

# At the edge of extinction: a first herpetological assessment of the proposed Serra do Pingano Rainforest National Park in Uíge Province, northern Angola

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## Abstract

We systematically assess the herpetofaunal diversity of the Serra do Pingano Forest Ecosystem (SPFE) and additional localities throughout the northern Angolan province of Uíge during four independent Rapid Assessment (RA) field campaigns held between 2013 and 2019. These assessments represent the first systematic surveys of amphibians and reptiles from the province, and thus we provide the first province-wide species list. We collected data on the status and current threats to amphibians and reptiles in the proposed Serra do Pingano Rainforest National Park and were able to document 33 species of reptiles from Uíge province. Of the 33 species recorded from the province, 10 species are exclusively found in the SPFE. Amphibian surveys yielded 47 amphibian species from the province. These include 14 new country records and additional records that may represent undescribed species. This raises the amphibian count for Angola to at least 133 species, which includes 18 species exclusively found within the SPFE. Species-richness estimators indicate that more species should be detected if survey efforts are intensified. The species composition in the SPFE is unique and consists of a high proportion of forest specialists with restricted ranges and species found nowhere else in the country. This emphasizes today's paramount importance of the SPFE, which is threatened by increasing agricultural encroachment and uncontrolled timber extraction and charcoal production. These principal factors need to be controlled and/or abandoned in already impacted areas. Conservation strategies should particularly consider the strict protection of remaining intact forests and both lentic and lotic aquatic systems. They are not only crucial for safeguarding a significant number of species that depend on these habitats for reproduction; they also provide key ecosystem services to the local population. Angola, and Uíge province in particular, is at a crossroads concerning decisions and trade-offs among utilization, conservation, and preservation of its forests and, thus, substantial parts of the country's biodiversity. The establishment of a National Protected Area in the Serra do Pingano Ecosystem is therefore a necessary and urgently needed first step towards protecting Angola's national biodiversity heritage.

## Key Words

Amphibia, biodiversity survey, conservation, new country records, rainforest fragments, Reptilia

## Introduction

Northern Angola, including the provinces of Cabinda, Lunda Norte, Uíge, and to a lesser extent Malanje and Cuanza Norte, harbours the last remaining tracts of al-

ready heavily fragmented rainforest. These forest ecosystems have been largely neglected in biodiversity surveys. However, due to an assumed link with the large Congolese Forest Bioregion and their unique position within the range of Angolan ecosystems, they promise to har-

bour an exceptionally rich flora and fauna. Today, sizable and important patches can only be found in Cabinda and Uíge. The latter province is particularly known for the Serra do Pingano Forest Ecosystem (SPFE), a site of recent herpetological explorations (Ernst et al. 2014, 2015). The amphibian and reptile fauna of this area was largely unknown until these first surveys were conducted. All species reported during these surveys, therefore, either represent first records for Uíge province or for Angola as a whole (Marques et al. 2018).

Amphibians and reptiles are amongst the world's most threatened organisms (Stuart et al. 2004, 2008; Böhm et al. 2013). The reasons for their dramatic decline are multifaceted, but unarguably the most important factor is land-use change, and to a lesser extent, climate change, direct exploitation, and pollution (IPBES 2019). The SPFE, formerly probably a vast and continuous area of intact rainforest, is now under severe pressure from deforestation, encroachment, and land conversion for agriculture.

Amphibians, due to their peculiar biology and diversity of reproductive strategies (Wells 2007), are affected by small changes in their microhabitats and are, therefore, prone to the effects of changes in land-use. Amphibians can be used to predict the response of other, less sensitive taxonomic groups (Roque et al. 2018), and they have been previously proven to be a suitable, sensitive organismal model system for analysing the impacts of environmental change on community structure, composition, and diversity at both taxonomic and functional levels (Ernst et al. 2006; Ernst and Rödel 2008; Hölting et al. 2016). For these reasons, amphibians were specifically selected as a model indicator group to assess the status, potential, and perspectives of the larger Serra do Pingano Forest Ecosystem with respect to safeguarding and developing biological diversity in the last remaining rainforest systems of northern Angola within the context of a prospective National Protected Area Network Strategy. A feature film presenting current threats and perspectives developed during our activities can be accessed online: <https://vimeo.com/405416258>.

## Herpetological research in Angola

Today's knowledge of Angola's national biodiversity remains poor compared to that of other Sub-Saharan countries. This is particularly true for herpetofaunal diversity. Although herpetological research in Angola dates back to the late 19<sup>th</sup> century (e.g. Bocage 1867, 1879; Boulenger 1905, 1907; Ferreira 1906; Monard 1937; Laurent 1952, 1954, 1964; Hellmich 1957), it was only until recently that Bocage's (1895) landmark book was updated by more recent research (see Baptista et al. 2019a for a summary). The war of independence from 1961–1974 and a subsequent civil war (1975–2002) largely prevented any scientific exploration. Very few papers were published during this period (Poynton and Haacke 1993; Ruas 1996, 2002). After the war, numerous researchers initiated several independent research projects and a constant flow of papers,

reporting faunistic data (Ceríaco et al. 2014, 2016a, b, 2018a; Conradie et al. 2016; Baptista et al. 2019b; Butler et al. 2019), new country records (Ernst et al. 2014, 2015; Branch and Conradie 2015), and new species descriptions (Conradie et al. 2012, 2013; Stanley et al. 2016; Ceríaco et al. 2018b, 2020a, b; Branch et al. 2019a; Marques et al. 2019a, b) has been published. An updated atlas for the Angolan herpetofauna was recently published by Marques et al. (2018), and, together with Branch et al. (2019b) and Baptista et al. (2019a), these sources can now be used as a general reference and overview that is constantly being updated as new discoveries are published. Both rapid biodiversity surveys in neglected parts of the country and long-term monitoring routines in previously assessed sites are urgently needed to obtain a better understanding of the largely underappreciated herpetofauna. This is particularly true for the fragile forest remnants of the northern provinces, as data established there can provide the basis for a more comprehensive assessment of Angola's biodiversity in general and is a prerequisite for the development of sound and sustainable conservation strategies of its most precious and unique ecosystems.

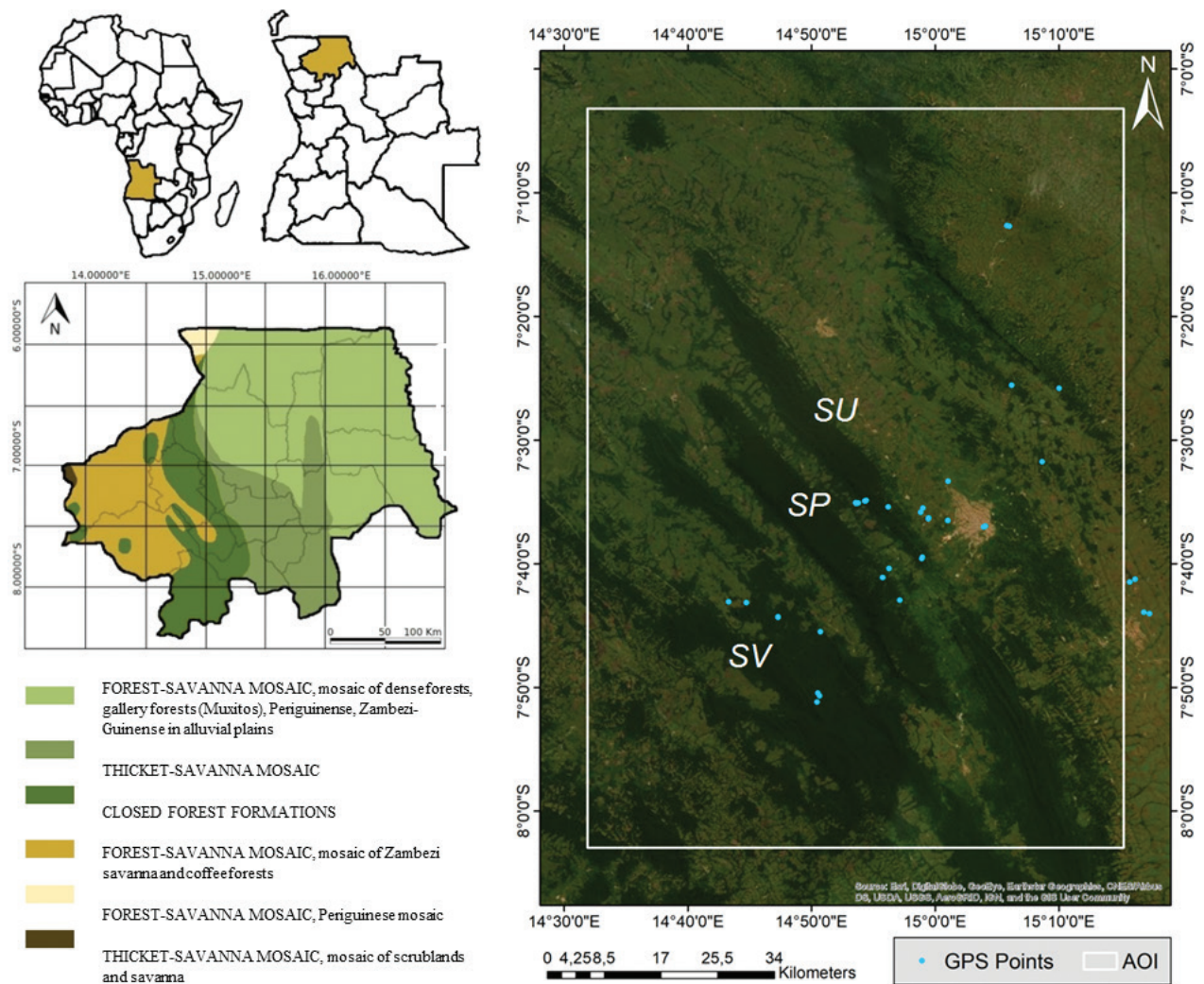
## Material and methods

### Study sites

Herpetofaunal diversity of the Serra do Pingano Forest Ecosystem (SPFE) was systematically assessed during four independent Rapid Assessment (RA) field campaigns (1<sup>st</sup> campaign: 2–16 October 2013; 2<sup>nd</sup> campaign: 30 October–17 November 2014; 3<sup>rd</sup> campaign: 15 September–3 October 2018; 4<sup>th</sup> campaign: 11–22 November 2019) and opportunistically between 2013 and 2019. Sampling was conducted at three core localities forming the larger Serra do Pingano Forest Ecosystem (from north to south: 1. Serra do Uíge (SU; core location: 7.6173S, 15.0658E), 2. Serra do Pingano (SP; core location: 7.6845S, 14.9298E), and 3. Serra Vamba (SV; core location: 7.8412S, 14.8422E), Fig. 1). Geographic coordinates use the WGS84 datum. Sampling was performed along an elevation gradient that covered both riparian as well as terrestrial forest habitats (for a selection of habitats, see Fig. 7). Additional surveys were conducted in different ecosystems (savannah, moorland, urban, and agricultural land) throughout the larger Uíge province to assess the Serra do Pingano herpetofauna in a province-wide context. Additional localities include the Planalto de Mucaba (wet savannah high plains with moorland) and savannah and forest ecosystems of Maquela do Zombo and Quimbele in the far north, bordering the Democratic Republic of Congo (DRC).

