looking species, we describe the form from Ambodivoaony as a new species.

Platypelis ando sp. nov.

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Figs 1–4, Table 1

Holotype. ZSM 293/2010 (FGZC 4285), adult male, collected on 3 April 2010 in Ambodivoaony (15.28995, 49.6203, ca. 100 m a.s.l.), Analanjirofo Region, northeastern Madagascar, by P.-S. Gehring, F. Glaw, J. Köhler, M. Pabijan, and F. M. Ratsoavina.

Paratypes. ZSM 291/2010 (FGZC 4200), adult male, and ZSM 292/2010 (FGZC 4226), probably a male, collected on 31 March 2010 from the same locality as the holotype by the same collectors.

Diagnosis. The new species is assigned to the genus Platypelis based on molecular phylogenetic relationships (Fig. 1). Platypelis ando sp. nov. is characterised by the following combination of characters: (1) Small size, with adult male SVL 16.9–18.7 mm; (2) manus with second finger shorter than fourth, pes with fifth toe shorter than third; (3) discs of fingers and toes yellowish to orangish in life; (4) presence of a dark dorsal chevron; (5) presence of dorsal tubercles; (6) short supratympanic dark brown marking; (7) males with prepollical tubercle but lacking a finger-like prepollex as typical for Anodonthyla Müller, 1892.

The new species is distinguished from Platypelis cowanni, P. mavomavo, P. grandis, P. tsaratanaaenasenis, P. pollicaris, P. alticola, P. olgae, P. tuberifera, P. barbouri and P. milloti by considerably smaller size (16.9–18.7 vs >25 mm). Among Platypelis species of similar size, it can be distinguished from P. tetra by its smaller dorsal tubercles, absence of large white spots on the dorsum (vs presence), and presence of a brown chevron-shaped marking on the dorsum (vs absence); and from P. karenae by its brown colouration and dorsal patterning (vs yellow colouration and lack of dorsal patterning), short supratympanic dark brown marking (vs extended along the flank), and less pointed snout. Morphologically and genetically, P. ando sp. nov. most closely resembles P. ravus. It differs from that species in the lack of yellowish colour on its venter (vs present), yellowish to orangish dorsal finger and toe tip colouration (vs brownish), and by a chevron-shaped brown marking on dorsum (vs W-shaped).

From all members of the externally similar Cophyla, except C. occultans and C. sp. ‘fortuna’ (Rakotoarison et al. in press), the new species differs in having a smaller body size (16.9–18.7 mm vs 21.6–33.6 mm). This includes C. maharipelo, which is similar in having yellow or orange finger and toe tips, but is larger in size. From C. occultans, P. ando sp. nov. differs in several call parameters (see below), but is very difficult to distinguish in external morphology, despite clear genetic evidence that these two species are not closely related. From C. sp. ‘fortuna’, it differs in having the fifth toe distinctly shorter than the third (vs slightly longer than the third), and presence of a brown chevron on the dorsum (vs absence). From all members of the genus Anodonthyla, the species can be distinguished by the absence of a distinct finger-like prepollex in males.

The new species differs bioacoustically from other Platypelis species with known advertisement calls as follows: from P. barbouri, P. karenae, P. milloti, P. pollicaris, P. tsaratanaaenasenis, and P. tuberifera by significantly longer call duration (= note duration; single note calls); and in addition from P. barbouri, P. milloti, P. pollicaris, P. ravus, P. tsaratanaaenasenis, and P. tuberifera by sig-
Table 1. Measurement data on *Platypelis ando* sp. nov. All measurements in mm. For abbreviations, see the material and methods. 

<table>
<thead>
<tr>
<th>Voucher</th>
<th>Field no</th>
<th>Sex</th>
<th>SVL</th>
<th>HW</th>
<th>HL</th>
<th>TD</th>
<th>ED</th>
<th>END</th>
<th>NSD</th>
<th>NND</th>
<th>FORL</th>
<th>HAL</th>
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<th>FOTL</th>
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<td>5.2</td>
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<td>1.5</td>
<td>1.2</td>
<td>1.9</td>
<td>10.0</td>
<td>4.4</td>
<td>23.1</td>
<td>10.0</td>
<td>6.0</td>
<td>7.1</td>
</tr>
<tr>
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<td>FGZC 4200</td>
<td>M</td>
<td>16.9</td>
<td>5.1</td>
<td>5.3</td>
<td>NA</td>
<td>2.2</td>
<td>1.6</td>
<td>1.1</td>
<td>1.7</td>
<td>9.3</td>
<td>4.4</td>
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</tr>
<tr>
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<td>FGZC 4226</td>
<td>M?</td>
<td>17.9</td>
<td>5.1</td>
<td>5.0</td>
<td>NA</td>
<td>2.1</td>
<td>1.3</td>
<td>1.2</td>
<td>1.9</td>
<td>10.2</td>
<td>4.4</td>
<td>22.5</td>
<td>10.6</td>
<td>7.0</td>
<td>7.3</td>
</tr>
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</table>

