**Universidade de Évora - Escola de Ciências e Tecnologia**

Mestrado em Biologia da Conservação

Dissertação

# Contributions to the taxonomic revision of the African Olive-Whip snakes (Squamata: Lamprohiidae) belonging to the Psammophis sibilans-mossambicus-phillipsii species complex

Diogo Miguel dos Santos Parrinha

Orientador(es) | Paulo Sá Sousa
Luís Miguel Pires Ceríaco
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UNIVERSIDADE DE ÉVORA

## ESCOLA DE CIÊNCIAS E TECNOLOGIA

## DEPARTAMENTO DE BIOLOGIA

# Contributions to the taxonomic revision of the African Olive-Whip snakes (Squamata: Lamprophiidae) belonging to the *Psammophis sibilans-mossambicus-phillipsii* species complex

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Évora, 2020

*À minha mãe e aos meus avós, a quem devo tudo.*

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# Contributions to the taxonomic revision of the African Olive-Whip snakes (Squamata: Lamprophiidae) belonging to the *Psammophis sibilans-mossambicus-phillipsii* species complex

## Abstract

*Psammophis sibilans* is a taxonomically problematic snake species. The wide distribution and phenotypic variation led to the description of several “varieties” that comprise the *sibilans* species complex, resulting in a confusing and unstable taxonomic history. While some problems have been solved in previous revisions, the status of populations from West and Central Africa remains uncertain. Morphological data for more than 700 specimens of the *sibilans* complex was analyzed, together with available molecular data, to better understand species delimitation and diagnosis. A combination of color pattern, scalation and geographic location is the best method to diagnose species of the *sibilans* complex. Morphological and molecular data support the distinction of West African populations as a new species, and populations from Central Africa are assigned to *P. mossambicus*. We clarify and summarize the taxonomic history of the group, providing updated descriptions and distribution maps. A tentative key to problematic taxa is presented.

**Keywords:** *Psammophis*, taxonomy, nomenclature, Africa, diagnosis, distribution

## Contribuições para a revisão taxonómica das serpentes-chicote africanas (Squamata: Lamprophiidae) pertencentes ao complexo de espécies *Psammophis sibilans-mossambicus-phillipsii*

# Resumo

*Psammophis sibilans* é uma espécie taxonomicamente problemática. A ampla distribuição e variedade fenotípica conduziram à descrição de inúmeras "variedades" que constituem o complexo de espécies *sibilans*, resultando numa história taxonómica confusa e instável. O estatuto das populações da África Ocidental e Central permanece incerto. Foram analisados dados morfológicos de mais de 700 espécimes do complexo *sibilans*, a par com os dados moleculares disponíveis, de modo a compreender melhor a delimitação e diagnose das espécies envolvidas. A combinação do padrão de coloração, merística e distribuição geográfica é a melhor forma de diagnosticar as espécies do complexo. Dados morfológicos e moleculares suportam a distinção das populações da África Ocidental como uma espécie nova, e as populações da África Central são atribuídas a *P. mossambicus*. A história taxonómica do complexo é clarificada e sumarizada, e são apresentadas descrições e mapas de distribuição actualizados. É ainda apresentada uma chave provisória para as espécies problemáticas.

**Palavras-chave:** *Psammophis*, taxonomia, nomenclatura, África, diagnose, distribuição

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# Introduction

The genus *Psammophis* Boie, 1825 comprises at least 34 species of diurnal snakes, widespread throughout the African continent and extending to some parts of Asia through Arabia, occupying a wide variety of habitats (Brandstätter 1995, 1996a; Branch 1998; Geniez 2018; Spawls *et al.* 2018; Uetz *et al.* 2019). It is amongst the most taxonomically challenging African snake genus, as noted by many authors (Schmidt 1923; Bogert 1940; Loveridge 1940; Broadley 1963, 1983; Largen & Rasmussen 1993; Hughes 1999; Largen & Spawls 2010; Spawls *et al.* 2018).

Within the genus, *Psammophis sibilans* (Linnaeus, 1758) is the most commonly cited species and the most problematic. It was formally described by Linnaeus (1758) as *Coluber sibilans*, and later placed in the newly erected genus *Psammophis* Boie, 1825 *in* Oken, becoming the type-species of the genus (Anderson 1898; FitzSimons 1962; Broadley 1983; Brandstätter 1996b). For a long time, *P. sibilans* was considered a species widespread throughout most of sub-Saharan Africa with variable coloration (Günther 1858; Bocage 1866, 1895; Boulenger 1896). This incredible phenotypic variation across its wide distribution range led to the description of several “races”, varieties and subspecies (*e.g.* Peters 1882; Fischer 1884; Bocage 1895; Boulenger 1896; Werner 1919), some of them were shown to have no support, while others are currently considered full species (Loveridge 1940; Broadley 1963, 2002; Kelly *et al*. 2008). However, this situation often leads to misidentifications and the excessive synonymization, resulting in a highly confusing taxonomic history (Bogert 1940; Broadley 1963; Hughes 2004).

A first attempt to provide a detailed review of the genus in Africa was made by Loveridge (1940), who summarized all the available data and presented a thorough bibliographic review, as well as a key to the recognized taxa. Among other taxonomic changes respecting other groups within the genus, Loveridge (1940) recognized six subspecies within *Psammophis sibilans*: *P. s. schokari* (Forskal, 1775), *P. s. sibilans* (Linnaeus, 1758), *P. s. phillipsii* (Hallowell, 1844), *P. s. notostictus* Peters, 1867, *P. s. trinasalis* Werner, 1902, and *P. s. leightoni* Boulenger, 1902. A subsequent revision was provided by Broadley (1963), who recognized east and southern African populations of *P. sibilans* as a distinct taxon, provisionally treated by the author as “Olive Grass Snake” (*Psammophis* sp.). In the following decades, Broadley continued to work towards a clarification of *Psammophis* taxonomy in southern Africa (Broadley 1966, 1975, 1977, 2002). Half a century after Loveridge’s (1940) revision, Brandstätter’s (1995) unpublished PhD thesis presented a much-needed revision of the genus *Psammophis* and its close allies. The thesis was subsequently adapted and published as a book (Brandstätter 1996a), however, the taxonomic proposals presented by Brandstätter (1995, 1996a) were not entirely followed and accepted by the scientific community. An extensive review of Brandstätter’s works published by Hughes (1999) evidenced several taxonomic and nomenclatural issues regarding his proposals.

The first molecular based phylogeny of the Psammophiids was presented by Kelly *et al*. (2008) and focused in some of the most problematic taxa, as the *sibilans* species complex. This phylogeny was of uttermost importance to the taxonomic and nomenclature understanding of the group, as it validated many existing species and synonymized others. According to the authors the *sibilans* complex is composed by two clades: the *phillipsii* clade (with *P. leopardinus* Bocage, 1887, *P. brevirostris* Peters, 1881, *P.* cf. *phillipsii occidentalis* Werner, 1919, *P. p. phillipsii* and *P. mossambicus* Peters, 1882) and the *subtaeniatus* clade (including *P. rukwae* Broadley, 1966, *P.* cf. *sibilans, P. subtaeniatus* Peters, 1882*, P. sudanensis* Werner, 1919 and *P. orientalis* Broadley, 1977).

Kelly *et al*. (2008) phylogeny provided the first molecular data for most species of the genus *Psammophis*, however, no attempt was made at combining their results with the available morphological data. For this reason, the *sibilans* complex remains unresolved in many parts of its distribution, especially in West and Central Africa, as well as those regions where two or more species may be sympatric and interbreed. Previous revisions of the genus (Loveridge 1940; Brandstätter 1995, 1996a) or specific groups within the genus (Broadley 1966, 1975, 1977, 2002; Hughes 1999; Hughes & Wade 2002, 2004) were based only on morphological data and unable to provide any definitive answer to the problem. Even though Kelly *et al.* (2008) restricted the distribution of *P. sibilans* to northeastern Africa, this species was still recently cited from West (Trape & Mané 2015, 2017), Central (Jackson & Blackburn 2010) and East Africa (Vats & Safari 2014). For East and Southern Africa, Kelly *et al*. (2008) synonymized *P. mossambicus* with *P. phillipsii*, turning it into a widespread species from Senegal to South Africa. However, most authors still assign these populations to *P. mossambicus* (*e.g.* Bates *et al.* 2014; Branch 2018; Marques *et al.* 2018; Spawls *et al.* 2018), and its distribution limits are poorly known.

The status of populations from Central Africa has never been fully resolved, and even though Kelly *et al*. (2008) validated the specific status of *P. occidentalis*, data on this species is scarce and inconsistent. Specimens from Nigeria to Uganda and southwards to southern Congo have been referred to *P. sibilans* (de Witte 1941, 1952, 1953, 1962, 1966; Laurent 1954, 1956, 1964; Jackson & Blackburn 2010), *P. phillipsii* (de Witte 1962; Akani *et al*. 1999, 2002a, 2002b, 2003; Luiselli *et al*. 2004; Pauwels *et al.* 2004, 2006, 2016, 2017a, 2017b, 2018a, 2018b, 2019; Jackson *et al*. 2007; Kelly *et al.* 2008), *P. occidentalis* (Hughes & Wade 2004; Chirio and LeBreton 2007; Kelly *et al.* 2008) and *P. mossambicus* (Broadley 1991; Broadley & Cotterill 2004; Spawls *et al.* 2018). This generates taxonomic instability with implications for species distribution limits, species checklists and ultimately conservation efforts (Duarte *et al*. 2014; Romero *et al*. 2014; Oates & Ting 2015).

We follow Kelly *et al*. (2008) in considering *P. sibilans* to be restricted to Egypt and northeastern Africa. However, contrary to Kelly *et al*. (2008), we think that *Psammophis phillipsii sensu stricto* is restricted to West Africa and follow other authors in assigning eastern and southern populations to *Psammophis mossambicus* (Bates *et al*. 2014; Marques *et al*. 2018; Spawls *et al*. 2918). Due to the lack of a coherent description that might allow a confident identification, we include in this group specimens from the putative distribution range of *P. occidentalis* (Hughes & Wade 2004; Kelly *et al*. 2008). Even though Kelly *et al.* (2008) validated this species, few are the specimens that display all characters used by Hughes & Wade (2004) to diagnose *P. occidentalis*. We include *Psammophis sudanensis* and *P. rukwae* in this review due to the high number of misidentifications and their problematic taxonomic history.

The present work aims to take the first steps towards a taxonomic revision of the *sibilans* complex, starting with a comprehensive bibliographic compilation in order to solve problems associated with nomenclature and synonymy in this group. An integrative approach is conducted, combining morphological and molecular methods to better understand species delimitations and diagnosis, with the aim of stabilizing problematic taxa. An updated key for the group is also provided.

[**Shortly before the conclusion of the present dissertation, Trape *et al.* (2019) published a review of the *sibilans* complex north of latitude 12ºS, solving most of the problems that are dealt with in this work. Due to the advanced stage of this dissertation at the time the above-mentioned paper was published it is not considered for the present work. We do, however, discuss it on the Results and Discussion sections.**]

# Materials and Methods

## Material examined

Newly collected specimens were euthanized following an approved IACUC protocol (Villanova University #1866) and preserved in 10% buffered formalin in the field and subsequently transferred to 70% ethanol. Liver tissue was removed before formalin fixation and preserved in 95% ethanol. Additional material was also consulted for morphological analysis, which includes mensural and meristic data, from specimens deposited in European, American and African museum collections: **AMNH** – American Museum of Natural History, New York (USA); **ANSP** – the Academy of Natural Sciences, Philadelphia (USA); **BMNH** – Natural History Museum, London (UK); **CAS** – California Academy of Sciences, San Francisco (USA); **CM** – Carnegie Museum of Natural History, Pittsburgh (USA); **FMNH** – Field Museum of Natural History, Chicago (USA); **IRSNB** – Institut Royal des Sciences Naturelles de Belgique, Brussels (Belgium); **IICT** – Instituto de Investigação Científica Tropical, Lisboa (Portugal); **LACM** – Natural History Museum of Los Angeles County, Los Angeles (USA); **MCZ** – Museum of Comparative Zoology, Harvard University, Cambridge (USA); **MHNC-UP** – Museu de História Natural e da Ciência, Universidade do Porto (Portugal); **MHNG** – Muséum d'Histoire Naturelle, Genève (Switzerland); **MNHN** – Muséum Nationale d'Histoire Naturelle, Paris (France); **MRAC** – Musée Royal de l'Afrique Centrale, Tervuren (Belgium); **MSNM** – Museu Civico di Storia Naturale di Milano (Italy); **MUZM** – Makerere University Zoology Museum, Kampala (Uganda); **MVZ** – Museum of Vertebrate Zoology, University of California, Berkeley (USA); **MWNH** – Museum Wiesbaden, Naturhistorische Sammlungen (formerly Staatliches Museum, Wiesbaden) (Germany); **MZUF** – Museo di Storia Naturale di Firenze, Sezione di Zoologia "La Specola" (Italy); **NHMAA** – Natural History Museum, Addis Ababa (Ethiopia); **NMK** – National Museums of Kenya, Nairobi (Kenya); **NMW** – Naturhistorisches Museum, Wien (Austria); **NMZB** – Natural History Museum of Zimbabwe, Bulawayo (Zimbabwe) (including former National Museum of Southern Rhodesia, Umtali Museum and Queen Victoria Memorial Museum); **SAM** – South African Museum, Cape Town (South Africa); **SMF** – Senckenbergische Naturforschende Gesellschaft, Frankfurt am Main (Germany); **SRI** – Serengeti Research Institute, Seronera (Tanzania); **TMP** – Ditsong National Museum of Natural History, Pretoria (formerly Transvaal Museum, Northern Flagship Institution) (South Africa); **UMMZ** – University of Michigan Museum of Zoology, Ann Arbor (USA); **UUZM** – Evolutionsmuseet, Uppsala Universitet, Uppsala (Sweden); **USNM** – National Museum of Natural History, Smithsonian Institution, Washington D.C. (formerly United States National Museum) (USA); **V-F** – Vasey FitzGerald Collection. Institutional acronyms follow Sabaj (2016), with the execption of MHNC-UP, MUZM, NHMAA and V-F.

We also examined high quality photographs of the type specimens of *Psammophis occidentalis* and *Psammophis sudanensis* from the collections of the NMW; *Psammophis leucogaster* Spawls, 1983, from the collections of the BMNH; and *Psammophis sibilans* from the UUZM. Even though the Linnaeus specimens cannot be called true "types" (Brandstätter 1996b), for the purpose of this work we refer the specimen UUZM42 as the type specimen of *Psammophis sibilans*. All specimens examined and used in the analysis are listed in the Appendix 1.

### Specimens identification

Most specimens were originally examined and identified by Donald G. Broadley (DGB), whose data and identification were subsequently reviewed by the first author (Diogo Parrinha) in light of the most recent literature (*e.g.* Trape & Mané 2006; Chirio & LeBreton 2007; Kelly *et al.* 2008; Spawls *et al*. 2018). The identification of specimens was based on meristic data (scalation) - namely the number of infralabials in contact with the anterior sublinguals - and color patterns - presence of head markings, dorsolateral and ventral stripes - as well as geographic location in some cases. Due to the morphological similarity of the species in question and their poorly known delimitation, the identification of some of the specimens was preliminary, especially in those regions where several species may be sympatric, and the occurrence of intermediate specimens is frequent. For most literature records it is nearly impossible to ascertain the true identity without careful reexamination of the specimens. Older literature records generally lack detailed descriptions and information that might allow us to reach a conclusive and unmistakable identification. Besides the species once hidden under the *sibilans* complex, that would distort data referring to this species, this group is prone to misidentifications, as pointed out by Hughes (2004). Under chresonymy we try to include only citations that we confidently assign to the species in question, confirmed either by reexamination of the specimens, detailed description or geographical location. Pending comparative material from West African forests to clarify the status of *P. phillipsii*, we provisionally assign populations from east of the Dahomey Gap to *Psammophis mossambicus*. We follow Kelly *et al*. (2008) by assigning West African populations of *"P. sibilans*" to *P.* cf. *rukwae,* and treat them as a distinct taxon.

## Morphological methods

Morphological analysis (scale nomenclature, scale counts and measurements) follows Broadley (1977, 2002). Morphometric data was collected from preserved specimens, using digital calipers (0.1mm) and a stereo-microscope. Head scales terminology and disposition is illustrated in Figure 1. Whenever possible, the following characters were recorded for each specimen: snout-vent length (SVL); tail length (TL); number of ventrals following the Dowling system (Dowling 1951) (V); number of subcaudals pairs, excluding the cloacal scale (SC); state of the cloacal scale, "E" for entire or "D" for divided (CS); neck scale rows, measured one head length behind the head (NSR); midbody scale rows (MSR); vent scale rows, measured one head length before the vent (VSR); number of supralabials (SL), and which of those that enter the orbit; number of infralabials (IL), and how many of those in contact with the anterior sublinguals (IL-ASL); number of preoculars (Preoc); number of postoculars (Postoc); number of nasals; temporal formula; type of contact between preocular and frontal scales (Preoc-F). The presence and type of head markings, dorsolateral stripes, and ventral lines was also recorded and coded as detailed in Table 1.

Regarding the temporal formula, most authors (*e.g.* Schmidt 1923; Laurent 1964; Marais 2004; Trape & Mané 2006) give 2+2 or 2+3 as the most common formula, considering the anterior temporals as those scales immediately after the postoculars. However, this study follows Broadley (1966, 2002) in considering ½+3 as the usual arrangement, which means that there are usually 2 anterior temporals, of which the lower is vertically divided. The temporal formula would be recorded as ½+3 by Broadley (Fig. 2-A), and 2+2 by other authors (Fig. 2-B). Despite ½+3 being the most common arrangement, fusion of scales is frequent, giving rise to a variety of possible formulas.

**Table 1** – Numerical coding used for variables associated with color pattern.

| Variable | Description | Numerical code |
|---|---|---|
| **Head markings** | Head markings absent or reduced to scattered dark spots | 0 |
| | Faint to distinct head markings present | 1 |
| **Dorsolateral stripes** | Dorsolateral stripes absent | 0 |
| | Faint to distinct dorsolateral stripes present | 1 |
| **Ventral stripes** | Ventral lines absent | 0 |
| | Broken lines formed by series of dark dots or dashes (discontinuous) | 1 |
| | Faint to distinct ventral lines (continuous) | 2 |

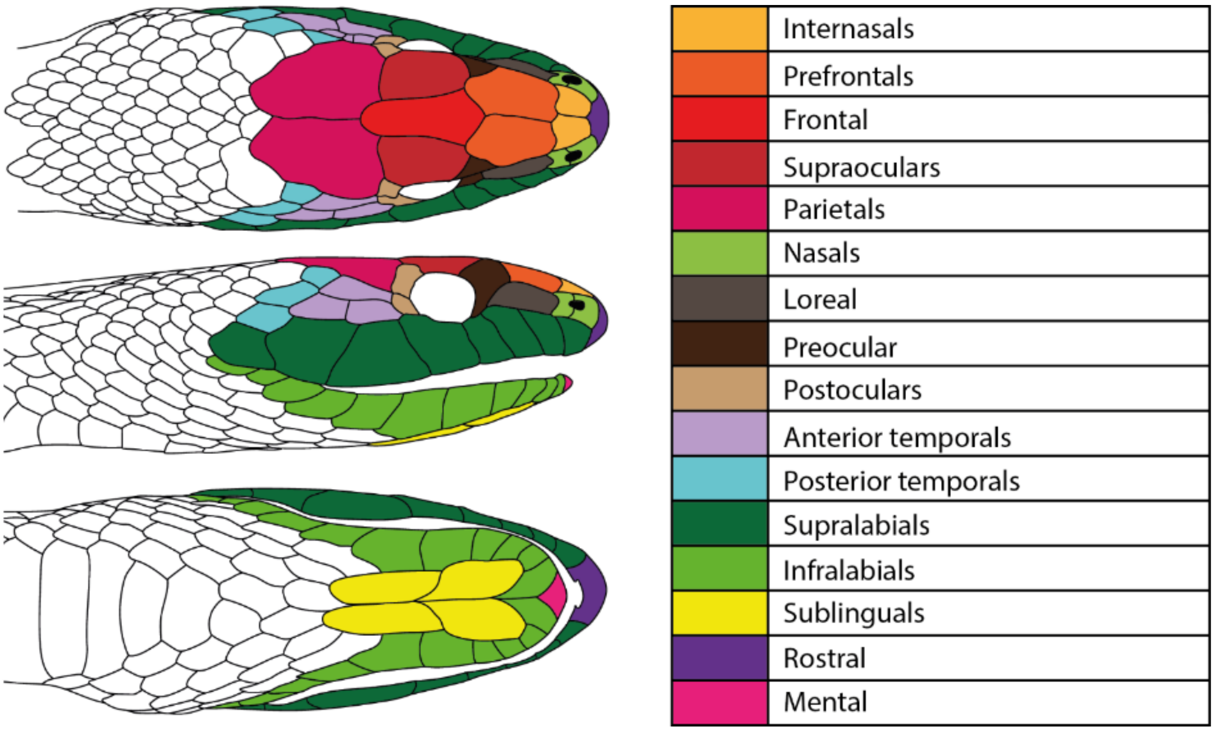

**Figure 1 –** Head scales arrangement common in *Psammophis* spp. and nomenclature adopted in this study.

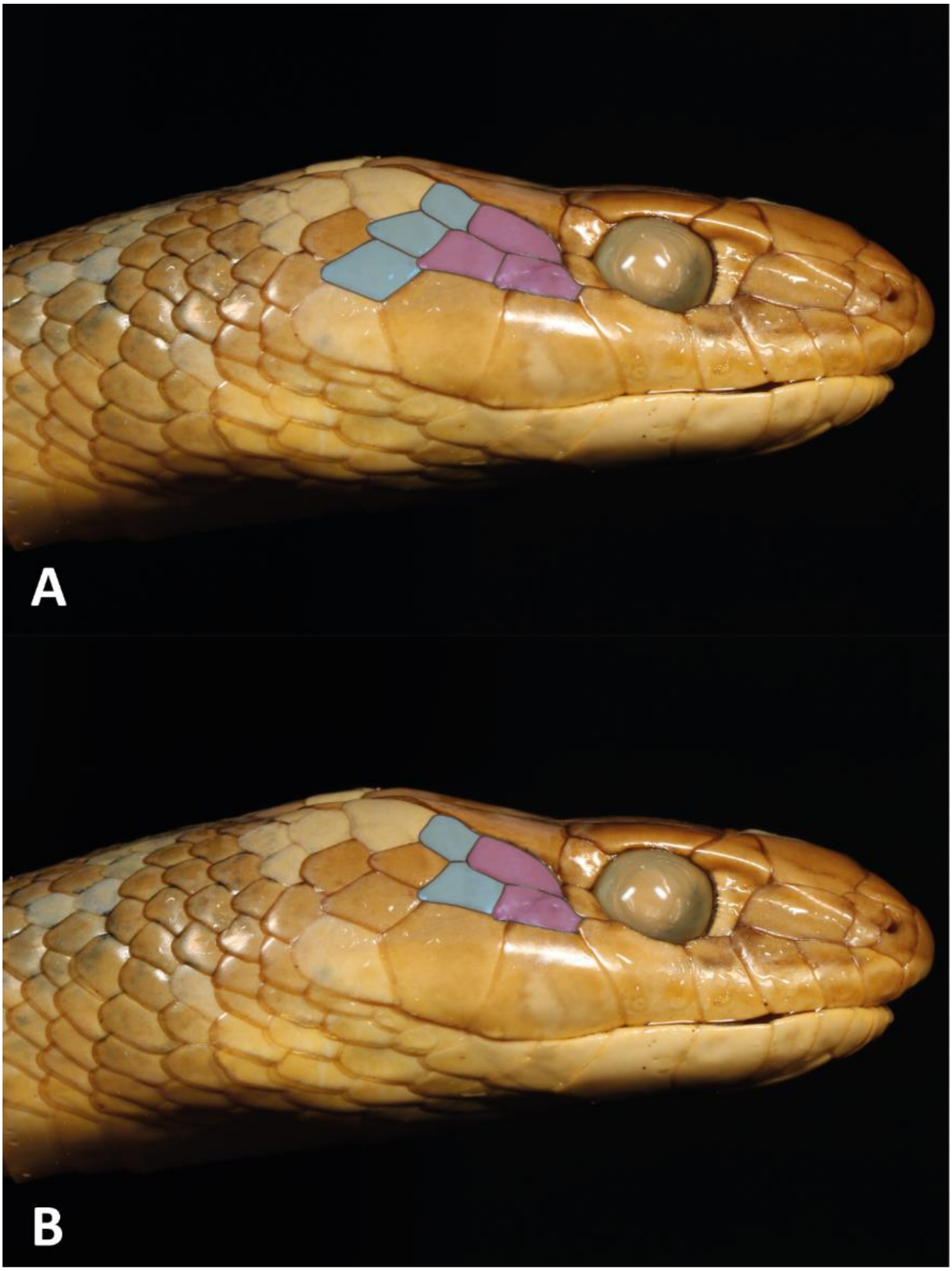

**Figure 2 –** Comparison between temporal formula as considered by Broadley (**A**) and other authors (**B**).

Loveridge (1940) and Broadley (1977, 1987) drew attention to caudal autotomy and incomplete subcaudal counts in the genus *Psammophis*. When caught by the tail, these snakes have the ability to spin on their own axis and break the tail at the point where it is held, remodeling the terminal point to form a blunt cone (see Fig. 3). While in some cases it may be easy to identify a truncated tail, it becomes harder if the injury occurred early in life and the missing portion is a short one, thus an effort was made in order to reject incomplete subcaudal counts and tail lengths, as well as unusually low subcaudal counts.

**Figure 3 –** Terminal point of a complete tail: **A.** *Psammophis* cf. *rukwae* (IICT/R GB9); and a truncated tail: **B.** *Psammophis mossambicus* (IICT/R 29-1958) (Photos by Diogo Parrinha).

### Statistical analysis

Due to the high number of asymmetrical specimens (*e.g.* with a different number/arrangement of scales on both sides of the head), statistical analysis was conducted independently for each side of the specimens (left and right). Multivariate analysis was conducted using the FactoMineR software package (Le *et al.* 2008). Some specimens were badly damaged, in some cases only the head was available, which results in incomplete meristic counts and missing data. To address this issue, missing values were imputed using the missMDA software package (Josse & Husson 2016).

### Phylogenetic analysis

For phylogenetic analysis we used sequences previously published by Rato *et al.* (2007) and Kelly *et al.* (2008) available on GenBank. The dataset included the mitochondrial gene NADH dehydrogenase subunit 4 (ND4) and the tranfer RNA (tRNA) genes for serine (tRNA$^{Ser}$), histamine (tRNA$^{His}$) and leucine (tRNA$^{Leu}$). Sequences of *Malpolon monspessulanus* (Hermann, 1804) and *Ramphiophis rostratus* Peters, 1854 were downloaded from GenBank and used as outgoups, as both genera are closely related to *Psammophis* (Kelly *et al.* 2008). All sequences used are detailed in the Appendix 2.

Sequences were aligned using the ClustalW alignment tool in MEGA 6.06 (Tamura *et al.* 2013). A phylogenetic tree was inferred by performing a Maximum Likelyhood (ML) analysis on the ND4 and tRNA dataset in MEGA 6.06 (Tamura *et al*. 2013). The best substitution model (HKY + G) was determined with MEGA using the Bayesian information criterion (BIC). Phylogenetic robustness was estimated by running 1000 random bootstrap replicates (Felsenstein 1985).

# Results

### Morphology

Most meristic characters show little or no variation among the studied groups, as can be seen in Tables 2, 3 and 4. The number of dorsal scale rows is almost invariably 17 NSR, 17 MSR and 13 VSR. Despite some minor variation, there are usually eight SL, with the fourth and fifth scales in contact with the eye; one preocular and two postoculars; two nasal scales, of which the posterior may be divided or present a horizontal ridge. The cloacal scale is divided in all species (Table 4), although 6% of *Psammophis mossambicus* specimens present an entire cloacal scale. In rare cases the cloacal scale may be half divided or even divided in more than one place. Temporals are usually ½+3, but fusion of scales gives rise to a variety of temporal arrangements, regardless of the species. Infralabials are usually 10(4) in *P. mossambicus* and *P. sudanensis*, while *P. sibilans*, *P. rukwae* and *P.* cf. *rukwae* have 11 infralabials, with the first five in contact with the anterior sublinguals (Tables 3 and 4). The type of contact between the preocular and frontal scales (Preoc-F) shows considerable variation in *P. sibilans*, *P. sudanensis* and *P.* cf. *rukwae*, while in most *P. mossambicus* and *P. rukwae* specimens there is no contact between the preocular and frontal scales (Table 4, Fig. 5-A).

The results evidenced morphological differences between topotypical *P. rukwae* and what we provisionally treat as *P.* cf. *rukwae* from West Africa, which encourage us to treat them as distinct taxa. The differences in the number of ventrals and subcaudals shown in Figures 4-A and 4-B result in a higher ventrals:subcaudals ratio in topotypical *P. rukwae* (Fig. 4-D). Furthermore, while in most East African specimens there is no contact between the preocular and frontal scales, in more than 50% of West African *P.* cf. *rukwae* there is contact between these two scales (Fig. 5-A, Tab. 3).

*Psammophis mossambius* can attain the largest SVL, followed by *P. sibilans* (Table 3, Fig. 4-C). Table 2 shows a considerable overlap in the ranges of ventrals (Fig. 4-A) and subcaudals (Fig. 4-C), however, *P. rukwae* seems to have slightly more ventrals and less subcaudals, on average, than other species, consequently resulting in a higher ventrals:subcaudals ratio.