### Data acquisition and processing

We used opportunistic visual and acoustic encounter surveys (VES and AES) both during the day and at



**Figure 1.** Study area depicting the larger Serra do Pingano Forest Ecosystem (SPFE) with core herpetological survey sites (white rectangle) and sampling localities (blue dots, 50 independent localities). From north to south: SU: Serra do Uíge, SP: Serra do Pingano, SV: Serra Vamba. The inset left provides a coarse overview on major vegetation formations in Uíge province according to Barbosa 1970. Carta fitogeográfica de Angola. Instituto de Investigação Científica de Angola, Luanda.

night, supplemented by arrays of pitfall traps placed along drift fences in combination with funnel traps (Rödel and Ernst 2004; Ernst et al. 2005), to obtain basic faunistic data. Additionally, sound recordings of anuran calls were taken using a Marantz PMD661 digital field recorder and a Sennheiser ME66 directional shotgun microphone. Frog calls are species specific and can be used to identify species and qualitatively and quantitatively assess frog populations in an area. Recordings were processed following standardized routines using Raven Pro 1.5 software (Cornell Lab of Ornithology, Bioacoustics Research Program). Amphibian larvae were assessed by dip-netting in all potentially available breeding sites, both lentic and lotic. Our sampling strategy only provided qualitative and semi-quantitative data. For calculations of estimated species richness and sampling efficiency using species accumulation curves and statistical estimators, we exclusively used incidence based non-parametric procedures and estimators (1<sup>st</sup> and 2<sup>nd</sup> order Jackknife, Chao 2, and bootstrap) on presence/

absence data for the combined SPFE and in comparison for the entire Uíge province. Estimators were corrected for small sample sizes to yield more realistic results. We performed all statistical analyses using R statistical software, v. 3.4.4 (R Core Team 2018), with the “vegan” (Oksanen et al. 2012) and “BiodiversityR” (Kindt 2016) packages. As sample sizes for reptiles were too small, statistical analyses are restricted to the amphibian data set. Thus, reptile data are presented as occurrence data for respective core sites. The nomenclature for amphibians follows Frost (2020) and for reptiles Uetz et al. (2019). Voucher specimens and tissue samples (stored in 99.9% ethanol) were collected for *ex situ* identification of problematic taxa that cannot unambiguously be identified in the field or based on morphological and acoustic data, using a mt 16S rRNA-barcoding approach (Vences et al. 2005). Available sequences will be published elsewhere. All collected specimens were euthanized using commercially available toothache pain relief gel containing 20% benzocaine and subsequently preserved in



70% ethanol (denatured with 10% isopropanol). Specimens are stored in the herpetological collection of the Museum für Tierkunde, Senckenberg Natural History Collections Dresden (MTD). Tissue samples used in molecular analyses are additionally stored in the tissue bank of the MTD. The combination of RA methods and lab-based molecular identification techniques is crucial to resolve basic taxonomic questions and provide baseline data on actual species richness and distribution within and among the focus localities and the wider national and cross-regional context.

## Results

While we were able to obtain a very solid overview of the amphibian fauna of the region, reptiles are largely underrepresented in our sampling and reptile data must be considered too incomplete to allow comprehensive conclusions. Nonetheless, we recorded several unique species and species of conservation concern in both taxonomic groups.

### Reptiles

Of the more than 280 species of reptiles reported for Angola today, we were able to record 33 species from Uíge province. Although this is a significant increase compared to the previously reported seven species (Marques et al. 2018), this figure is still comparatively moderate. This is partially because more arid and open environments generally tend to support higher reptile diversity than closed forest ecosystems. This is particularly true for lizards. However, with respect to snakes, more intensified surveys in other seasons will likely yield additional species that are expected to occur in the region. Of the 33 species recorded from the province, eight species were exclusively found in the SPFE. Even though the recorded reptile diversity is moderate, a significant proportion of the recorded species are unique for the country and can only be found in the forested areas of the northern provinces and in adjacent regions of West-Central Africa. For a summary of records, see Table 1. As most species have not yet been formally assessed by the IUCN, we refrain from presenting respective categories here.

### Annotated species list (Reptilia)

Numbers listed in parentheses refer to voucher specimens deposited in the MTD herpetological collection. Table 1 summarizes all species recorded throughout Uíge province (UP) and in three core localities within SPFE. These include the Serra do Uíge (SU), Serra do Pingano (SP), and Serra Vamba (SV).

### Reptilia Testudines Pelomedusidae

#### *Pelusios rhodesianus* Hewitt, 1927; (MTD 49953, 49954)

Only two specimens were collected by local villagers in a pond, and this species was not frequently observed in aquatic habitats. Densities are probably low due to hunting pressure.

### Testudinidae

#### *Kinixys belliana* Gray, 1831

Carapaces of unconfirmed origin were for sale in local markets or in the possession of villagers. We never observed this species alive during our surveys. This species is apparently heavily hunted. *Kinixys belliana* is associated with open savannah habitats and is unlikely to occur in the closed-forest systems of the SPFE, where it might be replaced by the forest-dwelling *Kinixys erosa*. However, we have no indication yet of the occurrence of *K. erosa* in Uíge province. More field surveys and interviews with local hunters are required to confirm the presence of *K. belliana* within the wider SPFE area.

### Crocodylia Crocodylidae

#### *Crocodylus niloticus* Laurenti, 1768

A single skull of unclear origin was found at a local village, but occurrence of this species in Uíge province is unconfirmed. Despite intensive searches and interviews with the local population, we were unable to unambiguously establish the existence of any crocodylian in the SPFE. However, it is likely that up to three species, *Crocodylus niloticus*, *Mecistops leptorhynchus*, and *Osteoleaemus tetraspis*, occur or have occurred within the boundaries of the SPFE.

### Sauria Agamidae

#### *Agama agama*-complex

This complex of species is mainly found in populated areas, such as within the provincial capital of Uíge, and largely associated with anthropogenic habitats, such as junkyards and buildings. Because of the unresolved taxonomy of this group in northern Angola, we refrain from

**Table 1.** Reptile species recorded in the Serra do Pingano Forest Ecosystem (SPFE) and the wider province of Uíge (in alphabetic order) with occurrence in respective core areas (SU: Serra do Uíge, SP: Serra do Pingano, SV: Serra Vamba, UP: Uíge province outside SPFE), general range (ANG: Angola including Cabinda, WCA: West-Central Africa, SSA: Sub-Saharan Africa (any range beyond WCA)) and general habitat type (PF: primary forest, DF: degraded forest, OH: open habitats, including natural savannahs as well as anthropogenic habitats and peri-urban sites). \* = species listed under CITES II. ? = status questionable/not yet confirmed.

Taxa	SU	SP	SV	UP	Restricted to			Habitat		
					ANG	WCA	SSA	PF	DF	OH
<b>Reptilia</b>										
<b>Testudines</b>										
<b>Pelomedusidae</b>										
<i>Pelusios rhodesianus</i>	x			x			x			x
<b>Testudinidae</b>										
<i>Kinixys belliana</i> *	?	?	?	x			x	?	?	?
<b>Crocodylia</b>										
<b>Crocodylidae</b>										
<i>Crocodylus niloticus</i>	?	?	?	X?			x		x	x
<b>Sauria</b>										
<b>Agamidae</b>										
<i>Agama agama</i> -complex	x			x			x			x
<b>Chamaeleonidae</b>										
<i>Chamaeleo gracilis etiennei</i>	x		x	x	x into DRC				x	x
<b>Gekkonidae</b>										
<i>Hemidactylus paivae</i>	x	x	x		x			x		
<i>Hemidactylus longicephalus</i>		x				x		x		
<b>Gerrhosauridae</b>										
<i>Gerrhosaurus cf. nigrolineatus</i>	x			x			x		x	x
<b>Lacertidae</b>										
<i>Holaspis guentheri</i>		x					x	x		
<b>Scincidae</b>										
<i>Panaspis cabindae</i>	x				x into DRC					x
<i>Trachylepis cf. affinis</i>	x	x	x	x		x			x	x
<i>Trachylepis maculilabris</i>				x			x			x
<b>Varanidae</b>										
<i>Varanus niloticus</i> *		x					x	x	x	
<b>Serpentes</b>										
<b>Colubridae</b>										
<i>Crotaphopeltis hotamboeia</i>				x			x		x	x
<i>Dispholidus typus punctatus</i>				x	x into DRC				x	x
<i>Grayia ornata</i>	x	x				x		x		
<i>Philothamnus carinatus</i>				x			x		x	x
<i>Philothamnus dorsalis</i>	x					x			x	x
<i>Thelotornis kirtlandii</i>				x			x		x	x
<i>Thrasops jacksonii</i>				x			x		x	x
<i>Toxicodryas blandingii</i>	x						x		x	x
<b>Elapidae</b>										
<i>Dendroaspis jamesoni</i>	x			x			x		x	x
<i>Elapsoidea semiannulata</i>	x			x	x into Zambia & Namibia				x	x
<i>Naja melanoleuca</i>		x					x	x	x	
<b>Lamprophiidae</b>										
<i>Boaedon angolensis</i>	x			x	x					x
<i>Boaedon olivaceus</i>				x			x			x
<i>Lycophidion cf. multimaculatum</i>				x		x				x
<b>Natricidae</b>										
<i>Natriciteres olivacea</i>		x					x	x		
<b>Pythonidae</b>										
<i>Python sebae</i> *	x			x			x		x	x
<b>Viperidae</b>										
<i>Atheris squamigera</i>		x				x		x		
<i>Bitis gabonica</i>		x				x into East A		x	x	
<i>Bitis nasicornis</i>				x		x into East A			x	
<i>Causus maculatus</i>				x			x		x	

assigning our records to a one of the currently recognized species. Marques et al. (2018) and Branch et al. (2019) have referred to individuals from northern Angola as

*A. congica*, which is currently recognized as a subspecies of *A. agama* but may deserve full species status pending further investigations.

## Chamaeleonidae

***Chamaeleo gracilis etiennei* Schmidt, 1919;  
(MTD 49658, 49874)**

This subspecies is endemic to Angola and is previously mainly reported from open or bush savannah habitats. We observed that *C. g. etiennei* had a clear preference for open forest type habitats or habitats at the savannah-forest interface. We frequently recorded this species in degraded forests, mainly along roads.

## Gekkonidae

***Hemidactylus longicephalus* Bocage, 1873;  
(MTD 48613)**

This species was recently revised by Ceriaco et al. (2020), who designated a neotype and provided a redescription. We exclusively recorded it from forest habitats where it is mainly ground dwelling in the leaf litter or perching on stems of small trees.

***Hemidactylus paivae* Ceriaco, Agarwal, Marques & Bauer, 2020; (MTD 48932, 49660, 49868, 49869, 49870)**

Fig. 6a, b

This species was recently described by Ceriaco et al. (2020). Specimens collected in the SPFE genetically match this taxon. We observed two different morphs which are genetically identical: a darker morph that inhabits forest habitats and an almost unpigmented morph that comes from an extensive calcareous inselberg cave system at the north-western edge of the Serra Vamba. Both the dark and light morphs can occur almost syntopically, but they were found to inhabit different microhabitats (caves vs closed forest). The difference in pigmentation was stable even under different, day/night light conditions and is still observable in ethanol-preserved material. The environmental drivers of this colour dimorphism deserve further study (see Griffing et al. 2020).

## Gerrhosauridae

***Gerrhosaurus cf. nigrolineatus* Hallowell, 1857;  
(MTD 48934)**

Fig. 6c

The taxonomic status of *Gerrhosaurus nigrolineatus* is not well established and requires further research (Bates et al. 2013). We found mainly juvenile specimens in a variety of habitats ranging from urban settings on wasteland in the city of Uíge to savannah habitats farther north, and even forest edges in degraded forest of the Serra do Uíge.

## Lacertidae

***Holaspis guentheri* Gray, 1863**

This is only the third record of the species for Angola (Branch et al. 2019). A single individual of this arboreal lizard was observed in a freshly burnt, closed forest patch on top of the Serra do Pingano. This species may be more widespread within the SPFE, but it may have been overlooked in our surveys due to its elusive habits and association with forest canopies.

## Scincidae

***Panaspis cabindae* (Bocage, 1866); (MTD 48612)**

The genus, of which *P. cabindae* is the type species, was recently revised by Medina et al. (2016). This revision included material from Uíge, assigned to this nominal species. Ceriaco et al. (2020b) provided an overview of the Angolan taxa, including the description of a new species. We recorded *P. cabindae* in degraded savannah habitats near agricultural areas and urban wasteland near and within the city of Uíge, but we have no clear evidence for this species' occurrence within the SPFE.

***Trachylepis cf. affinis* (Gray, 1838); (MTD 48611,  
48928, 48930, 48931, 49784)**

The taxonomic status of this species, particularly with respect to the relationship between its synonyms and the Angolan populations, is far from being resolved and requires a revision, in which Angolan material is included (Welton and Bauer 2019). This species found to be widespread throughout the province but was more frequently associated with degraded forest or forest-edge habitats than with open savannah. It was the most abundant diurnal lizard encountered during our surveys.

