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Life in the spray zone – overlooked diversity in West African torrent-frogs (Anura, Odontobatrachidae, *Odontobatrachus*)

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Abstract

West African torrent-frogs of the genus *Odontobatrachus* currently belong to a single species: *Odontobatrachus natator* (Boulenger, 1905). Recently, molecular results and biogeographic separation led to the recognition of five Operational Taxonomic Units (OTUs) thus identifying a species-complex. Based on these insights, morphological analyses on more than 150 adult specimens, covering the entire distribution of the family and all OTUs, were carried out. Despite strong morphological congruence, combinations of morphological characters made the differentiation of OTUs successful and allowed the recognition of five distinct species: *Odontobatrachus natator*, and four species new to science: *Odontobatrachus arndti* **sp. n.**, *O. fouta* **sp. n.**, *O. smithi* **sp. n.** and *O. ziama* **sp. n.** All species occur in parapatry: *Odontobatrachus natator* is known from western Guinea to eastern Liberia, *O. ziama* **sp. n.** from eastern Guinea, *O. smithi* **sp. n.** and *O. fouta* **sp. n.** from western Guinea, *O. arndti* **sp. n.** from the border triangle Guinea-Liberia-Côte d'Ivoire. In addition, for the first time the advertisement call of a West African torrent-frog (*O. arndti* **sp. n.**) is described.

Introduction

For a long time all West African torrent-frogs have been assigned to the genus *Petropedetes* Reichenow, 1874, until their generic distinctiveness from Central African species was revealed by Barej et al. (2014a). Based on molecular and osteological characters Barej et al. (2014b) even placed them in their own family, the Odontobatrachidae, which is endemic to West Africa and the Upper Guinea region.

West African torrent-frogs are nocturnal, inhabit lotic waters and usually occur close to streams with strong currents, cascades or rapids in forested areas. However, Rödel (2003) also collected specimens in gallery forests surrounded by savannah in Mont Sangbé National Park, Côte d'Ivoire. While females are usually found in close proximity to rapids and waterfalls, males may sit on rocky surfaces further away (Rödel 2003). Tadpoles are well adapted to life in torrents. With a dorso-ventrally depressed body and sucker-like mouthparts with enlarged labials, they live attached to rocks in strongest currents or adhere to rock-surfaces in the spray zone. These special mouthparts are only reduced at the very last stages of metamorphosis, which is typical for rheophilous larvae (Lamotte and Zuber-Vogeli 1954; Guibé and Lamotte 1958; Channing et al. 2012). The adult frogs are characterised by a medium to large body length (females reaching > 60 mm snout-urostyle length), the possession of dilated, heart-shaped toe tips, a rough dorsal skin texture with glandular ridges, mandibular fangs in both sexes and femoral glands in males (Boulenger 1905; Barej et al. 2014a). These frogs have a patchy distribution within the Upper Guinea forest region, roughly ranging from western Guinea through Sierra Leone and Liberia to western Côte d'Ivoire (Boulenger 1905; Guibé and Lamotte 1958; Böhme 1994b; Rödel 2003; Rödel et al. 2004a; Hillers and Rödel 2007; Hillers et al. 2008a).

Since the first description, West African torrent-frogs have been regarded as a single species: *Odontobatrachus natator* (Boulenger, 1905). Although inter-population differences in colouration and shape of dorsal glands have been reported (Rödel and Bangoura 2004; Rödel et al. 2004a), this has not resulted in taxonomic actions. Based on molecular data, five distinct lineages (therein treated as Operational Taxonomic Units, OTUs) were recognised in this supposedly monospecific family, indicating hitherto overlooked cryptic species (Barej et al. 2015). All samples from Sierra Leone, the type locality of *O. natator*, are grouped in a single clade which has consequently been assigned to the nominate taxon. Two OTUs occur in the westernmost and two more in the easternmost distribution of the family Odontobatrachidae. While the largest area is occupied by the nominate taxon *O. natator*, OTUs show a tendency to parapatric distribution with little overlap in their potential distribution areas; exceptionally the two western OTUs possess a similar range according to modelled distribution. The recognition of a potential species-complex in the presumably monospecific frog family Odontobatrachidae demonstrated that the current threat classification as "Near Threatened (NT)" (IUCN 2011) is insufficient as recognised OTUs possess very small distribution ranges, demanding a higher threat classification. However, a reassessment of threat categories and subsequent conservation actions require formal description of new species.

We herein present morphological results gathered from more than 150 specimens, covering the entire geographic distribution of the family Odontobatrachidae. Morphological characteristics were analysed and interpreted in combination with the published molecular data and biogeographic insights after Barej et al. (2015). Consequently, we re-describe *Odontobatrachus natator* (Boulenger, 1905), describe four new species, and provide the first call analysis for *Odontobatrachus*.

Material and methods

Species concept and species delimitation

We herein follow the General Lineage Concept of species (de Queiroz 1998, 1999) and accept distinctiveness on species level based on both morphological and genetic data. The genetic data have already been presented by Barej et al. (2015), indicating four undescribed candidate species and their relationships (compare Vieites et al. 2009). OTUs defined by Barej et al. (2015) were the basis of our morphological analyses. Consequently these molecular clades were taken as *a priori* group assignments to ensure understanding of the overall morphological character diversity within and between OTUs. Herein, we accept all five OTUs sensu Barej et al. (2015) and consequently four new species are described in the following. We re-describe the nominate species *Odontobatrachus natator* (blue colour code) and describe OTU1 as *O. ziama* sp. n. (red), OTU2 as *O. smithi* sp. n. (yellow), OTU3 as *O. fouta* sp. n. (green) and OTU4 as *O. arndti* sp. n. (orange). For convenience we will use these names without the suffix sp. n. throughout the manuscript, anticipating their formal description below. Environmental Niche Models (see Barej et al. 2015) confirm the overall distribution pattern of the family. No major range extensions are expected and modelled niches of the individual species are very similar. Interestingly niche similarity identified two groups: *O. smithi* and *O. fouta* in the first and the remaining three taxa in the second. The distribution of all five OTUs and herein recognised species is illustrated in Figure 1.

Morphology

Collected frogs were anesthetized either with chlorobuthanol or benzocaine solutions and thereafter fixed in 4% formalin or 70% ethanol. All voucher specimens have been transferred to 75% ethanol for long-term storage. Abbreviations of museum collections hosting the investigated vouchers are as follows: The Natural History Museum (BMNH), London, United Kingdom; Natural History Museum of Geneva (MHNG), Geneva, Switzerland; Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn and Museum für Naturkunde Berlin (ZMB), Berlin, both Germany.

Measurements follow standard procedures and were taken on preserved material with an electronic dial calliper (± 0.1 mm) by one person (MFB). Webbing formulae are composed as follows: dividing different toes by a '-'

and differentiating inner and outer side of toe by a '/', thus the example 0-0.5/0-1/0-1/1-0 translates to: the webbing reaches the disc at toe I, webbing extends halfway between the most proximate tarsal tubercle to the disc at the external side of toe II and the disc at the internal side of this toe, etc. Tarsal tubercles are counted from tip of the toe to toe base. Additional qualitative characters such as skin granulation were recorded, but not always ascertainable in all vouchers, probably due to different preservation procedures.

Recorded measures comprise: snout–urostyle length (SUL); head width at level of jaw articulation (HW); horizontal orbita diameter (O); interorbital distance (ID); horizontal tympanum diameter (TD); eye–nostril distance (EN); eye–snout distance (ES); length of femur (FM); femoral gland length (GL); femoral gland width (GW); tibiofibula length (TI); foot length without tarsus (FL); inner tarsal tubercle (IT). Additionally, the following ratios have been calculated and analysed: TI/SUL, FM/TI, FL/SUL, GL/FM, GL/GW, HW/SUL, TD/O, FM/SUL, IT/FL, O/EN, ES/O, TD/SUL. Measurements are summarised separately for males (Table 1) and females (Table 2).

Statistical analyses

Potential statistical discrimination of OTUs by morphological data was tested in SPSS 20 and R 3.1.0 (default packages; R Core Team 2013). We only included complete data sets in statistical analyses; damaged specimens or specimens with preservation artefacts were excluded. Furthermore, only measurements of adult frogs were taken into consideration. In order to consider sex-specific characters, e.g. femoral glands (present in males only) or size dimorphism (females growing larger than males), sexes were analysed separately.

Natural Log (ln) transformations were applied on measurements before analysis to obtain a homogeneous data distribution. Principal component analyses (PCA) were performed to explore the overall morphological variation between the putative taxa. Subsequently, we tested for significance of differences between OTUs with non-parametric tests (Kruskal-Wallis H test) since morphological datasets often violated the assumptions of standard parametric statistics and non-parametric tests are generally considered to be more conservative, not relying on assumptions such as random sampling, normality and homogeneity of variance (Anderson 2001). We finally tested for sex-based morphological characteristics within each OTU (Mann-Whitney U test). A Type I error of $p < 5\%$ was chosen to reject the null hypothesis. Sampling of included vouchers per OTU/species was as follows (N_{male}/N_{female}): *Odontobatrachus natator* (22/29), *O. ziama* (11/30), *O. smithi* (3/6), *O. fouta* (3/4) and *O. arndti* (26/24).

Finally, canonical discriminant function analyses (CDA) were performed on ln-transformed mensural variables to test whether our *a priori* groupings could be confirmed. These analyses maximised separations between groups based on within-group variance and correlation. CDA were again implemented on female and male datasets independently. Both the PCA analyses and the CDA were performed separately on absolute values and morphometric ratios.

Advertisement calls

Odontobatrachus call recordings were collected from specimens in terraria (vouchers collected on Nimba Mts., Guinea). Oscillograms (waveforms) and audiospectrograms (sonograms) as results of the Fast Fourier Transformation (FFT; frequency spectrum) were examined for spectral and temporal characters (analysis settings: 44.1 kHz sample ratio, 16 bits resolution, FFT length = 256). Call recordings were analysed with the software package Soundruler v0.9.6 (Gridi-Papp 2007), spectrograms and oscillograms were prepared with the software package Seewave for R (Sueur et al. 2008). Values of call duration, dominant frequency, fundamental frequency and number of notes are presented as minimum and maximum only, because of low numbers of recorded calls.

Genetics

Phylogeographic analyses included samples from the entire family range and were based on mitochondrial (12S, 16S, CYTB) and nuclear (BDNF, SIA, RAG1) genes (Barej et al. 2015). Herein, we present uncorrected 16S p-distances between species from Barej et al. (2015); a table providing inter and intra-species distances is provided in the Appendix 1: Table A. A list of samples gathered in addition to Barej et al. (2015) and respective GenBank numbers are given in Appendix 2: Table B. For laboratory procedures see Barej et al. (2014a).

Conservation status

Following IUCN Red List criteria, Barej et al. (2015) calculated the Extent of Occurrence (EOO) and the Area of Occupancy (AOO) using GeoCat (2011) for *Odontobatrachus natator* and four additional OTUs, herein described as new species. While EOO, often measured by a minimum convex polygon, corresponds to the contained area of a species, AOO refers to the area within the species EOO, excluding cases of unoccupied or unsuitable habitat. According to IUCN regulation, the higher of the two classifications is crucial for assessing global extinction risk.

Results and discussion

All specimens have been assigned to five OTUs *a priori* (OTUs at the putative species level following molecular results in Barej et al. 2015). Phenetic differences of all OTUs were assessed by carrying out a principal component analysis (PCA) on the respective datasets of a total of 65 males and 93 females. Due to the low number of available data points for *O. smithi* and *O. fouta*, placement of their centroids has to be regarded with caution.

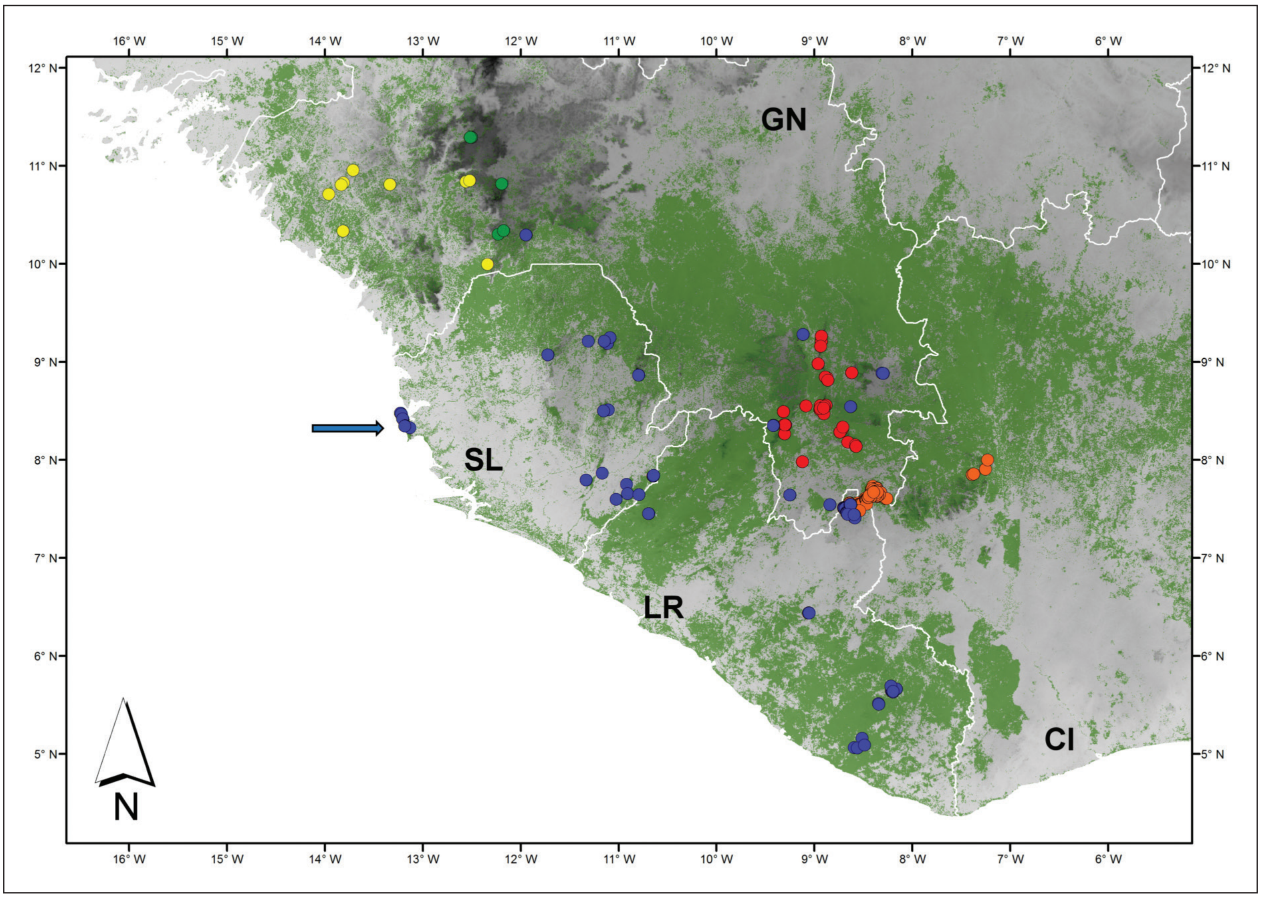

Figure 1. Distribution of *Odontobatrachus* spp. in the western Upper Guinea forest zone (country code: GN = Guinea, SL = Sierra Leone, LR = Liberia, CI = Côte d'Ivoire). The map shows forest cover (Arino et al. 2012; green shading) and elevation (increasing from light to dark grey). The arrow indicates the restricted type locality of *O. natator*. Colour code reads as follows: blue = *O. natator*, red = *O. ziama* sp. n., yellow = *O. smithi* sp. n., green = *O. fouta* sp. n., orange = *O. arndti* sp. n.

PCA results of absolute values in male *Odontobatrachus* (Fig. 2a) revealed that GL and GW contributed most to axis 1 and axis 1 accounted for 52.84% of the total variance. Axis 2 contributed an additional 23.23%, summing up to a total of more than 75% of the variance explained (Table 3). Axis 2 consisted mostly of contributions by EN, TD and GW. All contributors to axes 1 and 2 in the analysis of absolute values in males are given in Table 3. Axis 3 increased the total explained variance by only 6.60% (contributors not shown). The centroid of *O. ziama* was separated from those of *O. natator* and *O. smithi* on the second axis and from that of *O. arndti* by the first axis. Centroids of *O. ziama* and *O. fouta* were separated on both axes. The centroid of *O. smithi* was separated from that of *O. fouta* on the second axis and from that of *O. arndti* on both axes. The centroid of *O. fouta* was separated from those of *O. natator* and *O. smithi* on the second axis and from that of *O. arndti* on the first axis. Centroids of *O. fouta* and *O. arndti* were separated on the second axis. Centroids of *O. arndti* and *O. natator* were separated on both axes (Fig. 2a).

PCA results of morphometric ratios in male *Odontobatrachus* (Fig. 2b) revealed that main contributors to axis 1 were GL/FM, OD/EN, TD/OD and TD/SUL and axis 1 accounted for 41.28% of the total variance. Axis 2 contributed an additional 17.06%, summing up to a total of 58.35% of the variance explained (Table 4). The loading of this axis was mostly made up of contributions by GL/FM and TD/SUL. All contributors to axes 1 and 2 in the analysis of morphometric ratios in males are given in Table 4. Axis 3 explained an additional 13.44% of the variance (contributors not shown). The centroid of *O. ziama* from was separated from those of *O. natator*, *O. smithi* and *O. fouta* on the first axis and from that of *O. arndti* on the second axis. The centroid of *O. arndti* was separated from those of *O. natator*, *O. smithi* and *O. fouta* on both axes. Individuals of *O. natator*, *O. smithi* and *O. fouta* strongly overlapped in this plot (Fig. 2b).

PCA results of absolute values in female *Odontobatrachus* (Fig. 2c) revealed that IT and TD contributed mostly to axis 1 and axis 1 accounted for 59.02% of the total variance. Axis 2 contributed an additional

Table 1. Summary of morphological measures (in mm) of adult male *Odontobatrachus* species. Minimum (min), maximum (max), mean values (mean), standard deviation (SD) and number of included vouchers (N) are given. Measurements of holotypes are provided separately. For abbreviations see material and methods section.