**Table 2** – Variation in the number of ventrals and subcaudals in the studied species.

| | **Ventrals** | | | | **Subcaudals** | | | |
|---|---|---|---|---|---|---|---|---|
| | ***n*** | **Range** | **Mean** | **S.D.** | ***n*** | **Range** | **Mean** | **S.D.** |
| *P. sibilans* | 144 | 151–190 | 167,1 | 6,8 | 102 | 89–129 | 107,3 | 7 |
| *P. mossambicus* | 177 | 156–188 | 170 | 5,5 | 147 | 81–121 | 97,6 | 5,1 |
| *P. sudanensis* | 21 | 153–180 | 165 | 7,4 | 12 | 92–110 | 103,8 | 5,9 |
| *P. rukwae* | 61 | 160–179 | 171,1 | 4,3 | 30 | 83–112 | 92,9 | 5,7 |
| *P.* cf. r*ukwae* | 98 | 154–183 | 167,3 | 5,5 | 61 | 87–116 | 103,2 | 5,1 |

**Table 3** – Percentage of occurrence of each class for Cloacal Scale (CS), type of contact between Preocular and Frontal scales (Preoc-F) and the number of Infralabials in contact with the anterior Sublinguals (IL-ASL).

| | **CS** | | **Preoc-F** | | | **IL-ASL** | |
|---|---|---|---|---|---|---|---|
| | **E** | **D** | **NC** | **SPC** | **C** | **4** | **5** |
| *Psammophis sibilans* | 4% | 96% | 61% | 11% | 28% | 16% | 84% |
| *Psammophis mossambicus* | 6% | 94% | 91% | 1% | 3% | 95% | 4% |
| *Psammophis sudanensis* | 0 | 100% | 24% | 12% | 64% | 95% | 4% |
| *Psammophis rukwae* | 0 | 100% | 89% | 2% | 9% | 9% | 93% |
| *Psammophis* cf. *rukwae* | 3% | 97% | 30% | 9% | 61% | 5% | 95% |

**Table 4** – Variation in size and meristic characters (**SVL** – snout vent length; **TL** – tail length; **NSR** – neck scale rows; **MSR** – midbody scale rows; **VSR** – vent scale rows; **SL** – number of supralabials; **IL** – number of infralabials; **IL-ASL** – number of infralabials in contact with the anterior sublinguals; **Preoc** – number of preoculars; **Postoc** – number of postoculars; **Nasals** – number of nasals) for each species (mean ± standard deviation [min; max]).

| | *Psammophis sibilans* | *Psammophis mossambicus* | *Psammophis sudanensis* | *Psammophis rukwae* | *Psammophis* cf. *rukwae* |
|---|---|---|---|---|---|
| **SVL** | 539,6 ± 231,6 [211; 1380]<br>(n=86) | 698,3 ± 280 [153; 1415]<br>(n=181) | 569,4 ± 253,1 [217; 1010]<br>(n=14) | 648,5 ± 301 [205; 1200]<br>(n=42) | 589,1 ± 261,7 [195; 1010]<br>(n=64) |
| **TL** | 235,3 ± 89,3 [87; 460]<br>(n=75) | 248,3 ± 109,4 [53; 490]<br>(n=113) | 240 ± 106 [95; 405]<br>(n=11) | 220,7 ±102 [70; 388]<br>(n=30) | 212 ± 115,2 [75; 445]<br>(n=37) |
| **NSR** | 17 ± 0,2 [17; 19]<br>(n=114) | 17 ± 0,2 [15; 17]<br>(n=249) | 17 ± 0 [17; 17]<br>(n=25) | 17 ± 0 [17; 17]<br>(n=47) | 17 ± 0,1 [17; 18]<br>(n=102) |
| **MSR** | 17 ± 0 [17; 17]<br>(n=115) | 17 ± 0,2 [15; 17]<br>(n=288) | 17 ± 0 [17; 17]<br>(n=27) | 17 ± 0 [17; 17]<br>(n=62) | 17 ± 0,1 [16; 17]<br>(n=103) |
| **VSR** | 13 ± 0 [13; 13]<br>(n=114) | 13 ± 0,2 [11; 13]<br>(n=250) | 13 ± 0 [13; 13]<br>(n=25) | 13 ± 0 [13; 13]<br>(n=43) | 13 ± 0,1 [12; 13]<br>(n=103) |
| **SL** | 8 ± 0,3 [7; 9]<br>(n=119) | 8 ± 0,2 [7; 9]<br>(n=297) | 8 ± 0,3 [7; 9]<br>(n=28) | 8 ± 0 [8; 8]<br>(n=58) | 8 ± 0 [8; 8]<br>(n=105) |
| **IL** | 10,9 ± 0,4 [10; 12]<br>(n=114) | 9,9 ± 0,4 [8; 11]<br>(n=294) | 10,1 ± 0,5 [9; 11]<br>(n=27) | 10,9 ± 0,2 [10; 11]<br>(n=55) | 10,9 ± 0,3 [10; 12]<br>(n=104) |
| **IL-ASL** | 4,8 ± 0,4 [4; 5]<br>(n=135) | 4 ± 0,2 [4; 5]<br>(n=269) | 4,2 ± 0,4 [4; 5]<br>(n=28) | 4,9 ± 0,3 [4; 5]<br>(n=56) | 5 ± 0,2 [4; 5]<br>(n=106) |
| **Preoc** | 1 ± 0 [1; 1]<br>(n=116) | 1 ± 0,1 [1; 2]<br>(n=295) | 1 ± 0 [1; 1]<br>(n=27) | 1 ± 0,1 [1; 2]<br>(n=56) | 1 ± 0,1 [1; 2]<br>(n=104) |
| **Postoc** | 2 ± 0,1 [2; 3]<br>(n=113) | 2 ± 0,1 [1; 3]<br>(n=296) | 2 ± 0 [2; 2]<br>(n=27) | 2 ± 0 [2; 2]<br>(n=56) | 2 ± 0 [2; 2]<br>(n=104) |
| **Nasals** | 2 ± 0,2 [2, 3]<br>(n=86) | 2,1 ± 0,3 [1; 3]<br>(n=209) | 2 ± 0,2 [2; 3]<br>(n=24) | 2 ± 0,1 [2; 3]<br>(n=45) | 2 ± 0,2 [2; 3]<br>(n=74) |

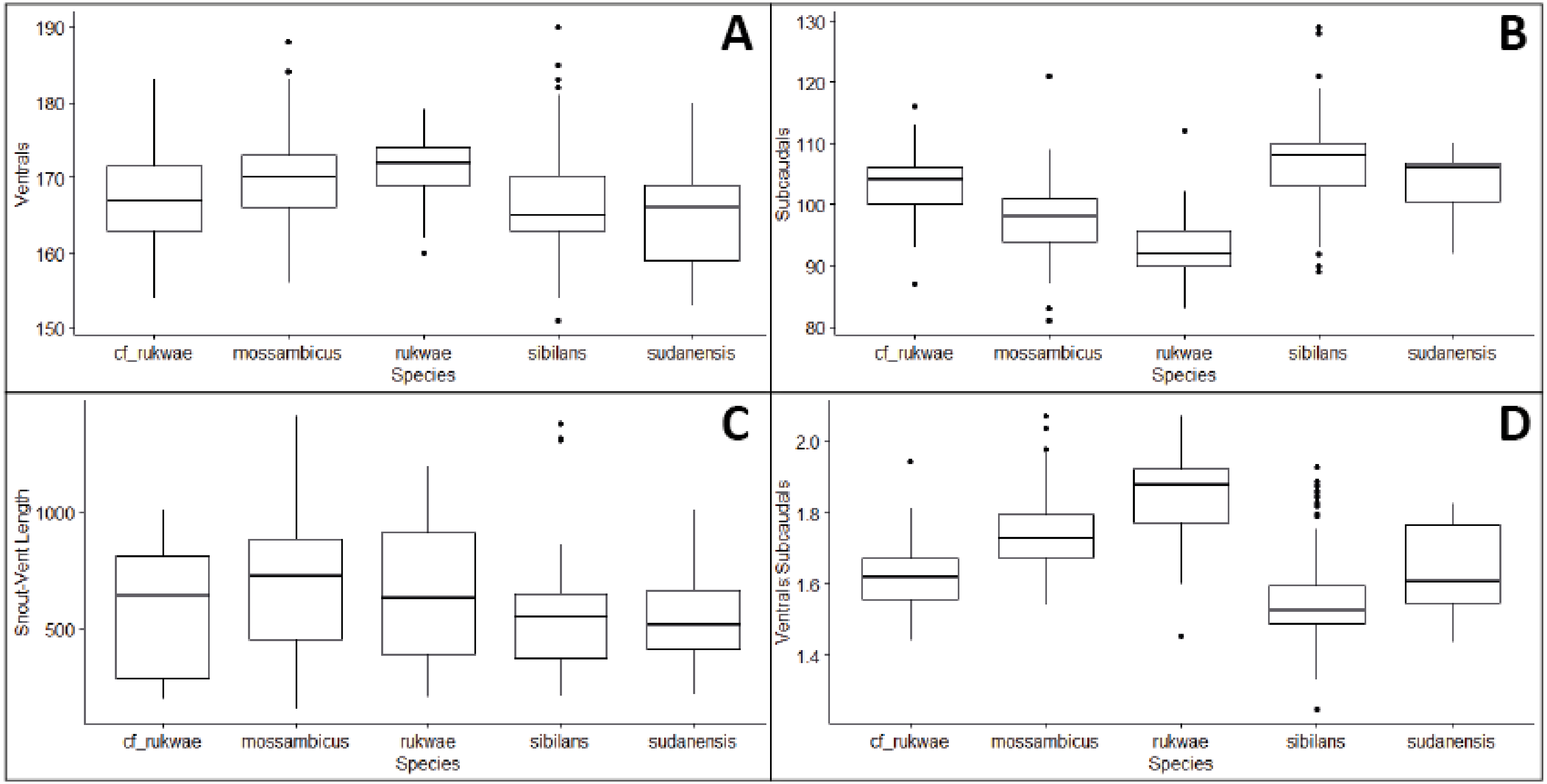

**Figure 4 –** Variation in size and meristic characters among the species studied: **A.** number of ventrals; **B.** number of subcaudals pairs; **C.** snout-vent length (in mm); **D.** ventrals:subcaudals ratio.

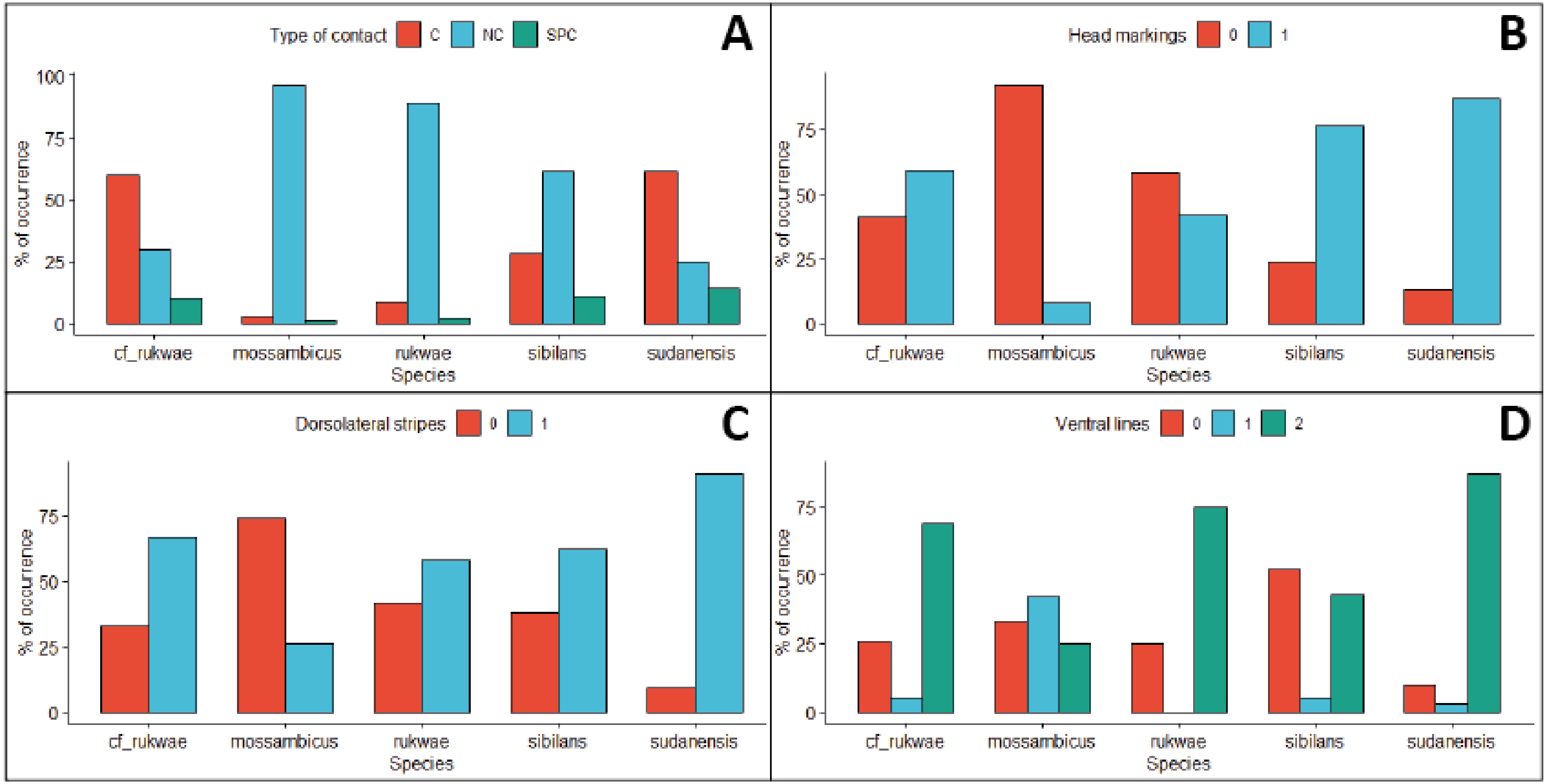

**Figure 5 –** Variation in the percentage of occurrence of each class for the type of contact between preocular and frontal scales (**A**), head markings (**B**), dorsolateral stripes (**C**) and ventral lines (**D**). Numerical coding is described in table 1.

The results produced from data associated with color pattern (presence and type of head markings, dorsolateral stripes, and ventral lines) show considerable variation in all species (Figs. 5). In *P. sibilans* there are usually distinct head markings and dorsolateral stripes, however, completely uniform specimens are not rare (Figs. 5-B and 5-C). Specimens with a uniform ventrum and continuous ventral stripes occur in similar proportions, but discontinuous lines or series of dots are uncommon (Fig. 5-D). In *P. mossambicus* the top of the head is almost always uniform (Fig. 5-B). Even though the results show the occurrence of dorsolateral and ventral stripes in *P. mossambicus* (Figs. 5-C and 5-D), these specimens are mostly restricted to Central Africa, so that outside this area *P. mossambicus* is almost always dorsally uniform and without continuous ventral lines. *P. sudanensis* shows the least variation in color pattern, with most specimens displaying well-defined head markings, as well as dorsal and ventral stripes (Figs. 5-B, 5-C and 5-D). We did not find differences in coloration between East African *P. rukwae* and *P.* cf. *rukwae* from West Africa. Both taxa may be striped or uniform, with or without head markings, and more than 50% of specimens of both species display thin ventral lines (Figs. 5-B, 5-C and 5-D).

In the multivariate analysis the first two Principal Components (PC) explained most of the variance (55%), however, neither species formed a clearly distinct cluster (Fig. 6). Instead, the plot shows 3 clusters: one formed by *P. mossambicus*, another formed by *P. sibilans*, *P. rukwae* and *P.* cf. *rukwae*, and a third one somewhat intermediate between the former two formed by *P. sudanensis*. All clusters overlap considerably but are partially distinguishable along PC 1 for which head markings, dorsolateral stripes and the number of infralabials in contact with the anterior sublinguals had the highest loadings (Table 5).

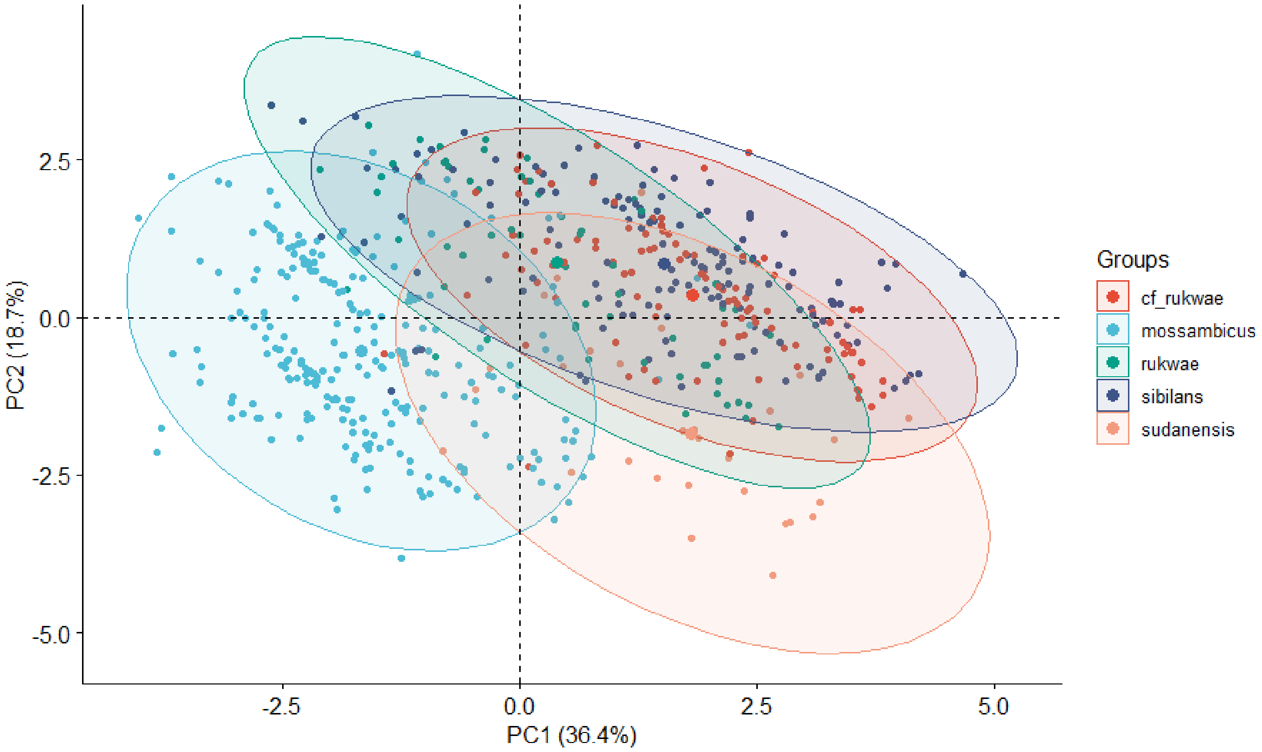

**Figure 6 –** Ordination of individual specimens in a Factor Analysis of Mixed Data.

**Table 5** – Loading scores of variables used in Factor Analysis of Mixed Data.

| | **PC1** | **PC2** |
|---|---|---|
| **Snout-Vent Length** | 0,3840 | 0,4183 |
| **Tail Length** | 0,3121 | 0,5235 |
| **Subcaudals** | 0,4102 | 0,0747 |
| **Infralabials** | 0,4799 | 0,2773 |
| **Infralabials in contact with anterior sublinguals** | 0,4930 | 0,2698 |
| **Preocular-Frontal Contact** | 0,3623 | 0,0118 |
| **Head markings** | 0,5992 | 0,0004 |
| **Dorsolateral stripes** | 0,5091 | 0,0130 |
| **Ventral stripes** | 0,4488 | 0,4626 |

## Phylogeny

Molecular phylogenetic analysis suggests that West African specimens represent an undescribed species of *Psammophis*. The resulting tree (Fig. 7) has a similar topology to that previously published by Kelly *et al*. (2008) showing five distinct taxa. The sequences from West African specimens (*P.* cf. *rukwae*) formed a monophyletic clade, and both *P. rukwae* and *P*. cf. *rukwae* are sister taxa to true *P. sibilans* from Ethiopia.

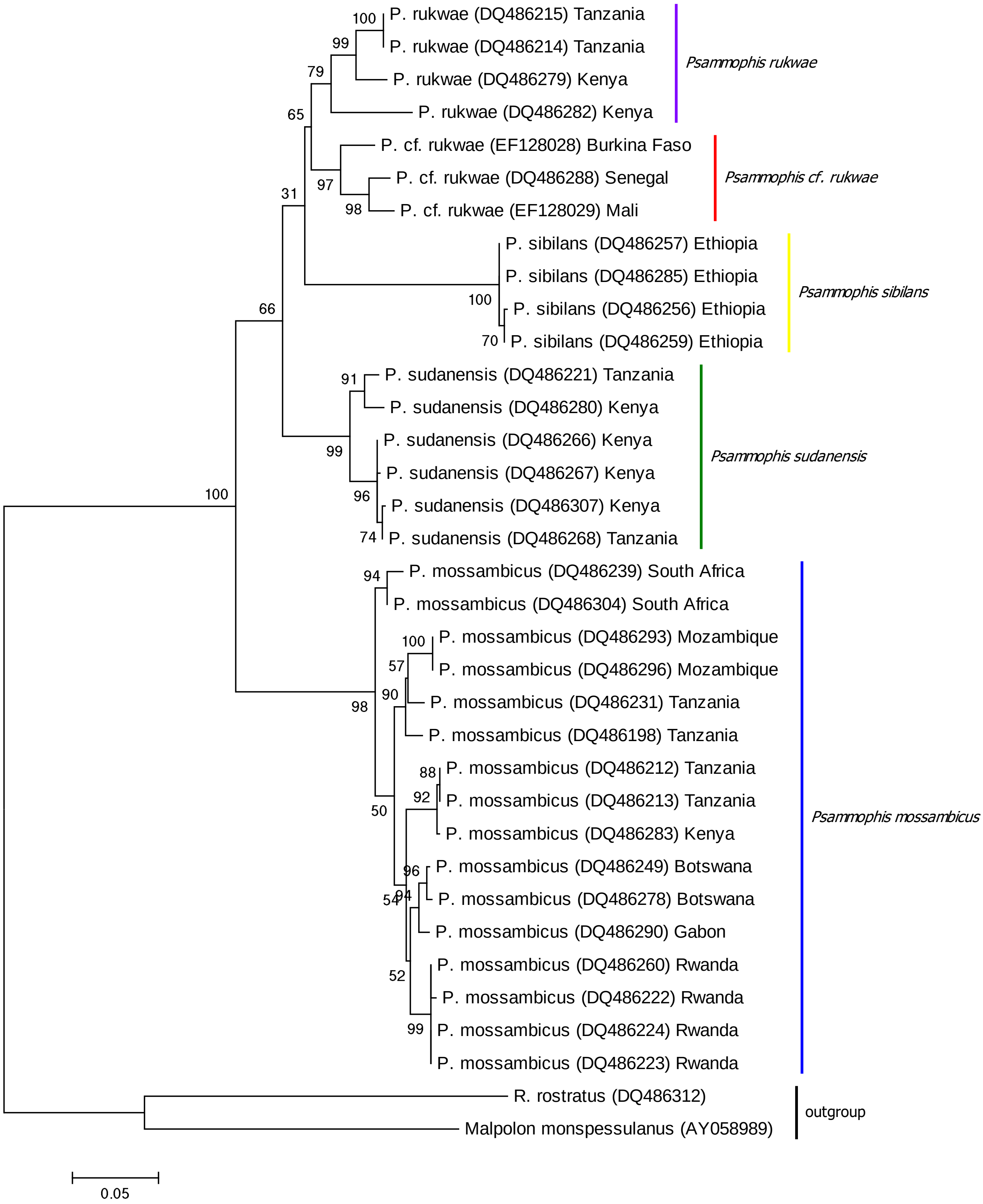

**Figure 7** – Maximum Likelihood phylogeny of the *Psammophis* species studied using the ND4 and tRNA dataset. Values on branches indicate bootstrap support.

# Taxonomic accounts

## *Psammophis sibilans* (Linnaeus, 1758)

**(Figs. 8–9)**

*Coluber sibilans* Linnaeus, 1758:222. "Holotype": UUZM 42 (Fig. 8). Type locality: "Asia" (= "Egypt", see Brandstätter 1996b).

*Coluber moniliger* Daudin 1803:69.

*Coluber auritus* Saint-Hilaire 1829:63, pl. viii, fig. 4 & 4'. Type locality: Egypt.

*Psammophis sibilans*: Günther (1858:136) (part), Anderson (1898:302), Barbour (1913:148), Flower (1933:824), Parker (1949:70), Algauhari (1967:395), Largen & Rasmussen (1993:366), Brandstätter (1995:173, 1996a:92) (part), Largen & Spawls (2010:564), Wallach *et al.* (2014:591) (part), Geniez (2018:244) (part).

*Psammophis sibilans sibilans*: Loveridge (1940:30) (part), Marx (1958:198, 1968:37), Isemonger (1968:174) (part), Welch (1982:170) (part), Lanza (1983:227, 1990:440), Broadley (1994:205), El Din (2006:266).

*Psammophis phillipsii*: Broadley (1994:205).

*Psammophis* cf. *sibilans*: Kelly *et al*. (2008:1046).

**Original description:** " 160 – 100. *Amaen. acad.* I. *p.* 302. *n.* 30.

*Seb. mus.* 2. *t.* 52. *f.* 4.

*t.* 56. *f.* 4.

*t.* 107. *f.* 4.

*Habitat in* Asia.

*Caerulescens vittis nigris, subtus albus.*" Linnaeus (1758).

**Nomenclatural history:**

After the original description as *Coluber sibilans*, this species was later designated as the type species of the newly erected genus *Psammophis* Boie (FitzSimons 1962; Broadley 1983 Brandstätter 1996b; Wallach *et al.* 2014). The type locality "Asia", discussed by Brandstätter (1996b), was later corrected to "Africa" by Anderson (1898) after comparison of Egyptian populations with the type specimen (Fig. 8), that was also pictured in Brandstätter (1995). Flower (1933) followed Anderson (1898) and Loveridge (1957) restricted the type locality to Egypt.

Up until the middle of the 20th century this species was recorded from several localities across most of the African continent, from West (*e.g.* Günther 1858; Bocage 1866; Manaças 1955), Central (*e.g.* Schmidt 1923; de Witte 1941, 1952, 1953, 1962, 1966; Laurent 1956, 1960), eastern (*e.g.* Boulenger 1895; Loveridge 1928, 1929, 1942, 1953, 1955) and southern Africa (*e.g.* Günther 1858; Bocage 1895; Monard 1937; Laurent 1954, 1964; Manaças 1959), and several color variants, "races" and subspecies were described (Peters 1882; Bocage 1887, among others). A more thorough list of records prior to 1939 is presented by Loveridge (1940).

Only in Angola, Bocage (1895) recognized 5 varieties of *P. sibilans* to which he attributed letters from A to E, corresponding to what are now recognized as *P. leopardinus* (var. C and E), *P. notostictus* (var. B), *P. subtaeniatus* (var. A) and *P. mossambicus* (var. D) (Marques *et al*. 2018). Boulenger (1896) synonymized *P. phillipsii* and *P. sibilans* var. *mossambica*, among others, with *P. sibilans* and recognized six color variants of the latter. In his revision of the genus, Loveridge (1940) recognized 6 subspecies of *P. sibilans*: *schokari, sibilans, phillipsii, nototstictus, trinasalis* and *leightoni*. All of these were later recognized as valid species plus another from East and southern Africa that would be assigned to *P. phillipsii* and later to *P. mossambicus* (Marx 1958; Laurent 1960; Broadley 1963, 1977, 1983, 2002).

By then *P. sibilans* was thought to be widespread across West Africa, reaching its southern limit in central Tanzania (Broadley 1983). Brandstätter (1995) would restrict its distribution to Egypt and northeastern Africa (from the Sudan and Ethiopia southwards to Tanzania) even suggesting a possible distinction between these two populations isolated by the Aswan Dam, in Egypt. However, both Broadley (1977, 1983) and Brandstätter (1995, 1996a) considered *P. sudanensis* and *P. sibilans* as synonyms, a decision that led them to assign Kenyan and Tanzanian populations to *P. sibilans*. Considering that these populations are most likely referable to *P. sudanensis*, this decision rendered their estimated distributions for *P. sibilans* inaccurate.

Largen & Rasmussen (1993) discussed the status of the *sibilans* complex in Ethiopia, and despite the morphological variation, they assign all populations in their area to *P. sibilans*. Following these authors, the specimens from eastern Sudan identified by Broadley (1994) as *P. phillipsii* should be assigned to *P. sibilans*.

Before Brandstätter's (1995) revision, the most common snake in west African savannas was generally referred to *P. sibilans* (*e.g.* Manaças 1958; Condamin 1958; Perret 1961). Since then, West African specimens have been identified as *P. rukwae* by some authors (Leaché 2005; Leaché *et al*. 2006; Kelly *et al*. 2008) and *P. sibilans* by others (Trape & Mané 2002, 2006; Chippaux 2006; Chirio & LeBreton 2007), and their status is still unresolved (discussed below).

Although lacking genetic material from Egypt, Kelly *et al. (*2008), in the lack of topotypical *P. sibilans*, referred to Ethiopian populations as *P.* cf. *sibilans* based on their morphological similarity to typical *P. sibilans* from Egypt. On the other hand, the authors associated a West African specimen to *P. rukwae*, validating the occurrence of this species in West Africa and restricting *P. sibilans* to northeastern Africa, down to the southern border of Ethiopia and South Sudan. However, while some authors have followed Kelly *et al*. (2008) in assigning West African specimens to *P. rukwae* (Chirio 2009; Sow *et al.* 2017), others still refer them to *P. sibilans* (Brito *et al*. 2008; Segniagbeto *et al*. 2011; Trape & Mané 2015, 2017). The status and distribution of *P. sibilans* remains so unresolved that in recent years it has been recorded from central Tanzania (Vats & Safari 2014) and from the coastal region of the Congo (Jackson & Blackburn 2010).