Figure 1. Maximum Likelihood phylogenetic tree of *Platypelis* and *Cophyla*, based on a fragment of the mitochondrial 16S rRNA gene (total alignment length 633 bp, of which 301 bp available for the new taxon). Numbers at nodes are support values in percent from a bootstrap analysis (500 pseudoreplicates). *Madecassophryne* cf. *truebae* was used as the outgroup. *Cophyla* sp. ‘fortuna’ (formerly C. sp. Ca04) is under description by Rakotoarison et al. (in press).

significantly higher dominant frequency (see bioacoustics section below).

Description of the holotype. Adult male in a good state of preservation, tongue taken as tissue sample. Snout-vent length 18.7 mm; for other measurements, see Table 1. Body long and rather round in preservative (more slender in life; see Fig. 2a–b); head slightly wider than long (HW/HL 1.04), snout rounded in dorsal and lateral view; nostrils not protuberant, nearer to tip of snout than to eye; canthus rostralis distinct, concave; loreal region slightly concave; tympanum hidden; supratympanic fold indistinct, starting at the posterior corner of the eye and ending anterior to the insertion of the forelimb, dark in colour; tongue attached anteriorly and was posteriorly free; maxillary teeth present; vomerine teeth not visible or palpable (presence of rudimentary vomerine teeth cannot be excluded and would require osteological examination); choanae diminutive, round. Forelimbs slender; subarticular tubercles small, single; outer metacarpal tubercle not visible, inner metacarpal tubercle distinct, forming a large and distinct protuberance at the base of the first finger; hand without webbing; finger discs distinctly broadly rounded, somewhat truncate, with small lateral fringes; relative length of fingers 1<2<4<3; nuptial pads absent. Hindlimbs slender, tibiotarsal articulation reaching tympanum when hindlimb adpressed along body; tibia length 37.9% of SVL; inner metatarsal tubercle small, oblong; outer metatarsal tubercle absent; webbing between third, fourth, and fifth toes rather well devel-
Figure 2. *Platypelis* specimens in life. (a–b) Holotype (ZSM 293/2010) of *Platypelis ando* sp. nov. in (a) dorsolateral and (b) ventral view; (c–d) paratype of *P. ando* sp. nov. (ZSM 292/2010) in (c) lateral and (d) ventral view; (e–f) holotype (ZSM 349/2005) of *P. rarus* in (e) dorsolateral and (f) ventral view.
oped, webbing formula 1(1) 2i(2) 2e(2) 3i(3) 3e(2) 4i(2.5) 4e(2.5) 5(1); subarticular tubercles on toes indistinct; toes flattened and their discs relatively broad and truncate; relative length of toes 1<2<5<3<4; third toe distinctly shorter than fifth. Dorsal skin smooth, without dorsolateral folds. A very weak mid-dorsal ridge was present in life, but is not evident in preservative. Ventral skin smooth on throat, weakly granular on abdomen and ventral legs.

In life, the holotype was olive brown in dorsal colouration with a slightly green-tinged cream saddle marking on its middle, demarcated posteriorly with a dark brown broken border, and anteriorly bordering a dark brown chevron over the supracapular region that extended to the middle of the eyes, where it stopped abruptly behind an olive-green bar between the eyes (Fig. 2a). The lateral head surface was as the surface of the snout, mottled olive and brown. The same colour was present on the dorsum behind the saddle marking. The dorsal surface of the hindlimbs was a more muted version of this colour, with several dark grey crossbands on each limb segment. The forelimbs were yellowish over the brachium, becoming more orange-tinged distally, with a single, nearly black crossband on the antebrachium and a spot of the same colour on the outer manus. A whitish annulus was present at the base of each terminal phalange. Finger and toe tips were yellowish in colour. Ventrally, it was pale mauve in colour, and the skin was quite transparent, flecked with diminutive cream spots. The digit tips were ventrally also clearly yellow in colouration (Fig. 2b). The iris was gold with black reticulations.

