

Contributions to the herpetofauna of the Angolan Okavango-Cuando-Zambezi river drainages. Part 3: Amphibians

^{1,2,3,*}Werner Conradie, ^{2,3,4}Chad Keates, ^{3,5,6}Luke Verburgt, ^{3,7,8,9,10,11}Ninda L. Baptista, and ^{3,12}James Harvey

Port Elizabeth Museum, Beach Road, Humewood, Port Elizabeth 6013, SOUTH AFRICA ²Department of Nature Conservation Management, Natural Resource Science and Management Cluster, Faculty of Science, George Campus, Nelson Mandela University, George, SOUTH AFRICA ³National Geographic Okavango Wilderness Project, Wild Bird Trust, SOUTH AFRICA ⁴South African Institute for Aquatic Biodiversity (SAIAB), Makhanda, SOUTH AFRICA ⁵Enviro-Insight CC, Unit 8 Oppidraai Office Park, Pretoria 0050, SOUTH AFRICA ⁶Department of Zoology and Entomology, University of Pretoria, Pretoria, 0001, SOUTH AFRICA ⁷Instituto Superior de Ciências da Educação da Huíla (ISCED), Rua Sarmento Rodrigues, Lubango, ANGOLA ⁸CIBIO/InBio, Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-661 Vairão, PORTUGAL ⁹Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4169-007, Porto, PORTUGAL ¹⁰BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, PORTUGAL ¹¹Museum für Naturkunde—Leibniz Institute for Evolution and Biodiversity Science, Invalidenstr. 43, 10115 Berlin, GERMANY ¹²Harvey Ecological, 41 Devonshire Avenue, Howick, 3290, SOUTH AFRICA

Abstract.—This article is the third and final installment of the herpetofaunal results obtained from a series of rapid biodiversity surveys of the upper Cuito, Cubango, Cuando, Zambezi, and Kwanza River basins in Angola. The amphibian survey results are presented along with an updated checklist of the historical and current records of amphibians from the southeastern region of Angola. A total of 1,114 new amphibian records were documented, comprising 37 species, bringing the total number of recognized amphibian species in this region to 49. These surveys documented two new country records (*Hyperolius* cf. *inyangae* and *Kassinula wittei*) and at least two candidate new species, and elevated *Amnirana adiscifera* stat. nov. (which now encompasses the western green form formerly regarded as *A. darlingi*). Finally, updated distribution maps for all of Angola are provided for all the species encountered within the study region.

Keywords. Africa, Cuanavale, Cuito, Okavango, headwaters, frogs

Resumo.—Este trabalho é a terceira e última parte dos resultados obtidos de uma série de levantamentos rápidos de biodiversidade realizados nas bacias dos rios Cuito, Cubango, Cuando, Zambeze e Kwanza em Angola. Aqui apresentamos uma lista atualizada de registos anfíbios do sudeste de Angola, consistindo em registos históricos e actuais. Ao todo foram obtidos 1,114 novos registos, relativos a 37 espécies, elevando o número total de espécies de anfíbios reconhecidas nesta região para 49. Duas espécies foram registadas no país pela primeira vez (Hyperolius cf. inyangae, Kassinula wittei). Os nossos resultados sugerem a existência de pelo menos duas potenciais espécies novas, e elevaram o estatuto de Amnirana adiscifera stat. nov. para abranger a forma verde ocidental de A. darlingi. Por fim, produzimos mapas de distribuição actualizados para todas as espécies encontradas neste estudo para o país inteiro.

Palavras-chave. África, Cuanavale, Cuito, Okavango, nascentes, sapos

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Introduction

In recent years, knowledge on the Angolan herpetofauna has increased dramatically (Marques et al. 2018; Baptista et al. 2019; Branch et al. 2019a). Although reptiles have been the main focus (Conradie et al. 2012a, 2020a, 2021, 2022a,b,c; Stanley et al. 2016; Ceríaco et al. 2020a,b,c;

Marques et al. 2019a,b, 2020, 2022a,b, 2023; Branch et al. 2019a,b, 2021; Hallermann et al. 2020; Lobón-Rovira et al. 2021, 2022; Parrinha et al. 2021; Wagner et al. 2021), several amphibian-focused studies have been published (Conradie et al. 2012b, 2013, 2020b; Ernst et al. 2014, 2015; Conradie and Bills 2016; Ceríaco et al. 2018, 2021; Nielsen et al. 2020; Baptista et al. 2021).

Correspondence. *werner@bayworld.co.za; wernerconradie@gmail.com

From these studies, only six new species of amphibians have been described for Angola since 2012, compared to 35 new species of reptiles (29 lizards and six snakes).

Recent syntheses on the amphibians of Angola documented between 111 and 117 anuran species within the country (Marques et al. 2018; Baptista et al. 2019), although the taxonomic status and presence within Angola remains uncertain for several of these frogs. Approximately 22 species are known only from the type description, singleton records, or incorrect species assignments which no longer apply to the Angolan material (Marques et al. 2018; Baptista et al. 2019). A large proportion of historical type material was lost or destroyed during the Natural History Museum Lisbon fire (Marques et al. 2018), complicating matters further, thus new topotypic material is needed to validate the taxonomical status of various species (Baptista et al. 2019).

Over the last few years, additional amphibian species have been either recorded for the first time from Angola (Conradie et al. 2020b; Ernst et al. 2020) or described as new species (Ceríaco et al. 2018, 2021; Nielsen et al. 2020; Baptista et al. 2021), raising the number of amphibian species known from Angola by at least 13. As more work is done in the country and remote regions are surveyed, a trend similar to reptiles is expected, with the predicted discovery and description of multiple new species.

Southeastern Angola remains amongst the most poorly known regions in Africa (Conradie et al. 2016; Marques et al. 2018; Baptista et al. 2019). Historical amphibian records from this region included only opportunistic collections, most of which were restricted to the western tributaries of the Cubango River basin (Bocage 1895; Monard 1937), and the eastern and northern sections of Moxico Province (Laurent 1964; Monard 1937; Mertens 1938; Ruas 1996, 2002), with only a few records from the Cuito and Cuando river basins (Angel 1924). Recently, based on the outcome of several biodiversity surveys (Brooks 2012, 2013; NGOWP 2017) to document the biodiversity of the Angolan catchment of the Okavango River basin, which comprises the Cubango, Cuito, and Cuando rivers, an updated herpetofauna checklist was compiled (Conradie et al. 2016). A total of 34 species of amphibians were recorded, four of which were new for Angola (Ptychadena mossambica, Sclerophrys poweri, *Xenopus muelleri*, and X. poweri).

The present work serves as the third and final installment of a series of papers documenting the herpetofauna of southeastern Angola, based on surveys performed for the National Geographic Okavango Wilderness Project. The first two installments focused on snakes (Conradie et al. 2021) and on lizards, chelonians, and crocodiles (Conradie et al. 2022c), while this article is restricted to amphibians. The overarching aim of these articles is to document and quantify the herpetofauna of the region, and to contribute to the knowledge of its

conservation importance in both regional and national contexts.

Materials and Methods

For this study, we present amphibian material and associated data collected during five National Geographic Okavango Wilderness Project (NGOWP) expeditions to south-eastern Angola from 2016 to 2019. See Conradie et al. (2021) for more details on these surveys, a description of the study area, sampling techniques (trapping and visual encounter surveys), and species mapping. Below are some specific methods pertaining to this article.

Identification and morphology. Upon completion of the fieldwork component of the study, species were identified based on external morphology, using relevant field guides or published identification keys (Poynton and Broadley 1985a,b, 1987, 1988; Channing 2001; Du Preez and Carruthers 2017; Channing and Rödel 2019) and orginal type descriptions when needed, and through direct comparisons with material housed in the Port Elizabeth Museum (PEM). Identifications of tadpoles were problematic, as the tadpoles of many of the species collected as adults remain undescribed (see Channing et al. 2012). We tentatively assigned tadpoles based on morphotypes and locality data to the known species until their true identities can be confirmed by genetic analysis. In certain cases, a 16S rRNA barcoding approach was employed to aid in the identification of tadpoles and adults. Laboratory and sequencing protocols followed Conradie et al. (2020b). The Basic Local Alignment Search Tool (BLAST; Altschul et al. 1990) was used to compare our material to the GenBank (https://www.ncbi. nlm.nih.gov/genbank/; Benson et al. 2013) repository and our unpublished Angolan dataset. Taxonomy follows Frost (2023) and was updated as needed. Common names follow Channing (2001), Du Preez and Carruthers (2017), and Marques et al. (2018).

The snout-urostyle length (SUL, measured from the tip of the snout to the posterior tip of the urostyle) of adult specimens and the total length of tadpoles were measured to the nearest 0.1 mm, using a digital calliper. All specimens were examined using a Nikon SMZ1270 binocular stereo microscope. For adult frogs, the following information was documented: skin texture, position and number of hand/ feet tubercles, webbing condition, and coloration. The webbing formula follows the scheme provided by Rödel (2000). Adult specimens were sexed by confirming the presence/absence of eggs, a gular flap or darkened throats, and nuptial pads. As needed, a small ventral incision was made to look for gonads or testes. No attempt was made to examine stomach contents (which will be the focus of another study). Additionally, the labial tooth rows and oral papillae condition were recorded for tadpoles. Tadpoles are catalogued as 'lots,' with specimens from the same locality and collecting event grouped together.



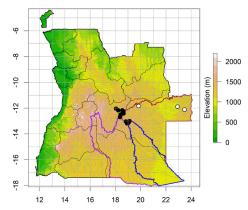
Fig. 1. Adult male *Arthroleptis stenodactylus* from Lungwebungu River. *Photo by Werner Conradie*.

Results

We documented a total of 1,114 (1,011 adult frogs and 103 tadpole lots) individual amphibian records from ~189 unique localities in southeastern Angola, particularly around the source lakes of the Cuito, Cuanavale, Cuando, and Quembo rivers. A total of 36 species of amphibians (comprising eight families and 20 genera, all from the order Anura) were recorded during this study (Table 1). Information is also reported for one additional species (Hyperolius quinquevittatus) that was not collected from within the core study area as previously defined. Updated species occurrence maps are provided for each of the 37 species, reflecting all known localities in Angola (Maps 1–37). For the mapping exercise, a total of 2,507 unique records were collated: 1,062 historical records from Marques et al. (2018), 522 additional literature records, 149 citizen science platform records, 296 records from other sources (GBIF ~ https://www. gbif.org/, unpublished records of the PEM, SAIAB, and ZMB collections), and 925 unpublished records from our surveys. This mapping exercise increased the number of new or previously undocumented amphibian records in this study by 58%.

Below we provide a checklist of the amphibians found during these surveys, with each entry including a list of the material examined and comments on identification, habitat, distribution, taxonomy, and natural history notes. Material not collected by the core team or examined for this paper are referred to under 'Additional material.' New data used to compile distribution maps can be found in Supplementary Table 1 at: https://doi.org/10.6084/m9.figshare.23544306.v1. Abbreviation used: asl – above sea level. Museum and collectors' codes used: INBAC – Instituto Nacional de Gestão Ambiental; PEM – Port Elizabeth Museum; ZMB – Museum für Naturkunde Berlin (Zoological Collections); SAIAB – South African Institute for Aquatic Biodiveristy; P – Pedro vaz Pinto, WC – Werner Conradie.

Amphibia Arthroleptidae



Map 1. Distribution of *Arthroleptis stenodactylus* in Angola. Historical records (Marques et al. 2018) are indicated by white dots, while new records are indicated by black dots. Axis values are in degrees (°). Purple polygon – Okavango River basin, Blue polygon – Cuando River basin, Brown polygon – Zambezi River basin.

Arthroleptis stenodactylus Pfeffer, 1893 Common Squeaker (Fig. 1; Map 1)

Material (43 specimens): PEM A12495, 4 km upstream from Cuanavale River source lake, -13.05084° 18.89726°, 1,395 m asl; PEM A12501-4, river crossing before Samboano village, -12.30700° 18.62350°, 1,397 m asl; PEM A12526, Munhango village, -12.16310° 18.55430°, 1,421 m asl; PEM A12527, Protea stop en route to Cuito River source, -12.30040° 18.62070°, 1,429 m asl; PEM A12528-36, INBAC: (no number x4), Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl; PEM A12585, 10 km north of Cuemba village, -12.03481° 18.04869°, 1,372 m asl; PEM A13815, en route to Lungwebungu River, -12.25034° 18.63742°, 1,506 m asl; PEM A12616-7, en route road to Cuito River source, -12.55152° 18.41434°, 1,507 m asl; PEM A12618, en route road to Cuito River source, -12.25050° 18.63730°, 1,519 m asl; PEM A12620, drive to Cuanavale River camp from Samanunga village, -13.03803° 18.82977°, 1,623 m asl; PEM A12644, Cuanavale River source lake, -13.18067° 18.92172°, 1,340 m asl; PEM A12647, stop on road to Cuito River source, -12.50584° 18.41382°, 1,556 m asl; PEM A12648–9, camp 1 en route to Cuito River source, -12.35920° 18.56280°, 1,510 m asl; PEM A12729, Cuando River source, -13.00346° 19.12751°, 1,346 m asl; PEM A12803–4, Lake Tchanssengwe, -12.41402° 18.64418°, 1,415 m asl; PEM A12843-50, INBAC: (no number x2), Quembo River source lake, -13.13624° 19.04591°, 1,411 m asl. Additional records: P2-276 (photograph and tissue sample), wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl. **Description:** Medium sized *Arthroleptis*; stocky build; rounded snout; tympanum clearly visible; welldeveloped inner metatarsal tubercle; no webbing; toe tips not dilated. Dorsum uniformly beige to pink, with scattered white speckles; no darker hourglass pattern

observed on dorsum; yellow vertebral stripe either

Amphibians of the Okavango Delta headwater area in Angola

Table 1. Records of amphibians for the Angolan Okavango-Cuando-Zambezi river basins. ? = not recorded from the core study area, but expected to occur based on peripheral records.

| Species | Okavango River Basin | Cuando River Basin | Zambezi River Basin | Source of records |
|--|-------------------------|--------------------------|------------------------|--|
| ARTHROLEPTIDAE | | | | |
| Arthroleptis stenodactylus Pfeffer, 1893 | X | X | X | This study; Ruas 1996 |
| Arthroleptis xenochirus Boulenger, 1905 | X | X | X | This study; Ruas 1996 |
| | | | | This study; Monard 1937; Conradie |
| Leptopelis anchietae (Bocage, 1873) | X | | | et al. 2016 |
| Leptopelis bocagii (Günther, 1865) | X | X | X | This study |
| Leptopelis sp. | X | X | X | This study |
| BREVICIPITIDAE | | | | |
| Breviceps ombelanonga Nielsen, | | | | |
| Conradie, Ceríaco, Bauer, Heinicke, | | | | This study; Bocage 1895; Monard |
| Stanley, and Blackburn, 2020 | X | X | X | 1937; Ruas 1996 |
| BUFONIDAE | | | | |
| Mertensophryne melanopleura (Schmidt | | | | |
| and Inger, 1959) | | | X | Ruas 1996 |
| Poyntonophrynus kavangensis (Poynton | | | | |
| and Broadley, 1988) | | | X | Ruas 1996 |
| Schismaderma carens (Smith, 1848) | | | X | Laurent 1964 |
| | | | | Monard 1937; Laurent 1964; Ruas |
| Sclerophrys funerea (Bocage, 1866) | X | | X | 1996; Conradie et al. 2016 |
| | | | | This study; Monard 1937; Ruas |
| Sclerophrys gutturalis (Power, 1927) | X | X | X | 1996; Conradie et al. 2016 |
| Sclerophrys pusilla (Mertens, 1937) | X | X | X | This study |
| Sclerophrys poweri (Hewitt, 1935) | X | | X | This study; Conradie et al. 2016 |
| Sclerophrys lemairii (Boulenger, 1900) | X | | X | Ruas 1996; Conradie et al. 2016 |
| HEMISOTIDAE | | | | |
| | | | | This study; Monard 1937; Laurent |
| Hemisus guineensis Cope, 1865 | X | X | X | 1964 |
| HYPEROLIIDAE | | | | |
| Hyperolius benguellensis (Bocage, 1893) | X | X | X | This study; Conradie et al. 2016 |
| Hyperolius cinereus Monard, 1937 | X | | | This study; Conradie et al. 2016 |
| Hyperolius cf. inyangae Channing, 2013 | | X | X | This study This study; Monard 1937; Conradie |
| Hyperolius nasutus Günther, 1865 | X | X | X | et al. 2016 |
| Hyperolius parallelus Günther, 1858 | X | X | X | This study; Conradie et al. 2016 |
| Hyperolius raymondi Conradie, Branch, | 71 | 11 | 11 | This study, Confudio of al. 2010 |
| and Tolley, 2013 | X | X | X | This study |
| Hyperolius quinquevittatus Bocage, 1866 | ? | 71 | ? | This study |
| Hyperolius aff. bocagei Steindachner, | : | | • | This study |
| 1867 | X | X | X | This study |

Conradie et al.