**Diagnosis:**

Given the complex taxonomic history of *P. sibilans*, literature data should be interpreted with caution. Older records may contain data belonging to other species, and therefore result in the incorporation of incorrect data in species descriptions. Considering this, we provide an updated diagnosis to the species based only on our data and literature records that refer to those populations that we consider to represent true *P. sibilans* (namely those from Egypt, Ethiopia and eastern Sudan).

The preocular is either separated or in contact with the frontal (separated in around 60% of our specimens, see Fig. 5-A) and there are usually 11 infralabials, of which the first five are in contact with the anterior pair of sublinguals (Anderson 1898; Marx 1958). Other authors give slightly different ranges for ventrals and subcaudals in Egypt (Anderson 1898; Marx 1958; El Din 2006) and Ethiopia (Largen & Rasmussen 1993; Largen & Spawls 2010), but generally agree with our combined data that shows a range of 151–190 and 89–129 for ventrals and subcaudals, respectively. Marx (1958) records a maximum SVL of 98,2cm in Egyptian specimens. Our largest specimen (NMK 0/3234/2) is a male from eastern Sudan with an SVL of 138cm, assigned by Broadley (1994) to *P. phillipsii*, but, following the opinion of Largen and Rasmussen (1993) and our results, we interpret it as true *P. sibilans*.

The typical and most common coloration in *P. sibilans* corresponds to that illustrated by Anderson (1898) and agrees with the type specimen (Fig. 8). It consists of an olive brown dorsum, with most scales black edged, a narrow pale vertebral line and a pair of well-defined, broader, light dorsolateral stripes (Fig. 8-A) (Anderson 1898; El Din 2006; Largen & Spawls 2010). The supralabials are yellowish, uniform or with brown spots, the preocular and postoculars are usually pale and there is also a pale line along the *canthus rostralis*. The top of the head is usually distinctly marked (Figs 8-D and 21-E), with a pale longitudinal stripe along the internasal and prefrontal sutures that ends or splits at the frontal.

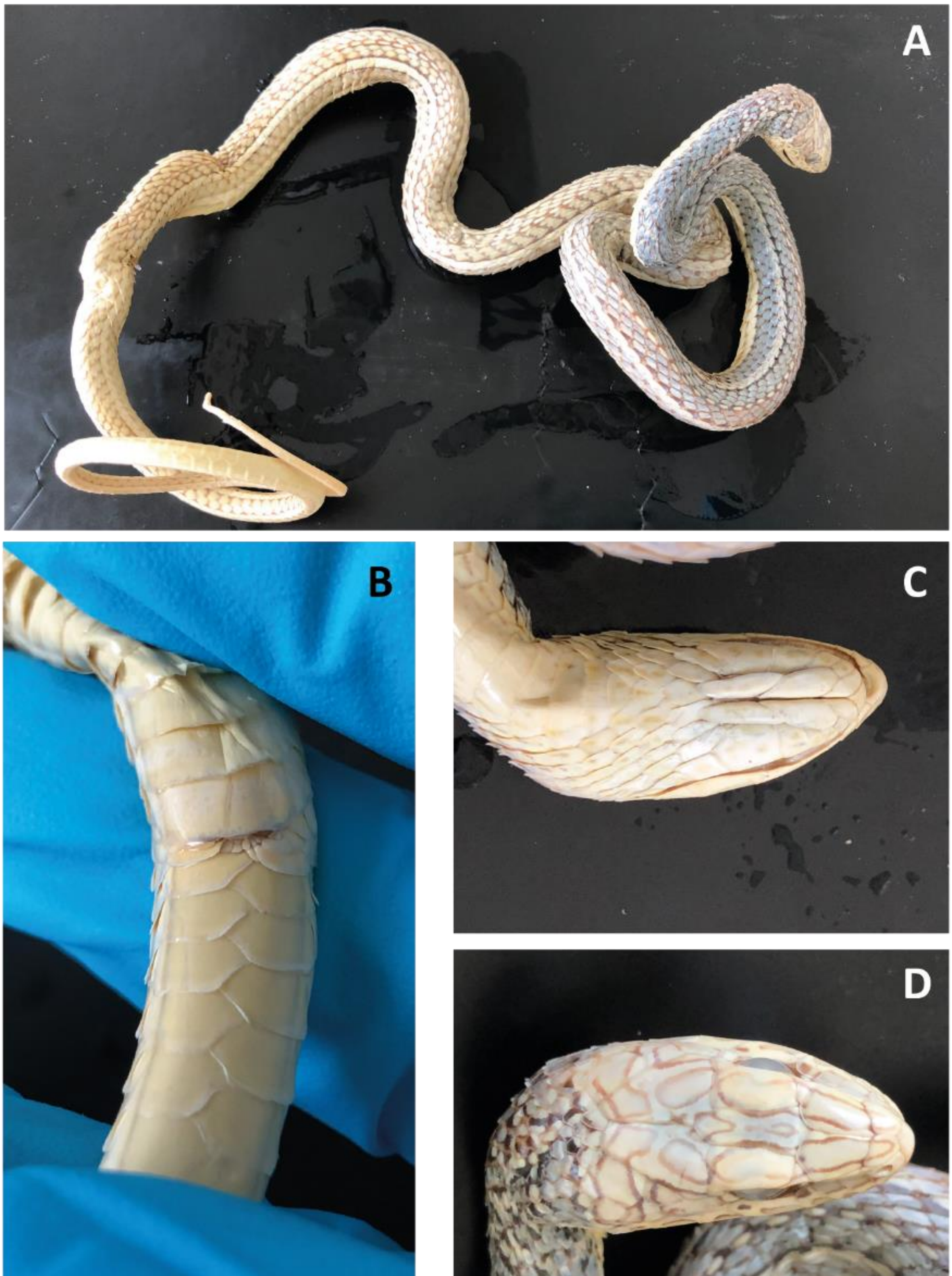

**Figure 8** – “Holotype” of *Psammophis sibilans* (UUZM 42): **A.** dorsal view; **B.** close-up view of cloacal region, showing faint and continuous ventral lines; **C.** close-up view of gular region; **D.** top of head, showing faint “*sibilans”* head markings (Photos by Erica Mejlon).

There are more or less regular but distinct longitudinal dark lines from the internasals to the parietals, usually followed by pale transverse bars on the posterior of the head and neck, forming two ovoid brown patches in the temporal region (Anderson 1898; Marx 1958; El Din 2006; Geniez 2018). However, specimens can also be uniform above, and some authors suggest an ontogenetic effect on color pattern that results in all markings fading with age, leaving older individuals patternless and similar to *P. mossambicus* (Largen & Rasmussen 1993; Largen & Spawls 2010; Geniez 2018). Although without detailed descriptions, Barbour (1913) recorded three specimens from eastern Sudan, all with distinct coloration. As for the ventral coloration, it is usually uniform yellowish or cream, often with dark ventral lines (Anderson 1898; Marx 1958; El Din 2006). Faint but continuous ventral lines can still be seen in the posterior ventral region of the type specimen (Fig. 8-B). Some specimens have a ventral pattern typical of the *"subtaeniatus"* group, consisting of a bright yellow midventral region bordered by dark ventral lines, followed by a pair of white ventrolateral bands that encompass the ends of the ventrals and a portion of the first dorsal scale row. It has been suggested that this may be a juvenile pattern that fades with age, although it remains unsubstantiated (Largen & Rasmussen 1993; Largen & Spawls 2010).

Although subject to some variation and ignored by many authors, we tend to agree with Largen and Rasmussen (1993) in considering infralabial arrangement as the best character to distinguish *P. sibilans* from *P. mossambicus* and *P. sudanensis*. When it comes to *P. rukwae*, however, diagnosis is not straightforward. In most cases, geographic location should be enough to know if we are dealing with *P. sibilans* or *P. rukwae*, but since distribution limits are poorly known, there are areas where both species may be sympatric, such as South Sudan. As *P. rukwae* shares the infralabial pattern typical of *P. sibilans*, there are no evident meristic characters that allow a distinction between these two species. According to Broadley (1966), *P. rukwae* should be readily diagnosed by a consistent pair of thin ventral lines, but as noted above, *P. sibilans* may also display ventral lines. The similarity of these two species makes the diagnosis problematic in sympatric areas and explains the confusion between both species in West Africa.

### Distribution and habitat:

Although distribution limits are poorly known, based on the available data (Fig. 9) we can conclude that *P. sibilans* is limited to Egypt, where it is restricted to the Nile valley and irrigated zones, such as the Delta and Fayum areas, south to Aswan (El Din 2006). Apparently, this species is absent along the Nile cataracts, but is also found in eastern Sudan, from Khartoum southwards along the Blue and the White Nile (Flower 1933; Loveridge 1955; Broadley 1994), eastwards to Eritrea and down to the southern border of Ethiopia (Largen & Rasmussen 1993; Largen & Spawls 2010), with the southernmost records from the lower Juba, Somalia (Hoevers & Johnson 1982; Lanza 1983, 1990). The status of specimens from South Sudan remains problematic, as both *P.*

*sibilans* and *P. rukwae* could occur there, and distinction of both species is not straightforward.

In Egypt this species is largely restricted to the wetlands and cultivated fields associated with the Nile Valley (Flower 1933; El Din 2006), although further south it occupies a wide range of habitats from dry savannas to moist grasslands, being absent only in closed forests and the most arid areas of eastern Ethiopia (Largen & Rasmussen 1993; Largen & Spawls 2010).

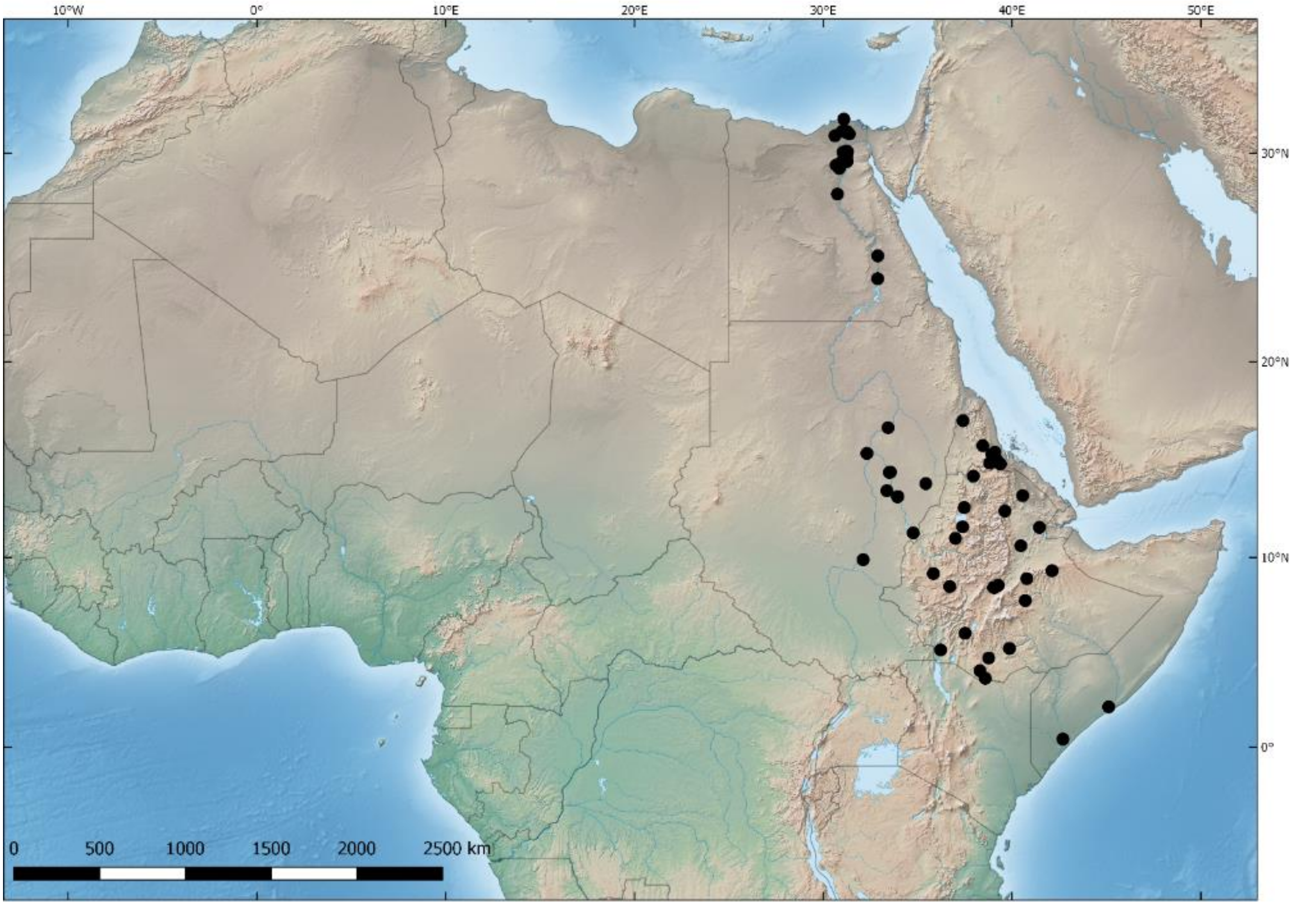

**Figure 9 –** Estimated distribution of *Psammophis sibilans* based on examined specimens.

## *Psammophis phillipsii* (Hallowell, 1844)

**(Figs. 10–12)**

*Coluber Phillipsii* Hallowell, 1844:169. Lectotype: ANSP 5112; Paralectotype: ANSP 5112, designated by Broadley (1977:24). Type locality: Liberia.

*Psammophis irregularis* Fischer, 1856:92. Holotype lost (Hughes and Wade 2004). Type locality: Peki, Ghana. Günther (1858:137), Jan & Sordelli (1870: livr. 34, pl. IV).

*Psammphis regularis* Sternfeld 1908a:412 (part). Type locality: “Cameroon and Togo”.

*Psammophis Phillipsii*: Hallowell (1854:100).

*Psammophis phillipsii*: Cope (1860:554), Ineich (2003:619), Trape & Mané (2006:150), Segniagbeto *et al*. 2011:346, Auliya *et al*. (2012:280), Wallach *et al*. (2014:589) (part).

*Psammophis* sp. (*Phillipsii* Hall ?): Müller (1885:686).

*Psammophis* sibilans: Boulenger (1905:113) (part), Chabanaud (1921:470).

*Psammophis sibilans phillipsii*: Loveridge (1940:41) (part), Briscoe (1949:17), Villiers (1950a: 98, 1950b:103), Condamin (1958:255), Taylor & Weyer (1958:1217), Menzies (1966:175), Cansdale (1973:38).

*Psammophis sibilans philippsi*: Villiers (1950a:98).

*Psammophis sibilans phillipsi*: Doucet (1963:307).

*Psammophis phillipsi*: Leston & Hughes (1968:754), Brandstätter (1995:75) (part), Ullenbruch *et al.* (2010).

*Psammophis* cf. *sibilans*: Rödel *et al.* (1995:7).

**Original description:** "Head elongated, flattened, covered above with nine plates; the rostral plate is hexagonal, rounded above, incurvated beneath, there are two anterior and two posterior frontal plates; the anterior are pentagonal; their posterior margin is the broadest. The posterior frontal are very large, pentagonal; there are two supra-orbitar, and one vertical plate; the supra-orbitar are of moderate size, the occipital are very large, triangular; there are two nasal plates, with the nostril placed between them; there is an anterior frontal, and a loral plate; there are two posterior orbitar plates; the eyes are large, the neck is narrow, the body is long and tapering, the scales upon the body are smooth and quadrangular; the tail is of moderate length.

Colour – Body and tail greenish-olive above, with numerous black points; chin and throat light yellow; under surface of abdomen and tail tea-green. Abdominal scuta 172: subcaudal 22." (Hallowell 1844)

**Nomenclatural history:**

After the original description as *Coluber phillipsii*, based on specimens from Liberia (Hallowell 1844), this species was recorded in West Africa as *Psammophis phillipsii*, and its distribution extended to the Gabon (Hallowell 1857; Cope 1860; Müller 1885). Boulenger (1896), however, considered *P. phillipsii* to be a synonym of *P. sibilans*, and this species was again recorded as *P. sibilans* from Guinea (Chabanaud 1921).

Loveridge (1940) recovered *phillipsii* as a valid subspecies of *P. sibilans* from rainforest regions, with an entire cloacal scale and uniform coloration. Its distribution range was thought to correspond to the rainforest belt from Senegal to the Congo, with

*P. regularis* Sternfeld, 1908 and *P. sibilans* var. *occidentalis* as synonyms. Subsequent authors followed the opinion of Loveridge and *P. s. phillipsii* was recorded from Liberia (Briscoe, 1949; Taylor & Weyer 1958), Sierra Leone (Menzies 1966), Ivory Coast (Doucet 1963) and the Democratic Republic of the Congo (de Witte 1962). Due to the fact that Loveridge (1940) recorded *P. s. sibilans* and *P. s. phillipsii* from the same localities, Laurent (1960) proposed the elevation of *phillipsii* to species status. Leston & Hughes (1968) treat it as a valid species, sympatric with *P. sibilans* in some areas of Ghana.

After a revision of the status of populations from southern Africa (Broadley 1963), these were assigned to *P. phillipsii* by several authors, turning it into a widespread species from Senegal to South Africa (Broadley 1977, 1983, 1994; Pienaar 1978; Branch & McCartney 1992; Spawls & Branch 1992). However, Brandstätter (1995) and Hughes (1999) considered *P. phillipsii* to be restricted to West Africa, and Branch (1998) recovered Peters' name *P. mossambicus* to refer to populations from East and southern Africa.

At this point *P. phillipsii* was thought to occupy forest regions from Senegal to the Congo, and Hughes (1999) evidenced an abrupt change in the incidence of an entire cloacal scale between Ghana and Nigeria. Based on this character and differences in coloration, the author suggested the split of *P. phillipsii* in two forms: "one essentially West African would remain under Hallowell's name, the other, centered on Central Africa but perhaps entering some way into West Africa may require another name". This central African form would later be assigned to *P. phillipsii occidentalis* Werner, 1919, a subspecies resurrected by Hughes & Wade (2004) based on two specimens (Figs. 12 and 13) from the "Congo" present in the NMW collections. According to the authors, *P. p. occidentalis* would be distributed from the Cameroon to Uganda, however, most authors continued to use the name *P. phillipsii* to refer to specimens with a divided cloacal scale from Nigeria (Akani *et al.* 2002a, 2002b, 2003), Gabon (Pauwels *et al.* 2004, 2006, 2017a, 2017b, 2018a, 2018b, 2019; Pauwels & David 2008) and the Republic of Congo (Jackson *et al.* 2007). Furthermore, Luiselli *et al*. (2004) did not find any ecological differences between the entire cloacal scale and divided cloacal scale in "*phillipsii"* from southern Nigeria. Chirio and LeBreton (2007) assign populations from the Cameroon to *P. occidentalis*, but later reassign them to *P.* cf. *phillipsii* (Ineich *et al.* 2015).

Kelly *et al*. (2008) revealed a sequence from the Gabon (identified as *P.* cf. *phillipsii phillipsii*), to be deeply nested within *P. mossambicus* from East and southern Africa and suggested that *P. mossambicus* is a synonym of *P. phillipsii*, a widespread species from Senegal to South Africa. Considering the lack of topotypical *P. phillipsii* sequences from West African forests, we disagree with this option, and would rather interpret their results as a restriction of *P. phillipsii* to West Africa. This goes in line with morphological and ecological data: populations from west of the Dahomey Gap have an entire cloacal scale and are restricted to forest regions, while those east of the Dahomey Gap have a divided cloacal scale and are habitat generalists (Leston & Hughes 1968; Hughes 1999; Broadley 2002; Hughes & Wade 2004; Luiselli *et al*. 2004; Trape & Mané 2006; Spawls *et al*. 2018). Few authors followed Kelly's *et al*. (2008) proposal (*e.g.*

Broadley & Baylock 2013), and most still assign populations from East and southern Africa to *P. mossambicus* (Broadley & Cotterill 2004; Bates *et al.* 2014; Marais 2014; Wallach *et al.* 2014; Schleicher 2015; Conradie *et al*. 2016; Branch 2018; Marques *et al.* 2018; Spawls *et al*. 2018). Likewise, some authors still assign populations from Central Africa to *P. phillipsii* (*e.g.* Pauwels *et al.* 2016, 2017a, 2017b, 2018a, 2018b, 2019).

**Diagnosis:**

*P. phillipsii* has 10 infralabials, of which the first 4 are in contact with the anterior sublinguals; an entire cloacal scale; 162 to 185 ventrals; 89 to 109 pairs of subcaudals; and a maximum length of 180 cm. The preocular is usually separated from the frontal (Villiers 1950b; Trape & Mané 2006).

This snake is dorsally uniform (Fig. 10-A), sometimes with a vertebral line; the dorsal scales are olive-brown to olive-green, and sometimes are edged black. The labials and throat may be shades of orange, with or without dark spotting; the venter is described as yellow to greenish, uniform, with series of lateral dots or with each scale transversely marked with black. Some authors argue that true *phillipsii* from rainforest areas have the ventrals shaded with blueish grey (Villiers 1950a; Böhme 1978; Brandstätter 1995; Wagner *et al.* 2008; Ullenbruch *et al*. 2010; Böhme *et al.* 2011) and are relatively small and slender arboreous snakes when compared to *P. mossambicus* and *P.* cf. *rukwae* (Wagner & Böhme 2007; Wagner *et al.* 2008).

The head pattern is what we call "*phillipsii*" head markings (Figs 10-B, 23-B and 23-D), common to *P. phillipsii* and *P. mossambicus*. This pattern consists of brown/chestnut patches covering the internasals, prefrontals and supraoculars, that become more irregular and reticulated posteriorly. The brown head markings are bordered with black, but the outline is usually weakly defined and without great contrast. These markings may persist in some adults, but most individuals have the top of the head uniform brown (Figs. 14-C and 23-F), or with traces of a head pattern reduced to a few scattered black spots.

**Figure 10 –** Dorsal view (**A**) and head pattern (**B**) of *P. phillipsii* from Liberia (FMNH 58091) (Photo by FMNH, available at https://www.gbif.org/occurrence/668621539).

**Distribution and habitat:**

*Psammophis phillipsii* is a West African species that occupies forest regions from the Gambia eastwards to Ghana (Fig. 11), where the rainforest belt is interrupted by the Dahomey Gap and the savannas and dry conditions of the interior reach the coast (Loveridge 1940; Hakansson 1981; Trape & Mané 2006). Wagner & Böhme (2007) and Wagner *et al.* (2008) claim to present the easternmost record of *P. phillipsii*, that they consider distinct from *P. mossambicus*, from forest remnants in western Kenya, but this remains unsubstantiated. Some records from West African savannas, usually as *Psammophis* cf. *phillipsii* (*e.g.* Böhme *et al.* 1996; Ullenbruch *et al.* 2010), are to be assigned to *P.* cf. *rukwae* (discussed below). As discussed above, in our view, records from Nigeria eastwards are to be assigned to *P. mossambicus* (*e.g.* de Witte 1962; Akani *et al*. 1999, 2002a, 2002b, 2003; Luiselli *et al*. 2004; Pauwels *et al.* 2004, 2006, 2016, 2017a, 2017b, 2018a, 2018b, 2019; Jackson *et al*. 2007). Many authors consider *P. phillipsii* to be a forest dwelling species that is found in primary and gallery forests (Böhme 1978; Hakansson 1981; Brandstätter 1995; Wagner & Böhme 2007; Wagner *et al*. 2008). On the other hand, some consider this to be a penetrant savanna species, found in forest-savanna mosaic and forest clearings but not in primary forest (Briscoe 1949; Cansdale 1973; Menzies 1966; Trape & Mané 2006; Ineich *et al.* 2015). In Ghana, Leston & Hughes (1968) consider grass clearings within the forest zone to be the habitat and hypothesize that this species may become more abundant with increasing human population and deforestation in eastern Ghana.

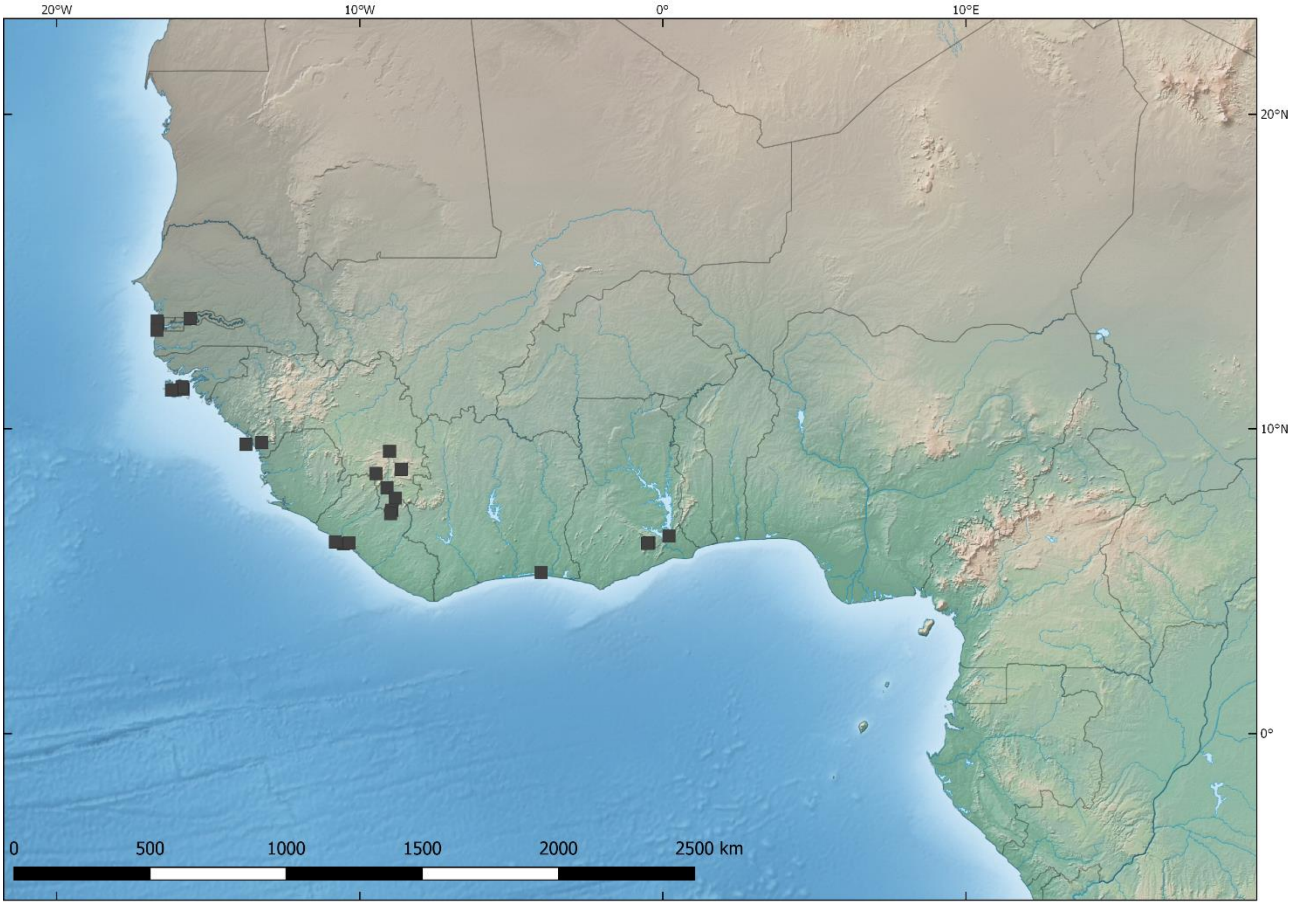

**Figure 11 –** Estimated distribution of *Psammophis* phillipsii based on literature records (grey squares).

## *Psammophis mossambicus* Peters, 1882

**(Figs. 12–17)**

*Psammophis sibilans* var. *mossambica* Peters, 1882:122. Lectotype: ZMB 2468A, designated by Broadley (1977:24). Type locality: Mozambique Island.

*Psammophis sibilans* var. *tettensis* Peters, 1882:122. Type locality: Tete, Mozambique.

*Psammophis sibilans* var. *intermedius* Fischer 1884:14. Type locality: Arusha, Tanzania.

*Psammophis thomasi* Gough 1908:30. Type locality: “Salisbury, Rhodesia” [=Harare, Zimbabwe].

*Psammphis regularis* Sternfeld 1908a:412 (part). Type locality: “Cameroon and Togo”.

*Psammophis sibilans occidentalis* Werner, 1919:504. Lectotype: NMW 19245.2 (Fig. 12), designated by Hughes & Wade (2004:129). Paralectotype: NMW 19241.1, designated by Hughes & Wade (2004: 129). Type locality: “Congo”.

*Psammophis Phillipsii*: Hallowell (1857:69).

*Psammophis sibilans*: Günther (1858:136) (part), Bocage (1866:48, 1895:114) (part), Boulenger (1905:113, 1915:213) (part), Schmidt (1923:111) (part), Loveridge (1928:55, 1929:32, 1936:262), Monard (1937:132), Laurent (1960:55), Broadley & Cock (1975:70), Jackson & Blackburn (2010:424).

*Psammophis sibilans phillipsii*: Loveridge (1940:41) (part).

