Zootaxa 5759 (5): 501–525
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5759.5.1
http://zoobank.org/urn:lsid:zoobank.org:pub:8306ACD4-E550-456B-8677-BF65F49B712A

A new polymorphic species of *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from southern Ivory Coast, a West African biodiversity hotspot

N'GORAN GERMAIN KOUAMÉ[1,*] & ALICE PETZOLD[2, 3]
[1]*Université Jean Lorougnon Guédé, Laboratoire de Biodiversité et Ecologie Tropicale, UFR-Environnement, BP 150, Daloa, Côte d'Ivoire*
[2]*Institute of Biochemistry and Biology, University of Potsdam, Karl-Liebknecht-Str. 24–25, 14476 Potsdam, Germany*
[3]*Museum für Naturkunde – Leibniz Institute for Evolution and Biodiversity Science, Invalidenstr. 43, 10115 Berlin, Germany*
alice.petzold@mfn.berlin; https://orcid.org/0000-0002-0743-2004
[*]*Corresponding author. ngoran_kouame@yahoo.fr; https://orcid.org/0000-0003-3007-605X*

Abstract

We describe a new species of puddle frog, genus *Phrynobatrachus*, from southern Ivory Coast. The new species, which we designate as *Phrynobatrachus moroedeli* **sp. nov.**, exhibits striking variation in colour pattern of the ventral surface with either very few small black dots or large dark or even black blotches along the edges, and differs from all other West African species of the genus by the combination of unique morphological characters: small sized (snout–vent length of 13.9–23 mm), compact-bodied frog with a short rounded to pointed snout; rough to slightly warty dorsal skin with variable colouration; males with greyish dark, deep dark to completely black throats absence of a spiny eyelid tubercle; absence of femoral gland; presence of narrow X-shaped pair of scapular ridges; presence of light or whitish vertebral line or band; distinct black lateral band on flanks; distinct but rudimentary pedal webbing and small but distinct discs on fingers and toes; spinulae on dorsal surfaces of thighs and lower legs. It is further distinguished by mitochondrial 16S rRNA genetic distances ranging from 4.05–11.43% relative to other West African species of *Phrynobatrachus*, and by the absence of haplotype sharing within the analysed fragment of the nuclear RAG1 gene. Phylogenetically, the new lineage is closely related to but genealogically exclusive from *Phrynobatrachus afiabirago*, *P. fraterculus*, *P. gutturosus*, *P. maculiventris*, and *P. pintoi*, all of which are endemic to the Upper Guinean forest zone of West Africa. One formerly recognized distinct lineage (*P.* aff. *gutturosus* 1) may further correspond to the newly described species (mean 16S genetic distance 1.96%), but it is currently represented by a single sample from an unvouchered specimen. Additional specimens are thus needed to clarify its taxonomic identity and morphological characteristics.

Key words: Côte d'Ivoire, integrative taxonomy, *Phrynobatrachus moroedeli* **sp. nov.**, Tanoé-Ehy, Upper Guinean forests, Yakassé-Mé

Résumé

Nous décrivons une nouvelle espèce de grenouille des flaques d'eau, du genre *Phrynobatrachus*, provenant du sud de la Côte d'Ivoire. La nouvelle espèce, que nous désignons sous le nom de *Phrynobatrachus moroedeli* **sp. nov.**, présente une variation remarquable du motif de couleur de sa face ventrale marquée par très peu de petits points noirs ou de grandes taches sombres ou noires côtoyant les bords. Elle se distingue de toutes les autres espèces ouest-africaines du genre *Phrynobatrachus* par la combinaison de caractères morphologiques uniques: grenouille de petite taille (longueur museau-anus comprise entre 13,9–23 mm), corps compact avec un museau court, arrondi à pointu; peau dorsale rugueuse à légèrement verruqueuse avec une coloration variable; mâles avec gorge grisâtre foncé, très sombre jusqu'à complètement noire; absence de masque latéral noir; absence de tubercule épineux sur la paupière; absence de glande fémorale; présence d'une paire de crêtes étroites en forme de X au niveau de la région scapulaire; présence d'une ligne ou bande vertébrale claire ou blanchâtre; bande latérale noire distincte sur les flancs; palmure pédale distincte mais rudimentaire et petits disques distincts sur les doigts et les orteils; présence de spicules sur les surfaces dorsales des cuisses et des parties inférieures des pattes arrières. Elle se distingue en outre par des distances génétiques mitochondriales ARNr 16S variant de 4,05 à 11,43% par rapport aux autres espèces ouest-africaines, et par l'absence de partage d'haplotypes dans le fragment

Accepted by W. Conradie: 6 Jan. 2026; published: 19 Feb. 2026

analysé du gène nucléaire RAG1. Sur le plan phylogénétique, la nouvelle lignée est étroitement liée à *Phrynobatrachus afiabirago*, *P. fraterculus*, *P. gutturosus*, *P. maculiventris* et *P. pintoi*, toutes endémiques de la zone forestière de la Haute-Guinée en Afrique de l'Ouest. Une lignée distincte précédemment reconnue (*P.* aff. *gutturosus* 1) pourrait correspondre à l'espèce nouvellement décrite (distance génétique moyenne de 1,96 % pour le gène 16S), mais elle n'est actuellement représentée que par un seul échantillon provenant d'un spécimen non déposé. Des spécimens supplémentaires sont donc nécessaires pour clarifier son identité taxonomique et ses caractères morphologiques.

Mots-clés: Côte d'Ivoire, forêts de Haute-Guinée, *Phrynobatrachus moroedeli* **sp. nov.**, Tanoé-Ehy, taxonomie intégrative, Yakassé-Mé

Introduction

The monotypic family Phrynobatrachidae Laurent, 1941 currently comprises 96 small to medium-sized species of the genus *Phrynobatrachus* Günther, 1862, with members being endemic to savannas and forests of sub-Saharan Africa (Poynton 1999; Frost 2025). Several phylogenetic studies of the genus across the continent, however, revealed numerous cryptic and undescribed species, especially in West and Central Africa (Rödel *et al*. 2009a; Zimkus *et al*. 2010; Rödel *et al*. 2015). In West Africa, west of the Dahomey Gap, 22 valid species are known to occur (Channing & Rödel 2019), with most showing a patchy distribution, often restricted to particular types of habitats (e.g., Rödel & Ernst 2004; Hillers & Rödel 2007; Hillers *et al*. 2009; Rödel *et al*. 2009a; Kouamé *et al*. 2014; Kpan *et al*. 2018; Ofori-Boateng *et al*. 2018). As members of the leaf-litter dwelling frog community, they serve as valuable model organisms to study forest degradation effects in Ghana (Ofori-Boateng *et al*. 2012) and Ivory Coast (Ernst & Rödel 2005, 2006; Hillers *et al*. 2008a; Kouamé *et al*. 2018) to inform conservation efforts.

In Ivory Coast, members of the genus *Phrynobatrachus* currently comprise 18 species: *Phrynobatrachus alleni* Parker, 1936, *P. annulatus* Perret, 1966, *P. calcaratus* (Peters, 1863), *P. francisci* Boulenger, 1912, *P. fraterculus* (Chabanaud, 1921), *P. ghanensis* Schiøtz, 1964, *P. guineensis* Guibé & Lamotte, 1962, *P. gutturosus* (Chabanaud, 1921), *P. latifrons* Ahl, 1924, *P. liberiensis* Barbour & Loveridge, 1927, *P. maculiventris* Guibé & Lamotte, 1958, *P. natalensis* (Smith, 1849), *P. phyllophilus* Rödel & Ernst, 2002, *P. plicatus* (Günther, 1858), *P. taiensis* Perret, 1988, *P. tanoeensis* Kpan, Kouamé, Barej, Adeba, Emmrich, Boateng & Rödel, 2018, *P. tokba* (Chabanaud, 1921), and *P. villiersi* Guibé, 1959 (Channing & Rödel 2019). The '*P. gutturosus*' group forms a species complex of several undescribed species (M.-O. Rödel, *pers. comm*) found in a variety of habitats, ranging from primary rainforests to humid savannas and located in both lowland and highland areas of West Africa (Rödel 2000; Nago *et al*. 2006; Kouamé *et al*. 2007; Zimkus *et al*. 2010). *Phrynobatrachus afiabirago* Ofori-Boateng, Leaché, Obeng-Kankam, Kouamé, Hillers & Rödel, 2018, which is a member of this group, was recently described and is known only from a few localities in southern Ghana (Ofori-Boateng *et al*. 2018).

Between the 14th and 18th of March 2018, towards the end of the dry season, we surveyed amphibians in the Dohouan village forest, a patch of the Tanoé-Ehy swamp forest, in the easternmost part of Ivory Coast. During this field work, we collected a series of small individuals found in the leaf-litter that could morphologically be assigned to the genus *Phrynobatrachus*. They resembled most members of the '*P. gutturosus*' group by sharing the main morphological traits, such as the presence of warty dorsal skin, vertebral band, a distinct black lateral band on the flanks, short X-shaped scapular ridges, rudimentary pedal webbing, and males with a black throat. The specimens collected in field were tentatively assigned to *P. afiabirago* due to the proximity of the Tanoé-Ehy swamp forest to the Ghanaian border (see Fig. 1), where that species occurs. Additional *Phrynobatrachus* individuals were found in Mabi-Yaya Forest Reserve, Taboth, and Yakassé-Mé village forest, all in south-eastern Ivory Coast, and in Tiassalé in the south-central part of the country. They likewise shared the general morphology of members of the '*P. gutturosus*' group, but they all differed in colouration from the frogs collected in Tanoé-Ehy swamp forest. Subsequent morphological investigations and genetic analyses revealed that specimens from Tanoé-Ehy and Yakassé-Mé forests belong to a single species previously unknown to science, which we formally described herein as a new species.

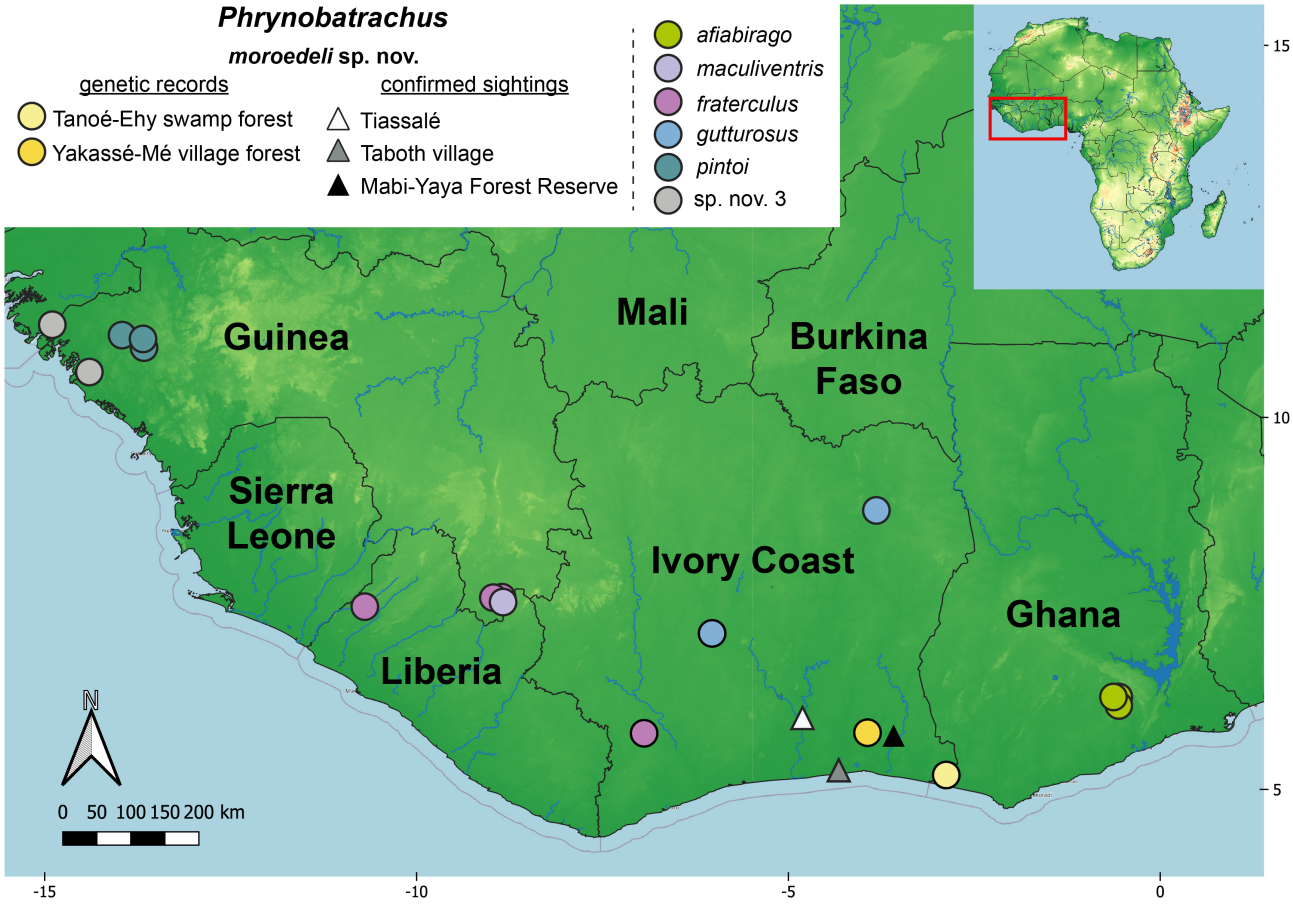

FIGURE 1. Map of West Africa indicating the geographic location of the five known sites of *Phrynobatrachus moroedeli* **sp. nov.** in southern Ivory Coast, along with the sampling localities of its closest congeners from Upper Guinean Forest, except the lineages *P.* aff. *gutturosus* 1 and 2, for which no detailed coordinates were available. The map was created in QGIS version 3.32.0 (https://www.qgis.org/en/site/about/index.html), based on the EPSG: 4326 model coordinates given in decimal WGS84 format.