Table 1 (continued). Records of amphibians for the Angolan Okavango-Cuando-Zambezi river basins. ? = not recorded from the core study area, but expected to occur based on peripheral records.

| Species | Okavango River Basin | Cuando River Basin | Zambezi River Basin | Source of records |
|--|-------------------------|--------------------------|------------------------|---|
| | | | | This study; Monard 1933, 1937; |
| Kassina kuvangensis (Monard, 1937) | X | X | X | Conradie et al. 2016 |
| Kassina senegalensis (Duméril and | | | | This study; Monard 1933, 1937; |
| Bibron, 1841) | X | X | X | Conradie et al. 2016 |
| Kassinula wittei Laurent, 1940 | X | X | X | This study; Conradie et al. 2021 |
| MICROHYLIDAE | | | | |
| Phrynomantis affinis Boulenger, 1901 | | | X | Ruas 1996 |
| PHRYNOBATRACHIDAE | | | | |
| Phrynobatrachus mababiensis | | | | |
| FitzSimons, 1932 complex | X | X | X | This study; Conradie et al. 2016 |
| | | | | This study; Monard 1937; Ruas |
| Phrynobatrachus natalensis (Smith,1849) | X | X | X | 1996; Conradie et al. 2016 |
| Phrynobatrachus parvulus (Boulenger, | | | | |
| 1905) | X | X | | Conradie et al. 2016 |
| PIPIDAE | | | | |
| Xenopus muelleri (Peters, 1844) | X | X | | Conradie et al. 2016 |
| | | | | This study; Monard 1937; Ruas |
| Xenopus petersii Bocage, 1895 | X | X | X | 1996; Conradie et al. 2016 |
| Xenopus poweri Hewitt, 1927 | | X | X | This study; Conradie et al. 2016 |
| PTYCHADENIDAE | | | | |
| Hildebrandtia ornatissima (Bocage, 1879) | X | | | Bocage 1895; Monard 1937a; Ruas 1996 |
| Ptychadena anchietae (Bocage, 1868) | | | X | Ruas 1996 |
| Ptychadena bunoderma (Boulenger, 1907) | X | X | | This study |
| Ptychadena grandisonae Laurent, 1954 | X | | X | This study, Ruas 1996 |
| Ptychadena guibei (Laurent, 1954) | | | X | Ruas 1996 |
| Ptychadena keilingi (Monard, 1937) | X | X | X | This study; Ruas 1996 |
| Ptychadena nilotica (Seetzen, 1855) | X | | X | Ruas 1996; Conradie et al. 2016 |
| Ptychadena mossambica (Peters, 1854) | | X | | Conradie et al. 2016 |
| | | | | This study; Monard 1937a; Conradie |
| Ptychadena oxyrhynchus (Smith, 1849) | X | X | | et al. 2016 |
| Ptychadena porosissima (Steindachner, | | | | |
| 1867) | X | | X | This study |
| | | | | This study; Ruas 1996; Conradie et |
| Ptychadena subpunctata (Bocage, 1866) | X | X | X | al. 2016 |
| | | | | This study; Ruas 1996; Conradie et |
| Ptychadena taenioscelis Laurent, 1954 | X | X | X | al. 2016 |
| Ptychadena upembae (Schmidt and Inger, | 3 7 | | 37 | This study; Ruas 1996; Conradie et |
| 1959) | X | | X | al. 2016 (as <i>P. guebei</i>) |

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Amphibians of the Okavango Delta headwater area in Angola

Table 1 (continued). Records of amphibians for the Angolan Okavango-Cuando-Zambezi river basins. ? = not recorded from the core study area, but expected to occur based on peripheral records.

| Species | Okavango River Basin | Cuando River Basin | Zambezi River Basin | Source of records |
|---|-------------------------|--------------------------|------------------------|------------------------------------|
| Ptychadena uzungwensis (Loveridge, | | | | This study; Ruas 1996; Conradie et |
| 1932) | X | X | X | al. 2016 |
| PYXICEPHALIDAE | | | | |
| | | | | This study; Ruas 1996; Conradie et |
| Amietia angolensis (Bocage, 1866) | X | | X | al. 2016 |
| Tomopterna tuberculosa (Boulenger, | | | | This study; Bocage 1895; Monard |
| 1882) | X | | X | 1937; Ruas 1996 |
| RANIDAE | | | | |
| Amnirana adiscifera (Schmidt and Inger, | | | | This study; Ruas 1996; Conradie et |
| 1959) stat. nov. | X | X | X | al. 2016 |
| Amnirana lemairei (De Witte, 1921) | | | X | Ruas 1996 |
| Species total: 51 | 40 | 31 | 42 | |

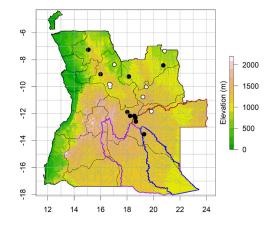
absent (n = 23) or present (n = 12); faint dark facial mask from tip of snout to the eye, continuous to the arm; ventrum immaculate. Breeding males with dark throats; minute spines on lower back; elongated 3rd finger, with spines on the inner side and to the tip. Adult females (n = 11) varied from 32.6-37.7 (34.6 average) mm SUL (largest female: PEM A12846); adult males (n = 4) varied from 19.5–23.6 (21.5) mm (largest male: PEM A12804). Habitat and natural history notes: All specimens were collected in miombo woodland. Gravid females were collected in October/November. Males were heard calling on overcast days and evenings after rain. In February/March, juveniles and subadults were abundant, but no adults were collected or heard calling. Comments: Historically, this species was only known from three records from eastern Angola (Marques et al. 2018). Our new material shows that this species is more common in eastern Angola than previously recognized. This was expected as it is widespread to the east of the Zambian border (Poynton and Broadley 1985a, 1991; Channing 2001). Additionally, these are the first confirmed records from the Okavango River basin. Studies have shown that *A. stenodactylus* comprises two distinct ecomorphs that occur in different habitats. One form, to which our material belongs, prefers drier savanna, while the other form is known from montane forests (Loveridge 1953; Pickersgill 2007; Bittencourt-Silva et al. 2020).

Arthroleptis xenochirus Boulenger, 1905 Plain Squeaker (Fig. 2; Map 2)

Material (8 specimens): PEM A12505–7, river crossing before Samboano Village, -12.30700° 18.62350°, 1,398 m asl; PEM A12910–1, Muhango village, -12.16067° 18.55042°, 1,430 m asl; PEM A14696–7, Lungwebungu



Fig. 2. Adult male Arthroleptis xenochirus from Muhango town. Photo by Werner Conradie.

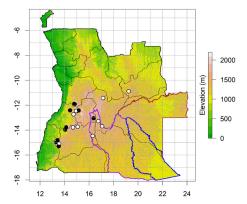


Map 2. Distribution of *Arthroleptis xenochirus* in Angola.

River camp, -12.58439° 18.66748°, 1,297 m asl; PEM A14777, Quembo River bridge camp, -13.52746° 19.2806°, 1,241 m asl. **Additional material:** P2-272 (photograph and tissue sample), wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl. Description: A small species of Arthroleptis; slender body; pointed snout; small tympanum, not always clearly visible; well-developed inner metatarsal tubercle; no webbing; slightly dilated toe tips. Dorsal color varies from beige to brown, with some red infusion; dark facial mask from snout to eye, continuing to just above arm; white markings on grey colored jawline; all specimens have a darkened hour-glass pattern on the back; ventrum immaculate. Breeding males with dark throats; elongated 3rd finger, with no spines. Single adult female measured 20.9 mm (PEM A14777); adult males (n = 4) varied from 19.5–23.6 (21.5) mm (largest male: PEM A14697). Habitat and natural history notes: All specimens were collected in miombo woodland. Males were heard calling in October/November. Gravid female collected in November, while only juveniles and subadults were collected in February/March. Comments: Known from central and northern Angola (Marques et al. 2018). The record from lower Quembo River represents the southernmost record for the species, and the first record associated with the Okavango River basin.

Leptopelis anchietae (Bocage, 1873) Anchieta's Tree Frog (Map 3)

Material (1 tadpole lot): PEM A14174 (five tadpoles), Cubango River campsite below rapids, west of Fundo village, -13.04260° 16.37476°, 1,559 m asl. **Description:** Elongated tadpoles; 20.8–30.6 mm total length, with tail 2.6–3.1 times the body length. Body is dark brown to black, ventrum with scattered light golden spots; lateral tail muscle dark brown to black, with two lighter bands from body to tail tip; posterior half of tail black. The labial tooth row formula (LTRF) is 3(2–3)/3(1); jaw sheaths are heavily keratinized; anterior part of mouth free of elongated marginal papillae. **Habitat and natural history notes:** Tadpoles were collected in a flooded grassland next to the main river. **Comments:**



Map 3. Distribution of Leptopelis anchietae in Angola.

Identification of tadpoles was confirmed by 16S rRNA barcoding (N. Baptista, unpub. data) and compared to the description in Channing et al. (2012). This Angolan endemic species occurs mostly in the highlands of central and western Angola (Becker et al., in prep.), and many of the old historical records (e.g., Marques et al. 2018) are based on incorrect identifications or erroneous locality data (Pedro vaz Pinto, pers. comm.).

Leptopelis bocagii (Günther, 1865) Bocage's Tree Frog (Figs. 3–4; Map 4)

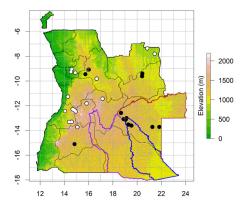
Material (46 specimens): PEM A12701–10, Lungwebungu River camp bridge crossing, -12.58347° 18.66598°, 1,304 m asl; PEM A12742–6, Cuando



Fig. 3. Adult male *Leptopelis bocagii* (brown form) from Cuando River source. *Photo by James Harvey*.



Fig. 4. Adult male *Leptopelis bocagii* (green form) from Cuanavale River side tributary source. *Photo by Luke Verburgt*.



Map 4. Distribution of Leptopelis bocagii in Angola.

River source, -13.00346° 19.12751°, 1,346 m asl; PEM A12772-4, INBAC: WC-4634, Cuanavale River side tributary source, -13.07452° 18.88345°, 1,385 m asl; PEM A12873-80, INBAC: WC-4669 and 4672, Quembo River source lake, -13.13624° 19.04591°, 1,411 m asl; PEM A14688–9, Lungwebungu River camp, massambas on left side of river, -12.58276° 18.66556°, 1,295 m asl; PEMA14701–4, INBAC: WC-6763, Lungwebungu River camp, -12.58439° 18.66748°, 1,297 m asl; PEM A14723, PEM A14742, Quembo River bridge camp, -13.52746° 19.28060°, 1,241 m asl; PEM A14741, Quembo River bridge camp, trap 3, -13.52778° 19.27455°, 1,256 m asl; PEM A14755-6, PEM A14758-9, INBAC: WC-6994, Quembo River right side tributary (Micongo River) past village, -13.51877° 19.28487°, 1,248 m asl; PEM A14823, camp at side tributary (Luandai River) of the Luanguinga River, -13.70885° 21.26234°, 1,116 m asl; PEM A14891, Luvu River camp, -13.71200° 21.83538°, 1,082 m asl. **Description:** Large terrestrial tree frog; broad rounded head; large protruding eyes; tympanum clearly visible; large well-developed inner metatarsal tubercle; no webbing or expanded toe tips. Dorsum varied from green to brown, with dark horseshoe pattern on the back, and dark interorbital bar; dark facial mask from snout to eye, continuing to above arm; sides of body with scattered black spots or continuous black bar between limbs; scattered white speckles on dorsum; ventrum immaculate. Breeding males with dark throat and weakly developed pectoral glands. Adult females (n = 12) varied from 41.5-67.8 (57.9) mm (largest female: PEM A12746); adult males (n = 34) varied from 43.0–56.8 (48.6) mm (largest male: INBAC: WC-4669). Habitat and natural history notes: Collected along the sandy margins of source lakes or rivers associated with miombo woodland. Frequently encountered in the clearings of agricultural fields near water sources. Males were found calling from the ground. Comment. These are the first records from eastern Angola, bridging the distribution gap between western Angola and Zambia (Broadley 1971; Marques et al. 2018; Baptista et al. 2019).

Leptopelis sp.

Unidentified Tree Frog (Figs. 5–6; Map 5)

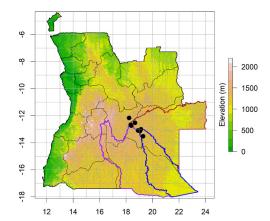
Material (34 specimens, 2 tadpole lots): PEM A12801–2, Cuanavale River source lake, -13.08934° 18.89485°, 1,359 m asl; PEM A12882–8, Quembo River source lake, -13.13624° 19.04591°, 1,396 m asl; PEM A12794–5, INBAC: WC-4685 and no number, Cuanavale River source lake, -13.09442° 18.89372°, 1,368 m asl; PEM A12747–51, INBAC: WC-4754 and no number, Cuando River source, -13.00346° 19.12751°, 1,353 m asl; PEM A14118 (tadpoles), Calua River source, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,446 m asl; PEM A13845–6, PEM A14123 (tadpoles), Cuiva River source, -12.66825° 18.35282°, 1,407 m asl; PEM A12786, Cuando River source, trap



Fig. 5. Adult male *Leptopelis* sp. from Cuanavale River source. *Photo by Luke Verburgt.*



Fig. 6. Tadpole of *Leptopelis* sp. from Cuiva River source. *Photo by Werner Conradie*.



Map 5. Distribution of Leptopelis sp. in Angola.

4, -13.00164° 19.12960°, 1,361 m asl; PEM A12819–21, Cuiva River source, -12.66856° 18.35307°, 1,433 m asl; PEM A14775, INBAC: WC-6852, Quembo River bridge camp, -13.52746° 19.28060°, 1,241 m asl; PEM A14767–74, Quembo River right side tributary (Micongo River) past village, -13.51877° 19.28487°, 1,248 m asl. **Additional material (3 specimens):** P2-277, wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl; SAIAB 209098 (2 specimens),

Quembo River source lake, -13.14025° 19.04822°, 1,365 m asl. **Description:** Small terrestrial tree frog; large protruding eyes; tympanum clearly visible; welldeveloped rounded inner metatarsal tubercle; reduced webbing; digit tips slightly dilated (slightly wider than finger), finger tips more dilated than toe tips. Dorsum tan-brown; dark brown interorbital bar often present; dark brown vertebral stripe from just behind head to vent; some individuals with extra paravertebral bands; dark brown facial mask extending past arm onto side of body; scattered white speckles; groin with scattered unpigmented skin, extending onto the limbs; throat darkly pigmented; ventrum immaculate. Males with weakly developed pectoral glands and darkened throats. Adult females (n = 2) varied from 36.6-40.7 (38.7) mm (largest female: PEM A12786); adult males (n = 35) varied from 29.0-34.6 (31.1) mm (largest male: PEM A12883). Elongated brown tadpoles; 40.7–52.2 mm total length, with tail 3.2 times body length; strong tail muscle starting just behind eye; thin fin margin above and below; LTRF 2(1)/3(1); jaw sheaths heavily keratinized, anterior part free of elongated marginal papillae. Habitat and **natural history notes:** Males were found calling in trees and shrubs (0.5–3 m above the ground), which were often located far from water, in grasslands with sparse tree cover. As the rainy season progressed, calls were heard progressively closer to water bodies, until eventually being heard among vegetation in the wetlands. The call resembles a chuckle. The eel-like tadpoles were found in wetlands among dense aquatic vegetation. Comments: Unusual light pink/red eel-like tadpoles were initially found in wetlands at the source of two different river systems, the Cuito and Kwanza rivers, in February 2016. A small number of these tadpoles were raised to adults in captivity. Nearly seven months were required to reach metamorphosis, during which time they changed from light pink/red to a more brownish coloration. They seemed to be sensitive to light as they swam eratically when removed from a dark environment and exposed to bright light. During the start of the rainy season in October 2016, unusual calls were heard which could not



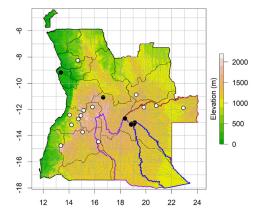
Fig. 7. Adult male *Breviceps ombelanonga* from Cuanavale River source. *Photo by Luke Verburgt*.

be assigned to a known species. After triangulation, several individuals were found calling from trees or shrubs, which were often far from water. On closer inspection, these specimens were found to be morphologically identical to the ones raised in captivity. We subsequently found these frogs at all major river sources and along rivers. Barcode analysis (16S rRNA) recovered the unknown Leptopelis as similar to L. ocellatus (94% similarity; KY080253), but the latter is a forest species with well-developed discs on toes. Schmidt and Inger (1959) described Leptopelis parvus from the Democratic Republic of the Congo (DRC), which resembles our Leptopelis sp. because of its small size and the shared absence of a white stripe above the vent that stretches onto the legs. However, our specimens differ from L. parvus in dorsal coloration pattern (para- and vertebral stripe present versus absent in L. parvus), lack of discs (dilated toe tips, but no clear discs versus clear discs in L. parvus), and pectoral glands (present versus absent in L. parvus). Further phylogenetic and morphological work is needed to resolve the taxonomic status of this species.

Brevicipitidae

Breviceps ombelanonga Nielsen, Conradie, Ceríaco, Bauer, Heinicke, Stanley, and Blackburn, 2020 Angolan Rain Frog (Fig. 7; Map 6)

Material (4 specimens): PEM A12787, Quembo River source lake, -13.13544° 19.04397°, 1,374 m asl; PEM A12800, Cuanavale River source lake, -13.08934° 18.89485°, 1,359 m asl; PEM A12770, Cuando River source, -13.00334° 19.13564°, 1,362 m asl; PEM A12537, Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl. Additional material (1 specimen): SAIAB 204537, Quembo River source lake, -13.13583° 19.04528°, 1,370 m asl. Description: Medium sized *Breviceps*; stout body; snout extremely shortened; pupils horizontally elliptical; tympanum not visible; outer metacarpal tubercle flat and undivided; short limbs; webbing absent; well-developed inner metatarsal tubercle fused with the outer metatarsal tubercle, with no deep cleft present, elongated, and



Map 6. Distribution of *Breviceps ombelanonga* in Angola.

protruding outwards. Coloration varied from red with scattered black blotches, dark brown with red spots and markings, and light brown with red spots and black blotches (Nielsen et al. 2020). The only female collected measured 30.1 mm (PEM A12770); adult males (n = 3) varied from 18.3-26.6 (26.2) mm (largest male: PEM A12787). Habitat and natural history notes: Males were only heard calling during the day, especially after heavy rains; calling did not continue into the evenings. Call sites were among leaf litter in dense miombo woodland. **Comments:** The taxonomic status of Angolan Breviceps was recently addressed, leading to the description of this material as a new species, B. ombelanonga (Nielsen et al. 2020). Broader sampling across Angola may detect the presence of other species (e.g., B. adspersus to the south and B. poweri to the east) and even additional undescribed species. For now, all historical records are mapped as B. ombelanonga, until their taxonomic status can be confirmed.