***Trachylepis maculilabris* (Gray, 1845); (MTD 48927)**

Fig. 6d

Given its wide distribution, this may represent a complex of species. We collected a single specimen on the Kimpa Vita University campus in Uíge.

## Varanidae

***Varanus niloticus* (Linnaeus, 1758); (MTD 49258)**

According to Dowell et al. (2016), Angolan populations of *V. niloticus* belong to a broadly distributed southern lineage, which includes individuals previously recognized as *V. ornatus*. Specimens observed in Uíge province had bluish tongues but only 5 or 6 transverse rows of spots or cross-bands between the extremities. They

were always observed in the vicinity of degraded forest patches. We conservatively refer to these individuals as *V. niloticus* until more extensive sampling from across Angola can clarify their taxonomic status. Once data are available, a reassessment of the Angolan material with respect to genetic lineages identified by Dowell et al. (2016) and the available names, *V. niloticus* and *V. ornatus*, will become possible.

## Serpentes Colubridae

### *Crotaphopeltis hotamboeia* (Laurenti, 1768); (MTD 48608)

This is one of the most widespread African snake species. A thorough revision recently assigned the Angolan populations to two distinct clades (“clade 2” and “clade 3” of Engelbrecht et al. 2020). The affiliation of the specimen collected in Uíge to one of these clades (or another) remains to be determined. We recorded this species from urban wasteland near a heavily polluted pond in Uíge city.

### *Dispholidus typus punctatus* Laurent, 1955; (MTD 48963)

Both currently recognized subspecies, *D. t. typus* and *D. t. punctatus*, are known to occur in Angola. However, we exclusively encountered *D. t. punctatus*, which is widespread throughout the province. A reassessment of the Angolan material and the distributional boundaries of the two subspecies is required. Several specimens were collected as roadkill.

### *Grayia ornata* (Bocage, 1866); (MTD 48961, 49659) Fig. 6f

Originally described from Angola by Bocage (1866), only a few individuals of this species were recorded since (Branch and Conradie 2015; Branch 2018; Branch et al. 2019). This species was exclusively recorded in closed-forest riparian systems within the SPFE, where individuals were either foraging in streams and rock pools at night or resting on branches overhanging streams, from which they dropped into the water when encountered. Due to the habitat preference of *G. ornata*, it is unlikely that this species occurs outside closed-forest patches and far from lotic rainforest habitats.

### *Philothamnus carinatus* (Andersson, 1901); (MTD 49872)

A single specimen, which is only the second record for Angola, was collected near Quimbele. This species is distinguishable from other members of its genus in having an undivided anal scale.

### *Philothamnus dorsalis* (Bocage, 1866); (MTD 49873)

A single specimen was collected near a village in the south-eastern foothills of the Serra do Pingano.

### *Thelotornis kirtlandii* (Hallowell, 1844); (MTD 48609, 49774)

This species is widespread throughout the province. We have several observations of *T. kirtlandii* from villages in which it was observed hunting for weaverbirds (*Ploceus* spp.).

### *Thrasops jacksonii* Günther, 1895; (MTD 48755, 48991, 49166, 49661)

This species has only been reported from Lunda Norte (Branch 2018). We recorded it within the SPFE, as road kill, as well as outside the SPFE.

### *Toxicodryas blandingii* (Hallowell, “1844” 1845); (MTD 49871)

This species is until now only known from Lunda Norte (Marques et al. 2018). The only record that we were able to obtain from Uíge is the head of a decapitated specimen which was given to us by a local from a village in the south-eastern foothills of the Serra do Pingano.

## Elapidae

### *Dendroaspis jamesoni* (Traill, 1843); (MTD 48844, 48962)

This species is recorded from sites only outside the core SPFE, including urban wasteland near the campus of Kimpa Vita University, Uíge.

### *Elapsoidea semiannulata* Bocage, 1882; (MTD 48607)

A single specimen was collected on the campus of Kimpa Vita University, Uíge.

### *Naja melanoleuca* Hallowell, 1857; (MTD 49164)

What was known as *Naja melanoleuca* has recently been split into four distinct species (Wüster et al. 2018). The few individuals we recorded correspond to *N. melanoleuca* sensu stricto. These were observed in degraded forest habitats.

## Lamprophiidae

### *Boaedon angolensis* Bocage, 1895; (MTD 48606, 48960, 49253)

The material from Angola, including specimens collected in Uíge, is currently being revised (Hallermann et al. in

prep.). We collected this species in a variety of open-savannah habitats near the city of Uíge and in the planalto de Mucaba.

***Boaedon olivaceus* (Duméril, 1856); (MTD 48990, 49657)**

The species has only been reported from Cabinda, and a single record exists from Lunda Norte. We collected two specimens near Maquela do Zombo, confirming the presence of *B. olivaceus* in Angola.

***Lycophidion cf. multimaculatum* Boettger, 1888; (MTD 49632)**

This species was previously often reported as *L. capense*. The differentiation and distributional limits of these two species require investigation.

## Natricidae

***Natriciteres olivacea* (Peters, 1854); (MTD 48610)**

Only a few historical records of this species exist for Angola (Marques et al. 2018), and there is a single recent record from south-eastern part of the country (Conradie et al. 2016). We recorded the species from within closed forest in the Serra do Pingano, in the vicinity of a recently cleared forest patch.

## Pythonidae

***Python sebae* (Gmelin, 1789)**

This species is probably restricted to northern Angola and replaced by *P. natalensis* in the south. It is heavily hunted and frequently seen in bushmeat markets. We recorded this species in areas of wet savannah, which are often associated with larger river systems.

## Viperidae

***Atheris squamigera* (Hallowell, “1854” 1855)**

This is a true forest species, which is rarely recorded from Angola. Only four records exist, one of which is from Cabinda (Marques et al. 2018). This small, aboreal viper was exclusively found in the Serra do Pingano. A re-examination of this species across its geographic range is necessary to determine if it is a geographically variable species or a species complex (Ernst and Rödel 2002; Menegon et al. 2014). The Angolan populations might be found to be a distinct lineage. We have a single photographic record of this species in closed forest near a large waterfall in the Serra do Pingano.

***Bitis gabonica* Duméril, Duméril & Bibron, 1854; (MTD 49875)**

Fig. 6e

This species is commonly associated with forest-savannah mosaics of West and Central Africa. We recorded this species from forest fringes within an agricultural matrix in the Serra do Pingano. The distribution of the species across Angola is not well known and knowledge is fragmentary, but recent surveys by de Oliveira et al. (2016) added records from as far south as Benguela. Unlike *B. nasicornis*, *B. gabonica* is usually associated with forest-savannah mosaics, whereas *B. nasicornis* is usually a leaf-litter dwelling forest species (but see below).

***Bitis nasicornis* (Shaw, 1792); (MTD 49251)**

Our records from Uíge represent the third and fourth record of this species from Angola. These records are all based on animals killed by local hunters within small gallery forest remnants within a wet savannah matrix. So far, we have no records from within closed-forest systems of the SPFE, but it is likely that intensified surveys within the SPFE will eventually detect this species.

***Causus maculatus* (Hallowell, 1842); (MTD 48845)**

We have a single record, which is based on a road-killed individual from outside the SPFE.

## Amphibians

Prior to the recent explorations outlined above, the amphibian diversity of Angola was considered moderate, with 101 amphibian species known. Of these, 11 species are endemic. As a comparison, the Democratic Republic of Congo has 224 amphibian species, with 48 of these endemic to that country (Frétey et al. 2011). Recent contributions by Conradie et al. (2012, 2013) and Ceríaco et al. (2018b) have added several newly described species, which raise to about 117 the number of amphibian species in Angola, with 18 species endemic (Marques et al. 2018; Baptista et al. 2019a)

Our systematic herpetological assessment for Uíge province yielded 47 amphibian species in various localities and ecosystems throughout the province (Table 2). This increases by 41 the number of species recorded, from only six, as previously reported by Marques et al. (2018). Uíge province is now known to be the second-most species-rich province in Angola. The records include 14 new country records and an additional five species with questionable taxonomic status that may represent undescribed species. This increases the amphibian count for Angola to at least 133 species. Of these 133 species, 18 species are so far exclusively found within the SPFE.

Species-richness estimators showed that our surveys yielded approximately between 70–80% of the species es-



**Table 2.** Amphibian species recorded in the Serra do Pingano Forest Ecosystem (SPFE) and the wider province of Uíge (in alphabetical order) with occurrence in respective core areas (SU: Serra do Uíge, SP: Serra do Pingano, SV: Serra Vamba, UP: Uíge province outside SPFE), general range (ANG: Angola including Cabinda, WCA: West-Central Africa, SSA: Sub-Saharan Africa (any range beyond WCA)) and general habitat type (PF: primary forest, DF: degraded forest, OH: open habitats, including natural savannahs as well as anthropogenic habitats and peri-urban sites). \* = first country records for Angola.

Taxa	SU	SP	SV	UP	Restricted to			Habitat		
					ANG	WCA	SSA	PF	DF	OH
<b>Amphibia</b>										
<b>Anura</b>										
<b>Pipidae</b>										
<i>Xenopus andrei</i> *		x				x			x	
<i>Xenopus mellotropicalis</i> *	x	x		x		x			x	x
<i>Xenopus petersii</i>				x		x				x
<b>Arthroleptidae</b>										
<i>Arthroleptis carquejai</i>	x	x	x			x			x	x
<i>Arthroleptis poecilnotus</i>		x	x			x			x	x
<i>Arthroleptis sylvaticus</i> *			x			x				x
<i>Arthroleptis xenochirus</i>				x	x into Malawi				x	
<i>Cardioglossa gracilis</i> *		x				x			x	x
<i>Leptopelis aubryi</i> *		x	x			x			x	x
<i>Leptopelis calcaratus</i> *	x					x			x	x
<i>Leptopelis</i> sp 1		x				?	?	?	x	x
<i>Leptopelis millsoni</i> *	x	x								x
<i>Leptopelis ocellatus</i> *	x			x		x				x
<i>Leptopelis</i> sp.2						?	?	?		
<i>Trichobatrachus</i> cf. <i>robustus</i> *		x				x			x	
<b>Bufonidae</b>										
<i>Sclerophrys pusilla</i>	x	x	x	x				x		x
<i>Sclerophrys regularis</i>	x	x		x				x		x
<i>Sclerophrys</i> cf. <i>superciliaris</i> *	x	x				x			x	
<i>Sclerophrys</i> sp.1				x	?	?	?			x
<b>Dicoglossidae</b>										
<i>Hoplobatrachus occipitalis</i>	x	x		x				x		x
<b>Hyperoliidae</b>										
<i>Afraxalus osorioi</i>			x	x		x				x
<i>Afraxalus wittei</i>				x				x Central A. into ANG		x
<i>Afraxalus</i> aff. <i>fulvovittatus</i>				x		x				x
<i>Alexteroon hypsiphonus</i> *	x	x	x			x			x	x
<i>Hyperolius bocagei</i>				x	x East to Uganda					x
<i>Hyperolius cinnamomeoventris</i>				x		x				x
<i>Hyperolius dartevellei</i>				x		x				x
<i>Hyperolius</i> cf. <i>guttulatus</i>				x		x				x
<i>Hyperolius parallelus</i>				x	x to Zambia & Namibia					x
<i>Hyperolius pardalis</i>				x		x				x
<i>Hyperolius platyceps</i>				x		x				x
<i>Hyperolius</i> sp. 1		x				?	?	?	x	
<i>Kassina kuvangensis</i>				x	x into Zambia					x
<i>Kassina senegalensis</i>				x		x				x
<b>Phrynobatrachidae</b>										
<i>Phrynobatrachus</i> cf. <i>natalensis</i>				x	?	?	?			x
<i>Phrynobatrachus</i> cf. <i>africanus</i>		x			?	?	?			x
<i>Phrynobatrachus</i> cf. <i>mababiensis</i>				x	?	?	?			x
<i>Phrynobatrachus</i> aff. <i>mayokoensis</i> sp. 1*		x		x	?	?	?			x
<i>Phrynobatrachus</i> aff. <i>mayokoensis</i> sp. 2*				x	?	?	?			x
<b>Ptychadenidae</b>										
<i>Ptychadena anchietae</i>				x						x
<i>Ptychadena bunoderma</i>				x	x into Zambia					x
<i>Ptychadena oxyrhynchus</i>	x	x	x	x				x		x
<i>Ptychadena</i> „ <i>mascareniensis</i> “-complex	x	x	x	x				x		x
<b>Pyxicephalidae</b>										
<i>Amietia angolensis</i>	x	x				x			x	x
<b>Ranidae</b>										
<i>Amnirana albolabris</i>	x			x						x
<i>Amnirana lepus</i>	x	x				x			x	
<b>Rhacophoridae</b>										
<i>Chiromantis rufescens</i> *			x			x			x	

timated for Uíge province,  $62 \pm 9.1$  (Chao  $2 \pm SE$ ),  $62 \pm 9.5$  (Jackknife1  $\pm SE$ ),  $68.7$  (Jackknife2 no SE available), and  $54.0 \pm 5.2$  (bootstrap  $\pm SE$ ), and between 70–90% of esti-

mated for the SPFE,  $34.1 \pm 5.5$  (Chao  $2 \pm SE$ ),  $34.8 \pm 4.8$  (Jackknife1  $\pm SE$ ),  $37.6$  (Jackknife2 no SE available), and  $31.2 \pm 2.6$  (bootstrap  $\pm SE$ ). Together with the statistical

species accumulation curves, which show a steady increase (Fig. 2), this indicates that the species lists for both Uíge province and the SPFE are incomplete and that additional species can be expected with intensified surveys. However, surveys yielded a very good representation of amphibian species active during the time of the surveys.