Materials and methods

Vouchers and measurements. Vouchers were euthanized in a MS222 solution, fixed in 95% ethanol and thereafter preserved in 75% ethanol. Samples of tissue (liver, muscle from lower side of thighs or toe tips) were taken from preserved specimens and stored in 1.5 ml vials filled with 96% ethanol. Measurements of morphological features were taken by NGK with a dial calliper (accuracy ± 0.1 mm) under a binocular dissecting microscope (± 0.1 mm), as follows: snout–vent length (SVL), head width measured directly behind the eyes (HW), head length in straight line from snout–tip to posterior edge of skull (HL), inter-orbital distance between eye-balls on dorsal side of head (IOD), distance from anterior corner of the eye to the nostril (EN), distance from anterior corner of the eye to the snout–tip (ES), horizontal eye diameter (ED), inter-nostril distance (IND), horizontal tympanum diameter (TD); thigh length from vent to knee (TL), crus length from knee to articulation with foot (CL), foot length including longest toe (FTL). Additionally, we determined the sex on the basis of external morphological characters, i.e., males mainly differ from females by possessing throats with a dark or black subgular vocal disc-like sac, and nuptial pads on digit II. We recorded the texture of the dorsal and ventral skin, relative finger and toe lengths, and the colour of preserved specimens. Descriptions of colour pattern of frogs in life and their habitats were based on photos taken in the field. Specimens investigated are deposited in the collection (ZMB) of the Museum für Naturkunde (MfN), Berlin, Germany. For comparative material investigated see Appendix 1.

Molecular datasets and phylogenetic analyses. A BLAST search of the 16S ribosomal RNA against sequences in GenBank, performing a similarity check among sequences, identified the West African taxa

P. afiabirago, *P. fraterculus*, *P. gutturosus*, *P. maculiventris*, and *P. pintoi* Hillers, Zimkus & Rödel, 2008 as the closest matches to the specimens of Tanoé-Ehy and Yakassé-Mé forests. Those five taxa have been shown to form a highly supported clade within this speciose genus (Zimkus *et al*. 2010, 2012). In addition to these recognized species, we included sequences of undescribed lineages clustering within the same clade (*P.* sp. nov. 3; Zimkus *et al.* 2010), and lineages co-occurring in Ivory Coast (*P*. aff. *gutturosus* 1 and 2), to assess whether any of them correspond to the newly described species. Accordingly, our molecular comparisons and phylogenetic assessment of the previously unstudied populations from Tanoé-Ehy and Yakassé-Mé focused on these five taxa and three distinct lineages. Specimens from Mabi-Yaya Forest Reserve, Taboth, and Tiassalé have not been sampled in this study and need to be genetically confirmed. Details for all herein studied individuals can be found in Table 1.

Total genomic DNA was extracted from thigh muscle samples taken from 10 individuals (five from each location; see Table 1) of the new lineage and four specimens of *P. afiabirago*, using the DNeasy tissue extraction kit (Qiagen) following the manufacturer protocols. The primers 16SA-L and 16SB-H of Palumbi *et al*. (1991) were used to amplify the mitochondrial 16S ribosomal RNA gene (16S) using the cycling protocol 94°C (90 s), [94°C (60 s), 51°C (60 s), 72°C (90 s)] x 35, 72°C (300 s). In addition, a fragment of the nuclear recombination-activating gene 1 (RAG1) was amplified using the primers and following the protocol of Zimkus *et al*. (2010). However, the samples of three *P. afiabirago* specimens (ZMB 73708; ZMB 86154; ZMB 86159) yielded only highly fragmented DNA, preventing the successful amplification of both markers. For all other samples (see Table 1), PCR products of both markers were purified using the QIAquick purification kit (Qiagen). Purified templates were sequenced in forward and reverse direction using an automated sequencer (ABI 377 or ABI 3100). Sequences were checked for reliability using the original chromatograph data in the program BioEdit (Hall 1999), aligned using ClustalX (Thompson *et al*. 1997) and subsequently checked by eye. All newly generated sequences were submitted to GenBank (PX890422-PX890432 (16S) and PX907657-PX907864 (RAG1); see Table 1).

The identification of distinct mitochondrial lineages was based on the 16S alignment (length = 540 bp; N = 40). Phylogenetic relationships were inferred using a Maximum Likelihood (ML) approach in IQ-TREE version 1.6.12 (Nguyen *et al*. 2015) with 1000 bootstrap replicates, under the best-fit substitution model selected using the command -m TEST in the integrated program ModelFinder (Kalyaanamoorthy *et al*. 2017). The tree was rooted using publicly available sequences for two individuals of *Phrynobatrachus ungujae* Pickersgill, 2007 (MCZ A-138442 and MCZ A-138444) as outgroups and visualised in FigTree version 1.4.4 (https://github.com/rambaut/figtree). The taxonomic identity was further corroborated by the calculation of uncorrected pairwise distances (*p*-distances) based on the 16S sequences in TaxI2 (Vences *et al*. 2024a), which is part of the iTaxoTools toolkit (Vences *et al*. 2021). In order to avoid biased results due to high amounts of missing data, sequences for five specimens had to be removed for distance calculations: *Phrynobatrachus afiabirago* ZMB 86160, *P. fraterculus* 135 and T34, *P. maculiventris* ZMB 71594, and *P. pintoi* ZMB 76881. We considered our new samples to represent an undescribed species if genetic distances to previously described species exceeded 3%, which is a commonly applied species threshold in anurans (e.g., Fouquet *et al*. 2007; Vieites *et al*. 2009; Rödel *et al*. 2015).

Mitochondrial distinction was contrasted with the assessment of diversity in nuclear encoding DNA, using a haplotype network approach based on a fragment of the protein-coding nuclear gene RAG1 (length = 664 bp; N = 18) in the program Hapsolutely (Vences *et al*. 2024b) from the iTaxoTools toolkit (Vences *et al*. 2021). Alleles (haplotypes) were inferred using the PHASE algorithm (Stephens *et al*. 2001) implemented in the program, using a phase (-p) and allele (-q) threshold of 0.7 with 1000 MCMC iterations and 10% burn-in. Subsequently, the network was visualised using the Median-Joining algorithm (Bandelt *et al*. 1999) and edited in Adobe Illustrator version 29.5.1 to match the colour code of the mitochondrial phylogeny.

Molecular diagnostic sites differentiating all species were determined using MolD (Fedosov *et al*. 2022), as implemented in iTaxoTools (Vences *et al*. 2021). For this purpose, the 16S alignment was trimmed to equal length of all sequences and samples with large numbers of missing data (same as for distance calculations) were removed. *Phrynobatrachus keniensis* Barbour & Loveridge, 1928 served as an indexing reference, for which the complete 16S gene was extracted from yet the most complete mitochondrial genome for the genus available on GenBank (15136 bp; JX564885.1). Gaps were considered as non-diagnostic sites (Gaps_as_chars = no) and a percent difference of 1% was used for the inference of rDNC's (Pdiff = 1). The input file for MolD along with the input files for other analyses can be downloaded from the Zenodo repository (https://doi.org/10.5281/zenodo.18214534).

TABLE 1. *Phrynobatrachus* specimens used for genetic inferences in this study, including locality information, and GenBank accession numbers for each marker. Holotype specimens are highlighted in boldface and newly generated sequences are indicated by an asterisk.

Taxon	Voucher	Field N°	Sex	Country	Locality	Lat.	Long.	16S	RAG1	Source
P. moroedeli sp. nov.	ZMB 94956	NGK 049 | TEF 01	F	Ivory Coast	Tanoé-Ehy swamp forest	5.1939	-2.8758	PX890423*	–	this study
P. moroedeli sp. nov.	ZMB 94957	NGK 050 | TEF 02	F	Ivory Coast	Tanoé-Ehy swamp forest	5.1939	-2.8759	PX890424*	–	this study
P. moroedeli sp. nov.	ZMB 94960	NGK 053 | TEF 05	F	Ivory Coast	Tanoé-Ehy swamp forest	5.1939	-2.8762	PX890425*	PX907858*	this study
***P. moroedeli* sp. nov.**	**ZMB 94963**	**NGK 056 | TEF 08**	**F**	**Ivory Coast**	**Tanoé-Ehy swamp forest**	**5.1939**	**-2.8765**	**PX890426***	PX907859*	**this study**
P. moroedeli sp. nov.	ZMB 94964	NGK 057 | TEF 09	M	Ivory Coast	Tanoé-Ehy swamp forest	5.1939	-2.8766	PX890427*	–	this study
P. moroedeli sp. nov.	ZMB 94911	NGK 004	M	Ivory Coast	Yakassé-Mé forest	5.7622	-3.9357	PX890428*	PX907860*	this study
P. moroedeli sp. nov.	ZMB 94912	NGK 005	M	Ivory Coast	Yakassé-Mé forest	5.7622	-3.9357	PX890429*	PX907861*	this study
P. moroedeli sp. nov.	ZMB 94914	NGK 007	M	Ivory Coast	Yakassé-Mé forest	5.7622	-3.9357	PX890430*	PX907862*	this study
P. moroedeli sp. nov.	ZMB 94915	NGK 008	M	Ivory Coast	Yakassé-Mé forest	5.7622	-3.9357	PX890431*	PX907863*	this study
P. moroedeli sp. nov.	ZMB 94916	NGK 009	M	Ivory Coast	Yakassé-Mé forest	5.7622	-3.9357	PX890432*	PX907864*	this study
P. afiabirago	**UWBM 5925**	**ADL 3999**	**M**	**Ghana**	**Atewa Range**	**6.2425**	**-0.5571**	**MF167602**	**–**	**Ofori-Boateng *et al.* (2018)**
P. afiabirago	UWBM 9041	-	F	Ghana	north-western part of Atewa Range	6.1280	-0.5571	MF167603	–	Ofori-Boateng *et al.* (2018)
P. afiabirago	UWBM 9042	-	M	Ghana	north-eastern part of Atewa Range	6.2425	-0.6289	MF167604	–	Ofori-Boateng *et al.* (2018)
P. afiabirago	UWBM 9043	-	M	Ghana	north-eastern part of Atewa Range	6.2425	-0.6289	MF167605	–	Ofori-Boateng *et al.* (2018)
P. afiabirago	UWBM 9044	-	M	Ghana	north-eastern part of Atewa Range	6.2425	-0.6289	MF167606	–	Ofori-Boateng *et al.* (2018)
P. afiabirago	UWBM 9045	-	M	Ghana	north-eastern part of Atewa Range	6.2425	-0.6289	MF167607	–	Ofori-Boateng *et al.* (2018)
P. afiabirago	UWBM 9046	-	M	Ghana	north-eastern part of Atewa Range	6.2425	-0.6289	MF167608	–	Ofori-Boateng *et al.* (2018)
P. afiabirago	ZMB 86160	JP 0014	M	Ghana	Atewa Range, Atiwiredu	6.2006	-0.5775	PX890422*	PX907857*	this study
P. fraterculus	-	135	-	Guinea	Diécké Forest Reserve	7.5833	-8.8500	FJ798828	–	Rödel *et al.* (2004)
P. fraterculus	-	GO31	M	Liberia	Gola National Forest	7.4563	-10.6956	EU718721	–	Hillers & Rödel (2007)
P. fraterculus	-	T34	-	Ivory Coast	Taï National Park	5.7543	-6.9398	AY902378	–	Rödel & Ernst (2004)
P. fraterculus	ZMB 73759	MOR 30	-	Ivory Coast	District des Montagnes, Taï National Park	5.7543	-6.9398	GU457550	GU457659	Zimkus *et al.* (2010)

.....continued on the next page

TABLE 1. (Continued)

Taxon	Voucher	Field N°	Sex	Country	Locality	Lat.	Long.	16S	RAG1	Source
P. fraterculus	ZMB 73761	GU133	-	Guinea	Nzérékoré Region, Diécké Forest	7.5775	-8.9676	GU457551	GU457660	Zimkus *et al*. (2010)
P. gutturosus	-	MOR C9	F	Ivory Coast	Comoé National Park	8.7500	-3.8167	EU718724	–	Rödel & Spieler (2000)
P. gutturosus	-	MOR C11	-	Ivory Coast	Marahoué National Park	7.0972	-6.0256	GU457556	GU457674	Rödel & Ernst (2003)/ Zimkus *et al*. (2010)
P. aff. *gutturosus* 1	-	MOR T33	–	Ivory Coast	–	–	–	GU457522	GU457598	Zimkus *et al*. (2010)
P. aff. *gutturosus* 2	-	MOR S01.38	–	Ivory Coast	–	–	–	GU457523	GU457599	Zimkus *et al*. (2010)
P. maculiventris	ZMB 71592	LS022	M	Guinea	Nzérékoré Region, Yonsono, Diécké Forest	7.5181	-8.8358	FJ798825/ GU457563	GU457701	Rödel *et al*. (2004)/ Zimkus *et al*. (2010)
P. maculiventris	ZMB 71593	LS023	M	Guinea	Nzérékoré Region, Yonsono, Diécké Forest	7.5181	-8.8358	FJ798826/ GU457564	GU457702	Rödel *et al*. (2004)/ Zimkus *et al*. (2010)
P. maculiventris	ZMB 71594	-	tadpole	Guinea	Nzérékoré Region, Yonsono, Diécké Forest	7.5181	-8.8358	FJ798827	–	Rödel *et al*. (2004)
P. pintoi	**ZMB 70689**	**BO167**	**-**	**Guinea**	**Boké Préfécture/ Sangarédi**	**11.1063**	**-13.9599**	**EU718711/ GU457571**	**GU457740**	**Hillers *et al*. (2008)/ Zimkus *et al*. (2010)**
P. pintoi	ZMB 76879	KD112	-	Guinea	Télimélé Préfecture	10.9351	-13.6612	JN813914	–	Rödel *et al*. (2011) - unpublished
P. pintoi	ZMB 76881	KD114	-	Guinea	Télimélé Préfecture	10.9351	-13.6612	JN813915	–	Rödel *et al*. (2011) - unpublished
P. pintoi	ZMB 76883	KD116	-	Guinea	Télimélé Préfecture	10.9380	-13.6645	JN813916	–	Rödel *et al*. (2011) - unpublished
P. pintoi	ZMB 76885	KD118	-	Guinea	Télimélé Préfecture	10.9380	-13.6645	JN813917	–	Rödel *et al*. (2011) - unpublished
P. pintoi	ZMB 76878	KD123	-	Guinea	Télimélé Préfecture	11.0549	-13.6779	JN813913	–	Rödel *et al*. (2011) - unpublished
P. sp. nov. 3	ZMB 73704	MOR BO107	juvenile	Guinea	Boké Prefecture, Kamsar	10.62385	-14.524483	GU457579	GU457756	Zimkus *et al*. (2010)
P. sp. nov. 3	ZMB 73707	MOR BO121	juvenile	Guinea	Boké Prefecture, Kamsar	11.1141	-14.961333	GU457580	GU457757	Zimkus *et al*. (2010)

Nomenclatural act. The electronic version of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new name contained herein is available under that Code from the electronic edition of this article. This published work and the nomenclatural act it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is on the first page of this article. The electronic edition of this work was published in a journal with an ISSN, has been archived and is available from the following digital repositories: mapress.com/zt/index, zenodo.org.