Bufonidae

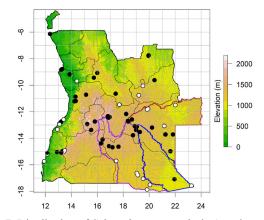
Sclerophrys gutturalis (Power, 1827) Guttural Toad (Fig. 8; Map 7)

Material (69 specimens): PEM A12484, INBAC: WC-4841-2. Cuanavale River source lake, -13.08537° 18.89098°, 1,360 m asl; PEM A12498, drive back from Cuchi to Menongue, -14.67986° 17.17512°, 1,404 m asl; PEM A12573-5, Cuito River source lake, -12.68935° 18.36012°, 1,431 masl; PEMA12612, Calua River source, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,442 m asl; PEM A12625-6, HALO Cuito, -12.39584° 16.96067°, 1,697 m asl; PEM A12629, roadside ditch 10 km SW of Cuito town, -12.44815° 16.88118°, 1,742 m asl; PEM A12639, PEM A12643, Cuanavale River, -13.37406° 18.99269°, 1,304 m asl; PEM A12677–9, INBAC: WC-5232, Camp 3, Malova Village, Mipanha River, -14.09140° 16.41476°, 1,553 m asl; PEM A12685, Huambo HALO training camp, -12.73726° 15.81828°, 1,665 m asl; PEM A12698, Cuando River bridge, -13.60757° 19.53257°, 1,277 m asl; PEM A12719–25,



Fig. 8. Adult male *Sclerophrys gutturalis* from Lungwebungu River source. *Photo by Werner Conradie.*

Lungwebungu River camp bridge crossing, -12.58346° 18.66598°, 1,304 m asl; PEM A12796-7, Cuanavale River source lake camp side, -13.09442° 18.89372°, 1,368 m asl; PEM A12907-8, INBAC: no number (x2), Quembo River source lake, -13.13624° 19.04591°, 1,366 m asl; PEM A13763, Lungwebungu River, trap 2, -12.58199° 18.66562°, 1,208 m asl; PEM A13781, Lungwebungu River, trap 3, -12.58056° 18.66419°, 1,302 m asl; PEM A13784, Cuquema River, downstream, -12.47021° 16.82334°, 1,644 m asl, PEM A13790, Dam/ Hydroplant on Cuquema River, -12.42556° 16.81856°, 1,640 m asl; PEM A14680, Menongue, -14.63015° 17.63465°, 1,373 m asl; PEM A14685, wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl; PEM A14712-5, INBAC: WC-6975, Lungwebungu River camp, -12.58439° 18.66748°, 1,297 m asl; PEM A14724, Quembo River bridge, -13.52746° 19.28060°, 1,241 m asl; PEM A14739, Quembo River bridge camp, trap 1, -13.52801° 19.28147°, 1,236 m asl; PEM A14740, Quembo River bridge camp, -13.52746° 19.28060°, 1,241 m asl; PEM A14744, Quembo River bridge camp, trap 4, -13.52658° 19.27810°, 1,248 m asl; PEM A14818– 22, INBAC: WC-7004, Luio River camp floodplains, -13.19711° 20.22194°, 1,181 m asl; PEM A14824-6, INBAC: WC-7029, Camp at side tributary (Luandai River) of the Luanguinga River, -13.70885° 21.26234°, 1,116 m asl; PEM A14831, Luanguinga River waterfall, -13.71132° 21.24914°, 1,118 m asl; PEM A14851-5, INBAC: WC-7044, Lake Hundo, -14.97431° 21.62966°, 1,100 m asl; PEM A14889-90, INBAC: WC-7079, Luvu River camp, -13.71200° 21.83538°, 1,082 m asl. **Description:** Large robust toad; snout rounded; elevated parotoid glands. Dorsum dark brown with pairs of dark paravertebral patches; pairs of dark patches on snout and behind eyes that create the appearance of a pale cross on head; in PEM A12724 and A12720 a continuous dark interorbital bar is present; back of thighs often with red infusions (not always present in females or juveniles). In breeding males, the dorsum becomes yellow, with numerous small black-tipped asperites; throat darkened; enlarged arms; black nuptial pads present on palm and



Map 7. Distribution of Sclerophrys gutturalis in Angola.

first finger. Adult females (n = 22) varied from 54.4-109.7 (78.3) mm (largest female: PEM A12575); adult males (n = 37) varied from 56.7–89.2 (74.6) mm (largest male: PEM A14890). Habitat and natural history notes: Found in miombo woodland. Males were heard calling from margins of the source lakes. Comments: Widespread species across most of south-central Africa (Channing and Rödel 2019). Most historical Angolan material has been referred to as Bufo regularis Reus, 1833. Since the description of *Bufo regularis gutturalis* Power, 1927 (subsequently elevated to full species), the Angolan material has only partly been reassigned (Ruas 1996), and the rest of the extant material needs to be reassessed to verify the taxonomic status. Additionally, this species needs to be reassessed as other authors have demonstrated that cryptic species may be present in this taxon (Pickersgill 2007; Telford et al. 2019).

Sclerophrys pusilla (Mertens, 1937) Flat-backed Toad (Fig. 9; Map 8)

Material (41 specimens): PEM A12425-6, INBAC (no number), Cunde waterfall, -13.77364° 18.75514°, 1,287 masl; PEMA12434, south of Menongue en route to Cuebe River, -14.96288° 17.69090°, 1,319 m asl; PEM A12446, Cuchi River gorge, -14.59000° 16.90758°, 1,375 m asl; PEM A12494, HALO Menongue, -14.66317° 17.66521°, 1,386 m asl; PEM A12499, INBAC (no number), drive back from Cuchi to Menongue, -14.67986° 17.17512°, 1,404 m asl; PEM A12623-4, HALO Cuito, -12.39584° 16.96067°, 1,697 m asl; PEM A12630-1, roadside ditch 10 km SW of Cuito, -12.44815° 16.88118°, 1,742 m asl; PEM A12636, Quembo River source camp, -13.52653° 19.28368°, 1,242 m asl; PEM A12640, Cuanavale River, -13.37406° 18.99269°, 1,297 m asl; PEM A12642, Cuanavale River, -13.29236° 18.96283°, 1,313 m asl; PEM A 12650-1, Kwanza River bridge, -11.99348° 17.66965°, 1,273 m asl; PEM A12652, Kuvango Hydro Plant Site, wetland to east, -14.38755° 16.30166°, 1,451 m asl; PEM A12658, old Kuvango Hydroplant site, -14.38775° 16.29365°, 1,440 m asl; PEM A12659–60, Campsite 2 near Cuvango Mission, -13.32887 16.41167, 1,537 m asl; PEM A12668, Campsite 1 below rapids,

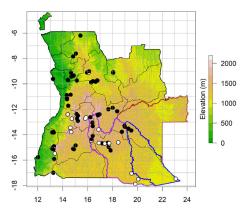


Fig. 9. Adult male *Sclerophrys pusilla* from Cuito town. *Photo by Werner Conradie*.

west of Fundo village, -13.04483° 16.37520°, 1,565 m asl; PEM A12680, Camp 3, Malova Village, Mipanha River, -14.09140° 16.41476°, 1,553 m asl; PEM A12686-7, Huambo HALO training camp, -12.73726° 15.81828°, 1,665 m asl; PEM A12690, Cubango 2017 launch site, -12.61700° 16.22132°, 1,727 m asl; PEM A12839, 31 km W of Menongue, Cueli River, -14.70511° 17.38014°, 1,392 m asl; PEM A13791, Dam/Hydroplant on Cuquema River, -12.42556° 16.81856°, 1,640 m asl; PEM A14681– 2, Menongue, -14.63015° 17.63465°, 1,373 m asl; PEM A14720–1, 14725, Quembo River bridge, -13.52746° 19.28060°, 1,241 m asl; PEM A14745-7, Quembo River bridge camp, -13.52746° 19.28060°, 1,241 m asl; PEM A17761–2, Quembo River right side tributary (Micongo River) past village, -13.51877° 19.28487°, 1,478 m asl. **Description:** Medium sized toad; sharp snout profile; small flattened parotoid glands. Light brown dorsal coloration, with irregular darker markings; no interorbital bar; thin light dorsal stripe may be present; no red markings on the back of the thighs. Males with darkened throats; dorsum with black tipped asperites. Adult females (n = 16) varied from 52.1-79.3 (65.9) mm (largest female: PEM A14745); adult males (n = 9)varied from 35.5-58.7 (50.3) mm (largest male: PEM A12839). Habitat and natural history notes: Found in miombo woodland, sympatric with S. gutturalis. Comments: Poynton et al. (2016) recently split West Africa S. maculata from central and southern African S. pusilla. All the historical Angolan material referred to under the former name, S. maculata, now represents S. pusilla.

Sclerophrys poweri (Hewitt, 1935) Western Olive Toad (Fig. 10; Map 9)

Material (8 specimens): PEM A14876-82, INBAC: WC-7076, wetland south of Lake Hundo, -15.01099° 21.63608°, 1,100 m asl. **Description:** Large robust toad; snout rounded; large elevated parotoid glands. Dorsum of females tan with distinct black-edged dark brown to deep red paired dorsal markings; in males it can be more olive-yellow; red infusions on the back of the thighs. Males with dark throat and dorsal surface spinose with



Map 8. Distribution of Sclerophrys pusilla in Angola.



Fig. 10. Adult female *Sclerophrys poweri* from Lake Hundo. *Photo by Werner Conradie.*

small black tipped asperites. Adult females (n = 3) varied from 101.0–102.3 (101.8) mm (largest female: PEM A14876; maximum recorded size); adult males (n = 5) varied from 85.5–97.0 (93.3) mm (largest male: PEM A14877; maximum recorded size). **Habitat and natural history notes:** This species was heard calling during early evenings in a flooded wetland and from margins of large natural lakes. **Comments:** Only a few records exist for southern and eastern Angola (Marques et al. 2018; Baptista et al. 2019). These specimens represent the easternmost records in Angola, and only the second record for Moxico Province (Ruas 1996).

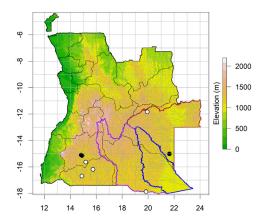
Hemisotidae

Hemisus guineensis Cope, 1865 Guinea Shovel-snouted Frog (Fig. 11; Map 10)

Material (6 specimens): PEM A14955, Cuando River, CUD2018 AC Camp 27, -16.09006° 21.83947°, 1,038 m asl; PEM A14832–3, INBAC: WC-6948, Lake Hundo, -14.97431° 21.62966°, 1,100 m asl; PEM A13831, Cuando River, camp 18, -14.66105° 20.16858°, 1,124 m asl; PEM A12771, Cuando River Source, trap 3, -13.00334° 19.13564°, 1,360 m asl. Additional material (1 tadpole lot): SAIAB 209095 (7

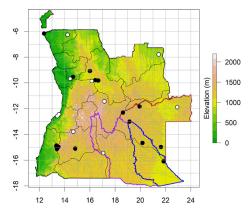


Fig. 11. Adult female *Hemisus guineensis* from Cuando River source. *Photo by Werner Conradie*.



Map 9. Distribution of *Sclerophrys poweri* in Angola.

tadpoles), small wooden bridge across wetland on road between Cuanavale River source camp and Munhango, -12.30714° 18.62333°, 1,397 m asl. **Description:** Small to medium sized frog; hardened pointed snout; small eyes; tympanum hidden; smooth dorsum (except PEM A12771, in which the yellow spots are slightly elevated); transverse skin ridge between posterior corners of eye, extending behind eye to above the arm; reduced webbing; large inner metatarsal and outer metacarpal tubercles. Grey dorsum with yellow mottling or spots; yellow vertebral stripe present; ventrum granular, with small irregular spots. Males with dark throats. Adult females (n = 3) varied from 40.5–49.2 (43.4) mm (largest female: PEM A12771); adult males (n = 3) varied from 26.7–31.6 (29.8) mm (largest male: PEM A14955). Habitat and natural history notes: No calls were heard. Specimens were either caught in traps or by hand while they were active at night after heavy rains in November, near open grassland and pans. One female (PEM A13831) collected in November was gravid. Comments: Laurent (1972) assigned all Angolan material he examined to the subspecies H. guineensis microps, and this was followed by Ruas (1996). However, Channing (2001) and Marques et al. (2018) documented two species of Hemisus occuring in Angola, Hemisus guineensis in the



Map 10. Distribution of Hemisus guineensis in Angola.



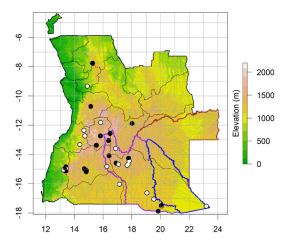
Fig. 12. Adult female *Hyperolius benguellensis* from Cubango River rapids near Fundo village. *Photo by Werner Conradie*.

north and *H. marmoratus* in the south-central region. We follow Laurent (1972) and assign all Angolan material to *Hemisus guineensis* until an in-depth phylogenetic work is conducted to assess the taxonomic status of the available material.

Hyperoliidae

Hyperolius benguellensis (Bocage, 1893) Benguela Reed Frog (Fig. 12; Map 11)

Material (8 specimens, 1 tadpole lot): PEM A12438–41, INBAC (no number x2), Cuchi River gorge, -14.59000° 16.90758°, 1,365 m asl; PEM A12661, PEM A14172, Campsite 2 near old Cuvango Mission, -13.33451° 16.41280°, 1,356 m asl; PEM A12675–6, Camp 3, Malova Village, Mipanha River, -14.09140° 16.41476°, 1,553 m asl; PEM A12666, Cubango River campsite 1 below rapids, west of Fundo village, -13.04790° 16.37896°, 1,568 m asl. Additional specimens (1 tadpole lot): SAIAB 209058 (18 tadpoles), Cuvango power station, entrance to canal, -14.38650° 16.28767°, 1,457 m asl. **Description:** Small reed frog; sharp but truncated snout, with small to no anterior protrusion; pedal webbing formula: I(1), II i/e (1-0.5), III (1–0.5), IV (1–1), V (0.75). Dorsum green with white dorso-lateral stripes (mostly males) or uniformly green with scattered brown spots (mostly females); ventrum transparent. Males with yellow gular disc. Single adult female measured 24.7 mm (PEM A12438); adult males (n = 7) varied from 16.2-22.8 (19.7) mm (largest male: PEM A12440). Habitat and natural history notes: Found on margins of rivers and in wetlands. Restricted to the western side of the study area, associated with the Cubango River system. Comments: In the most recent revision of the *Hyperolius nasutus*-complex, 16 species have been recognized (Channing et al. 2013). At least four species are expected to occur in Angola (Channing et al. 2013; Marques et al. 2018; Baptista et al. 2019), namely H. benguellensis, H. nasutus, H. adspersus, and H. dartevellei. Two clear morphotypes exist based on the general snout shape: sharp (benguellensis group) and



Map 11. Distribution of *Hyperolius benguellensis* in Angola.

rounded (nasutus group). Of the sharp snouted form, we distinguished between two morphotypes in southeastern Angola: the 'shark'-like profile (H. benguellensis, this species account) and the acutely pointed snout, with a distinct protruding tip (H. cf. invangae, see species account below). These identifications were confirmed by comparing 16S rRNA barcodes (W. Conradie, unpub. data) to published sequences (Channing et al. 2012). The remaining material is assigned to the nasutus group (see species account below). However, it must be noted that these little green frogs have been the subject of rigorous taxonomic debate over the years due to their cryptic nature, molecular and morphological similarity, and substantial geographic overlaps (see Channing et al. 2012 for overview). The taxonomic status of Angolan species belonging to these groups needs to be assessed in a broadscale phylogenetic study.

Hyperolius cinereus Monard, 1937 Ashy Reed Frog (Fig. 13; Map 12)

Material (12 specimens, 1 tadpole lot): PEM A12442-4, INBAC (no numbers x 2), Cuchi River gorge, -14.59000° 16.90758°, 1,375 m asl; PEM A12664, PEM A12670, Cubango River, campsite 1 below rapids, west of Fundo village, -13.04790° 16.37806°, 1,565 m asl; PEM A13787-9, INBAC: WC-520, Dam/ Hydroplant on Cuquema River, -12.42556° 16.81856°, 1,640 m asl; PEM A14128 (10 tadpoles), old Kuvango Hydroplant Site, wetland to east, -14.38755° 16.30166°, 1,438 m asl; INBAC: WC-5169, Cubango River source site, -12.66256° 16.09324°, 1,771 m asl. Description: Medium sized reed frog. No sexual dichromatism observed; both sexes with lime green to olive dorsum; protruding yellow eyes; red inner thighs; ventrum yellow. Males with yellow gular disc. Adult females (n = 3) varied from 20.3–29.1 (25.0) mm (largest female PEM A13789); adult males (n = 9) varied from 19.1– 22.8 (21.6) mm (largest male: PEM A12443). Habitat and natural history notes: Only recorded from the western side of the study area, where it was associated



Fig. 13. Adult *Hyperolius cinereus* from Cubango River rapids near Fundo village. *Photo by Werner Conradie*.

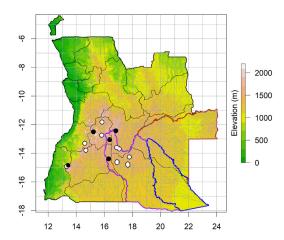
with the Cubango and Cuito rivers. **Comments:** Widely recorded from the interior highlands of Angola (Conradie et al. 2013). The map in Marques et al. (2018) incorrectly plotted records from southern Cuando Cubango Province. The southeasternmost Angolan record of this species is close to the town of Menongue (Conradie et al. 2013).