*Psammophis sibilans sibilans*: Loveridge (1940:30, 1942:51, 1953:274, 1955:48) (part), de Witte (1941:213, 1952:20, 1953:235, 1962:117, 1966:82), Laurent (1954:59, 1956:249, 1964:113), Manaças (1959:151, 1974:196), FitzSimons (1962:227, 1966:60) (part), Isemonger (1968:174) (part), Pitman (1974:156), Vasey-FitzGerald (1975:20).

*Psammophis sibilans phillipsi*: Perret (1961:136), Böhme (1975:40).

*Psammophis sibilans philippsi*: de Witte (1962:117).

"Olive Grass Snake" (*Psammophis* sp.): Broadley (1963:6).

*Psammophis phillipsii*: Broadley (1977:24, 1983:145, 1990:486, 1991:530), Pienaar (1978:170), Broadley & Howell (1991:28), Branch & McCartney (1992:2), Spawls & Branch (1995:42), Akani *et al*. (2002a:143), Jackson *et al.* (2007:82), Broadley & Baylock (2013:199), Wallach *et al*. (2014:589) (part).

*Psammophis* cf. *brevirostris tettensis*: Brandstätter (1995:60).

*Psammophis mossambicus*: Branch (1998:92, 2005:44, 2018:62), Haagner *et al*. (2000:15), Broadley (2002:96), Broadley *et al.* (2003:167), Broadley & Cotterill (2004:50), Marais (2004:153, 2014:84), Branch *et al*. (2005:213), Spawls *et al.* (2006:124, 2018:434), Bates *et al.* (2014:377), Wallach *et al*. (2014:588), Schleicher (2015:167), Ceríaco *et al*. (2016:14, 2018:414), Conradie *et al.* (2016:22), Branch (2018:62), Marques *et al.* (2018:348).

*Psammophis phillipsi*: Akani *et al.* (1999:629, 2002b:63, 2003:208), Luiselli *et al*. (2004:415), Chirio & Ineich (2006:28), Jackson *et al*. (2007:77), Wagner & Böhme (2007:138), Wagner *et al.* (2008:1353).

*Psammophis phillipsii phillipsii*: Hughes & Wade (2004:130).

*Psammophis phillipsii occidentalis*: Hughes & Wade (2004:130).

*Psammophis* cf. *phillipsii*: Pauwels *et al.* (2004:121, 2006:184, 2016:183, 2017a:5, 2017b:136, 2018a:108, 2018b:148, 2019:154), Pauwels & David (2008:22), Ineich *et al.* (2015:30).

*Psammophis occidentalis*: Chirio & LeBreton (2007:532), Wallach *et al*. (2014:589).

*Psammophis* sp. 1: Chirio & LeBreton (2007:538).

*Psammophis phillipsii phillipsii*: Kelly *et al*. (2008:1049).

**Original description:** "Die zweite (var. *mossambica*) zeigt auch die spinale Reihe gelber Flecke, aber keine Seitenbinden. Die Schuppen, einschliesslich der unteren Halfte der letzten Schuppenreihe sind olivenbraun oder olivengrun und an den Randern schwarz. Die Bauchschilder haben, wie die von Dr. J.G. Fischer beschriebene Varietat *irregularis*, an den aussersten Enden und mehr nach innen einen schwarzen Punkt, aber an jeder Seite des Bauches zwei Punktlinien. Die Mitte des Bauches zwischen den beiden inneren Linien ist noch feiner unregelmassig punktirt und im Ganzen dunkler. Bei den alten Exemplaren verbleichen diese Punktlinien. Die Kopfschilder mit Ausschluss des oberen Theils des Schnauzenschildes, sind schwarzgefleckt. Das Anteorbitale und die Postorbitalia sind am Auge hellgelb. Die Supralabialia, Infralabialia, Submentalia und die vorderen seitlichen Kehl- und Halsschuppen sind schon gelb mit einem schwarzen Fleck. Von den Linienzeichnungen des Kopfes, welche an den agyptischen Exemplaren stets so deutlich sind, findet sich nur bei den jungen Exemplaren eine Spur. 7 oder 8 Supralabialia, von denen das 3te uns 4te, oder das 4te und 5te ans Auge stossen. 161 Abdominalschilder, ein getheiltes Anale und 91 Paar Subcaudalschuppen." (Peter 1882)

**Nomenclatural history:**

Peters (1882) described two new varieties of *P. sibilans* from Mozambique: *P. sibilans* var. *mossambica* and *P. sibilans* var. *tettensis*. With several varieties of *P. sibilans* being described, Fischer (1884) suggested that most of them, as *"mossambica", "tettensis", "brevirostris", "irregularis"*, and perhaps even *"subtaeniatus"* could represent the same species, distributed across tropical Africa, and proposed the name *P. sibilans* var. *intermedius*. Boulenger (1896), however, considered all of the above to be synonyms of *Psammophis sibilans*, and was followed by most authors by assigning populations from East and Southern Africa to *P. sibilans* (Schmidt 1923; Loveridge 1929, 1940, 1942; de Witte 1941, 1952, 1953, 1962, 1966; Laurent 1954, 1956, 1964; FitzSimons 1962).

Broadley (1963), on the other hand, upon comparing specimens from Zimbabwe and Egypt, concluded that the former were distinct from topotypical *P. sibilans*. Broadley (1963) refers to this taxon only as the "Olive Grass Snake" (*Psammophis* sp.), occurring from the Sudan southwards through East Africa to northeastern South Africa, and west through southern Congo to Angola and northern Namibia. These populations would later be assigned to *P. phillipsii* by several authors (Broadley 1977, 1983, 1994; Pienaar 1978; Branch & McCartney 1992; Spawls & Branch 1992). Brandstätter (1995, 1996a), however, considered *P. phillipsii* to be restricted to west Africa, and applied the name *Psammophis* cf. *brevirostris tettensis* to populations from southeastern Africa, south of Lake Malawi (Mozambique, Zambia, Zimbabwe, Botswana and northeastern South Africa), but the name was inadequate and his proposals were not followed (Hughes 1999). Branch (1998) was the first to recover Peters' (1882) name *P. mossambicus* to refer to those populations from East and southern Africa previously assigned to *P. sibilans* and then *P. phillipsii*, and was followed by most authors since (Hughes 1999; Broadley 2002; Broadley *et al*. 2003; Marais 2004).

The status of populations from Central Africa is the most problematic. In the past these were assigned to *P. sibilans* (de Witte 1941, 1952, 1953, 1962, 1966; Laurent 1954, 1956, 1964; Jackson & Blackburn 2010), *P. phillipsii* (de Witte 1962; Akani *et al*. 1999, 2002a, 2002b, 2003; Luiselli *et al*. 2004; Pauwels *et al.* 2004, 2006, 2016, 2017a, 2017b, 2018a, 2018b, 2019; Jackson *et al*. 2007; Kelly *et al.* 2008), *P. occidentalis* (Hughes & Wade 2004; Chirio and LeBreton 2007; Kelly *et al.* 2008) and *P. mossambicus* (Broadley 1991; Broadley & Cotterill 2004; Spawls *et al.* 2018). Hughes and Wade (2004) recovered *P. occidentalis* as a subspecies of *P. phillipsii,* with a divided cloacal scale, occurring from the Cameroon to Uganda. The description, however, is quite confusing, as only the lectotype (Fig. 12) is referred to *P. p. occidentalis*; despite referring the second specimen (Fig. 13) to *P. p. phillipsii*, the authors still designate it as paralectotype of *P. p. occidentalis*. Furthermore, all characters used for diagnosing *P. occidentalis* (*i. e.* head markings, dorsolateral stripes, double row of dots on each side of the ventrals and a grey obfuscation of the midventral region) are known to occur in other species outside the putative distribution range of *P. occidentalis*, and few specimens within this range display all the diagnostic characters. Kelly *et al*. (2008) validate the specific status of *occidentalis* and suggest an approximated distribution from the Cameroon to Uganda, and then southwards to Zambia. However, the authors only used genetic data and do not discriminate the characters used in specimen identification, stating only that "the identification of our *P.* cf. *p. occidentalis* specimens was based on potentially labile characters associated with pattern and colouration, and is thus uncertain". Considering this, we did not find any consistent morphological differences that support the distinction of populations from Central Africa as a valid species, and provisionally assign them to *P. mossambicus*.

As discussed above, Kelly *et al*. (2008) also propose the synonymization of *P. mossambicus* with *P. phillipsii* but this was only followed by Broadley & Baylock (2013). Our interpretation of their results, instead, leads us to assign populations from Central Africa to *P. mossambicus*, a species with a wide distribution range from Nigeria to Kenya, and southwards to South Africa. Following this view, records from Nigeria (Akani *et al*. 1999, 2002a, 2002b, 2993; Luiselli *et al*. 2004), Cameroon (Chirio &LeBreton 2007; Ineich *et al*. 2015), Central African Republic (Chirio & Ineich 2006), the Gabon (Pauwels *et al.* 2004, 2006, 2016, 2017a, 2017b, 2018a, 2018b, 2019) and the Republic of the Congo (Jackson *et al.* 2007; Jackson & Blackburn 2010) should be assigned to *P.mossambicus*.

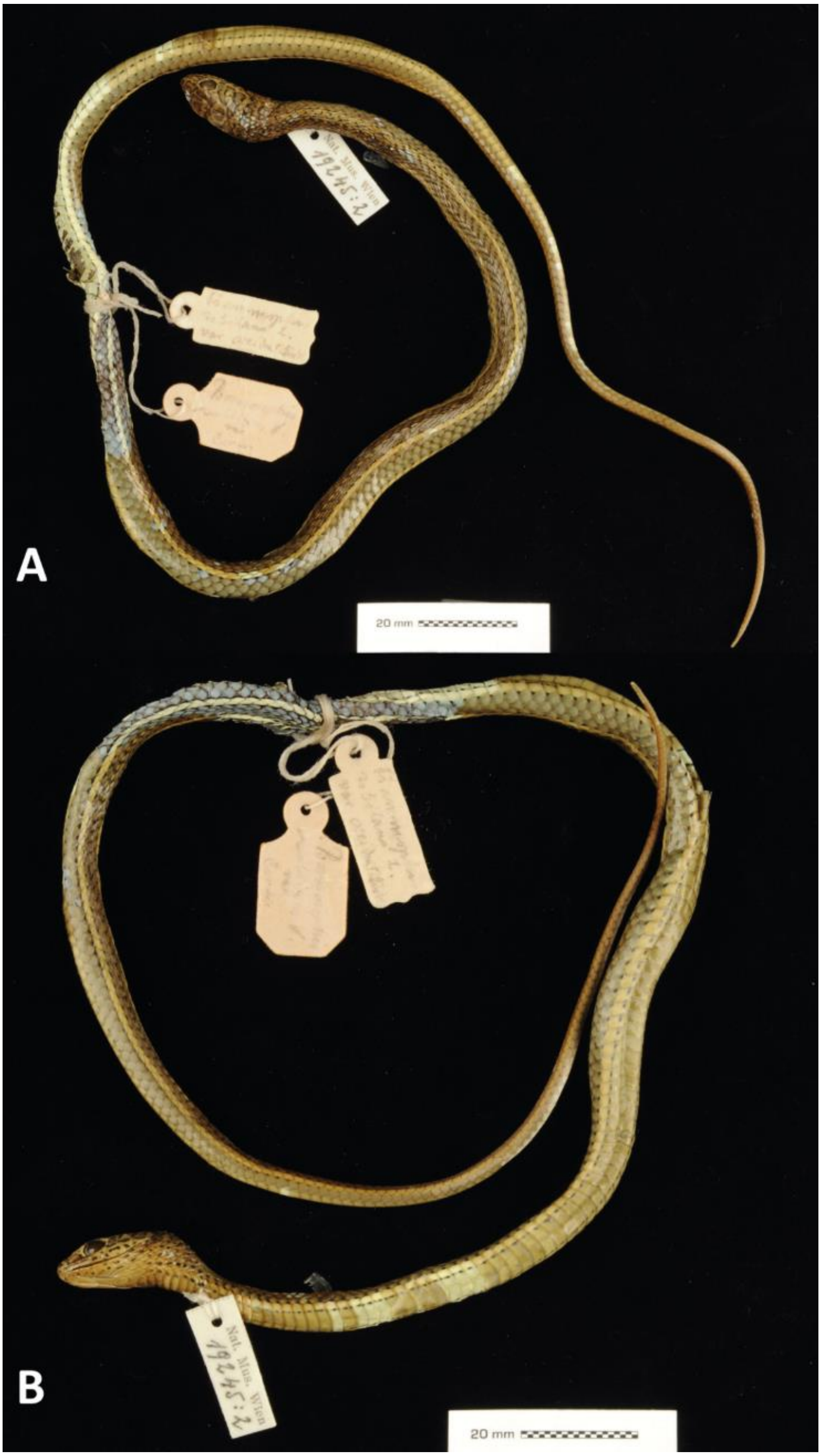

**Figure 12** – Lectotype of *Psammophis occidentalis* (NMW 19245.2). **A.** dorsal view, showing well-defined dorsolateral stripes; **B.** ventral view, showing discontinuous ventral lines (Photos by Alice Schumacher).

**Figure 13** – Paralectotype of *Psammophis occidentalis* (NMW 19245.1). **A.** dorsal view; **B.** ventral view (Photos by Alice Schumacher).

**Diagnosis:**

There are usually 10 infralabials present, the first 4 in contact with the anterior sublinguals; the preocular is usually well separated from the frontal (Broadley 1963, 1977, 1983, 2002; Brandstätter 1995; Spawls *et al.* 2018). Our results show a range of 156–188 ventrals and 81–121 paired subcaudals, and generally agree with those given by other authors for East (Loveridge 1929, 1937, 1953; Spawls *et al.* 2018) and southern (Broadley 1963, 1977, 1983, 2002) Africa. The cloacal scale is divided in most specimens (Loveridge 1929, 1937, 1953; Broadley 2002; Pauwels *et al.* 2004, 2018b, 2019; Spawls *et al*. 2018). This species reaches a maximum length of 180cm (Spawls *et al*. 2018), maybe more, and a specimen from Zimbabwe (NMZB 3893) has the largest recorded snout to vent length of 141.5cm.

In terms of coloration, *P. mossambicus* is generally characterized by an unstriped olive dorsum, usually with scattered black points on the flanks, sometimes with a vertebral line but very rarely with dorsolateral stripes (FitzSimons 1962; Broadley 1963, 1977, 1983, 2002; Spawls *et al*. 2018). Dorsal scales (including the lower third of the first scale row, as can be seen in Figure 15-A) may be of a variety of shades from olive-brown to olive-grey, often progressively paler or yellowish towards the tail; completely uniform or with black edged middorsal scales, often forming thin longitudinal lines or "V" shaped black marks (Fig. 14-A) (Broadley 1977, 1983, 2002; Spawls *et al.* 2018). Juveniles often have scattered black scales or irregular patches on the dorsum that disappear within the first months of life (Cesare Colli *pers. comm*.). These may resemble *Psammophis irregularis* Fischer, 1856, as illustrated by Jan and Sordelli (1970), or even the dark "saddle" of the European/North African species *Malpolon monspessulanus*. Sometimes these marks persist in adults, and largely black individuals are known from Zimbabwe and Mozambique, with Broadley (2002) claiming to have seen "what appeared to be an all black *P. mossambicus* on the road between Victoria Falls and Kazungula". When dorsolateral stripes are present, which is rare, they are usually faint and never well-defined like in *P. sibilans* or *P. subtaeniatus*.

Juveniles may display "*phillipsii*" head markings (discussed above, see Figs. 10-B, 23-B and 23-D) that usually fade with age, leaving most adults with the top of the head uniform brown (Figs. 14-C and 23-F), or with traces of a head pattern reduced to a few scattered black spots. However, this pattern persists in some adults, especially in Central Africa, as is well illustrated by Ward *et al*. (2003). Labials and throat are usually spotted, with supralabial spots paler in the center or even solid black, however, specimens with uniform yellow labials are known (Fig. 14-B); the throat and sides of the head may be orange (Broadley 2002; Spawls *et al*. 2018).

Ventral pattern in East and southern Africa is usually cream to yellowish, uniform or with lateral rows of more or less distinct dots or dashes, but never forming well-defined continuous lines; sometimes with irregular dark speckling or blotching, or even partially black (Broadley 2002; Spawls *et al.* 2018).

Even though we did not find any meristic differences between populations from Central Africa and those from East and southern Africa, specimens from Gabon, Congo and Uganda display exceptional color patterns. Specimens from the Congo and the Great Lakes Region, unlike *P. mossambicus* from East and southern Africa, may have well-marked continuous dark ventral lines (Fig. 16-C) and/or clear dorsolateral stripes (Fig. 12-A). De Witte (1962) shows a black and white picture of what seems to be a *P. mossambicus* with clear dorsolateral stripes from Virunga National Park. However, de Witte has been known to mistakenly identify *P. lineatus* as *P. sibilans* in the past (Hughes 2004). Schmidt (1923) recorded 13 specimens from Uele district, northeastern Democratic Republic of the Congo, that he describes has being uniform above with well-marked ventral lines. A ventral pattern of more or less distinct dark lines is also mentioned by de Witte (1966), concerning specimens from Garamba National Park, northeastern Democratic Republic of the Congo. Loveridge (1936, 1940, 1942) also mentions a ventral pattern of dark ventral lines as being common in specimens from forest edges in Uganda and Central Lake Region, and Pitman (1974) describes a population from Central Lake Region that "appear to be intermediates, not hybrids, between *Psammophis sibilans* and *Psammophis subtaeniatus*". He describes specimens of these "intermediates" from Lake Edward and Lake Albert as having more or "less conspicuous, but broken, ventro-lateral dark-brown or black line, with well-developed dorso-lateral stripes shades brown and yellow, approximating *P. subtaeniatus*, but lacking any pale crossbars behind head and on neck". Specimens from rainforest regions and their surroundings, like Budongo Forest, Mabira Forest and lake-shore forests of Lake Victoria, are described as generally larger, without distinct dorsolateral stripes and ventrolateral lines "usually broader, mainly indistinct and considerably broken". Specimens from the Cameroon are described by Chirio & LeBreton (2007) as follows: "Four infralabials in contact with the anterior sublinguals. Supralabials, throat and sides of the neck stained with black, an elongated black patch on the mental scale. Dorsum olive green, venter pigmented with dark grey-blue in the middle, at least at the base of each ventral. In general, two broad, black vontrolateral lines, limiting two yellowish lateral bands."

**Figure 14** – Live *P. mossambicus* from Angola (AMB 11691). **A.** dorsal view; **B.** close-up of right the side of head; **C.** close-up of top of head; **D.** close-up of ventral section. (Photos by Luis Ceríaco).

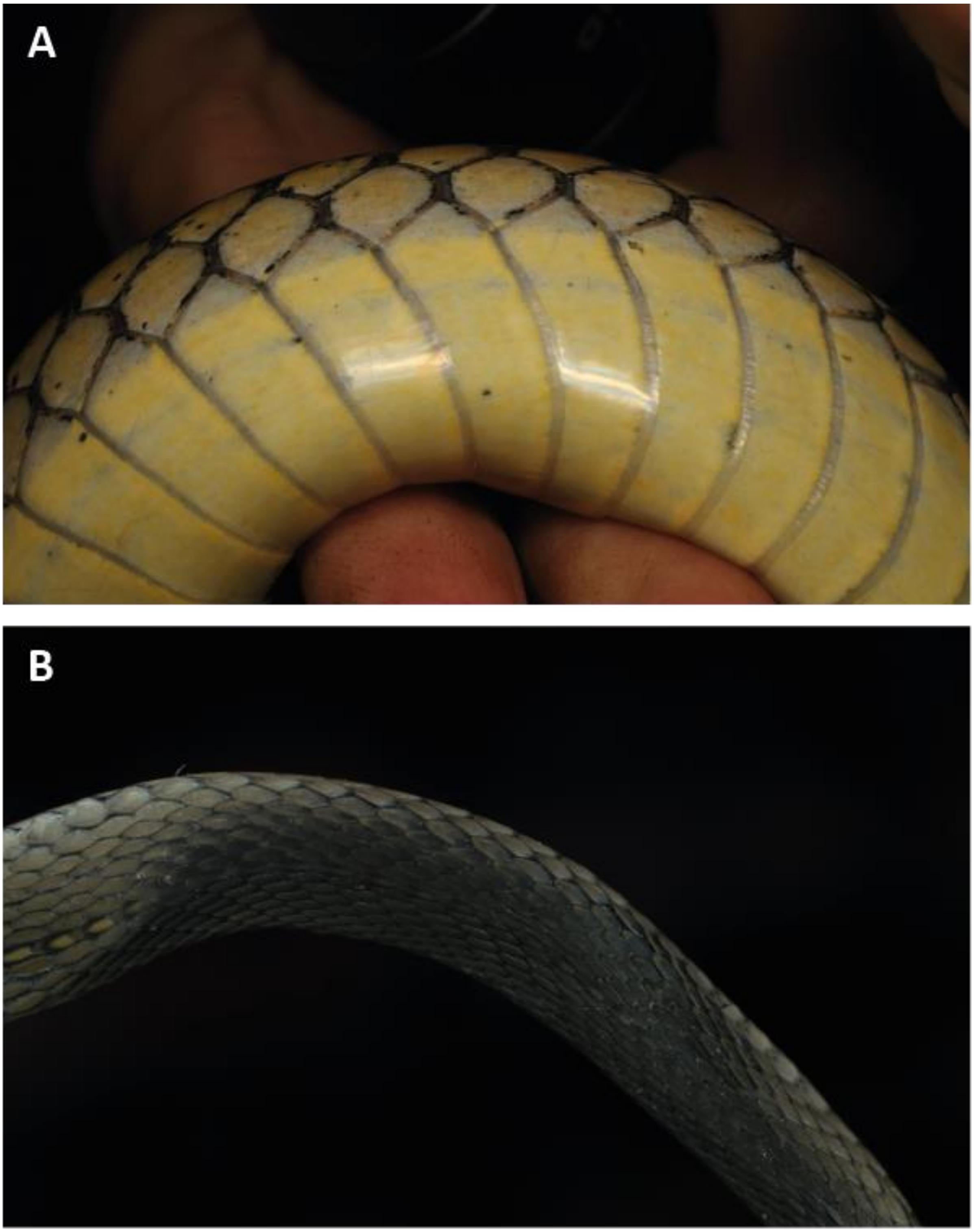

**Figure 15 – A.** Detail of the transition between dorsal and ventral coloration in *P. mossambicus* from Angola (AMB 11691) (Photo by Luis Ceríaco); **B.** Anterior dorsum of juvenile *P. mossambicus* from Angola (AMB 9644), showing a large patch of black scales (Photo by Diogo Parrinha).

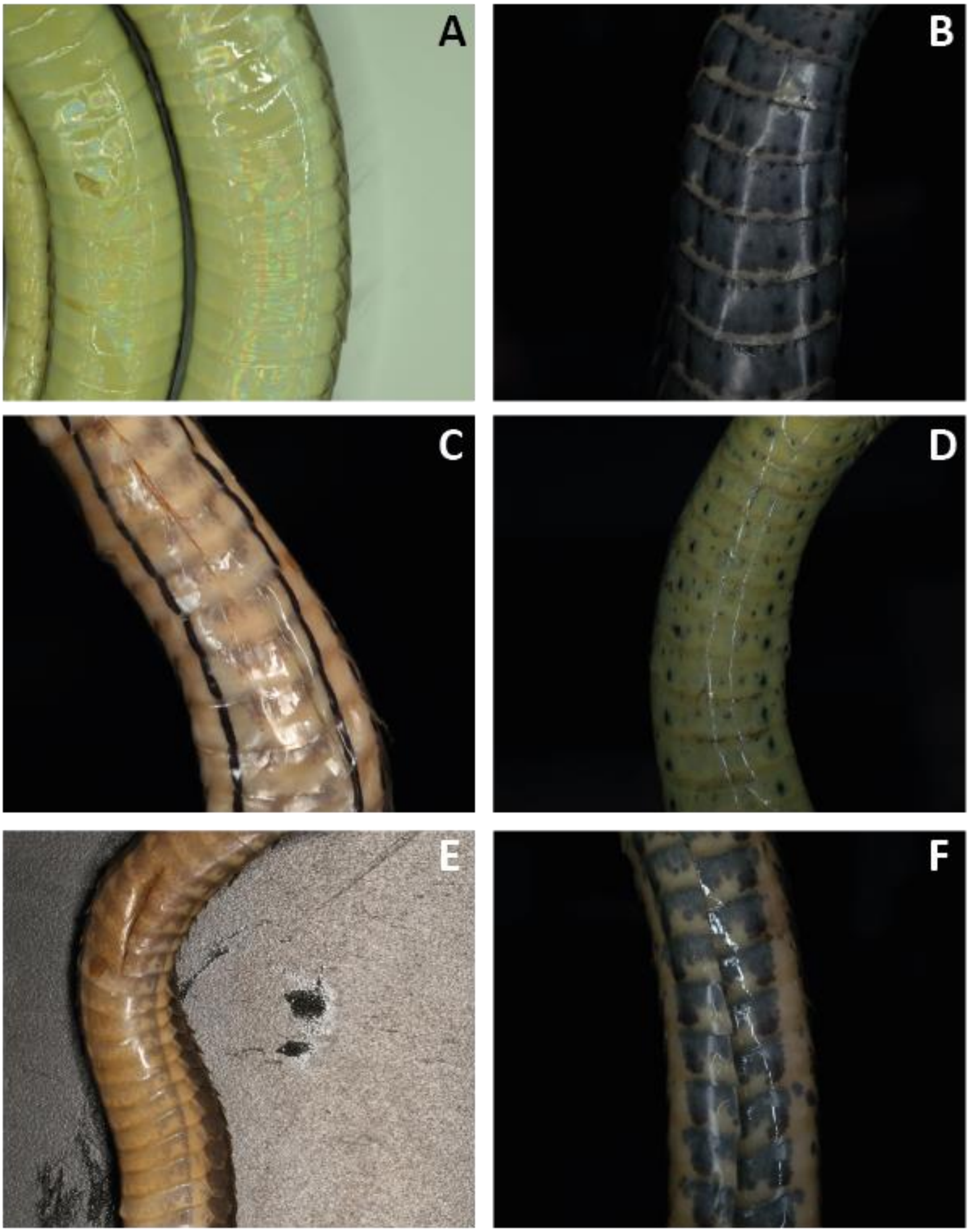

**Figure 16 –** Ventral pattern variation in *Psammophis mossambicus*: **A.** AMB 9665 from Angola (Photo by Diogo Parrinha); **B.** IICT/R 12-1958 from Angola (Photo by Diogo Parrinha); **C.** ANSP 20341 from the Central African Republic (Photo by Luis Ceríaco); **D.** IICT/R 7-1955 from Mozambique (Photo by Diogo Parrinha); **E.** MHNC-UP 040696 from Angola (Photo by Diogo Parrinha); **F.** IICT/R 47-1955 from Mozambique (Photo by Diogo Parrinha).

**Distribution and habitat:**

Common and widespread from Nigeria eastwards to Kenya and southwards to northern Namibia, Botswana and northeastern South Africa (Fig. 17). *P. mossambicus* seems to be a generalist species that occupies a variety of habitats from urban areas, derived savannas and farmlands, to mature forests and mangroves (Luiselli *et al*. 2004; Chirio & Ineich 2006; Chirio & LeBreton 2007; Ineich *et al*. 2015). In East and southern Africa, it is especially common in riparian habitats and is absent only from dryer desert and closed forest (Broadley 2002; Spawls *et al*. 2018).

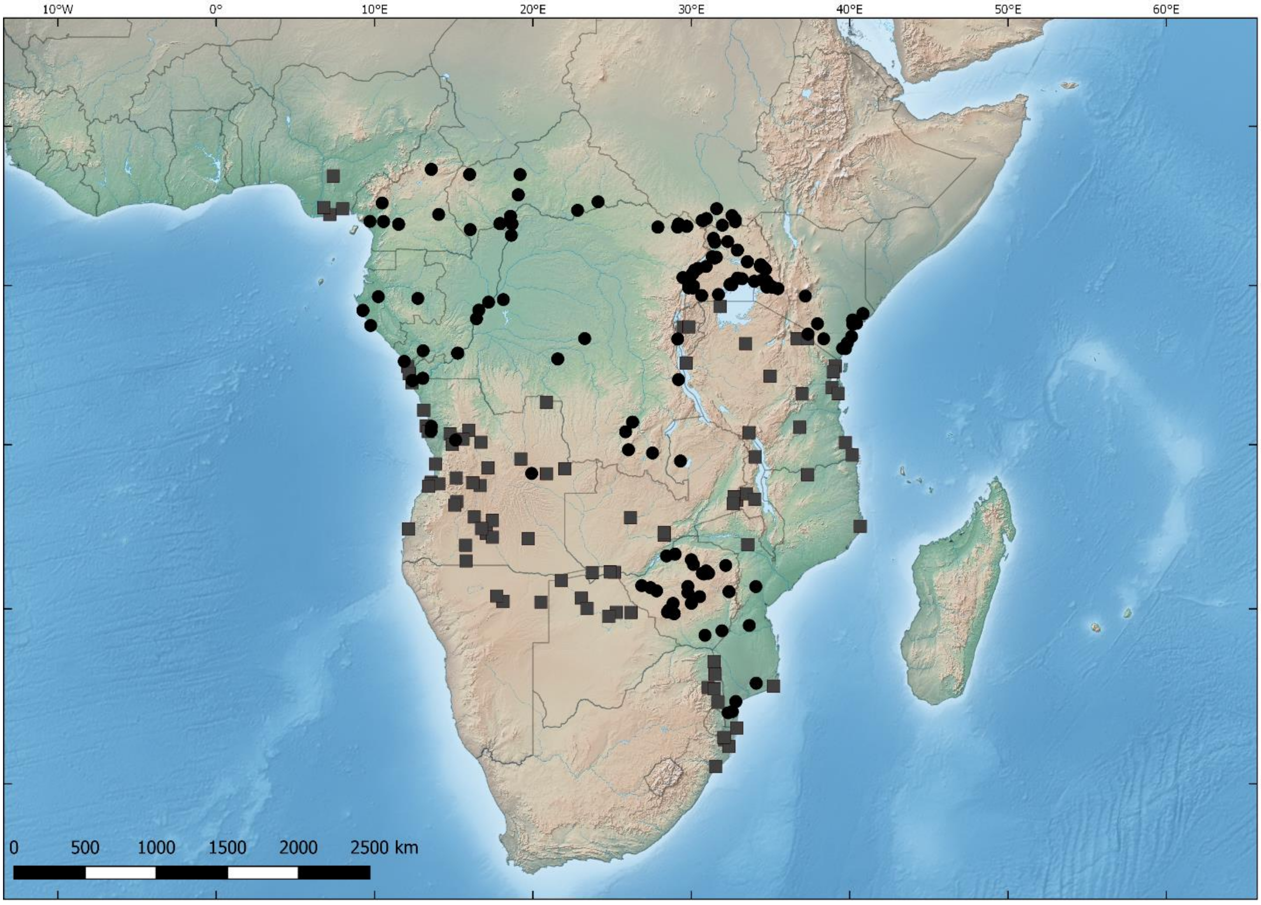

**Figure 17 –** Estimated distribution of *Psammophis mossambicus* based on examined specimens (black circles) and literature records (grey squares).