After almost nine years in preservative, the specimen has faded considerably, resulting in the loss of distinction in its pattern (Fig. 3). The body and legs are overall beige, with dark oval markings in the supracapular region, curving over the tympanum, and scattered irregularly over the rest of the dorsum, including some markings in the inguinal region. Faint crossbands on limbs, one of which is distinct on the forearm. A broad, poorly-defined, pale chevron is indistinctly visible on the dorsum.

**Variation.** For variation in measurements, see Table 1. In general, the paratypes agree well with the holotype, but with the following noteworthy differences: The holotype is the plumpest specimen in the type series, with ZSM 291/2010 and ZSM 292/2010 (Fig. 2) being rather slim. In colouration, the holotype is the lightest specimen of the type series in preservative. Its pattern resembles strongly those of ZSM 291/2010 and 292/2010 (Fig. 2). ZSM 292/2010 in life (Fig. 2c–d) apparently possessed a distinctly greenish marking in its inguinal region, of which there are unfortunately no clear photographs. This specimen also had a whiter venter than the holotype.

**Bioacoustics.** The advertisement call recorded on the night of the 3rd of April 2010 in Ambodivoangy (estimated air temperature ca. 25 °C) from the holotype, ZSM 293/2010, consists of a single moderately long, high-pitched tonal whistle, repeated at regular intervals (Fig. 4). Numerical call parameters of 14 calls are as follows: call duration (= note duration) 433 ± 5.8 ms (424–441 ms); inter-call intervals 2655 ± 365 ms (2200–3567 ms); call repetition rate within call series approximately 20 calls/minute; dominant frequency 5402 ± 22 Hz (5380–5432 Hz); prevalent bandwidth 5100–5550 Hz; second frequency band at app. 7800–8200 Hz, and third at 10200–11000 Hz, the latter with the lowest energy of all three recognisable bands. Each note is characterized by a distinct upward modulation of the dominant frequency, starting at around 5250 Hz and increasing up to 5440 Hz before ending with a slight final drop in dominant frequency at around 5300 Hz.

Call comparison: The advertisement call of the sister species *P. ravus* (see Glaw et al. 2012) is rather similar and...
temporal call parameters overlap with those of *P. ando* sp. nov.: call duration 384–443 ms (vs. 424–441 ms); inter-call interval 2504–3200 ms (vs. 2200–3567 ms). However, *P. ravus* has a distinctly lower dominant frequency, with a mean value of 4010 Hz versus 5402 Hz in the new species. Despite the great similarity in structure of the calls of both species, such differences in dominant frequency are barely explainable with the slight differences in body size of calling males (SVL 19.1 versus 18.7 mm) and thus argue for species-specific differences (see Köhler et al. 2017).

Compared to the call of *P. ando* sp. nov., the advertisement calls of other *Platypelis* species differ significantly. The call of *P. tuberifera* is shorter (280 ms) and has a lower dominant frequency of 2300–3000 Hz (Glaw and Vences 1994). The call of *P. barbouri* has significantly shorter duration (160 ms) and is repeated at much longer intervals (3200 ms), with a lower dominant frequency of 3850 Hz (Glaw and Vences 1994). Calls of *P. milloti* are very short (55–65 ms) and exhibit a dominant frequency of approximately 3000 Hz (Glaw and Vences 1994). Calls of *P. pollicaris* from Andasibe have shorter call duration (160–180 ms) and a dominant frequency of about 3000 Hz (Glaw and Vences 1994). The call of *P. tsaratanaanaensis* is very short (79–145 ms duration) at a dominant frequency of 3057–3186 Hz (Rakotoarison et al. 2012), that of *P. karennae* has a duration of 131–145 ms and a dominant frequency 4600–5200 Hz (Rosa et al. 2014). The call of the morphologically similar *Cophyla occultans* from Nosy Be differs by a slightly longer note duration of 500–550 ms and shorter inter-call intervals (1210–1360 ms) at a dominant frequency of approximately 4000 Hz (Glaw and Vences 1994).

**Natural history.** As is typical for *Platypelis* species, calling activity was only heard after dusk. ZSM 291/2010 was found calling 1.8 m above the ground. Nothing further is known about the habits of this species, but based on the reproductive ecology of congeners, it is likely to reproduce in phytotelmata and have endotrophic nidicolous tadpoles.