The amphibian fauna of the SPFE is comparatively rich and unique for the country, consisting of species that otherwise are only known from the Central African forest systems of Cameroon and/or Gabon (e.g. *Trichobatrachus robustus*, *Xenopus andrei*, and *Sclerophrys superciliaris*) or the Congolese rainforest realm, with faunal elements connecting to locations as far as the Albertine Rift in Eastern Africa (Ernst unpubl.). These elements make up roughly 80% of the recorded species, and represent exceptional range extensions in some cases. Apart from previously published records of the SPFE amphibians (Ernst et al. 2014, 2015; Channing et al. 2016; Jongsma et al. 2018), additional, unpublished records are particularly noteworthy, as they represent enigmatic taxa in need of distributional and taxonomic revision (e.g. *Alexeteron hypsiphonus*, Ernst et al. in prep., and *Leptopelis millsoni*, Bell et al. in prep.) or taxa, in which the southernmost distribution lies in the SPFE (e.g. *Chiromantis rufescens*, first country records). Some records can only tentatively be assigned to nominal species, as they belong to cryptic species complexes in need of revision or unrecorded and potentially undescribed taxa. This particularly involves the diverse frog families Arthroleptidae (especially *Leptopelis* spp.) and Hyperoliidae (especially *Hyperolius* spp.), as well as the monotypic Phrynobatrachidae (*Phrynobatrachus* sp.) (Table 2). Most amphibian species recorded by us have not been formally assessed by the IUCN Red List or are at lower risk. As an update to the original IUCN assessments is underway, we refrain from including Red List categorization of species.

## Annotated species list (Amphibia)

Numbers listed in parentheses refer to voucher specimens deposited in the MTD herpetological collection. Table 2 summarizes all species recorded in Uíge province (UP) and in three core localities within the SPFE. These include the Serra do Uíge (SU), Serra do Pingano (SP), and Serra Vamba (SV).

### Amphibia

#### Anura

##### Pipidae

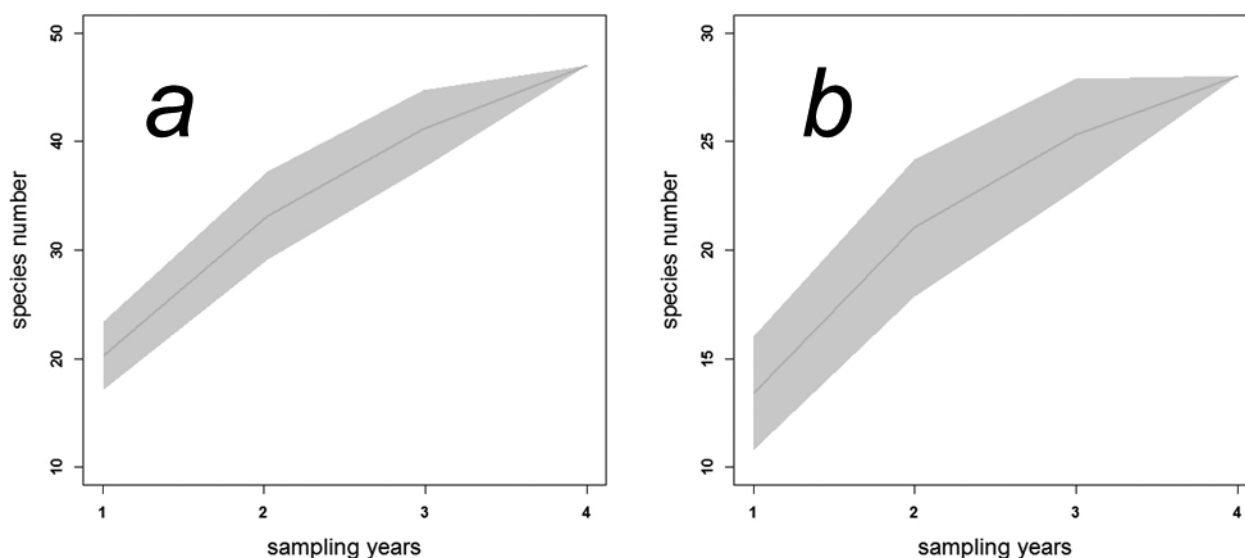
#### *Xenopus andrei* Loumont, 1983; (MTD 48661)

This is a small member of the aquatic genus *Xenopus*. The specimen recorded in the SPFE represents the first record for Angola and south of the Congo Basin (Ernst et al. 2015). Historically this species was confused with *X. fraseri*, whose taxonomic status and distribution was only recently reassessed (Evans et al. 2019)

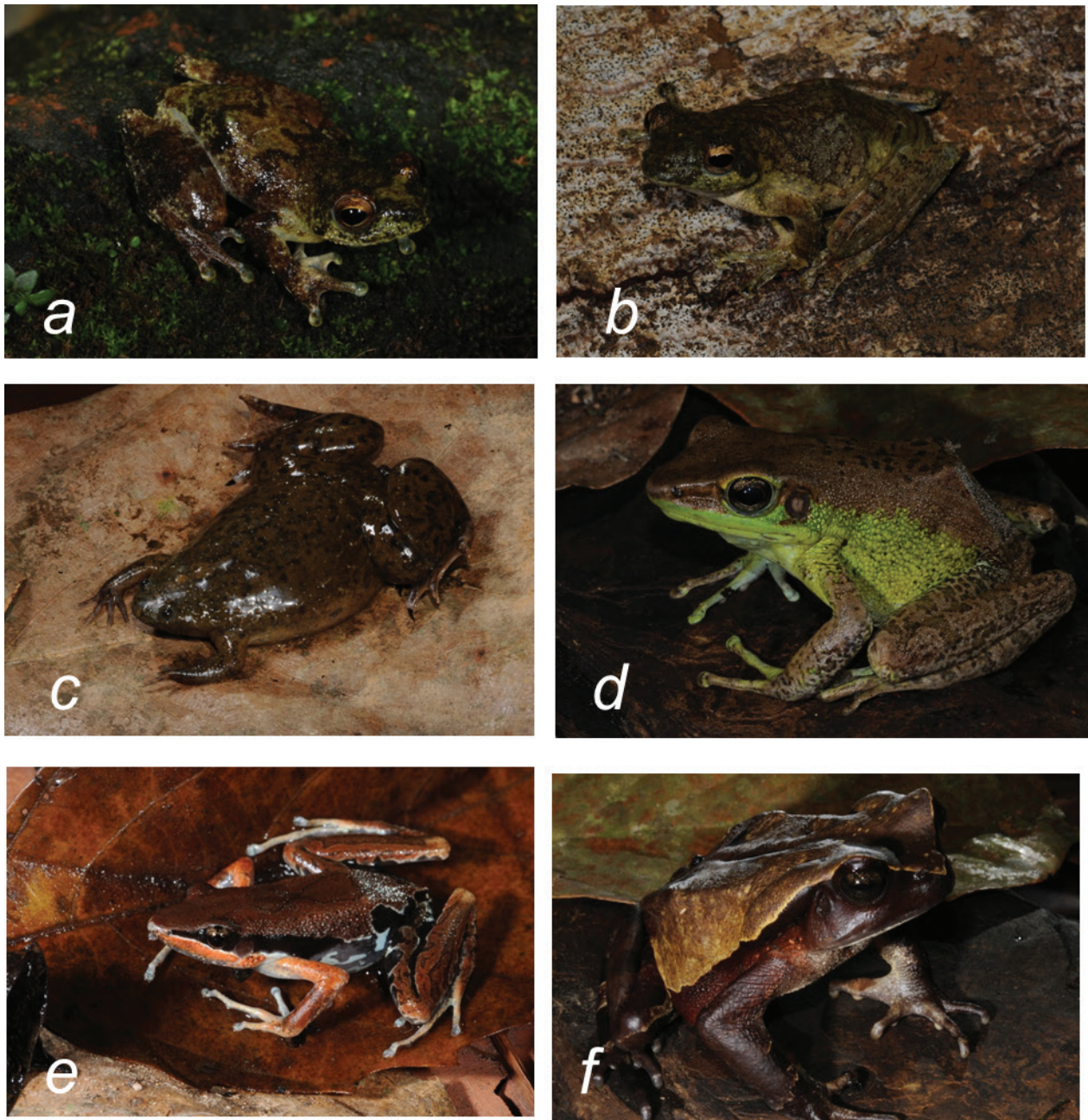
#### *Xenopus melloptropicalis* Evans, Carter, Greenbaum, Gvoždík, Kelley, McLaughlin, Pauwels, Portik, Stanley, Tinsley, Tobias & Blackburn, 2015; (MTD 48840, 48841, 48842, 48843, 48850, 49833)

Fig. 3c

This species is widespread throughout Uíge province, occurring from Quimbele in the far north, bordering the DRC, south to the SPFE. This species was always found to be associated with lotic habitats in both primary and disturbed forest (SPFE) and upland forest-savannah mosaics (Quimbele). Individuals were observed migrating into puddles along small roads and streamside ditches



**Figure 2.** Permuted species accumulation curves (species-based rarefaction curve, grey envelop represents SE based confidence intervals) of amphibian species richness for **a.** Uíge province and **b.** the SPFE. y-axis: estimated species richness, x-axis: sampling years (1-4: 2013, 2014, 2018, 2019).



**Figure 3.** Anuran species recorded within the SPFE **a.** Male *Alexteroon hypsiphonus* from transition between SP & SU **b.** female *Chiromantis rufescens* from SV **c.** female *Xenopus mellotropicalis* from transition between SP & SU **d.** female *Amnirana lepus* from SP **e.** male *Cardioglossa gracilis* from SP **f.** *Sclerophrys* cf. *superciliaris* from SP.

after and during heavy rain, where they likely feed on larvae of syntopic *Ptychadena* sp. This is the first record of the species for Angola.

*Xenopus petersii* Bocage, 1895; (MTD 48851, 48852, 48853, 48854, 48855, 48856, 49673, 49766)

This is a moderate- to large-bodied species. It is widespread throughout Angola. In Uíge, this species was exclusively found in heavily disturbed and/or anthropogenic aquatic habitats in open areas. These range from water-filled sand extraction pits in the moorlands of the Mucaba highlands to large, heavily polluted ponds (used

for car washing, etc.) in open savannah areas near the town of Negage.