## *Psammophis sudanensis* Werner, 1919

### (Figs. 18–22)

*Psammophis subtaeniatus sudanensis* Werner, 1919:504. Lectotype: NMW 19086 (Fig. 18) [not NKW 19086 as in Broadley (1977), nor NMW 1986 as in Ullenbruch *et al*. (2010)], designated by Tiedemann and Haupl (1980). Type locality: "Kasugli, S-Kordofan, Anglo-ägyptischer Sudan" [=Kadugli, South Kordofan State, Sudan], via lectotype selection.

*Psammophis leucogaster* Spawls, 1983:311. Holotype: BMNH 1980.261 (Figs. 19 and 20). Type locality: Wa, Upper West Region, Ghana.

*Psammophis subaeniatus*: Loveridge (1928:55, 1929:32) (part), de Witte (1941:212), Böhme (1975:39), Chippaux (2006:179).

*Psammophis subtaeniatus sudanensis*: Loveridge (1940:50) (part), Laurent (1956:248), Perret (1961:136), de Witte (1962:117), Broadley (1966:5) (part), Isemonger (1968:177) (part), Pitman (1974:159), Böhme (1975), Vasey-FitzGerald (1975:20).

*Psammophis sibilans sibilans:* Broadley (1977:17), Broadley and Howell (1991:28).

*Psammophis* cf. *rukwae*: Böhme (1978:402), Joger (1981:332, 1982:332).

*Psammophis rukwae leucogaster*: Böhme (1986:178), Böhme & Schneider (1987:259).

*Psammophis subtaeniatus* ssp.: Böhme (1987:85).

*Psammophis sibilans*: Branstatter (1995, 1996a) (part).

*Psammophis sudanensis*: Trape and Mané (2002:149, 2015:45), Branch (2005:45), Trape (2005:42), Chippaux (2006:180), Chirio and Ineich (2006:52), Spawls *et al*. (2006:126, 2018:437), Chirio and LeBreton (2007:536), Ullebruch *et al*. (2010:44), Wallach *et al*. (2014:592).

*Psammophis sudanensis leucogaster*: Trape and Mané (2006:156).

**Original description:** "An diese Form Schlie sich dann ohneweiters die Sudanform des *P. subtaeniatus* an, mit deutlicher, an *schokari* erinnernder Kopfzeichnung, deutlichen, aber im erwachsenen Zustande stets braun gefärbten Längslinien der Ventralen, mit einer Reihe von schwarzen Punkten der Supralabialia oder diese ungefleckt. Ich nenne diese Form var. *sudanensis*. Sie wird wenig über 1 m lang." (Werner 1919)

**Nomenclatural history:**

After Werner's (1919) original description, based on a specimen from Sudan, the species was recorded from eastern Africa as *P. subtaeniatus* (Loveridge 1928, 1929; de Witte 1941). These East African records would be reassigned by Loveridge (1940) to *P. subtaeniatus sudanensis*, a northern form of *P. subtaeniatus* ranging from southern Sudan to northern Mozambique. Loveridge (1942, 1953, 1955, 1957) would continue to cite this species from East Africa and was followed by other authors (Laurent 1956; Manaças 1959; de Witte 1962; Broadley 1966; Isemonger 1968; Broadley & Cock 1975; Vasey-Fitzgerald 1975). Some of these records would later be reassigned to *P. orientalis* (discussed below). In the meanwhile, this species was also recorded from the savanas of Cameroon (Perret 1961; Böhme 1975), extending westwards to Senegal (Pitman 1974).

However, after examination of the type specimen, Broadley (1977) synonymized *P. subtaeniatus sudanensis* with *P. sibilans sibilans*, and described *P. subtaeniatus orientalis* to accommodate coastal and southern populations previously referred to *P. s. sudanensis* in eastern Africa, from coastal Kenya southwards to Malawi and Mozambique. Upon examination of the type it is understandable why Broadley referred those populations to *P. sibilans*, given that it has the lower labial pattern typical of the group (11 IL, the first 5 in contact with the anterior sublinguals), and the ventral pattern shows faded ventral lines instead of the distinct and contrasting "*subtaeniatus"* pattern (*i.e.* a bright yellow midventral region bordered by thick, well defined ventral lines) typical of *P. orientalis* and *P. subtaeniatus* in east and southern Africa, respectively.

At this point, and after Broadley's description of *P. rukwae* and the identification of Senegalese specimens as such (Broadley 1966, 1977), Böhme (1978) refers his specimens from Senegal to *P. rukwae*, as well as the Cameroon specimens he had previously identified as *P. subtaeniatus sudanensis* (Böhme 1975), a decision that was later followed by Joger (1981, 1982). Spawls (1983) described *P. leucogaster* based on a single specimen from northern Ghana. This snake resembled *P. sudanensis* in coloration but differed considerably in scalation, being a highly irregular and asymmetric specimen with an entire cloacal scale, 7(3, 4) supralabials, three fused infralabials on the right side and a single anterior temporal. Considering that at the time *P. sudanensis* was considered a synonym of *P. sibilans*, Böhme (1986) recognized *P. leucogaster* to be identical to the specimens from Cameroon and Senegal that he had previously called *P. subtaeniatus* and later *P. rukwae*, and suggested the name *P. rukwae leucogaster* to distinguish these western populations from the nominal *P. rukwae rukwae* in East Africa, with the specimens from Cameroon being intermediate between the two forms (Böhme & Schneider 1987). Böhme (1987) addressed once more the status of "*P. subtaeniatus*" from the Sudan, commenting on the description of *P. orientalis* by Broadley (1977) and calling for an urgent revision of northern populations associated with the "*subtaeniatus*" group. The status of West African populations was also discussed by Hughes (1999) and Trape (2005), with both authors considering these to represent *P. sudanensis*, a decision that we follow based on the descriptions and photos provided by earlier authors (Böhme 1978, 1986, 1987; Joger 1982; Spawls 1983). As for the status of *P. leucogaster*, based on my interpretation it should be regarded as a synonym of *P. sudanensis*, and not *P. rukwae* as in Wallach *et al.* (2014). Even though the holotype is a peculiar specimen when it comes to scalation, the dorsal and head patterns (Figs. 19-A and 20) match the diagnosis of *P. sudanensis* (see below). Many authors followed this view by recording *P. sudanensis* from several localities in West and Ccentral Africa (Trape & Mané 2002, 2015; Trape 2005; Chirio & Ineich 2006; Chirio & LeBreton 2007).

Trape & Mané (2006) recognize *P. sudanensis leucogaster*, without ventral markings, as the subspecies occurring in West Africa. On the other hand, Ullenbruch *et al*. (2010) record *P. sudanensis* from southern Benin and comment on the ventral pattern, suggesting that "if there is a distinction between typical *sudanensis* and *leucogaster* in West Africa, this is a question of a north-south rather than a west-east disjunction".

Kelly's *et al*. (2008) genetic assessment proved *P. sudanensis* to be a valid species, distinct from *P. sibilans, P. rukwae* and *P. orientalis*. However, genetic data was limited to East Africa (Kenya and Tanzania), so whether West African specimens truly represent *sudanensis* or an undescribed species remains to be confirmed. In the eventuality of West and East African populations representing distinct species, the name *P. leucogaster* might be available for the West African species (Spawls 1983).

**Diagnosis:**

Even though the lectotype has 11(5) infralabials, which may be one of the reasons that led Broadley (1977) to synonymize *P. sudanensis* with *P. sibilans*, most of the examined specimens, as well as literature records (Laurent 1956; Broadley 1966; Pitman 1974; Trape 2005; Trape & Mané 2006), have 10 infralabials, of which the first 4 are in contact with the anterior sublinguals. There is contact between the preocular and frontal scales in more than half of the specimens, but these may be separated as well. Between 153–180 ventrals and 92–110 pairs of subcaudals; the cloacal scale is divided. Spawls *et al.* (2018) give a lower limit for ventrals (142–180) and a wider range of subcaudals (182–129). The largest examined specimen is the lectotype (NMW 19086), which is a male from Sudan, with a total length of 135cm (101 SVL + 33 TL), followed by a male (MNHN 1904.67) and a female (FMNH 58389) from South Sudan, with an SVL of 92,5cm and 92cm, respectively. Trape & Mané (2007) give 137cm as the maximum length. It is a rather slender snake, when compared to bigger and robust species like *P. sibilans* and *P. mossambicus* (Loveridge 1940; Laurent 1956; Chirio & LeBreton 2007; Spawls *et al.* 2018).

A vertebral stripe may be present, usually a continuous white stripe, contrary to an interrupted vertebral stripe common in other species. Usually, but not always, with well-defined dorsolateral stripes, sometimes outlined with black. Both vertebral and dorsolateral stripes are usually wider than in other species, as can still be seen in the type specimens (Figs. 18-A, 19-A and 20-B). The dorsal coloration covers only the upper half of the first dorsal scale row, and there may be a black line separating dorsal and ventral coloration (Fig. 21-A).

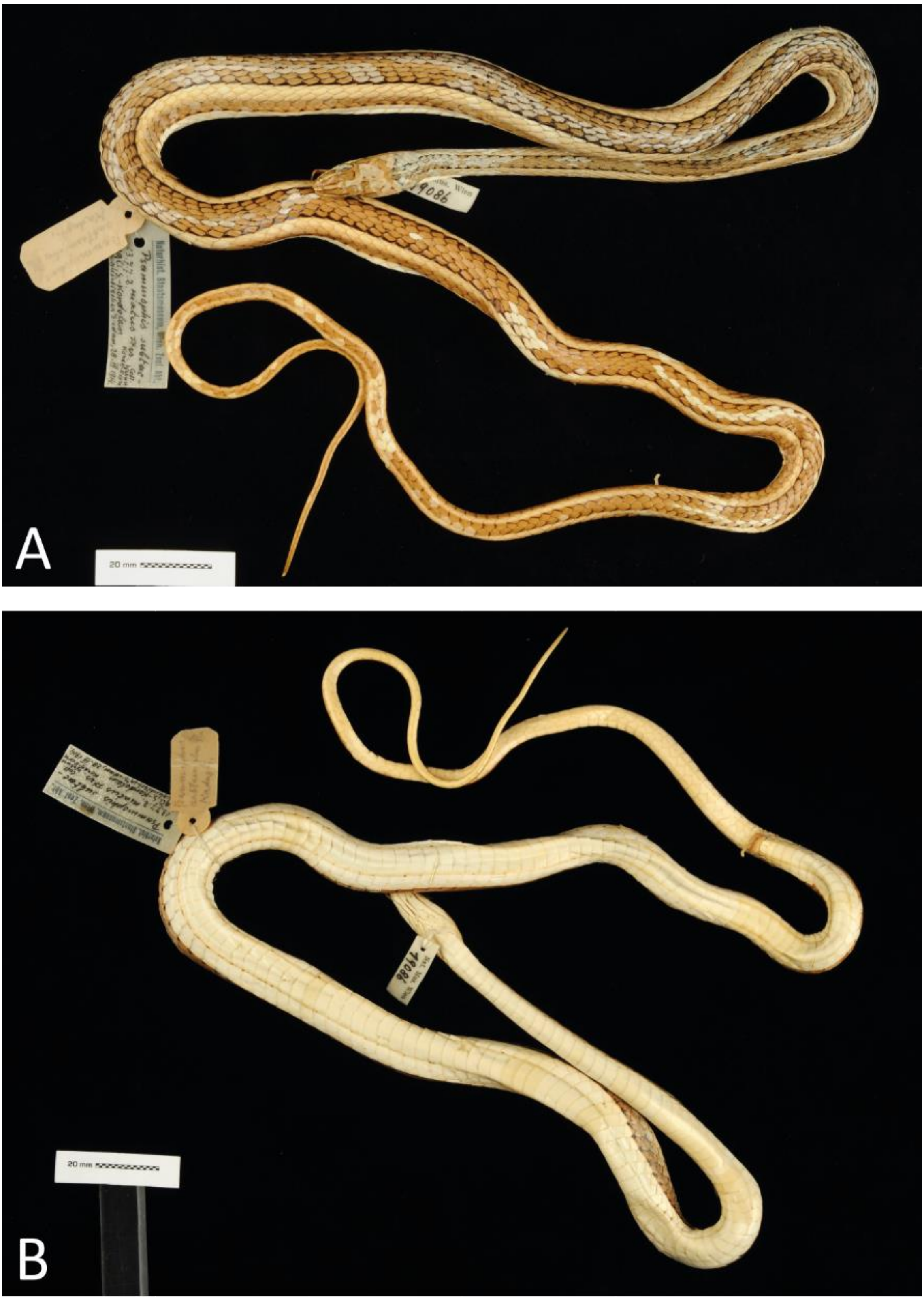

**Figure 18** – Dorsal (**A**) and ventral (**B**) view of the lectotype of *P. sudanensis* (NMW 19086) (Photos by Alice Schumacher).

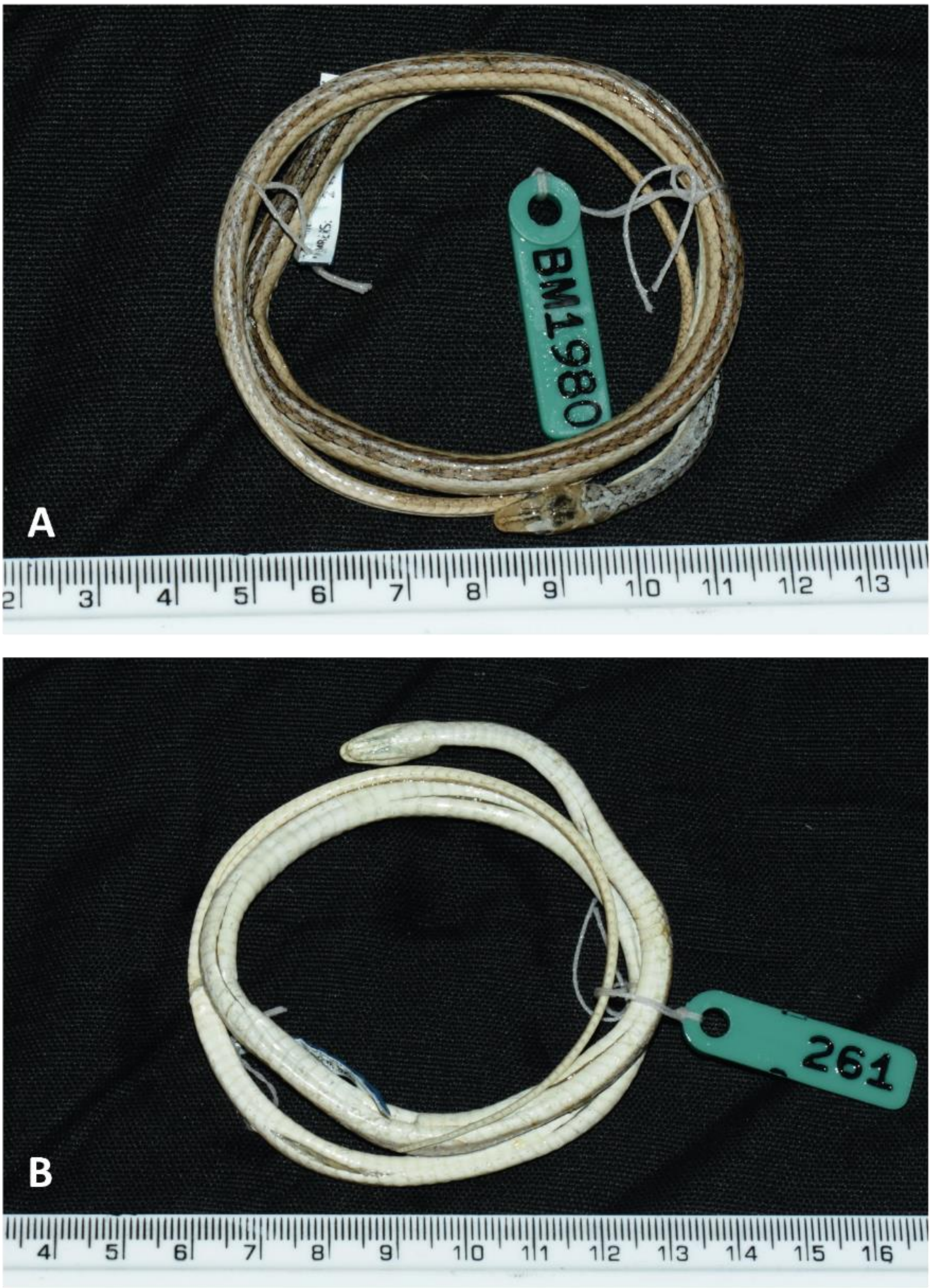

**Figure 19** – Dorsal (**A**) and ventral (**B**) view of the holotype of *P. leucogaster* (BMNH 1980.261) (Photos by Patrick Campbell).

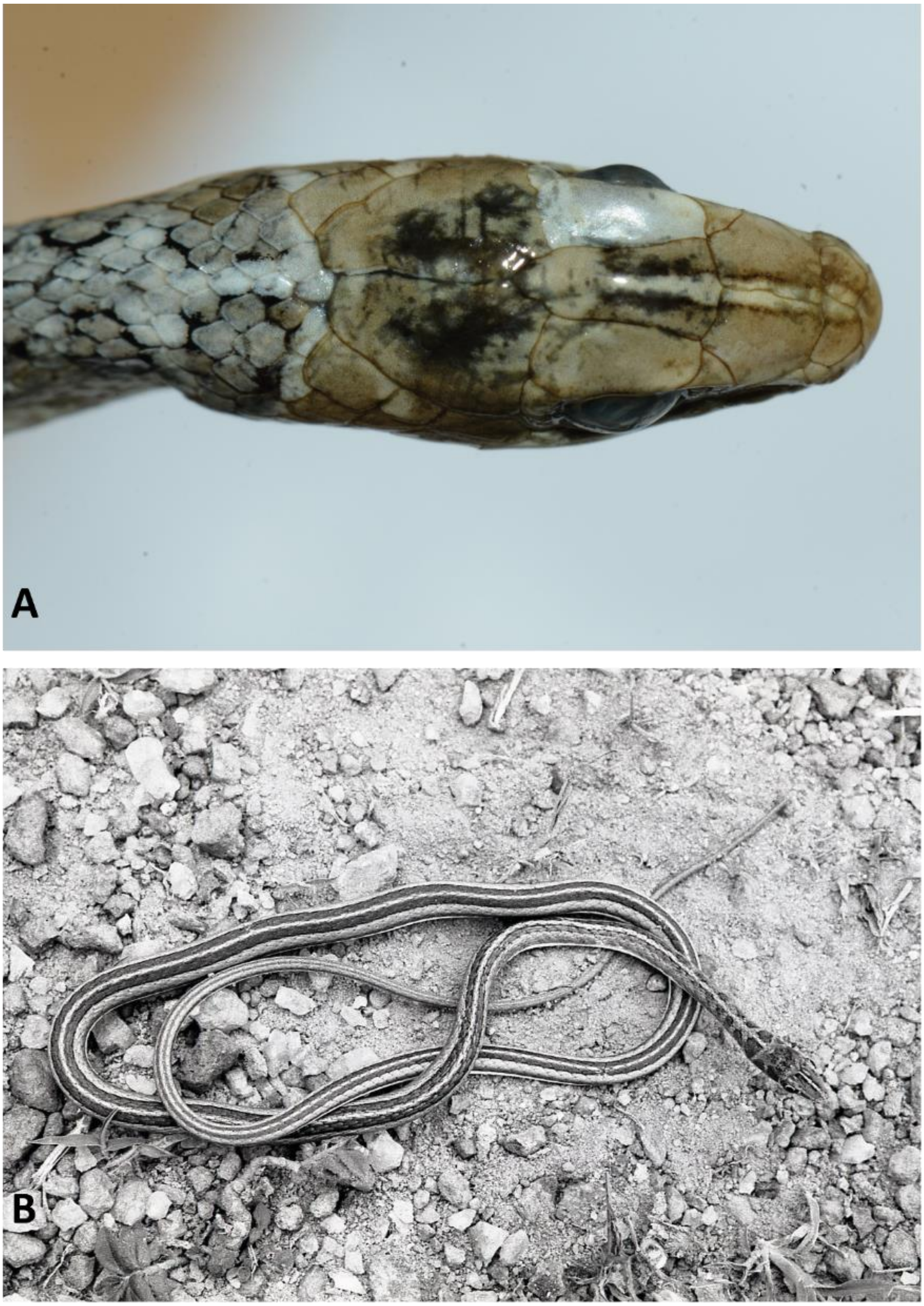

**Figure 20** – **A.** Top of head of the holotype of *P. Leucogaster* (BMNH 1980.261) (Photo by Patrick Campbell); **B.** Holotype of *P. leucogaster* (BMNH 1980.261) in life (Photo by Stephen Spawls).

This snake is sometimes diagnosed by a striking ventral pattern typical of the "*subtaeniatus*" group, consisting of a bright yellow midventral region bordered by distinct black lines, followed by white ventrolateral bands encompassing the ends of the ventrals and the lower half of the first dorsal scale row (Pitman 1974; Spawls *et al*. 2018). This is not always the case, however, as there are several records of specimens without ventral lines, especially in west Africa (Spawls 1983; Trape & Mané 2006). In the original description, Werner (1919) mentions only a pair of brown ventral lines, which are not very distinct and can still be seen in the lectotype (Fig. 18-B).

There is an argument regarding the distinction between nominal *sudanensis* and *leucogaster* based on differences in the ventral pattern. Some authors consider *leucogaster*, with a uniform white ventrum, to represent a west African subspecies of *P. sudanensis* (Böhme 1986; Trape & Mané 2006), while Ullenbruch *et al*. (2010) record both "forms" from Benin and suggest that if a distinction is to be made, it is a question of latitude rather than longitude. Most of our specimens from East Africa have clear ventral lines, but the small number of West African specimens examined makes it impossible to reach conclusive results regarding this issue at the moment. The idea of an ontogenetic effect on ventral pattern should not be discarded either.

Considering this, ventral pattern should not be regarded as a good diagnostic character, as it is quite variable within *P. sudanensis*, and the typical "*subtaeniatus*" pattern is also known to occur in other species (Largen & Rasmussen 1993; Largen & Spawls 2010).

The most unique character to *P. sudanensis* seems to be a typical head pattern of a pale stripe going from the tip of the snout, through the middle of the frontal, to the anterior margin of the parietals, usually followed by pale transverse lines (Figs. 21-B and 23-A). This head pattern is mentioned by some authors (Loveridge 1940; Broadley 1966, 1977; Trape & Mané 2006, 2015; Chirio & LeBreton 2007; Spawls *et al*. 2018) but few acknowledge it as a diagnostic character, which may be due to the long-lasting confusion with *P. orientalis* and *P. sibilans* in East Africa and *P. rukwae* in West Africa. However, despite its taxonomic value, this is not a constant character and identification should not be based solely on the presence of the head stripe.

**Figure 21 – A.** Lateral view of *P. sudanensis* from West Africa (MHNC-UP 017461) showing a black line through the middle of the first dorsal scale row that separates dorsal and ventral coloration, plus a pair of faded ventral hairlines (Photo by Diogo Parrinha); **B.** Typical *P. sudanensis* head pattern in a specimen from South Sudan (FMNH 62317) (Photo by FMNH, available at https://www.gbif.org/occurrence/668625612).

**Distribution and habitat:**

In East Africa it is known from central Tanzania northwards to central Kenya and eastern Uganda, with a few isolated records from northern Kenya, South Sudan and eastern Democratic Republic of Congo (Fig. 22) (Laurent 1956; de Witte 1962; Pitman 1974; Spawls *et al.* 2018). Records from Mozambique and Malawi (*e.g.* Loveridge 1953; Manaças 1959) are to be assigned to *P. orientalis*. Although not yet recorded for the country, it is possible that this species occurs further north to some parts of Ethiopia (Pitman 1974; Largen & Rasmussen 1993; Largen & Spawls 2010). The type specimen comes from Kadugli, southern Sudan, and although distribution limits are poorly known, isolated records from Cameroon to Senegal lead to an estimated distribution from East Africa to Senegal through the Sahel (Pitman 1974; Böhme 1975, 1978; Trape & Mané 2006, 2015; Chirio & LeBreton 2007; Ullenbruch *et al.* 2010). *P. sudanensis* shows Sudanian and Sahelian zoogeographical affinities, preferring dryer habitats in relation to the other species of the group. This species is usually found in dry savannas with scattered bushes or thicket, which the snake often climbs to bask or seek refuge (Loveridge 1940; Broadley 1966; Böhme 1975; Broadley & Howell 1991; Trape & Mané 2006; Chirio & LeBreton 2007; Spawls *et al.* 2018). This seems to be a rather uncommon snake throughout its range, especially in West Africa (Laurent 1956; Trape & Mané 2002).

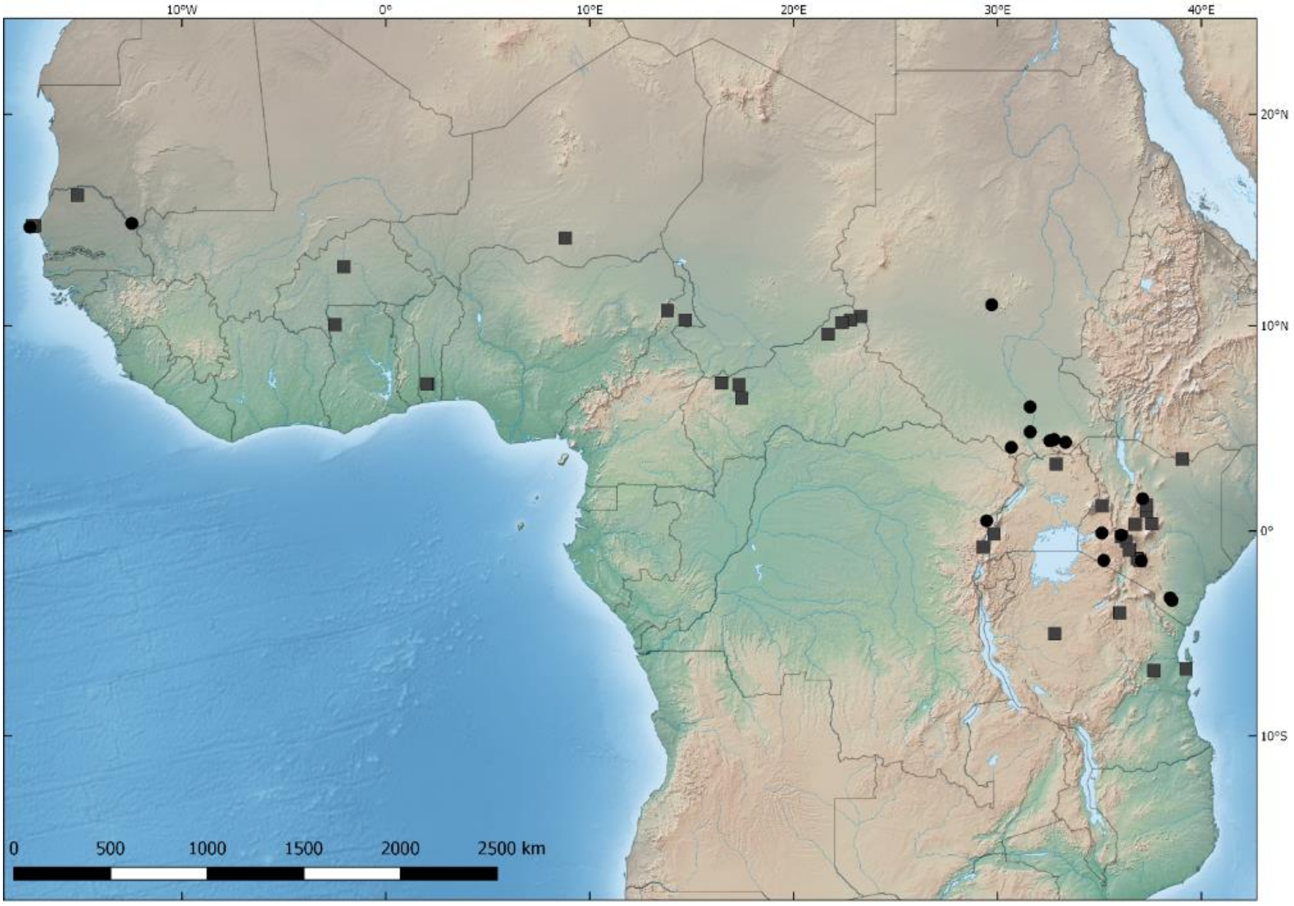

**Figure 22 –** Estimated distribution of *Psammophis sudanensis* based on examined specimens (black circles) and literature records (grey squares).