**Available names.** Only two available synonyms of any *Cophyla* or *Platypelis* refer to small-sized species that could possibly refer to our new species. *Cophyla tuberculata* Ahl, 1929 ‘1928’ is currently a synonym of *P. grandis.* The two syntypes are juveniles according to Blommers-Schlösser and Blanc (1991), but have an SVL of 26 mm, and are therefore larger than the new species. *Paracophyla tuberculata* Millot & Guibé, 1951 is currently considered a synonym of *P. barbouri.* The holotype of that species, MNHN-RA-1957.715, differs from our new species in having a more rugose dorsum, broader finger discs, and a darker venter. Additionally, it is from Périnet (=Analamazaotra) in the Central East of Madagascar, more than 400 km south of Ambodivoangy. Blommers-Schlösser and Blanc (1991) concluded that it is conspecific with *P. barbouri,* and we agree that it is a member of that species complex, which is in need of revision.

**Etymology.** We dedicate this species to our friend and colleague, Dr. Andolalao Rakotoarison, in recognition of her valuable contributions to the systematics and taxonomy of the Malagasy microhylid fauna. The name is to be treated as an invariable noun in the nominative singular.

**Distribution.** The new species is reliably known only from the type locality Ambodivoangy, but the species is likely to be more widespread in low altitude forest of the adjacent Makira Natural Park. Glaw and Vences (1992) found a small *Platypelis* species (assigned to and figured as *P. occultans*) near Voloina (15.5775S, 49.6042S; voucher specimens ZFMK 52777–52779), ca. 30 km south of the type locality with similar calls and morphology, which is possibly conspecific with *Platypelis ando,* but further studies are necessary to confirm its identity.

**Discussion.** The new species, *Platypelis ando,* is genetically, bio-acoustically, morphologically, and chromatically distinct from all other members of the genus *Platypelis* and *Cophyla,* being a small frog with yellow fingers and toes but without yellow on its hindlimbs. It is one of the smallest members of this group, with a maximum size under 20 mm, although currently *P. karennae* remains the smallest member of the genus, with a SVL ranging from 16.1–18.3 mm (Rosa et al. 2014).

*Platypelis ando* occurs at low elevation, ca. 100 m a.s.l., in the rainforest of Ambodivoangy. Its sister species, *P. ravus,* is from considerably higher elevation (ca. 1350 m a.s.l.) on Marojejy. A similar biogeographic pattern has not yet been reported for any other *Platypelis* or *Cophyla,* but is known for another cophyline genus, *Stumpfiella:* three species, *S. fusca* Rakotoarison et al., 2017, *S. pardus* Rakotoarison et al., 2017, and *S. contumelia* Rakotoarison et al., 2017 from Ambodivoangy are also sister to species from Marojejy (*S. achillei* Rakotoarison et al., 2017, *S. diutissima* Rakotoarison et al., 2017, and *S. tridactyla* Guibé, 1975, respectively), and most notably, *S. contumelia* and *S. tridactyla* differ in elevation to the same degree as *P. ando* and *P. ravus,* namely ca. 1200 m in elevation (Rakotoarison et al. 2017, 2019). It therefore provides further support for the biogeographic connection of these areas. Although elevational differences and the resulting differences in biotic and abiotic conditions may have triggered the species-level differentiation of these species pairs, two of them, namely *S. achillei-S. fusca* and *S. pardus-S. diutissima,* do not differ much in elevation. Thus, these pairs may have diverged as a result of previous shifts in range that separated their populations at different elevations, due to isolation by distance, or as a result of ecological differences between their respective localities.

The low-elevation forest of Ambodivoangy is under pressure from anthropogenic habitat destruction, and the current knowledge of *P. ando* from this single location makes it potentially highly threatened, although the type
locality is very close to the border of the Makira reserve, where *P. ando* is likely to occur as well. Despite our considerable uncertainty regarding the full distribution of the species, we follow the rationale applied by Rakotoarison et al. (2017) for species of *Stumpffia* from this area with a similar distribution, and consider the species to qualify as Critically Endangered (reliably known from a single location, with ongoing threats, and a very small currently known range, i.e. IUCN Red List criterion B1ab(iii)), but urge that further survey work be conducted in the forests around the northern end of Makira and western side of Masoala. These areas could potentially yield additional populations of the several amphibian species from Anbo-divoangy that are thought to be highly threatened.

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