Results

Molecular species delimitation. The ML tree inferred from sequences of the mitochondrial barcoding marker 16S (540 bp) for 38 ingroup specimens is shown in Figure 2. The obtained phylogeny confirmed the distinctiveness of all focal *Phrynobatrachus* species from Upper Guinean Forest, with all being recovered as highly supported monophyletic groups: *P. afiabirago* (BS = 98), *P. maculiventris* (BS=100), *P. fraterculus* (BS = 96), *P. pintoi* (BS=99), *P. gutturosus* (BS = 100) and the newly analysed populations from Tanoé-Ehy forest and Yakassé-Mé village forest forming a single clade (BS = 98). Interestingly, specimens from Yakassé-Mé cluster as a separate group within the clade of the newly described species (dark yellow Fig. 2), although with low support (BS = 70). The sister lineage to the whole clade is *P.* aff. *gutturosus* 1, a specimen previously identified as a candidate species (Zimkus *et al*. 2010), with strong support for a shared ancestry with all members of the newly identified lineage (BS = 96).

The basis of the tree is formed by *P. fraterculus* and the other lineages can be further divided into two weakly supported groups, one comprising all members of *P. pintoi* and *P. gutturosus* (BS = 75), and the other including the remaining three species and three candidate species (BS = 52). Interestingly, this grouping does not correspond to a geographic pattern of species distribution but may rather reflect polymorphic traits and/or life-histories.

Uncorrected pairwise distances (Table 4) between lineages exceed the 3% divergence threshold for 16S, which is commonly applied to identify anuran species (e.g., Vieites *et al.* 2009). The sole exception is found for the newly identified lineage from Tanoé-Ehy forest, Yakassé-Mé village forest and *P.* aff. *gutturosus* 1, with distances ranging from 1.81–2.22%. Interspecific distances among all other lineages range from 5.04% (new lineage vs. *P. afiabirago*) to 12.66% (*P. fraterculus* vs. *P. pintoi*). Intraspecific distances were expectedly low, ranging from 0% to 0.61% (*P. gutturosus*).

The haplotype network based on RAG1 alleles (664 bp) of 18 specimens showed no haplotype sharing between lineages (Fig. 3). The highest diversity was found among specimens of the newly identified lineage, with eight distinct haplotypes and no haplotype sharing between individuals from Tanoé-Ehy (light yellow) and Yakassé-Mé (dark yellow). Individuals of the new lineage differ from *P. afiabirago* by 2–8 mutations with two individuals sharing a single haplotype from Tanoé-Ehy being closest related. The lineage *P. gutturosus* 1, although recovered as closest related in the mitochondrial phylogeny, is distinct from the new lineage by four mutational steps in the haplotype network. From other species described for the genus, it differs by a minimum of 5 (*P. maculiventris*) up to 17 mutations (*P. pintoi*), which is comparable to the divergence observed among other species (e.g., a maximum of 11 mutations between *P. gutturosus* and *P. maculiventris*, and a maximum of 14 mutations between *P. fraterculus* and *P. pintoi*).

Morphological differentiation. Individuals of the new species are of rather compact, small size, with SVL ranging from 13.9–21.0 mm. The colour pattern shows some variation, in particular the dorsal part of the body ranges from bronze to either greyish brown or brown with some black or dark spots scattered particularly along edges of warts. The belly exhibits a striking colour pattern variation, ranging from very few small black dots to being intensively beset with large dark or black blotches along the edges. The ventral sides of hind legs have some dark to black blotches of variable sizes. The new species is morphologically most similar to members of the '*P. gutturosus*' group by possessing the combination of the following morphological characters: narrow X-shaped pair of ridges in the scapular region, black throat in adult males, black lateral band on flanks, well visible light vertebral line or band, and hind legs with rudimentary webbing.

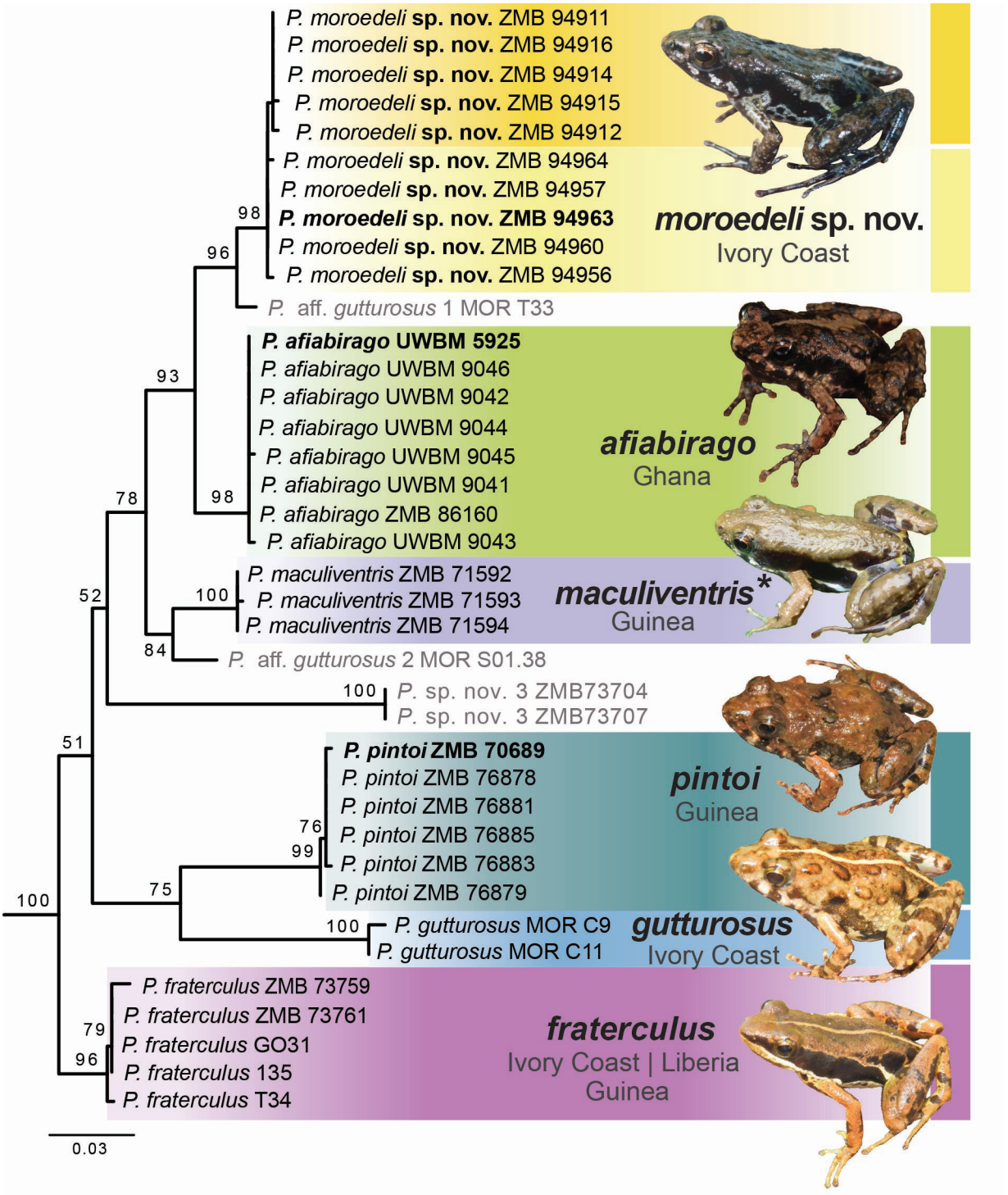

FIGURE 2. Maximum Likelihood tree calculated from the mitochondrial 16S ribosomal DNA gene (N= 40, length = 540 bp) for *Phrynobatrachus moroedeli* **sp. nov.** and its closest congeners from Upper Guinean Forest. Values at the main nodes indicate percent bootstrap support (BS) and are indicated if BS>75. Two individuals of *P. ungujae* were used as outgroups (not shown for graphical reasons). Photographs not to scale. * = original photograph mirrored.

Taxonomic conclusion. In light of congruence between molecular and morphological results indicating distinction from other species of the Upper Guinean Forest, we consider the individuals from populations of Tanoé-Ehy swamp forest and Yakassé-Mé to represent a distinct species new to science, which we formally describe in the following.

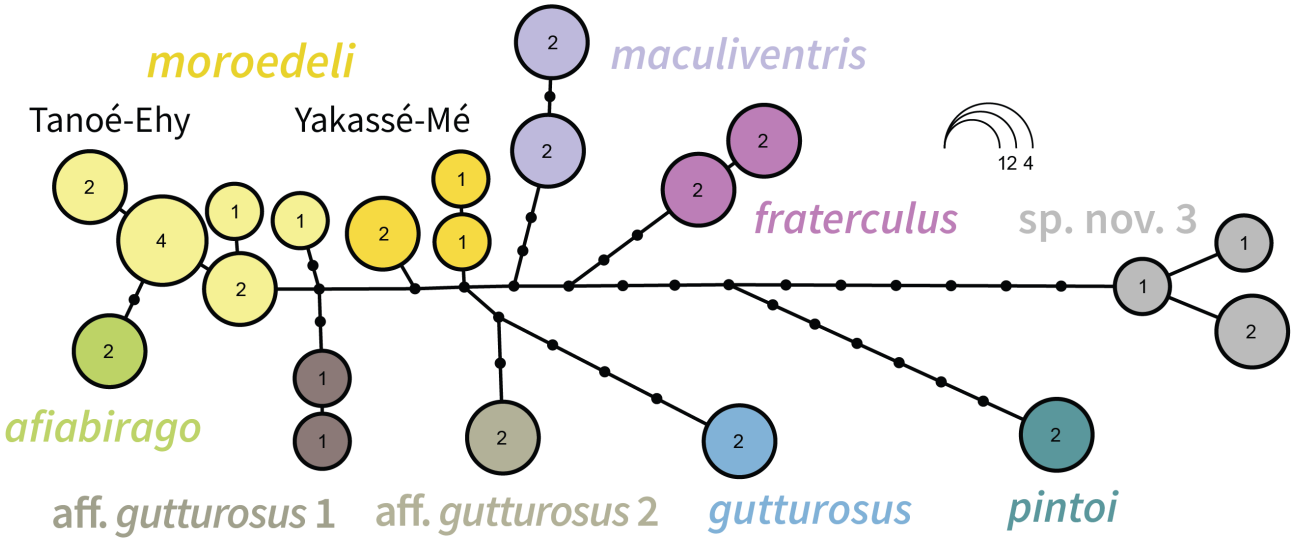

FIGURE 3. Haplotype network inferred from the phased DNA sequences of 18 individuals for the nuclear-encoded RAG1 gene (664 bp) between *Phrynobatrachus moroedeli* **sp. nov.** and its closest congeners from Upper Guinean Forest. Circles represent haplotypes, with size proportional to their frequency in the individuals sequenced. Small black dots in-between haplotypes represent mutational steps. Individuals were coloured according to the mitochondrial phylogeny.

***Phrynobatrachus moroedeli* sp. nov.**
Figs 4–6

Holotype. ZMB 94963 (field and tissue #: NGK 056, TEF08), adult female, Ivory Coast, Dohouan village forest, a patch of the Tanoé-Ehy swamp forests, 05°11′38.04″N, 02°52′32.9″W, (datum: WGS84), swamp forest dominated by *Raphia* palms with large canopy gaps, shallow water, and the leaf-litter, 14 March 2018, coll. N.G. Kouamé.

Paratypes (21 specimens). ZMB 94956–94957 (NGK 049–050), ZMB 94959–94960 (NGK 052–053), 94962 (NGK 055), 94965 (NGK 058), six adult females, same data as holotype; ZMB 94958 (NGK 051), ZMB 94961 (NGK 054), ZMB 94964 (NGK 057), ZMB 94966–94968 (NGK 059–061) six adult males, same data as holotype; ZMB 94911–94919 (NGK 001–009), nine adult males, Ivory Coast, Yakassé-Mé village forest, 05°45′43.8″N, 03°56′08.5″W, (datum: WGS84), thick vegetation alongside a deep swamp, bamboo patches with small brooks running through degraded forest, 20 July 2024, coll. N.G. Kouamé.

Diagnosis. The 16S rRNA sequence data confirmed that the new species is a member of the genus *Phrynobatrachus*. Compared to other West-African members of the genus *Phrynobatrachus*, the new species can be characterised by exclusive synapomorphies in 16S (see below), and the lack of haplotype sharing with other species from the region in the nuclear RAG1 gene. *Phrynobatrachus moroedeli* **sp. nov.** is morphologically most similar to a variety of small, compact West African *Phrynobatrachus* species with warty dorsal skin: *Phrynobatrachus alleni*, *P. francisci*, *P. ghanensis*, *P. guineensis*, *P. latifrons*, and *P. phyllophilus*. The new species is however smaller (< 23 mm) than *P. intermedius* Rödel, Boateng, Penner & Hillers, 2009, *P. liberiensis*, *P. natalensis*, *P. plicatus*, and *P. tanoeensis*.