Hyperolius cf. inyangae Laurent, 1943 Nyanga Reed Frog (Fig. 14; Map 13)

Material (30 specimens): PEM A12730–3, INBAC: WC-4839; INBAC (no number x3), Cuando River source, -13.00346° 19.12751°, 1,353 m asl; PEM A14793–803, INBAC: WC-7023, INBAC: WC-7025, Luio River camp floodplains, -13.19711° 20.22194°, 1,181 m asl; PEM A13741, Lungwebungu River campsite, -12.58319° 18.66570°, 1,284 m asl; PEM A14887–8, Luvu River camp, -13.71200° 21.83538°, 1,082 m asl; PEM A12858–9, Quembo River source lake, -13.13624° 19.04591°, 1,366 m asl; PEM A12500, PEM A12513, river crossing before Samboano Village, -12.30700° 18.62350°, 1,398 m asl; PEM A14892–3, wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl. Additional material (1 specimen): P2-

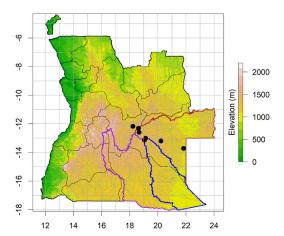


Fig. 14. Adult male *Hyperolius* cf. *inyangae* from Cuando River source. *Photo by Werner Conradie*.



Map 12. Distribution of *Hyperolius cinereus* in Angola.

274 (photograph and tissue sample), wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl. **Description:** Small slender species of reed frog; very sharp snout with a small anterior protrusion, which extends well beyond the margin of the mouth; small black asperites on throat; pedal webbing formula: I(1), II i/e (1–0.75), III (1–0.75), IV (0.75–0.75), V (0.5). Dorsum lime green with white dorsolateral stripes; ventrum transparent; toe tips and webbing yellow. Adult females (n = 9) varied from 15.0-19.6 (16.7) mm (largest female: PEM A12500); adult males (n = 21) varied from 12.8-17.9 (15.1) mm (largest male: PEM A14893). Habitat and natural history notes: Found sympatric with Hyperolius nasutus at the Lungwebungu, Cuando, and Quembo rivers, where they were distinguished by microhabitat preference. Hyperolius cf. inyangae was found among vegetation associated with slow running water, while H. nasutus was found on margins of source lakes or flooded areas with larger bodies of open water. Comments: Bittencourt-Silva (2019) assigned a specimen from western Zambia to H. nasicus based on head shape and webbing, but mentioned that molecularly it is most like H. inyangae. The new material documented



Map 13. Distribution of Hyperolius cf. inyangae in Angola.

here is molecularly identical (16S rRNA: 97.5–100%) to the published sequences of H. inyangae (Channing et al. 2013; Bittencourt-Silva 2019) and agrees with the description, especially regarding the sharp snout usually with a pointed protrusion, but differs in the pedal webbing condition (Channing et al. 2013). It is reported to have reduced webbing and is illustrated as such, while the specimens here have more extensive webbing. This is either an error or there is a degree of variation in the webbing condition. The presence of this species so far to the west is an unexpected result, as *H. inyangae* is currently only known from the Eastern Highlands of Zimbabwe. These new records thus represent a range extension of over 1,500 km westward. Further phylogenetic work is underway to fully document the taxonomic status of this population and other species assigned to the *H. nasutus* or *H. benguellensis* complexes.

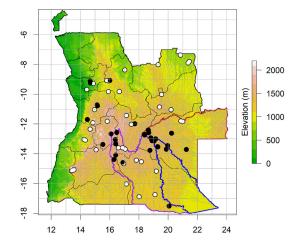
Hyperolius nasutus Günther, 1865 Large-nosed Reed Frog (Fig. 15; Map 14)

Material (64 specimens, 1 tadpole lot): PEM A12599–601, Calua River source, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,445 m asl; PEM A12424, Cunde waterfall, -13.77390° 18.75520°, 1,285 m asl; PEM A14107 (tadpoles), PEM A12435, confluence of Cuito and Calua rivers, -13.12458° 18.20909°, 1,345 m asl; PEM A12461-3, INBAC (no number x 4), Cuanavale River source lake, -13.08537° 18.89098°, 1,360 m asl; PEM A12738-40, INBAC (no number), Cuando River source, -13.00346° 19.12751°, 1,353 m asl; PEM A12693, Cubango River source site, -12.66256° 16.09324°, 1,771 m asl; PEM A12445, Cuchi River gorge, -14.5900° 16.90758°, 1,365 m asl; PEM A12550-1, Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl; PEM A12427, INBAC (no number), Cuiva River bridge on EN250, -11.98345° 17.72367°, 1,267 m asl; PEM A12490, Dala River, near Samanunga village, -12.93169° 18.81458°, 1,363 m asl; PEM A12665, Cubango River campsite 1 below



Fig. 15. Adult male *Hyperolius nasutus* from Cuanavale River source. *Photo by Werner Conradie*.

rapids, west of Fundo village, -13.04790° 16.37896°, 1,568 m asl; PEM A12805-6, PEM A13804-12, Lake Tchanssengwe, -12.41402° 18.64418°, 1,393 m asl; PEM A14827-8, INBAC (no number), Luanguinga River waterfall, -13.71132° 21.24914°, 1,118 m asl; PEM A13773-80, Lungwebungu River old oxbows, -12.58129° 18.67162°, 1,304 m asl; PEM A14750–52, Quembo River right side tributary (Micongo River) past village, -13.51877° 19.28487°, 1,248 m asl; PEM A12860-62, INBAC (no number), Quembo River source lake, -13.13624° 19.04591°, 1,366 m asl; PEM A14729-35, INBAC (no number x2), Quembo River, oxbow near small waterfall, -13.54257° 19.29551°, 1,233 m asl. Additional material (13 specimens, 8 tadpole lots): SAIAB 209057 (1 specimen), Cuanavale River near confluence, -13.12478° 18.90017°, 1,346 m asl; SAIAB 204573 (2 specimens), Quembo River source lake, -13.13586° 19.04492°, 1,369 m asl; SAIAB 209053 (7 tadpoles), outlet River from Kuembo River source lake, -13.13689° 19.03144°, 1,392 m asl; SAIAB 209173 (3 tadpoles), Quembo River source, -13.13583° 19.04528°, 1,370 m asl; SAIAB 209051 (5 specimens), Quembo River source lake, -13.14025° 19.04822°, 1,365 m asl; SAIAB 209045 (6 tadpoles), stream outflow about 2.6 km downstream of source lake, -13.00317° 19.15153°, 1,331 m asl; SAIAB 209056 (3 specimens), SAIAB 209087 (1 specimen), small stream 3 km below Cuanavale River source camp, -13.12539° 18.89914°. 1,344 m asl; SAIAB 209049 (5 tadpoles), south west of Cambuta on main track, -13.44678° 19.96403°, 1,229 m asl; SAIAB 209055 (1 tadpole), river bridge at Cangamba, -13.69611° 19.87503°, 1,193 m asl; SAIAB 209050 (1 tadpole), Calua lagoon, -12.73600° 18.39394°, 1,448 m asl; SAIAB 209026 (1 tadpole), Cuanavale River lake outlet, -13.09414° 18.89612°, 1,357 m asl; SAIAB 209054 (4 tadpoles), Cuando River source bog, -13.00383° 19.12719°, 1,350 m asl. **Description:** Small reed frog; rounded snout. Dorsum green, with white dorso-lateral stripes and small scattered black spots;



Map 14. Distribution of *Hyperolius nasutus* in Angola.

ventrum transparent; pedal webbing formula: **I**(1), **II** i/e (1–0.25), **III** (0.75–0.5), **IV** (0.75–0.5), **V** (0.5). Male throat is white. Adult females (n = 14) varied from 15.9–20.2 (18.5) mm (largest female: PEM A13810); adult males (n = 21) varied from 13.7–20.3 (17.2) mm (largest male: INBAC no number). **Habitat and natural history notes:** Found on the margins of source lakes, larger rivers, and cut-off oxbows. **Comments:** Found at certain localities in sympatry with *Hyperolius* cf. *inyangae* (see above), but can easily be distinguished based on the rounded snout and larger overall size.

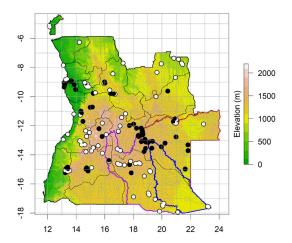
Hyperolius parallelus Günther, 1858 Angolan Reed Frog (Fig. 16; Map 15)

Material (80 specimens, 6 tadpole lots): PEM A12436-7, INBAC (no number), Cuchi River gorge, -14.59000° 16.90758°, 1,365 m asl; PEM A12448–54, Cuanavale River source lake, -13.08537° 18.89098°, 1,360 m asl; PEM A12488, Dala River, near Samanunga village, -12.93169° 18.81458°, 1,363 m asl; PEM A12525, Muhango village, -12.16310° 18.55430°, 1,430 m asl; PEM A12520, PEM A12538-42, INBAC (no number), Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl; PEM A12586-91, PEM A12827, Calua River source lake, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,445 m asl; PEM A12683–4, Huambo HALO training camp, -12.73726° 15.81828°, 1,665 m asl; PEM A12851–56, INBAC: WC-4626, INBAC (no number x2), Quembo River source lake, -13.13624° 19.04591°, 1,366 masl; PEMA13737 (tadpoles), Comba River, -12.62442° 18.65159°, 1,299 m asl; PEM A13765–6, Lungwebungu River, old oxbows, -12.58129° 18.67162°, 1,304 m asl; PEM A13794-8, PEM A13799 (tadpoles), INBAC: WC-4555, Lake Tchanssengwe, -12.41402° 18.64418°, 1,393 m asl; PEM A14097 (tadpoles), Dala River, near Samanunga village, -12.93169° 18.18146°, 1,315 m asl; PEM A14105 (tadpoles), Confluence of Cuito and Calua rivers, -13.12458° 18.89989°, 1,345 m asl; PEM A14113 (tadpoles), Cuiva River, -11.98346° 17.72841°, 1,264 m asl; PEM A14683–4, wetland near old quarry



Fig. 16. Adult male *Hyperolius parallelus* from Cuanavale River source. *Photo by Werner Conradie*.

east of Quemba, -12.16960° 18.22965°, 1,353 m asl; PEM A14698-9, wetland west of Lungwebungu River camp, -12.55855° 18.6377°, 1,308 m asl; PEM A14726, Quembo River, oxbow near small waterfall, -13.54257° 19.29551°, 1,233 m asl; PEM A14783-92, INBAC: WC-7012, INBAC: WC-7008, INBAC: WC-7014, Luio River camp floodplains, -13.19711° 20.22194°, 1,181 m asl; PEM A14834-43, INBAC: WC-6928, INBAC: WC-6928, Lake Hundo, -14.97431° 21.62966°, 1,100 m asl; PEM A14883-5, PEM A14886 (tadpoles), INBAC: WC-7083, Luvu River camp, -13.712° 21.83538°, 1,082 m asl; INBAC (no number), Cuiva River bridge on EN250, -11.98345° 17.72367°, 1,267 m asl. **Additional** material (1 specimen, 14 tadpole lots): SAIAB 204515 (9 tadpoles), below the outlet of the Cuanavale River source lake, -13.09364° 18.89597°, 1,357 m asl; SAIAB 209030 (10 tadpoles), small bridge on road to Cuanavale River source, -12.30714° 18.62333°, 1,399 m asl; SAIAB 204563 (5 tadpoles), SAIAB 204566 (1 tadpole), Quembo River source lake, -13.13611° 19.04500°, 1,367 m asl; SAIAB 209025 (1 tadpole), Quembo River source lake outlet, -13.14025° 19.04822°, 1,365 m asl; SAIAB 209027 (1 tadpole), Cunde waterfall, -13.77364° 18.75514°, 1,287 m asl; SAIAB 209065 (8 tadpoles), swamp near Cuanavale River source, -13.10750° 18.86089°, 1,386 m asl; SAIAB 209085 (1 specimen), Cuanavale River source lake , -13.08997° 18.89561°, 1,358 m asl; SAIAB 204471 (16 tadpoles), frog pan 30 km below Cuando River source camp, -13.06831° 19.34369°, 1,297 m asl; SAIAB 209024 (1 tadpole), Samununga village, -12.93228° 18.81672°, 1,364 m asl; SAIAB 209029 (3 tadpoles), south west of Cambuta on main track, -13.44678° 19.96403°, 1,229 m asl; SAIAB 209028 (4 tadpoles), Cueve River source, peat bog source, -12.66949° 18.35203°, 1,420 m asl; SAIAB 209034 (5 tadpoles), Calua River lagoon, -12.73600° 18.39394°, 1,448 m asl; SAIAB 208959 (7 tadpoles), Cuanavale River source lake outlet, -13.09414° 18.89612°, 1,357 m asl; SAIAB 209031 (6 tadpoles), Cuanavale River bog above lake, -13.08575° 18.89215°,



Map 15. Distribution of *Hyperolius parallelus* in Angola.

1,356 m asl; SAIAB 209035 (7 tadpoles), Cuvango River - Power station camp, -14.38720° 16.28760°, 1,456 m asl. Description: Large reed frog. Dorsal coloration varied from finely vermiculated to boldly patterned; base color mostly orange to brick red with irregular black-edged white-cream markings that were often fused to form irregular stripes, the centers of these markings exhibited a small red or yellow spot or formed a thin line; feet and webbing red; ventrum white. Adult females (n = 24) varied from 26.8–37.2 (32.2) mm (largest female: PEM A14789); adult males (n = 52) varied from 22.8– 34.7 (29.2) mm (largest male: PEM A12542). Habitat and natural history notes: All specimens were found around larger water bodies. Males started calling in the early evening, high up in trees around the water bodies, and slowly moved to the water edge during the evening. Conradie et al. (2021) recorded predation of this species by the following species of snakes: Crotaphopeltis hotamboeia, Philothamnus ornatus, Philothamnus semivariegatus, and Kladirostratus acutus. Comments: This species was by far the most common frog from all major waterbodies surveyed. As in the larger viridiflavus group, many color variations have been described in the parallelus subgroup (see Channing 2022). The material from this study conforms to the color pattern recorded for Hyperolius angolensis Steindachner, 1867, which is now a synonym of H. parallelus.

Hyperolius raymondi Conradie, Branch, and Tolley, 2013 Raymond's Reed Frog (Fig. 17; Map 16)

Material (27 specimens, 3 tadpole lots): PEM A12464–7, INBAC (no number x 2), Cuanavale River source lake, -13.08537° 18.89098°, 1,360 m asl; PEM A12514–8, river crossing before Samboano village, -12.30700° 18.62350°, 1,398 m asl; PEM A12521–2, PEM A14124 (tadpoles), Cuiva River source, -12.66825° 18.35282°, 1,407 m asl; PEM A12553–8, INBAC (no number x2), Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl; PEM A12602–3, PEM A14120 (tadpoles), Calua River source lake, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,445 m asl; PEM

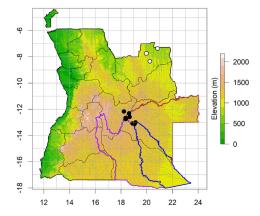


Fig. 17. Adult male (above) and female (below) *Hyperolius raymondi* from river crossing before Samboano village. *Photo by Luke Verburgt*.

A12741, Cuando River source, -13.00346° 19.12751°, 1,353 m asl; PEM A12816, Cuiva River source, -12.66856° 18.35307°, 1,433 m asl; PEM A13742-3, Lungwebungu River campsite, -12.58319° 18.66573°, 1,284 m asl; PEM A14127 (tadpoles), confluence of Cuito and Calua rivers, -12.74878° 18.35433°, 1,393 m asl. Additional material (1 specimen, 1 tadpole lot): P2-275 (photograph and tissue sample), wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl; SAIAB 209041 (2 tadpoles), Quembo River source lake, -13.13586° 19.04492°, 1,372 m asl. **Description:** Medium sized reed frog. Most males possess two paravertebral and two dorsolateral black stripes on lime green to olive background; three males (PEM A12515, A13742-3) did not exhibit any dorsal stripes, and in one male (PEM A12816) the stripes faded mid-dorsally and eventually disappeared. All females devoid of dorsal markings. Adult females (n = 3) varied from 21.2–23.7 (22.6) mm (largest female: PEM A12555); adult males (n = 19) varied from 16.5–21.4 (18.8) mm (largest male: PEM A12816). Habitat and natural history notes: Found among inundated tall grass next to slow flowing water. Comments: This recently described species is currently regarded as endemic to Angola, but is expected to occur in adjacent DRC (Conradie et al. 2013). Initially, it was only known from the rivers draining northwards into the Congo basin (Conradie et al. 2013), and it was therefore thought to be associated with the Congo fauna. The discovery of this species in southeastern Angola corroborates Cei's (1977) findings that the amphibian fauna located within the Cubango River system and has affinities with Congo fauna, due to the apparent lack of natural barriers between these regions. This is the southernmost record for Angola for this species, and the first from the Okavango and Zambezi River catchments.

Hyperolius quinquevittatus Bocage, 1866 Five-striped Reed Frog (Fig. 18; Map 17)

Material (1 specimen): P2-273 (photograph and tissue sample only), wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl. **Description:**



Map 16. Distribution of Hyperolius raymondi in Angola.

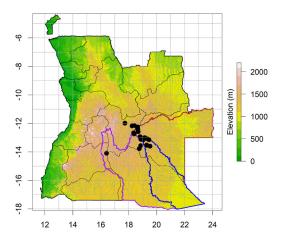


Fig. 18. Adult male *Hyperolius quinquevittatus* from wetland east of Quemba town. *Photo by Pedro Vaz Pinto*.