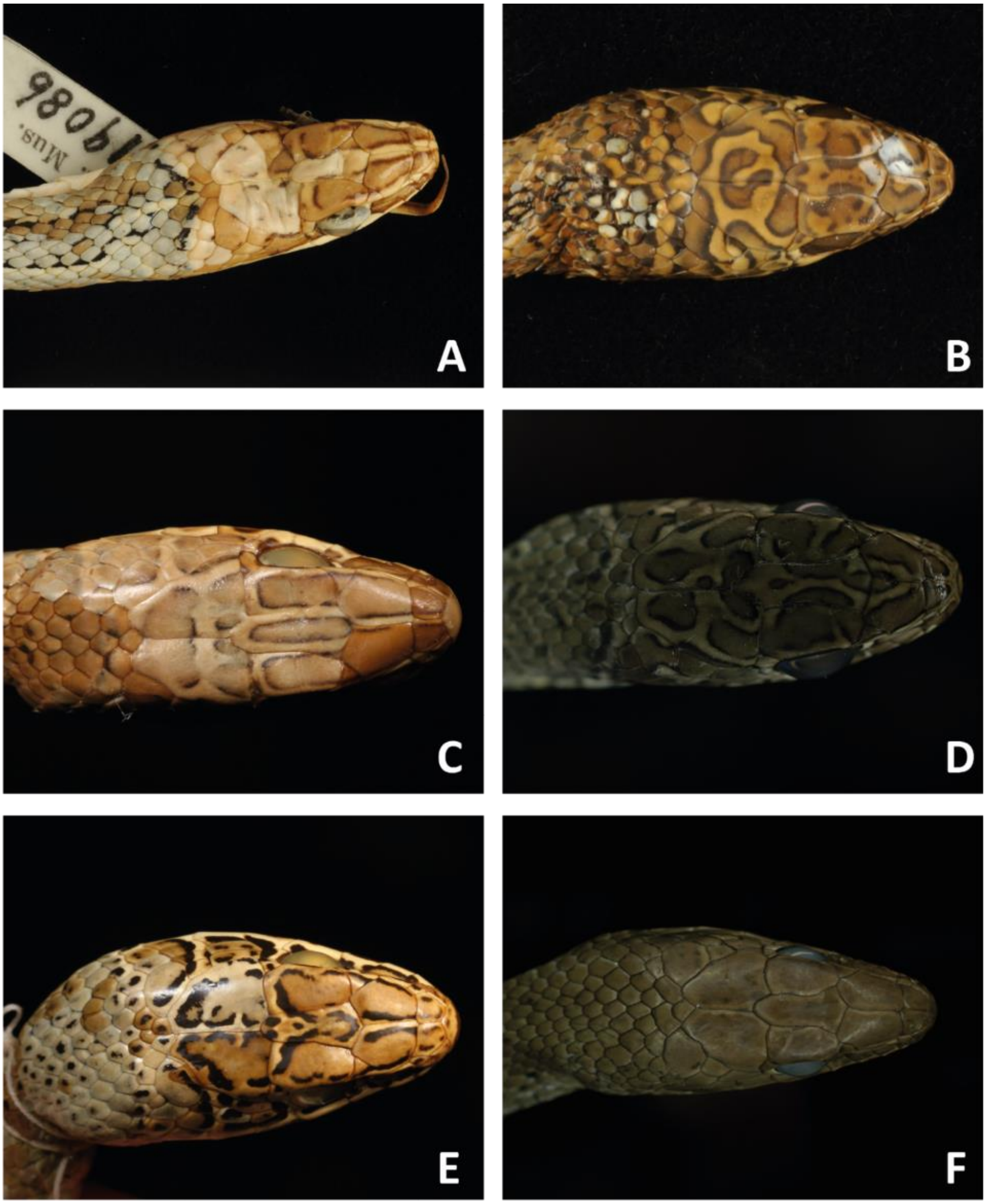

**Figure 23 –** Head markings in: **A.** lectotype of *P. sudanensis* (NMW 19086), from Sudan (Photo by Alice Schumacher); **B.** lectotype of *Psammophis occidentalis* (NMW 19245.2), from "Congo" (Photo by Alice Schumacher); **C.** *P.* cf. *rukwae* (IICT/R 34-1946), from Guinea-Bissau (Photo by Diogo Parrinha); **D.** juvenile *P. mossambicus* (AMB 9644), from Angola (Photo by Diogo Parrinha); **E.** *P.* cf. *sibilans* (ANSP 4835) (Photo by Luis Ceríaco); **F.** adult *P. mossambicus* (AMB 9665), from Angola (Photo by Diogo Parrinha).

## *Psammophis rukwae* Broadley, 1966

**(Figs. 24–25)**

*Psammophis sibilans rukwae* Broadley, 1966:3. Holotype: NMSR 4212. Type locality: Kafukola, Rukwa Valley, Tanzania.

*Psammophis subtaeniatus sudanensis*: Vasey-FitzGerald (1958:62), Broadley & Pitman (1960:446), Robertson *et al.* (1962:428) (*fide* Broadley 1966).

*Psammophis rukwae*: Welch (1982:170) (part), Branch (2005:47), Spawls *et al.* (2006:128, 2018:436), Wagner & Böhme (2007:138), Wagner *et al.* (2008:1353), Wallach *et al.* (2014:590).

*Psammophis rukwae rukwae*: Broadley & Howell (1991:28), Broadley (1993:42).

**Original description:** "Diagnosis – A race of *Psammophis sibilans* distinguished by consistent ventral pattern of a pair of black lateral hairlines similar to that found in *Psammophis subtaeniatus* Peters. This form differs from all related south-eastern forms of *Psammophis* in having the first five lower labials in contact with the anterior sublinguals, an arrangement common in Egyptian populations of *P. sibilans* (Marx, 1958) and typical of the species *elegans, punctulatus, trigrammus, schokari* and *biseriatus* (Loveridge, 1940).

Description (paratype variations in parentheses) – Snout twice as long as the orbital diameter (but only $1^{1/2}$ times in juveniles); nostril pierced between two nasals; loreal more than twice as long as deep; preocular 1, well separated from the frontal; postoculars 2; temporals ½+3 (i.e., lower anterior temporal vertically divided); upper labials 8, the fourth and fifth entering the orbit; lower labials 11 (10–11), the first 5 (5 on 33 sides; 4 on 3) in contact with the anterior sublinguals; dorsal scale row formula $17\,\frac{3+4(98)}{3+4(98)}\,15\,\frac{6+7(100)}{6+7(102)}\,13$; ventrals 166 (165-177); anal divided; subcaudals 91 (83-96). Dental formula (from skulls of two paratyes): maxillary 4+2+3+II; palatine 10; pterygoid 16; dentary 17-18.

Coloration – Head uniform pale brown, body dark olive brown, becoming paler caudad with faint pale dorso-lateral bands, vertebral scale row with a pale spot at the base of each scale, labials, chin and throat uniform white, ventrals with lateral dark hairlines which fade out caudad. Juvenile paratypes all have well defined *P. subtaeniatus* markings – a pair of pale dorso-lateral bands and a pair of black lateral hairlines on the ventrals and subcaudals, the head markings are variable, but usually the frontal has a pale margin and a pale stripe extends forward along the prefrontal-internasal sutures, there may be pale transverse bands on the back of the head. All markings gradually fade with increasing size, but dorso-lateral light bands are usually distinguishable, and the ventral hairlines persist in all the adults that I have examined." Broadley (1966)

## Nomenclatural history:

After the original description as a subspecies of *P. sibilans* (Broadley 1966), based on specimens from the Rukwa Valley, Tanzania, Broadley (1977) gave it specific status and extended its distribution across the Sudanese savanna to Senegal. However, as discussed above, this range extention led some authors to mistakenly record *P. sudanensis* as *P.* cf. *rukwae* from West Africa (*e.g.* Böhme 1978; Joger 1981, 1982). Likewise, *P. leucogaster* is to be associated with *P. sudanensis* rather than *P. rukwae*, contrary to what is suggested by Böhme (1986). Some authors followed Broadley (1977) by assigning West African specimens to *P. rukwae* (Welch 1982; Brandstätter 1995, 1996a; Pauwels & Meirte 1996; Leaché 2005; Leaché *et al.* 2006).

Kelly *et al.* (2008) proved *P. rukwae* to be a valid species in East Africa and showed a single sample from Senegal to be genetically closer to *P. rukwae* than to *P. sibilans*. Some authors followed Kelly *et al*. (2008) by referring West African populations to *P. rukwae* (Chirio 2009; Wallach *et al*. 2014; Sow *et al*. 2017).

## Diagnosis:

The infralabial arrangement of 11 infralabials, with the first five in contact with the anterior sublinguals, is the best way to distinguish *P. rukwae* from related species in eastern Africa. Preocular separated from the frontal. Between 160 and 179 ventral scales and 83 to 112 subcaudals pairs, and the cloacal scale is divided. Our largest specimen (NMZB 8310) is a male with a truncated tail measuring 120cm from snout to vent, but the largest recorded measures 122.7cm from snout to vent, with a total length of 165,5cm (Broadley 1966).

*Psammophis rukwae* is often described as morphologically intermediate between *P. sibilans* and *P. mossambicus* (Broadley 1977; Largen & Rasmussen 1993), with juveniles showing a striped pattern that fades with age, leaving old individuals more similar to *P. mossambicus*, with dorsolateral stripes indistinct and head pale brown. As can be seen in Figure 24, faint or weakly defined reddish dorsolateral stripes are usually noticeable in most individuals, as well as a pair of thin ventral lines (unlike the thick ventral lines typical of *P. subtaeniatus* and *P. orientalis*) (Broadley 1966). However, this remains a rare and uncommon species in east Africa, known mostly from literature records (Wagner & Böhme 2007; Spawls *et al.* 2018).

**Figure 24 –** Dorsal (**A**) and ventral (**B**) view of a *Psammophis rukwae* (ZMUC R631333) from Tanzania in the collections of the Zoological Museum, Natural History Museum of Denmark (photos by Geert Møller Brovad, Natural History Museum of Denmark, available at https://www.gbif.org/occurrence/462395126).

**Distribution and habitat:**

In East Africa this remains a rare and uncommon species known only from a few scattered localities (Fig. 25). From Lake Rukwa in western Tanzania northwards to Torit in South Sudan, in woodland and medium-altitude moist savanna (Broadley 1966; Broadley & Howell 1992; Branch 2005; Spawls *et al*. 2018). Distribution limits are poorly known, and it may extend westwards to the Central African Republic (Chirio 1997; Chirio & Ineich 2006). The status of populations from Central Africa, between Chad and South Sudan, remains unclear.

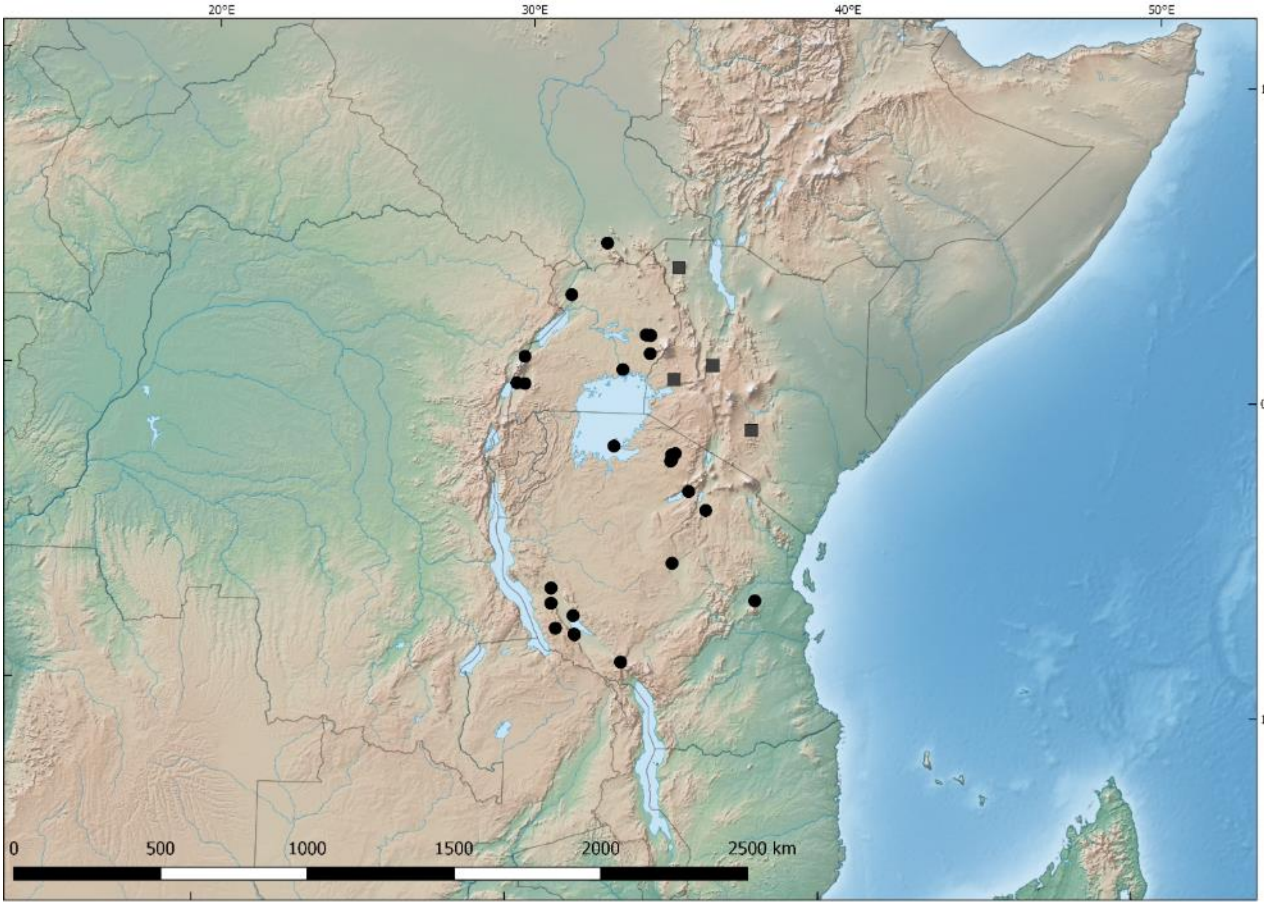

**Figure 25 –** Estimated distribution of *Psammophis rukwae* based on examined specimens (black circles) and literature records (grey squares).

## *Psammophis* cf. *rukwae* Broadley, 1966

**(Figs. 26-29)**

***Psammophis afroccidentalis* Trape, Böhme & Mediannikov, 2019:68. Holotype: MNHN 2018.0013 (formerly IRD 7631.S). Type locality: Dakkar Hann, Senegal. [Described during the writing of this dissertation]**

*Psammophis sibilans*: Günther (1858:136) (part), Bocage (1866:48, 1896a:177, 1896b:78) (part), Chabanaud (1917:12), Monard (1940:177), Böhme (1975:40, 1978:398), Roman (1980:61), Trape & Mané (2002:149, 2006:154, 2015:45), Chippaux (2006:175), Chirio & LeBreton (2007:534), Rato *et al*. (2007:113), Brito *et al.* (2008:22), Segniagbeto *et al*. 2011:346, Auliya *et al*. (2012:280).

*Psammophis phillipsii*: Joger (1881: 331, 1882:331), Leaché (2005:18), Leaché *et al*. (2006:39).

*Psammophis sibilans sibilans*: Villiers (1950a:92, 1950b:103; 1951:827, 1952:892, 1953:1119, 1956:880) (part), Manaças (1955:24), Condamin (1958:255), Perret (1961:136), Doucet (1963:306), Isemonger (1968:174) (part), Welch (1982:170) (part).

*Psammophis rukwae*: Broadley (1977:2) (part), Welch (1982:170) (part), Brandstätter (1995:151, 1996a:83) (part), Leaché (2005:18), Leaché *et al.* (2006:39), Chirio (2009:30), Wallach *et al.* (2014:590) (part).

*Psammophis rukwae* cf. *silvomarginata* (*nomen ineditum*): Brandstätter (1995:85).

*Psammophis* cf. *phillipsii*: Rödel *et al.* (1995:7).

*Psammophis sibilans* (cfr. *rukwae*): Pauwels & Meirte (1996:30).

*Psammophis* cf. *phillipsi*: Böhme *et al.* (1996), Ullenbruch *et al.* (2010:43).

*Psammophis* aff. *phillipsii:* Rödel *et al*. (1999:170).

*Psammophis* cf. *rukwae*: Rödel *et al.* (1999:170), Kelly *et al*. (2008:1046), Sow *et al*. (2017:105).

*Psammophis* aff. *sibilans*: Trape & Mané (2017:120).

**Nomenclatural history:**

West African populations of the *sibilans* complex are one of the most taxonomically unstable, and its status remains unresolved. Specimens were assigned either to *P. sibilans* or *P. phillipsii* based mostly on coloration and habitat (Cansdale 1973; Menzies 1966). Specimens from West African savannas have been referred to *P. sibilans* by most authors (*e.g.* Bocage 1866, 1896a, 1896b; Boulenger 1896; Loveridge 1940; Villiers 1950a; Manaças 1955; Doucet 1963; Papenfuss 1969; Roman 1980). Although without commenting on the status and distribution of *P. sibilans* in West Africa, Broadley (1977) assigns specimens from Senegal to *P. rukwae*, extending its distribution from Tanzania across the Sudanese savanna to Senegal. This range extension led other authors to record *P.* cf. *rukwae* from west Africa (Böhme 1978; Joger 1981, 1982), although these are misidentifications referable to *P. sudanensis* (discussed above). This snake was also recorded from West African savannas as *P.* cf. *phillipsii* (Böhme 1978; Schätti 1986; Joger 1981; Böhme *et al*. 1996; Rödel *et al*. 1995, 1999). The confusion between *P. phillipsii* and *P.* cf. *rukwae* in West Africa is due to the morphological similarities between the two species. Older individuals of *P.* cf. *rukwae* are usually uniformly colored, and therefore similar to *P. phillipsii*, which led authors to record monochrome specimens from savanna regions regions as *P.* cf. *phillipsii*. A good way to distinguish *P. phillipsii* from *P.* cf. *rukwae* and *P. sibilans* is to look at the infralabial arrangement (Broadley 1966; Largen & Rasmussen 1993), but unfortunately most older records didn't mention this character.

Brandstätter (1995) followed Broadley (1977) in assigning West African specimens to *P. rukwae* rather than *P. sibilans* (although it should be noted that *P. sudanensis* was considered a synonym of *P. sibilans* by both authors). Furthermore, while the striped specimens are assigned to nominal *P. rukwae rukwae*, the uniform specimens from savanna, forest margins and cultivated areas, recorded as *P.* cf. *phillipsii* by some authors (*e.g.* Böhme 1978; Schätti 1986; Joger 1981), are treated by Brandstätter (1995) as *P. rukwae* cf. *silvomarginata*. However, no formal description is made, neither is there any reference to it in the subsequently published book (Brandstätter 1996a). Hughes (1999) is skeptical about earlier records of *P. rukwae* from West Africa, and prefers to assign those populations to *P. sibilans*, as did other authors (Trape & Mané 2002, 2006; Chirio & LeBreton 2007; Rato *et al*. 2007; Brito *et al*. 2008). Meanwhile, the presence of *P. rukwae* in west Africa remains unsubstantiated, but there are still those who follow Broadley (1977) by recording this species from Ghana (Leaché 2005) and Togo (Leaché *et al*. 2006).

Based on genetic data, Kelly *et al*. (2008) showed a single specimen from Senegal to be closer related to *P. rukwae* rather than *P. sibilans*. Despite the considerable intraspecific divergence, the authors provisionally treat it as *P.* cf. *rukwae*, validating the occurrence of this species in West Africa. Some authors followed Kelly *et al.* (2008) by assigning West African specimens to *P. rukwae* (Chirio 2009; Sow *et al*. 2017), while others continue to consider *P. sibilans* as the species occurring in West Africa (Trape & Mané 2015, 2017; Segniagbeto *et al*. 2011; Auliya *et al.* 2012). Furthermore, Ullenbruch *et al.* (2010) still follow Böhme *et al*. (1996) by referring specimens from West African savannas to *P.* cf. *phillipsii*. In our phylogenetic analysis, the two samples from Burkina Faso and Mali previously published by Rato *et al*. (2007) formed a monophyletic group with Kelly's *et al.* (2008) sample from Senegal, genetically closer to *P. rukwae* than to *P. sibilans* (Fig. 7). Taking these results in consideration, as well as morphological and ecological differences, we think that West African populations may represent a valid species, distinct from *P. sibilans* and topotypical *P. rukwae*. Therefore, most records of *P. sibilans* from West Africa are to be provisionally assigned to *P.* cf. *rukwae* (*e.g.* Doucet 1963; Papenfuss 1969; Roman 1980; Rödel *et al*. 1995; Trape & Mané 2002 2006, 2015, 2017; Chippaux 2006; Chirio & LeBreton 2007; Rato *et al*. 2007; Brito *et al*. 2008; Segniagbeto *et al.* 2011).

Combining morphological and molecular data, Trape *et al*. (2019) confirmed our hypothesis by describing and naming West African populations from Mauritania to Chad as *Psammophis afroccidentalis* Trape, Böhme & Mediannikov, 2019.

**Diagnosis:**

The infralabial arrangement is like that of *P. sibilans*, with 11 infralabials, of which the first five are in contact with the anterior sublinguals. It should be noted that specimens from Guinea-Bissau display this infralabial arrangement, contrary to what is described by Manaças (1955). Unlike *P. rukwae* from east Africa, there is usually contact between the preocular and frontal scales. There are 154 to 183 ventrals and 87 to 116 subcaudals pairs, and the cloacal scale is divided. Our largest specimen (USNM 161972) measures 101cm from snout to vent and has a truncated tail, but according to other authors this snake can reach total lengths up to 185cm (Trape & Mané 2006; Chirio & LeBreton 2007).

This species is usually characterized by a distinctly striped juvenile pattern that fades with age, resulting in uniformly colored adults that may resemble *P. phillipsii* and *P. mossambicus* (Böhme *et al*. 1996; Trape & Mané 2006; Ullenbruch *et al.* 2010). However, the presence of dorsal stripes may not be entirely related to ontogeny, as there are several juvenile specimens among our data, measuring less than 30cm from snout to vent, that are dorsally uniform (Fig. 28-A). Considering this, the dorsum may be either monochrome or longitudinally striped (Fig. 27-A), with or without a vertebral line. Dorsolateral stripes become less distinct with age, but weakly defined reddish stripes are usually perceptible in most specimens (Fig. 26-A). Some specimens from Guinea-Bissau, Benin and Burkina Faso have a considerably darker anterior dorsum, that progressively becomes paler posteriorly and contrasts with a pale brown head (Fig. 27-B). Pictures of both juvenile and adult live specimens from Mali are shown in Böhme *et al*. (1996). The underside is yellowish white, uniform or with thin lateral lines, commonly faint and broken, only perceptible posteriorly in adults (Figs. 26-A and 28-B). Although less common, the midventral region between these lateral lines may be yellow, leaving a white ventrolateral band that covers the ends of the ventrals and a portion of the first dorsal scale row.

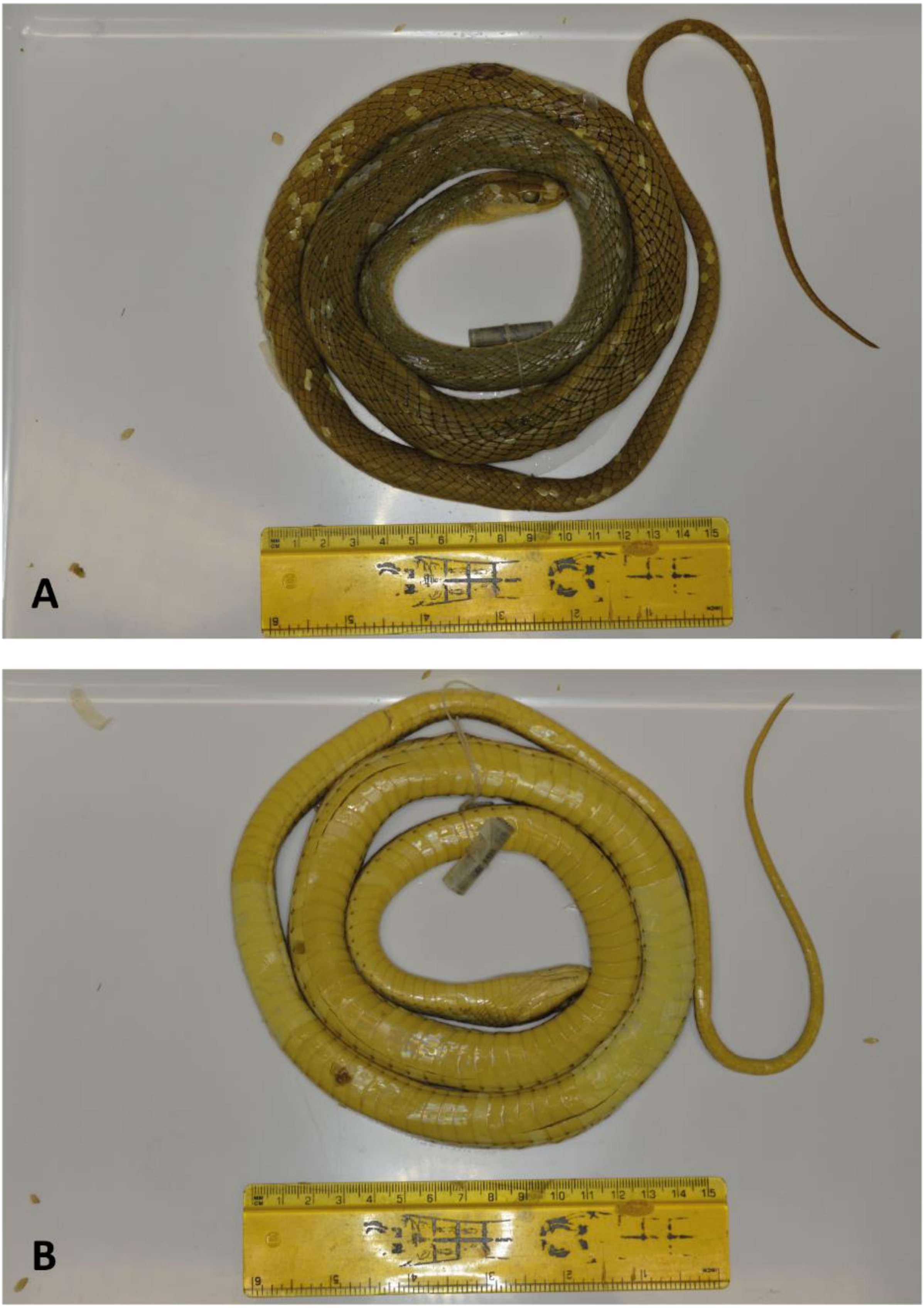

**Figure 26 –** Dorsal (**A**) and ventral (**B**) view of a *P.* cf. *rukwae* specimen from Guinea-Bissau (IICT/R 25-1945) (Photos by Diogo Parrinha).

**Figure 27 –** Dorsal pattern variation in *P.* cf. *rukwae* from Guinea-Bissau: **A.** IICT/R 143-1945, from Tor; **B.** IICT/R GB9, from Mandinga (Photos by Diogo Parrinha).