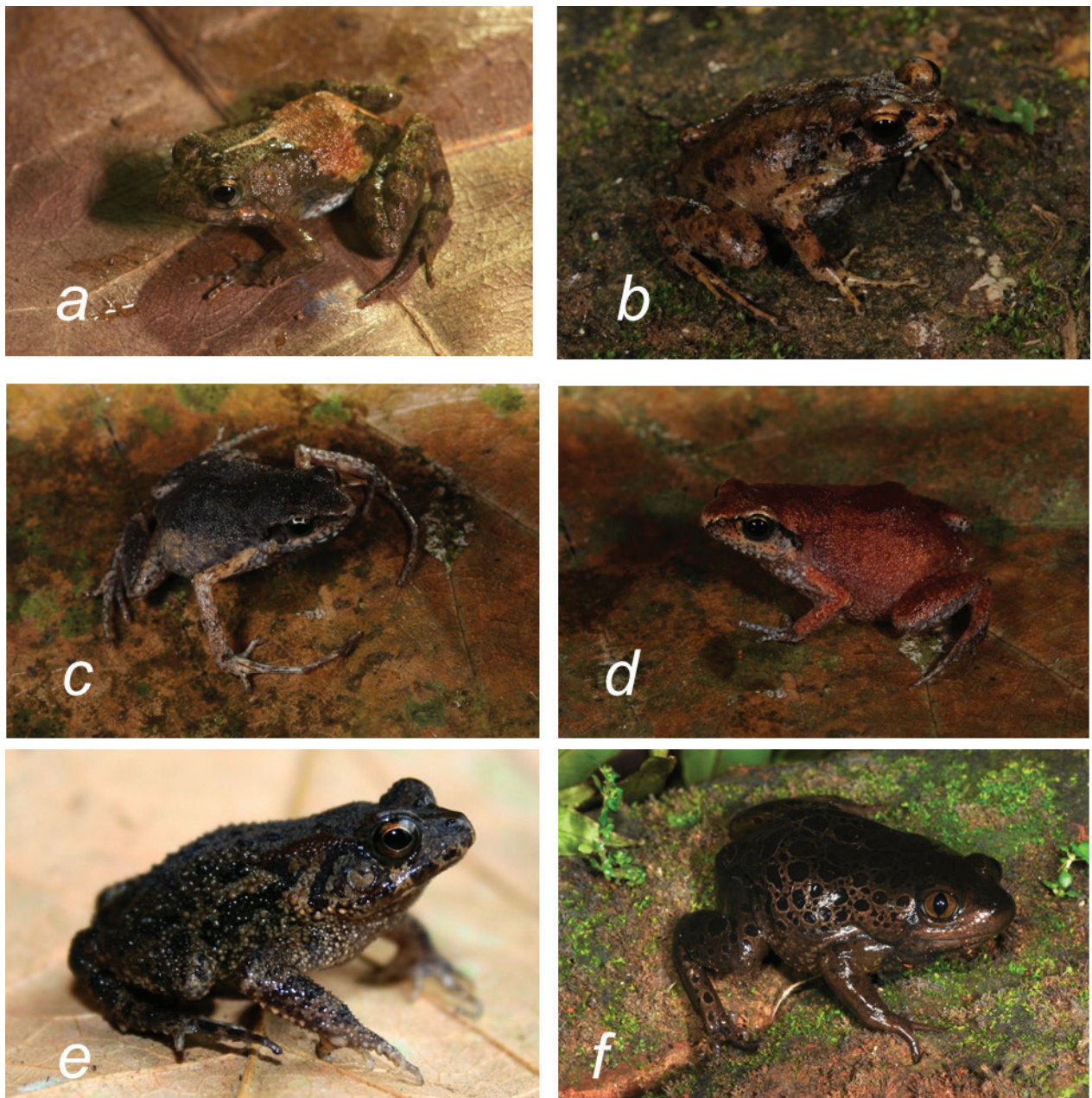
### Arthroleptidae

*Arthroleptis carquejai* Ferreira, 1906; (MTD 49851, 49852, 49853, 49854, 49855, 49705, 49706, 49707, 49708)

Fig. 4b

This is a bulky, medium-sized species. Males have only a slightly elongated middle finger. *Arthroleptis carquejai* was recently recognized as valid, distinct species, sepa-





**Figure 4.** Anuran species recorded within and outside the SPFE **a.** Male *Phrynobatrachus* aff. *mayokoensis* sp. 1 from the planalto de Mucaba UP **b.** *Arthroleptis carquejai* from SV **c.** male *Arthroleptis xenochirus* from planalto de Mucaba with elongated middle finger **d.** female *Arthroleptis xenochirus* from planalto de Mucaba, found to be associated with ponerine ants **e.** undescribed *Sclerophrys* sp. from Quimbunda swamp UP **f.** male *Kassina kuvangensis* from moorland in planalto de Mucaba.

rate from *A. variabilis*. In Uíge province, *A. carquejai* was found in a variety of mainly disturbed forest habitats and along logging roads. It was frequently attracted by light-traps installed to catch nocturnal lepidopterans.

***Arthroleptis* aff. *poecilnotus*; (MTD 49796, 49797, 49798)**

This is likely a species complex, which has been referred to as pseudo-mottled squeaker by Channing and Rödel (2019). It is usually associated with degraded forest and savannah

transition habitats. Single males were often found calling hidden in dense vegetation from roadsides. The call consists of a long high pitched, frequency modulated whistle.

***Arthroleptis sylvaticus* (Laurent, 1954); (MTD 49849)**

This is a small, variable species with yellowish belly and mottled throat and ventro-laterals. So far, it has been exclusively found at forest edges near large calcareous inselberg outcrops in the Serra Vamba. This is the first record of this species from Angola.



***Arthroleptis xenochirus* Boulenger, 1909; (MTD 48890, 48879, 48925, 48926, 49735, 49736, 49737)**

Fig. 4c, d

This is a well-documented species from north-eastern Angola. Males have extremely elongated middle fingers. In Uíge, *A. xenochirus* is restricted to more arid, open upland habitats in the Mucaba highland. Here, it is frequently found in small quarries, hiding underneath stones during the day and becoming active at dawn. In the planalto de Mucaba, a single female specimen (MTD 48925) was associated with the ponerine ant *Paltothyreus tarsatus*. Both the frog and several ants emerged when lifting a flat stone covering the ants' nest entrance. The frog and the ants were subsequently transferred to a terrarium for further observations. The frog remained unharmed and did not attack even when encountered by ants. Associations with ponerine ants have previously been reported for the West African microhylid *Phrynomantis microps* (Rödel and Braun 1999), but in *A. xenochirus*, preliminary analyses of EtOH skin extractions (MTD 48925, 48926) did not yet reveal potential chemically camouflaging compounds (Mebs and Ernst unpubl.).

***Cardioglossa gracilis* Boulenger, 1900; (MTD 48878, 48887)**

Fig. 3e

The records from SPFE represent the southernmost ones for the genus *Cardioglossa* and, thus, are the first records from Angola. This species was recorded from two localities in the Serra do Pingano but may be more widespread in the province. In the SPFE, it was associated with closed forest habitats on steep terrain. Males were calling while hidden in vegetation or leaf-litter, usually in the vicinity but several meters from the banks of fast running creeks.

***Leptopelis aubryi* (Duméril, 1856); (MTD 49827, 49828, 49829, 49830, 49831, 49832, 49863, 49864, 49865, 49866, 49867)**

Fig. 5f

There is a single record of the species from Angola, from outside Cabinda in the far north-eastern corner of Lunda Norte (Laurent 1954), but this record cannot unambiguously be confirmed. However, this species is relatively common throughout the SPFE and may be more widespread in the province. It was restricted to degraded forest and forest edges where males were frequently observed calling from low vegetation. Pending clarification of the record from Cabinda, the Uíge records can be considered the first confirmed from Angola.

***Leptopelis calcaratus* (Boulenger, 1906); (MTD 48738)**

Only a single record was found, from the Serra do Uíge near Cassechi, in a small forest patch near the Zeu River. Represents the first record for Angola.

***Leptopelis millsoni* (Boulenger, 1895); (MTD 49689, 49690, 49691, 49692, 49693, 49694, 49695, 49696, 49825, 49826, 48922, 48867, 48868, 48869, 48870, 48871, 48872, 48866)**

Fig. 5a–d

Large-bodied females of this species were associated with dense forest. Within SPFE, the species is restricted to closed forest habitats in the vicinity of fast-running rainforest creeks. Males call from vegetation overhanging creeks. Locally, this species is fairly abundant. Coloration and pattern are extremely variable, usually brown-olive with dorsal crossbars, but also uniform green with white and yellow bands. The ventral side is mostly uniform yellowish-white but sometimes also bright orange or with dark-reticulations on a white background. Individuals from Uíge may be part of a larger unresolved complex in need of a thorough revision (Bell et al. in prep.).

***Leptopelis ocellatus* (Mocquard, 1902); (MTD 48738, 48728, 48729, 48730, 48737)**

This is a small species mainly found in more open, savannah-like habitats, where males call from low vegetation, often in the vicinity of larger lentic aquatic habitats. There is pronounced sexual size dimorphism. An amplexant pair (MTD 48728, MTD 48728), that were transferred to a plastic terrarium, later produced three separate, cylindrical clutches, containing 62, 65, and 87 yolk-rich eggs. Our records of this species represent the first from Angola.

***Leptopelis* sp. 1; (MTD 48873)**

Fig. 5e

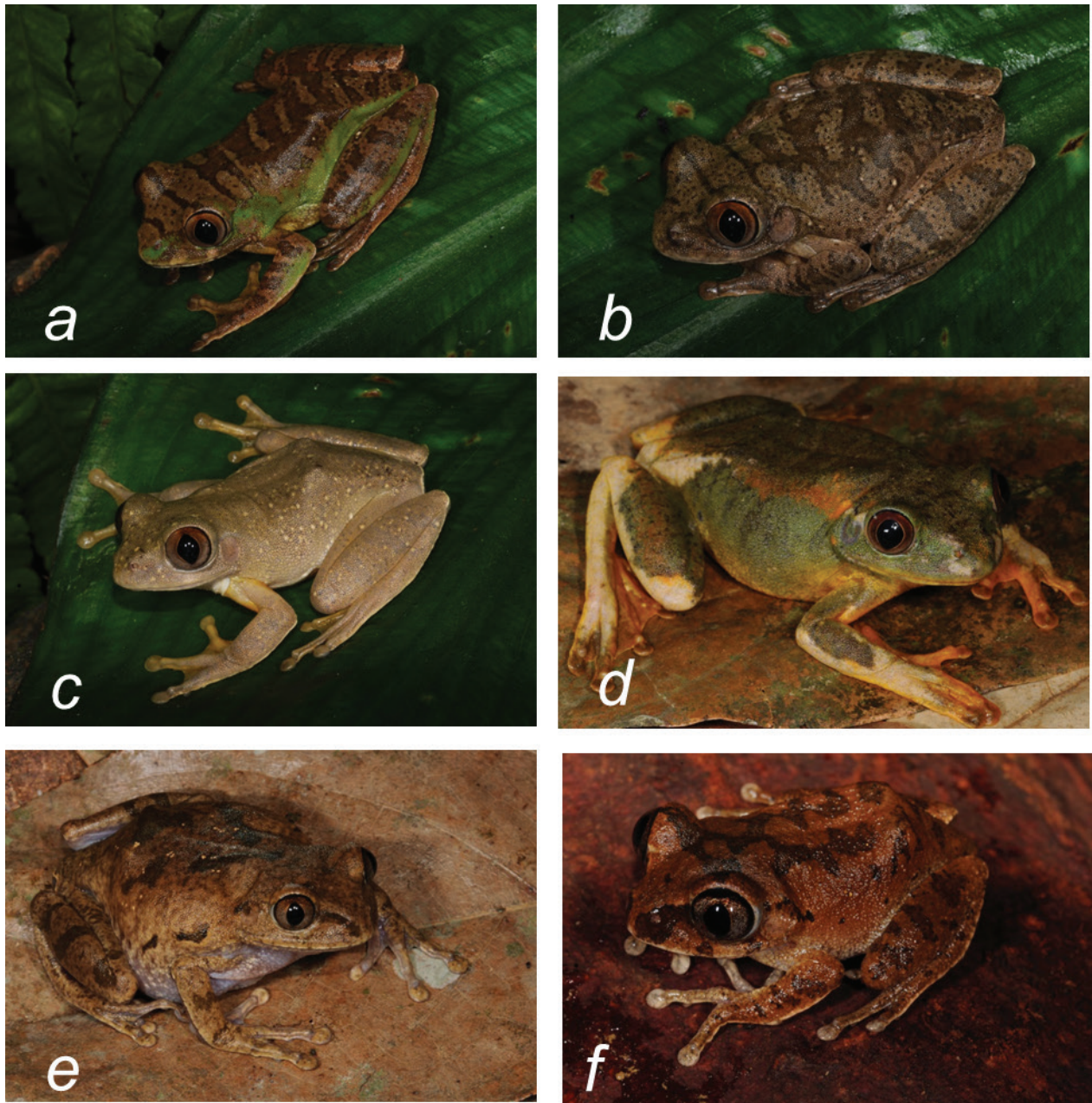
This possibly undescribed species superficially resembles *L. jordani* but genetically does not match any known taxon for which sequence data are available. A single specimen was found in a forest patch connecting the Serra do Uíge with the Serra do Pingano.