Taxon		SUL	HW	FM	GL	GW	TI	FL	IT	TD	O	ID	EN	ES	TI/SUL	FM/TI	FL/SUL	GL/FM	GL/GW	HW/SUL	TD/O	FM/SUL	IT/FL	O/EN	ES/O	TD/SUL
O. natator	min	42.6	16.1	21.9	8.7	4.0	23.3	19.6	2.8	2.4	6.1	4.6	3.2	5.9	0.49	0.91	0.42	0.36	1.71	0.34	0.33	0.47	0.14	1.55	0.84	0.05
	max	52.5	19.0	25.5	13.7	7.4	26.8	23.1	4.3	3.1	7.5	5.9	4.1	6.8	0.57	1.02	0.51	0.56	2.32	0.39	0.47	0.54	0.20	2.06	1.03	0.06
	mean	48.0	17.3	23.8	10.9	5.6	24.8	21.4	3.6	2.7	6.8	5.2	3.7	6.2	0.52	0.96	0.45	0.46	1.96	0.36	0.40	0.50	0.17	1.82	0.92	0.06
	SD	2.2	0.8	1.0	1.3	0.8	1.1	0.9	0.4	0.2	0.4	0.3	0.2	0.2	0.02	0.03	0.02	0.06	0.16	0.01	0.04	0.02	0.02	0.11	0.05	0.00
	N	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23
O. ziama sp. n.	ZMB 78300 (holotype)	46.1	15.5	24.1	12.8	7.6	24.4	21.4	3.7	2.4	6.5	5.2	3.3	6.4	0.53	0.99	0.46	0.53	1.69	0.34	0.37	0.52	0.17	2.00	0.98	0.05
	min	43.0	15.0	19.6	7.5	4.7	22.4	19.0	2.4	1.8	6.3	4.0	2.7	5.3	0.49	0.86	0.42	0.38	1.60	0.34	0.27	0.45	0.12	1.95	0.84	0.04
	max	50.3	17.5	24.9	13.7	7.7	24.8	23.2	3.9	2.7	7.1	5.2	3.4	6.7	0.54	1.00	0.53	0.59	2.13	0.37	0.40	0.52	0.18	2.51	1.00	0.06
	mean	45.10	15.86	22.24	11.54	6.31	23.52	20.83	3.29	2.25	6.54	4.75	3.05	5.95	0.52	0.95	0.46	0.51	1.83	0.35	0.34	0.49	0.16	2.16	0.91	0.05
	SD	1.99	0.70	1.46	1.77	0.83	0.65	1.17	0.43	0.26	0.25	0.37	0.25	0.44	0.01	0.05	0.02	0.07	0.17	0.01	0.04	0.02	0.02	0.17	0.05	0.01
	N	12	12	12	11	11	12	12	12	12	12	12	12	12	12	12	12	11	11	12	12	12	12	12	12	12
O. smithi sp. n.	ZMB 78310 (holotype)	60.4	21.9	29.9	15.6	7.2	30.4	25.7	4.3	3.3	7.9	5.7	4.7	7.7	0.50	0.98	0.42	0.52	2.17	0.36	0.42	0.49	0.17	1.69	0.98	0.05
	min	40.1	15.0	19.4	7.4	3.8	19.8	17.4	3.1	2.3	5.6	4.5	3.5	5.8	0.49	0.92	0.42	0.38	1.95	0.36	0.41	0.48	0.15	1.51	0.98	0.05
	max	60.4	21.9	29.9	15.6	7.2	30.4	25.7	4.3	3.3	7.9	5.7	4.7	7.7	0.53	0.98	0.45	0.52	2.24	0.39	0.49	0.49	0.19	1.69	1.07	0.06
	mean	48.9	18.3	23.9	11.3	5.3	24.8	21.3	3.6	2.8	6.4	4.9	4.0	6.6	0.51	0.96	0.44	0.46	2.12	0.38	0.44	0.49	0.17	1.60	1.03	0.06
	SD	10.4	3.5	5.4	4.1	1.7	5.3	4.2	0.6	0.5	1.2	0.7	0.6	1.0	0.02	0.03	0.01	0.07	0.16	0.01	0.04	0.01	0.02	0.09	0.05	0.00
	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
O. fouta sp. n.	ZMB 78314 (holotype)	55.6	21.6	27.8	14.3	8.4	28.9	25.8	4.1	3.1	7.7	5.9	3.7	7.1	0.52	0.96	0.46	0.51	1.70	0.39	0.41	0.50	0.16	2.07	0.93	0.06
	min	47.8	17.3	23.1	8.9	5.3	25.6	22.1	3.2	2.8	6.3	5.3	3.7	5.8	0.52	0.90	0.44	0.35	1.69	0.36	0.40	0.48	0.14	1.49	0.92	0.05
	max	57.0	21.6	27.9	14.4	8.4	29.8	25.8	4.2	3.1	7.8	5.9	4.3	7.4	0.53	0.97	0.46	0.52	1.79	0.39	0.46	0.51	0.18	2.07	1.06	0.06
	mean	52.5	19.6	26.0	12.5	7.2	27.6	23.8	3.9	3.0	7.0	5.6	4.0	6.8	0.53	0.94	0.45	0.46	1.72	0.37	0.43	0.50	0.16	1.78	0.96	0.06
	SD	4.5	2.3	2.3	3.2	1.7	2.0	1.9	0.5	0.2	0.8	0.3	0.2	0.7	0.01	0.03	0.01	0.10	0.06	0.01	0.03	0.01	0.02	0.26	0.06	0.00
	N	4	4	4	3	3	4	4	4	4	4	4	4	4	4	4	4	3	3	4	4	4	4	4	4	4
O. arndti sp. n.	ZMB 78355 (holotype)	48.8	17.1	24.6	13.0	7.9	26.3	24.1	3.7	2.7	7.6	5.2	3.4	6.0	0.54	0.93	0.49	0.53	1.65	0.35	0.36	0.50	0.15	2.24	0.78	0.06
	min	43.5	15.2	22.5	10.4	5.1	23.4	20.0	2.9	2.2	6.0	4.2	3.0	5.2	0.50	0.80	0.44	0.40	1.50	0.33	0.32	0.45	0.13	1.81	0.76	0.04
	max	53.6	19.3	27.2	15.1	8.7	28.6	24.8	4.4	3.0	7.6	5.7	3.8	7.0	0.59	1.04	0.50	0.59	2.14	0.36	0.44	0.56	0.19	2.47	1.05	0.07
	mean	49.1	17.3	24.9	12.8	6.9	26.2	23.0	3.5	2.6	7.0	5.0	3.4	6.1	0.5	0.95	0.47	0.51	1.86	0.35	0.37	0.51	0.15	2.05	0.89	0.05
	SD	2.3	1.0	1.3	1.3	1.1	1.2	1.2	0.3	0.2	0.4	0.4	0.2	0.4	0.0	0.04	0.02	0.05	0.17	0.01	0.03	0.02	0.01	0.17	0.07	0.01
	N	28	28	28	26	26	28	28	28	28	28	28	28	28	28	28	28	26	26	28	28	28	28	28	28	28

Table 2. Summary of morphological measures (in mm) of adult female *Odontobatrachus* species. Minimum (min), maximum (max), mean values (mean), standard deviation (SD) and number of included vouchers (N) are given. For abbreviations see material and methods section.

Taxon		SUL	HW	FM	TI	FL	IT	TD	O	ID	EN	ES	TI/SUL	FM/TI	FL/SUL	HW/SUL	TD/O	FM/SUL	IT/FL	O/EN	ES/O	TD/SUL
O. natator	min	44.6	15.9	22.0	23.7	20.2	2.5	2.4	6.2	4.6	3.4	5.4	0.45	0.87	0.39	0.32	0.34	0.43	0.12	1.60	0.82	0.04
	max	61.1	21.2	28.1	29.8	26.1	4.9	3.4	7.9	6.4	4.7	7.5	0.58	1.01	0.51	0.38	0.46	0.55	0.20	2.18	1.11	0.06
	mean	53.6	18.6	26.0	27.2	23.7	3.8	2.9	7.1	5.4	3.9	6.6	0.51	0.96	0.44	0.35	0.40	0.49	0.16	1.80	0.93	0.05
	SD	5.0	1.4	1.6	1.5	1.6	0.5	0.3	0.5	0.5	0.3	0.5	0.03	0.03	0.03	0.02	0.03	0.03	0.02	0.13	0.07	0.00
	N	31	31	31	31	31	29	31	31	31	31	31	31	31	31	31	31	31	29	31	31	31
O. ziama sp. n.	min	44.3	15.1	21.9	23.9	20.7	2.7	1.9	6.0	4.3	2.9	5.8	0.45	0.88	0.38	0.30	0.29	0.41	0.12	1.69	0.84	0.04
	max	60.3	19.8	27.7	29.7	25.4	4.2	2.7	7.7	5.8	3.8	7.4	0.56	1.03	0.49	0.40	0.40	0.53	0.18	2.38	1.10	0.06
	mean	52.1	17.5	24.8	26.3	22.8	3.6	2.4	6.9	5.0	3.4	6.5	0.51	0.94	0.44	0.34	0.34	0.48	0.16	2.03	0.94	0.05
	SD	4.3	1.2	1.6	1.4	1.2	0.3	0.2	0.4	0.4	0.2	0.5	0.03	0.03	0.03	0.02	0.02	0.03	0.01	0.17	0.08	0.00
	N	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30
O. smithi sp. n.	min	48.7	18.1	22.7	24.7	21.8	3.0	2.7	6.7	4.2	3.8	5.9	0.49	0.91	0.42	0.35	0.39	0.45	0.14	1.61	0.87	0.05
	max	61.9	22.4	28.6	31.2	27.9	5.1	3.7	7.8	6.3	4.8	8.1	0.57	0.96	0.51	0.39	0.48	0.52	0.19	1.79	1.12	0.07
	mean	54.1	20.1	25.9	27.9	24.7	4.0	3.2	7.1	5.6	4.2	7.0	0.52	0.93	0.46	0.37	0.44	0.48	0.16	1.69	0.98	0.06
	SD	4.4	1.7	2.4	2.6	2.5	0.8	0.4	0.5	0.7	0.3	0.8	0.03	0.02	0.03	0.01	0.03	0.03	0.02	0.07	0.10	0.01
	N	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
O. fouta sp. n.	min	44.1	16.8	22.5	23.7	20.9	2.4	2.8	6.0	4.7	3.6	5.9	0.48	0.95	0.41	0.34	0.41	0.47	0.11	1.57	0.97	0.05
	max	62.5	22.2	29.4	30.2	26.3	4.8	3.9	7.7	6.4	4.5	8.5	0.55	0.98	0.49	0.40	0.50	0.52	0.18	1.88	1.10	0.07
	mean	51.1	18.6	24.8	25.8	22.5	3.6	3.1	6.6	5.3	3.9	6.8	0.51	0.96	0.44	0.37	0.47	0.49	0.16	1.71	1.02	0.06
	SD	8.2	2.4	3.2	3.0	2.6	1.0	0.5	0.8	0.8	0.4	1.2	0.03	0.01	0.03	0.03	0.04	0.02	0.03	0.13	0.06	0.01
	N	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
O. arndti sp. n.	min	45.9	16.2	22.3	24.7	20.6	3.1	2.4	6.1	4.5	3.0	5.7	0.47	0.88	0.42	0.31	0.31	0.44	0.13	1.65	0.75	0.04
	max	64.0	20.9	29.8	31.3	27.7	4.7	3.4	8.3	5.9	4.3	7.3	0.56	0.97	0.51	0.37	0.45	0.53	0.18	2.59	1.00	0.06
	mean	56.1	18.9	27.1	29.2	25.7	3.8	2.8	7.4	5.3	3.6	6.5	0.52	0.93	0.46	0.34	0.38	0.48	0.15	2.04	0.89	0.05
	SD	4.5	1.2	2.0	1.9	1.8	0.4	0.2	0.6	0.4	0.3	0.4	0.02	0.03	0.02	0.01	0.04	0.02	0.01	0.19	0.06	0.00
	N	25	25	25	25	25	24	25	25	25	25	25	25	25	25	25	25	25	24	25	25	25

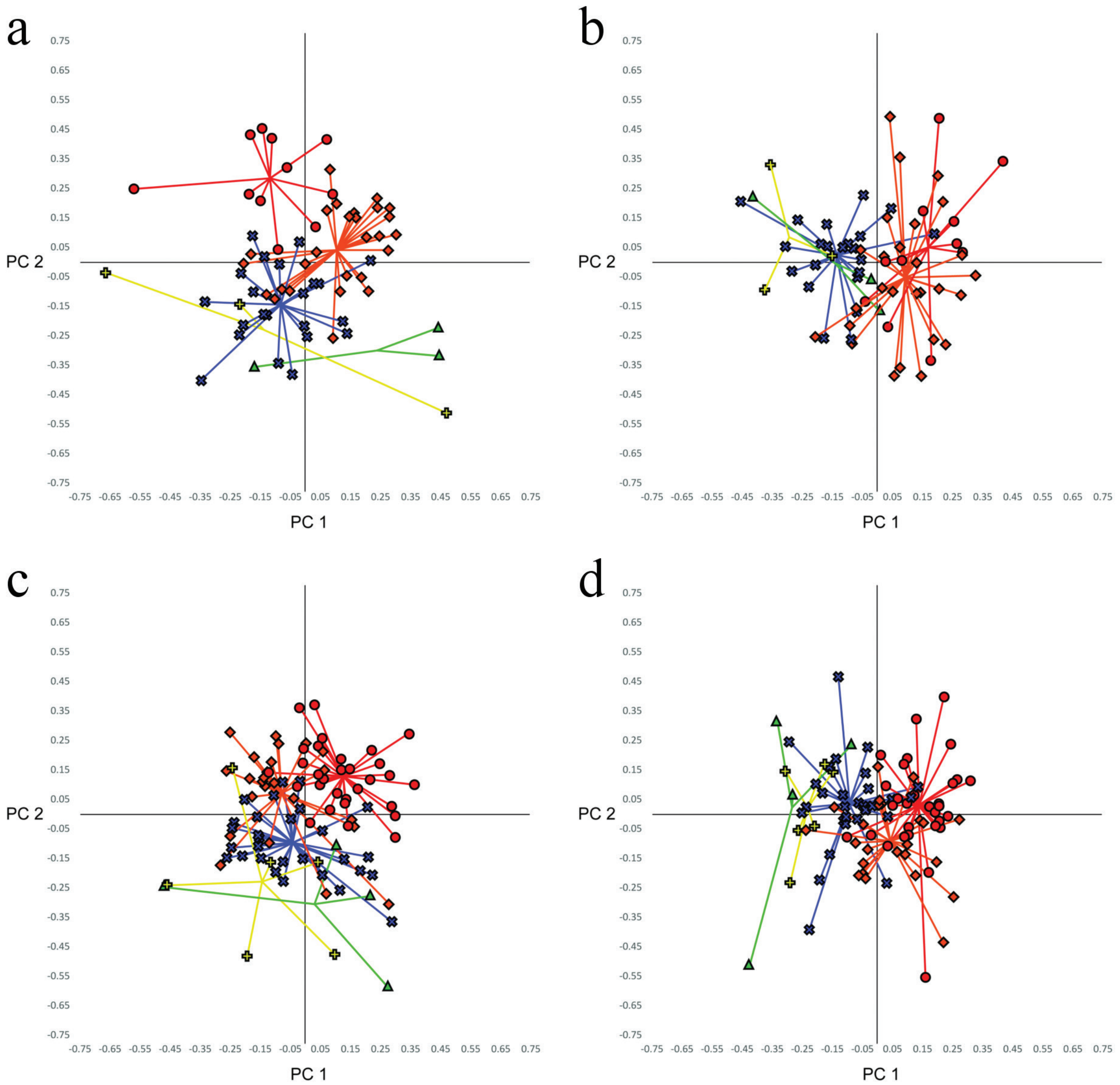

Figure 2. Scatter plot of the first and second axis of the principal component analyses for absolute values of morphological measurements in males (**a**) and females (**c**), and respective ratios in males (**b**) and females (**d**). For PCA loadings see Tables 3 and 4. Lines are drawn to indicate the centroid of points for each species. For colour code see Fig. 1.

14.27%, summing up to a total of more than 73% variance explained (Table 3). Axis 2 was mostly made up of contributions by TD and EN. All contributors to axes 1 and 2 in the analysis of ratios in males are given in Table 3. Axis 3 increased the total explained variance by only 8.79% (contributors not shown). The centroid of *O. ziama* was separated from those of *O. natator* and *O. smithi* on both axes, from that of *O. fouta* on the second axis and from that of *O. arndti* on the first axis. Centroids of *O. smithi* and *O. natator* were separated from that of *O. fouta* on the first axis and from that of *O. arndti* on the second axis. Centroids of *O. arndti* and *O. fouta* were separated on both axes from each other (Fig. 2c).

PCA results of morphometric ratios in female *Odontobatrachus* (Fig. 2d) revealed that main contributors to axis 1 were TD/O and TD/SUL and axis 1 accounted for 48.38% of the total variance. Axis 2 contributed additional 17.84%, summing up to a total of 66.22% of the variance explained (Table 4). Axis 2 was mostly made up of IT/FL. All contributors to axes 1 and 2 in the analysis of ratios in females are given in Table 4. Axis 3 explained an additional 12.49% (contributors not shown). The centroid of *O. ziama* was separated from those of *O. natator*, *O. smithi* and *O. fouta* on the first axis and from that of *O. arndti* on the second axis. The centroid of *O. arndti* was separated from those of *O. natator*, *O. smithi* and *O. fouta* on both axes (Fig. 2d).

Table 3. Principle component loadings for male (left) and female (right) absolute values. Eigenvalues, percent of explained variance for the first two axis and the cumulative variance are given.

	male		female	
	PC1	PC2	PC1	PC2
Eigenvalue	0.0766	0.0337	0.0581	0.0141
Percent variance	52.84	23.23	59.02	14.27
Cumulative variance	52.84	76.07	59.02	73.29
Loadings (absolute values)				
Snout-urostyle length (SUL)	0.2444	-0.1534	-0.4375	0.1178
Head width (HW)	0.2224	-0.2185	-0.4029	-0.0173
Femur length (FM)	0.2774	-0.1283	-0.3644	0.1217
Femoral gland length (GL)	0.6581	0.1982	---	---
Femoral gland width (GW)	0.7881	0.3470	---	---
Tibiofibula length (TI)	0.2547	-0.1241	-0.3523	0.1340
Foot length (FL)	0.2796	-0.0701	-0.3901	0.1429
Inner metatarsal tubercle length (IT)	0.2712	-0.2628	-0.5340	0.2196
Tympanum diameter (TD)	0.1145	-0.3954	-0.4940	-0.4614
Orbita diameter (OD)	0.2316	-0.0549	-0.3427	0.0844
Interorbital distance (ID)	0.2106	-0.1749	-0.3683	-0.0191
Distance eye to naris (EN)	0.0921	-0.3951	-0.3608	-0.3051
Distance eye to snout (ES)	0.1818	-0.1573	-0.3180	0.0216

Table 4. Principle component loadings for male (left) and female (right) ratios. Eigenvalues, percent of variance for the first two axes (PC1 and PC2) and the cumulative variance are given.

	male		female	
	PC1	PC2	PC1	PC2
Eigenvalue	0.0362	0.0150	0.0338	0.0124
Percent variance	41.28	17.06	48.38	17.84
Cumulative variance	41.28	58.35	48.38	66.22
Loadings (ratios)				
Tibiofibula length to snout-urostyle length (TI/SUL)	0.0345	-0.0091	-0.0750	-0.1917
Femur length to tibiofibula length (FM/TI)	-0.0043	0.0246	0.0024	-0.0115
Foot length to snout-urostyle length (FL/SUL)	0.1005	-0.0628	-0.0746	-0.2220
Femoral gland length to femur length (GL/FM)	0.4487	-0.3126	---	---
Femoral gland length to femoral gland width (GL/GW)	-0.1595	0.0494	---	---
Head width to snout-urostyle length (HW/SUL)	-0.0784	0.0093	-0.1872	-0.1029
Tympanum diameter to orbita diameter (TD/OD)	-0.5397	-0.2602	-0.6797	0.0372
Femur length to snout-urostyle length (FM/SUL)	0.0302	0.0155	-0.0726	-0.2032
Inner tarsal tubercle length to foot length (IT/FL)	-0.1794	0.0933	-0.0964	0.5165
Orbita diameter to distance eye naris (OD/EN)	0.4411	-0.2198	0.4463	-0.0762
Distance eye snout to orbita diameter (ES/OD)	-0.1440	0.2105	-0.1403	0.1742
Tympanum diameter to snout urostyle length (TD/SUL)	-0.4402	-0.3605	-0.6957	-0.0986

Generally, PCA results on morphology supported the separation of the five molecular OTUs sensu Barej et al. (2015; *O. natator*, *O. ziama*, *O. smithi*, *O. fouta*, *O. arndti*), although males and females often showed overlap in the variance in both analyses (absolute values and ratios) between OTUs. Two major morphological groupings *O. natator*, *O. smithi*, *O. fouta* vs. *O. ziama*, *O. arndti* were uncovered in all analyses, with the groups being separated from each other on at least one of the two major axes (Fig. 2).

We tested for statistical differences in particular morphological characters and ratios between species (Kruskal-Wallis H test), considering potential sex-dependant characters (Appendix 3: Table C). These non-parametric tests revealed significant differences in males and females of the five species highlighting their morphological distinctness (Table 5).

Due to the overlap in morphological variation of species (see above), the correct assignment of single individuals would be difficult if their geographic origin is unknown. We therefore applied Detrended Correspondence Analyses (DCAs) to assess how reliably individuals can be assigned to a particular species. DCA results showed high levels of correctly assigned males and females, based on absolute values and ratios of mensural data sets, respectively (Table 6). Combined correct assignments of all five species for absolute values in male *Odontobatrachus* summed up to 89.2% and combined values of ratios referred to 87.7%. DCA results in female *Odontobatrachus* were 82.9% for absolute values and 74.2% in ratios. The lowest percentages of correctly assigned individuals were recovered in the species with the lowest voucher numbers (Table 6). Despite the high percentage of correct assignments, the persisting mismatches reflected the PCA results and highlight the morphological overlap between some species.

Based on the combination of the molecular data recognising five OTUs and their respective distribution patterns (indicating spatial partitioning) presented in Barej et al. (2015), as well as morphological distinction presented herein, we consider the five *Odontobatrachus* OTUs as distinct species. Until now, all Upper Guinean populations were assigned to *Odontobatrachus natator* (Boulenger, 1905) and thus no synonyms are available. We provide diagnostic characters (Table 7) and formally describe four new species.