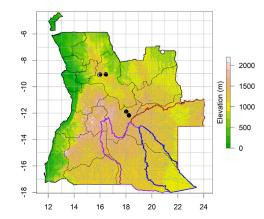
Medium sized reed frog; pointed snout; long slender limbs. Dorsum dark brown, with a single vertebral and two dorsolateral light green stripes. **Habitat and natural history notes:** Found in a flooded grassland, surrounded by miombo woodland. Founded syntopically with *Kassinula wittei, Hyperolius raymondi,* and *H.* cf. *inyangae*. **Comments:** This record represents an eastward range extension in Angola. It has been recorded from northwestern Zambia (Poynton and Broadley 1987, 1991; Channing 2001; Bittencourt 2019), and like *Kassinula wittei* and *Kassina kuvangensis*, this species is thus expected to occur to the north and east of the defined study area.

Hyperolius aff. bocagei Steindachner, 1867 Bocage's Reed Frog (Figs. 19–21; Map 18)

Material (74 specimens, 10 tadpole lots): PEM A12423, Cunde waterfall, -13.77390° 18.75520°, 1,287 m asl; PEM A12455–60, PEM A14085–6 (tadpoles) Cuanavale River source lake, -13.08537° 18.89098°, 1,340 m asl; PEM A12489, PEM A14098 (tadpoles), INBAC (no number), Dala River, near Samanunga village, -12.93169° 18.81458°, 1,363 m asl; PEM A12508–12, river crossing before Samboano village, -12.30700° 18.62350°, 1,397 m asl; PEM A12543–52, INBAC



Map 18. Distribution of Hyperolius aff. bocagei in Angola.



Map 17. Distribution of *Hyperolius quinquevittatus* in Angola.



Fig. 19. Adult male *Hyperolius* aff. *bocagei* (green form) from Cuito River source. *Photo by Werner Conradie*.



Fig. 20. Adult male *Hyperolius* aff. *bocagei* (red form) from Cuanavale River source. *Photo by Werner Conradie*.



Fig. 21. Adult male *Hyperolius* aff. *bocagei* (brown form) from Cuito River source. *Photo by Werner Conradie*.

(no number x2), Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl; PEM A12592-8, Calua River source lake, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,446 m asl; PEM A12619, Stop 1: road to Cuito River source, -12.25050° 18.63730°, 1,556 m asl; PEM A12674, Camp 3, Malova Village, Mipanha River, -14.09140° 16.41476°, 1,553 m asl; PEM A12734-7, INBAC: WC-4833, INBAC (no number x2), Cuando River source, -13.00346° 19.12751°, 1,553 m asl; PEM A12788-9, INBAC: WC-4614, Quembo River, source trap 2, -13.13544° 19.04397°, 1,374 m asl; PEM A14112 (tadpoles), Cuiva River, -11.98346° 17.72841°, 1,264 m asl; PEM A12815, PEM A14125 (tadpoles), Cuiva River source, -12.66856° 18.35307°, 1,407 m asl; PEM A12857, INBAC: WC-4616; INBAC (no number x5) Quembo River source lake, -13.13624° 19.04591°, 1,411 m asl; PEM A13767-72, INBAC: WC-6979 Lungwebungu River, old oxbows, -12.58129° 18.67162°, 1,304 m asl; PEM A13800–2, PEM A13803 (tadpoles), Lake Tchanssengwe, -12.41402° 18.64417°, 1,415 m asl; PEM A14090 (tadpoles), 4 km upstream from Cuanavale River source, -13.05084° 18.89726°, 1,394 m asl; PEM A14103 (tadpoles), 4 km downstream from Cuanavale River source camp, -13.11585° 18.90246°, 1,354 m asl; PEM A14106 (tadpoles), confluence of Cuito and Calua rivers, -13.12458° 18.89989°, 1,345 m asl; PEM A14686, detour route just across bridge over Cuiva River, -12.13942° 18.39393°, 1,385 m asl; PEM A14693 (tadpoles), Lungwebungu River camp, first oxbow on right side, -12.58117° 18.67106°, 1,294 m asl; PEM A14717, en route from Samanunga village to Cuanavale River source, -12.94331° 18.81118°, 1,407 m asl; PEM A14727–8, Quembo River, oxbow near small waterfall, -13.54257° 19.29551°, 1,233 m asl; PEM A14748-9, PEM A14763-65, PEM A14778, Quembo River right side tributary (Micongo River) past village, -13.51877° 19.28487°, 1,248 m asl; PEM A14757, left side tributary (Condinde River) at Cuando River bridge, -13.60076° 19.52675° 1,219 m asl. Additional material (16 tadpole lots): SAIAB 204553 (7 tadpoles), Cuanavale River source lake, -13.08997° 18.89389°, 1,358 m asl; SAIAB 209059 (15 tadpoles), Cuanavale River near confluence, -13.12478° 18.90017°, 1,347 m asl; SAIAB 204509 (29 tadpoles), outlet from Kuembo River source lake, -13.13689° 19.03144°, 1,375 m asl; SAIAB 204564 (25 tadpoles), SAIAB 209074 (1 tadpole), Quembo River source lake, -13.13611° 19.04500°, 1,366 m asl; SAIAB 209066 (9 tadpoles), Quembo River source lake, -13.14025° 19.04822°, 1,365 m asl; SAIAB 209062 (2 tadpoles), swamp near Cuanavale River source lake camp, -13.10750° 18.86089°, 1,386 m asl; SAIAB 204465 (19 tadpoles), Cuando River source pool, -13.00383° 19.12719°, 1,350 m asl; SAIAB 209060 (2 tadpoles), stream outflow about 2.6 km downstream of source lake, -13.00317° 19.15153°, 1,331 m asl; SAIAB 204472 (13 tadpoles), Cuando River, -13.09142° 19.35850°, 1,283 m asl; SAIAB 209067 (8 tadpoles), on Cuanavale River

road, -13.14190° 19.44503°, 1,301 m asl; SAIAB 209070 (10 tadpoles), pan near Cuanavale River camp, seepage, -13.10750° 18.86089°, 1,387 m asl; SAIAB 204569 (13 tadpoles), Samununga village, -12.93228° 18.81672°, 1,365 m asl; SAIAB 209063 (6 tadpoles), small stream 3 km below Cuanavale River source camp, -13.12539° 18.89914°, 1,344 m asl; SAIAB 209069 (11 tadpoles), pool in wetland on road edge, west of Munhango, -12.17806° 18.24306°, 1,370 m asl; SAIAB 209075 (18 tadpoles), Cuando River source bog, -13.00383° 19.12719°, 1,350 m asl. **Description:** Medium sized reed frog; rounded snout; reduced webbing; ventrum granular. Three different color forms were observed, i.e., plain light to dark green, brown, and bright red; thin dorsolateral white stripe present; small white specks on dorsal side of legs; toes and webbing red. Tadpoles with ventrum spotted and ventral blotches remain present in juveniles but fade in adults. Adult females (n = 11) varied from 16.7–21.9 (19.6) mm (largest female: PEM A12549); adult males (n = 52) varied from 14.8-21.1 (18.7) mm (largest male: PEM A12592). Habitat and natural **history notes:** Found at the margins of large rivers and source lakes within dense emergent wetland vegetation. Sympatric with other species of *Hyperolius*, mostly *H*. nasutus and H. parallelus. Comments: Initially we assigned these specimens to H. bocagei (NGOWP 2017), however it is generally regarded as a larger species that is associated with the *viridiflavus* group (see Schiøtz 1999). This new material differs in size (smaller) and webbing (less webbing) from H. bocagei (Schiøtz 1999). Phylogenetic work is currently underway to determine its taxonomic status.

Kassina kuvangensis (Monard, 1937)

Kuvangu Kassina (Fig. 22; Map 19)

Material (9 specimens, 5 tadpole lots): PEM A12496-7, unnamed side-triburaty source of Cuanavale River, -13.07518° 18.88481°, 1,374 m asl; PEM A12775-6, Quembo River, trap 4, -13.13586° 19.04709°, 1,369 m asl; PEM A12781, Quembo River trap 1, -13.13592° 19.04417°, 1,369 m asl; PEM A12825, Quembo River, trap 3, -13.13073° 19.03725°, 1,445 m asl; PEM A14116 (tadpoles), river crossing before Sombanana village, -12.30710° 18.62350°, 1,407 m asl; PEM A12828, PEM A14119 (tadpoles), Calua River source 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,446 m asl; PEM A14089 (tadpoles), 4 km upstream from Cuanavale River source, -13.05084° 18.89726°, 1,394 m asl; PEM A14096, Dala River, near Samanga village, -12.93169° 18.81458°, 1,363 m asl; PEM A14101 (tadpoles), 4 km downstream from Cuanavale River source camp, -13.11585° 18.90246°, 1,354 m asl; PEM A14104 (tadpoles), confluence of Cuito and Calua rivers, -13.12458° 18.89989°, 1,345 m asl; PEM A14804, Luio River camp floodplains, -13.19711° 20.22194°, 1,181 m asl. Additional material (4 tadpole lots): SAIAB 209127 (1 tadpole), SAIAB 209107 (2 tadpoles), swamp

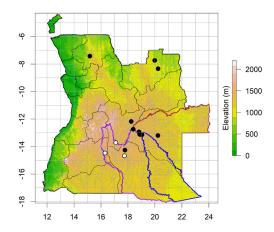


Fig. 22. Adult female *Kassina kuvangensis* from Cuanavale River source. *Photo by Werner Conradie*.

near Cuanavale River lake camp, -13.10750° 18.86089°, 1,386 m asl; SAIAB 209108 (22 tadpoles), pool in wetland on road edge west of Munhango, -12.17806° 18.24306°, 1,381 m asl; SAIAB 209089 (4 tadpoles), Calua lagoon, -12.73599° 18.39394°, 1,448 m asl. **Description:** Large sized Kassina; tympanum visible; elliptical vertical pupils; large inner metatarsal tubercle; subarticular tubercle well-developed. Dorsum very dark olive-brown, with scattered large darker brown yellow-edged irregular shaped spots; ventrum yellow, but in some individuals has black-edged white/yellow spots. In females, the cloaca sides are swollen. In males, the gular flap is dark and the glands behind eye/head are enlarged. Adult females (n = 2) varied from 51.9–53.3 (52.6) mm (largest female: PEM A14096); adult males (n = 7) varied from 38.4–52.9 (43.7) mm (largest male: PEM A12781). Tadpoles can get very large (up to 135 mm total length); LTRF 1/2(1), with strong jaw sheaths. Habitat and natural history notes: In the evenings, males call from the margins of source lakes and flooded areas while clinging to vegetation, and quickly submerge themselves when disturbed. Comments: These new records and other records from Uíge Province, which are the northwesternmost records (Ernst et al. 2020), represent the first adult K. kuvangensis



Fig. 23. Adult female *Kassina senegalensis* from Culua River source. *Photo by Werner Conradie*.

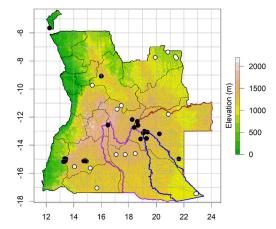


Map 19. Distribution of Kassina kuvangensis in Angola.

for Angola since the original species description (Monard 1937). The new localities recorded here lie between the species type locality in Angola (Kuvango, Monard 1937) and western Zambia (Poynton and Broadley 1987, 1991; Channing 2001).

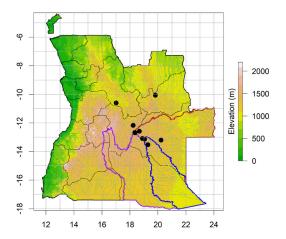
Kassina senegalensis (Duméril and Bibron, 1841) Bubbling Kassina (Fig. 23; Map 20)

Material (56 specimens, 3 tadpole lots): PEM A12604-7, Calua River source, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,445 m asl; PEM A12621, Cutata River, -12.56916° 16.49334°, 1,647 m asl; PEM A12699-700, Lungwebungu River camp bridge crossing, -12.58347° 18.66598°, 1,304 m asl; PEM A12785, Cuando River source trap 4, -13.00164° 19.12960°, 1,374 m asl; PEM A12790, Quembo River trap 2, -13.13544° 19.04397°, 1,374 m asl; PEM A12829–30, Culua River source, -12.73723° 18.39340°, 1,444 m asl; PEM A12863–9, INBAC (no number x2), Quembo River source lake, -13.13624° 19.04591°, 1,366 m asl; PEM A13744 (tadpoles), Lungwebungu River campsite, -12.58319° 18.66573°, 1,284 m asl; PEM A13757-62, INBAC: WC-6261, Lungwebungu River, trap 2, -12.58199° 18.66562°, 1,208 m asl; PEM A14094



Map 20. Distribution of Kassina senegalensis in Angola.

(tadpoles), series of pans south of Tempué, -13.55719° 18.85519°, 1,315 m asl; PEM A14109 (tadpoles), Cutata River, -12.56916° 16.49334°, 1,647 m asl; PEM A14687, PEM A14700, INBAC: WC-6759, Lungwebungu River camp, -12.58439° 18.66748°, 1,297 m asl; PEM A14718, PEM A14722, Quembo River bridge camp, -13.52746° 19.28060°, 1,241 m asl; PEM A14753-4, PEM A14766, Quembo River right side tributary (Micongo River) past village, -13.51877° 19.28487°, 1,248 m asl; PEM A14805-9, INBAC: WC-7017, Luio River camp floodplains, -13.19711° 20.22194°, 1,181 m asl; PEM A14844-50, PEM A14867-72, INBAC: WC-6916, INBAC: WC-6917, INBAC: WC-6953, Lake Hundo, -14.97431° 21.62966°, 1,100 m asl. **Additional** material (1 tadpole lot): SAIAB 209106 (28 tadpoles), small wooden bridge across wetland on road between Cuanavale River source camp and Munhango, -12.30714° 18.62333°, 1,399 m asl. **Description:** Medium sized *Kassina*; elliptical vertical pupils; tympanum visible. Dorsum yellow-mustard, with irregular shaped dark brown blotches, sometimes fused to form a vertebral stripe; ventrum white. In females, the cloaca is swollen, with papillae pointed downward. Male throats are black. Adult females (n = 16) varied from 27.9-41.1 (37.6) mm (largest female: INBAC: WC-6759); adult males (n = 34) varied from 35.2–43.6 (39.2) mm (largest male: PEM A14809). Habitat and natural history notes: This species was found in sympatry with K. kuvangensis in the study area, although not syntopically. Kassina senegalensis was found in more open habitat or sparse vegetation, calling from the edges of waterbodies, while K. kuvangensis was only heard calling from wellvegetated floodplains and source lakes. Comments: Schiøtz (1999) divided material of K. senegalensis into different forms, based on the dorsal markings. As pointed out by Poynton and Broadley (1987), there is considerable overlap in these color forms between and within populations. Due to the large distributional range of this species from Senegal to South Africa (Channing and Rödel 2019), spanning many different habitats and



Map 21. Distribution of Kassinula wittei in Angola.

biomes, cryptic species are expected, and this species needs a broad-scale phylogeographic study.

Kassinula wittei Laurent, 1940

De Witte's Clicking Frog (Figs. 24–25; Map 21)

Material (48 specimens): PEM A12468-5, PEM A12792-3, INBAC (no number x2), Cuanavale River source lake, -13.08537° 18.89098°, 1,360 m asl; PEM A12807–12, INBAC (no number x3), Cuito River source lake, -12.68727° 18.36067°, 1,423 m asl; PEM A12817– 8, Cuiva River source, -12.66856° 18.35307°, 1,433 m asl; PEM A12870-2, INBAC (no number x2), Quembo River source lake, -13.13624° 19.04591°, 1,366 m asl; PEM A14271-3, INBAC: WC-6743, Lungwebungu River camp, first oxbow on right side, -12.58117° 18.67106°, 1,294 m asl; PEM A14274-5, Cuanavale River source, -13.08537° 18.89098°, 1,357 m asl; PEM A14276–80, Quembo River right side tributary (Micongo River) past village, -13.51877° 19.28487°, 1,248 m asl; PEM A14281-4, INBAC: WC- 6958-60, Luio River camp floodplains, -13.20191° 20.22144°, 1,181 m asl; PEM A14270, PEM A14285, wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl. Additional material (4 specimens): P2-278, P2-279,



Fig. 24. Adult male *Kassinula wittei* from Cuanavale River source. *Photo by Werner Conradie*.



Fig. 25. Adult male *Kassinula* cf. *wittei* from wetland east of Quemba town. *Photo by Chad Keates*.

P2-280, P2-281, wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl. **Description:** Minute hyperoliid species. See Conradie et al. (2020b) for a detailed description of this material. The only female measured 14.7 mm (PEM A14284); adult males varied from 12.3-22.0 (14.2) mm (largest male: PEM A14270). Habitat and natural history notes: Found in flooded grassland and peat wetlands. Comments: The occurrence of this species in northeastern Angola was expected from a biogeographical point of view, but these are the first records of the species for the country. These new records extend the known range of this species from northwestern Zambia and southern DRC to central Angola by more than 400 km (see Conradie et al. 2020b). The taxonomic status of this genus has recently been validated phylogenetically and the species is considered to be closely related to Afrixalus, although its exact systematic placement remains unclear (see Conradie et al. 2020b; Nečas et al. 2022).

Two specimens (PEM A14270, PEM A14285) differ in the dorsal coloration pattern (vertebral band broken and no darker stipples in lighter bands versus continuous dark vertebral band and lighter bands, with fine dark stipples), maximum size (22 mm versus 16.7 mm), and potential differences in habitat preference from other K. wittei collected. These two specimens are similar in appearance to a specimen collected from Congolo River, Luando Strict Nature Reserve (FHK091) (see Conradie et al. 2020b). While Nečas et al. (2022) pointed out the relatively deep divergence between the specimen from Congolo River and the eastern Angolan and topotypic DRC samples, this difference was not considered in Conradie et al. (2020b). Preliminary unpublished genetic results (W. Conradie, unpub. data) show that the two specimens listed here agree genetically with the western Angolan sample (Congolo River) and may represent an undescribed cryptic species. These specimens occur syntopically with typical K. wittei east of Quemba, although collected from different habitats and different times of the year.