***Leptopelis* sp. 2; (MTD 49605)**

This species superficially resembles *L. bocagei* but genetically does not match any known taxon for which sequence data are available. A single specimen was collected in the north-eastern municipality of Milunga.

***Trichobatrachus* cf. *robustus* Boulenger, 1900; (MTD 48622, 48623, 48624, 48958)**

A single adult and several tadpoles were recorded in the Serra do Pingano. SPFE populations belong to a lineage that is genetically distinct from populations in Cameroon and Gabon. Further studies are required to clarify the status of the SPFE populations (Ernst et al. 2014).



**Figure 5.** Different *Leptopelis* sp. species recorded within the SPFE a.–d. Differently colored and patterned *Leptopelis millsoni* from the same locality in SP e. *Leptopelis* sp. 1 from transition between SP & SU f. *Leptopelis aubryi* from SV.

## Bufonidae

*Sclerophrys pusilla* (Mertens, 1937); (MTD 48686, 48688, 48678, 48679, 48680, 48681, 49835, 48874, 48875, 48876, 48877, 49669, 49670)

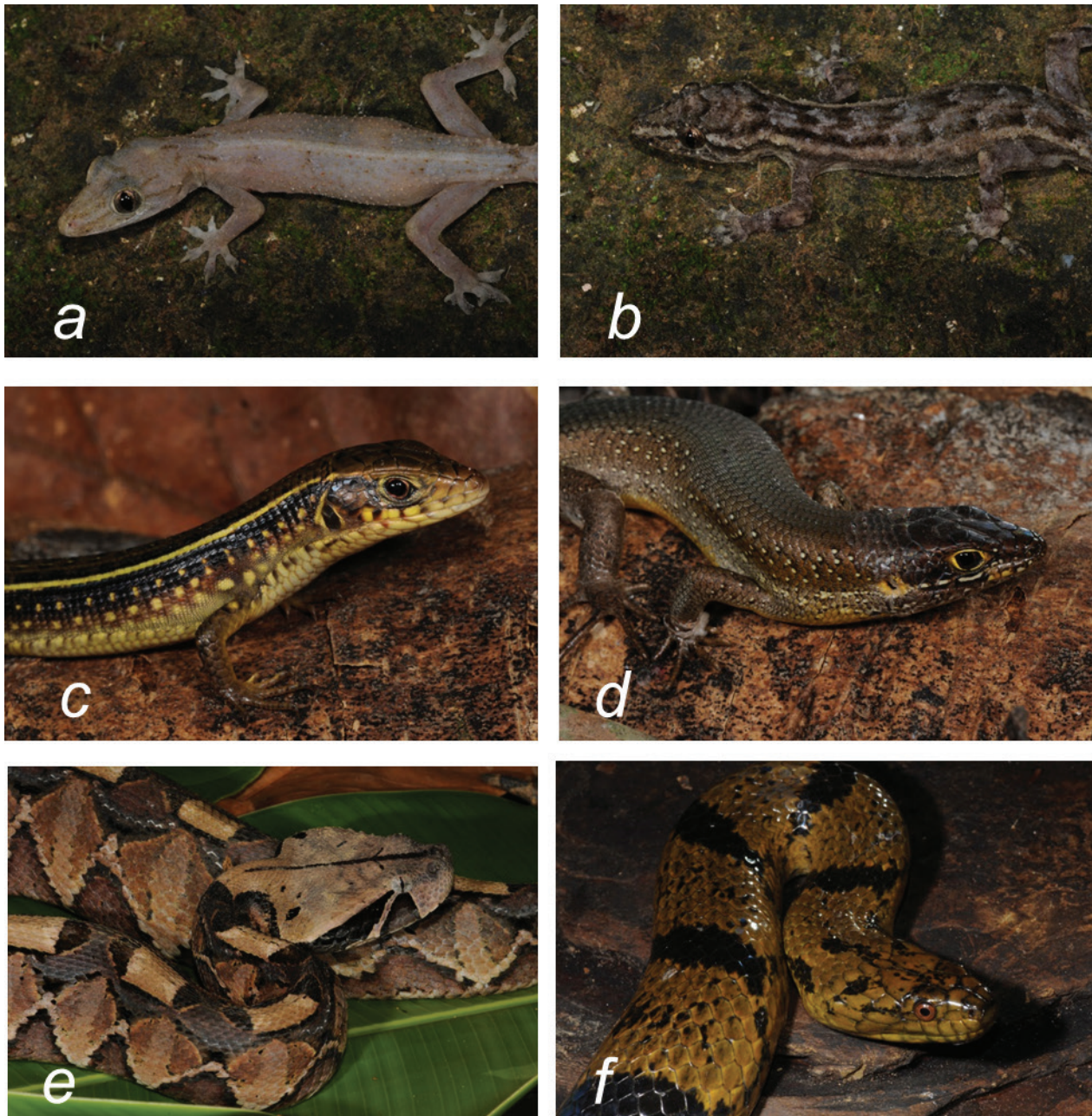
The species was previously recorded as *S. maculata* but removed from synonymy by Poynton et al. (2016). Angolan records were sometimes confused with *S. funerea*, a species commonly associated with forest habitats. Although widespread throughout the province and occurring in a wide array of different habitats, *S. pusilla* was more frequently found in degraded forest habitats and the

bordering open matrix, always in the vicinity of rivers and small streams, than in open savannah habitats.

*Sclerophrys regularis* (Reus, 1833); (MTD 48687, 48685, 48682, 48683, 48684, 49668)

Unlike the previous species, *S. regularis* was exclusively found in disturbed or open savannah habitats, including rural settlements and peri-urban or urban areas. The taxonomic boundaries between *S. regularis*, *S. gutturalis*, and even *S. pusilla* in Angola are poorly understood and further studies are needed to clarify the actual status of the northern Angolan populations.





**Figure 6.** Reptile species recorded within the SPFE **a.** *Hemidactylus paivae* (“cave-morph”) from calcereous inselberg cave systems of SV **b.** *Hemidactylus paivae* (“forest-morph”) from forest patch in the same locality in the SV **c.** Juvenile *Gerrhosaurus* cf. *nigrolineatus* from SU. **d.** *Trachylepis maculilabris* from UP **e.** *Bitis gabonica* from SP **f.** *Grayia ornata* from SP.

***Sclerophrys* cf. *superciliaris* (Boulenger, 1888); (MTD 48908, 48909, 49662, 49663, 49664)**

Fig. 3f

This species was recorded from two localities within the SPFE, always associated with fast-flowing streams. Adults were frequently found at night on rocks in the middle of streams, and during the day, they were sleeping on branches overhanging these streams. Freshly metamorphosed toadlets were recorded in November. Although this species was previously collected in the Angolan provinces of

Cuanza Norte and Huambo during the “Deutsche Angola Expedition 1952–1953”, with vouchers deposited in the herpetological collection of the Zoologisches Museum Hamburg (ZMH A03799, ZMH A03854, ZMH A09489), there are no published records of *S. superciliaris* for Angola. The thorough revision by Barej et al. (2011) did not include specimens from Angola. These authors originally designated individuals of the Lower Guinean forest block populations as *S. superciliaris superciliaris* and those of the Upper Guinean forest block populations as *S. superciliaris chevalieri*. Recently, Channing and





**Figure 7.** Pristine and disturbed habitats in the Serra do Pingano Forest Ecosystem (SPFE). **a.** Intact forest cover in the Serra do Pingano. **b.** Riparian forest system with waterfall on steep terrain in the Serra do Pingano. **c.** Clearcut after slash-and-burn activity at higher elevations (upper slope and ridge) of the Serra do Pingano. **d.** Intentional burning on the northeastern slope of the Serra do Pingano. **e.** Mosaic of previously burnt and still forested patches on northeastern slope of the Serra do Pingano. **f.** Freshly cleared forest patch at transition between the Serra do Pingano and the Serra do Uíge, now used for plantation agriculture. Locality, in which several amphibian species (e.g. *Alexeroon hypsiphonus*, *Sclerophrys* cf. *superciliaris*) had been recorded for the first time in Angola only 3-4 years prior to the impact. .

Rödel (2019) treated *S. chevalieri* and *S. superciliaris* as separate species. Barej et al. (2011) distinguished the subspecies based on several morphological characteristics. Individuals collected in the SPFE show intermediary

characteristics between these former subspecies but are genetically closer to the West African *S. s. chevalieri* (Ernst and Schmitz unpubl.). The Angolan specimens unmistakably indicate that a revision is required to clearly



separate the species and subspecies of African horned toads across the known range. *Sclerophrys superciliaris* is the only African amphibian that is currently listed under CITES I.

***Sclerophrys* sp. 1; (MTD 48743)**

Fig. 4e

A single specimen of a possibly undescribed species *Sclerophrys* was recorded from Quimbunda swamp near Negage. The morphology and habitus of this taxon superficially resembles *Sclerophrys gracilipes*, but it does not genetically match any known species for which sequence data are currently available.

Dicroglossidae

***Hoplobatrachus occipitalis* (Günther, 1858); (MTD 48718, 48910, 49841)**

This species is widespread throughout the province. We previously recorded this species exclusively from open savannah type and degraded habitats near larger rivers (Ernst unpubl.). In 2019, the species was found in an area of the Serra do Pingano that had been forested but was cleared and converted to a mixed crop plantation in 2017. This species was absent at this site in all previous recording years, and it seemed to have replaced the large-river associated pyxicephalid *Amietia angolensis*, which was previously recorded and observed to reproduce in that segment of the river. Whether this absence is the result of direct competition, or even larval predation by the carnivorous tadpoles of *H. occipitalis*, remains unclear. *Amietia angolensis* was still recorded in other upstream segments of this river still bordered by degraded forest remnants; this indicates that the replacement process is at least in part directly driven by habitat alteration.

Hyperoliidae

***Afrixalus osorioi* (Ferreira, 1906); (MTD 49709, 49710, 49711, 49856, 49857, 49859, 49860, 49861, 49862, 48861, 48862, 48863, 48864, 48865)**

In Angola, this species was previously only recorded from its type locality at Quilombo, Cuanza Norte, but apparently it is more widespread. We frequently recorded this species in degraded forest.

***Afrixalus wittei* (Laurent, 1941); (MTD 48720, 48721, 48722, 48723, 48724)**

This species was recorded in open savannah and farm bush habitats, even in urban areas such as the campus of Kimpa Vita University in Uíge.

***Afrixalus* aff. *fulvovittatus* sensu Channing and Rödel 2019; (MTD 48857, 48858, 48859, 48860, 49676, 49677, 49678, 49679, 49681)**

This species was found in wet savannahs and open grasslands in the planalto de Mucaba. Its status and distribution remain unclear and require further investigation. Until the taxonomic status of the species recorded in Uíge has been clarified, we tentatively assign it to the *Afrixalus* aff. *fulvovittatus* lineage as construed by Channing and Rödel (2019).