The new species may share vertebral line or band with *P. calcaratus*, *P. francisci*, *P. fraterculus*, *P. ghanensis*, *P. gutturosus*, *P. latifrons*, and *P. tokba*. However, in all these seven species the vertebral line or band may be present or absent, while the characteristic light or white vertebral line or band is always present in the new species. When present, the vertebral line or band is light or reddish in *P. calcaratus*, *P. fraterculus*, *P. ghanensis*, and *P. gutturosus*, light, reddish, or green in *P. francisci*, red, green, orange, beige or bright yellow in *P. latifrons*, and light, reddish or green in *P. tokba*. The new species shares distinct lateral band on flanks with *P. afiabirago*, *P. fraterculus*, *P. latifrons*, *P. maculiventris*, and *P. phyllophilys*. Whereas the dorsal skin is smooth in *P. fraterculus*, *P. hieroglyphicus* Rödel, Ohler & Hillers, 2010, most often discernible in breeding *P. latifrons* and *P. tokba*, and somewhat granular in *P. maculiventris*, the new species has rough to warty dorsal skin. The new species possesses

short X-shaped scapular or dorsal ridges, while scapular ridges in *P. alleni*, and *P. plicatus* are long and converging towards mid-body, almost X-shaped. The new species differs from *P. annulatus*, *P. calcaratus*, *P. pintoi*, *P. taiensis*, and *P. villersi* by lacking a spine-like wart on upper eyelid (eyelid cornicle). In addition to these characters, *P. moroedeli* **sp. nov.** differs from *P. intermedius*, *P. plicatus*, *P. liberiensis* and *P. rainerguentheri* Rödel, Onadeko, Barej & Sandberger, 2012, by lacking a black lateral face mask. Males of the new species have dark to completely black throats, while the throat in *P. alleni* and *P. latifrons* males is yellow and the throat in *P. annulatus* males is either white or greyish. *Phrynobatrachus afiabirago*, *P. annulatus*, *P. fraterculus*, *P. ghanensis*, *P. maculiventris*, *P. pintoi*, *P. taiensis* and *P. villiersi* all have very characteristic, species-specific patterning on the belly, different to the new species which exhibits exceptional dark markings varying in intensity from very few small black dots to being densely beset with large dark or black blotches along the edges. In contrast, *P. alleni* (only females, males with yellow belly), *P. francisci*, *P. latifrons*, *P. natalensis*, and *P. rainerguentheri* have predominantly white bellies with at best some rare minute black points. The belly and pectoral region of *P. phyllophilus* is whitish, often with smaller black spots. Femoral glands are discernible in males of *P. fraterculus*, *P. gutturosus*, *P. maculiventris*, *P. phyllophilus*, and *P. taiensis*, but absent in males of the new species. The webbing is more developed in *P. alleni*, *P. francisci*, *P. intermedius*, *P. latifrons*, *P. liberiensis*, *P. natalensis*, *P. plicatus*, and *P. rainerguentheri* than in the new species, which has distinct but rudimentary pedal webbing.

Two other taxa that have earlier been reported to occur in southern Ivory Coast are *P. parogoensis* Loveridge, 1955 and *P. aelleni* Loveridge, 1955. The type locality for the first taxon is 'a banana plantation at N'zida' in Grand-Lahou, approximately 126 km from Abidjan westwards, while the type locality for the second taxon is 'a temporary pool on a forest trail near the research centre of the Centre Suisse de Recherches Scientifiques (C.S.R.S.)' in Adiopodoumé, approximately 18 km from Abidjan westwards (Loveridge 1955; Schätti *et al*. 2002). *Phrynobatrachus parogoensis* was relegated into the synonymy of *P. accraensis* by Guibé & Lamotte (1963), while Rödel (2000) considered *P. parogoensis*/*accraensis*-like frogs to represent a junior synonym of *P. latifrons*. *Phrynobatrachus parogoensis*/*accraensis*/*latifrons*-like frogs can be differentiated morphologically from *P. moroedeli* **sp. nov.** by the yellow to bright yellow throats of their males (Rödel 2000; Rödel & Agyei 2003); throats being greyish dark, deep dark to completely black in males of the new species (Figs. 4d, f; 5b, d). In addition, the webbing is more developed in *P. parogoensis*/*accraensis*/*latifrons*-like frogs than in the new species, which has distinct but rudimentary pedal webbing. Concerning *P. aelleni*, it was treated by Lamotte & Xavier (1966) as a junior synonym of *P. plicatus*. *Phrynobatrachus aelleni*/*plicatus*-like frogs mainly differ from *P. moroedeli* **sp. nov.** by possessing the following characters: SVL up to 42 mm, black or dark lateral face mask, and long X-shaped scapular or dorsal ridges converging towards mid-body (Channing & Rödel 2019). These morphological characters are completely absent in the newly described species.

Description of the holotype (measurements in mm; Figs. 4a, b, 6). Adult female in good state of preservation with slender-oval, compact body shape; very short and round snout; large eyes; SVL: 21.0; snout rounded in dorsal, moderately pointed in lateral view; HW: 7.2, shorter than HL: 9.9; IOD: 2.7; ED: 3.1, larger than TD: 2.0; tympanum distinct, round with round median annuli; EN: 1.2; ES: 2.3; nostrils closer to snout tip than to eye; IND: 1.8; canthus rostralis rounded; loreal region straight; eyelids without spiny tubercles, but faintly granular; CL: 11.5, longer than TL: 7.9; FTL: 17.2; hand with oval palmar and thenar tubercles; fingers with small roundish subarticular tubercles, no additional tubercles on hands; small round tarsal tubercle; finger tips roundish, not enlarged to discs; manual webbing absent; larger internal and smaller external metatarsal tubercle; toe-tips expanded forming slightly roundish discs; relative toe length: I<II<V<III<IV; only palmar webbing rudimentary between the most basal phalanx of each toe; dorsal skin slightly warty, spinulae on posterior part of back indistinct; spinulae on dorsal surfaces of thighs and lower legs; narrow X-shaped pair of ridges in scapular region, anterior one small and roundish, posterior one larger and elongated; pair of very small warts on back edges, and upper part of flanks; ventral skin otherwise smooth; relative finger length: I<II<IV<III; only traces of webbing.

Colour in life. Dorsal surface basically dark brown; light vertebral line or band starting from the scapular region to vent; orange-golden iris; area between inter-orbital to snout tip light; black bars alternating with white bars on upper lip, whereas lower mandible almost completely black with few minute white spots; broad black longitudinal band extending from behind eye across tympanum region and running along flank to groin; narrow area between this band and back light in upper part but faint yellow in groin region; upper arms dorsally brownish to light; lower arms dorsally brownish, beset with minute light spots; outer parts of hind legs brownish with three broad black cross bars on thighs, and several narrow black cross bars on lower legs; lower part of flank white with large black dots towards

FIGURE 4. Dorsolateral and ventral views of live specimens of *Phrynobatrachus moroedeli* **sp. nov.** from south-eastern Ivory Coast: female holotype (ZMB 94963) from the type locality in Tanoé-Ehy swamp forest (a, b); male specimen (ZMB 94966) from the type locality (c, d); male specimen (ZMB 94971) from Yakassé-Mé village forest (e); ventral view of male (ZMB 94913) from Yakassé-Mé village forest with some parasitic, subcutaneous mites on the lower parts of the ventral side of thighs (d, f); female (not collected) from Mabi-Yaya Forest Reserve (g); female specimen (not collected) from Yakassé-Mé village forest (h).

of venter; throat greyish with brownish mottling reaching sides of pectoral region; belly whitish with dark brown blotches on sides; groin area yellow; ventral parts of thighs grey with dark spots, while ventral parts of lower legs grey with variable size of dark brown botches; ventral parts of feet including rudimentary webbing, phalanges and articular tubercles dark brown.

Colour in preservation (Fig. 6). After being preserved for more than six years in 75% ethanol, the colour pattern as in life has notably faded. The dorsal surface exhibits a predominantly rusty colouration, whereas the ventral surface turned into beige or whitish colour.

Variation. Paratype individuals are morphologically similar to the holotype, but with contrasting colour morphs in some males' ventral pattern. Snout-vent lengths in adults range from 18.0–21.0 mm (mean ± sd: 19.1 ± 1.2 mm; N = 7) in females, and 13.9–18.2 mm (mean ± sd: 16.4 ± 1.1 mm; N = 15) in males. Females are significantly larger than males (Mann-Whitney *U*-test, $Z = 3.418801$, $P = 0.000141$, N = 22). Snout-vent lengths of paratype males from the type locality range from 13.9–16.5 mm (mean ± sd: 15.8 ± 0.9 mm; N = 6). In contrast paratype males originated from Yakassé-Mé range between 15.1–18.2 mm (mean ± sd: 16.8 ± 1.0 mm; N = 9), thus being larger in size than males from the type locality. Further measures are summarised in Tables 1 and 2. The frogs have a compact body shape with a short rounded to pointed snout. The dorsal skin structure between both sexes may vary from rough to warty. The skin roughness changes within individuals, dorsal skin of fore-and-hind legs being rough to slightly granular. A short X-shaped pair of scapular ridges is always present on back. Some individuals possess a row of warts on edges of the back. The different colourations are illustrated in Figures 4 and 5. The basic dorsal colour ranges from bronze to either greyish brown or brown with some black or dark spots scattered particularly along edges of warts; the black lateral bands are always present, often with wave-like border. Likewise, a light vertebral line is well visible. The thighs and shanks may carry more than two broad dark cross bars, these bars are smaller on lower parts of hind legs. The lower and upper mandibles in both sexes are most often dark cross-barred. All males have nuptial pads on digit II, but lack femoral glands. Some females have a ventral border of flanks with black dots. All females from the type locality share a greyish smooth throat with irregular dark brown spots and patches that occasionally may nearly cover the whole throat, and some brown spots on the pectoral region. They have a white or almost white belly with some large dark brown spots in the lateral parts. Some exhibit some large dark brown spots in the pectoral region. Females from Yakassé-Mé and Mabi-Yaya Forest Reserve have a more contrasting smooth dark spotted-throat, ranging from densely dark brown to being beset with huge black blotches separated by narrow whitish lines. In some individuals, the region between the junction of arms and shoulders is yellow. Some females exhibit some large black spots in the lateral parts of the belly. The groin area is beige to yellow. The ventral sides of thighs, crus and feet are beige to yellowish and are dark-spotted. The throat of males from the type locality is either completely black or dark grey ground densely covered with large black spots. Sometimes, the pectoral region is entirely black. The central parts of belly may vary from almost uniform white to rose-coloured. Edges of belly, inner parts of thighs, crus, and feet of males exhibit numerous black markings, which range from small black dots to being densely beset with huge black blotches. Sometimes, the ventral surface of males may be rose-coloured with some dark spots. However, males from Yakassé-Mé and some males from Tiassalé differ to males of the type locality by having an almost uniform brown dorsal colour. Their throats are most often dusted in dark greyish with a well discernible subgular vocal disc-like. The belly is white with a few black dots on the lateral parts, while the groin area is yellow and carries a few black spots. The inner parts of thighs, crus, and feet are beige with some black spots.

In preservation, all paratypes from the type locality mirror exactly the holotype (Fig. 4). The colour in preservation of paratypes from Yakassé-Mé is likely a bit fainted, otherwise it is not different to colour in life.

Genetics. *Phrynobatrachus moroedeli* **sp. nov.** can be distinguished from congeners of the Upper Guinean Forest clade by one minimal diagnostic nucleotide combinations (mDNCs) in the mitochondrial 16S gene used for molecular taxonomic identification (positions relative to the whole respective marker extracted from the almost complete mitochondrial genome of *P. keniensis*, JX564885.1): 'G' at site 1015.

Distribution, threats and conservation status. The new species has been so far recorded from four localities in south-eastern Ivory: the type locality in Tanoé-Ehy swamp forest (05°11′38.04″N, 02°52′32.9″W), Yakassé-Mé village forest (05°45′43.8″N, 03°56′08.5″W), Mabi-Yaya Forest Reserve (05°43′16.8″N, 03°35′6.72″W), and a very small pocket of forest from Taboth village in Jacqueville district (05°15′21.24″N, 04°19′22.01″W). A viable population of *P. moroedeli* **sp. nov.** was also found in Tiassalé (05°41′40″N, 04°52′08″W) in south-central Ivory Coast (Fig. 1). However, it is likely that the new species also occurs in Ankasa Conservation Area in south-western Ghana, near the border with Ivory Coast. In Taboth village, the small pocket of forest, where the new species was

found, falls entirely within a non-protected area, rendering the local specimens highly vulnerable to habitat loss following the rapid urbanisation of Jacqueville district. Similarly, the Yakassé-Mé village forest and Tiassalé are also not under formal protection but are rather owned and managed by local communities. Therefore, the long-term survival of the new species in Taboth, Yakassé-Mé, and Tiassalé is highly uncertain. Only the Tanoé-Ehy swamp forest and Mabi-Yaya Forest Reserve remain the two promising sites for conservation of viable populations of the new species. Given these concerns, the new species likely qualifies for the category Endangered according to the IUCN RedList criteria (IUCN 2017).

TABLE 2. Measurements (in mm) of the type series of *Phrynobatrachus moroedeli* **sp. nov.** (holotype in bold); ZMB = ZMB accession number; M = male, F = female; SVL = snout–vent length; HW = head width; HL = head length; IOD = inter-orbital distance; EN = distance anterior corner of eye to nostril; ES= distance anterior corner of eye to snout-tip; ED = horizontal eye diameter; IND = inter-nostril distance; TD = horizontal tympanum diameter; TL = thigh length; CL = crus length; FTL = foot length incl. longest toe; * = specimens from Tanoé-Ehy swamp forest; ** = specimens from Yakassé-Mé village forest.