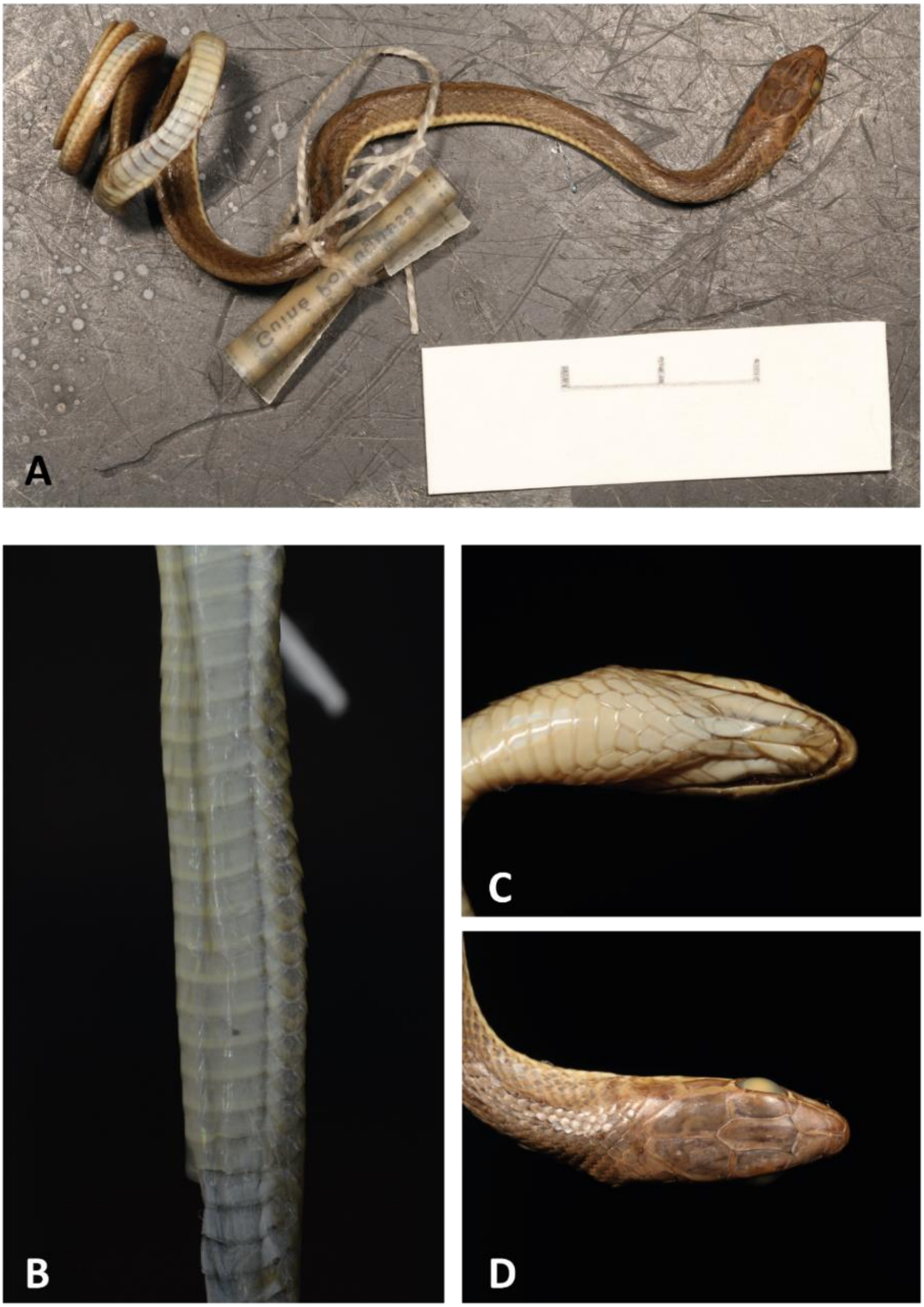

**Figure 28 –** Juvenile specimen of *P.* cf. *rukwae* from Guinea-Bissau (IICT/R 126-1946): **A.** Dorsal view; **B.** Close-up of ventral section, showing faint ventral lines and pigmented midventral region; **C.** Close-up of gular region; **D.** Top of head (Photos by Diogo Parrinha).

**Distribution and habitat:**

This is a common and widespread species from Senegal westwards to the Cameroon (Fig. 29) (Brandstätter 1995, 1996a; Chippaux 2006; Trape & Mané 2006; Chirio & LeBreton 2007). It occupies a variety of habitats, from dry savannas to forest clearings and cultivated fields, being absent only from rainforest regions (Brandstätter 1995; Böhme *et al*. 1996; Trape & Mané 2006; Chirio & LeBreton 2007).

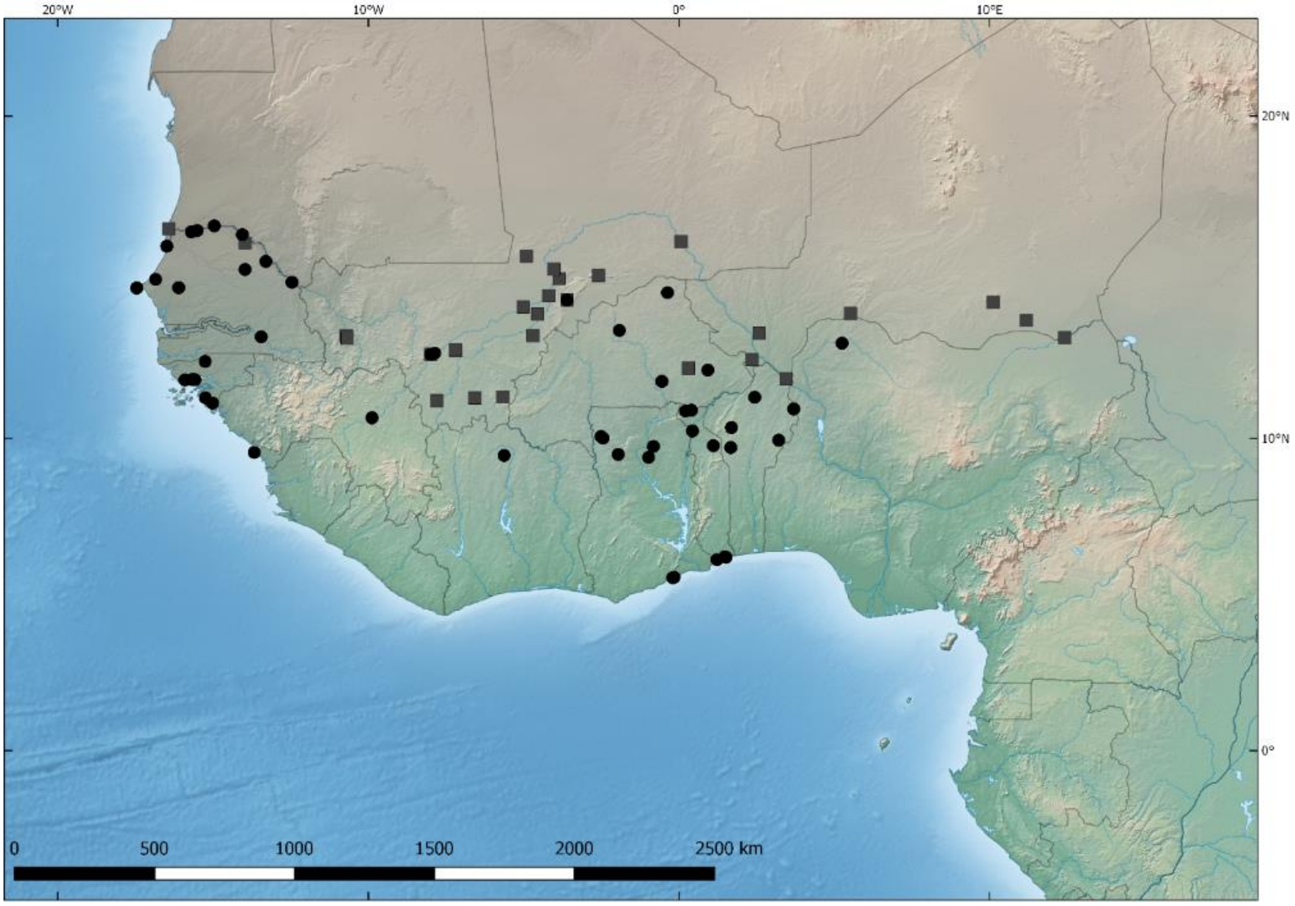

**Figure 29 –** Estimated distribution of *Psammophis* cf. *rukwae* in west Africa based on examined specimens (black circles) and literature records (grey squares).

# Discussion and final considerations

The *Psammophis sibilans* species complex has been a taxonomic problem in African herpetology for decades (Schmidt 1923; Bogert 1940; Loveridge 1940; Broadley 1963, 1983; Largen & Rasmussen 1993; Hughes 1999; Largen & Spawls 2010; Spawls *et al.* 2018). Several species and subspecies have been described over the years (*e.g.* Peters 1882; Fischer 1884; Bocage 1895; Boulenger 1896; Werner 1919; Broadley 1966, 1977; Spawls 1983), but most of them are now considered synonyms, while others still have an uncertain taxonomic and nomenclatural status. This over description of species within the *sibilans* complex is mostly explained by the considerable variation in color pattern across its range (Bogert 1940). Even though Broadley (1963, 1966, 1975, 1977,

2002) clarified the situation in southern Africa, the status of populations from West and Central Africa remained unclear. The result was a taxonomic instability, that compromised any conservation efforts that depended on a precise identification of the species that occur at any given area, such as the evaluation of conservation status and priorities (Duarte *et al*. 2014; Romero *et al*. 2014; Oates & Ting 2015).

The morphological data presented in this study illustrates the intraspecific variability within a group of species of the *sibilans* complex, which combined with the lack of a clear morphological distinction and the poorly know distribution limits, are the main cause of taxonomic and nomenclatural uncertainties for these taxa. After an extensive bibliographic research, compiling relevant information scattered in dozens of works, we were able to clarify and summarize the taxonomic history of this problematic group of snakes. We provide updated descriptions and distribution maps that will aid in the identification of specimens belonging to the *sibilans* species complex.

Morphological results indicate that most meristic characters have little or no taxonomic value for diagnosing the species of the *sibilans* complex (Tabs. 2 and 4). We found that *P. rukwae* in East Africa has, on average, a higher ventrals:subcaudals ratio than the other species studied (Fig. 4-D). However, as the ranges of ventrals and subcaudals overlap in all species (Figs. 4-A and 4-B), this character alone does not allow a confident identification. The infralabial arrangement and the type of contact between the preocular and frontal scales proved to be the most useful meristic characters for diagnosis (Tab. 3). Although useful for diagnosing certain species, color pattern is very variable and should be interpreted with caution (Figs. 5-B to 5-D). Despite being used to diagnose *P. sudanensis* in East Africa (Spawls *et al*. 2018), the "*subtaeniatus*" ventral pattern is not present in all specimens of *P. sudanensis*, and is also known to occur in other species of the *sibilans* complex, such as *P. sibilans* and *P.* cf. *rukwae*. The same can be said for the "grey obfuscation" of the midventral region, used by Hughes and Wade (2004) to diagnose *P. occidentalis*. This grey obfuscation is not present in all specimens from Central Africa, and is also known, even if to a lesser extent, from specimens of *P. sibilans* from Eritrea, *P. phillipsii* from Liberia, P. cf. *rukwae* from Guinea-Bissau (Fig. 26-B) and *P. mossambicus* from Angola (Fig. 12-D).

Contrary to what has been suggested by some authors, we did not find any evidence of an ontogenetic effect on color pattern. It has been hypothesized that *P. sibilans* displays a juvenile ventral pattern like that of *P. subtaeniatus* (Largen & Rasmussen 1993; Largen & Spawls 2010) that gradually fades with age, as well as other dorsal and head markings (Geniez 2018). However, among the specimens we examined there are several juveniles that are already uniform. Similarly, it has been suggested that *P.* cf. *rukwae* displays a juvenile striped pattern that fades with age (Böhme *et al*. 1996), but as we show in Fig. 28-A, not all juveniles are striped.

While most *P. mossambicus* specimens are uniformly colored above, those from Central Africa commonly display well-defined dorsolateral stripes, making them more similar to *P. sibilans*. This may be what led Jackson & Blackburn (2010) to record *P. sibilans* from the vicinity of Pointe-Noire, Republic of the Congo, which reinforces the need for caution when interpreting coloration in these species. Instead, a combination of color pattern and meristic characters, as well as geographic location, is the best way to identify species of the *sibilans* complex. We found that the presence and type of head markings, the infralabial arrangement and the type of contact between the preocular and frontal scales are the most useful morphological characters. Even though distribution limits are poorly known, sympatry is restricted to specific regions, so that geographic location is usually useful for identification. Broadley (1966, 1977) suggested the occurrence of hybrids where distribution ranges overlap, but further molecular studies are yet to shed light on this subject.

Even though we follow previous authors by provisionally assigning West African specimens to *P.* cf. *rukwae* (Broadley 1977; Brandstätter 1995; Kelly *et al*. 2008), molecular and morphological data support the distinction of West African populations as a valid species, and further analyses are needed in order to allow a formal description.

Shortly before the conclusion of this dissertation, Trape *et al*. (2019) published a review of the *sibilans* complex north of latitude 12ºS. Combining morphological and molecular data covering most of the distributional range of the species considered, they solved the problems identified in the present work, and their results are comparable to ours.

Through the sampling of Egyptian specimens, Trape *et al*. (2019) were able to restrict *P. sibilans* to northeastern Africa, from Egypt to Ethiopia. However, the status of *Coluber lacrymans* Reuss, 1834 is problematic. All specimens used by Reuss (1834) to describe *C. lacrymans* have eight supralabials, the fourth and fifth touching the eye, an arrangement typical of most *Psammophis* species, including *P. sibilans*. However, *P. schokari* and *P. aegyptius* are the only species of the genus known to occur in the area (El Tor, Sinai Peninsula), and both species are characterized by having nine supralabials, the fifth and sixth in contact with the eye. The coloration described by Reuss (1834) leads to *P. schokari* and explains why most authors consider *C. lacrymans* as a synonym of *P. schokari* (Boulenger 1896; Loveridge 1940; El Din 2006; Wallach *et al*. 2014). However, this species has been referred to *P. sibilans* by some authors (Broadley pers. comm.; Brandstätter 1995; Trape *et al*. 2019), a decision that would imply a range extension across the Eastern Desert and Gulf of Suez, for the closest *P. sibilans* records are from the Nile valley and Delta (El Din 2006). Parker (1949) showed that 10% of *P. schokari* from southern Arabia have atypical labial arrangements, and following Reuss' description of the color pattern, we consider *C. lacrymans* to be a synonym of *P. schokari*.

Additional sampling from West and Central Africa allowed a reevaluation of the status of topotypical populations of *P. rukwae* as well as the West African populations treated here as *P.* cf. *rukwae*. This new data revealed that *P. rukwae* is restricted to Central and eastern Africa from Chad to Tanzania, and populations from Chad westwards to Senegal (*P.* cf. *rukwae*) are in fact a new species, that the authors described and named as *Psammophis afroccidentalis* Trape, Böhme & Mediannikov, 2019. The elevation of these populations to full species status is in line with our findings and conclusions. The authors reached the same diagnostic characters as we did, namely the infralabial arrangement, color pattern and the ranges of ventrals and subcaudals. *P. afroccidentalis* is readily distinguishable from *P. phillipsii*, *P. mossambicus* and *P. sudanensis* by the number of infralabials in contact with the anterior sublinguals (five in *P. afroccidentalis,* four in the other species) and the type of head markings. It is distinguishable from *P. rukwae* by a higher number of subcaudals (usually less than 100 in *P. rukwae*). Although variable in *P. afroccidentalis*, the type of contact between the preocular and frontal scales may be useful for separating *P. afroccidentalis* from *P. phillipsii* and *P. rukwae* (rarely in contact in *P. phillipsii* and *P. rukwae*). *P. afroccidentalis* can be better distinguished from *P. sibilans* based on differences in mitochondrial haplotypes and geographical location.

The same authors showed *P. phillipsii sensu stricto* from West Africa to form a monophyletic clade sister to *P. mossambicus*, supporting our option of treating them as distinct taxa. The distribution range of *P. phillipsii* is restricted to West Africa and the problematic status of *Psammophis irregularis* Fischer is resolved. Fischer (1856) described *P. irregularis* based on a specimen from Peki, Ghana, with a divided cloacal scale and extensive black patches on the anterior dorsum, which was illustrated by Jan & Sordelli (1870: livr. 34, pl. IV) and is now lost (*fide* Hughes and Wade 2004). Broadley (2002) suggested that *P. irregularis* might be the earliest available name for populations assigned to *P. mossambicus*, but by sequencing a specimen from Togo that fits the description of *P. irregularis* (*i.e.* divided cloacal scale and extensive black patches dorsally), Trape *et al*. (2019) synonymized *P. irregularis* with *P. phillipsii*. The status of *P. regularis* was also clarified. Sternfeld (1908b) described *Psammophis regularis* based on two specimens from Cameroon and four from Togo, all monochrome, with an entire cloacal scale and four infralabials in contact with the anterior sublinguals. Following Trape *et al*. (2019), Sternfeld's (1908b) type series is most likely a combination of *P. phillipsii* (Togo) and *P. mossambicus* (Cameroon).

Despite the variation in color pattern discussed in this work, Trape's *et al*. (2019) results show little genetic structure between *P. mossambicus* populations from southern Africa and those from Central Africa north of the Congo forest block. Among the sequenced specimens there is one from coastal Republic of the Congo that has a reticulated head pattern and distinct dorsolateral stripes (similar to the lectotype of *P. occidentalis*, see Fig. 12), which encouraged the authors to consider *P. occidentalis* as a synonym of *P. mossambicus*, as we do in this work. Considering this, it seems that *P. mossambicus* is a widely distributed and polymorphic species, with striped specimens (with dorsolateral stripes and/or continuous ventral lines) concentrated in the Congo region. This distribution of color patterns could be correlated to environmental variables such as rainfall, solar radiation and vegetation, as is the case of *Psammophis schokari* in Sinai and Israel (Kark *et al*. 1997).

Even though Trape *et al*. (2019) consider *P. sudanensis* to range from Senegal to Tanzania, East African specimens formed a distinct clade in their phylogenetic tree, suggesting that populations from East Africa may represent an undescribed cryptic species. Populations from Chad are assigned to typical *P. sudanensis*, given the close geographical and ecological proximity to the type locality. However, as no specimens from West Africa were sequenced, the status of those populations remains to be genetically clarified.

The authors also revealed the existence of at least two undescribed cryptic species in Ethiopia, which illustrates how much diversity remains to be uncovered. One of these species could possibly represent what Chirio & LeBreton (2007) treat as *Psammophis* sp. 2, from the mountains of Cameroon and Ethiopia. Trape *et al*. (2019) included in their analysis two sequences from Zambia and Burundi published by Kelly *et al*. (2008) and reluctantly assigned by the same authors to *P.* cf. *phillipsii occidentalis*. Unfortunately, the authors don't offer a morphological description, and the sequenced specimens are not deposited in accessible museum collections. However, as discussed above, Trape *et al*. (2019) showed specimens from the putative distribution range of *P. occidentalis* to belong to *P. mossambicus*, leaving the identity of Kelly's *et al*. (2008) "*P.* cf. *p. occidentalis*" unknown. Based on the close genetic proximity of these sequences to *P. brevirostris* and *P. leopardinus*, Trape *et al*. (2019) suggest that these may belong to *P. zambiensis* Hughes and Wade, 2002, a species that was not yet molecularly studied. On the other hand, these could represent yet another undescribed cryptic species from eastern Africa.

Works like the one presented here are important for improving the knowledge and conservation of biodiversity. Our current taxonomic knowledge is incomplete and inaccurate in most cases, but especially in African biodiversity, which leads to the ignoring and underestimating of conservation needs (Dubois 2003). We can only protect what we know, and taxonomy plays the fundamental role of uncovering and describing biodiversity, allowing the establishment of regional species lists that are necessary to effectively develop and implement conservation measures (Mace 2004). The taxonomic split of widespread species complexes calls for a reevaluation of conservation status. While the originally widespread species may not have been threatened, this may not be the case for newly described species, often with much more restricted distribution ranges (Melzer *et al*. 2017; Wüster *et al*. 2018). This can be the case of *P. phillipsii* that is now restricted to West African forest regions, a habitat that is increasingly threatened by expanding human population and economic activities (*e.g.* logging and agriculture) (Barnes 1990; Norris *et al.* 2010). The urgent need to develop taxonomic research is reinforced by the current rate of biodiversity loss (Dubois 2003).

Further research is necessary in order to describe the cryptic diversity uncovered by Trape *et al*. (2019) in Ethiopia. Likewise, the status of *P. sudanensis* also needs to be clarified, starting with the sequencing and allocation of West African populations. Populations from East Africa should be further investigated and if necessary, formally described as a new species. Still in eastern Central Africa, the sequences identified by Kelly *et al*. (2008) as *P.* cf. *p. occidentalis* are still to be correctly identified. A first step towards the clarification of this subject should be the reexamination of specimens from the Great Lakes Region available in museum collections, and if possible, the sampling of

*P. zambiensis* and comparison with the resulting sequences. A phylogeographic study of *P. phillipsii* and *P. mossambicus* could help improve our knowledge on the evolution processes in African snakes, by identifying the transition zone between both species and evaluating any eventual genetic structure linked to ecological and morphological variation. A more detailed study of pattern variation to evaluate geographical correlation and ontogenetic effect could help improve species delimitation and diagnosis.

# Tentative key to problematic species of the *sibilans* complex

**1a.** Usually the first five infralabials in contact with the anterior sublinguals……………2

**1b.** Usually the first four infralabials in contact with the anterior sublianguals…………4

**2a.** Northeastern Africa, from Egypt to Ethiopia; usually striped, all markings fading with age; preocular in contact or separated from the frontal……………………………………………………………………………..*Psammophis sibilans*

**2b.** West and East Africa ………………………………………………………………………………………3

**3a.** West Africa; preocular often in contact with the frontal; striped or uniform; often with thin ventral lines………………………………………………….*Psammophis* cf. *rukwae*

**3b.** East Africa; usually with thin ventral lines and reddish dorsolateral stripes; preocular separated from the frontal; lower number of subcaudals in comparison to related species, on average less than 95……………..………….*Psammophis rukwae*

**4a.** From Senegal to Tanzania, on dryer habitats; Usually with broad dorsal stripes; in East Africa the midventral region is usually bright yellow and bordered by distinct black lines; in west Africa often ventrally uniform, or with thin ventral lines; ventral coloration covers the lower half of the first dorsal scale row, and is often separated from dorsal coloration by a black line; a pale longitudinal stripe on the head, from the snout to the frontal, is usually diagnostic.…………………………….……………………….…….*Psammophis sudanensis*

**4b.** Dorsum uniform olive, with or without a vertebral stripe, often with black edged scales or scattered black scales; top of head uniform or with reticulated *"phillipsii"* pattern; ventrum very variable but never with well-defined continuous lines; preocular separated from the frontal ..……………….……………5

**5a.** Forest regions in West Africa from the Gambia to Ghana; cloacal scale entire…………………………………………...…………………………..*Psammophis phillipsii*

**5b.** From Nigeria to Kenya and southwards to South Africa, in a variety of habitats; cloacal scale divided; exceptionally, specimens from Central Africa often have well marked dorsal and ventral stripes………………………*Psammophis mossambicus*

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# Appendix 1 – Material examined

## *Psammophis sibilans* (Linnaeus, 1758)

**"EGYPTIAN SUDAN":** FMNH 21692-3, FMNH 25405 [without specific locality]. **EGYPT:** USNM 131153 [0.5mi W of Abu Rawash, Giza, N: 30.0456, E: 31.0925, WGS-84]; USNM 124728 [10km W of Simbillawein, Dagahlia Province, N: 30.8819, E: 31.3789, WGS-84]; BMNH 1897.10.28.603 [Abbasiyah, near Cairo, N: 30.069073, E: 31.276256, WGS-84]; BMNH 1897.10.28.604-5, NMZB-UM 6882-98, USNM 131151-2, USNM 131154-9, USNM 134685 [Abu Rawash, Giza, N: 30.03333333, E: 31.10000000, WGS-84]; ANSP 19442 [Aswan, N: 24.08333333, E: 32.88333333, WGS-84]; BMNH 1897.10.28.602 [Baltim, Between Rosetta and Damietta, N: 31.554632, E: 31.090936, WGS-84]; AMNH 2184, AMNH 31654, CM 22545, SMF 32636-7, USNM 37333, UUZM (10 specimens) [Cairo, N: 30.08333333, E: 31.25000000, WGS-84]; NMZB-UM 3158 [El Aiyat, Sakkara, N: 29.619722, E: 31.2575, WGS-84]; BMNH 1897.10.28.606-7 [Fayoum, N: 29.309949, E: 30.841804, WGS-84]; NMW [Fayoum Oasis, N: 29.450787, E: 30.682648, WGS-84]; UMMZ 174786 [Giza, N: 30.01666667, E: 31.21666667, WGS-84]; USNM 131213 [Imbaba, Giza, N: 30.076247, E: 31.206662, WGS-84]; NMZB-UM 3159 [Kom Hammada, N: 30.80000000, E: 30.61666667, WGS-84]; FMNH 58490 [Kom Oshim, N: 29.56666667, E: 30.91666667, WGS-84]; USNM 128206 [Lower Nile Valley, from Cairo to Alexandria, N: 30.9987, E: 31.2468, WGS-84]; BMNH 1897.10.28.611 [Mahalla El Kubra, N: 30.974495, E: 31.164987, WGS-84]; BMNH 1897.10.28.610 [Minia, N: 28.109884, E: 30.750299, WGS-84]; USNM 56450 [near Giza, N: 30.0861, E: 31.2122, WGS-84]; CAS 38719 [Nile Delta, N: 31, E: 31, WGS-84]; CAS 156664 [Sakkara-Dashur Road, N: 29.833333, E: 31.233333, WGS-84], NMW [Umgeb, Cairo]; BMNH 1914.8.17.12 [Wadi Hilal (Upper Egypt), N: 25.184189, E: 32.887557, WGS-84]; AMNH 3867, MZUF 2515-16, SMF 20077, USNM 5438, UUZM [without specific locality]. **ERITREA:** MZUF 172, MZUF 2500-1 [Adi Caieh, N: 14.844444, E: 39.377222, WGS-84]; MSNM 2750 [Adi Ugri (now Mendefera), N: 14.887222, E: 38.815278, WGS-84]; BMNH 1869.11.4.33 [Anseba Valley, N: 17.05, E: 37.4, WGS-84]; MSNM 2787/1-2 [Asmara, N: 15.338046, E: 38.93184, WGS-84]; MSNM 2746 [Cunama Region]; MSNM 2741 [Ghinda, N: 15.449167, E: 39.088611, WGS-84]; ANSP 25205 [Gura, N: 15.015117, E: 39.060209, WGS-84]; MZUF 646 [Keren, N: 15.777923, E: 38.451074, WGS-84]; MSNM 2737 [Saganeiti, N: 15.052778, E: 39.187222, WGS-84]; MSNM 2761, NMW 19094:3 [without specific locality]. **ETHIOPIA:** BMNH 1972.798 [25km S of Scheraroti, N: 14.21666667, E: 37.95, WGS-84]; NHMAA H. 731 [32km E of Neghelli, Sidamo, N: 5.230174, E: 39.862154, WGS-84]; USNM 218617 [Alamatta, Welo, N: 12.42, E: 39.62, WGS-84]; MZUF 621 [Arero, N: 4.724852, E: 38.762079, WGS-84]; USNM 218618 [ Aseita (= Asayita), Welo, N: 11.57, E: 41.45, WGS-84]; MZUF 12287 [Aware Melca]; BMNH 1902.12.13.88 [Bahar Dar, N: 11.6, E: 37.383333, WGS-84]; MNHN 1905.214 [Bourka, N: 10.616667, E: 40.466667, WGS-84]; NHMAA H. 568 [Didessa River, Wollega, N: 8.483333, E: 36.7, WGS-84]; BMNH 1964.1083-4 [Gamu-Gofa, N: 6.030366, E: 37.513013, WGS-84]; BMNH 1973.3180-1

[Ghimbi, Wollega, N: 9.166667, E: 35.833333, WGS-84]; MCZ 84326 [Gojam, Bahar Dar, N: 11, E: 37, WGS-84]; AMNH 20343 [Golêlé River, near Harar]; MSNM 2731/1-4 [Gondar, N: 12.6, E: 37.466667, WGS-84]; FMNH 4045, NMW 19094:1-2 [Harar, N: 9.313866, E: 42.118151, WGS-84]; MCZ 84327 [Kilometer 400 along road, from Gondar to Asmara]; NHMAA H. 911 [Koka, Shoa, N: 8.433955, E: 39.067248, WGS-84]; MNHN 1905.216 [Laga-Hardine]; MSNM 2756 [Mega, N: 4.05, E: 38.3, WGS-84]; SMF 55548 [Modjo River, 20km S of Modjo, N: 8.435308, E: 39.022819, WGS-84]; MSNM 2749 [Murle, N: 5.15, E: 36.216667, WGS-84]; NMZB 13982 (duplicated) [Nazareth, N: 8.55, E: 39.266667, WGS-84]; BMNH 1905.10.16.3 [Polkom, Baro River (Sobat)]; NMW ["S.E. Ethiopia"]; BMNH 1902.12.13.89 [Serba, Lake Tana (Abyssinia)]; ANSP 4834-5 [Sheikh Hussein, N: 7.75, E: 40.7, WGS-84]; MNHN 1905.215 [Tedetchamalka]; MSNM 1740 [Upper Uelle Valley]; MSNM 2760 [Zilo, Luacaba]. **SOMALIA:** CM 83287 [Afgoi, near Mordine, N: 2.1381, E: 45.1212, WGS-84]; CAS 153412, CAS 153416 [Lower Juba River, near Mareri, Juba Sugar Project, N: 0.4335000000, E: 42.6945000000, WGS-84]. **SOUTH SUDAN:** BMNH 1901.7.31.5 [Kodok (formely Fashoda), Upper Nile, N: 9.888889, E: 32.109444, WGS-84]. **SUDAN:** NMW [Barboy, N: 15.38, E: 32.31, WGS-84]; NMK 0/3234/2 [near Dabkara Manshia, Singa, N: 13.15, E: 33.933333, WGS-84]; MCZ 8783 [Fazughli, N: 11.283333, E: 34.766667, WGS-84]; BMNH 1900.9.22.30 [Gabt-el-Magahid, White Nile]; BMNH 1924.5.21.21 [Gebel Moya, N: 13.466667, E: 33.366667, WGS-84]; BMNH 1949.1.2.92 [Gezirat el Fil, Wad Madani, N: 14.422226, E: 33.558595, WGS-84]; BMNH 1924.5.21.22 [Hosh, Blue Nile Province]; NMK 0/3234/1 [Kassab, Blue Nile, N: 13.833333, E: 35.433333, WGS-84]; NMW (5 specimens) [Khor Attar]; MCZ 8784 [Magangani, Sennar Province]; NMK 0/3233 [Meina el Mek, Blue Nile, N: 13.166667, E: 33.95, WGS-84]; BMNH 1930.11.12.12 [Shendi, N: 16.6915, E: 33.4341, WGS-84]; BMNH 1927.8.18.1 [Wad Medani, Blue Nile Province, N: 14.4056, E: 33.4989, WGS-84].