Systematics of the *Odontobatrachus natator*-complex

Frogs belonging to the genus *Odontobatrachus* are all characterised by the following external morphological characters: tusk-like odontoids on the lower mandible in both sexes; posteriorly curved teeth on premaxillaries and anterior maxillaries; presence of vomerine teeth; eye diameter distinctly larger than tympanum diameter; pupil horizontally elliptical; tympanum rather indistinct; skin

Table 5. Morphological comparison of absolute measurements and ratios in males (lower left corner) and females (upper right corner). Number of samples per sex in each species and level of significance are given; lack of significant differences in absolute values or ratios is marked with "X". See material and methods section for abbreviations.

Taxon	***O. natator*** **($N_{male,female}$= 22/29)**	***O. ziama* sp. n.** **($N_{male,female}$= 11/30)**	***O. smithi* sp. n.** **($N_{male,female}$= 3/6)**	***O. fouta* sp. n.** **($N_{male,female}$= 3/4)**	***O. arndti* sp. n.** **($N_{male,female}$= 26/24)**
O. natator		♀♀ *O. natator* < *O. ziama*: O/EN (p< 0.001) ♀♀ *O. natator* > *O. ziama*: HW (p< 0.05), TD (p< 0.001), ID (p< 0.05), EN (p< 0.001), HW/SUL (p< 0.01), TD/O (p< 0.001), TD/SUL (p< 0.001)	X	X	♀♀ *O. natator* < *O. arndti*: TI (p< 0.05), FL (p< 0.01), O/EN (p< 0.001) ♀♀ *O. natator* > *O. arndti*: EN (p= 0.06), FM/TI (p< 0.05), HW/SUL (p< 0.05)
***O. ziama* sp. n.**	♂♂ *O. ziama* < *O. natator*: HW (p<0.01), TD (p< 0.01), EN (p< 0.001), HW/SUL (p< 0.01), TD/O (p< 0.01), TD/SUL (p< 0.05) ♂♂ *O. ziama* > *O. natator*: O/EN (p< 0.01)		♀♀ *O. ziama* < *O. smithi*: HW (p< 0.01), TD (p< 0.001), ID (p< 0.05), EN (p< 0.001), HW/SUL (p< 0.001), TD/O (p< 0.001), O/EN (p< 0.001), TD/SUL (p< 0.001)	♀♀ *O. ziama* < *O. fouta*: TD (p< 0.001), HW/SUL (p= 0.07), TD/O (p< 0.001), TD/SUL (p< 0.001) ♀♀ *O. ziama* > *O. fouta*: O/EN (p< 0.05)	♀♀ *O. ziama* < *O. arndti*: HW (p< 0.01), FM (p< 0.001), TI (p< 0.001), FL (p< 0.001), TD (p< 0.001), O (p< 0.05), ID (p= 0.09), TD/O (p< 0.05)
***O. smithi* sp. n.**	X	♂♂ *O. smithi* < *O. ziama*: O/EN (p< 0.01) ♂♂ O. smithi > O. ziama: EN (p< 0.01), GL/GW (p< 0.01), HW/SUL (p< 0.05), TD/O (p< 0.05)		X	♀♀ *O. smithi* < *O. arndti*: O/EN (p< 0.01) ♀♀ O. smithi > O. arndti: EN (p< 0.05), HW/SUL (p< 0.01), TD/O (p< 0.05), TD/SUL (p< 0.05)
***O. fouta* sp. n.**	♂♂ *O. fouta* > *O. natator*: FL (p= 0.08)	♂♂ *O. fouta* < *O. ziama*: GL/GW (p= 0.05) ♂♂ *O. fouta* > *O. ziama*: SUL (p< 0.001), HW (p< 0.01), TI (p< 0.001), FL (p< 0.05), TD (p< 0.01), ID (p< 0.05), EN (p< 0.01), HW/SUL (p= 0.07)	♂♂ *O. fouta* > *O. smithi*: GL/FM (p< 0.05)		♀♀ *O. fouta* < *O. arndti*: FL (p< 0.05), O/EN (p< 0.05) ♀♀ *O. fouta* > *O. arndti*: TI (p< 0.05), TD/O (p= 0.06), ES/O (p< 0.05), TD/SUL (p= 0.06)
***O. arndti* sp. n.**	♂♂ *O. arndti* < *O. natator*: EN (p< 0.01), HW/SUL (p= 0.06), TD/SUL (p= 0.05), TD/O (p= 0.06), IT/FL (p< 0.01) ♂♂ *O. arndti* > *O. natator*: GL (p< 0.01); GW (p< 0.01), TI (p<0.01), FL (p< 0.001), TI/SUL (p< 0.05), FL/SUL (p< 0. 01), O/EN (p< 0.001)	♂♂ *O. arndti* > *O. ziama*: SUL (p< 0.01), HW (p< 0.01), FM (p< 0.01), TI (p< 0.001), FL (p< 0.001), TD (p= 0.08), O (p< 0.01)	♂♂ *O. arndti* > *O. smithi*: FL/SUL (p= 0.06), GL/GW (p< 0.05), O/EN (p< 0.01), ES/O (p< 0.05)	♂♂ *O. arndti* < *O. fouta*: TD (p= 0.06), EN (p= 0.08) ♂♂ *O. arndti* > *O. fouta*: GL/GW smaller (p= 0.05)	

Table 6. Results from statistical discrimination of species (DCA) using morphological data and pooling individuals according to sex. Percentage of correct assignments, number of cases (N) and overall correct classification rate for absolute values and ratios in males and females are given.

male absolute values	***O. ziama* sp. n.**	***O. smithi* sp. n.**	***O. fouta* sp. n.**	***O. arndti* sp. n.**	***O. natator***	**N**
O. ziama sp. n.	100.0	0.0	0.0	0.0	0.0	11
O. smithi sp. n.	0.0	66.7	33.3	0.0	0.0	3
O. fouta sp. n.	0.0	0.0	100.0	0.0	0.0	3
O. arndti sp. n.	3.8	0.0	0.0	84.6	11.5	26
O. natator	0.0	4.5	0.0	4.5	90.9	22
all taxa (combined)	89.2%					
male ratios						
O. ziama sp. n.	81.8	0.0	0.0	18.2	0.0	11
O. smithi sp. n.	0.0	100.0	0.0	0.0	0.0	3
O. fouta sp. n.	0.0	0.0	100.0	0.0	0.0	3
O. arndti sp. n.	7.7	0.0	3.8	80.8	7.7	26
O. natator	0.0	0.0	0.0	4.5	95.5	22
all taxa (combined)	87.7%					
female absolute values						
O. ziama sp. n.	93.3	3.3	0.0	3.3	0.0	30
O. smithi sp. n.	0.0	83.3	16.7	0.0	0.0	6
O. fouta sp. n.	0.0	0.0	75.0	0.0	25.0	4
O. arndti sp. n.	0.0	0.0	0.0	83.3	16.7	24
O. natator	10.3	10.3	3.4	3.4	72.4	29
all taxa (combined)	82.8%					
female ratios						
O. ziama sp. n.	83.3	3.3	0.0	10.0	3.3	30
O. smithi sp. n.	0.0	83.3	16.7	0.0	0.0	6
O. fouta sp. n.	0.0	25.0	50.0	0.0	25.0	4
O. arndti sp. n.	12.5	0.0	0.0	70.8	16.7	24
O. natator	10.3	6.9	3.4	10.3	69.0	29
all taxa (combined)	74.2%					

texture granular and heterogeneous; males with femoral glands, external vocal sacs, velvety nuptial excrescences on finger I. These characters apply to all species treated herein and are not repeated in the specific diagnoses below. For further osteological characters see Barej et al. (2014a, b).

Odontobatrachus natator (Boulenger, 1905)

OTU *natator* sensu Barej et al. (2015)

Syntypes. BMNH 1947.2.30.65-69 (syntypes: 1 male, 3 females, subadult), Sierra Leone, no more details available, coll. Major F. Smith.

Examined material. Sierra Leone: BMNH 1961.1248-54 (5 juveniles), Western Area; BMNH 1963.1047 (female), Southern Province; BMNH 1964.178 (female), Western Area; ZMB 78196 (juvenile), Western Area Peninsula Forest (Latitude: 8.35; Longitude: -13.18), 178 m a.s.l.; ZMB 78197 (female), Western Area Peninsula Forest (8.47; -13.22), 367 m a.s.l.; ZMB 78198 (female), Northern Province (9.21; -11.14), 1325 m a.s.l.; ZMB 78199 (female), Eastern Province (8.86; -10.79), 748 m a.s.l.; ZMB 78200 (male), Northern Province (9.21; -11.14), 1345 m a.s.l.; ZMB 78202, ZFMK 95469 (2 females), ZMB 78203, MHNG 2731.51, ZFMK 95470 (3 males), Eastern Province (7.66; -10.90), 334 m a.s.l. Guinea: ZMB 78207 (juvenile), ZMB 78208 (female), N'Zérékoré Region (8.89; -8.31), 1019 m a.s.l.; ZMB 78209 (female), Kankan Region (9.28; -9.11), 637 m a.s.l.; ZMB 78210 (juvenile), ZMB 78211 (female), N'Zérékoré Region (7.54; -8.84), 403 m a.s.l.; ZMB 78212 (female), ZMB 78213 (male), N'Zérékoré Region (8.88; -8.29), 939 m a.s.l.; ZMB 78214 (male), ZMB 78215-6 (2 females), N'Zérékoré Region (7.64; -9.25), 533 m a.s.l.; ZMB 78217-19 (3 males) Mamou Region (10.30; -11.94), 527 m a.s.l.; ZMB 78303 (female), N'Zérékoré Region (8.35; -9.42), 487 m a.s.l. Liberia: BMNH 1982.631 (male), Iti Valley; ZMB 78220 (female), Grand Cape Mount County (7.45; -10.69), 299 m a.s.l.; ZMB 78221 (female), ZMB 78222 (male), Nimba County (7.54; -8.63), 595 m a.s.l.;

ZMB 78223-24, ZMB 78232, ZMB 78234, ZMB 78236-7, ZMB 78239 (7 females), ZMB 78227, ZMB 78229-31, ZMB 78233, ZMB 78235, ZMB 78238, ZMB 78240-42 (10 males), ZMB 78228 (juvenile), Nimba County (7.44; -8.66), 634 m a.s.l.; ZMB 78225 (female), Nimba County (7.44; -8.59); ZMB 78226 (female), Nimba County (7.46; -8.67), 591 m a.s.l.; ZMB 78244 (female), ZMB 78245 (male), Grand Gedeh County (5.66; -8.16), 316 m a.s.l.; ZMB 78246 (juvenile) Grand Gedeh County (5.69; -8.21), 247 m a.s.l.; ZMB 78247 (male), Grand Gedeh County (5.64; -8.19), 367 m a.s.l.; ZMB 78248 (juvenile), Grand Gedeh County (5.64; -8.19), 345 m a.s.l.; ZMB 78249 (female), ZMB 78250 (female, juvenile), Grand Gedeh County (5.63; -8.19), 388 m a.s.l.; ZMB 80504 (male), Nimba County (7.51; -8.70), 429 m a.s.l.; ZMB 80505 (female), Nimba County (6.44; -9.06), 533 m a.s.l.

Boulenger's (1905) species description is based on a series of five specimens in the BMNH collection (1947.2.30.65-69, formerly: 1905.1.27.4-5 and 1905.2.2.15-17). The type series collected by Major F. Smith Royal Army Medical Corps (R.A.M.C.) contains one male, three females and a subadult female. The type locality is given as "Sierra Leone".

During his service in western Africa, Captain (Local Major) F. Smith researched tropical diseases, prepared species lists of pests and elaborated respective preventive measures (Smith 1902, 1905). A part of his contribution contains the local fauna around barracks (Smith 1905) and Major F. Smith mentioned "a local frog (a new species named *Petropedetes natator*)…". He was based in Freetown predominantly surveying the area of Mt. Aureol, Tower Hill and Kortright but likewise carried out short travels to Port Lokkoh (today: Port Loko) and Rotifunk in the close hinterland (Smith 1902). However, Smith (1902) searched in the latter region for swampy areas as potential breeding habitats of the mosquito genus *Anopheles*, a habitat type inappropriate for torrent-frogs. Consequently, we herein restrict the type locality of *Petropedetes natator* Boulenger, 1905 to the Freetown area, Sierra Leone. A more detailed restriction appears unreasonable.

We refrain from designating a single lectotype as subsequent species descriptions are possible with comparison to the whole syntype series.

Genetics. *Odontobatrachus natator* is genetically well differentiated from all congeners and known populations form a well-supported and monophyletic clade (Barej et al. 2015). Uncorrected 16S p-distances between *O. natator* and other *Odontobatrachus* species range from 3.40–5.40% (Appendix 1: Table A), while maximum intrataxon differences of *O. natator* reach 1.98% (one-to-one pairwise comparisons N = 703), maximum intra-subclade difference values for the two subclades of *O. natator* are 0% (N = 1) and 0.72% (N = 630) respectively (Appendix 1: Table A). These two subclades correspond to the disjunct distribution of I) the Freetown area and II) all remaining localities further inland; divided by unsuitable habitat in-between (Barej et al. 2015). In case taxonomic changes are made in the future, the Freetown clade should retain the nominate form following the restriction of the type locality.

Description of male syntype. The male syntype (BMNH 1947.2.30.68) has been assigned to this taxon in both DCA analyses (absolute values and ratios). The male syntype has a robust body shape: snout-urostyle length of 46.1 mm; head width 17.0 mm; head slightly longer than broad; snout in lateral view short, slightly rounded at the snout tip (Fig. 3); snout in dorsal view fairly rounded; lower jaw with sharp tusk-like prolongations and single small knob at lower jaw symphysis with corresponding socket in-between premaxillae; upper premaxillae and maxillae with numerous teeth, posteriorly curved; vomerine teeth present, arranged in two small odontophores, closer to each other than to choanae; tongue broadly heart shaped; horizontal eye diameter 6.4 mm; interorbital distance 5.3 mm; pupil horizontally elliptical; eye diameter distinctly larger than tympanum diameter (Fig. 3); tympanum indistinct (horizontal diameter 2.7 mm); nares closer to snout than to eye; snout as long as eye diameter; *canthus rostralis* rounded; loreal region concave; paired lateral vocal sacs (Fig. 3); forelimbs moderately slender, forearms slightly hypertrophied, fingers slender; prepollex absent; relative finger lengths III>IV≥II>I (Fig. 3); velvety nuptial excrescences on finger I weakly developed; subarticular tubercles large, subconical; supernumerary tubercles absent; fingertips dilated, triangular, notched in the middle; femur length 23.2 mm; tibia length 23.8 mm; femoral glands large (length × width: left: 10.3 × 5.4 mm, right: 9.5 × 5.5 mm); femoral glands positioned on the posterior part of the ventral side of femur (Fig. 3); relation femoral gland length to femur length: 0.43; minuscule circular glands running along upper side of tibia; foot length (incl. longest toe) 29.9 mm; relative toe lengths IV>III≥V>II>I; inner metatarsal tubercle elliptical; toe tips broadened forming triangular dilated discs; inner metatarsal tubercle prominent (2.8 mm); number of subconical subarticular tubercles on toes I-V: 1, 1, 2, 3, 2; supernumerary tubercles absent (Fig. 3); prominent skin fold on posterior side of feet; dorsal skin texture heterogeneous; dorsum and flanks covered with slender dorsal ridges of app. 3.0 mm length (partially flattened on the dorsum due to preservation); venter smooth; flank texture as on dorsum; webbing fully developed (0-0.5/0-1/0-1/1-0), running as a skin fold along toes III and IV to the disc, webbing between toes hardly concave, almost straight.

Colouration in preservation. Specimen overall brownish in colour (Fig. 3); dorsum darker than ventrum; throat darker than belly, ventrum lacking any marbling or patterns. Damage of the male syntype: third toe of left foot (in dorsal view) cut off (Fig. 3); left side (in dorsal view)

Figure 3. Male syntype of *Odontobatrachus natator* (BMNH 1947.2.30.68) in ventral and dorsal view (top from left to right, scale bar: 10 mm); head in lateral view, details of pedal webbing, details of hand (bottom left to right, scale bar: 5 mm).

with cut along flank; transverse cut on throat; discs on toes and fingers partially shrivelled due to drying-out.

Variation. Females are significantly larger than males (SUL: $Z = -3.814$, $p < 0.001$, $N_{males} = 22$, $N_{females} = 29$), mean SUL in females 53.6 mm and 48.0 mm in males, and consequently possess longer extremities (FM: $Z = -4.395$, $p < 0.001$; TI: $Z = -4.746$, $p < 0.001$; FL: $Z = -4.623$, $p < 0.001$), broader heads (HW: $Z = -3.570$, $p < 0.001$) and longer snouts (EN: $Z = -2.533$, $p < 0.01$; ES: $Z = -3.285$, $p < 0.05$) in absolute measurements (Tables 1 and 2). However, ratios are predominantly similar between the two sexes, with males only showing higher values in HW/SUL ($Z = -2.796$, $p < 0.01$), IT/FL ($Z = -1.978$, $p < 0.05$) and TD/SUL ($Z = -2.701$, $p < 0.01$); for details see Tables 1 and 2. Both sexes possess enlarged tusk-like prolongations in the lower jaw as well as the name-bearing ‘teeth’ on the upper jaw. Male secondary sexual characters are femoral glands, velvety nuptial excrescences on finger I and presence of vocal sacs.

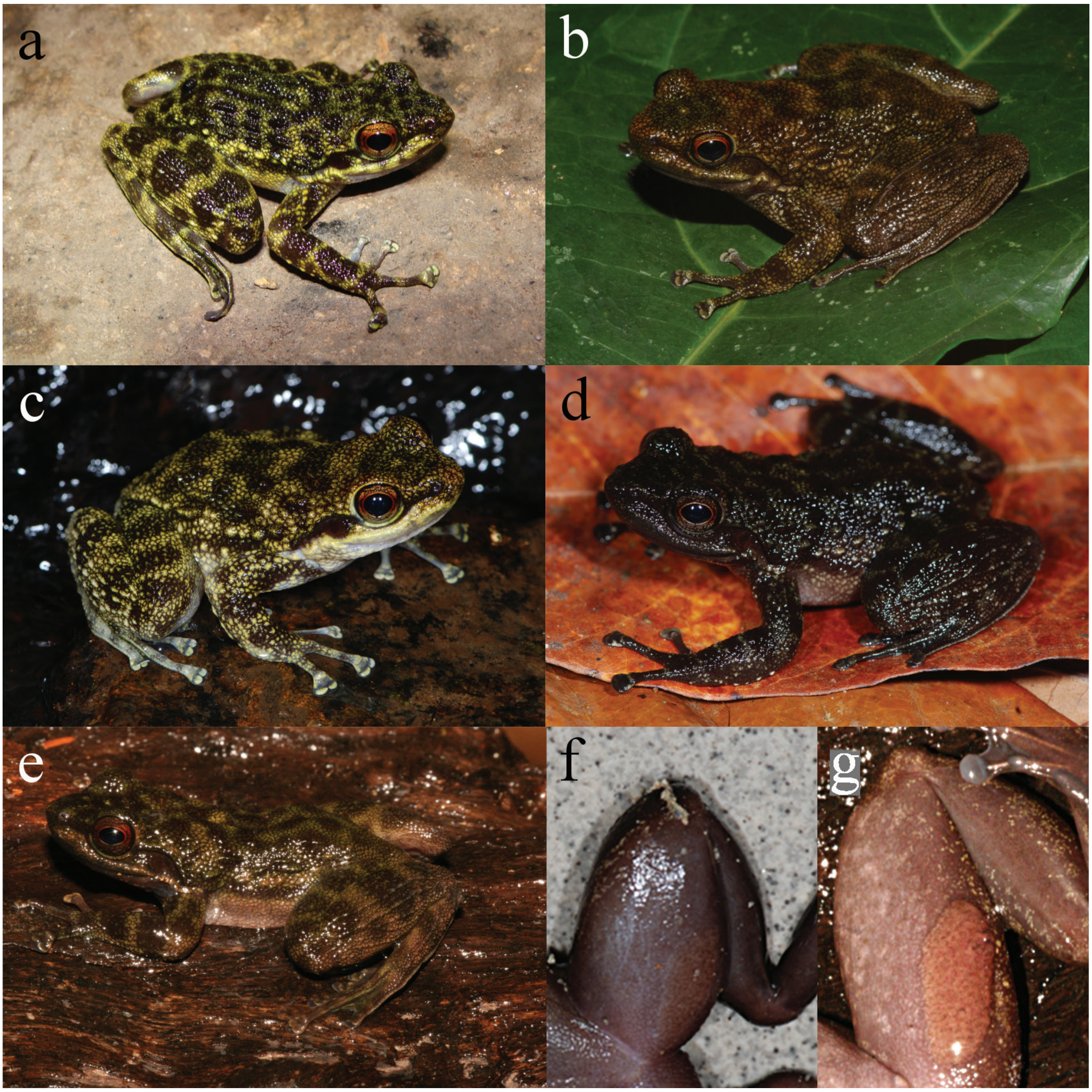

Figure 4. *Odontobatrachus natator* in life: **a**) female ZMB 78303, Ziama Forest, Guinea; **b**) male ZMB 78214, N'Zérékoré Region, Guinea; **c**) Gola Rainforest National Park, Sierra Leone; **d**) Freetown Area (type locality of *Petropedetes natator* Boulenger, 1905), Sierra Leone; **e**) ZMB 80504, Nimba County, Liberia; **f**) colouration of male femoral glands hardly visible (male shown in **d**); **g**) colouration distinctly contrasted against the femur (male shown in **e**).