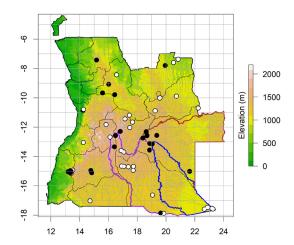
Fig. 26. Adult female *Phrynobatrachus mababiensis* from Cutatu River. *Photo by Werner Conradie*.

Phrynobatrachidae

Phrynobatrachus mababiensis FitzSimons, 1932 complex

Dwarf Puddle Frog (Fig. 26; Map 22)

Material (14 specimens, 1 tadpole lot): PEM A12429, series of pans south of Tempué, -13.55719° 18.85519°, 1,315 m asl; PEM A12608, Calua River source, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,445 m asl; PEM A12622, Cutata River, -12.56916° 16.49334°, 1,647 m asl; PEM A12662, Campsite 2 near old Cuvango Mission, -13.33451° 16.41280°, 1,542 m asl; PEM A12688, Cubango 2017 launch site, -12.61700° 16.22133°, 1,727 m asl; PEM A12777, Quembo River source, trap 4, -13.13586° 19.04709°, 1,373 m asl; PEM A12840-1, west of Cuito town on Aludungo rd, -12.28700° 16.81716°, 1,739 m asl; PEM A12889, Quembo River source lake, -13.13624° 19.04591°, 1,366 m asl; PEM A13739, Lungwebungu River, new campsite, -12.58445° 18.66538°, 1,308 m asl; PEM A14743, Quembo River bridge camp, trap 2, -13.52816° 19.28067°, 1,240 m asl; PEM A14779, Quembo River bridge camp, trap 1, -13.52801° 19.28147°, 1,236 m asl; PEM A14873, wetland south of Lake Hundo, -15.01099° 21.63608°, 1,100 m asl; PEM A14114 (tadpoles), river before Sombanana village, -12.30710° 18.62350°, 1,407 m asl; INBAC: WC-5221, Campsite 2 near old Cuvango Mission, -13.33451° 16.41280°, 1,542 m asl. Additional material (3 tadpole lots): SAIAB 209079 (14 tadpoles), road to Cuanavale River camp, -12.54990° 18.67444°, 1,333 m asl; SAIAB 209105 (10 tadpoles), swamp near Cuanavale River source lake camp, 1,386 m asl; SAIAB 209111 (9 tadpoles), small wooden bridge across wetland on road between Cuanavale River source camp and Munhango, -12.30714° 18.62333°, 1,399 m asl. **Description:** Small *Phrynobatrachus*; scattered small warts present on the back; up to three and a half phalanges of longest toe free of webbing. Dorsum light brown, with scattered darker brown markings; lower lip barred in black and white; ventrum varied from immaculate to mottled



Map 22. Distribution of *Phrynobatrachus mababiensis* complex in Angola.

with black. Males with black throats. Adult females (n = 3) varied from 12.8–18.0 (16.2) mm (largest female: PEM A14743); adult males (n = 3) varied from 12.6–17.2 (14.7) mm (largest male: PEM A14779). **Habitat and natural history notes:** Found on edges of rivers and source lakes among marginal vegetation. **Comments:** Numerous cryptic species have been documented within *P. mababiensis* as currently recognized (Zimkus and Schick 2010; Zimkus et al. 2010), and the new material recorded here may represent more than one species (N. Baptista et al., unpub. data). Until further phylogenetic studies are conducted, this material is all included in the *P. mababiensis* complex.

Phrynobatrachus natalensis (Smith, 1849) Snoring Puddle Frog (Fig. 27; Map 23)

Material (20 specimens): PEM A12637–8, Cuanavale River, -13.37406° 18.99269°, 1,297 m asl; PEM A12711, Lungwebungu River camp bridge crossing, -12.58347° 18.66598°, 1,304 m asl; PEM A12890-3, INBAC: WC-4599, INBAC (no number), Quembo River source lake, -13.13624° 19.04591°, 1,366 m asl; PEM A13738, Comba River, -12.62442° 18.65159°, 1,299 m asl; PEM A13745-8, Lungwebungu River old campsite, -12.58319° 18.66573°, 1,284 m asl; PEM A14690, PEM A14705-6, INBAC: WC-6740, Lungwebungu River camp, -12.58439° 18.66748°, 1,297 m asl; PEM A14707, wetland west of Lungwebungu River camp, -12.55855° 18.63770°, 1,308 m asl; PEM A14810-1, Luio River camp floodplains, -13.19711° 20.22194°, 1,181 m asl. Additional material (1 specimen): SAIAB 209104 (1 specimen), swamp near Cuanavale River source lake camp, -13.10750° 18.86089°, 1,386 m asl. **Description:** Medium sized Phrynobatrachus; dorsum with scattered elevated tubercles; reduced webbing; heel spine present; small outer metatarsal tubercle; large inner metatarsal tubercle; ridge running along outer toe; small tarsal ridge; mid-tarsal tubercle present; well-developed elevated subarticular tubercle. Dorsum coloration varies from grey to brown and even green; ventrum white. Female throats



Fig. 27. Adult male *Phrynobatrachus natalensis* from Luio River. *Photo by Chad Keates*.

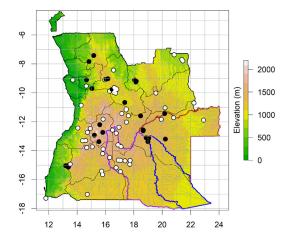
are speckled, while throats of males are uniformly grey to black. Adult females (n = 15) varied from 23.6–32.6 (28.1) mm (largest female: PEM A13745); adult males (n = 5) varied from 26.3–30.4 (28.2) mm (largest male: PEM A14705). **Habitat and natural history notes:** Found in flooded grasslands associated with miombo woodland. **Comments:** This species is widespread in Angola (Marques et al. 2018). Although there were no records for southeastern Angola prior to Conradie et al. (2016), they are widespread east of the Zambian border (Poynton and Broadley 1985b, 1991; Channing, 2001). This is another complex within *Phrynobatrachus* containing several cryptic species, and thus deserving of further investigation (Zimkus et al. 2010; Bittencourt-Silva 2019).

Pipidae

Xenopus petersii Bocage, 1895

Peters' Clawed Frog (Fig. 28; Map 24)

Material (40 specimens): PEM A11617-9, PEM A12576–84, INBAC (no number x 4), Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl; PEM A12430–3, pans south of Tempue, -13.55719° 18.85519°, 1,315 m asl; PEM A12519, river crossing before Samboano village, -12.30700° 18.62350°, 1,397 m asl; PEM A12613-5, Calua River source, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,446 m asl; PEM A12634-5, roadside ditch 10 km SW of Cuito town, -12.44815° 16.88118°, 1,742 m asl; PEM A12682, Camp 3, Malova Village, Mipanha River, -14.09140° 16.41476°, 1,553 m asl; PEM A12691-2, INBAC: WC-5175, Cubango River launch site, -12.61700° 16.22133°, 1,727 m asl; PEM A12694, Cubango River source site, -12.66256° 16.09324°, 1,771 m asl; PEM A12695, INBAC: WC-5173, New dam, Katchingo, -12.60587° 16.22003°, 1,373 m asl; PEM A12697, Chicala Choloanga roadside quarry, -12.63611° 16.04282°, 1,858 m asl; PEM A12779-80, Quembo River, trap 4, -13.13586° 19.04709°, 1,373 m asl;

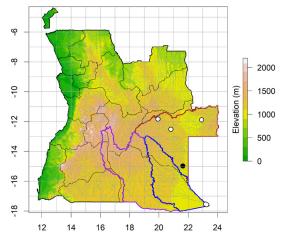


Map 23. Distribution of *Phrynobatrachus natalensis* in Angola.

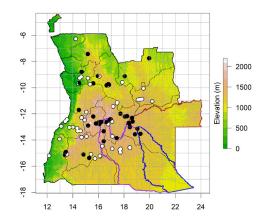


Fig. 28. Adult female *Xenopus petersii* from Cuito town. *Photo by Werner Conradie*.

PEM A12909, Quembo River source lake, -13.13624° 19.04591°, 1,411 m asl; PEM A13756, Lungwebungu River old campsite, -12.58319° 18.66573°, 1,284 m asl; PEM A13817, river crossing before Samboano village, -12.20672° 18.06236°, 1,387 m asl; PEM A14776, Quembo River right side tributary (Micongo River) past village, -13.51877° 19.28487°, 1,248 m asl. Additional material (9 specimens, 1 tadpole lot): SAIAB 204517 (1 specimen), Lungwebungu River Bridge, -12.58397° 18.66536°, 1,295 m asl; SAIAB 204468 (1 tadpole), main road bridge over upper Kwanza east of cuito, -11.98433° 17.72197°, 1,267 m asl; SAIAB 204500 (1 specimen), small wooden bridge across wetland on road between Cuanavale source camp and Munhango, -12.30714° 18.62333°, 1,399 m asl; SAIAB 204502 (6 specimens), pool in wetland on road edge west of Munhango, -12.17806° 18.24306°, 1,370 m asl; SAIAB 209086 (1 specimen), Cuvango mission rapids camp, -13.32782° 16.41106°, 1,538 m asl. **Description:** Medium to large sized pipid; dorsum smooth; eyes on top of head; three clawed toes, no claw on prehallux; extensive webbing. Dorsum varies from light to dark brown; posterior half of ventrum and thighs with orange pigmentation. Adult females (n = 24) varied from 34.2–



Map 25. Distribution of *Xenopus poweri* in Angola.



Map 24. Distribution of *Xenopus petersii* in Angola.

74.2 (52.4) mm (largest female: PEM A12682); adult males (n = 16) varied from 37.9–51.2 (45.5) mm (largest male: PEM A11619). **Habitat and natural history notes:** Aquatic species found in all major waterbodies surveyed. **Comments:** Furman et al. (2015) split *X. petersii* and *X. poweri*, restricting the former mostly to western Angola northward to Gabon. In Angola, this species seems to be absent from the south and east, where it is replaced by *X. muelleri* and/or *X. poweri*.

Xenopus poweri Hewitt, 1927 Powers' Clawed Frog (Map 25)

Material (13 specimens): PEM A14856-66, INBAC: WC-7040, INBAC: WC-7043, Lake Hundo, -14.97431° 21.62966°, 1,100 m asl. Description: Medium sized pipid; dorsum smooth; eyes on top of head; three clawed toes, no claw on prehallux; extensive webbing. Dorsum varies from light to dark brown, with scattered darker markings; ventrum grayish, with scattered darker blotches. Adult females (n = 6) varied from 55.6–65.9 (59.8) mm (largest female: PEM A14861); adult males (n = 6) varied from 43.1–51.2 (48.8) mm (largest male: PEM A14858). Habitat and natural history notes: After a heavy thunderstorm, numerous X. poweri were found moving over land away from the waterbodies. Comments: Only recorded from lower elevations of eastern Angola, associated with open and dry savanna. Only a limited number of records exist of this species from eastern Angola (Conradie et al. 2016; Marques et al. 2018).

Ptychadenidae

Ptychadena bunoderma (Boulenger, 1907) Rough Ridged Frog (Fig. 29; Map 26)

Material (2 specimens): PEM A12778, Quembo River source, trap 4, -13.13586° 19.04709°, 1,369 m asl; PEM A12476, Cuanavale River source lake, -13.08537° 18.89100°, 1,360 m asl. **Description:** Small stocky *Ptychadena*; dorsum warty, with no clear ridges as in other *Ptychadena* species; short stubby legs; very reduced



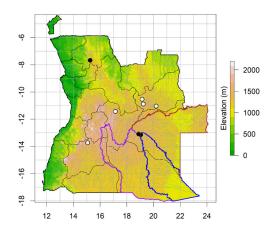
Fig. 29. Adult male *Ptychadena bunoderma* from Cuanavale River source lake. *Photo by Werner Conradie*.

webbing, four phalanges of the 4th toe free of webbing. Dorsum dark brown to olive, with scattered white to brown elevated tubercles; lower lip gray with white bars; back of thighs with scattered light spots. The only adult male measured 25.6 mm (PEM A12778). Habitat and natural history notes: Specimens were found in trap arrays (see Conradie et al. 2021) set up next to flooded areas of source lakes. They were never heard calling, and either have a very cryptic call or were not vocal during the survey periods. Comments: In Angola, this species is only known from the east, based on historical records (Marques et al. 2018). No new collections were made until Ernst et al. (2020) recorded a series of specimens from northwestern Angola. Elsewhere, it is known from northwestern Zambia (Channing 2001; Channing and Rödel 2019). Our new material represents a new record for southeastern Angola and the Okavango River basin.

Ptychadena grandisonae Laurent, 1954 Many-ridged Grass Frog (Fig. 30; Map 27) Material (3 specimens): PEM A12696, INBAC: WC-5185, Chicala Choloanga roadside quarry, -12.63611° 16.04282°, 1,858 m asl; PEM A12689, Cubango River launch site, -12.61700° 16.22133°, 1,727 m asl.



Fig. 30. Adult male *Ptychadena grandisonae* from upper Cubango River. *Photo by Werner Conradie*.

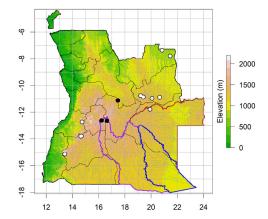


Map 26. Distribution of Ptychadena bunoderma in Angola.

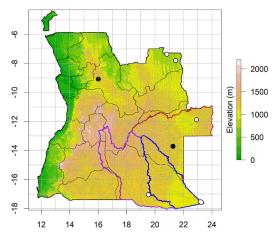
Description: Medium sized *Ptychadena*; narrow body; ridges present on thigh; two and a half phalanges of the longest toe free of webbing. Dorsum light brown, with darker brown blotches; back of thighs with pale stripes; yellow infusion in groin. Only adult male measured 36.2 mm (PEM A12689). **Habitat and natural history notes:** This species was only encountered along the Cubango River in flooded grassland. **Comments:** The identification was based on the key provided by Poynton and Broadley (1985b) and needs genetic verification.

Ptychadena upembae (Schmidt and Inger, 1959) Upemba Ridged Frog (Map 28)

Material (1 specimen): PEM A14829, camp at side tributary (Luandai River) of the Luanguinga River, -13.70885° 21.26234°, 1,116 m asl. **Description:** Medium sized *Ptychadena*; elongated body; longitudinal dorsal ridges present; long toes; reduced webbing, with up to three phalanges of longest toe free of webbing. Dorsum brown to beige with black and brown spots; black facial mask, from snout through eye to forearm; broad light vertebral band present; thin light line on dorsal tibia; back of thighs with light and dark bands; ventrum light yellow. Only adult male measured 37.7



Map 27. Distribution of Ptychadena grandisonae in Angola.



Map 28. Distribution of Ptychadena upembae in Angola.

mm (PEM A14829). **Habitat and natural history notes:** Found in grassland alongside a large river during the day. **Comments:** Identification was based on the key provided by Poynton and Broadley (1985b). Only a few records of this species exist for central and eastern Angola (Marques et al. 2018). Re-examination of material recorded by Conradie et al. (2016) of *Ptychadena guibei* also conform to this species.

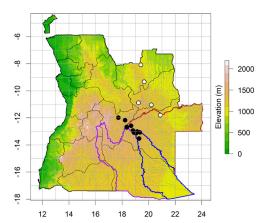
Ptychadena keilingi (Monard, 1937) Keiling's Ridged Frog (Fig. 31; Map 29)

Material (38 specimens): PEM A12428, Cuiva River bridge on EN250, -11.98345° 17.72367°, 1,267m asl; PEM A12477–8, INBAC (no number x2), Cuanavale River source lake, -13.08537° 18.89098°, 1,360 m asl; PEM A12491, Dala River, near Samanunga village, -12.93170° 18.81458°, 1,363 m asl; PEM A12559–61, Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl; PEM A12646, outlet of Cuito River source lake, -12.70453° 18.35445°, 1,429 m asl; PEM A12752–9, INBAC: WC-4797, (no number x2), Cuando River source, -13.00346° 19.12751°, 1,353 m asl; PEM A12782, Quembo River, trap 1, -13.13592° 19.04417°, 1,369 m asl; PEM A12822–4, Cuiva River source, -12.66856° 18.35307°, 1,433 m



Fig. 31. Adult male *Ptychadena keilingi* from Cuito River source. *Photo by Werner Conradie*.

asl; PEM A12894-6, INBAC: WC-4691, INBAC: (no number x1), Quembo River source lake, -13.13624° 19.04591°, 1,366 m asl; PEM A13818-19, en route to Cuemba Village, -11.96587° 17.76176°, 1,302 m asl; PEM A14694, Lungwebungu River camp, right bank past first oxbow, -12.57956° 18.67761°, 1,295 m asl; PEM A14736, Quembo River, walk back from small waterfall, -13.52988° 19.28340°, 1,242 m asl; PEM A14780, Quembo River bridge camp, trap 1, -13.52801° 19.28147°, 1,236 m asl; PEM A14781, INBAC: WC-6962, Quembo River right side tributary (Micongo River) past village, -13.51877° 19.28487°, 1,248 m asl; PEM A14894, wetland near old quarry east of Quemba, -12.16960° 18.22965°, 1,353 m asl. Additional specimens (2 specimens): SAIAB 204561 (2 specimens), Quembo River source lake, -13.13611° 19.04500°, 1,367 m asl. **Description:** Medium sized Ptychadena; elongated body; longitudinal dorsal ridges present; rostrum protruding well beyond lower jaw and forming a very pointed and elongated keratinized protrusion; long toes; reduced webbing, with up to four phalanges of longest toe free of webbing. Dorsum colorful; red infusions on the flanks; black facial mask, from snout through eye to forearm; broad light vertebral band present; thin light line on dorsal tibia; top of thighs with light and dark bands; ventrum immaculate, with black spots on chest in some specimens; black spot in front of arm that connects with lower jaw; lower jaw with spots; back of thighs with irregular longitudinal black and yellow stripes. Adult females (n = 19) varied from 24.6-39.9 (34.8) mm (largest female: PEM A12755); adult males (n = 14) varied from 25.3-31.5 (27.9) mm (largest male: PEM A14894). Habitat and natural history notes: Found in the flooded margins of rivers and lakes. Comments: Originally described from Dala, in north-eastern Angola (Laurent 1964). It is only known from northeastern Angola (Laurent 1964; Marques et al. 2018), western Zambia (Channing 2001), and southwestern DRC (Channing and Rödel 2019). This is the southernmost record for this species, and a new species record for southeastern Angola and the Okavango River basin.