***Alexteroon hypsiphonus* Amiet, 2000; (MTD 48923, 48924, 49697)**

Fig. 3a

The Angolan records represent the southernmost records of the genus and the first records for the country. This species occurs throughout the SPFE but is restricted to riparian habitats in both primary and degraded forests. Males were heard calling from trees overhanging streams by several metres. Calling perches were very often in myrmecophytic *Macaranga* sp. trees. Therefore, our attempts to catch individuals often resulted in attacks by associated ants. Whether this calling site selection was coincidental or represents a predator avoidance strategy is unclear and requires testing. Although the morphology of males of the SPFE population largely corresponds to Amiet's (2000) description of the type, they differ in at least one prominent feature used to distinguish *Alexteroon* from the related *Hyperolius*, to which *Alexteroon obstetricans* was originally assigned by Ahl (1931). Gular coloration in *Alexteroon* was originally described as always being white or partially translucent but never yellow, as in some *Hyperolius* species. However, males of the SPFE population feature a yellow-colored throat which fades when preserved in ethanol. The status of the Angolan populations, the true distribution of *Alexteroon*, and the position of this genus within the larger hyperoliid phylogeny is currently being comprehensively revised (Ernst et al. in prep.); this will include the re-analysis of the type material of the three previously described *Alexteroon* species.

***Hyperolius bocagei* Steindachner, 1867; (MTD 48941, 48942, 48943, 48944, 48945, 48946)**

This species was exclusively found in open savannah habitats outside the core SPFE area. It was previously suggested to be part of the *Hyperolius viridiflavus* super-species (Marques et al. 2018). Only Angolan populations should probably be regarded as the currently recognized nominal species, *Hyperolius bocagei*.

***Hyperolius cinnamomeoventris* Bocage, 1866; (MTD 48935, 48936)**

This species was recorded from degraded open habitats in peri-urban settings, such as the campus of Kimpa Vita

University, and open savannah habitats in the northern region of Quimbele. Bell et al. (2017) considered *H. cinna-momeoventris* to be a complex of several species in need of revision.

***Hyperolius dartevellei* Laurent, 1943; (MTD 49703, 49704, 49727, 49728, 49729, 49730, 49731, 49732, 49733, 49734, 49159, 49162, 49163, 49257)**

This is a small species of the *nasutus*-complex and was removed from the synonymy of *Hyperolius adspersus* by Channing et al. (2013). It was recorded from open savannah habitats outside the core SPFE, such as the planalto de Mucaba region north to Makela do Sombo.

***Hyperolius cf. guttulatus* Günther, 1858; (MTD 48954, 48955, 48956, 48939, 48940)**

This is a bulky, variable species, which was recorded from open wet and mixed forest savannah in the northern region of Quimbele. The main color patterns observed were either uniform yellowish or orange-brown with small dark spots. Both sexes lack the dark stripe extending from snout tip to eye, typical for *H. guttulatus* or *H. phantasticus*. *Hyperolius cf. guttulatus* also differs from *H. phantasticus* in its ventral coloration, which is uniformly translucent in the former and yellowish with black spots as in the later.

***Hyperolius parallelus* Günther, 1858; (MTD 49156, 49157, 48765, 48766, 48767, 48768, 48783, 48784, 48785, 48786, 48787, 48798, 48799, 48800, 48918, 48919, 48920, 48921, 49682, 49683, 49684, 49685, 49686, 49687, 49688)**

This species is widespread throughout the province in a wide array of open and degraded habitats, including peri-urban farming areas with fishponds. It is a greatly variable species. Marques et al. (2018), referred to this species as *Hyperolius angolensis*, and Channing and Rödel (2019) and Dehling and Sinsch (2019) considered it to belong to the *Hyperolius viridiflavus* superspecies. Given the complex and challenging taxonomy of this group, we collectively refer to the population in Uíge province as *Hyperolius parallelus*, realizing that this assignment may be provisional until species and corresponding distributions have been clarified.

***Hyperolius pardalis* Laurent, 1948; (MTD 48947, 48948, 48949, 48950, 48951, 48952)**

This species was recorded from open wet and mixed forest savannah in the northern region of Quimbele, where it was syntopic with *Hyperolius cf. guttulatus* and *Kassina senegalensis*. Individuals in these populations differ in coloration from Cameroonian individuals by having a darker, copper-brown dorsal coloration (versus cream brown to yellowish in the Cameroonian ones) and smaller white spots on venter extending ventrolaterally.

***Hyperolius platyceps* (Boulenger, 1900); (MTD 49702)**

This species was only recorded from Mucaba swamp, planalto de Mucaba, and there only within a tiny swamp forest fragment that is severely impacted by logging. This is the only forest fragment remaining in an otherwise cleared moorland system which is heavily exploited for sand extraction for road construction.

***Hyperolius sp. 1*; (MTD 49858)**

This is the only *Hyperolius* species recorded from dense forest within a core SPFE locality connecting the Serra do Pingano with the Serra do Uíge. Males emit high-pitched metallic calls that are tonally similar to the syntopically occurring *Alexteroon hypsiphonus*. The single individual collected superficially resembles *Hyperolius koehleri* but shows >10% sequence divergence in the 16S gene with sequences publicly available on GenBank.

***Kassina kuvangensis* (Monard, 1937); (MTD 49671, 49672)**

Fig. 4f

This species was only recorded from Mucaba swamp, planalto de Mucaba but is probably more widespread throughout Uíge province. *Kassina kuvangensis* was previously thought to be restricted to south-central Angola and northern Zambia, but it apparently has a much wider distribution. It has also been recorded in Lunda Norte (W. Conradie pers. comm.). Calling males in the Mucaba swamp population were concealed in small holes or burrows near sedge tussocks. Whether the Mucaba swamp population is a disjunct northern population or continuous with populations of central Angola and northern Zambia in the south to Uíge in the north, needs to be clarified by surveys in the interlying areas.

***Kassina senegalensis* (Duméril & Bibron, 1841); (MTD 48902, 48903)**

This is the most widespread *Kassina* species, but across its range it likely comprises several cryptic species. Populations in different geographic regions, including those from Angola, require a thorough revision. In Uíge, the species was encountered in open wet savannahs in Quimbele, planalto de Mucaba, and savannah patches between M'Banza Congo and Songo, as well as the north-western fringes of the Serra Vamba.

## Phrynobatrachidae

***Phrynobatrachus cf. natalensis* (Smith, 1849); (MTD 48897, 48898, 48899, 48788, 48789, 48790, 48901, 49674, 49675, 49713, 49848)**

In the SPFE, this species was only found in roadside ditches and puddles in disturbed forest and open habi-

tats. It is variable in color, but most frequently there is a broad, green dorsal band. *Phrynobatrachus natalensis* comprises several cryptic species. The Angolan records have been referred to the “natalensis-A” lineage by Zimkus and Schick (2010). The true identity of the Uíge populations remains questionable.

***Phrynobatrachus* cf. *africanus* (Hallowell, 1858); (MTD 49834)**

This is a compact-bodied species. There are only a few records from the SPFE, all from degraded or recently cleared forest. This species is apparently locally not abundant, but it may be more widely distributed than currently known.

***Phrynobatrachus* cf. *mababiensis* FitzSimons, 1932; (MTD 48880, 48881, 48882, 48883, 48884, 48885, 48886, 49738, 49739, 49740, 49741, 49742, 49743, 49744, 49745, 49746, 49747, 49748, 49749, 49750, 49751, 49767)**

This widespread species occurs throughout Uíge province, except in fully forested areas. It is restricted to open savannahs and heavily disturbed grasslands, such as in the planalto de Mucaba. It is locally very abundant. Males were heard calling from the ground near small puddles and water-filled rills.

***Phrynobatrachus* aff. *mayokoensis* sp. 1; (MTD 49667)**  
Fig. 4a

A single individual was collected from the planalto de Mucaba, outside the SPFE core, in a freshly cleared forest patch near a large pond. Superficially this individual resembles *P. mayokoensis* but shows approximately 6% divergence in the 16S gene sequence (Ernst unpubl.); additionally, it can be differentiated by several morphological characters: there are three regular tubercles on the eyelid; there is a broad orange transversal band on the back but a red-orange spot is lacking on the thighs; and the throat is yellowish but with the belly uniform white. This probably is an undescribed species.

***Phrynobatrachus* aff. *mayokoensis* sp. 2; (MTD 49665, 49666)**

Two individuals, resembling *P. mayokoensis*, were collected, in the planalto de Mucaba and outside the SPFE core. These were found in a freshly cleared forest patch near a large pond. Superficially resembling *P. mayokoensis*, these individuals (compare *P. aff. mayokoensis* sp. 1) show approximately 4.5% divergence in the 16S gene sequence (Ernst unpubl.) and are also differentiated by several morphological characters: the eyelid is warty but without regular tubercles or spines; the dorsal coloration is uniformly olive-brown with irregularly arranged orange tubercles, and there is a narrow, white dorsal line; and the ventral coloration is

white, with the throat and first third to half of the body bearing irregular black blotches. The relationship of this species to *P. mayokoensis* and *P. aff. mayokoensis* sp. 1 is in need of clarification.

## Ptychadenidae

***Ptychadena anchietae* (Bocage, 1868); (MTD 48706, 48707, 48726, 48727)**

In Uíge province, this species is restricted to open savannah habitats outside core SPFE sites. Individuals from Angolan populations are clearly distinct from those of East African populations. The *P. anchietae* complex currently comprises at least three distinct lineages in East Africa, including a separate lineage in Mozambique. Therefore, Angola populations likely represent the nominal *P. anchietae* (Hübler 2016; Ernst unpubl.). Individuals from Zambia referred to as *P. anchietae* by Bittencourt-Silva (2019) likely belong to the Angolan clade, but this needs to be confirmed. The taxonomy of these frogs is currently being revised.

***Ptychadena bunoderma* (Boulenger, 1907); (MTD 48690, 48691, 48692, 48693, 48694, 48695, 48696, 48697, 48698, 48699, 48700)**

This is a very small and compact species. It is restricted to open savannah habitats outside core SPFE sites. Individuals from Uíge province mostly correspond to the holotype, both morphologically and genetically (Hübler 2016; Ernst unpubl.).

***Ptychadena oxyrhynchus* (Smith, 1894); (MTD 48702, 48846, 48847, 48849, 49845, 49846, 49847)**

This species was recorded in both open savannah habitats and degraded forest. In the latter, it was found mainly along roads. *Ptychadena oxyrhynchus* is a species complex, which consists of at least four deeply divergent lineages having distinct geographic ranges (Hübler 2016; Ernst unpubl.). The specimens from Uíge form a distinct clade that may be undescribed. The taxonomy of these frogs is currently being revised.

***Ptychadena* “*mascareniensis*” complex; (MTD 48703, 48704, 48705, 48848, 49724, 49725, 49799, 49800, 49850, 49714, 49715)**

This taxon was recorded in both open savannah habitats and degraded forest. In the latter, it was mainly along roads. *Ptychadena mascareniensis* is a complex of species which has not been fully resolved (Zimkus et al. 2017). Specimens from Uíge match “*mascareniensis*” Clade D of Vences et al. (2004), whereas specimens from southern Angola should be assigned to *P. nilotica* (Hübler 2016; Ernst unpubl.). The taxonomy of these frogs in Angola is currently being revised.

## Pyxicephalidae

*Amietia angolensis* (Bocage, 1866); (MTD 48893, 48717, 48725, 48761, 48904, 48905, 48906, 48907, 48957, 48959, 49161, 49726, 49764, 49842, 49843, 49844)

This species is an Angolan endemic (Channing et al. 2016). This species was found exclusively within the SPFE, where it is associated with fast-flowing creeks, often in steep terrain. Males were frequently observed at the edge of small rock pools below waterfalls.

## Ranidae

*Amnirana albolabris* (Hallowell, 1856); (MTD 48719, 48739, 48740, 48741, 48742, 49699, 49700, 49701, 49765)

In Uíge, this species was frequently found in small, riparian forest pockets in otherwise open, degraded savannah habitats; however, it was also found in agricultural areas near fishponds. This species ranges widely from Uíge in the south to Maquela do Zombo in the north. Northern Angolan individuals are part of a cryptic complex of several species (Jongsma et al. 2018).