Variation in webbing formulae of examined specimens in the covered distribution range corresponds to the extent in the type series (Table 7); although skin folds running along toes in the male syntype are more distinct than in many other specimens, showing an almost fully extended webbing state. Dorsal ridges form either slender lines as in the male syntype (Fig. 3, see also Fig. 4b, c) or are short and knob like (Fig. 4a). Number of distinct dorsal ridges (counted from spine to flank) range between two and six, usually three to five ridges per body site. However, both characters were not recognisable due to preservation artefacts in many specimens. Glandular ridges on tibia are usually built of small to large conic glands and form more or less interrupted lines (Fig. 4a–e). Dorsal colouration (in life) varies from uniform brownish, to mottled patterns with greenish or light brownish background and darker spots, usually arranged along dorsum. Male femoral glands are rose-coloured but colouration may be attenuated by the ventral colouration (Fig. 4e). Belly colouration (in alcohol) ranges from completely pale, dirty whitish, dark throat and pale belly, dark with few pale markings, to entirely dark colouration, showing no sex-dependant colour differentiation.

Distribution. *Odontobatrachus natator* has the widest distribution of all congeners (Fig. 1). The species is known from Sierra Leone, Liberia and Guinea. While the species distribution overlaps with *O. ziama* and *O. arndti* in eastern Guinea, westernmost localities reach extensions of the Fouta Djallon area, close to the range of *O. fouta*. Two distinct molecular clades have been uncovered in *O. natator* (Barej et al. 2015), one of them being restricted to the Freetown Peninsula in coastal Sierra Leone (FP sensu Barej et al. 2015) and the other covering all remaining localities (IL sensu Barej et al. 2015) of this taxon.

Conservation status. The EOO, combining both subclades of *O. natator* (Barej et al. 2015; therein *natator*) sums up to 180,231 km^2, resulting in the IUCN Red List category "Least Concern (LC)". However, due to the habitat requirements of this family the AOO is restricted to 224 km^2 and thus classifies the species as "Endangered (EN)". When considering the genetic subdivision of *O. natator* (see Barej et al. 2015), the distribution areas further diminish dramatically, especially for the Freetown Peninsula subclade. While IUCN categories remain constant for the widely distributed subclade, the Freetown Peninsula subclade possesses an AOO of only 20 km^2 classifying it as EN and an EOO of 34 km^2 placing it as "Critically Endangered (CR)" if treated as its own taxonomic unit.

Odontobatrachus ziama Barej, Schmitz, Penner, Doumbia, Hirschfeld, Brede, Bangoura & Rödel, sp. n.

http://zoobank.org/89BB73CC-EC8E-42E9-A075-990A52E711C5
OTU1 sensu Barej et al. (2015)

Holotype. ZMB 78300 (male), Republic of Guinea, Ziama Classified Forest (Latitude: 8.35790; Longitude: -9.29993), 668 m a.s.l., 22 November 2008, coll. C. Brede, M.A. Bangoura and J. Doumbia.

Paratypes. Guinea: ZMB 78298 (female), N'Zérékoré Region (8.36; -9.31), 878 m a.s.l., 11 July 2011; ZMB 78299 (female), same data as holotype; ZMB 78301, ZFMK 95464-65, MHNG 2731.46 (4 females), N'Zérékoré Region (8.36; -9.29), 558 m a.s.l., 30 July 2010; ZMB 78302, MHNG 2731.45 (2 males), N'Zérékoré Region (8.49; -9.31), 960 m a.s.l., 5 August 2010.

Additional material. Guinea: ZMB 78251 (male), ZMB 78252 (female), Kankan Region (9.21; -8.93), 1119 m a.s.l.; ZMB 78253-58 (5 females), N'Zérékoré Region (7.98; -9.12), 472 m a.s.l.; ZMB 78259 (female), Kankan Region (8.982; -8.96), 606 m a.s.l.; ZMB 78260, ZMB 78263, ZMB 78264 (juvenile), ZMB 78265-7 (5 females), ZMB 78261-2, ZMB 78268-9 (4 males), Kankan Region (9.26; -8.93), 754 m a.s.l.; ZMB 78271 (juvenile), N'Zérékoré Region (8.55; -9.08), 529 m a.s.l.; ZMB 78272 (male), Kankan Region (9.16; -8.93), 999 m a.s.l.; ZMB 78273 (male), ZMB 78274-5 (2 females), N'Zérékoré Region (8.89; -8.62), 646 m a.s.l.; ZMB 78276-7 (2 females), ZMB 78278 (juvenile), N'Zérékoré Region (8.55; -8.90), 1201 m a.s.l.; ZMB 78279-80 (2 females), N'Zérékoré Region (8.85; -8.89), 937 m a.s.l.; ZMB 78281 (female), ZMB 78282 (male), N'Zérékoré Region (8.82; -8.86), 726 m a.s.l.; ZMB 78283 (juvenile), N'Zérékoré Region (8.52; -8.94), 600 m a.s.l.; ZMB 78284 (male), ZMB 78285-6, ZMB 78288 (3 females), ZMB 78287 (juvenile), N'Zérékoré Region (8.53; -8.91), 1310 m a.s.l.; ZMB 78289-91 (3 males) ZMB 78292 (female), N'Zérékoré Region (8.14; -8.57), 622 m a.s.l.; ZMB 78295 (female), N'Zérékoré Region (8.28; -8.74), 908 m a.s.l.; ZMB 78296 (male), ZMB 78297 (female), N'Zérékoré Region (8.33; -8.71), 701 m a.s.l.

Diagnosis. Medium sized frogs, robust body shape; head narrow, smallest tympanum diameter/eye diameter ratio in the family, webbing fully developed, leaving up to 0.5 of the distal phalange free at the inner side of toe II, leaving up to 0.5-0.75 of the distal phalange free at toe IV; male femoral glands dark orange; glandular lines on tibia contain minuscule to small conic glands forming a pretty continuous line, belly pattern highly variable. Genetically *O. ziama* differs by a minimum of 2.89% in the mitochondrial 16S gene from its congeners.

Differential diagnosis. *Odontobatrachus ziama* can be distinguished from its congeners by a combination of characters (for all significant differences see Table 5): SUL in *O. ziama* is smaller than in *O. smithi* and *O. fouta* (Tables 1 and 2); male *O. ziama* differ from their congeners in the following ratios (Table 1): HW/SUL smaller than in *O. natator*, *O. smithi* and *O. fouta*; TD/O smaller than in *O. natator* and *O. smithi*; O/EN larger than in *O. natator* and *O. smithi*; TD/SUL smaller than in *O. natator*; GL/GW smaller than in *O. smithi* but larger than in *O. fouta*; female *O. ziama* differ from their congeners by the following ratios (Table 2): HW/SUL smaller than in *O. natator*, *O. smithi* and *O. fouta*; TD/O smaller than in *O. natator*, *O. smithi*, *O. fouta* and *O. arndti*; O/EN larger than in *O. natator*, *O. smithi* and *O. fouta*; TD/SUL smaller than in *O. natator, O. smithi* and *O. fouta*. Webbing of *O. ziama* is more more extensive than in *O. natator*, less extensive than in *O. smithi* and *O. fouta* and possesses a similar extent to *O. arndti* (Table 7). Femoral glands are dark orange in *O. ziama* but rose-coloured in *O. natator*, pale orange in *O. smithi* and bright orange in *O. fouta* (Figs 4, 6, 8, 10). Glandular lines on tibia contain minuscule to small conic glands forming almost continuous lines (Fig. 6a–d), while small to large glands form more or less interrupted lines in *O. natator* (Fig. 4a–e), small to mean conic glands form predominantly interrupted lines in *O. smithi* (Fig. 8a, b), small to large glandular conic glands, rather interrupted lines in *O. fouta* (Fig. 10b, c). and similar to *O. ziama* small to mean glandular conic glands form hardly interrupted lines in *O. arndti* (Fig. 12b, c). Morphologically the species is most similar in size and colour pattern to *O. arndti* (Table 7); however, they differ in several mensural characters: male *O. ziama* have larger SUL, but smaller HW, TD, O and extremities (FM, TI,

Figure 5. Male holotype of *Odontobatrachus ziama* sp. n. (ZMB 78300) in ventral and dorsal view (top from left to right, scale bar: 10 mm); head in lateral view, details of pedal webbing, details of hand (bottom left to right, scale bar: 5 mm).

FL); female *O. ziama* have smaller HW, O, ID and extremities (FM, TI, FL).

Genetics. The species is genetically well differentiated from all congeners and known populations form a well-supported and monophyletic clade (Barej et al. 2015). Uncorrected 16S p-distances between *O. ziama* and other *Odontobatrachus* species range from 2.89–5.41%, while maximum intrataxon differences of *O. ziama* add up to 0.38% (mean value 0.18%; N = 496; Appendix 1: Table A).

Holotype description. The male holotype has been correctly assigned to this taxon in both DCA analyses (absolute values and ratios). The holotype is an adult male with a moderately robust body shape (Fig. 5): snout-urostyle length of 46.1 mm; head width 15.5 mm; head slightly longer than broad; snout in lateral view short, flattened and slightly pointed at the snout tip; snout in dorsal view pointed; lower jaw with sharp tusk-like prolongations and single small knob at lower jaw symphysis with corresponding socket in between premaxillae; upper premaxillae and maxillae with numerous teeth, posteriorly curved; vomerine teeth present, arranged in two small odontophores, closer to each other than to choanae; tongue broadly heart shaped; horizontal eye diameter 6.5 mm; interorbital distance 4.8 mm; pupil horizontally elliptical; eye diameter distinctly larger than tympanum diameter; tympanum indistinct (horizontal diameter 3.5 mm); nares closer to snout than to eye; snout as long as eye diameter; *canthus rostralis* rounded; loreal region concave; paired lateral vocal sacs; forelimbs moderately slender, forearms slightly hypertrophied, fingers slender; prepollex absent; relative finger lengths III>IV>II>I; velvety nuptial excrescences on finger I weakly developed; subarticular tubercles large, subconical; supernumerary tubercles absent; fingertips dilated, triangular, notched in the middle; femur length 24.1 mm; tibia length 24.4 mm; femoral glands large (length × width: left: 12.7 × 7.6 mm, right: 12.8 × 7.5 mm); femoral glands positioned on the posterior part of the ventral side of femur; relation femoral gland length to femur length: 0.53; minuscule circular glands running along upper side of tibia; foot length (incl. longest toe) 32.0 mm; relative toe lengths IV>III≥V>II>I; shortest toe 5.5 mm; inner metatarsal tubercle elliptical; toe tips broadened forming triangular dilated discs; inner metatarsal tubercle prominent (3.7 mm); number of subconical subarticular tubercles on toes I-V: 1, 1, 2, 3, 2; supernumerary tubercles absent; prominent skin fold on posterior side of feet; dorsal skin texture heterogeneous; dorsum and flanks covered with slender dorsal ridges of app. 2.6 mm length (partially flattened, but recognisable as darker spots); venter smooth; flank texture as on dorsum; webbing fully developed (0-0.25/0-0.75/0-1/1.25-0); webbing between toes hardly concave. Damage to the male holotype: left femur (in dorsal view) with short cut; third toe of left foot (in dorsal view) clipped for tissue sample; glandular dorsal ridges partially not recognisable due to preservation.

Colouration of holotype in alcohol (Fig. 5). Dorsum brownish, marbled with small dark spots (partially indicating presence of former dorsal gland ridges), a pale marking between shoulders; hind limbs on upper side with large dark blotches, surrounded with blurred pale lines; throat dark showing pale markings of scratches (scars); venter dark; femoral glands pale, clearly contrasted against femora, with few minuscule dark dots; femora and tibia dark as belly.

Variation. Females are significantly larger than males (SUL: $Z = -4.164$, $p < 0.001$, $N_{males} = 11$, $N_{females} = 30$), mean SUL in females 52.1 mm and 45.1 mm in males, and consequently possess longer extremities (FM: $Z = -3.649$, $p < 0.001$; TI: $Z = -4.665$, $p < 0.001$; FL: $Z = -3.694$, $p < 0.001$), broader heads (HW: $Z = -3.638$, $p < 0.001$), longer snouts (EN: $Z = -3.261$, $p < 0.01$; ES: $Z = -2.402$, $p < 0.05$) and larger eyes (O: $Z = -2.431$, $p < 0.05$) in absolute measurements (Tables 1 and 2). However, ratios are predominantly similar between the two sexes, although males show higher values in FL/SUL ($Z = -2.119$, $p < 0.05$), FM/SUL ($Z = -1.883$, $p = 0.06$), HW/SUL ($Z = -3.119$, $p < 0.01$) and TD/SUL ($Z = -1.942$, $p = 0.52$). Both sexes possess enlarged tusk-like prolongations in the lower jaw as well as the name-bearing 'teeth' on the upper jaw. Male secondary sexual characters are femoral glands, velvety nuptial excrescences on finger I and presence of vocal sacs. Male femoral glands are dark orange (Fig. 6f). Several specimens marked as males in the field lacked obvious secondary sexual characters (femoral glands) and flanks were opened to assess primary sexual characters. Probably due to preservation, femoral glands were not contrasted against the femora, and skin of vocal sacs shrivelled and retracted; however, one male showed no trace of skin modification on femora even if the typical gland position was cut open (ZMB 78262). Webbing formulae show very extensive webbing (Table 7). However, few specimens show a little reduced webbing on toe IV leaving almost the whole distal phalange free (1/1). Dorsal ridges are either long and slender (Fig. 6a–c) or are roundish and knob-like (Fig. 6d). Number of distinct dorsal ridges (counted from spine to flank) ranges between three and seven, usually four to five ridges per body site. However, both characters were not recognisable due to preservation artefacts in many specimens. Glandular ridges on tibia are usually built of small to large conic glands and form more or less interrupted lines (Fig. 6a–d). Dorsal colouration (in life) varies from uniform dark brown or olive, to dark brownish with pale irregular markings, to ochre with brownish spots and dorsal ridges are set off in terms of colour by usually being darker than the remaining dorsum (Fig. 6; Rödel and Bangoura 2004). Male femoral glands are dark orange (Fig. 6f). Belly colouration (in alcohol) is very variable, ranging from completely pale, to dirty smeared pale-dark, to pale reticulation on dark belly, to dark throat and pale belly, to dark throat and belly with pale longitudinal lines to dark with few pale markings, to completely dark, showing no sex-dependant differentiation.

Distribution. Distribution of *Odontobatrachus ziama* is restricted to isolated mountains north of the Nimba Mts. in south-eastern Guinea (Fig. 1). Its range apparently overlaps with *O. natator* as the latter is found in proximity to the Simandou Mountain Range, Massif du Ziama or Mt. Going. However, no syntopic populations are known so far. At present no differing habitat requirements or ecological adaptations are known (Barej et al. 2015), which could explain their spatial separation. Presence of *O. natator* in lower altitudes (e.g. Liberia, Grand Gedeh 250-500 m a.s.l.) could be a factor but both species co-occur in altitudes of app. 500–1300 m a.s.l. in the distribution range of *O. ziama*.

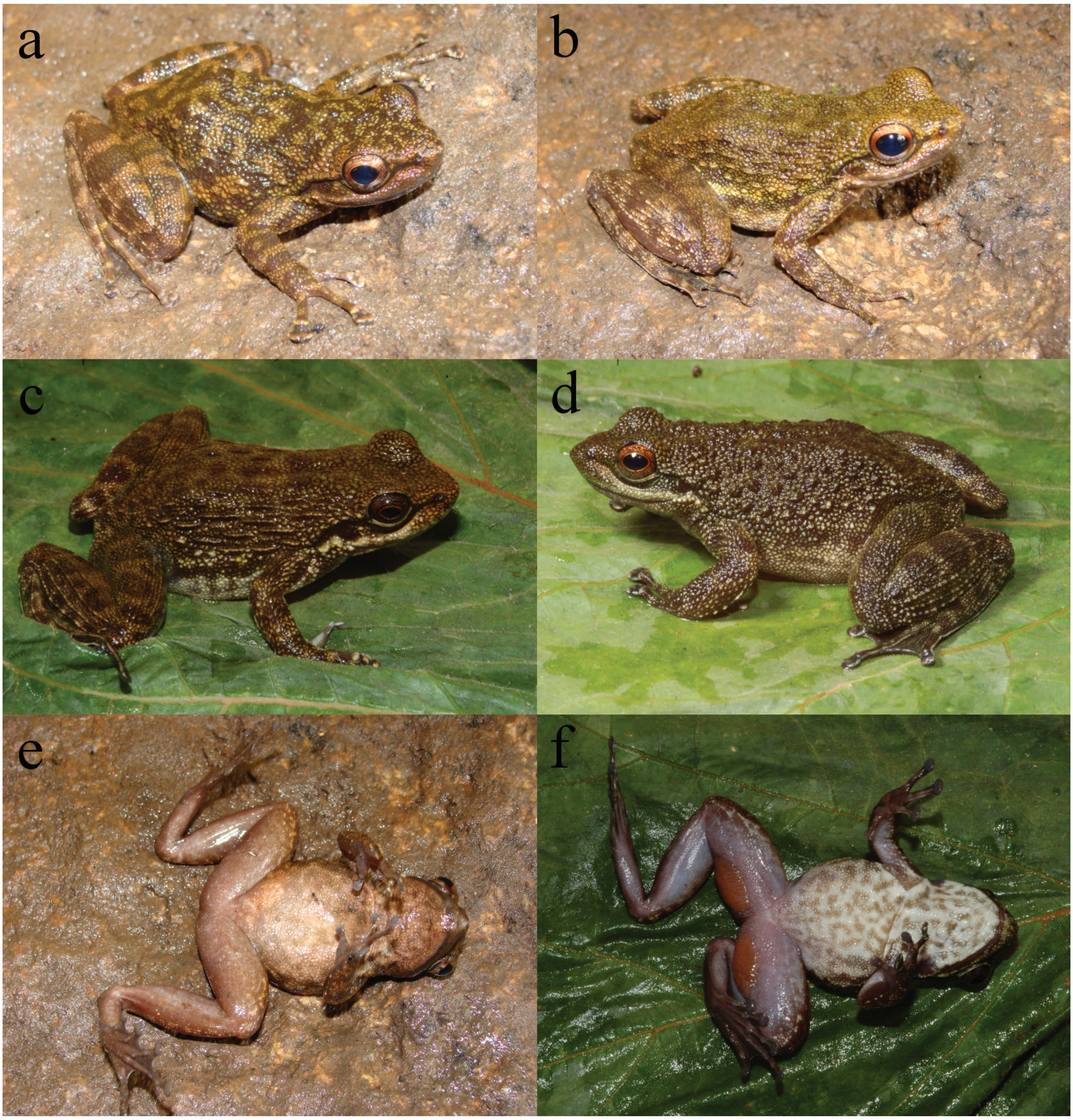

Figure 6. *Odontobatrachus ziama* sp. n. in life: **a**) female paratype ZFMK 95465 Ziama Forest, Guinea; **b**) female paratype MHNG 2731.46, from Ziama Forest, Guinea; **c**) female ZMB 78267, Kankan Region, Guinea; **d**) female ZMB 78263, Kankan Region, Guinea; **e**) ventral view of ZFMK 95465; **f**) colouration of femoral glands in male ZMB 78269. Mind the variation in shape of snout in lateral view from rounded (**b**) to pointed (**d**) and the variation in shape of dorsal ridges ranging from sub-elliptical (**a, b**), elongated (**c**) to conic (**d**).