ZMB	status	sex	SVL	HW	HL	IOD	EN	ES	ED	IND	TD	TL	CL	FTL
94956*	paratype	F	18.0	6.0	7.4	2.9	1.0	1.9	2.5	1.5	1.1	7.8	8.9	14.0
94957*	paratype	F	19.8	6.3	8.8	2.9	1.2	2.1	3.0	1.5	1.1	8.8	10.8	15.9
94958*	paratype	M	15.9	5.2	7.0	1.2	1.0	1.5	2.2	1.5	1.0	6.3	8.5	13.0
94959*	paratype	F	18.0	6.0	7.9	2.5	1.5	2.6	2.9	2.0	1.2	7.8	9.0	13.8
94960*	paratype	F	19.8	6.0	9.0	2.5	1.2	2.2	3.4	1.5	1.1	9.8	11.1	15.5
94961*	paratype	M	13.9	4.4	5.9	1.9	1.0	1.6	2.5	1.5	0.9	6.1	8.1	11.0
94962*	paratype	F	18.1	5.5	6.9	2.0	1.0	1.7	2.3	1.9	1.9	7.9	10.5	16.9
94963*	**holotype**	**F**	**21.0**	**7.2**	**9.9**	**2.7**	**1.2**	**2.3**	**3.1**	**1.8**	**2.0**	**7.9**	**11.5**	**17.2**
94964*	paratype	M	16.0	5.3	7.1	1.9	1.5	2.4	2.2	1.5	1.5	7.4	9.0	13.5
94965*	paratype	F	19.0	6.0	7.4	2.0	1.2	1.7	3.0	1.5	1.6	9.1	10.1	14.5
94966*	paratype	M	16.1	5.5	7.9	2.0	1.5	2.0	2.6	1.6	1.4	7.5	9.2	13.0
94967*	paratype	M	16.5	5.0	7.2	2.0	1.2	1.7	2.2	1.9	1.0	7.9	9.0	15.0
94968*	paratype	M	16.2	5.5	7.9	2.5	1.0	1.9	2.1	2.0	1.0	8.5	9.0	14.0
94908**	paratype	M	15.9	5.8	6.8	2.0	1.5	2.5	2.1	1.9	1.1	9.0	10.0	13.8
94909**	paratype	M	15.1	5.0	6.5	2.1	1.5	2.4	2.9	1.5	1.0	8.5	9.5	13.2
94910**	paratype	M	16.0	5.9	6.8	2.0	1.5	2.3	3.0	1.5	1.0	8.1	9.5	13.8
94911**	paratype	M	16.9	5.5	6.9	2.1	1.5	2.4	2.5	1.1	1.0	8.5	10.0	15.0
94912**	paratype	M	18.2	5.8	6.4	3.1	1.4	2.2	3.5	1.5	1.2	9.5	10.5	15.5
94913**	paratype	M	17.0	5.5	6.2	3.0	1.4	1.9	3.0	1.5	1.0	7.9	8.9	14.0
94914**	paratype	M	17.5	5.9	6.5	2.9	1.5	2.4	2.5	1.5	1.1	8.5	9.5	14.0
94915**	paratype	M	16.5	5.5	8.0	2.9	1.5	2.5	2.5	1.5	1.0	8.2	9.5	15.0
94916**	paratype	M	18.0	6.5	6.9	2.5	1.5	2.4	3.0	2.1	1.0	8.5	10.0	15.0

Natural History. *Phrynobatrachus moroedeli* **sp. nov.** inhabits true primary forests as well as degraded and fragmented forests. However, the new species seems to be more common in degraded forests, where it can often be found in the leaf-litter of drier parts, either close to open water, or close to slow flowing forest streams (Fig. 7). Habitats of the new species in Tanoé-Ehy swamp forest and Taboth village in Jacqueville district are predominantly swamp forests with *Raphia* palms. The forest area in Tanoé-Ehy and the small pocket of forest in Taboth are influenced by the brackish water backflow respectively from the Ehy and Ebrié lagoons. In Tiassalé, adults and froglets of the new species were mainly found, well concealed, between thick layers of the leaf-litter alongside a forest swamp. This forest patch had a low canopy and comprised some stands of *Raphia* palms. The forest area in Tiassalé is crossed by the Bandama River, which may represent a natural limit of the westernmost populations of *P. moroedeli* **sp. nov.**, approximately 217 km from the type locality. The mean annual temperature of the geographic area in south-eastern Ivory Coast is 26°C, the mean annual precipitation is about 2000 mm. This region is characterized by a longer dry

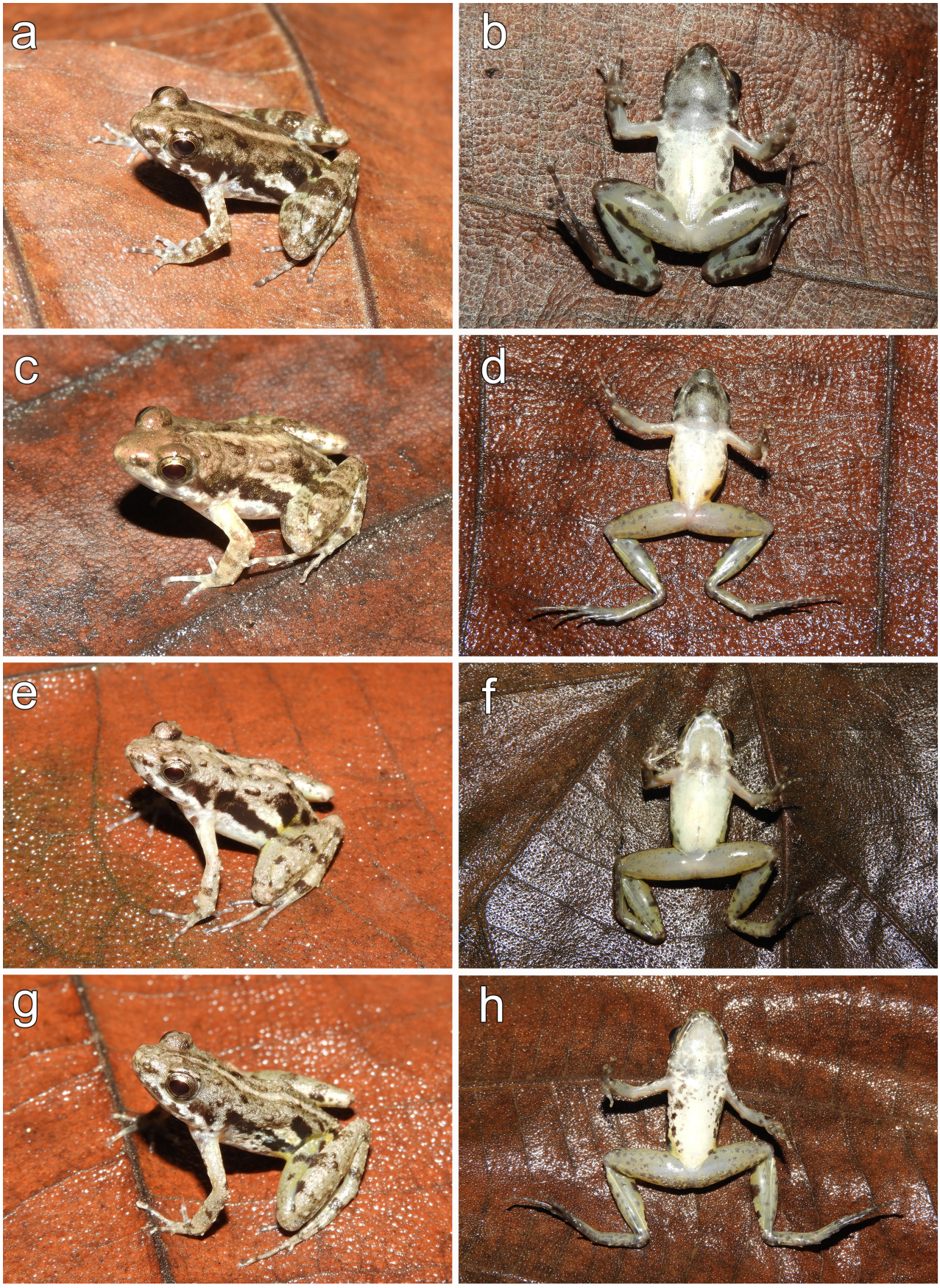

FIGURE 5. Dorsolateral and ventral views of live specimens of *Phrynobatrachus moroedeli* **sp. nov.** from Tiassalé, in the south-central part of Ivory Coast: male variations, not collected (a–d); female variations, not collected (e–h).

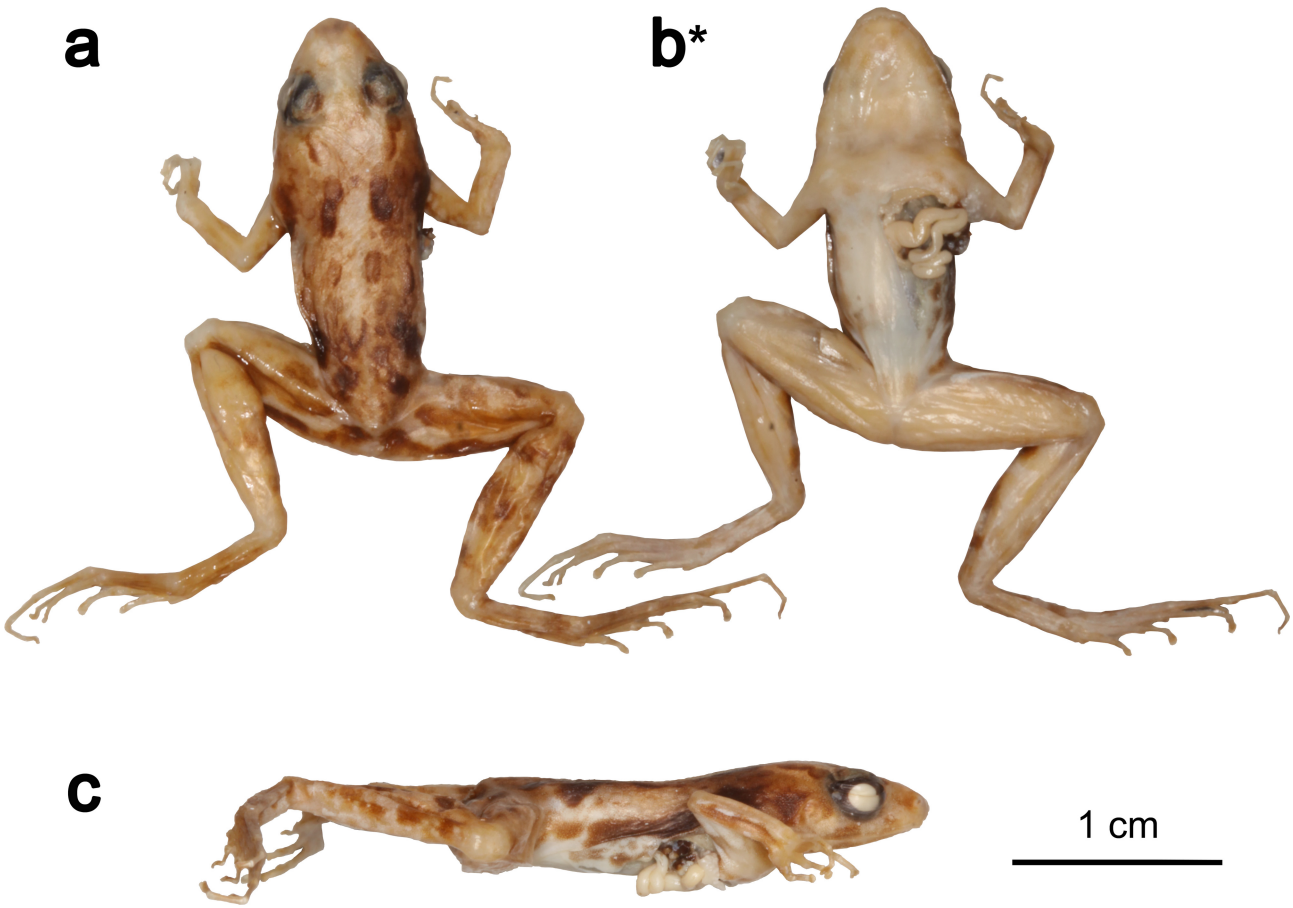

FIGURE 6. Preserved holotype specimen of *Phrynobatrachus moroedeli* **sp. nov.** (ZMB 94963, female) from Tanoé-Ehy swamp forest, the type locality, in south-eastern Ivory Coast in dorsal (a), ventral (b), and dorsolateral views. Photos by F. Tillack. * = original photograph mirrored.

season (December to March), followed by the period with high precipitation (March to July). A short rainy season extends from October to November (Avenard *et al*. 1971). The forest region mainly consists of moist, partly primary forests on predominantly sandy soil, with characteristic vegetation (Béligné 1994). During the rainy season, the water level is particularly high in Tanoé-Ehy swamp forest because water from the Tanoé River flows into the swamp. A large part of the small pocket of forest from Taboth village in Jacqueville district is not accessible in the core rainy season because of deep water. Likewise, during the rainy season the level of the Mafou River usually increases and inundates several patches of the forest in Yakassé-Mé. Rivers draining the Mabi-Yaya Forest Reserve are the Kossan and Yaya, two tributaries of the Comoé, and other smaller streams, i.e., Ebohoa, Foussin, N'tchibié, Abouan and Kloukro, and brooks.

Phrynobatrachus moroedeli **sp. nov.** seems to be a host for parasitic, subcutaneous mites of the genus *Endotrombicula* Ewing, 1931, in particular on the lower parts of the ventral side of thighs (Fig. 4d, f), where endoparasitic mites were detected in one male from Tanoé-Ehy swamp forest (Fig. 4d), as well as one male (Fig. 4f) and one female from Yakassé-Mé (not collected, picture not shown).

The advertisement call of the species remains unrecorded.

Etymology. The specific epithet '*moroedeli*' was chosen to honour PD Dr. rer. nat. habil. Mark-Oliver Rödel, alias MO. He is currently Curator of Herpetology at the MfN, Berlin, Germany. During his career, he has made outstanding contributions to amphibian research, with a publication record exceeding 400 scientific articles, including several books. His herpetology lab at the MfN comprises researchers and students of various career stages, from bachelor students to postdocs, with whom he conducts projects in Germany, Ecuador, Cameroon, Guinea, Ivory Coast, and Mozambique. MO has particularly contributed to our knowledge of West African amphibians by participating in field surveys in crucial areas and providing expert taxonomic advice, being actively involved in the description of many new species, and applying molecular techniques to tackle puzzling taxonomic cases. He has also trained several West African students, supporting the completion of their PhD projects in collaboration with national universities. In recognition of his substantial scientific contributions and mentorship, the authors feel

honoured and proud to dedicate this new species to him. The first author was one of his first African students dating back to 2001 and their collaboration has remained ongoing throughout the years. The second author is currently a postdoctoral researcher in his working group at the MfN, Berlin, Germany. The specific epithet is treated as a noun in apposition. The suggested common name for this new species is 'MO Rödel's Puddle Frog.'