*Amnirana lepus* (Andersson, 1903); (MTD 48888, 48911, 48912, 48913, 48914, 48915, 48916, 49698)

Fig. 3d

This species has marked sexual size dimorphism, with females larger. It was found exclusively in closed forest, along creeks and waterfalls, within the SPFE. Tadpoles were frequently found in larger pools at the bottom of waterfalls. The population in the SPFE probably represents the southernmost distribution of the species (Jongsma et al. 2018).

## Rhacophoridae

*Chiromantis rufescens* (Günther, 1869); (MTD 49836, 49837, 49838, 49839, 49840)

Fig. 3b

Leaché et al. (2019) showed that this species, which is widespread throughout West and Central Africa, is a complex. The SPFE population was not known to Leaché et al. and was not included in their study. The SPFE records represent the first from Angola, as well as the southernmost records for the species. The assignment of Angolan frogs, to one of the lineages identified by Leaché et al. (2019) remains to be determined. In Angola, we recorded this species only at a single location in the Serra Vamba. We observed reproduction in a water-filled rut created by logging machinery in a recently logged forest patch.

## Discussion

With the exceptions of perhaps Lunda Norte (Laurent 1952, 1954, 1964; Branch and Conradie 2015) and the mostly unpublished material from Cuanza Norte collected during the “Deutsche Angola-Expedition 1952–53” and deposited in the collection of the Zoological Museum Hamburg, northern Angola, and particularly Uíge province, has been largely neglected in biodiversity surveys. Apart from a very few records and observations, no comprehensive treatment of the local herpetofauna existed until today (e.g. see distribution maps by Marques et al. 2018, which have almost no entries for Uíge province). Yet, as data are acquired from throughout the province, more evidence accumulates that northern Angola, and Uíge province in particular, is central in shaping and ultimately understanding the biogeography of the entire West Central African realm. We define this realm as the region roughly extending from southern Mauritania south along the Atlantic coastline to northern Angola and including islands in the Gulf of Guinea. To the west it includes Mali, Burkina Faso, Niger, and Chad, as well as the western parts of the Central African Republic, Congo, and the Democratic Republic of Congo. Uíge province may even be important in understanding historic connections between East and West Africa, mediated by the dynamic history of the large drainage system of the Congo River (Ernst 2016). For many taxa, the Congo river basin was thought to represent a natural barrier and the southern boundary of their distribution. Our findings challenge this assumption, at least for amphibians (Ernst et al. 2014, 2015; Jongsma et al. 2018; this study) and for plants (Lautenschläger et al. 2020). Additional evidence is also available for reptiles (e.g. Wagner et al. 2008, 2009); increasingly, the number of species found outside their previously reported distributions is proof that current biogeographical delimitations of Sub-Saharan taxa are, to a considerable extent, simply a reflection of sampling gaps and taxonomic misidentifications rather than true biogeographical patterns. Moreover, these new floral and faunal data shed light on the forest history of the whole region. While Pliocene or even Miocene dynamics may have been more important for speciation events in many African amphibian and reptile groups (e.g. Tolley et al. 2008; Bell et al. 2015), geologically younger events may have significantly shaped the present-day distribution of taxa. If included in larger biogeographical models, the findings from northern Angola may contribute to solving questions about early-Pleistocene glaciation dynamics, which are assumed to have been responsible for the recent and historic extent of the Guineo-Congolian tropical forest phytogeographic region. A Late Quaternary connection between Central African rainforest patches has previously been hypothesized from palaeoenvironmental reconstructions (Maley 1991). Maley’s (1987) analyses have also clearly shown that montane vegetation extended to low altitudes, particularly in northern Angola and the southern DRC, making a previous link between central African forest biomes as far apart as Cameroon and



the forest remnants of northern likely Angola (see also Wagner et al. 2008). This seems to be supported by the occurrence of forest-associated amphibian species, which have a suggested distributional centre in Central Africa (e.g. Ernst et al. 2014). Without doubt, the palaeoenvironmental history of the region is much more complex than previously assumed, and the debate surrounding the precise location of late-Pleistocene forest refuges has not yet been convincingly settled (Colyn et al. 1991). In the case of Angola, even more recent accounts of forest dynamics and fragmentation are lacking, and the disentangling of recent and historic drivers of biogeographical patterns poses an additional challenge. Thus, data derived from various taxonomic groups are badly needed to reduce existing knowledge gaps. The challenge will be to gather these data through intensified surveys.

### Management and conservation recommendations

Evidence from our herpetofaunal field surveys in the SPFE supports an assumed Late Quaternary connection with Central African forest systems and its potential role as late-Pleistocene forest refuge. Our results highlight the prominent role of northern Angola, and the SPFE in particular, in protecting and safeguarding significant and unique portions of Angola's biodiversity. However, if deforestation and habitat degradation continue at the alarming rates observed during 2018 and 2019, this exceptional African rainforest ecosystem, including much of its amphibian and reptile diversity, will be lost forever. A closed rainforest site, which connected the Serra do Uíge with the Serra do Pingano, where we visited in 2016, and where *Alexeteron hysiphonus* was recorded for the first time in Angola, had been cleared for agricultural use two years later (Fig. 7f). Slash-and-burn agriculture is very prominent in the region. Such burning is particularly harmful to the steep and still forested slopes of the cordilleras, as the chimney effect can lead to rapid, uncontrolled spread of fires upslope that then destroy huge areas of intact forest (Fig. 7c–e). Consumption of amphibians (e.g. *Amietia angolensis*) has been reported by local inhabitants, but amphibians are not frequently seen in the extensive bush-meat markets, nor are they important elements in the diets of local people, as is the case in West Africa (e.g. Mohneke et al. 2010). The situation is somewhat different for reptiles (Gonçalves et al. 2019), and larger species, in particular, such as *Python sebae*, *Varanus niloticus*, and *Kinixys* sp., and to a lesser extent, the large vipers of the genus *Bitis*, are frequently observed in bush meat markets and hunted and consumed locally. Apart from direct consumption, snakes, whether venomous or non-venomous, are particularly prone to being killed out of fear. This also applies to chameleons (*Chamaeleo* spp.), which according to popular belief, are associated with death. They are sometimes even considered venomous and are often killed as a result.

In contrast to large mammals and more mobile organisms, such as birds, habitat size seems less important than habitat diversity in conserving amphibian diversity (Brüning et al. 2018). This may be one of the reasons why both diversity and species composition in the SPFE indicate high potential for preserving amphibian and reptile species unique to the West-Central African biogeographic realm and northern Angolan forest ecosystems, despite that habitats are being degraded and lost at alarming rates, leaving only very small patches of still intact forest. The species composition in the amphibian and, to a lesser degree, reptile assemblages partially resembles that of submontane Central African rainforests of Cameroon and Gabon. A few faunal elements indicate a connection to the larger Congolian rainforest. In some cases the closest relatives are found in the Albertine Rift of East African Uganda or even Kenya. However, in several cases species recorded from Uíge province show distinct lineage divergence and may actually represent distinct taxa, endemic to the northern Angolan forest of Uíge province. Yet, the presence of typical farm-bush and savannah species is a clear indication that the respective habitats are already seriously damaged. Habitat loss through uncontrolled slash-and-burn agriculture and encroachment into pristine forest patches is a major concern everywhere we visited. It is most dramatic in the Serra do Uíge and the eastern slope of the Serra do Pingano, where virtually all low-lying forests were either disturbed or completely cleared, with only forest on steep slopes remaining relatively intact. The lowland corridors connecting all three serras have been entirely cleared for agriculture. The only existing links are small pockets of gallery forest along rivers (e.g. Rio Loge), which probably represent the only corridors for migration and genetic exchange between otherwise disconnected populations (potential for river-associated species, such as *Amietia angolensis* or *Sceloporphrys cf. superciliaris*). Continued logging also leads to high levels of disturbance and severe alteration of the microclimate and water balance. Due to the physiology and biphasic lifecycle of amphibians, they are especially susceptible to these changes and prone to local extinctions. Although habitat size may not be of utmost importance for the protection of amphibians, habitat diversity, which is important, is likely to increase with habitat size. A minimum habitat size is essential to maintain key ecosystem properties that directly affect amphibians. Our observations clearly show that some disturbance-tolerant species usually associated with savannah habitats have managed to invade closed forest areas within very short time using logging roads and agricultural areas as dispersal corridors; examples are *Hoplobatrachus occipitalis* and the *Ptychadena "mascareniensis"* complex), which are now well established within the SPFE, and it is likely that they will compete and eventually displace truly forest species.

Thus, the highest priority should be given to halting or strictly controlling ongoing encroachment and uncontrolled farming activities, such as slash-and-burn agriculture, as well as logging. One legislative issue requiring

attention involves the frequent noncompliance of official forestry laws and uncontrolled logging outside designated times. Core areas surrounding lotic water systems (rivers, streams, waterfalls, etc.) are particularly sensitive and crucial to the protection of several high-priority species and should be spared from logging and burning. Improvement of infrastructure in the SPFE, especially road construction on the southern flank of the Serra do Pingano facing the Serra Vamba, is another serious concern. By allowing for easy access to forest sites, new roads into previously inaccessible forest lead to numerous impacts, including a massive increase in the illegal and unsustainable harvest of forest resources, especially bushmeat (Laurance and Edwards 2014). Both illegal logging and extensive road construction are already very evident in the SPFE. Although poaching may not be a direct threat to most amphibians, it strongly affects the population sizes of reptiles, some of which are included in the IUCN Red List and regulated under CITES (*Kinixys* spp., *Varanus* spp., and *Python* spp.). Many species are regularly hunted for food, medicinal, or ceremonial purposes. Hunting pressure on reptiles is likely to increase due to the severe over-exploitation and recent lack of more traditional game such as large and medium-sized mammals, and large birds.

## Conservation synthesis

In conclusion, the SPFE has an extraordinary conservation potential for amphibian and reptile diversity both in a national and pan-African context. The species composition in the SPFE is unique and consists of a high proportion of forest specialists with restricted ranges and found nowhere else in the country. Several species and species complexes require taxonomic revision, and additional undescribed species are to be expected pending results of studies already underway. Species estimates clearly show that more species are likely to be detected if survey efforts are increased. The newly recorded species shed light on the forest history of the whole region. If the newly obtained distributional data are included in larger biogeographic models, they may contribute to solving open questions concerning early-Pleistocene glaciation dynamics which are assumed to have affected the recent and historic extent of the Guineo-Congolian tropical forest phytogeographic region. This is particularly important as evidence accumulates that northern Angolan rainforests may have served as a refugium for forest taxa during periods of dramatic climatic fluctuations. This emphasizes the paramount importance of the remaining forest fragments, such as those still existent in the SPFE. The SPFE is currently threatened by increasing agricultural encroachment and uncontrolled timber extraction in the remaining forest patches, whose extent is dwindling at an alarming rate. These threats will likely push some of the rarer species to the brink of extinction within the next decade and ultimately jeopardize the long-term viability of the entire ecosystem and the services it provides to human wellbeing. In an urgent need to strictly

protect the remaining forests, destructive activities need to be controlled or abandoned. Our knowledge of the biodiversity contained in forest fragments is still patchy. Rapid biodiversity surveys, in combination with modern scientific techniques and long-term monitoring routines, are urgently needed to obtain a better understanding of the largely underappreciated biodiversity in these fragile forest remnants, to resolve both taxonomic and biogeographic questions, and to provide the basis for a more comprehensive assessment of Angola's biodiversity in general, which is a prerequisite for the development of sound and sustainable conservation strategies of its most precious and unique ecosystems. The Serra do Pingano Forest Ecosystem is central in developing and enhancing these strategies. Its protection will be the major challenge in the battle of ideas aimed at safeguarding Angola's biodiversity treasure trove for future generations of Angolan scientists who may eventually contribute to solving the pressing questions that will ultimately help fighting the life-threatening global biodiversity crisis that we experience today.

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