Map 29. Distribution of Ptychadena keilingi in Angola.



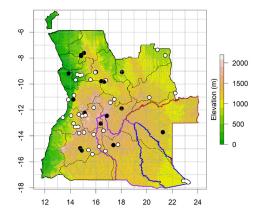
Fig. 32. Adult male *Ptychadena oxyrhynchus* from Cuito town. *Photo by Werner Conradie.*

Ptychadena oxyrhynchus (Smith, 1849) Sharp-nosed Ridged Frog (Fig. 32; Map 30)

Material (6 specimens): PEM A12628, roadside ditch 10 km SW of Cuito town, -12.44815° 16.88118°, 1,742 m asl; PEM A12667, Campsite 1 below Cubango River rapids, west of Fundo village, -13.04483° 16.37520°, 1,585 m asl; PEM A12835-6, 31 km W of Menongue, Cueli River, -14.70511° 17.38014°, 1,392 m asl; PEM A14830, camp at side tributary (Luandai River) of the Luanguinga River, -13.70885° 21.26234°, 1,116 m asl. Additional material (1 specimen): SAIAB 204559 (1 specimen), half-way house road just outside Munhango village, pools in road. Description: Large and robust Ptychadena; sharp pointed snout; clear longitudinal dorsal ridges; extensive webbing, with one phalange on outer toe (5th) free of webbing; large pointed subarticular tubercles on toes; small inner metatarsal tubercle; outer metatarsal tubercle absent; enlarged palmar tubercles; ventrum smooth. Dorsum light brown to gray, with scatted dark spots (PEM A12628 with unusual orange dorsum and yellow infusion in the outer thigh region); pale triangle on snout; lower jaw barred; back of thigh with irregular white blotches or spots that are sometimes fused; ventrum immaculate. Adult males (n = 5) varied from 44.1–51.9 (47.7) mm (largest male: PEM A12835).



Fig. 33. Adult male *Ptychadena porosissima* from Lungwebungu River crossing. *Photo by Werner Conradie*.

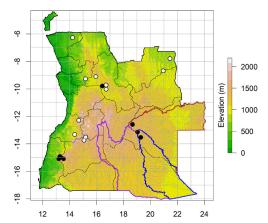


Map 30. Distribution of *Ptychadena oxyrhynchus* in Angola.

Habitat and natural history notes: Only found in open dry savanna. Comments: This species has a wide distribution, from Senegal to South Africa (Channing and Rödel 2019). Found across most of Angola (Marques et al. 2018), associated with a wide variety of habitats. Smith (1849) gave the type locality as 'Kaffirland and the region of Port Natal,' which is situated along the east coast of South Africa. Material from Angola differs molecularly from the topotypical material and warrants further phylogenetic investigation (Hübler 2015).

Ptychadena porosissima (Steindachner, 1867) Striped Ridged Frog (Fig. 33; Map 31)

Material (17 specimens): PEM A12712-6, Lungwebungu River camp bridge crossing, -12.58347° 18.66600°, 1,304 m asl; PEM A12901–2, PEM A12906, Quembo River source lake, -13.13624° 19.04591°, 1,366 m asl; PEM A13749-51, Lungwebungu River Campsite, -12.58319° 18.66573°, 1,284 m asl; PEM A13782-3, Lungwebungu River Trap 1, -12.58013° 18.66740°, 1,298 m asl; PEM A14708-9, INBAC: WC-6750, Lungwebungu River camp, -12.58439° 18.66748°, 1,297 m asl; PEM A14782, Quembo River bridge camp, -13.52746° 19.28060°, 1,241 m asl. **Description:** Medium sized *Ptychadena*; sharp snout; large tympanum,

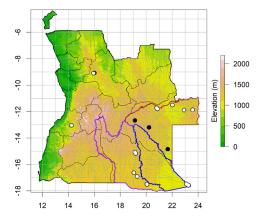


Map 31. Distribution of *Ptychadena porosissima* in Angola.

almost equal to eye diameter; three phalanges of longest toe free of webbing; webbing reaches first phalange of the outer toe; large inner metatarsal tubercle; outer metatarsal tubercle inconspicuous or absent; distinct inner tarsal ridge; subarticular tubercles single and prominent. Dorsum brown, with scattered black spots along ridges; snout paler than body; vertebral stripe broad; dorsolateral ridge pale, elevated, and prominent; white anterior bars on lower jaw; dark facial mask from snout to front of arms; dorsal pale stripe on tibia; back of thighs with light spots forming longitudinal lines; ventrum immaculate, except for scattered faint black blotches between arms. In males, ventrum covered in small brown asperites; thumbs and nuptial pads swollen. Adult females (n = 7)varied from 34.8-46.2 (41.1) mm (largest female: PEM A12716); adult males (n = 7) varied from 34.9-40.0(37.4) mm (largest male: PEM A14782). Habitat and natural history notes: Found in flooded grasslands or river margins. Comments: Found in sympatry with the closely related P. uzungwensis, but at lower abundance. The two species can be distinguished based on ventral asperites (present in *P. porosissima* versus absent in *P.* uzungwensis), dorsal coloration (striped in P. porosissima versus mostly spotted in *P. uzungwensis*), and dorsal tibia line (always present in *P. porosissima* versus mostly absent in *P. uzungwensis*).

Ptychadena subpunctata (Bocage, 1866) Speckled-bellied Ridged Frog (Map 32)

Material (2 specimens): PEM A14874, Ninda River, -14.84018° 21.66556°, 1,081 m asl; PEM A14812, Luio River camp floodplains, -13.19711° 20.22194°, 1,181 m asl. **Description:** Large robust *Ptychadena*; snout pointed; two phalanges of longest toe free of webbing; large tympanum; small elevated inner metatarsal tubercle; outer metatarsal tubercle absent. Dorsum brown, with large rounded dark brown spots; dorsal ridges pale; narrow vertebral stripe present; lower jaw barred; white spot below eye; back of thighs with two continuous black stripes below vent from knee to knee; white stripe on dorsal tibia; ventrum finely spotted. In males, the forearms and thumbs are swollen and nuptial pads are black. Adult



Map 32. Distribution of Ptychadena subpunctata in Angola.

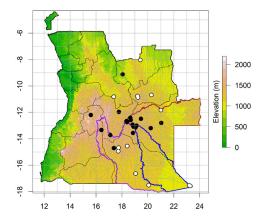
males (n = 2) varied from 44.6–61.0 (53.1) mm (largest male: PEM A14874). **Habitat and natural history notes:** Only found at Zambezi River tributaries to the east and clearly absent from the source lake area. **Comments:** Although originally described from Angola, only a few records are known from the country (Marques et al. 2018).

Ptychadena taenioscelis Laurent, 1954 Small Ridged Frog (Fig. 34; Map 33)

Material (39 specimens, 2 tadpole lots): PEM A12479– 81, Cuanavale River source lake, -13.08537° 18.89098°, 1,360 m asl; PEM A12492, Dala River, near Samanunga village, -12.93169° 18.81458°, 1,371 m asl; PEM A12523, Cuiva River source, -12.66825° 18.35282°, 1,407 m asl; PEM A11609, PEM A12562-69, INBAC (no number x 4), Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl; PEM A12663, Campsite 2 near old Cuvango Mission, -13.33451° 16.41280°, 1,534 m asl; PEM A12760, INBAC: WC-4750, INBAC (no number), Cuando River source, -13.00346° 19.12751°, 1,353 m asl; PEM A12767-8, Cuando River source trap 1, -13.00393° 19.12808°, 1,351 m asl; PEM A12783-4, INBAC: WC-4600, Quembo River trap 1, -13.13592° 19.04417°, 1,369 m asl; PEM A12837, 31 km W of Menongue, Cueli River, -14.70511° 17.38014°, 1,392 m asl; PEM A12897-8, INBAC (no number), Quembo



Fig. 34. Adult female *Ptychadena taenioscelis* from Cuito River source. *Photo by Werner Conradie.*



Map 33. Distribution of Ptychadena taenioscelis in Angola.

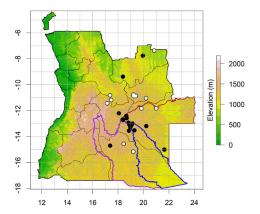
River source lake, -13.13624° 19.04591°, 1,367 m asl; PEM A13813, Lake Tchanssengwe, -12.41403° 18.64418°, 1,393 m asl; PEM A13820, en route to Cuemba Village, -11.96587° 17.76176°, 1,302 m asl; PEM A14092 (tadpoles), series of pans south of Tempué, -13.55719° 18.85519°, 1,315 m asl; PEM A14122 (tadpoles), Calua River source, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,446 m asl; PEM A14691, Lungwebungu River camp, first oxbow on right side, -12.58117° 18.67106°, 1,294 m asl; PEM A14813– 6, INBAC: WC-7009, Luio River camp floodplains, -13.19711° 20.22194°, 1,181 m asl. Additional material (2 specimens, 1 tadpole lot): SAIAB 204572 (2 specimens), Samaununga village, -12.93228° 18.81672°, 1,364 m asl; SAIAB 209102 (12 tadpoles), Calua lagoon, -12.73599° 18.39394°, 1,448 m asl. **Description:** Small Ptychadena; subarticular tubercles weakly developed; thin inner metatarsal tubercle; outer metatarsal tubercle absent or much reduced; three phalanges of longest toe free of webbing. Dorsum dark, with scattered black spots; broad vertebral band often present; white line above lip, from tip of snout to insertion of arm; bright green patch between eye and lip; dorsolateral ridge white; back of thighs with one continuous black stripe below vent from knee to knee; soles of feet, toes, forearms, and legs black; light line present on dorsal tibia; throat with scattered black spots; ventrum immaculate. Adult females (n = 21) varied from 21.5–33.2 (27.4) mm (largest female: PEM A12523); adult males (n = 9) varied from 23.1-28.2 (26.5) mm (largest male: PEM A13813). Habitat and natural history notes: Found along river margins and floodplains. Comments: The close morphological relationship between P. pumilio and P. taenioscelis has been discussed in the past, and no clear concensus has yet been reached (Perret 1979; Poynton and Broadley 1987), although the former is mostly restricted to West Africa and the latter to Southern Africa (Channing and Rödel 2019). Bittencourt-Silva (2019) alludes to the close genetic relationship between P. pumilio and this species. Additional investigation is needed to validate its taxonomic status.



Fig. 35. Adult male *Ptychadena uzungwensis* from Culua River source. *Photo by Werner Conradie*.

Ptychadena uzungwensis (Loveridge, 1932) Udzungwa Ridged Frog (Fig. 35; Map 34)

Material (56 specimens, 7 tadpole lots): PEM A12482-3, Cuanavale River source lake, -13.08537° 18.89098°, 1,360 m asl; PEM A12493, river crossing before Samanunga village, -12.93169° 18.81458°, 1,363 m asl; PEM A12570-2, Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl; PEM A12609–11, PEM A14117 (tadpoles), Calua River source, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,445 m asl; PEM A12641, Cuanavale River, -13.29236° 18.96283°, 1,314 m asl; PEM A12717-8, Lungwebungu River camp bridge crossing, -12.58347° 18.66598°, 1,304 m asl; PEM A12761-3, Cuando River Source, -13.00346° 19.12751°, 1,353 m asl; PEM A12769, Cuando River source, trap 1, -13.00393° 19.12808°, 1,351 m asl; PEM A12813-4, Cuito River source lake, -12.68727° 18.36067°, 1,424 m asl; PEM A12826, Quembo River, trap 3, -13.13073° 19.03725°, 1,453 m asl; PEM A12831–3, Culua River source, -12.73723° 18.39340°, 1,450 m asl; PEM A12838, 31 km W of Menongue, Cueli River, -14.70511° 17.38014°, 1,392 m asl; PEM A12899-900, PEM A12903-5, Quembo River source lake, -13.13624° 19.04591°, 1,366 m asl; PEM A13752-5, Lungwebungu River campsite, -12.58319° 18.66573°, 1,284 m asl; PEM A13814, Lake Tchanssengwe, -12.41403° 18.64418°, 1,393 m asl; PEM A13816, John's crossing before village, -12.20672° 18.06236°, 1,387 m asl; PEM A14083 (tadpoles), Longa rice paddies, Longa River, -14.56356° 18.44367°, 1,277 m asl; PEM A14084 (tadpoles), Cuanavale River source, -13.09033° 18.89396°, 1,359 m asl; PEM A14087 (tadpoles), 4 km upstream from Cuanavale River source, -13.05084° 18.89726°, 1,380 m asl; PEM A14093, (tadpoles) series of pans south of Tempué village, -13.55719° 18.85519°, 1,315 m asl; PEM A14095 (tadpoles), Dala River, near Samanunga village, -12.93169° 18.81458°, 1,363 m asl; PEM A14100 (tadpoles), 4 km downstream from Cuanavale River source camp, -13.11585° 18.90246°, 1,354 m asl; PEM A14692, Lungwebungu River camp, machamba (cultivated areas) on left side of river,



Map 34. Distribution of Ptychadena uzungwensis in Angola.

-12.58276° 18.66556°, 1,295 m asl; PEM A14695, Lungwebungu River camp, right bank past first oxbow, -12.58077° 18.67585°, 1,300 m asl; PEM A14710–11, Lungwebungu River camp, -12.58439° 18.66748°, 1,297 m asl; PEM A14719, PEM A14738, Quembo River bridge camp, -13.52746° 19.28060°, 1,241 m asl; PEM A14737, Quembo River bridge camp, trap 1, -13.52801° 19.28147°, 1,236 m asl; PEM A14760, Quembo River bridge camp, trap 2, -13.52816° 19.28067°, 1,240 m asl; PEM A14817, Luio River camp floodplains, -13.19711° 20.22194°, 1,181 m asl; PEM A14875, wetland south of Lake Hundo, -15.01099° 21.63608°, 1,100 m asl. Additional specimens (2 specimens): SAIAB 204568 (2 specimens), Quembo River source lake, -13.13611° 19.04500°, 1,367 m asl. **Description:** Medium sized *Ptychadena*; tympanum large, three-quarters the size of the eye; small inconspicuous metatarsal tubercle; large outer metatarsal tubercle; three phalanges of longest toe free of webbing; numerous irregular-sized palmar tubercles present; prominent longitudinal ridges; outer dorsolateral ridge broken anteriorly; no ventral asperites in males. Dorsum with scattered blotches, almost forming transverse bands; lower lip barred; vertebral stripe present or absent; snout distinctly marked, without pale triangle; back of thighs with large pale blotches, almost forming longitudinal stripes; light line on dorsal tibia often absent (present in PEM A12769, 12762, and 12900). Males with swollen and dark thumbs. Adult females (n = 25) varied from 27.5-43.7 (39.0) mm (largest females: PEM A12905, PEM A12831); adult males (n = 22) varied from 30.1-39.5 (35.0) mm (largest male: PEM A12611). Habitat and natural history notes: Commonly found in flooded grasslands adjacent to main rivers and source lakes. Comments: See P. porosissima account for information on sympatry between these two species.

Pyxicephalidae

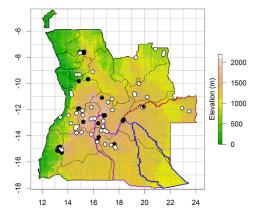
Amietia angolensis (Bocage, 1866) Angola River Frog (Fig. 36; Map 35)

Material (16 specimens): PEM A12627, roadside ditch 10 km SW of Cuito town, -12.44815° 16.88118°,



Fig. 36. Adult male *Amietia angolensis* from west of Menongue. *Photo by Werner Conradie.*

1,742 m asl; PEM A12645, confluence of Cuito and Calua rivers, -12.74878° 18.35433°, 1,413 m asl; PEM A12653-7, INBAC: WC-5245, Kuvango Hydro Plant Site, -14.38775° 16.29365°, 1,441 m asl; PEM A12669, Campsite 1 below rapids, west of Fundo village, -13.04359° 16.37439°, 1,571 m asl; PEM A12671-3, INBAC: WC-5228, Camp 3, Malova Village, Mipanha River, -14.09140° 16.41476°, 1,553 m asl; PEM A12834, 31 km W of Menongue, Cueli River, -14.70511° 17.38014°, 1,392 m asl; PEM A13785, Aquaculture farm outside Cuito, -12.43972° 16.89833°, 1,689 m asl; PEM A13786, Dam/Hydroplant on Rio Cuquema, -12.42556° 16.81856°, 1,640 m asl; PEM A14678, Villa Menongue, -14.63015° 17.63465°, 1373 m asl; bridge between Huambo and Cuito, -12.47056° 16.82389°, 1,643 m asl. Additional material (2 specimens): SAIAB 204011 (2 specimens), Cuchi River below bridge, -14.70272° 17.37864°, 1,393 m asl. **Description:** Large species; large tympanum, with an elevated ridge running from just behind the eye to arm; elevated paravertebral ridges continuous from behind eyes to groin, while the other ridges are broken (except in PEM A12834, where the dorsum is smooth); two and a half phalanges of longest toe free of webbing; small but conspicuous inner metatarsal tubercle; no outer metatarsal tubercle; well-developed subarticular tubercles; protruding eyes that are contained in outline of jaw viewed from below. Dorsum brown to dark green with scattered darker blotches; gular region dark with irregular white blotches that sometimes fuse to form lines; light vertebral stripe often present; dorsal tibia with dark crossbands; ventrum immaculate, except in two specimens (PEM A12654 and A12657) where the throat mottling extends onto the groin. In breeding males, the dorsum is yellowish, spiny with black-tipped asperites, and the nuptial pads on the thumbs are swollen. Adult males (n = 13) varied from 51.1-71.9 (63.9) mm (largest male: PEM A12671). Habitat and natural history notes: All material was found associated with the western tributaries of the Cubango River, where the substrate is rocky and the water is fast flowing. A single subadult specimen was found at the confluence of



Map 35. Distribution of Amietia angolensis in Angola.