Discussion

The lowland rainforest region from south-eastern Ivory Coast to neighbouring south-western Ghana is a biodiversity hotspot with a rich fauna of amphibians (Rödel *et al*. 2005; Assemian *et al*. 2006; Kouamé *et al*. 2014; Kpan *et al*. 2014). The amphibian diversity occurring in this ecoregion strongly differs from that observed in forest areas east of the Volta River and the western part of the Upper Guinea, especially in terms of species endemism (Penner *et al*. 2011). In particular between 1964 and 2018, at least nine rare and cryptic anuran species, which are endemic to various forest patches in-between eastern Ivory Coast and western Ghana, have been described. These endemic species are: *Astylosternus laticephalus* Rödel, Hillers, Leaché, Kouamé, Ofori-Boateng, Diaz & Sandberger, 2012, family Arthroleptidae Mivart, 1869, *Kassina arboricola* Perret, 1985, *Hyperolius laurenti* Schiøtz, 1967, *H. viridigulosus* Schiøtz, 1967, and *Morerella cyanophthalma* Rödel, Assemian, Kouamé, Tohé & Perret, 2009, family Hyperoliidae Laurent, 1943, and *Phrynobatrachus afiabirago*, *P. ghanensis*, *P. intermedius*, *P. tanoeensis*, family Phrynobatrachidae (Schiøtz 1964, 1967; Perret 1985; Rödel *et al*. 2009a, b, 2012a; Kpan *et al*. 2018; Ofori-Boateng *et al*. 2018).

Two other taxa that were recorded a few kilometers westwards from Abidjan are *P. parogoensis* and *P. aelleni* (see Loveridge 1955; Schätti *et al*. 2002). However, the lack of congruence in morphological data excludes the possibility that the names of these taxa apply for the newly described species. Our data thus support the recognition of *P. moroedeli* **sp. nov.** as a distinct species and exclude its assignment to the names *P. aelleni* and *P. parogoensis*. Likewise, the assignment of our newly described species to *P.* sp. nov. 3 and *P.* aff. *gutturosus* 2 are excluded by genetic analyses. By contrast, the taxon *P.* aff. *gutturosus* 1 might be a member of *P. moroedeli* **sp. nov.** but we rather stay conservative with only two markers and no physical specimen to check morphological features and/or convergence. In this study, we are adding with *P. moroedeli* **sp. nov.** another new cryptic species to the endemic anuran fauna of south-eastern Ivory Coast. Although the species is new to science, individuals from Yakassé-Mé village forest and Tanoé-Ehy swamp forest were collected in the past but got tentatively assigned to *P. gutturosus* (see Kouamé *et al*. 2014; Kpan *et al*. 2014) based on morphological similarities and co-occurrence in Ivory Coast (Fig. 1). Our newly generated data for the mitochondrial 16S gene, however, revealed that *P. moroedeli* **sp. nov.** is indeed closely related to *P. gutturosus*, forming a clade with four described species of the Upper Guinean forest zone of West Africa: *P. afiabirago*, *P. fraterculus*, *P. maculiventris*, *P. pintoi*, along with the three candidate species *P.* aff. *gutturosus* 1, *P.* aff. *gutturosus* 2 and *P.* sp. nov. 3 (Fig. 2). This phylogenetic relationship is further reflected in case of described species by a set of shared morphological traits. For instance, males of *P. moroedeli* **sp. nov.** share with all five species a disc-like vocal sac skin that extends to the anterior chest, and further exhibit alike the males of *P. afiabirago*, *P. gutturosus*, *P. maculiventris*, and *P. pintoi* a throat that is either dark or completely black (Figs. 8b, f, h, j), compared to an olive throat in *P. fraterculus* males (Fig. 8d). By contrast, the belly colouration of *P. moroedeli* **sp. nov.** is rather variable, but the common pattern of dark blotching or mottling is also observed in *P. afiabirago*, which consistently shows a range of dark patterning from small black dots to dense dark blotches. In terms of secondary sexual traits, males of *P. moroedeli* **sp. nov.**, *P. afiabirago*, and *P. pintoi* lack discernible femoral glands. All five species additionally have the absence of a thin, light longitudinal line on the upper surface of the thighs and crus in common.

The observed morphological similarities emphasize the region's high cryptic diversity and the limitations of morphology-based species identification, emphasizing the importance of integrative taxonomic approaches (Padial *et al*. 2010). Interestingly, our genetic analyses revealed that *P. moroedeli* **sp. nov.** is not most closely related to *P. gutturosus*, as initially assumed based on morphology, but to *P. afiabirago* (Figs. 2, 3). They can be delimited by a genetic distance ranging from 5.04–5.65%, which is substantially exceeding the 3% threshold used commonly for anuran species (e.g., Vieites *et al.* 2009). Interspecific genetic distances are overall remarkably high within this Upper Guinean clade, with interspecific distances ranging from 5.04–10.75% (Table 4). This high degree of mitochondrial divergence was found to be congruent with nuclear results, as no haplotype sharing could be detected among species (Fig. 3). Species-specific advertisement calls are likely a key mechanism of reproductive isolation, as distinct *Phrynobatrachus* species often differ markedly in their vocalizations (e.g., Kpan *et al*. 2018). However, available bioacoustic data are still pending for most species within the Upper Guinean clade, including *P. moroedeli* **sp. nov.**

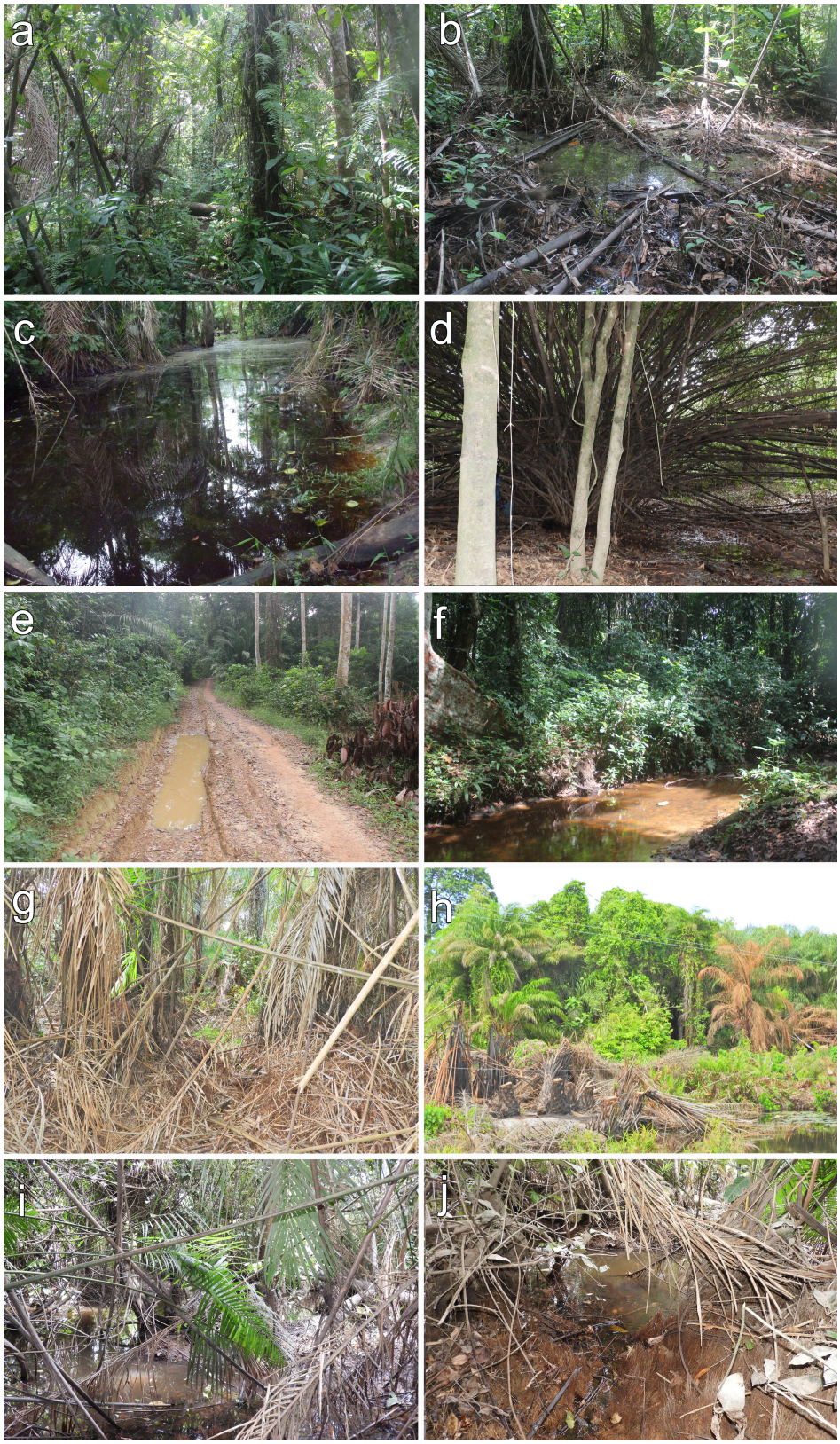

FIGURE 7. Habitat images of *Phrynobatrachus moroedeli* **sp. nov.** in southern Ivory Coast: in Tanoé-Ehy swamp forest (type locality), the new species was found in a swamp forest dominated by *Raphia* palms with large canopy gaps (a), and close to shallow water among the leaf-litter (b); in Yakassé-Mé, it was encountered most often among thick vegetation alongside a large swamp edged by *Raphia* palms (c), and also in a degraded forest with small brooks running through bamboo patches (d); in Mabi-Yaya Forest Reserve, the new species inhabited alongside a forest road with water filled tire tracks (e), and alongside a stream in a primary forest patch as well (f); in Taboth village, the new species was recorded in heavily degraded forest patches with predominantly *Raphia* palms (g, h); in Tiassalé the new species inhabited in a degraded forest patch with *Raphia* palms (i, j).

FIGURE 8. Photos in life of male Upper Guinean *Phrynobatrachus* species that are genetically and morphologically close to *P. moroedeli* **sp. nov.** in dorsolateral and ventral view: *P. afiabirago* from Atewa Range in Ghana (a, b); *P. fraterculus* from Yéalé in Ivory Coast side of Mounts Nimba (c, d); *P. maculiventris* from Diécké Classified Forest in Guinea (e, f); *P. gutturosus* from Daloa in Ivory Coast (g, h); and *P. pintoi* from Sangarédi in Guinea (i, j).

TABLE 3. Summary of measurements (in mm) taken for members of the Upper Guinean Forest clade including *Phrynobatrachus moroedeli* sp. nov., *P. afiabirago*, *P. maculiventris*, *P. fraterculus*, *P. gutturosus* and *P. pintoi*. Given are mean ± standard deviation and range (min-max); M = male, F = female, N = sample size; SVL = snout–vent length; HW = head width; TL = thigh length; CL = crus length; FTL = foot length incl. longest toe; ED = horizontal eye diameter; TD= horizontal tympanum diameter; IOD = inter-orbital distance; EN = distance anterior corner of eye to nostril; ES = distance anterior corner of eye to snout-tip.

Species	SVL	HW	HL	IOD	EN	ES	ED	IND	TD	TL	CL	FTL
P. moroedeli **sp. nov.**	16.4 ± 1.1	5.5 ± 0.5	6.9 ± 0.6	2.3 ± 0.5	1.4 ± 0.2	2.1 ± 0.3	2.6 ± 0.4	1.6 ± 0.3	1.1 ± 0.2	8.0 ± 0.9	9.3 ± 0.6	13.9 ± 1.1
M, N = 15	13.9–18.2	4.4–6.5	5.9–8.0	1.2–3.1	1.0–1.5	1.5–2.5	2.1–3.5	1.1–2.1	0.9–1.5	6.1–9.5	8.1–10.5	11.0–15.5
P. afiabirago	19.3 ± 0.8	6.0 ± 0.1	7.7 ± 0.5	2.3 ± 0.1	1.2 ± 0.2	1.3 ± 0.6	2.9 ± 0.2	1.9 ± 0.2	1.6 ± 0.2	9.0 ± 0.7	10.8 ± 0.7	14.8 ± 0.5
M, N = 5	18.5–20.2	5.8–6.1	7.1–8.4	2.8–3.1	1.0–1.5	0.5–2.1	2.6–3.2	1.5–2.0	1.5–1.9	8.0–10.1	10.4–12.0	14.2–15.5
P. maculiventris	19.3 ± 0.2	6.0 ± 0	7.2 ± 0.3	2.0 ± 0.1	1.2 ± 0.3	2.1 ± 0.3	3.3 ± 0.3	1.7 ± 0.3	1.5 ± 0	7.9 ± 0	9.7 ± 0.3	16.2 ± 1.8
M, N = 2	19.2–19.5	6.0	7.0–7.5	2.0–2.1	1.0–1.5	1.9–2.3	3.1–3.5	1.5–2.0	1.5	7.9	9.5–10.0	15.0–17.5
P. fraterculus	19.0 ± 2.0	6.2 ± 0.6	7.8 ± 0.5	2.4 ± 0.2	1.3 ± 0.2	2.2 ± 0.2	3.0 ± 0.1	2.0 ± 0.4	1.5 ± 0	9.1 ± 0.2	10.4 ± 1.0	14.6 ± 2.2
M, N = 3	16.9–21.0	5.5–6.5	7.5–8.4	2.2–2.5	1.1–1.5	2.1–2.5	2.8–3.1	1.5–2.4	1.5	9.0–9.4	9.5–11.5	12.0–15.9
P. gutturosus	18.2 ± 0.3	5.8 ± 0.1	8.7 ± 0.3	2.2 ± 0.2	1.2 ± 0.3	2.2 ± 0.5	2.5 ± 0.5	1.8 ± 0.1	1.5 ± 0.7	8.0 ± 1.3	9.0 ± 0.7	13.9 ± 1.3
M, N = 2	18.0–18.5	5.8–5.9	8.5–9.0	2.1–2.4	1.0–1.5	1.9–2.6	2.2–2.9	1.8–1.9	1.0–2.0	7.1–9.0	8.5–9.5	13.0–14.9
P. pintoi M, N = 1	16.1	5.1	7.5	2.2	1.2	1.7	2.5	1.8	1.1	7.4	8.4	12.0
P. moroedeli **sp. nov.**	19.1 ± 1.2	6.1 ± 0.5	8.2 ± 1.1	2.5 ± 0.4	1.2 ± 0.2	2.1 ± 0.3	2.9 ± 0.4	1.7 ± 0.2	1.4 ± 0.4	8.4 ± 0.8	10.3 ± 1.0	15.4 ± 1.4
F, N = 7	18.0–21.0	5.5–7.2	6.9–9.9	2.0–2.9	1.0–1.5	1.7–2.6	2.3–3.4	1.5–2.0	1.1–2.0	7.8–9.8	8.9–11.5	13.8–17.2
P. afiabirago F, N = 1	23.5	7.5	10.1	3.5	1.5	2.7	3.2	2.2	2.0	11.0	12.9	18.5
P. fraterculus	25.5 ± 1.2	8.1 ± 0.3	10.5 ± 0.9	3.5 ± 0.5	1.7 ± 0.3	3.1 ± 0.3	4.0 ± 0.1	2.7 ± 0.4	2.1 ± 0.1	11.5 ± 0.7	14.0 ± 0.5	20.0 ± 0.3
F, N = 5	24.0–26.9	7.8–8.5	9.5–11.8	3.0–4.0	1.4–2.0	2.8–3.5	3.9–4.2	2.1–3.0	2.0–2.2	10.6–12.5	13.4–14.5	19.5–20.5
P. gutturosus F, N = 1	22.5	6.9	10.0	2.9	1.9	3.4	3.0	1.9	1.5	11.1	11.6	17.4

TABLE 4. Uncorrected pairwise genetic distances in % (mean, with minimum and maximum in parentheses) within and between six genetically close *Phrynobatrachus* species of the Upper Guinean Forest, calculated from the alignment of the mitochondrial 16S rRNA gene (556 bp) containing 33 sequences without missing data. Cells along the diagonal show intra-specific variation highlighted in bold.