Natural history remark. *Odontobatrachus ziama* is known as a host of the endoparasitic mite *Endotrombicula pillersi*, otherwise known from members of the family Phrynobatrachidae (Wohltmann et al. 2007).

Etymology. The species epithet *ziama* is a noun in apposition, therefore invariable, referring to the species' type locality, the Ziama Forest, in eastern Guinea.

Common name. We advise to use the term "Ziama torrent-frog" in English and "grenouilles des torrents de Ziama" in French.

Conservation status. The EOO of *O. ziama* is 7797 km^2, placing the species in the category "Vulnerable (VU)" while the AOO of 104 km^2 classifies the species as "Endangered (EN)" (Barej et al. 2015).

Odontobatrachus smithi **Barej, Schmitz, Penner, Doumbia, Sandberger-Loua, Hirschfeld, Brede, Emmrich, Kouamé, Hillers, Gonwouo, Nopper, Adeba, Bangoura, Gage, Anderson & Rödel, sp. n.**

http://zoobank.org/94C996AB-8A52-4439-8F75-13938558A3EB
OTU2 sensu Barej et al. (2015)

Holotype. ZMB 78310 (male), Republic of Guinea, Fouta Djallon, Pita, Hörè Binti (Latitude: 10.83964; Longitude: -12.55572), 510 m a.s.l., 23 July 2010, coll. C. Brede and J. Doumbia.

Paratypes. Guinea: MHNG 2731.47 (female), Mamou Region (10.85; -12.52), 664 m a.s.l., 22 July 2010; ZFMK 95466, ZMB 78306 (2 females), Kindia Region (10.81; -13.34), 314 m a.s.l., 3 October 2010; ZMB 78311 (female), same data as holotype.

Additional material. Guinea: ZMB 78304-05 (2 juveniles), Kindia Region (10.83; -13.81), 253 m a.s.l.; ZMB 78307 (male), Kindia Region (10.81; -13.34), 314 m a.s.l.; ZMB 78308 (female), Kindia Region (10.96; -13.71), 312 m a.s.l.; ZMB 78309 (male), Kindia Region (10.00; -12.34), 92 m a.s.l.; ZMB 78312 (female), ZMB 78313 (juvenile), Mamou Region (10.85; -12.52), 664 m a.s.l.

Diagnosis. Medium to large sized frogs, robust body shape; head narrow, smallest tympanum-eye ratio in the family, highest eye diameter/eye-naris-distance ratio in the family, webbing fully developed, leaving up to 0.5 of the distal phalange free at the inner side of toe II, leaving 0.5-0.75 of the distal phalange free at toe IV; belly pattern very variable, male femoral glands pale orange; glandular lines on tibia contain mean conic glands forming frequently interrupted lines. Genetically *O. smithi* differs by a minimum of 3.79% in the mitochondrial 16S gene from its congeners.

Differential diagnosis. *O. smithi* can be distinguished from its congeners by a combination of characters (characters distinguishing *O. smithi* vs. *O. ziama* see above; for all significant differences see Table 5): growing larger than *O. natator* and *O. arndti* (Tables 1 and 2); male *O. smithi* differ from their congeners by the following ratios (Table 1): GL/GW larger than in *O. natator* and *O. fouta* but smaller than in *O. arndti*; TD/O larger than in *O. natator*; O/EN smaller than in *O. natator* and *O. arndti*; ES/O smaller than in *O. arndti*; female *O. ziama* differ from their congeners by the following ratios (Table 2): HW/SUL larger than in *O. natator* and *O. arndti*; larger TD/O than in *O. natator* and *O. arndti*; O/EN smaller than in *O. natator* and *O. arndti*; TD/SUL larger than in *O. arndti*. Webbing formulae of *O. smithi* are similar to *O. fouta* and *O. arndti*; however, *O. smithi* possesses less webbing on the inner side of toe II, and webbing in *O. natator* is more extensive (Table 7). Femoral glands are pale orange in *O. smithi* but rose-coloured in *O. natator*, dark orange in *O. ziama* and bright orange in *O. fouta* (Figs 4, 6, 8, 10). Glandular lines on tibia contain small to mean sized conic glands forming predominantly interrupted lines (Fig. 8a, b), while small to large glands form more or less interrupted lines in *O. natator* (Fig. 4a–e), small to large glandular conic glands, rather interrupted lines in *O. fouta* (Fig. 10b, c) and small to mean glandular conic glands form hardly interrupted lines in *O. arndti* (Fig. 12b, c). Morphologically, the species is most similar in size and colour pattern to *O. fouta*. However, they differ in a few characters, namely colouration in male femoral glands and belly pattern with both taxa possessing a dark belly colouration, but only *O. fouta* specimens show a smeared pattern.

Genetics. The species is genetically well differentiated from all congeners and known populations form a well-supported and monophyletic clade (Barej et al. 2015). Uncorrected 16S p-distances between *O. smithi* and other *Odontobatrachus* species range from 3.79–5.55%, while maximum intrataxon differences of *O. smithi* add up to 0.54% (mean value 0.20%; N = 45; Appendix 1: Table A).

Holotype description. The male holotype has been assigned to this taxon in the DCA analysis of ratios. The holotype is an adult male with a robust body (Fig. 7): snout-urostyle length of 60.4 mm; head width 21.9 mm; head slightly longer than broad; snout in lateral view short, flattened and slightly pointed at the snout tip; snout in dorsal view triangular, pointed; lower jaw with sharp tusk-like prolongations protruding the skin and single triangular knob at lower jaw symphysis, corresponding socket in between premaxillae weakly developed; upper premaxillae and maxillae with numerous teeth, posteriorly curved; vomerine teeth present, single prolongations; odontophores arranged in short lines, closer to each other than to choanae; tongue broadly heart shaped; horizontal eye diameter 7.9 mm; interorbital distance 5.6 mm; pupil horizontally elliptical; eye diameter distinctly larger than tympanum diameter; tympanum distinct (horizontal diameter 4.0 mm); nares closer to snout than to eye; snout as long as eye diameter; *canthus rostralis* rounded; loreal region concave; paired lateral vocal sacs; forelimbs robust, forearms hypertrophied, fingers slender; prepollex absent; relative finger lengths III>IV>II>I; velvety nuptial excrescences covering finger I; subarticular tubercles large, subconical; supernumerary tubercles absent; fingertips dilated, triangular, notched in the middle; femur length 29.9 mm; tibia length 30.4 mm; femoral glands large (length × width: left: 15.7 × 7.0 mm, right: 15.4 × 7.3 mm); femoral glands positioned on the posterior part of the ventral side of femur; relation femoral gland length to femur length: 0.52; minuscule circular glands running along upper side of tibia; foot length (incl. longest toe) 40.0 mm; relative toe lengths IV>III≥V>II>I; shortest toe (7.1 mm); inner

Figure 7. Male holotype of *Odontobatrachus smithi* sp. n. (ZMB 78310) in ventral and dorsal view (top from left to right, scale bar: 10 mm); head in lateral view, details of pedal webbing, details of hand (bottom left to right, scale bar: 5 mm).

metatarsal tubercle elliptical; toe tips broadened forming triangular dilated discs; inner metatarsal tubercle prominent (4.7 mm); number of subconical subarticular tubercles on toes I-V: 1, 1, 2, 3, 2; supernumerary tubercles absent; prominent skin fold on posterior side of feet; dorsal skin texture rough; dorsum and flanks covered with broad dorsal ridges of app. 3.0–4.0 mm (partially flattened, but recognisable as darker spots); venter somewhat rough and slightly granular; flank texture rough and granular as dorsum; webbing fully developed (0-1/0-1/0-1/1-0)), skin fringe running along toe III, webbing between toes hardly concave. Damage to the male holotype: transverse cut at pectoral region (liver tissue sampled) and skin cut on throat; glandular dorsal ridges partially not recognisable due to preservation.

Colouration of holotype in alcohol (Fig. 7). Dorsum dark brownish, few pale marblings recognisable; hind limbs with dark blotches on upper side; entire throat dark

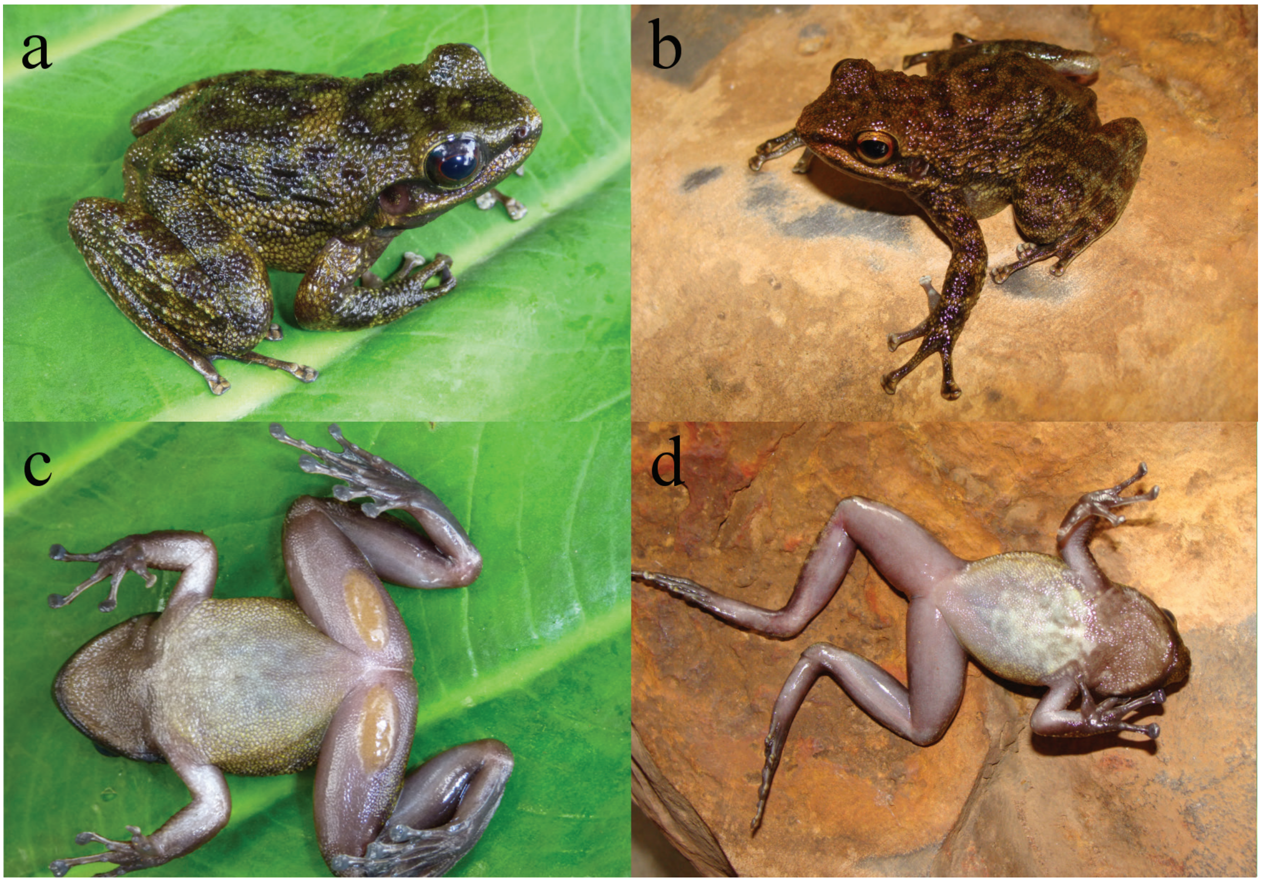

Figure 8. *Odontobatrachus smithi* sp. n. in life: **a**) male ZMB 78307, Kindia Region, Guinea; **b**) female paratype MHNG 2731.47, Fouta Djallon: Pita, Hörè Binti, Guinea); **c**) colouration of femoral glands in ZMB 78307; **d**) ventral view of female paratype MHNG 2731.47.

showing minuscule pale dots; venter dark; pale colouration between axillaries and elbows, femoral glands pale, clearly silhouetted from femora, with blurred minuscule dark dots; femora and tibia dark as belly.

Variation. Females ($N_{females}$ = 6) grow larger than males (N_{males} = 3), mean SUL in females 54.1 mm and 48.9 mm in males and accordingly absolute values for extremities are larger too. However, ratios between the two sexes overlap in their range, and are very similar in their mean values showing only minor differences (Tables 1 and 2). Both sexes possess enlarged tusk-like prolongations in the lower jaw as well as the name-bearing 'teeth' on the upper jaw. Male secondary sexual characters are femoral glands, velvety nuptial excrescences on finger I and presence of vocal sacs. Male femoral glands are pale orange (Fig. 8d). Webbing formulae showed little variance in this character (Table 7). Dorsal ridges are usually elongated and slender (Fig. 8a, b). Number of distinct dorsal ridges (counted from spine to flank) ranges between four and seven, usually five to six ridges per body site. However, this character was not recognisable in all vouchers due to preservation artefacts. Glandular ridges on tibia usually are built of small to large conic glands and form more or less interrupted lines (Fig. 8a, b). Dorsal colouration (in life) ochre coloured with dark brown markings along dorsal glandular ridges or greenish with dark grey markings. Male femoral glands are pale orange (Fig. 8c). Belly colouration (in alcohol) is mainly uniform dark, only few specimens possess paler markings or show a dirty smeared colouration, showing no sex-dependant differentiation.

Distribution. Distribution of *Odontobatrachus smithi* is restricted to localities in western Guinea on the western and southern edge of the Fouta Djallon Highlands and its western extensions to the Kindia region (Fig. 1). Its easternmost localities are in proximity of *O. fouta*. However, *O. smithi* seems to occupy lowland to mid-altitudes (app. 100–650 m a.s.l.) while *O. fouta* occurs in mid-altitudes (app. 650–900 m a.s.l.).

Etymology. The species epithet *smithi* refers to Major F. Smith of the Royal Army Medical Corps (R.A.M.C.). In addition to his studies on blackwater fever he contributed to our knowledge on West African amphibians and collected the first specimens of *Petropedetes natator* Boulenger, 1905 in Sierra Leone during his military service in West Africa.

Common name. We advise to use the term "Smith's torrent-frog" in English and "grenouilles des torrents de Smith" in French.

Conservation status. The EOO of *Odontobatrachus smithi* is 12673 km^2, placing the species in the category "Vulnerable (VU)" while the AOO of 40 km^2 even classifies the species as "Endangered (EN)" (Barej et al. 2015).

Odontobatrachus fouta Barej, Schmitz, Penner, Doumbia, Brede, Hillers & Rödel, sp. n.

http://zoobank.org/D7A22E4A-430A-45E6-81DC-8E0792B442A2
OTU3 sensu Barej et al. (2015)

Holotype. ZMB 78314 (adult male), Republic of Guinea, Fouta Djallon, Labé, Sala (Latitude: 11.29389; Longitude: -12.50178), 916 m a.s.l., 18 July 2010, coll. C. Brede and J. Doumbia.

Paratypes. Guinea: ZMB 78314, MHNG 2731.48 (2 females), same data as holotype.

Additional material. Guinea: ZMB 78316 (female), same data as holotype; ZMB 78317-18 (2 males), Mamou Region (10.82; -12.19), 760 m a.s.l.; ZMB 78319 (juvenile), Labé Region (11.29; -12.51), 882 m a.s.l.; ZMB 78320, ZMB 78323 (2 females), ZMB 78322 (male), ZMB 78321, ZMB 78324-5 (3 juveniles), Mamou Region (10.34; -12.17), 652 m a.s.l.

Diagnosis. Medium to large sized frogs, robust body shape; head narrow, low mean eye diameter/eye-naris distance ratio, highest tympanum diameter orbita diameter ratio in the family, webbing fully developed, leaving 0.75 of the distal phalange free at the inner side of toe II, leaving the distal phalange at toe IV free; belly colouration typically dark, male femoral glands bright orange; glandular lines on tibia contain mean conic glands forming frequently interrupted lines. Genetically *O. fouta* differs by a minimum of 3.79% in the mitochondrial 16S gene from its congeners.

Differential diagnosis. *O. fouta* can be distinguished from its congeners by a combination of characters (characters distinguishing *O. smithi* vs. *O. ziama* and *O. fouta* see above; for all significant differences see Table 5): SUL in *O. fouta* is larger than in *O. natator* and *O. arndti* (Tables 1 and 2); male *O. fouta* differ from their congeners by the following ratios (Table 1): GL/GW smaller than in *O. natator* and *O. arndti*; TD/O and O/EN smaller than in *O. natator*; female *O. fouta* differ from their congeners by the following ratios (Table 2): TD/O larger than in *O. natator* and *O. arndti*; O/EN smaller than in *O. natator* and *O. arndti*; ES/O and TD/SUL larger than in *O. arndti*. Webbing in *O. fouta* is generally less extensive than in *O. natator* and shows less webbing on the inner side of toe II than in *O. arndti* (Table 7). Femoral glands are bright orange in *O. fouta* but rose-coloured in *O. natator*, pale orange in *O. smithi* and dark orange in *O. ziama* (Figs 4, 6, 8, 10). Glandular lines on tibia contain small to large glandular conic glands, rather interrupted lines (Fig. 10b, c), while similar to *O. fouta* small to large glands form more or less interrupted lines in *O. natator* (Fig. 4a–e), and small to mean glandular conic glands form hardly interrupted lines in *O. arndti* (Fig. 12b, c).

Genetics. The species is genetically well differentiated from all congeners and known populations form a well-supported and monophyletic clade (Barej et al. 2015). Uncorrected 16S p-distances between *O. fouta* and other *Odontobatrachus* species range from 3.79–4.98%, while maximum intrataxon differences of *O. fouta* reach 0.36% (mean value 0.15%; N = 55; Appendix 1: Table A).

Holotype description. The male holotype has been assigned to this taxon in both DCA analyses (absolute values and ratios). The holotype is an adult male with a robust body (Fig. 9): snout-urostyle length of 55.6 mm; head width 21.6 mm; head slightly longer than broad; snout in lateral view short, flattened and slightly rounded; snout in dorsal view triangular, tip fairly rounded; lower jaw with sharp tusk-like prolongations protruding the skin and single triangular knob at lower jaw symphysis, corresponding socket in between premaxillae weakly developed; upper premaxillae and maxillae with numerous teeth, posteriorly curved; vomerine teeth present, single prolongations; odontophores arranged in short lines, closer to each other than to choanae, skin around vomerine teeth dark; tongue broadly heart shaped; horizontal eye diameter 7.7 mm; interorbital distance 5.9 mm; pupil horizontally elliptical; eye diameter distinctly larger than tympanum diameter; tympanum distinct (horizontal diameter 3.1 mm); nares closer to snout than to eye; snout as long as eye diameter; *canthus rostralis* rounded; loreal region concave; paired lateral vocal sacs; forelimbs robust, forearms hypertrophied, fingers slender; prepollex absent; relative finger lengths III>IV>II>I (Fig. 9); velvety nuptial excrescences covering finger I; subarticular tubercles large, subconical; supernumerary tubercles absent; fingertips dilated, slightly triangular; femur length 27.8 mm; tibia length 28.9 mm; femoral glands large (length × width: left: 14.2 × 8.0 mm, right 14.3 × 8.7 mm); femoral glands positioned on the posterior part of the ventral side of femur; relation femoral gland length to femur length: 0.51; minuscule circular glands running along upper side of tibia; foot length (incl. longest toe) 38.0 mm; relative toe lengths IV>III≥V>II>I (Fig. 9); shortest toe 7.2 mm; inner metatarsal tubercle elliptical; toe tips broadened forming triangular dilated discs; inner metatarsal tubercle prominent (4.5 mm); number of subconical subarticular tubercles on toes I-V: 1, 1, 2, 3, 2; supernumerary tubercles absent; prominent skin fold on posterior side of feet; dorsal skin texture rough; dorsum and flanks covered with slender dorsal ridges of app. 2.0–5.0 mm, mainly positioned dorsolaterally (partially

Figure 9. Male holotype of *Odontobatrachus fouta* sp. n. (ZMB 78314) in ventral and dorsal view (top from left to right, scale bar: 10 mm); head in lateral view, details of pedal webbing, details of hand (bottom left to right, scale bar: 5 mm).

flattened); venter somewhat rough and slightly granular; flank texture rough and granular as dorsum; webbing fully developed (0-0.75/0-1/0-1/1-0), skin fringe running along toe III, webbing between toes hardly concave. Damage of the male holotype: transverse cut at pectoral region (liver tissue sampled); glandular dorsal ridges partially not recognisable due to preservation.