Fig. 37. Adult male *Tomopterna tuberculosa* from west of Cuito town. *Photo by Werner Conradie*.

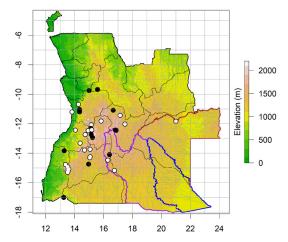
the Calua and Cuito rivers. This species is absent from the rivers and floodplains of the main Okavango River basin, possibly due to the sandier substrate. **Comments:** Recent phylogenetic revisions of the genus led to the identification and description of numerous cryptic species (Channing and Baptista 2013; Larson et al. 2016; Channing et al. 2016). In the process, *A. angolensis*, which was once considered to have a wide distribution across most of southern African, was restricted to Angola and is now regarded as a country endemic (Channing and Baptista 2013; Channing et al. 2016).

Tomopterna tuberculosa (Boulenger, 1882) Rough Sand Frog (Fig. 37; Map 36)

Material (5 specimens): PEM A12632–3, roadside ditch 10 km SW of Cuito, -12.44815° 16.88118°, 1,743 m asl; PEM A12681, INBAC: WC-5235, Camp 3, Malova Village, Mipanha River, -14.09140° 16.41476°, 1,553 m asl; PEM A13792–3, Dam/Hydroplant on Rio Cuquema, -12.42556° 16.81856°, 1,640 m asl. **Description:** Medium sized frog; short snout; tympanum clearly visible; elevated ridge from behind eye to arm; reduced webbing; inner metatarsal tubercle large; subarticular



Fig. 38. Adult male *Amnirana adiscifera* **stat. nov.** from Cuando River source. *Photo by James Harvey*.



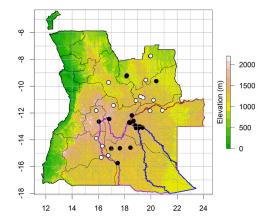
Map 36. Distribution of *Tomopterna tuberculosa* in Angola.

tubercles single. Dorsum brown with near-symmetrical dark brown markings with thin white border; dark brown interorbital bar; no light vertebral line. Adult females (n = 2) measured 45.4–46.3 (45.8) mm (largest female: PEM A12681); adult males (n = 4) varied from 31.9–36.5 (32.3) mm (largest male: PEM A12633). **Habitat and natural history notes:** This species was only found within the western side of the study area, associated with open and rocky habitats. **Comments:** This species occurs mostly in central and western Angola, with isolated records in the east (Marques et al. 2018). Elsewhere, it is known from northern Namibia and western Zambia to northern Tanzania and south to Zimbabwe (Channing and Rödel 2019).

Ranidae

Amnirana adiscifera (Schmidt and Inger, 1959) **stat. nov.** Green White-lipped Frog (Fig. 38; Map 37)

Material (18 specimens, 5 tadpole lots): PEM A11599, Cuito River source lake, -12.68935° 18.36012°, 1,431 m asl; PEM A12447, Cuanavale River source lake, -13.08537° 18.89098°, 1,360 m asl; PEM A12726, Cuando River source, -13.00346° 19.12751°, 1,353 m



Map 37. Distribution of *Amnirana adiscifera* **stat. nov.** in Angola.

asl; PEM A12727-8, Cuando River source, -13.00346° 19.12751°, 1,353 m asl; PEM A12764-6, Cuando River source, trap 1, -13.00393° 19.12808°, 1,351 m asl; PEM A12791, Cuanavale River source lake camp side, -13.09442° 18.89370°, 1,368 m asl; PEM A12798–9, Cuanavale River source lake opposite side, -13.08934° 18.89485°, 1,359 m asl; PEM A12842, west of Cuito town on Aludungo road, -14.64833° 16.97444°, 1,380 m asl; PEM A13736 (tadpoles), Comba River, -12.62442° 18.65159°, 1,299 m asl; PEM A13764, Lungwebungu River old oxbows, -12.58129° 18.67162°, 1,304 m asl; PEM A14082 (tadpoles), Luissinga River, -14.58899° 18.44367°, 1,311 m asl; PEM A14091 (tadpoles), Cuanavale River source, -13.09033° 18.89396°, 1,359 m asl; PEMA14099 (tadpoles), PEMA12485-7, Dala River, near Samanga village, -12.93169° 18.81458°, 1,363 m asl; PEM A14121 (tadpoles), Culua River source, 6 km SE of Cuito River source, -12.73675° 18.39310°, 1,446 m asl; PEM A14679, Menongue, -14.63015° 17.63465°, 1,373 m asl; PEM A14716, Cuanavale River source lake, -13.09052° 18.89394°, 1,357 m asl. Additional material (14 specimens, 4 tadpole lots): SAIAB 209135 (5 specimens), Kalilongue Dam inflow, -12.44722° 16.82428°, 1,429 m asl; SAIAB 209081 (1 specimen), swamp near Cuanavale River source, -13.10750° 18.86089°, 1,386 m asl; SAIAB 209080 (tadpoles), Cuito River source outlet, -12.70455° 18.35203°, 1,430 m asl; SAIAB 209088 (tadpoles), Calua River lagoon, -12.73599° 18.39394°, 1,448 m asl; SAIAB 209140 (tadpoles), Cuanavale River lake outlet, -13.09414° 18.89612°, 1,357 m asl; SAIAB 204541 (tadpoles), Cuanavale River source lake below fish fence, -13.09364° 18.89597°, 1,357 m asl; SAIAB 204567 (1 specimen), Quembo River source lake, -13.13611° 19.04500°, 1,363 m asl; SAIAB 204520 (2 specimens), SAIAB 204531 (1 specimen), SAIAB 204534 (1 specimen), Cuanavale River source lake, -13.08997° 18.89389°, 1,358 m asl; SAIAB 204484 (1 specimen), stream outflow about 2.6 km downstream of Cuando River source lake, -13.00317° 19.15153°, 1,333 m asl; SAIAB 204496 (2 specimens), river at Munhango lagoon, -12.17281° 18.54897°, 1,376 m asl. **Description:** Large ranid; large tympanum, nearly equal in size to eye; elevated upper lip ridge from snout tip to above arm; pair of dorsolateral ridges from eye to urostyle; some specimens have a small flap or ridge above the vent; smooth elevated subarticular tubercles on feet; small indistinct outer metatarsal tubercle, inner metatarsal tubercle present; pedal webbing formula: I (1), II i/e (1-2), III i/e (1-3), IV (2-3), V (1); no dilated toe tips or terminal discs, no horizontal grooves present on toe tips; no external vocal sacs. All the adults collected were green and not the typical golden-brown coloration as illustrated in Du Preez and Carruthers (2009). Metamorphs retain dorsal and ventral spots, which fade during growth. Tadpoles are orange with black scattered dots. Males with a small nuptial pad on the thumb and enlarged glands on the upper arm. Adult

females (n = 7) varied from 57.0–66.5 (61.6) mm (largest female: PEM A14716); adult males (n = 6) varied from 46.9–62.4 (55.0) mm (largest male: PEM A12799). Habitat and natural history notes: Males called in late afternoons and early evenings, from vegetation on the edge of open deep waters. Comments: Currently, five species of Amnirana have been recorded from Angola (Marques et al. 2018; Baptista et al. 2019): A. albolabris, A. darlingi, A. lemairei, A. lepus, and A. parkeriana. All except A. darlingi are forest-associated species, with toes that are dilated or have discs with horizontal grooves. The specimens found in our study do not exhibit dilated toes or terminal discs. Five specimens from Chitau that were initially referred to as Rana albolabris (see Schmidt 1936), were later described as Rana albolabris adiscifera by Schmidt and Inger (1959). Those authors only compared it to R. albolabris and R. a. lemairei, and differentiated it based on the condition of the toes (no dilated tips or discs), webbing (reduced versus extensive) and foot length (long versus short), respectively. Later, without much explanation, Laurent (1964) synonymised it with Rana darlingi [=Amnirana darlingi], and this was followed by Poynton (1964) and Perret (1977). Jongsma et al. (2018) showed that eastern (Malawi) and western (Angolan) A. darlingi material differ significantly enough on a molecular level to warrant taxonomic re-evaluation. However, no taxonomic action has been undertaken pending more evidence. The type locality of A. darlingi is 'Mazöe and between Umtali [Mutare] and Marandellas [= Marondera], Mashonaland, Zimbabwe' and represents the eastern material of Jongsma et al. (2018). The new series of specimens is in full morphological agreement with the description of R. a. adiscifera. However, no coloration details were provided in the original description or in Schmidt (1933). The newly collected material agrees in preserved coloration and morphology to photos of the holotype (https://collections-zoology. fieldmuseum.org/catalogue/1848393). The green Angolan form of A. darlingi is also in agreement with the green 'undescribed Hillwood frog' referred to by Channing (2001) and Channing and Rödel (2019). Recently, Ceríaco et al. (2016, 2018) also documented this green form of A. darlingi from central Angola. Based on the color differences, together with the typical form (green versus brown) and the genetic results by Jongsma et al. (2018), we here formally assign the green western material to Schmidt and Inger's (1959) adiscifera and elevate it to full species, Amnirana adiscifera stat. nov. This species is widely distributed in central Angola and northwestern Zambia (see Channing 2001; Channing et al. 2013; Marques et al. 2018; Channing and Rödel 2019). Similar distribution patterns have been observed in Kassinula wittei, Kassina kuvangensis, as well as the snake Limnophis bicolor (Conradie et al. 2020a,b; this study). Amnirana can be divided into two morphotypes: those with short feet, dilated toes, or terminal discs and extensive webbing (albolabris, amnicola, asperrima, fonensis, lemairei, lepus, occidentalis, and parkeriana), and those with long feet, reduced webbing, and no dilated toes or discs (adiscifera, darlingi, and galamensis). The former group is restricted to forests, while the latter prefers flooded grasslands in savanna (Poynton 1964). However, this pattern is not mirrored in the phylogenetic analysis, and indicates that adaptation from savanna to forest has occurred more than once (Jongsma et al. 2018).

Discussion

The material collected during this study contributes substantially to the knowledge of Angolan amphibians. Our findings have increased the number of documented amphibians for Angola by at least five species, three of which are potentially new (i.e., Hyperolius aff. bocagei, Kassinula cf. wittei, and Leptopelis sp.). A large collection of the green Amnirana 'darlingi' allowed us to reassess the taxonomic status of this material and led to both the reinstatement of Schmidt and Inger's (1959) adiscifera and its elevation to full species as Amnirana adiscifera stat. nov. The rain frogs (Breviceps sp.) collected represent the first modern (post civil unrest, ~2002) material for Angola, and allowed us to explore their taxonomic status, which led to the description of a new endemic species, Breviceps ombelanonga (see Nielsen et al. 2020). Furthermore, the *Kassinula wittei* specimens represent the first country records, a range extension of over 500 km, and further allowed us to revisit the taxonomic relationships of the group relative to other hyperoliids (Conradie et al. 2020b). Conradie et al. (2020b) and Nielsen et al. (2020) highlighted the relevance of these new collections on the national and continental levels, as well as the necessity for further studies to document the diversity and distribution of Angolan biodiversity.

Some of the species recorded here at the headwaters of the Okavango (e.g., Amnirana adiscifera stat. nov., Kassinula wittei, and Kassina kuvangensis) also occur in northwestern Zambia and eastern DRC (Poynton and Broadley 1985a,b, 1987, 1988; Channing 2001). Cei (1977) suggested that the amphibian fauna located south of the main Congo rivers to the Cubango rivers should have close affinities, given the lack of natural barriers. The limited genetic differences between Kassinula wittei from Angola and DRC (Nečas et al. 2022) provided support for this hypothesis, and this may also be reflected in other taxa.

On a more regional level, we increased the number of amphibian species recorded from the Cuito, Cuanavale, and Cuando rivers in Angola by Conradie et al. (2016) by nine species, and documented an additional 42 species associated with the Angolan Zambezi River basin. Ten of the species recorded here represent the southeasternmost records for Angola, some of which are also new records for the larger Okavango River basin (i.e., *Arthroleptis*

stenodactylus, A. xenochirus, Breviceps ombelanonga, Hyperolius raymondi, Kassinula wittei, Ptychadena bunoderma, P. keilingi, Leptopelis sp., and Hyperolius aff. bocagei).

In total, 125 nights, representing 240 total trapping nights, were spent surveying the region during both wet and dry seasons, without adding any additional species to the checklist. Thus, we now consider the upper catchments of the Cuito, Cuanavale, Cuando, and Lungwebungu rivers to be well surveyed for amphibians. However, the following species are expected to occur eastward to the Zambian border (compare to Broadley 1971; Pietersen et al. 2017; Bittencourt-Silva 2019), based the availability of appropriate habitat: Breviceps adspersus, Breviceps Chiromantis xerampelina, Hildebrandtia ornata, Hemisus marmoratus, Phrynomantis bifasciatus, Phrynomantis affinis, Poyntonophrynus fenoulheti, Poyntonophrynus kavangensis, Ptychadena mapacha, Pyxicephalus adspersus, and Tomopterna cryptotis.

The headwaters of the Okavango River basin, with peat lakes and extensive floodplains, harbor a high diversity of Hyperoliidae (three genera, comprising 12 species) and Ptychadenidae (nine species), compared to the more terrestrial families such as Bufonidae. Many of the species are regarded as local endemics to the headwaters (i.e., Hyperolius raymondi, Hyperolius aff. bocagei, Kassina kuvangensis, Kassinula wittei, and Ptychadena keilingi). The increased knowledge coupled with the presence of habitat specialist species will contribute to better conservation planning in these regions and the larger Okavango River basin.

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Werner Conradie has a Masters in Environmental Science (M.Env.Sc.) and 18 years of experience working with the southern African herpetofauna. His main research interests focus on the taxonomy, conservation, and ecology of amphibians and reptiles. Werner has published numerous principal and collaborative scientific papers, and has served on many conservation and scientific panels, including the Southern African Reptile and Amphibian Relisting Committees. He has undertaken research expeditions to many African countries, including Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Zambia, and Zimbabwe. Werner is currently the Curator of Herpetology at the Port Elizabeth Museum (Bayworld), South Africa.

Chad Keates is currently a Post-doctoral Fellow at the Port Elizabeth Museum, funded by research funds through Nelson Mandela University (Port Elizabeth, South Africa). Having recently completed his Ph.D. in Zoology, Chad's research focuses on the African herpetofauna and its evolutionary and ecological structuring. In Chad's short professional career, he has published several principal and collaborative peer-reviewed scientific papers and book chapters. As a strong advocate for reptile and amphibian awareness, Chad regularly conducts walks, talks, and presentations; and he has produced numerous popular scientific outputs on the subject. He has undertaken numerous expeditions in various African countries, such as Angola, Zambia, and South Africa, with a variety of both professional and scientific organizations.

Luke Verburgt is a consulting herpetologist in South Africa with over 19 years of herpetofauna survey experience across 23 African countries (Angola, Botswana, Cameroon, Democratic Republic of Congo, Ghana, Ivory Coast, Kenya, Lesotho, Liberia, Namibia, Madagascar, Malawi, Mali, Morocco, Mozambique, Republic of Guinea, São Tomé and Príncipe, Sierra Leone, South Africa, Swaziland, Tanzania, Uganda, and Zimbabwe). He is a co-owner of Enviro-Insight (Pretoria, South Africa), holds an M.Sc. in Zoology from the University of Pretoria, and is a registered scientific professional with the South African Council for Natural Scientific Professions (SACNASP). Luke has published more than 30 scientific articles, which include the descriptions of several new African herpetofauna species, and he is a co-author of the book *Snakes and other Reptiles of Zambia and Malawi* (Struik Random House Publishers, Cape Town, South Africa). He is also an extraordinary lecturer in the Department of Zoology & Entomology at the University of Pretoria.

Ninda Baptista is an Angolan biologist with an M.Sc. degree in Conservation Biology from the University of Lisbon (Portugal). She is currently pursuing a Ph.D. in Biodiversity, Genetics, and Evolution at the University of Porto (Portugal) that addresses the diversity of Angolan amphibians. Over the last 13 years, she has worked on research, *in-situ* conservation projects, and environmental consulting in Angola, including priority areas for conservation along the Angolan escarpment and highlands. She has conducted herpetological surveys throughout the country, and created a herpetological collection (Colecção Herpetológica do Lubango) that is currently deposited in Instituto Superior de Ciências da Educação da Huíla (ISCED – Huíla) in Angola. Ninda is an author of various scientific papers and book chapters on Angolan herpetology and ornithology. She also works on scientific outreach, producing magazine articles, books for children, and posters about the country's biodiversity in collaboration with Fundação Kissama (Luanda, Angola).

James Harvey lives in South Africa and works as an independent herpetologist, ecological researcher, and consultant. He holds degrees in Zoology, Hydrology, and Environmental Management, and has performed herpetological fieldwork widely, primarily within Africa, in such places as South Africa, Botswana, Zimbabwe, Angola, Malawi, Kenya, Mali, Democratic Republic of Congo, Madagascar, and Vietnam. His interests are diverse but center on the taxonomy, ecology, and conservation of herpetofauna and other biodiversity. James has contributed to conservation assessments, workshops, and Red Data publications for reptiles, amphibians, mammals, and plants for the southern and eastern African regions. James regularly attends herpetological conferences, has published several scientific papers, and has contributed to a number of herpetological publications as an author.

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