	1	2	3	4	5	6	7	8	9
1 *P. moroedeli sp. nov.*	0.27 (0.00–0.60)								
2 *P. afiabirago*	4.24 (4.05–4.66)	0.11 (0.00–0.40)							
3 *P.* sp. 3	10.24 (9.94–10.55)	10.55 (10.55–10.55)	0.00 (0.00–0.00)						
4 *P. aff. gutturosus 1*	1.96 (1.81–2.22)	4.05 (4.05–4.05)	10.14 (10.14–10.14)	NA					
5 *P. aff. gutturosus* 2	5.67 (5.44–5.85)	5.88 (5.85–6.05)	9.29 (9.29–9.29)	5.44 (5.44–5.44)	NA				
6 *P. gutturosus*	10.91 (10.34–11.43)	11.63 (11.36–12.04)	11.54 (11.41–11.68)	10.58 (10.55-10.61)	10.46 (10.32–10.59)	0.61 (0.61–0.61)			
7 *P. maculiventris*	7.08 (6.85–7.26)	5.20 (5.04–5.44)	10.10 (10.10–10.10)	6.65 (6.65–6.65)	3.92 (3.82–4.02)	10.86 (10.73–11.00)	0.20 (0.20–0.20)		
8 *P. fraterculus*	6.83 (6.48–7.48)	6.96 (6.48–7.69)	9.64 (9.37–10.11)	6.48 (6.28–6.84)	6.20 (6.07–6.41)	8.46 (8.20–8.86)	7.38 (7.09–7.91)	0.43 (0.00–0.64)	
9 *P. pintoi*	9.69 (9.11–10.17)	9.42 (9.11–9.75)	11.34 (11.20–11.48)	9.36 (9.11–9.54)	9.00 (8.91–9.13)	9.75 (9.13–10.22)	9.63 (9.31–9.96)	8.67 (8.20–9.47)	0.24 (0.00–0.40)

Beyond phylogenetic and morphological findings, our herpetological surveys also yielded new insights into the species' natural history. Notably, some parasitic, subcutaneous mites of the genus *Endotrombicula* were detected on the ventral side of thighs of some individuals of *P. moroedeli* **sp. nov.** (Fig. 4d, f), thus indicating that the species is indeed mostly living in swamps. The infestation of endoparasitic mites occurs on many *Phrynobatrachus* species but is most abundant on species dwelling in very wet or humid habitats (Spieler & Linsenmair 1999; Wohltmann *et al*. 2007; Rödel *et al*. 2012b; Kpan *et al*. 2019). In the type locality, syntopic *Phrynobatrachus* species were *P. ghanensis*, and *P. alleni*-complex. In Yakassé-Mé and Tiassalé, syntopic *Phrynobatrachus* species were *P. alleni*-complex, *P. calcaratus*-complex, *P. latifrons* and *P. plicatus*. In Mabi-Yaya Forest Reserve, syntopic *Phrynobatrachus* species were *P. ghanensis*, *P. latifrons*, *P. liberiensis*, and *P. plicatus*. In Taboth village, syntopic congener frogs were *P. ghanensis* and *P. latifrons*. The fact that the new species was found in syntopy with *P. alleni*-complex, *P. ghanensis*, and *P. liberiensis* is a hint that its habitat requirements may comprise some dense forest patches. However, most often *P. moroedeli* **sp. nov.** was found in syntopy with degraded forest species e.g., *P. calcaratus*-complex, *P. latifrons* and *P. plicatus*, thus indicating that natural habitats of the new species are prone to various states of degradation due to increasing human influence.

The rainforest region which extends from Abidjan eastwards to neighbouring western Ghana is supposed to represent a Pleistocene forest refugium (Maley 1996). The entire region lacks sufficient protected areas and consequently is highly threatened by intensive deforestation and habitat loss (Parren & de Graaf 1995; Bakarr *et al*. 2004; Mayaux *et al*. 2013). An alarming result is that two of the rare known sites of the new species, i.e., Yakassé-Mé village forest and the small forest pocket in Taboth village, are non-protected and potentially are expected to be lost because of ongoing development of the area. Hence, Tanoé-Ehy swamp forest and Mabi-Yaya Forest Reserve remain the only two more promising sites for a long-term persistence of the most viable populations of the new species. Likewise, in the south-central part of Ivory Coast, natural habitats in Tiassalé are increasingly threatened by anthropogenic impacts. Ongoing forest degradation and conversion of swamp forests into rice fields suggest that the viable population of the new species in Tiassalé is highly endangered.

We observed various signs of habitat degradation in several parts of the range where the new species is patchily distributed. Whereas the small pocket of forest where the new species was found is highly threatened due to the rapid urbanisation of Taboth in Jacqueville district, the Yakassé-Mé village forest was already considered as a threatened rainforest and is prone to agrochemicals, steadily increasing human encroachment, in particular logging, shifting agriculture and conversion of forests into plantations (Kouamé *et al*. 2014). *Raphia* palms are used by the local human population for extracting palm wine and as construction materials. Besides the close proximity to a human settlement and roads running through the forest, the Tanoé-Ehy swamp forest, Mabi-Yaya Forest Reserve, and Tiassalé are surrounded by heavily degraded forests (Kpan *et al*. 2014; Gongomin *et al*. 2019; Soro *et al*. 2019; this study). Considering the restricted range of *P. moroedeli* **sp. nov.** in southern Ivory Coast, and the potential loss of the non-protected forests in the forthcoming years i.e., Taboth, Tiassalé, and Yakassé-Mé forests, the IUCN categorization (e.g., IUCN 2017) of this species as Endangered is reasonable. A more in-depth study of the new species, in particular the call characteristics, the life-history, and the population sizes is urgently needed to understand the biology of *P. moroedeli* **sp. nov.** more clearly and to uncover its strategy to inhabit swamp forests. We thus argue for the subsequent protection of the Tanoé-Ehy swamp forest and Mabi-Yaya Forest Reserve which are irreplaceable ecosystems of national and regional importance.

Acknowledgements

We are much indebted to the 'Ministère des Eaux et Forêts de Côte d'Ivoire', in general, and Col.-Maj. Koné Salimata Tondossama, the Headmistress of the 'Direction de la Faune et des Ressources Cynégétiques (DFRC)' in particular for having delivered the CITES permit. We are also indebted to support from the ATINKOU project. We are especially grateful to Xavier Horiot for encouraging this study. Our gratitude goes to Abouo Béatrice Adepo-Gourène, Bodoua I. Kouassi Kanga and Koffi Ernest Konan for support and collaboration, and local guides during field work. We also thank Karla Neira-Salamea and Frank Tillack for providing access to the specimens. Caleb Ofori-Boateng, Adam D. Leaché, and Mareike Petersen permitted the use of their *P. afiabirago* and *P. maculiventris* pictures from Ghana and Guinea. This work got financially supported by the Taxonomiefonds of the MfN Berlin, Germany. We like to acknowledge the editor, as well as David C. Blackburn and Tadeáš Nečas for valuable comments which improved our manuscript.

References

Assemian, N.E., Kouamé, N.G., Tohé, B., Gourène, G. & Rödel, M.-O. (2006) The anurans of the Banco National Park, Côte d'Ivoire, a threatened West African rainforest. *Salamandra*, 42, 41–51.

Avenard, J.-M., Eldin, M., Girard, G., Sircoulon, J., Touchebeuf, P., Guillaumet, J.-L. & Adjanohoun, E. (1971) *Le milieu naturel de la Côte d'Ivoire*. ORSTOM, Paris, 391 pp.

Bakarr, M., Oates, J.F., Fahr, J., Parren, M., Rödel, M.-O. & Demey, R. (2004) Guinean forests of West Africa. *In*: Mittermeier, R.A., Gil, P.R., Hoffmann, X., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J. & da Fonesca, G.A.B. (Eds.), *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. Conservation International & CEMEX, Washington, D.C., pp. 123–130.

Bandelt, H.J., Forster, P. & Röhl, A. (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular biology and evolution*, 16, 37–48.
https://doi.org/10.1093/oxfordjournals.molbev.a026036

Béligné, V. (1994) *Etude de l'état du milieu naturel du Parc National du Banco: recommandation pour sa sauvegarde et son aménagement*. Rapport du Fonds Mondial pour la Nature (WWF), Abidjan, 48 pp.

Channing, A. & Rödel, M.-O. (2019) *Field guide to the frogs and other amphibians of Africa*. Struik Nature, Cape Town, 408 pp.

Ernst, R. & Rödel, M.-O. (2005) Anthropogenically induced changes of predictability in tropical anuran assemblages. *Ecology*, 86, 3111–3118.
https://doi.org/10.1890/04-0800

Ernst, R. & Rödel, M.-O. (2006) Community assembly and structure of tropical leaf-litter anurans. *Ecotropica*, 12, 113–129.

Fedosov, A., Achaz, G., Gontchar, A. & Puillandre, N. (2022) MOLD, a novel software to compile accurate and reliable DNA diagnoses for taxonomic descriptions. *Molecular Ecology Resources*, 22, 2038–2053.
https://doi.org/10.1111/1755-0998.13590

Fouquet, A., Gilles, A., Vences, M., Marty, C., Blanc, M. & Gemmell, N.J. (2007) Underestimation of species richness in Neotropical frogs revealed by mtDNA analyses. *PLoS ONE*, 2 (10), 1109.
https://doi.org/10.1371/journal.pone.0001109

Frost, D.R. (2025) *Amphibian Species of the World: an Online Reference. Version 6.2. Electronic Database*. American Museum of Natural History, New York, New York. Available from: https://amphibiansoftheworld.amnh.org/index.php (accessed 27 October 2025)
https://doi.org/10.5531/db.vz.0001

Gongomin, B.A.-I., Kouamé, N.G. & Rödel, M.-O. (2019) New records of the Togo toad, *Sclerophrys togoensis*, from south-eastern Ivory Coast. *Herpetology Notes*, 12, 501–508.

Guibé, J. & Lamotte, M. (1963) La Réserve Naturelle Intégrale du Mont Nimba. XXVIII. Batraciens du genre *Phrynobatrachus*. *Mémoire de l'Institut Français d'Afrique Noire*, 66, 601–627.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.

Hillers, A., Boateng, C.O., Segniagbeto, G.H., Agyei, A.C. & Rödel, M.-O. (2009) Assessment of the amphibians in the forests of southern Ghana and western Togo. *Zoosystematics and Evolution*, 85, 127–141.
https://doi.org/10.1002/zoos.200800019

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

Hillers, A., Veith, M. & Rödel, M.-O. (2008a) Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. *Conservation Biology*, 22, 762–772.
https://doi.org/10.1111/j.1523-1739.2008.00920.x

Hillers, A., Zimkus, B. & Rödel, M.-O. (2008b) A new species of *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from north-western Guinea, West Africa. *Zootaxa*, 1815 (1), 43–50.
https://doi.org/10.11646/zootaxa.1815.1.4

IUCN (2017) The IUCN Red List of Threatened Species. Version 2017-2. IUCN, Gland. Available from: http://www.iucnredlist.org (accessed 14 September 2017)

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K., Von Haeseler, A. & Jermiin, L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature methods*, 14, 587–589.
https://doi.org/10.1038/nmeth.4285

Kouamé, N.G., Konan, J.C.B.Y.N., Adepo-Gourène, A.B., Gourène, G. & Rödel, M.-O. (2014) The amphibians of the Yakassé-Mé village forest, a threatened rainforest of south-eastern Ivory Coast. *Herpetology Notes*, 7, 657–665.

Kouamé, N.G., Ofori-Boateng, C. & Rödel, M.-O. (2007) A rapid biological assessment of the Atewa Range, eastern Ghana. *In*: McCullough, J., Alonso, L.E., Naskrecki, P., Wright, H.E. & Osei-Owusu, Y. (Eds.), *A rapid biological assessment of the Atewa Range Forest Reserve, Eastern Ghana*. Conservation International, Washington D.C., *RAP Bulletin of Biological Assessment*, 47, pp. 76–83.

Kouamé, N.G., Tohé, B., Assemian, N.E., Gourène, G. & Rödel, M.-O. (2018) Spatio-temporal distribution of five species of West African leaf-litter frogs. *Salamandra*, 54, 21–29.