Colouration of holotype in alcohol (Fig. 9). Dorsum dark brownish; hind limbs with dark blotches on upper side, few pale lines recognisable; entire dirty blurred dark and pale, with several scratches (scars); venter as throat on the anterior part, more reticulated pattern on the belly; colouration between axillaries and elbows brighter; femoral glands pale, clearly silhouetted from femora, with blurred minuscule dark dots, posterior part darker; femora and tibia dark as belly.

Variation. Females ($N_{females}$ = 4) grow larger than males (N_{males} = 3), maximum SUL in females 62.5 mm and

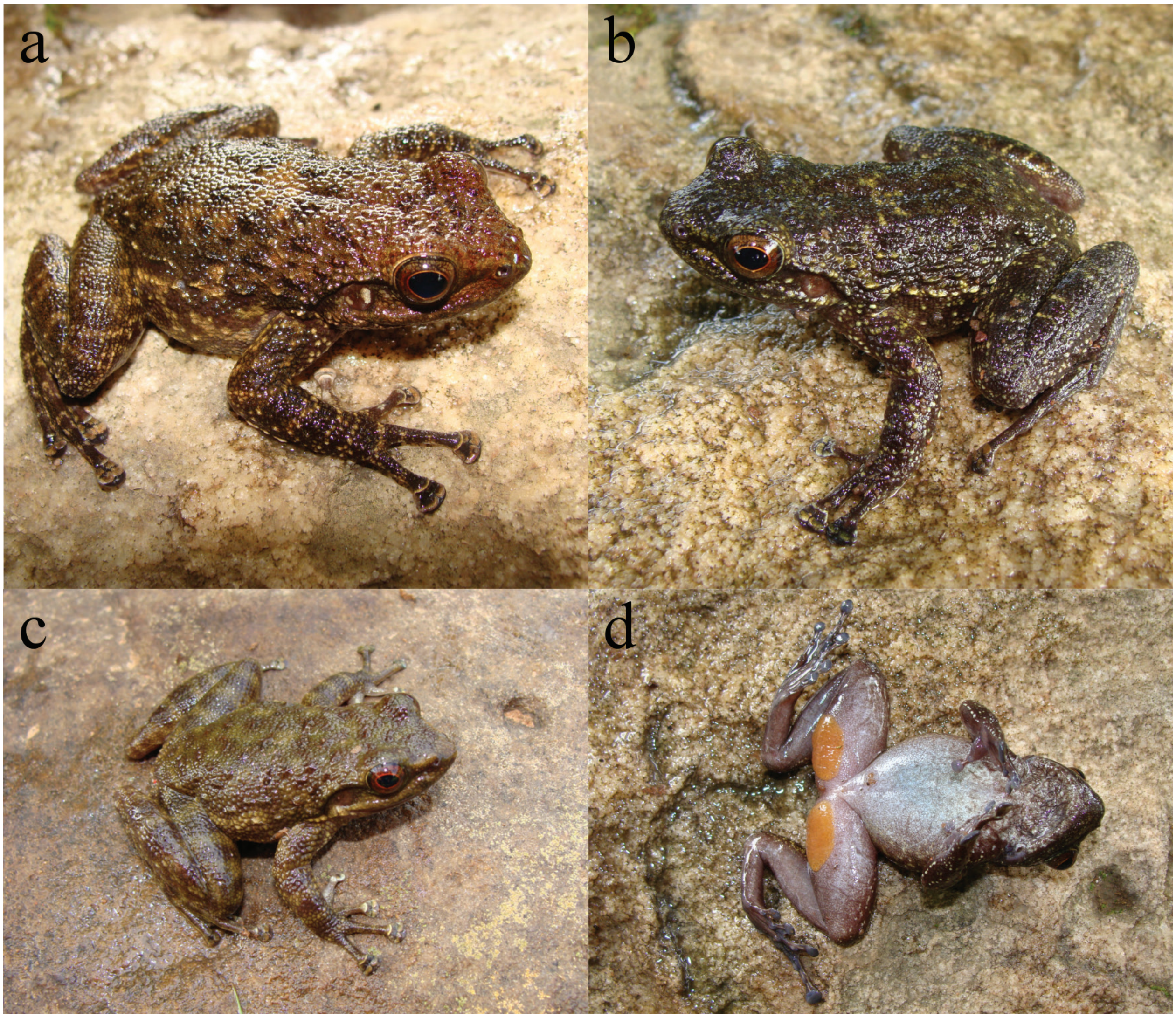

Figure 10. *Odontobatrachus fouta* sp. n. in life: **a**) female paratype ZMB 78315, Fouta Djallon: Labé, Sala, Guinea; **b**) male holotype ZMB 78314, Fouta Djallon: Labé, Sala, Guinea; **c**) male Dalaba\Chute de Ditinn, Guinea; **d**) colouration of femoral glands in the male holotype ZMB 78314.

57.0 mm in males, and absolute values for extremities are accordingly larger, too (Tables 1 and 2). However, males and females have similar ratios and mean values. Both sexes possess enlarged tusk-like prolongations in the lower jaw as well as the name-bearing 'teeth' on the upper jaw. Male secondary sexual characters are femoral glands, velvety nuptial excrescences on finger I and presence of vocal sacs. Webbing formulae showed little variance (Table 7). Dorsal ridges are short and knobbed (Fig. 10a) or elongated and slender (Fig. 10b). Number of distinct dorsal ridges (counted from spine to flank) ranges between three and six ridges per body site, usually four to five ridges per body site. However, this character was not recognisable due to preservation artefacts in all specimens. Glandular ridges on tibia usually are built of small to large conic glands and form rather interrupted lines (Fig. 10b, c). Dorsal colouration (in life) ochre coloured with dark brown markings along dorsal glandular ridges or almost uniform dark with few whitish markings along flanks and on dorsum. Male femoral glands are bright orange (Fig. 10d). Belly colouration (in alcohol) is mainly uniform dark, only few specimens possess paler markings or show a dirty smeared colouration, showing no sex-dependant differentiation.

Distribution. The distribution of *Odontobatrachus fouta* is restricted to isolated peaks in the central Fouta Djallon Highlands in western Guinea (Fig. 1). Localities of *O. natator* at the southern edge and of *O. smithi* close to western-central of the Fouta Djallon Highlands are in close proximity to *O. fouta.* However, *O. fouta* occurs in higher altitudes (southern edge: *O. natator* app. 500 m a.s.l. and *O. smithi* app. 92 m a.s.l. vs. *O. fouta* app. 650 m a.s.l.; western-central: *O. smithi* app. 510–650 m a.s.l. vs. *O. fouta* app. 750–900 m a.s.l.).

Etymology. The species epithet *fouta* is a noun in apposition, therefore invariable, referring to the species' type locality, the Fouta Djallon Highlands, in western Guinea.

Common name. We advise to use the term "Fouta Djallon torrent-frog" in English and "grenouilles des torrents de Fouta Djallon" in French.

Conservation status. Both, the EOO of 1318 km^2 and the AOO of 20 km^2 classify *O. fouta* as "Endangered (EN)" (Barej et al. 2015).

Odontobatrachus arndti Barej, Schmitz, Penner, Doumbia, Sandberger-Loua, Emmrich, Adeba & Rödel, sp. n.

http://zoobank.org/542C46CE-2B91-41AC-8314-5F84469AED04
OTU4 sensu Barej et al. (2015)

Holotype. ZMB 78355 (male), Republic of Guinea, Nimba Mts., River Mandey (Latitude: 7.64786; Longitude: -8.42397), 694 m a.s.l., 18 June 2009, coll. L. Sandberger-Loua and J. Doumbia.

Paratypes. Guinea: MHNG 2731.49 (male), ZMB 78356 (female), N'Zérékoré Region (7.65; -8.42), 670 m a.s.l., 18 June 2009; MHNG 2731.50, ZMB 78357 (2 females), N'Zérékoré Region (7.63; -8.41), 1121 m a.s.l., 4 November 2011; ZFMK 95467 (female), ZFMK 95468 (male), N'Zérékoré Region (7.65; -8.42), 674 m a.s.l., 2 January 2011; ZMB 78354 (female), same data as holotype.

Additional material. Côte d'Ivoire: ZMB 78326, ZMB 78329 (3 females), ZMB 78327-8 (2 males), Dix-Huit Montagnes Region (7.85; -7.39), app. 500 m a.s.l. Liberia: ZMB 78332 (male), Nimba County (7.56; -8.64), 647 m a.s.l.; ZMB 78333-35 (3 males), Nimba County (7.48; -8.58), 513 m a.s.l. Guinea: ZMB 78336 (female), ZMB 78337-39 (3 males), N'Zérékoré Region (7.61; -8.27), 400 m a.s.l.; ZMB 78340-41 (2 females), N'Zérékoré Region (7.61; -8.26), 460 m a.s.l.; ZMB 78342 (juvenile), N'Zérékoré Region (7.70; -8.40), 751 m a.s.l.; ZMB 78343, ZMB 78345 (2 females), ZMB 78344, ZMB 78346 (2 males), N'Zérékoré Region (7.70; -8.40), 760 m a.s.l.; ZMB 78347 (male), N'Zérékoré Region (7.71; -8.41), 518 m a.s.l.; ZMB 78348 (male), ZMB 78349 (female), N'Zérékoré Region (7.70; -8.40), 764 m a.s.l.; ZMB 78350-1 (2 females), ZMB 78352 (male), N'Zérékoré Region (7.68; -8.39), 1027 m a.s.l.; ZMB 78353 (juvenile), N'Zérékoré Region (7.65; -8.42), 670 m a.s.l.; ZMB 78358-59 (2 males), N'Zérékoré Region (7.65; -8.34), 577 m a.s.l.; ZMB 78360 (female), ZMB 78361 (male), N'Zérékoré Region (7.65; -8.36), 815 m a.s.l.; ZMB 78362 (female), ZMB 78363 (male), N'Zérékoré Region (7.63; -8.35), 652 m a.s.l.; ZMB 78364, ZMB 78367 (2 females), ZMB 78365-6 (2 males), N'Zérékoré Region (7.65; -8.37), 949 m a.s.l.; ZMB 78368 (female), ZMB 78369 (male), N'Zérékoré Region (7.67; -8.37), 1317 m a.s.l.; ZMB 78370 (male), ZMB 78371 (female), N'Zérékoré Region (7.67; -8.37), 1234 m a.s.l.; ZMB 78372 (female), ZMB 78373 (male), N'Zérékoré Region (7.62; -8.42), 1154 m a.s.l.; ZMB 78374 (female), ZMB 78375 (male), N'Zérékoré Region (7.62; -8.45), 701 m a.s.l.; ZMB 78376 (female), ZMB 78377 (male), N'Zérékoré Region (7.63; -8.44), 750 m a.s.l.; ZMB 78378 (female), ZMB 78379 (male), N'Zérékoré Region (7.67; -8.35), 786 m a.s.l.; ZMB 78380 (female), ZMB 78381 (male), N'Zérékoré Region (7.67; -8.40), 998 m a.s.l.

Diagnosis. Medium to large sized frogs, robust body shape; head narrow, highest eye diameter/eye-naris-distance ratio in the family, low mean tympanum diameter orbita diameter ratio, webbing almost fully developed, leaving 0.25–0.5 of the distal phalange free at the inner side of toe II, leaving 0.75–1 of the distal phalange free at toe IV, belly pattern very variable, glandular lines on tibia contain mean conic glands forming frequently interrupted lines. Genetically *O. arndti* differs by a minimum of 2.89% in the mitochondrial 16S gene from its congeners.

Differential diagnosis. *O. arndti* can be distinguished from its congeners by a combination of characters (characters distinguishing *O. arndti* vs. *O. ziama*, *O. smithi* and *O. fouta* see above; for all significant differences see Table 5): male *O. arndti* differ from *O. natator* by the following ratios (Table 1): larger TI/SUL, FL/SUL, O/EN and smaller HW/SUL, TD/O, IT/FL, TD/SUL in *O. arndti* than in *O. natator*; female *O. arndti* differ from *O. natator* by the following ratios (Table 2): smaller FM/TI, HW/SUL and O/EN larger in *O. arndti* than in *O. natator*. Webbing formulae are very similar in the two species (Table 7). Glandular lines on tibia contain small to mean conic glands forming hardly interrupted lines in *O. arndti* (Fig. 12b, c), while similar to *O. fouta* small to large glands form more or less interrupted lines in *O. natator* (Fig. 4a–e).

Genetics. The species is genetically well differentiated from all congeners and known populations form a well-supported and monophyletic clade (Barej et al. 2015). Uncorrected 16S p-distances between *O. arndti* and other *Odontobatrachus* species range from 2.89–5.55%, while maximum intrataxon differences of *O. arndti* add up to 0.58% (mean value 0.05%; N = 861; Appendix 1: Table A).

Holotype description. The male holotype has been assigned to this taxon in both DCA analyses (absolute values and ratios). The holotype is an adult male with a slightly robust body (Fig. 11): snout-urostyle length of 48.8 mm; head width 17.1 mm; head slightly longer than broad; snout in lateral view short, flattened and rounded at the snout tip; snout in dorsal view triangular, rounded; lower jaw with sharp tusk-like prolonga-

Figure 11. Male holotype of *Odontobatrachus arndti* sp. n. (ZMB 78355) in ventral and dorsal view (top from left to right, scale bar: 10 mm); head in lateral view, details of pedal webbing, details of hand (bottom left to right, scale bar: 5 mm).

tions protruding the skin and single triangular knob at lower jaw symphysis, corresponding socket in between premaxillae; upper premaxillae and maxillae with numerous teeth, posteriorly curved; vomerine teeth present, arranged in two small odontophores, closer to each other than to choanae; tongue broadly heart shaped; horizontal eye diameter 7.6 mm; interorbital distance 5.2 mm; pupil horizontally elliptical; eye diameter distinctly larger than tympanum diameter; tympanum distinct (horizontal diameter 2.7 mm); nares closer to snout than to eye; snout shorter than eye diameter; *canthus rostralis* rounded; loreal region concave; paired lateral vocal sacs; forelimbs robust, forearms hypertrophied, fingers slender; prepollex absent; relative finger lengths III>IV>II>I; velvety nuptial excrescences weakly developed on finger I; subarticular tubercles large, subconical; supernumerary tubercles absent; fingertips dilated, triangular, notched in the middle; femur length 24.6 mm; tibia length 26.3 mm; femoral glands large (length × width: left: 12.9 × 8.0 mm, right: 13.1 × 7.8

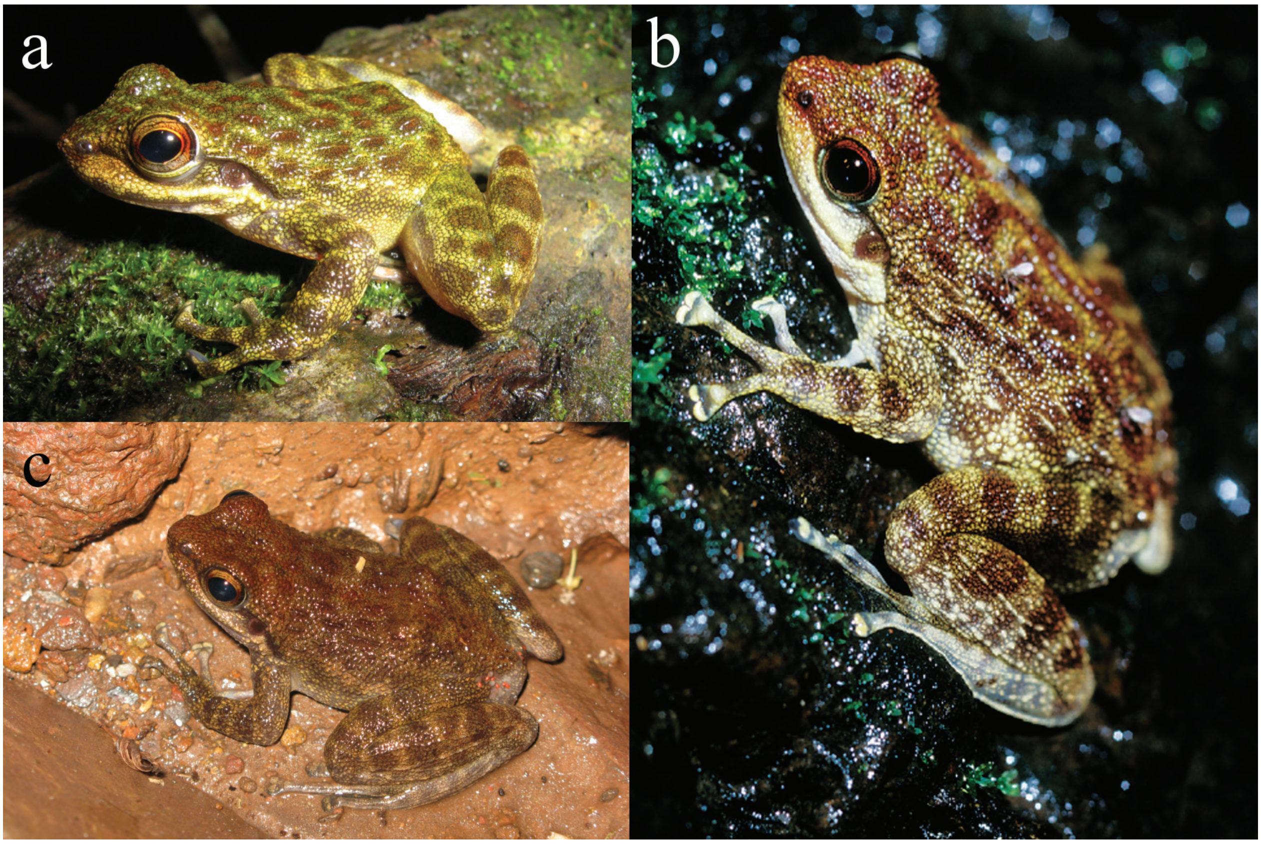

Figure 12. *Odontobatrachus arndti* sp. n. in life: **a**) and **c**) Nimba Mts, Guinea; **b**) Mt. Sangbé, Côte d'Ivoire. Non vouchered specimens. Note parasitic mites (minuscule red dots) close to the cloaca in (**c**).

mm); femoral glands positioned on the posterior part of the ventral side of femur; relation femoral gland length to femur length: 0.53; minuscule circular glands running along upper side of tibia; foot length (incl. longest toe) 34.9 mm; relative toe lengths IV>III>V>II>I; shortest toe 6.4 mm; inner metatarsal tubercle elliptical; toe tips broadened forming triangular dilated discs; inner metatarsal tubercle prominent (3.8 mm); number of subconical subarticular tubercles on toes I-V: 1, 1, 2, 3, 2; supernumerary tubercles absent; prominent skin fold on posterior side of feet; dorsal skin texture heterogeneous; dorsum and flanks covered with slender dorsal ridges of app. 2.5-3.5 mm (partially flattened); venter with fine granulation; flank texture rough and granular as dorsum; webbing fully developed (0-0/0-1/0-0.75/0.75-0); webbing between toes hardly concave. Damage of the male holotype: cut at pectoral region (liver tissue sampled) and skin cut on right lumbar region (in ventral view); glandular dorsal ridges partially not recognisable due to preservation.

Colouration of holotype in alcohol (Fig. 11). Dorsum dark brownish, few paler marblings; hind limbs coloured as dorsum; throat pale with few darker marblings; venter pale, area around incision darker; pale colouration between axillaries and elbows, femoral glands pale, clearly silhouetted from femora, with blurred minuscule reticulation; femora and tibia pale as belly.

Variation. Females are significantly larger than males (SUL: $Z = -4.933$, $p < 0.001$, $N_{males} = 26$, $N_{females} = 24$), max SUL in females 64.0 mm and 53.6 mm in males, and consequently possess longer extremities (FM: $Z = -3.894$, $p < 0.001$; TI: $Z = -4.458$, $p < 0.001$; FL: $Z = -4.264$, $p < 0.001$), broader heads (HW: $Z = -4.090$, $p < 0.001$), longer snouts (EN: $Z = -2.678$, $p < 0.01$; ES: $Z = -2.906$, $p < 0.01$) and larger eyes ($Z = -2.779$, $p < 0.01$), larger TD ($Z = -2.214$, $p < 0.05$). However, ratios are predominantly similar between the two sexes, although males show higher values in FL/SUL ($Z = -2.214$, $p < 0.05$), FM/SUL ($Z = -2.932$, $p < 0.01$), FM/TI ($Z = -3.010$, $p < 0.01$) and HW/SUL ($Z = -4.136$, $p < 0.001$). Both sexes possess enlarged tusk-like prolongations in the lower jaw as well as the name-bearing 'teeth' on the upper jaw. Male secondary sexual characters are femoral glands, velvety nuptial excrescences on finger I and presence of vocal sacs. Webbing formulae showed little variance (Table 7). However, some specimen possess a more extensive webbing on toe IV (0.5/0.5). Dorsal ridges are elongated and slender (Fig. 12a–c). Number of distinct dorsal ridges (counted from spine to flank) ranges between three and six, usually four to five ridges per body site. Glandular ridges on tibia usually are built of small to mean conic glands and form hardly interrupted lines (Fig. 12b, c). However, both characters were not recognisable due to preservation artefacts in many specimens. Dorsal colouration (in life) varies from almost black, beige with reddish-brown spots ar-

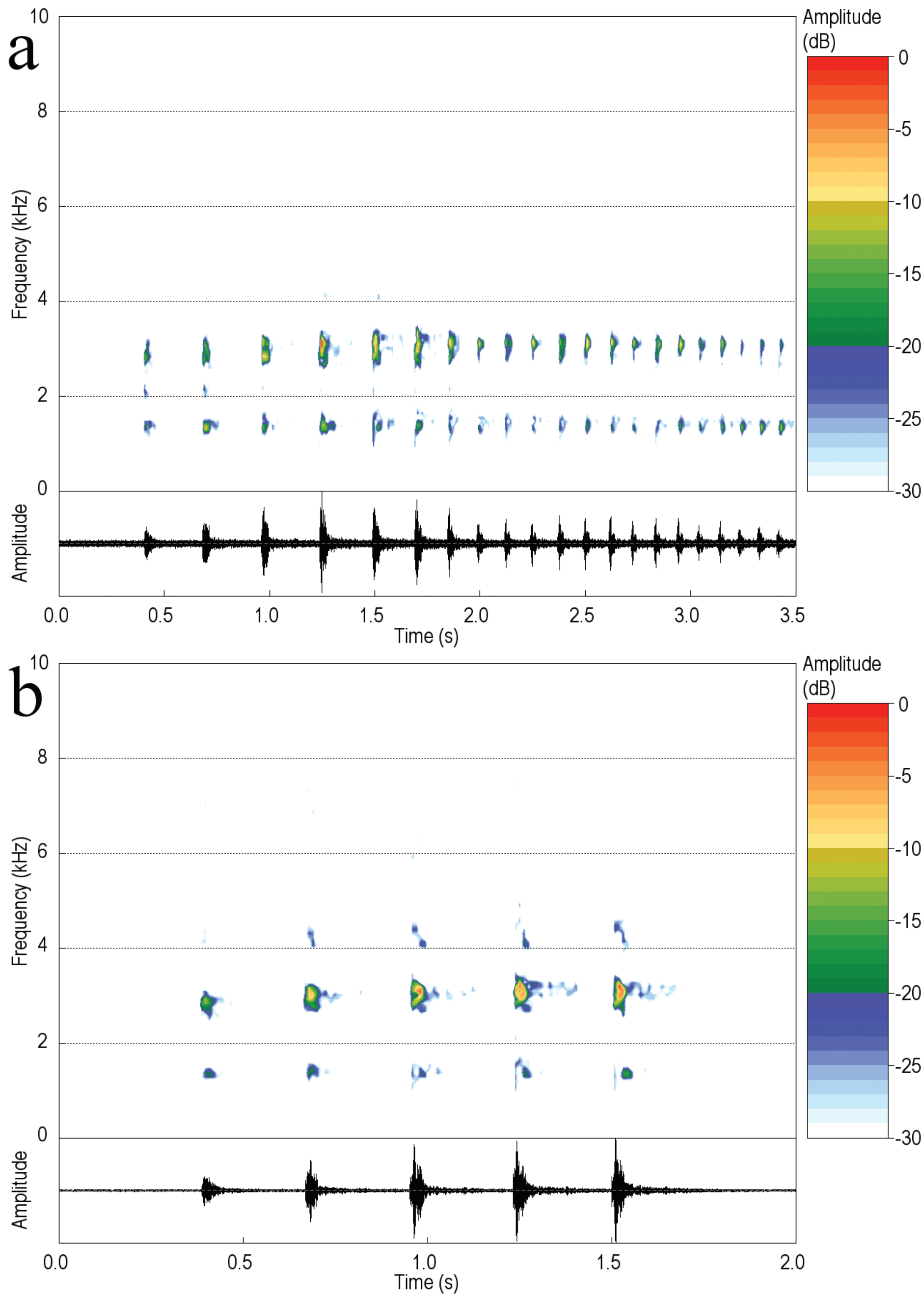

Figure 13. Spectrogram and oscillogram of two calls of *Odontobatrachus arndti* sp. n. from Nimba Mts., Guinea with a dominant frequency of app. 2800-3400 Hz, a fundamental frequency of app. 1400-1700 Hz and 22 notes showing decreasing pause duration between notes (**a**) and 5 notes with constant pauses between notes (**b**).

ranged in longitudinal lines (Fig. 12; Guibé and Lamotte 1958; Rödel and Bangoura 2004). Male femoral glands are yellow (Rödel 2003). Belly colouration (in alcohol) is very variable, ranging from completely whitish, dirty whitish, a distinct reticulation pattern, dark throat with marbling on belly, marbling on throat and belly blurring to paler colouration posteriorly, to completely dark throat and belly, showing no sex-dependant differentiation.

Acoustics. Three calls of *Odontobatrachus arndti* were recorded from specimens in terraria. Calls sound like a repeat of “chucks”, consisting of several tonal notes. Two harmonics were visible (Fig. 13), the second harmonic being the dominant frequency (2842.4–3359.2 Hz), the first being the fundamental frequency (1421.2–1679.6 Hz). The call duration ranged from 1.2 to 3.0 s. One call comprised 22 notes (Fig. 13a) and the other two comprised five notes each (Fig. 13b). Each note had a duration of 34.7 ± 0.01 ms (N = 32). The notes were separated from each other by pauses of 238.0 ± 0.01 ms (N = 12) with the two calls comprising five notes (Fig. 13b). Pause duration in the third call (22 notes) was decreasing from 160.0 to 67.0 ms from the beginning towards the end of the call (Fig. 13a). Rödel’s (2003) anecdotal report of a torrent frog call from Mt. Sangbé (Côte d'Ivoire) comprising a series of click sounds with ever-shorter intervals corresponds to the second call type (22 notes).

Distribution. *Odontobatrachus arndti* is known to occur on the Nimba Mts. in Guinea and Liberia, the adjacent areas at Mt. Gangra (Liberia) and Déré (Guinea), as well as the Mt. Sangbé in western Côte d'Ivoire (Fig. 1). This taxon represents the easternmost representative of the family. Localities at the southern end of the Nimba Mts. and along Mt. Gangra are in very close proximity to *O. natator*. Both species inhabit similar altitudes at the foot of the Nimba Mts. However, at present no differing habitat requirements or ecological adaptations are known (Barej et al. 2015), which could explain their spatial separation.

Etymology. The species epithet *arndti* was chosen in order to honour Prof. emerit. Dr. Rudolf G. Arndt, New Jersey USA, for his trust in young academics and his invaluable support of this study.

Common name. We advise to use the term "Arndt's torrent-frog" in English and "grenouilles des torrents d'Arndt" in French.

Conservation status. Both, the EOO of 2595 km^2 and the AOO of 156 km^2 classify *O. arndti* as "Endangered (EN)" (Barej et al. 2015).

Conclusive summary

Only recently, biogeographic separation of molecular lineages identified the monospecific West African torrent-frog family Odontobatrachidae as a complex of cryptic species (Barej et al. 2015). In contrast to studies that predominantly rely on genetics in diagnoses of new species (Jörger and Schrödl 2013; Satler et al. 2013; Petzold et al. 2014), no taxonomic actions were conducted in the case of the *Odontobatrachus natator*-complex. Phylogeographic insights formed the basis for our assessment of morphological characters which led to the formal description of four new species with distinguishing morphological characters.

Odontobatrachus species are phenetically very similar and show an overlap in their morphometrics. Nonetheless, males and females of all species are statistically distinguishable in their metrics and following McLeod et al. (2012), we could confirm that DCAs provided a reasonable method to assign individuals to single species when morphometrics and ratios show no obvious differentiation.

The application of qualitative characters for species differentiation was difficult and previously used diagnostic characters to distinguish *Odontobatrachus* populations (see Rödel and Bangoura 2004; Rödel et al. 2004a), which are appropriate and important in non-related genera, like shape arrangement of dorsal glandular ridges in *Ptychadena* (Guibé and Lamotte 1957; Perret 1979; Rödel 2000) or ventral colouration in *Phrynobatrachus* (Rödel et al. 2012b; Zimkus and Gvoždík 2013), are not applicable in this family. Specimens belonging to one species from a single locality for example, already show high character variability (see e.g. Fig. 6c, d for glandular ridges in *O. ziama*). Yet, despite problems due to preservation artefacts, a few qualitative diagnostic characters (e.g. shape of the glandular line on tibia, differences in webbing formulae) could be successfully used (Table 7). All subtle differences between *Odontobatrachus* species are supported genetically, with interspecies differences of 2.89–5.55% in 16S rRNA uncorrected p-distance (Barej et al. 2015; Appendix 1: Table A) corresponding to species-level in non-related taxa and additionally, *Odontobatrachus* species are geographically isolated.

Thus, knowledge of the origin of vouchers can narrow down the potential species assignment, because only *O. natator* is widely distributed, from western Guinea to eastern Liberia and southeastern Guinea, while *O. fouta* and *O. smithi* occur only in the westernmost range of that distribution and *O. arndti* and *O. ziama* occur only in the easternmost range. Still, it would be somewhat unsatisfactory, if solely genetics provided a warranted identification of single specimens in areas of distributional overlap between morphologically rather indistinguishable species (Real et al. 2005). Fortunately, following an integrative approach, the consideration of molecular data, distribution patterns, and morphology, rendered recognition of different *Odontobatrachus* species comprehensible despite their superficial similarity. The similarity in morphology of *Odontobatrachus* species likely results from speciation lacking distinct external changes (Bickford et al. 2007), probably because the most conspicuous characters are all adaptations to the habitat of fast flowing streams. The *Odontobatrachus* species all exhibit a torrent-frog'-habitus as likewise independently developed in various non-related taxa (e.g. Petropedetidae: *Petropedetes*, *Arthroleptides*, Barej et al. 2010, 2014a, b; Hylodidae: *Hylodes*, Haddad and Giaretta 1999; Heleophrynidae: *Heleophryne*, *Hadromophryne*, Minter et al. 2004; Ranidae: *Staurois*, Matsui et al. 2007). Adults usually possess a rather flattened body shape and head, allowing them to hide between crevices and under rocks. Their extremities are long, terminal phalanges enlarged and digits on hands and feet spatulated offering a larger contact area with the slippery substrate (Minter et al. 2004; Scott 2005; Kamermans and Vences 2009). Torrent-frog tadpoles have a streamlined habitus with distinct tail musculature and a sucker-like mouth which are used to cling or climb on rocks (Barej et al. 2010; Minter et al. 2004). It seems likely that any radical deviation from that morphotype could have negative effects on species survival.

Recognition and description of species is just a first step which provides the baseline for subsequent studies to gather further data on the ecology or behaviour – or

Table 7. Important morphological features and measurements (in mm) that can be applied for species identification in West African torrent-frogs *Odontobatrachus*. See material and methods section for abbreviations.

	O. natator	***O. ziama* sp. n.**	***O. smithi* sp. n.**	***O. fouta* sp. n.**	***O. arndti* sp. n.**
OTU sensu Barej et al. (2015)		OTU1	OTU2	OTU3	OTU4
distribution	western to eastern Upper Guinea	eastern Upper Guinea (Simandou Mtn. Range)	western Upper Guinea (Fouta Djallon, Boffa)	western Upper Guinea (Fouta Djallon)	eastern Upper Guinea (Nimba Mts., Mt. Sangbé)
femoral glands in males	present	present	present	present	present
tusk-like odontoids	present	present	present	present	present
skin texture	heterogeneous, granular	heterogeneous, granular	heterogeneous, granular	heterogeneous, granular	heterogeneous, granular
typical glandular line on tibia	small to large conic glands, more or less interrupted lines	minuscule to small conic glands, almost continuous lines	small to mean conic glands, predominantly interrupted lines	small to large glandular conic glands, rather interrupted line	small to mean glandular conic glands, hardly interrupted line
ventral colouration	uniform pale, dirty whitish, dark with pale markings, uniform dark	uniform pale, dirty whitish, reticulated, uniform dark, dark with paler markings	uniform dark or few paler markings	uniform dark, rarely paler markings or dirty smeared	uniform pale, dirty whitish, reticulated, fading posteriorly from throat to belly, uniform dark
colouration of male femoral glands	rose-coloured	dark orange	pale orange	bright orange	unknown
typical webbing formula	0-0.25/0-0.75/0-0.75/0.75-0 0-0.5/0-1/0-1/1-0	0-0/0-0.5/0-0.5/0.5-0 0-(0.25 to 0.5)/0-1/0-0.75/0.75-0	0-(0.75 to 1)/0-1/0-1/1-0	0-0.75/0-1/0-1/1-0	0-0.5/0-1/0-1/1-0 0-0.25/0-1/0-0.75/0.75-0
typical number of dorsal glandular ridges	3 to 5	4 to 5	5 to 6	4 to 5	4 to 5
max SUL (m / f)	52.5 / 61.1	50.3 / 60.3	60.4 / 61.9	57.0 / 62.5	53.6 / 64.0
GL/FM	0.46	0.51	0.46	0.46	0.51
GL/GW	1.96	1.83	2.12	1.72	1.86
HW/SUL (m / f)	0.36 / 0.35	0.35 / 0.34	0.38 / 0.37	0.37 / 0.37	0.35 / 0.34
TD/O (m / f)	0.40 / 0.40	0.34 / 0.34	0.44 / 0.44	0.43 / 0.47	0.37 / 0.38
O/EN (m / f)	1.82 / 1.80	2.16 / 2.03	1.60 / 1.69	1.78 / 1.71	2.05 / 2.04

simply: naming does not mean knowing a species. Our knowledge on the family is still incomplete, as calls of four species remain unknown and data on tadpole morphology is lacking. Lamotte and Zuber-Vogeli (1954) published a detailed description on tadpoles collected in Liberia and the Nimba Mts., thus we cannot rule out that their description is based on material from two different species (*O. natator* and *O. arndti*). Solely Guibé and Lamotte (1958) described a series of tadpoles from the River Zougue on the Nimba Mts. (described as *O. arndti* in the present work) and provided a short and superficial description of the habitus. Our insights on the ecology of adult *Odontobatrachus* are scarce, too. While streams with rapids in primary forests are the preferred habitat of torrent-frogs, detailed ecological studies are missing. Differences in habitat requirements and ecology have been recognised as further characters of importance to distinguish species in other genera (e.g. *Amietophrynus regularis* vs. *A. maculatus* Amiet 1976; Böhme 1994a; *Phrynobatrachus guineensis* and *P. phyllophilus* Rödel and Ernst 2002).

'West African Forests' are recognised as one of the world's biodiversity hotspots (Myers et al. 2000; Bakarr et al. 2001) and biogeographically demarcated from the Central African forest block (Penner et al. 2011). Although West Africa, defined as ranging from Senegal to Nigeria, is regarded as one of the better known regions on the continent, more than ten new amphibian species have been described in the last decade (e.g. Blackburn et al. 2008; Ernst et al. 2008; Hillers et al. 2008b; Rödel 2007; Rödel and Bangoura 2004; Rödel et al. 2003, 2009a, b, c, 2010, 2011, 2012a, b) and more await formal description (Rödel et al. unpubl. data.). We agree with McLeod et al. (2012) that it is crucial to identify the "true" biodiversity and although species that are morphologically difficult to tell apart become condemned, their scientific recognition is an indispensable tool for conservation management.

In the past, only a single torrent-frog species, *O. natator*, was known to occur in West Africa and it has been listed as "Near Threatened (NT)" according to the IUCN Red List (IUCN 2011). However, we herein demonstrated the presence of four new *Odontobatrachus* species with dramatically constrained distribution ranges. According to Barej et al. (2015) all five species (therein treated as OTUs) require the IUCN category "Endangered (EN)" resulting from analyses of the range criteria Extent of Occurrence and Area of Occupancy. Environmental Niche Modelling (Barej et al. 2015) confirmed large distributional gaps and thus justify the use of AOO as criterion. Both sub-clades of *O. natator* should be treated distinctly with regard to conservation concern as evolutionary significant units (Moritz 1996, 2002; Ennos et al. 2005) and if recognised as distinct species, the Freetown Peninsula population demands the category "Critically Endangered (CR)". As habitat loss is ongoing due to forest fragmentation and conversion (Chatelain et al. 1996; FAO 2006; Norris et al. 2010), conservation efforts need to be made soon. In the case of West African torrent-frogs, only *O. natator*, *O. ziama* and *O. arndti* occur in protected areas like National Parks and Biosphere Reserves (Barej et al. 2015) and even if lower priority areas are considered, they fail to protect all five species. Distribution patterns in *Odontobatrachus* cover ranges of various endemic species in the Fouta Djallon and the Nimba Mts.-Massif du Ziama-Simandou Mountain Range (Angel 1943; Porembski et al. 1994, 1995). Furthermore, these areas are assumed to have played an important role as forest refugia in Upper Guinea (Maley 1987; Porembski et al. 1994; Sosef 1994). Barej et al. (2015) suggested that the Loma Mts. and Tingi Hills in Sierra Leone, as the highest elevation occurrences in the Guinea Highlands, could represent a refugium in central Upper Guinea for *O. natator* and any conservation effort within these areas could consequently be beneficial in many non-related taxa and assure their long-term survival.

In summary, the diversity in the family Odontobatrachidae has been raised to five species. While our knowledge on this West African endemics is far from complete, nomination of OTUs recognised by Barej et al. (2015) is of importance for promoting immediate conservation actions as all species require the IUCN category "Endangered (EN)". West African torrent-frog species are at risk of becoming extinct because of habitat loss in the Upper Guinean biodiversity hotspot, whose "true" biodiversity is still far from being completely known.

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References

Amiet J-L (1976) Voix d'Amphibiens camerounais V. Bufonidae; genres *Bufo*, *Werneria* et *Nectophryne*. Annales de la Faculté de Sciences du Cameroun 21-22: 139–157.

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 2: 32–46. doi: 10.1111/j.1442-9993.2001.01070.pp.x

Angel F (1943) Description d'un nouvelle Amphibien anoure, ovovivipare, de la Haute Guinée Française. (Matériaux de la Mission Lamotte, au Mont-Nimba). 2e note. Bulletin du Museum National d'Histoire Naturelle, Série 2, 15: 167–169.

Arino O, Ramos Perez JJ, Kalogirou V, Bontemps S, Defourny P, van Bogaert E (2012) Global Land Cover Map for 2009 (GlobCover 2009). © European Space Agency (ESA) & Université catholique de Louvain (UCL).

Bakarr M, Bailey B, Byler D, Ham R, Olivieri S, Omland M (2001) From the forest to the sea: biodiversity connections from Guinea to Togo, Conservation Priority-Setting Workshop, December 1999. Conservation International, Washington, 78 pp.

Barej MF, Rödel M-O, Gonwouo NL, Pauwels OSG, Böhme W, Schmitz A (2010) Review of the genus *Petropedetes* Reichenow, 1874 in Central Africa with the description of three new species (Amphibia: Anura: Petropedetidae). Zootaxa 234: 1–49.

Barej MF, Rödel M-O, Loader SP, Menegon M, Gonwouo NL, Penner J, Gvoždík V, Günther R, Bell RC, Nagel P, Schmitz A (2014a) Light shines through the spindrift – Phylogeny of African Torrent Frogs (Amphibia, Anura, Petropedetidae). Molecular Phylogenetics and Evolution 71: 261–273. doi: 10.1016/j.ympev.2013.11.001

Barej MF, Schmitz A, Günther R, Loader SP, Mahlow K, Rödel M-O (2014b) The first endemic West African vertebrate family – a new anuran family highlighting the uniqueness of the Upper Guinean biodiversity hotspot. Frontiers in Zoology 11: 8. doi: 10.1186/1742-9994-11-8

Barej MF, Penner J, Schmitz A, Rödel M-O (2015) Multiple genetic lineages challenge the monospecific status of the West African endemic frog-family Odontobatrachidae. BMC Evolutionary Biology 15: 67. doi: 10.1186/s12862-015-0346-9

Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winke K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. Trends in Ecology & Evolution 22: 148–155. doi: 10.1016/j.tree.2006.11.004

Blackburn DC, Kosuch J, Schmitz A, Burger M, Wagner P, Gonwouo LN, Hillers A, Rödel M-O (2008) A new species of *Cardioglossa* (Anura: Arthroleptidae) from the Upper Guinean forests of West Africa. Copeia 2008: 603–612. doi: 10.1643/CH-06-233

Böhme W (1994a) Frösche und Skinke aus dem Regenwaldgebiet Südost-Guineas, Westafrika I. Einleitung; Pipidae, Arthroleptidae, Bufonidae. herpetofauna 16(92): 11–19.