Kpan, T.F., Adeba, P.J., Kouamé, N.G., Koné, I., Kouassi, K.P. & Rödel, M.-O. (2014) The anuran fauna of a Volunteer Nature Reserve: the Tanoé-Ehy Swamp Forests, south-eastern Ivory Coast, West Africa. *Zoosystematics and Evolution*, 90, 261–270.
https://doi.org/10.3897/zse.90.8796

Kpan, T.F., Ernst, R., Kouassi, P.K. & Rödel, M.-O. (2019) Prevalence of endoparasitic mites on four West African leaf-litter frogs depends on habitat humidity. *Biotropica*, 51, 432–442.
https://doi.org/10.1111/btp.12649

Kpan, T.F., Kouamé, N.G., Barej, M.F., Adeba, P.J., Emmrich, M., Ofori-Boateng, C. & Rödel, M.-O. (2018) A new puddle frog, genus *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae), from the eastern part of the Upper Guinea biodiversity hotspot, West Africa. *Zootaxa*, 4388 (2), 221–237.
https://doi.org/10.11646/zootaxa.4388.2.5

Lamotte, M. & Xavier, F. (1966) Étude comparée de deux espèces de *Phrynobatrachus* souvent confondues: *Phr. plicatus* Günther et *Phr. auritus* Boulenger. *Bulletin de l'Institut Fondamental d'Afrique Noire, Série A, Sciences Naturelles*, 28, 1605–1619.

Loveridge, A. (1955) On Amphibia Salientia from the Ivory Coast collected by Dr. V. Aellen. *Revue Suisse de Zoologie*, 62, 129–150.
https://doi.org/10.5962/bhl.part.75415

Maley, J. (1996) The African rain forest – main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Proceedings of the Royal Society of Edinburgh, Section B, Biological Sciences*, 104, 31–73.
https://doi.org/10.1017/S0269727000006114

Mayaux, P., Pekel, J.-F., Desclée, B., Donnay, F., Lupi, A., Achard, F., Clerici, M., Bodart, C., Brink, A., Nasi, R. & Belward, A. (2013) State and evolution of the African rainforests between 1990 and 2010. *Philosophical Transactions of the Royal Society B*, 368, 20120300.
https://doi.org/10.1098/rstb.2012.0300

Nago, S.G.A., Grell, O., Sinsin, B. & Rödel, M.-O. (2006) The amphibian fauna of the Pendjari National Park and surroundings, northern Benin. *Salamandra*, 42, 93–108.

Nguyen, L.T., Schmidt, H.A., Von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274.
https://doi.org/10.1093/molbev/msu300

Ofori-Boateng, C., Leaché, A.D., Obeng-Kankam, B., Kouamé, N.G., Hillers, A. & Rödel, M.-O. (2018) A new species of Puddle Frog, genus *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from Ghana. *Zootaxa*, 4374 (4), 565–578.
https://doi.org/10.11646/zootaxa.4374.4.6

Ofori-Boateng, C., Oduro, W., Hillers, A., Norris, K., Oppong, S.K., Adum, G.B. & Rödel, M.-O. (2012) Differences in the effects of selective logging on amphibian assemblages in three West African forest types. *Biotropica*, 45, 94–101.
https://doi.org/10.1111/j.1744-7429.2012.00887.x

Padial, J.M., Miralles, A., De la Riva, I. & Vences, M. (2010) The integrative future of taxonomy. *Frontiers in zoology*, 7, 1–14.
https://doi.org/10.1186/1742-9994-7-16

Palumbi, S., Martin, A., Romano, S., McMillan, W.O., Stice, L. & Grabowski, G. (1991) *The simple fool's guide to PCR. Version 2*. Honolulu, Hawai, 47 pp.

Parren, M.P.E. & de Graaf, N.R. (1995) *The quest for natural forest management in Ghana, Côte d'Ivoire and Liberia. Tropenbos Series 13*. The Tropenbos Foundation, Wageningen, 199 pp.

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.
https://doi.org/10.1111/j.1472-4642.2011.00801.x

Perret, J.-L. (1985) Description of *Kassina arboricola* n. sp. (Amphibia, Hyperoliidae) from Ivory Coast and Ghana. *South African Journal of Science*, 81, 196–199.

Poynton, J.C. (1999) Distribution of amphibians in sub-Saharan Africa, Madagascar, and Seychelles. *In*: Duellman, W.E. (Ed.), *Patterns of distribution of amphibians, a global perspective*. John Hopkins University Press, Baltimore, Maryland,pp. 483–539.

Rödel, M.-O. (2000) *Herpetofauna of West Africa. Vol. I. Amphibians of the West African Savanna*. Edition Chimaira, Frankfurt/F., 335 pp.

Rödel, M.-O. & Agyei, A.C. (2003) Amphibians of the Togo-Volta highlands, eastern Ghana. *Salamandra*, 39, 207–234.

Rödel, M.-O., Bangoura, M.A. & Böhme, W. (2004) The amphibians of south-eastern Republic of Guinea (Amphibia: Gymnophiona, Anura). *Herpetozoa*, 17, 99–118.
https://doi.org/10.1080/03946975.2004.10531206

Rödel, M.-O., Barej, M.F., Hillers, A., Leaché, A.D., Kouamé, N.G., Ofori-Boateng, C., Assemian, N.E., Tohé, B., Penner, J., Hirschfeld, M., Doumbia, J., Gonwouo, L.N., Nopper, J., Brede, C., Diaz, R., Fujita, M., Gil, M., Segniagbeto, G.H., Ernst, R. & Sandberger, L. (2012a) The genus *Astylosternus* in the Upper Guinean rainforests, West Africa, with the description of a new species (Amphibia: Anura: Arthroleptidae). *Zootaxa*, 3245 (1), 1–29.
https://doi.org/10.11646/zootaxa.3245.1.1

Rödel, M.-O., Boateng, C.O., Penner, J. & Hillers, A. (2009a) A new cryptic *Phrynobatrachus* species (Amphibia: Anura: Phrynobatrachidae) from Ghana, West Africa. *Zootaxa*, 1970 (1), 52–63.
https://doi.org/10.11646/zootaxa.1970.1.2

Rödel, M.-O., Burger, M., Zassi-Boulou, A.G., Emmrich, M., Penner, J. & Barej, M.F. (2015) Two new *Phrynobatrachus*

species (Amphibia: Anura: Phrynobatrachidae) from the Republic of the Congo. *Zootaxa*, 4032 (1), 55–80.
https://doi.org/10.11646/zootaxa.4032.1.3
Rödel, M.-O., Doherty-Bone, T., Kouete, M.T., Janzen, P., Garrett, K., Browne, R., Gonwouo, N.L., Barej, M.F. & Sandberger, L. (2012b) A new small *Phrynobatrachus* (Amphibia: Anura: Phrynobatrachidae) from southern Cameroon. *Zootaxa*, 3431 (1), 54–68.
https://doi.org/10.11646/zootaxa.3431.1.4
Rödel, M.-O., Doumbia, J., Kouamé, N.G. & Sandberger, L. (2011) A new small *Phrynobatrachus pintoi* Hillers, Zimkus & Rödel, 2008 (Amphibia: Anura: Phrynobatrachidae): additional morphological and distribution data. *Zootaxa*, 3098 (1), 59–63.
https://doi.org/10.11646/zootaxa.3098.1.6
Rödel, M.-O. & Ernst, R. (2003) The amphibians of Marahoué and Mont Péko National Parks, Ivory Coast. *Herpetozoa*, 16, 23–39.
Rödel, M.-O. & Ernst, R. (2004) Measuring and monitoring amphibian diversity in tropical forests. An evaluation of methods with recommendations for standardization. *Ecotropica*, 10, 1–14.
Rödel, M.-O., Gil, M., Agyei, A.C., Leaché, A.D., Diaz, R.E., Fujita, M.K. & Ernst, R. (2005) The amphibians of the forested parts of south-western Ghana. *Salamandra*, 41, 107–127.
Rödel, M.-O., Kosuch, J., Grafe, T.U., Boistel, R., Assemian, N.E., Kouamé, N.G., 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 (1), 23–45.
https://doi.org/10.11646/zootaxa.2044.1.2
Rödel, M.-O. & Spieler, M. (2000) Trilingual keys to the savannah-Anurans of the Comoé National Park, Ivory Coast. *Stuttgarter Beiträge zur Naturkunde*, Serie A, 620, 1–31.
Schätti, B., Perret, J.-L. & Mariaux, J. (2002) Catalogue commenté des types d'amphibiens et de reptiles du Muséum d'histoire naturelle de Genève. Version 4.0. Geneva, Switzerland. Available from: www.vill-ge.ch/musinfo/mhng/erpi/catl (accessed 24 January 2002)
Schiøtz, A. (1964) A preliminary list of amphibians collected in Ghana. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 127, 1–17.
Schiøtz, A. (1967) The treefrogs (Rhacophoridae) of West Africa. *Spolia Zoologica Musei Hauniense*s, 25, 1–346.
Soro, N., Kouamé, A.M., Adepo-Gourène, A.B. & Rödel, M.-O. (2019) *Morerella cyanophthalma* (Anura: Hyperoliidae) in south-eastern Ivory Coast: Additional data and implications for the species' conservation. *Herpetology Notes*, 12, 1215–1223.
Spieler, M. & Linsenmair, K.E. (1999) The larval mite *Endotrombicula pillersi* (Acarina: Trombiculidae) as a species-specific parasite of a West African savannah frog (*Phrynobatrachus francisci*). *American Midland Naturalist*, 142, 152–161.
https://doi.org/10.1674/0003-0031(1999)142[0152:TLMEPA]2.0.CO;2
Stephens, M., Smith, N.J. & Donnelly, P. (2001) A new statistical method for haplotype reconstruction from population data. *The American Journal of Human Genetics*, 68, 978–989.
https://doi.org/10.1086/319501
Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, 24, 4876–4882.
https://doi.org/10.1093/nar/25.24.4876
Vences, M., Miralles, A., Brouillet, S., Ducasse, J., Fedosov, A., Kharchev, V., Kostadinov, I., Kumari, S., Patmanidis, S., Scherz, M.D. & Puillandre, N. (2021) iTaxoTools 0.1: Kickstarting a specimen-based software toolkit for taxonomists. *BioRxiv*, 2021-03.
https://doi.org/10.1101/2021.03.26.435825
Vences, M., Patmanidis, S., Fedosov, A., Miralles, A. & Puillandre, N. (2024a) iTaxoTools 1.0: Improved DNA Barcode Exploration with TaxI2. *In*: DeSalle, R. (Ed.), *DNA Barcoding: Methods and Protocols*. Springer US, New York, New York, pp. 281–296.
https://doi.org/10.1007/978-1-0716-3581-0_18
Vences, M., Patmanidis, S., Schmidt, J.C., Matschiner, M., Miralles, A. & Renner, S.S. (2024b) Hapsolutely: a user-friendly tool integrating haplotype phasing, network construction, and haploweb calculation. *Bioinformatics Advances*, 4, vbae083.
https://doi.org/10.1093/bioadv/vbae083
Vieites, D.R., Wollenberg, K.C., 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*, 106, 8267–8272.
https://doi.org/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 and Madagascan anurans, with description of a new species. *Folia Parasitologica*, 54, 225–235.
https://doi.org/10.14411/fp.2007.031
Zimkus, B.M., Lawson, L., Loader, S.P. & Hanken, J. (2012) Terrestrialization, miniaturization and rates of diversification in African puddle frogs (Anura: Phrynobatrachidae). *PloS ONE*, 7 (4), e35118.
https://doi.org/10.1371/journal.pone.0035118

Zimkus, B.M., Rödel, M.-O. & Hillers, A. (2010) Complex patterns of continental speciation: molecular phylogenetics and biogeography of sub-Saharan puddle frogs (*Phrynobatrachus*). *Molecular Phylogenetics and Evolution*, 55, 883–900. https://doi.org/10.1016/j.ympev.2009.12.012

Appendix 1

Phrynobatrachus voucher specimens, examined for morphological comparison.

***Phrynobatrachus afiabirago*: Ghana**: ZMB 86160, JP 0014, adult male, Atewa Range, Atiwiredu, 06°12′22.7″N, 0°34′39.2″W, 817 m asl, primary forest, 7 June 2006, coll. N.G. Kouamé & C. Ofori-Boateng; ZMB 73708 (COB 057: adulte male), ZMB 73709 (COB 059, adult female), Jukwa forest, 05°14′44.13″N, 1°22′42.31″W, coll. C. Ofori-Boateng & A. Hillers; ZMB 86154-86159 (ATE 001: adult female; ATE 002: adult male; ATE 003: adult male; ATE 004: adult male; ATE 005: adult male; ATE 006: adult male), Atewa range, 06°10′N, 0°36′W, April 2016, coll. C. Ofori-Boateng & A.D Leaché.

***Phrynobatrachus fraterculus*: Guinea**: ZMB 73759, adult female, ZMB 73760, adult female, Simandou, Pic de Fon, N'zérékoré Region, 08°31.499′N, 08°56.204′W, 650 m asl, 02 December 2002, coll. M.A. Bangoura & M.-O. Rödel; ZMB 73761, adult female, Diécké Classified Forest, 07°35′46.9″N, 08°52′18.8″W, 24 November 2003, coll. M.A. Bangoura & M.-O. Rödel; ZMB 84230 adult male, ZMB 84231 adult female, ZMB 84232 adult female, Simandou, Pic de Fon, Banko, 08°31.432′N, 08°56.915′W, 3 April 2004, coll. M.A. Bangoura & K. Camara; **Sierra Leone:** ZMB 73801, JP 0180, adult male, Tingi Hills, Eastern Province, 08°51.871′N, 10°47.478′W, 4 June 2007, coll. J. Johnny & A. Hillers; ZMB 84227, GS 159, adult male, Gola Forest, Extension 2, 07°49.873′N, 10°38.894′W, 1 October 2009, coll. A. Hillers.

***Phrynobatrachus gutturosus*: Guinea**: ZMB 90011, Wata1 0221, adult male, N'zérékoré, Beyla, Wataférédou I (08.65633/0865221; -008.79488/ -008.79799), 9 May 2019, coll. J. Doumbia & K. Camara; **Ivory Coast**: ZMB 83859 adult male, ZMB 83860 adult female, Taï National Park, swampy primary rainforest, Transect 1, 05°50′03.5″N, 007°20′57.0″W, 22 July 2016, coll. M.-O. Rödel, T.F. Kpan & N.G. Kouamé.

***Phrynobatrachus maculiventris*: Guinea**: ZMB 71592-71593 (LS 022: adult male; LS 023: adult male), Diécké Classified Forest, Yonsono, N'zérékoré Region, 22 September 2008, coll. L. Sandberger.

***Phrynobatrachus pintoi*: Guinea**: ZMB 76878, Télimélé Prefecture, 11°03′17.5″N, 13°40′40.4″W, 255 m asl, grassy savanna within a forest zone, 17 October 2010, coll. N.G. Kouamé & J. Doumbia.