Böhme W (1994b) Frösche und Skinke aus dem Regenwaldgebiet Südost-Guineas, Westafrika. II. Ranidae, Hyperoliidae, Scincidae; faunistisch-ökologische Bewertung. herpetofauna 16(93): 6–16.

Boulenger GA (1905) Descriptions of new West-African frogs of the genera *Petropedetes* and *Bulua*. The Annals and Magazine of Natural History 15: 281–283. doi: 10.1080/03745480509443042

Chatelain C, Gautier L, Spichiger R (1996) A recent history of forest fragmentation in southwestern Ivory Coast. Biodiversity and Conservation 5: 37–53. doi: 10.1007/BF00056291

de Queiroz K (1998) The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. In: Howard DJ, Berlocher SH (Eds) Endless forms: species and speciation. Oxford University Press, Oxford, 57–75.

de Queiroz K (1999) The general lineage concept of species and the defining properties of the species category. In: Wilson RA (Ed.) Species: new interdisciplinary essays. MIT Press, Cambridge, Massachusetts, 49–89.

Ennos RA, French GC, Hollingsworth PM (2005) Conserving taxonomic complexity. Trends in Ecology & Evolution 20: 164–168. doi: 10.1016/j.tree.2005.01.012

Ernst R, Agyei AC, Rödel M-O (2008) A new giant species of *Arthroleptis* (Amphibia: Anura: Arthroleptidae) from the Krokosua Hills Forest Reserve, south-western Ghana. Zootaxa 1697: 58–68.

FAO (2006) Global Forest Resources Assessment 2005. Progress towards Sustainable Forest Management. FAO Forestry Paper N°147. Food and Agriculture Organization of the United Nations, Rome, 320 pp.

Gridi-Papp M (2007) SoundRuler: Acoustic analysis for research and teaching. Available at http://soundruler.sourceforge.net

Guibé J, Lamotte M (1957) Révision systématique des *Ptychadena* (Batraciens Anoures Ranidés) d'Afrique Occidentale. Bulletin de l'Institut Fondamental d'Afrique Noire (A) 19: 937–1003.

Guibé J, Lamotte M (1958) La réserve naturelle intégrale du Mont Nimba. XII. Batraciens (sauf *Arthroleptis*, *Phrynobatrachus* et *Hyperolius*). Mémoires de l'Institut fondamental d'Afrique noire 53: 241–273.

Haddad CFB, Giaretta AA (1999) Visual and acoustic communication in the Brazilian torrent frog, *Hylodes asper* (Anura: Leptodactylidae). Herpetologica 55: 324–333.

Hillers A, Rödel M-O (2007) The amphibians of three national forests in Liberia, West Africa. Salamandra 43: 1–10.

Hillers A, Loua N, Rödel M-O (2008a) A preliminary assessment of the amphibians of the Fouta Djallon, Guinea, West Africa. Salamandra 44: 113–122.

Hillers A, Zimkus BM, Rödel M-O (2008b) A new species of *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from north-western Guinea, West Africa. Zootaxa 1815: 43–50.

International Commission on Zoological Nomenclature (2012) Amendment of articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. ZooKeys 219: 1–10. doi: 10.3897/zookeys.219.3944

IUCN (2011) IUCN Red List of Threatened Species. Version 2011.2. http://www.iucnredlist.org [accessed on 02.01.2015]

Jörger KM, Schrödl M (2013) How to describe a cryptic species? Practical challenges of molecular taxonomy. Frontiers in Zoology 10: 59. doi: 10.1186/1742-9994-10-59

Kamermans M, Vences M (2009) Terminal phalanges in ranoid frogs: morphological diversity and evolutionary correlation with climbing habits. Alytes 26: 177–152.

Lamotte M, Zuber-Vogeli M (1954) Contribution à l'étude des batraciens de l'Ouest-Africain III. Le développement larvaire de deux espèces rhéophiles, *Astylosternus diadematus* et *Petropedetes natator*. Bulletin de l'Institut français d'Afrique Noire 16: 1222–1233.

Maley J (1987) Fragmentation de la forêt dense humide africaine et extension des biotopes montagnards ou Quartenaire récent:

nouvelles données polliniques et chronologiques. Implications paléoclimatiques et biogéographiques. Palaeoecology of Africa 18: 307–334.

Matsui M, Mohamed M, Shimada T, Sudin A (2007) Resurrection of *Staurois parvus* from *S. tuberilinguis* from Borneo (Amphibia: Ranidae). Zoological Science 24: 101–106. doi: 10.2108/zsj.24.101

McLeod DS, Kelly JK, Barley A (2012) "Same-Same but different": Another new species of the *Limnonectes kuhlii* complex from Thailand (Anura: Dicroglossidae). Russian Journal of Herpetology 19: 261–274.

Minter LR, Burger M, Harrison JA, Braack HH, Bishop PJ, Kloepfer D (2004) Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland. SI/MAB Series #9. Smithsonian Institution, Washington, DC, 360 pp.

Moritz C (1996) Defining 'evolutionary significant unit' for conservation. Trends in Ecology & Evolution 9: 373–375. doi: 10.1016/0169-5347(94)90057-4

Moritz C (2002) Strategies to protect biological diversity and the evolutionary processes that sustain it. Systematic Biology 5: 238–254. doi: 10.1080/10635150252899752.

Myers N, Mittermeier RA, Mittermeier CG, DaFonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–845. doi: 10.1038/35002501

Norris K, Asase A, Collen B, Gockowksi J, Mason J, Phalan B, Wade A (2010) Biodiversity in a forest-agriculture mosaic – The changing face of West African rainforests. Biological Conservation 143: 2341–2350. doi: 10.1016/j.biocon.2009.12.032

Penner J, Wegmann M, Hillers A, Schmidt M, Rödel M-O (2011) A hotspot revisited – a biogeographical analysis of West African amphibians. Diversity and Distributions 17: 1077–1088. doi: 10.1111/j.1472-4642.2011.00801.x

Perret J-L (1979) Remarques et mise au point sur quelques espèces de *Ptychadena* (Amphibia, Ranidae). Bulletin de la Société Neuchâteloise des Sciences Naturelles 102: 5–21.

Petzold A, Vargas-Ramírez M, Kehlmaier C, Vamberger M, Branch WR, du Preez L, Hofmeyr MD, Meyer L, Schleicher A, Široký P, Fritz U (2014) A revision of African helmeted terrapins (Testudines: Pelomedusidae: *Pelomedusa*), with descriptions of six new species. Zootaxa 3795: 523–548. doi: 10.11646/zootaxa.3795.5.2

Porembski S, Barthlott W, Dörrstock S, Biedinger N (1994) Vegetation of rock outcrops in Guinea: granite inselbergs, sandstone table mountains and ferricretes - remarks on species numbers and endemism. Flora 189: 315–326.

Porembski S, Biedinger N, Dörrstock S (1995) Zur Vegetation Guineas unter besonderer Berücksichtigung der Inselbergflora. Natur und Museum 125: 143–154.

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Real R, Barbosa AM, Martinez-Solano I, Garcia-Paris M (2005) Distinguishing the distributions of two cryptic frogs (Anura: Discoglossidae) using molecular data and environmental modeling. Canadian Journal of Zoology-Revue Canadienne de Zoologie 8: 536–545. doi: 10.1139/z05-040

Rödel M-O (2000) Herpetofauna of West Africa, Vol. I: Amphibians of the West African savanna. Edition Chimaira, Frankfurt am Main, 332 pp.

Rödel M-O (2003) The amphibians of Mont Sangbé National Park, Ivory Coast. Salamandra 39: 91–110.

Rödel M-O (2007) The identity of *Hylambates hyloides* Boulenger, 1906 and description of a new small species of *Leptopelis* from West Africa. Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologische Reihe 83 (Supplement): 90–100. doi: 10.1002/mmnz.200600031

Rödel M-O, Bangoura MA (2004) A conservation assessment of amphibians in the Forêt Classée du Pic de Fon, Simandou Range, southeastern Republic of Guinea, with the description of a new *Amnirana* species (Amphibia Anura Ranidae). Tropical Zoology 17: 201–232. doi: 10.1080/03946975.2004.10531206

Rödel M-O, Barej MF, Hillers A, Leaché AD, Kouamé NGG, Ofori-Boateng C, Assemian NGE, Gonwouo LN, Nopper J, Brede C, Diaz RE, Fujita MK, Gil M, Segniagbeto GH, Ernst R, Sandberger L (2012a) The genus *Astylosternus* in the Upper Guinea rainforests, West Africa, with the description of a new species (Amphibia: Anura: Arthroleptidae). Zootaxa 3245: 1–29.

Rödel M-O, Bangoura MA, Böhme W (2004) The amphibians of south-eastern Republic of Guinea (Amphibia: Gymnophiona, Anura). Herpetozoa 17: 99–118.

Rödel M-O, Boateng CO, Penner J, Hillers A (2009) A new cryptic *Phrynobatrachus* species (Amphibia: Anura: Phrynobatrachidae) from Ghana, West Africa. Zootaxa 1970: 52–62.

Rödel M-O, Doherty-Bone T, Kouete MT, Janzen P, Garrett K, Browne R, Gonwouo NL, Barej MF, Sandberger L (2012) A new small *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from southern Cameroon. Zootaxa 3431: 54–68.

Rödel M-O, Doumbia J, Johnson AT, Hillers A (2009a) A new small *Arthroleptis* (Amphibia: Anura: Arthroleptidae) from the Liberian part of Mount Nimba, West Africa. Zootaxa 2302: 19–30.

Rödel M-O, Ernst R (2002) A new *Phrynobatrachus* from the Upper Guinean rain forest, West Africa, including a description of a new reproductive mode for the genus. Journal of Herpetology 36: 561–571. doi: 10.1670/0022-1511(2002)036[0561:ANPFTU]2.0.CO;2

Rödel M-O, Kosuch J, Grafe TU, Boistel R, Assemian NGE, Kouamé NGG, Tohé B, Gourène G, Perret J-L, Henle K, Tafforeau P, Pollet N, Veith M (2009b) A new tree-frog genus and species from Ivory Coast, West Africa (Amphibia: Anura: Hyperoliidae). Zootaxa 2044: 23–45.

Rödel M-O, Kosuch K, Veith M, Ernst R (2003) First record of the genus *Acanthixalus* Laurent, 1944 from the upper Guinean rain forest, West Africa, with the description of a new species. Journal of Herpetology 37: 43–52. doi: 10.1670/0022-1511(2003)037[0043:FROTGA]2.0.CO;2

Rödel M-O, Kouamé NGG, Doumbia J, Sandberger L (2011) A new beautiful squeaker frog (Arthroleptidae: *Arthroleptis*) from West Africa. Zootaxa 3011: 16–26.

Rödel M-O, Ohler A, Hillers A (2010) A new extraordinary *Phrynobatrachus* (Amphibia, Anura, Phrynobatrachidae) from West Africa. Zoosystematics and Evolution 86: 257–261. doi: 10.1002/zoos.201000008

Rödel M-O, Onadeko AB, Barej MF, Sandberger L (2012b) A new polymorphic *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from western Nigeria. Zootaxa 3328: 55–65.

Satler JD, Carstens BC, Hedin M (2013) Multilocus species delimitation in a complex of morphologically conserved trapdoor spiders

(Mygalomorphae, Antrodiaetidae, *Aliatypus*). Systematic Biology 62: 805–823. doi: 10.1093/sysbio/syt041

Scott E (2005) A phylogeny of ranid frogs (Anura: Ranoidea: Ranidae), based on a simultaneous analysis of morphological and molecular data. Cladistics 21: 507–574. doi: 10.1111/j.1096-0031.2005.00079.x

Smith F (1902) Appendix: No. VIII The distribution of mosquito larvae on war department lands in Sierra Leone. In: Army Medical Department Report for the Year 1900. Volume XLII. Verlag HMSO, London, 495–501.

Smith F (1905) Certain forms of fever, and the conditions bearing thereon, in the hill stations of Sierra Leone. Journal of the Royal Army of Medical Corps 5: 688–702.

Sosef MSM (1994) Studies in Begoniaceae V. Refuge Begonias. Taxonomy, phylogeny and historical biogeography of *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia* in relation to glacial rain forest refuges in Africa. Wageningen Agricultural University Papers 94-1: i-xv + 1-306 + 8 pl.

Sueur J, Aubin T, Simons S (2008) Seewave: a free modular tool for sound analysis and synthesis. Bioacoustics 18: 213–226. doi: 10.1080/09524622.2008.9753600

Vieites DR, Wollenberg KC, Andreone F, Köhler J, Glaw F, Vences M (2009) Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. Proceedings of the National Academy of Sciences, USA 106: 8267–8272. doi: 10.1073/pnas.0810821106

Wohltmann A, du Preez L, Rödel M-O, Köhler J, Vences M (2007) Endoparasitic mites of the genus *Endotrombicula* Ewing, 1931 (Acari: Prostigmata: Parasitengona: Trombiculidae) from African an Madagascan anurans, with description of a new species. Folia Parasitologica 54: 225–235. doi: 10.14411/fp.2007.031

Zimkus BM, Gvoždík V (2013) Sky Islands of the Cameroon Volcanic Line: a diversification hot spot for puddle frogs (Phrynobatrachidae: *Phrynobatrachus*). Zoologica Scripta 42: 591–611. doi: 10.1111/zsc.12029

Appendix 1

Table summarising uncorrected p-distances within and between *Odontobatrachus* spp.

Table A. Uncorrected p-distances within (first column) and between *Odontobatrachus* spp. based on 567bp of the 16S rRNA gene. Minimum to maximum values (lower left corner), mean values with standard deviation and sample size (upper right corner) are given. For seemingly high intra-species differences in *Odontobatrachus natator* see Barej et al. (2015).

Taxon	intraspecies	***O. natator***	***O. ziama* sp. n.**	***O. smithi* sp. n.**	***O. fouta* sp. n.**	***O. arndti* sp. n.**
O. natator	0.00–1.98; 0.42 ± 051 (703)		4.36 ± 0.21 (1216)	4.88 ± 0.19 (1216)	4.34 ± 0.20 (418)	4.82 ± 0.27 (1596)
O. ziama sp. n.	0.00–0.72; 0.27 ± 0.21 (630)	3.74–4.87		5.03 ± 0.14 (320)	4.25 ± 0.13 (352)	3.36 ± 0.22 (1344)
O. smithi sp. n.	0.00–0.54; 0.20 ± 0.19 (45)	4.50–5.40	4.86–5.41		4.01 ± 0.11 (110)	5.21 ± 0.17 (420)
O. fouta sp. n.	0.00–0.36; 0.15 ± 0.15 (55)	3.97–4.88	3.99–4.53	3.79–4.15		4.52 ± 0.16 (462)
O. arndti sp. n.	0.00–0.58; 0.05 ± 0.11 (861)	3.40–5.40	2.89–3.97	4.60–5.55	4.17–4.98	

Appendix 2

Table summarising voucher specimens, and additional GenBank accession numbers.

Table B. List of additionally generated *Odontobatrachus* sequences and respective GenBank accession numbers. *Odontobatrachus* sequences analysed in Barej et al. (2015) refer to the following GenBank numbers and publications ([1]Barej et al. 2015; [2]Barej et al. 2014; [3]Loader et al. 2013; [4]Rödel et al. 2005): 16S: KP005071–124[1], KF693390–5[2], JX546953–4[3]; AY902379[4]; 12S: KP005195–243[1], KF693286–91[2], JX546938–9[3]; cytb: KP005418–32[1], KF693670–5[2], JX546968–9[3]; BDNF: KP005312–26[1], KF693488–93[2]; SIA: KP005377–KP005396[1], KF693550–5[2]; RAG1: KP005345–59[1], KF693610–5[2].

taxon	voucher	country	16S	RAG1
O. natator	ZMB 80505	Liberia	KP284862	---
O. natator	ZMB 80504	Liberia	KP284863	---
O. ziama sp. n.	MHNG 2731.45	Guinea	---	KP284864
O. ziama sp. n.	MHNG 2731.46	Guinea	---	KP284865
O. ziama sp. n.	ZFMK 95465	Guinea	---	KP284866
O. ziama sp. n.	ZMB 78299	Guinea	---	KP284867
O. ziama sp. n.	ZMB 78300	Guinea	---	KP284868
O. smithi sp. n.	ZMB 78311	Guinea	---	KP284869
O. fouta sp. n.	MHNG 2731.48	Guinea	---	KP284870
O. arndti sp. n.	MHNG 2731.50	Guinea	---	KP284871
O. arndti sp. n.	ZFMK 95467	Guinea	---	KP284872

Barej MF, Penner J, Schmitz A, Rödel M-O (2015) Multiple genetic lineages challenge the monospecific status of the West African endemic frog-family Odontobatrachidae. BMC Evolutionary Biology. doi: 10.1186/s12862-015-0346-9

Barej MF, Rödel M-O, Loader SP, Menegon M, Gonwouo NL, Penner J, Gvoždík V, Bell RC, Nagel P, Schmitz A (2014) Light shines through the spindrift – phylogeny of African Torrent Frogs (Amphibia, Anura, Petropedetidae). Molecular Phylogenetics and Evolution 71: 261–273. doi: 10.1016/j.ympev.2013.11.001

Loader SP, Ceccarelli FS, Wilkinson M, Menegon M, Mariaux J, de Sá RO, Howell KM, Gower DJ (2013) Species boundaries and biogeography of East African torrent frogs of the genus *Petropedetes* (Amphibia: Anura: Petropeditidae). African Journal of Herpetology 62: 40–48.

Rödel M-O, Kosuch J, Kouamé NG, Ernst R, Veith M (2005) *Phrynobatrachus alticola* Guibé & Lamotte, 1961 is a junior synonym of *Phrynobatrachus tokba* (Chabanaud, 1921). African Journal of Herpetology 54: 93–98.

Appendix 3

Table summarising Kruskal-Wallis test statistics.

Table C. Kruskal-Wallis test statistics for *Odontobatrachus* male and female absolute values (A) and ratios (B). χ^2-value, degree of freedom (DF) and the asymptotic significance (Asymp. Sig.) are given. See material and methods section for abbreviations.

A		SUL	HW	FM	GL	GW	TI	FL	IT	TD	O	ID	EN	ES
male	$\chi 2$	22.350	22.253	25.490	15.559	16.667	32.377	30.048	6.008	24.781	13.177	15.413	40.756	9.201
	DF	4	4	4	4	4	4	4	4	4	4	4	4	4
	Asymp. sig.	<0.001	<0.001	<0.001	<0.01	<0.01	<0.001	<0.001	0.20	<0.001	<0.05	<0.01	<0.001	0.06
female	$\chi 2$	8.675	20.808	19.819	---	---	29.519	28.719	8.745	53.107	11.852	14.913	40.751	4.604
	DF	4	4	4	---	---	4	4	4	4	4	4	4	4
	Asymp. sig.	0.07	<0.001	<0.01	---	---	<0.001	<0.001	0.07	<0.001	<0.05	<0.01	<0.001	0.33
B		**TI/SUL**	**FM/TI**	**FL/SUL**	**GL/FM**	**GL/GW**	**HW/SUL**	**TD/O**	**FM/SUL**	**IT/FL**	**O/EN**	**ES/O**	**TD/SUL**	
male	$\chi 2$	13.864	0.493	19.752	9.968	14.135	20.020	22.370	9.054	13.709	34.315	12.905	14.156	
	DF	4	4	4	4	4	4	4	4	4	4	4	4	
	Asymp. sig.	<0.01	0.98	<0.01	<0.05	<0.01	<0.001	<0.001	0.06	<0.01	<0.001	<0.05	<0.01	
female	$\chi 2$	5.743	11.946	7.465	---	---	30.977	49.876	1.398	8.857	41.359	12.499	45.160	
	DF	4	4	4	---	---	4	4	4	4	4	4	4	
	Asymp. sig.	0.22	<0.05	0.11	---	---	<0.001	<0.001	0.85	0.07	<0.001	<0.05	<0.001	