## *Psammophis mossambicus* Peters, 1882

**"CONGO":** NMW 19245.1 (Paralectotype of *Psammophos occidentalis*), NMW 19245.2 (Lectotype of *Psammophis occidentalis*) [without specific locality]. **"SUDAN"**: FMNH 58499. **ANGOLA:** MHNC-UP 017423 [Cabicula, Cazengo, S: 9.1667, E: 13.56667, WGS-84]; IICT/R 245-1959, IICT/R 431-1959, IICT/R 443-1959, IICT/R 452-1959, IICT/R 75-1959, IICT/R 77-1959, IICT/R 78-1959 [Calombe-Luso, Moxico, S: 11,833333, E: 19,916667, WGS-84]; IICT/R 77-1958 [Cameia, S: 11,716667, E: 20,8, WGS-84]; IICT/R 29-1958, IICT/R 12-1958 [L. Cameia, Moxico, S: 11,733333, E: 20,8, WGS-84]; IICT/R 127-1958 [L. Dilolo, Moxico, S: 11.5, E: 22.016667, WGS-84]; AMB 9644, AMB 9665 [Laúca, S: 9.71651, E: 15.114706, WGS-84]; IICT/R ANG8 [Luso (now Luena), Moxico, S: 11.783333, E: 19.916667, WGS-84]; IICT/R 14-1958, MHNC-UP 040698 [without specific locality]. **CENTRAL AFRICAN REPUBLIC:** CAS 143240 [N of Rafai, near Chinko-Vovodo rivers confluence, N: 5.2777611111, E: 24.1117472222, WGS-84]; CMP 60747 [Bangassou, N: 4.741324, E: 22.818383, WGS-84]; MHNG 1521.11, MHNG 1521.24 [Bangui, N: 4.366667, E: 18.583333, WGS-84]; MNHN 1964.489-500 [Boukoko, N: 3.904355, E: 17.917927, WGS-84]; MCZ 55420 [Fort Crampel, N: 6.989607, E: 19.187443,

WGS-84]; ANSP 20341, MCZ 44288 [Fort Sibut, N: 5.718013, E: 19.073889, WGS-84]; MCZ 52137 [Nola, N: 3.527155, E: 16.039996, WGS-84]; MNHN 1895.337 [Pays de Abiras, Haut-Oubangui]; BMNH 1918.11.12.28-29 [Shari River District, N: 7, E: 16, WGS-84]. **CAMEROUN:** MHNG 967.16 [Bangwa, N: 5.201337, E: 10.480973, WGS-84]; MHNG 1521.14 [Douala, N: 4.0469, E: 9.7084, WGS-84]; MHNG 1521.38 [Gabou Boulai]; BMNH 1937.1.1.47 [Gadji, 45km NW of Batouri, N: 4.483333, E: 14.05, WGS-84]; MHNG 1521.25 [Mbé]; MHNG 1521.20, MHNG 1521.22 [Ngaoundéré, N: 7.316667, E: 13.583333, WGS-84]; MCZ 14988, MCZ 22840 [Sakbayeme, N: 4.033333, E: 10.566667, WGS-84]; CM 15002, MHNG 1521.29, MHNG 1521.32, specimen without number [Yaounde, N: 3.866667, E: 11.516667, WGS-84]; SMF 20078 [without specific location]. **DEMOCRATIC REPUBLIC OF THE CONGO:** BMNH 1953.1.10.89 [Albertville (now Kalemie), S: 5.93504, E: 29.190044, WGS-84]; NMW, SMF 20068, SMF 20070-74 [Banana, S: 5.990376, E: 12.392104, WGS-84]; CAS 156709 [Beni, Kivu, N: 0.5, E: 29.466667, WGS-84]; NMW, MCZ 42963 [Boma, S: 5.85, E: 13.05, WGS-84]; FMNH 12990 [Bukama, S: 9.2, E: 25.85, WGS-84]; USNM 167082-84 [Bulape, Kasai, S: 4.633333, E: 21.566667, WGS-84]; SMF 20086 [Duma, Ubangui, N: 3.883333, E: 18.683333, WGS-84]; AMNH 12262, AMNH 12268, AMNH 12269, NMK (formerly AMNH 12267), AMNH 12270 [Faradje, N: 3.733333, E: 29.716667, WGS-84]; RG 30801 [Gangala-Na-Bodio, Parc National De La Garamba, N: 3.683333, E: 29.133333, WGS-84]; MCZ 42959 [Kansenia, S: 10.316667, E: 26.033333, WGS-84]; MCZ 42964 [Kunungu, S: 2.100017, E: 16.43425, WGS-84]; LACM 49507 [Lake Tumba, Bwalanga, S: 0.889015, E: 18.128839, WGS-84]; MCZ 42960 [Lukafu, S: 10.516667, E: 27.55, WGS-84]; AMNH 45915 [Lukolela, S: 1.05, E: 17.2, WGS-84]; BMNH 99.8.22.2 [Monsembe]; TMP 38189 [Mutsora, Virunga National Park, Kivu, N: 0.316667, E: 29.75, WGS-84]; AMNH 12258-60 [Niangara, N: 3.686124, E: 27.887095, WGS-84]; ANSP 20130A [Nijana Farm]; MCZ 42961, MCZ 42962 [Nyonga, S: 8.593174, E: 26.292549, WGS-84]; LACM 49543 [Omaniundu, near Lodja, Sankuru, S: 3.35, E: 23.266667, WGS-84]; RG 30805, RG 30806, RG 30807, RG 30813-815 [Parc National De La Garamba, N: 3.883333, E: 29.2, WGS-84]; SMF 20064 [Povo Netonna, Banana]; MNHN 1950.84-85 [Uvira, Kivu, S: 3.376616, E: 29.140243, WGS-84]; BMNH 1901.3.12.101 [Zambi, Lower Congo, N: 3.166667, E: 18.633333, WGS-84]. **GABON:** FMNH 75026, MHNG 1374.31, USNM 62156-59 [Fernan Vaz, S: 1.574642, E: 9.261836, WGS-84]; MCZ 51908 [Lambaréné (Ogowe River)]; MHNG 948.100 [Lastoursville, S: 0.817157, E: 12.732905, WGS-84]; USNM 62231-32 [Ntyonga]; BMNH 91.1.27.2 [Sette Cama, S: 2.525739, E: 9.753897, WGS-84]. **KENYA:** MCZ 40629, TMP 16592, MCZ 40628 [Bukori, Kitosh, N: 1.013048, E: 34.676452, WGS-84]; CAS 141542-44, CAS 148038-40, CAS 152799, CAS 154621, CAS 154770-71 [Chemelil, Kisumu District, S: 0.1, E: 35.116667, WGS-84]; MCZ 40637 [Golbanti, Tana River, S: 2.455439, E: 40.192176, WGS-84]; MCZ 40632 [Kaimosi, Kakamega, N: 0.129437, E: 34.841609, WGS-84]; CAS 141717 [Kakamega, N: 0.284219, E: 34.752285, WGS-84]; MCZ 40633 [Kibwezi, Ukamba, S: 2.411173, E: 37.965213, WGS-84]; BMNH 1953.1.1.83-84 [Kilifi, S: 3.630453, E: 39.849915, WGS-84]; BMNH 1887.11.3.22-23 [Kilimanjaro, S: 3.066667, E: 37.366667, WGS-84]; BMNH 1974.4216 [Kisumu, S: 0.10221, E: 34.761714, WGS-84]; MCZ 68884-85 [Lumbwa, S: 0.196749, E: 35.468473, WGS-84]; MCZ 40648 [Malindi, S: 3.217478, E: 40.1191, WGS-84]; MCZ 29435 [Mazeras, S: 3.963596, E: 39.55218, WGS-84]; LACM

93208-09 [Milimani, Boni Forest, Lamu District, S: 1.775833, E: 40.8375, WGS-84]; CAS 141541 [Mumias, Kakamega, N: 0.335107, E: 34.486396, WGS-84]; BMNH 1893.11.21.56 [Mwatchi, W of Mombasa]; BMNH 1893.11.21.66 [Ndi, Teita Hills, S: 3.367233, E: 38.358902, WGS-84]; MCZ 40642 [Witu, S: 2.388855, E: 40.43821, WGS-84]; MCZ 40644-46 [Ngatana, Tana River, S: 2.180833333, E: 40.18333333, WGS-84]; MCZ 137309 [Monbasa, S: 3.983333, E: 39.733333, WGS-84]; LACM 66154 [Sagana, Fort Hall (now Muranga), S: 0.666667, E: 37.2, WGS-84]. **MOZAMBIQUE:** IICT/R Moz1 [Boane, S: 26.041667, E: 32.325278, WGS-84]; IICT/R 241-1948 [Maputo, S: 25.965278, E: 32.589167, WGS-84]; IICT/R 7-1955 [Mambone, S: 20.9825, E: 33.658889, WGS-84]; IICT 1685-1948, IICT/R 1686-1948 [Manhiça, S: 25.402222, E: 32.807222, WGS-84]; IICT/R 1015-1948, IICT/R 157-1948 [Mauele, S: 24.35, E: 34.1, WGS-84]; IICT/R 47-1955 [Vila Paiva de Andrada, S: 18.675556, E: 34.072778, WGS-84]; IICT/R Moz9, IICT/R Moz21, IICT/R Moz22, IICT/R Moz23 [without specific locality]. **REPUBLIC OF THE CONGO:** CAS 16950, CAS 16951, MNHN 1886.223, MNHN 1892.120, MNHN 1959.33, MNHN 1965.19, MNHN 1966.744, MNHN 1966.745 [Brazzaville, S: 4.266589, E: 15.249681, WGS-84]; MNHN 1896.70 [Diéla, on Congo River at Alima Confluence, S: 1.553711, E: 16.58371, WGS-84]; MNHN 1907.38 [Sanga River between Loudima and Souborneau, S: 4.118122, E: 13.067249, WGS-84]. **SOUTH SUDAN:** FMNH 48082 [Katire, N: 4.026571, E: 32.775895, WGS-84]; FMNH 62318 [Torit, Equatoria, N: 4.41177, E: 32.570457, WGS-84]; MCZ 53439 [Loa, N: 3.806583, E: 31.959746, WGS-84]; MCZ 53444, MCZ 53445 [Imatong Mtn., Katire, Talanga Forest, N: 4.170839, E: 32.761496, WGS-84]; SMF 56220, SMF 56221 [Loka, Equatoria, N: 4.22363, E: 30.955902, WGS-84]; USNM 134446, USNM 134447 [7km East of Yei, Equatoria, N: 4.090624, E: 30.74058, WGS-84]; USNM 134448 [1ml N of Yei, Equatoria, N: 4.108944, E: 30.678782, WGS-84]. **UGANDA:** BMNH 1934.12.15.596-598 [Namanyama, Mabira Forest, N: 0.466667, E: 32.916667, WGS-84]; USNM 42225 [Between Uma and Khor rivers, West Nile Province]; BMNH 1936.7.3.36, BMNH 1930.7.3.35 [Budongo Forest, Bunyoro, N: 1.787139, E: 31.577437, WGS-84]; LACM 39047 [Bugoma Forest, N: 1.198056, E: 30.935278, WGS-84]; MCZ 47858-59, MCZ 47861-62, BMNH 1953.1.1.89 [Bundibugyo, Bwamba, N: 0.709463, E: 30.060378, WGS-84]; BMNH 1953.1.2.6-7 [Busingiro, Budongo Forest, N: 1.73027, E: 31.464545, WGS-84]; MCZ 40627 [Butandiga, western Mount Elgon, N: 1.2, E: 34.366667, WGS-84]; MCZ 47857 [Butiaba, Bunyoro, N: 1.818423, E: 31.326756, WGS-84]; BMNH 1930.6.11.47 [Bweramule, Semliki Valley, N: 0.966667, E: 30.2, WGS-84]; BMNH 1901.6.24.56, BMNH 1929.8.5.24, BMNH 1953.1.2.8-9 [Entebbe, N: 0.064444, E: 32.446944, WGS-84]; MCZ 47833 [Gulu, Acholi, N: 2.774569, E: 32.29899, WGS-84]; BMNH 1953.1.2.10 [Hakitengya, Bwamba, N: 0.733333, E: 30.05, WGS-84]; BMNH 1954.1.12.61 [Jinja, N: 0.424444, E: 33.204167, WGS-84]; BMNH 1951.1.5.30, NMK (R. 1513) [Kalanja, Lake Edward]; CAS-SU 21698, CAS-SU 21702 [Kasenyi, S: 0.035174, E: 30.139348, WGS-84]; BMNH 1953.1.2.16A [Kateboa, northwestern Lake Victoria]; BMNH 1953.1.1.80-81, NMK (R. 1523) [Katunguru, Kazinga Channel, S: 0.156389, E: 30.089167, WGS-84]; BMNH 1953.1.1.74-75, BMNH 1953.1.1.77, BMNH 1953.1.1.79, BMNH 1953.1.2.24-26 [Katwe, Lake Edward, S: 0.141667, E: 29.830278, WGS-84]; ANSP 20130 [Kitala, N: 0.116667, E: 32.516667, WGS-84]; MCZ 47803-805 [Lira, Lango, N: 2.235, E: 32.909722, WGS-84]; BMNH 1930.6.11.48-49 [Makoga, Semliki Valley, N: 1.016667, E: 30.333333, WGS-84]; MUK [Masaka to Mbarara]; MUZM 5409 [Mbarara, Ankole, S: 0.630583, E: 30.658179, WGS-84]; BMNH 1953.1.2.12, NMK (R. 1487) / NMZB 17544 [Mjanji, Lake Victoria, N: 0.264167, E: 33.978889, WGS-84]; BMNH 1934.5.25.412 [Mount Elgon, N: 1.157326, E: 34.532468, WGS-84]; BMNH 1903.12.2.24 [Mulema, S: 0.566667, E: 31.716667, WGS-84];

BMNH 1953.1.2.33 [Nakifulube, N: 0.044405, E: 32.560058, WGS-84]; USNM 42255 [Rhino Camp, N: 2.972786, E: 31.396332, WGS-84]; FMNH 4046 [southeastern Ruwenzori] BMNH 1953.1.2.11, MCZ 47821-824 [Serere, Teso, N: 1.497942, E: 33.542139, WGS-84]; MCZ 40622-626 [Sipi, Mount Elgon, N: 1.309722, E: 34.374167, WGS-84]; USNM 42250 [Sururu Village, N: 2.972786, E: 31.396332, WGS-84]; BMNH 87.12.1.14-15 [Wadelai, N: 2.729179, E: 31.485797, WGS-84]; USNM 206997 [Wasa Camp, Toro Game Reserve, N: 1.08333, E: 30.4167, WGS-84]. **ZAMBIA:** FMNH 12976 [Kabengere, Upper Luapula, S: 11.016667, E: 29.316667, WGS-84]. **ZIMBABWE:** NMZB-UM 855 [15km WNW of Umtali]; NMZB 4910 [5km W of Mtoko, S: 17.406509, E: 32.172907, WGS-84]; NMZB 1827, NMZB 1885, NMZB 871-2 [Bulawayo, S: 20.15, E: 28.583333, WGS-84]; NMZB 5153, NMZB 5156 [Bulawayo (Old Essexvale road), S: 20.289789, E: 28.922611, WGS-84]; NMZB 1251, NMZB 1475-6 [Bulawayo (Umgusa River), S: 20.067744, E: 28.595835, WGS-84]; NMZB 3598 [Bumi Confluence, Kariba Lake, S: 16.833333, E: 28.433333, WGS-84]; NMZB 4007 [Chinhoyi Caves, S: 17.35, E: 30.133333, WGS-84]; NMZB-UM 1671 [Chipinda Pools, S: 21.3, E: 31.933333, WGS-84]; NMZB 461 [Crosby Farm (40km N of Bulawayo)]; NMZB-UM 1469 [Dett, Hwange, S: 18.616667, E: 26.866667, WGS-84]; NMZB 478, NMZB 909-10 [Esigodini, S: 20.289789, E: 28.922611, WGS-84]; NMZB 1028 [Famona, Bulawayo, S: 20.183236, E: 28.576841, WGS-84]; NMZB 803 [Fatima Mission, S: 18.738346, E: 27.418071, WGS-84]; NMZB 5146 [Glenville, Bulawayo, S: 20.098889, E: 28.558889, WGS-84]; NMZB-QVM 34 [Hatfield, Harare, S: 17.875711, E: 31.092068, WGS-84]; NMZB 360, NMZB 874 [Hillside, Bulawayo, S: 20.199167, E: 28.6, WGS-84]; NMZB 2715 [Imbezu Park]; NMZB 287 [Inyati, S: 19.675634, E: 28.846873, WGS-84]; MCZ 67040-1 [Kariba Lake (eastern end), S: 16.71932, E: 28.973035, WGS-84]; NMZB-UM 1726 [Lake Chivero, S: 17.919658, E: 30.789294, WGS-84]; NMZB 5149 [Lupane, S: 18.931488, E: 27.806962, WGS-84]; NMZB-QVM 32-3 [Mount Hampden, S: 17.741667, E: 30.938889, WGS-84]; NMZB-QVM 582 [Msitkwe R., Mutorashanga, S: 17.066667, E: 30.000000, WGS-84]; NMZB 3893, NMZB 3982, NMZB-QVM 72 [Norton, S: 17.883333, E: 30.7, WGS-84]; NMZB-UM 1596 [Nuanetsi, S: 21.562429, E: 30.863495, WGS-84]; NMZB 423, NMZB-UM 10 [Odzi, S: 18.976931, E: 32.380852, WGS-84]; NMZB 5326 [Redcliff, Kwekwe, S: 19.033333, E: 29.783333, WGS-84]; NMZB 616, NMZB 967 [Sherugwi, S: 19.670156, E: 30.005894, WGS-84]; NMZB-UM 847 [Tynwald, Harare, S: 17.810278, E: 30.955, WGS-84]; NMZB 2643 [Umvuma, S: 19.279243, E: 30.528281, WGS-84]; NMZB 496 [Upper Rangemore, Bulawayo, S: 20.195002, E: 28.488565, WGS-84]; NMZB 3589 [West bank of Sanyati, Kariba Lake, S: 18.662389, E: 29.784175, WGS-84].

## *Psammophis sudanensis* Werner, 1919

**"SUDAN":** FMNH 58497 [Juba]; FMNH 62319 [without specific locality]. **"WEST AFRICA":** MHNC-UP 017431 [without specific locality]. **KENYA:** MHNG 1464.38 [10km N of Nakuru, S: 0.195788, E: 36.06985, WGS-84]; USNM 42490 [Lukenya Hills, S: 1.466667, E: 37.05, WGS-84]; LACM 65965 [ca. 24 mi. (by air) NE Barsaloi, Samburu District, N: 1.58033, E: 37.11208, WGS-84]; MZUF 27196 [Chemelil, Kisumu District, S: 0.1, E: 35.116667, WGS-84]; MCZ 40635-6 [Mt Mbololo, Taita Hills, S: 3.283333333, E: 38.46666667, WGS-84]; FMNH 216321 [Talek Gate, Masai Mara Reserve, S: 1.443269,

E: 35.208133, WGS-84]; FMNH 2250, MCZ 40634 [Voi, S: 3.399114, E: 38.554495, WGS-84]. **SENEGAL:** BMNH 1920.1.20.4094 A [Bakel, N: 14.902377, W: 12.459351, WGS-84]; MNHN 1953.43 [Dakar, N: 14.723612, W: 17.455302, WGS-84]. **SOUTH SUDAN:** FMNH 58386 [Nurruicurren (=Murukiron?), N: 4.34278, E: 33.335733, WGS-84]; FMNH 58387 [Terangore, 20 miles East of Torit, N: 4.475201, E: 32.775077, WGS-84]; FMNH 48075-6, FMNH 58385, FMNH 58388-9, FMNH 58421, FMNH 62313-17 [Torit, Equatoria, N: 4.41177, E: 32.570457, WGS-84]; FMNH 58320 [Yei, Equatoria, N: 4.094444, E: 30.676389, WGS-84]. **SUDAN:** BMNH 1912.7.13.2 [Malek, White Nile, N: 6.069397, E: 31.599747, WGS-84]; NMW 19086 (Holotype) [Kadugli, N: 11.016667, E: 29.716667, WGS-84].

## *Psammophis rukwae* Broadley, 1966

**“NILE”:** USNM 42151-2 [without specific locality]. **SOUTH SUDAN:** FMNH 52912, FMNH 58378, FMNH 58384, FMNH 62116, FMNH 62322 [Torit, Equatoria, N: 4.41177, E: 32.570457, WGS-84]. **TANZANIA:** IRSNB (2 specimens) ["Abercorn" (=Rukwa, fide Broadley 1966)]; SRI 46, SRI 48 [Banagi, Serengeti National Park, S: 2.266667, E: 34.85, WGS-84]; NMZB 5461 (Paratype) [Iku, Rukwa]; MCZ 54575, NMZB 4212 (Holotype), TMP 25301 (Paratype) [Kafukola, Rukwa, S: 8.083333, E: 31.95, WGS-84]; IRSNB/IG 17 (Paratype), IRSNB/IG 413 (Paratype) [Katisunga (Sitaliki), Rukwa, S: 6.633333, E: 31.15, WGS-84]; NMZB-UM 6676 (Paratype) [Kipangati, Rukwa, S: 7.483333, E: 31.883333, WGS-84]; NMZB 8310 [Mangola, Mbulu District, S: 3.416667, E: 35.433333, WGS-84]; MCZ 54097-100 [Mbeya, Lake Rukwa, S: 8.9, E: 33.45, WGS-84]; SRI [Mbuzi Mawe, Serengeti, S: 2.222481, E: 34.966279, WGS-84]; MCZ 54576 [Milepa, Rukwa, S: 8.066667, E: 31.933333, WGS-84]; UMMZ 612398, DOR [Morogoro, S: 6.816667, E: 37.666667, WGS-84]; SRI 47, SRI 49, SRI 50 [Oloserian, Serengeti, S: 2.434999, E: 34.853459, WGS-84]; SMF 20079 [Pentambili]; NMZB 5458 / BMNH (Paratype), TMP [Rukwa, S: 7.9, E: 31.333333, WGS-84]; MCZ 30338 [Saranda, Ugogo, S: 5.716667, E: 34.983333, WGS-84]; SRI [Seronera, S: 2.470543, E: 34.82256, WGS-84]; NMZB 7451 [Shinyanga]; USNM 72464-5 [Stet]; V-F 15241 [Tarangire Game Reserve, Arusha, S: 4, E: 36, WGS-84]; NMZB 1675-79 (Paratypes), NMZB 5459-60, NMZB 5462-4 (Paratypes), V-F 11226 (Paratype) [Tumba, Rukwa, S: 7.116667, E: 31.166667, WGS-84]; MCZ 30370 [Ukerewe Island, Lake Victoria, S: 2.05, E: 33, WGS-84]. **UGANDA:** BMNH 1954.1.12.62 [Bugungu, Jinja, Lake Victoria, N: 0.4, E: 33.2, WGS-84]; MCZ 47860 [Bundibugyo, Bwamba, N: 0.709463, E: 30.060378, WGS-84]; MCZ 127402 [ca. 3-4 mi N of Kumi on road to Soroti, N: 1.529378, E: 33.902616, WGS-84]; MUZM 103 [Doho Swamp, Tororo, N: 0.934253, E: 34.05336, WGS-84]; BMNH 1953.1.1.82 [Katunguru, Kazinga Channel Ankole, S: 0.156389, E: 30.089167, WGS-84]; BMNH 1953.1.1.76, BMNH 1953.1.1.78 [Katwe, Lake Edward, Toro District, S: 0.141667, E: 29.830278, WGS-84]; BMNH 1953.1.1.85-88 [Ongino, Teso, N: 1.516667, E: 34.05, WGS-84]; BMNH 87.12.1.16 [Wadelai, N: 2.729179, E: 31.485797, WGS-84].

## *Psammophis* cf. *rukwae*

**BENIN:** USNM 199594-5 [Banikoara, N: 11.298448, E: 2.438561, WGS-84]; MHNP 03-58 A, MNHN 1903.58 [Djougou, between Mangho and Niki, N: 9.708526, E: 1.665983, WGS-84]; USNM 223808-10 [Kouandé, N: 10.34168, E: 1.689238, WGS-84]; USNM 199599-600 [Nikki, N: 9.940086, E: 3.210749, WGS-84]; USNM 199596-8 [Segbana, N: 10.928213, E: 3.694293, WGS-84]; MNHN 1891.184, MNHN 1894.264-5, MNHN 1916.133 [without specific locality]. **BURKINA FASO:** USNM 199316 [6km SE of Seguenega, N: 13.4, W: 1.92, WGS-84]; MHNP 1965-70, MNHN 1965.60-63, MNHN 1965.66 [Garango, N: 11.8, W: 0.550556, WGS-84]; USNM 199317 [Ougarou, N: 12.154444, E: 0.929722, WGS-84]; USNM 199315 [Petoye, N: 14.58, W: 0.37, WGS-84]. **GHANA:** CM 24686 [Accra, N: 5.554828, W: 0.200086, WGS-84]; MVZ 75742 [Labadi, Eastern Region, N: 5.570153, W: 0.155921, WGS-84]; NMZB 12368 (duplicated) [Mole National Park, N: 9.488663, W: 1.955738, WGS-84]; USNM 223935-6 [Nabogo, Northern Province, N: 9.743273, W: 0.823039, WGS-84]; CAS 146309 [Nyankpala Agricultural Station (near Tamale), N: 9.395979, W: 0.979882, WGS-84]; CAS 154795 [Wa, Danko Valley, Upper West Region, N: 10.0058333333, W: 2.4441666667, WGS-84]; CAS 146201 [Wa, Northern Region, N: 10.0585000000, W: 2.5096666667, WGS-84]; MCZ 44093 [without specific locality]. **GUINEA:** MNHN 1921.472 [Dixinn, N: 9.551111, W: 13.673056, WGS-84]; MNHN 04-420 A, MNHN 1902.14-15, MNHN 1904.420 [Kouroussa, N: 10.65, W: 9.883333, WGS-84]. **GUINEA-BISSAU:** IICT/R 101-1945 [Bijimita, Bissau]; IICT/R 126-1946, IICT/R 176-1945 [Bissau, N: 11.85, W: 15.583333, WGS-84]; IICT/R 21-1946, IICT/R 22-1946, IICT/R 34-1946 [Cacine, N: 11.116667, W: 15.016667, WGS-84]; IICT/R GB9 [Mandinga, N: 12.426593, W: 15.254194, WGS-84]; IICT/R 25-1945 [Marques Mano, Bisau, N: 11.857795, W: 15.666495, WGS-84]; IICT/R 122-1945, IICT/R 134-1945, IICT/R 142-1945, IICT/R 143-1945 [Tor, N: 11.843602, W: 15.904442, WGS-84]. **IVORY COAST:** LACM 63549 [Korhogo, N: 9.458031, W: 5.629608, WGS-84]. **MALI:** FMNH 20819 [Bamako, N: 12.65, W: 8, WGS-84]; CAS 103195 [Bandiagara, N: 14.347998, W: 3.608787, WGS-84]; FMNH 20814 [Moribabougou, N: 12.686723, W: 7.86378, WGS-84]; FMNH 20821, FMNH 20824 [Sotuba, N: 12.661157, W: 7.91717, WGS-84]. **NIGER:** NMW [without specific locality]. **NIGERIA:** LACM 36799 [Sokoto, N: 13, E: 5.25, WGS-84]. **SENEGAL:** BMNH 1920.1.20.4086 A-C ["Haut Senegal"]; USNM 161963-5 [17km NE of Diourbel, N: 14.733858, W: 16.106755, WGS-84]; USNM 161994 [6km NW of Tivaouane, Thies, N: 14.992892, W: 16.849267, WGS-84]; BMNH 1920.1.20.4095, BMNH 1920.1.20.4097 [Bakel, N: 14.902377, W: 12.459351, WGS-84]; MNHN 1918.68 [between Matam and Kaédi, on Senegal River]; CM 23733-7 [Cape Vert, N: 14.723612, W: 17.455302, WGS-84]; MNHN 1884.267 [Cayou]; NMW [Dagana (On South bank of Senegal River), N: 16.503817, W: 15.50969, WGS-84]; CM 24751-3, CM 24760, CM 24775-6, CM 24784, NMZB 7861 [Dakar, N: 14.723612, W: 17.455302, WGS-84]; USNM 161972 [Kaskas, N: 16.378631, W: 14.056026, WGS-84]; USNM 161974 [Ogo, N: 15.549104, W: 13.299405, WGS-84]; USNM 161975 [Podor, N: 16.648918, W: 14.960732, WGS-84]; USNM 199231 [Ranerou, River Region, N: 15.3, W: 13.97, WGS-84]; USNM 161977-8 [Richard Toll, River Region, N: 16.4625, W: 15.700833, WGS-84]; NMW (3 specimens) [Saint-Louis, N: 16.021079, W: 16.48852, WGS-84]; NMW

[Tabadian, N: 13.2, W: 13.45, WGS-84]; NMW [without specific locality]. **TOGO:** USNM 223890 [Dapaong, N: 10.862254, E: 0.207616, WGS-84]; RG MAC 29641 [Kpeme, N: 6.209073, E: 1.514279, WGS-84]; RG MAC 29642 [Lomé, N: 6.131944, E: 1.222778, WGS-84]; RG MAC 29538 [Namoundjoga, N: 10.889248, E: 0.401357, WGS-84]; RG MAC 29507 [Niamtougou, N: 9.768056, E: 1.105278, WGS-84]; USNM 223889, USNM 223894-6 [Padori, Mango, N: 10.233333, E: 0.433333, WGS-84]; RG MAC 29637 [Togoville, N: 6.228056, E: 1.478056, WGS-84]; MZUF 36564 [without specific location].

# Appendix 2 – Sequences used in phylogenetic analysis

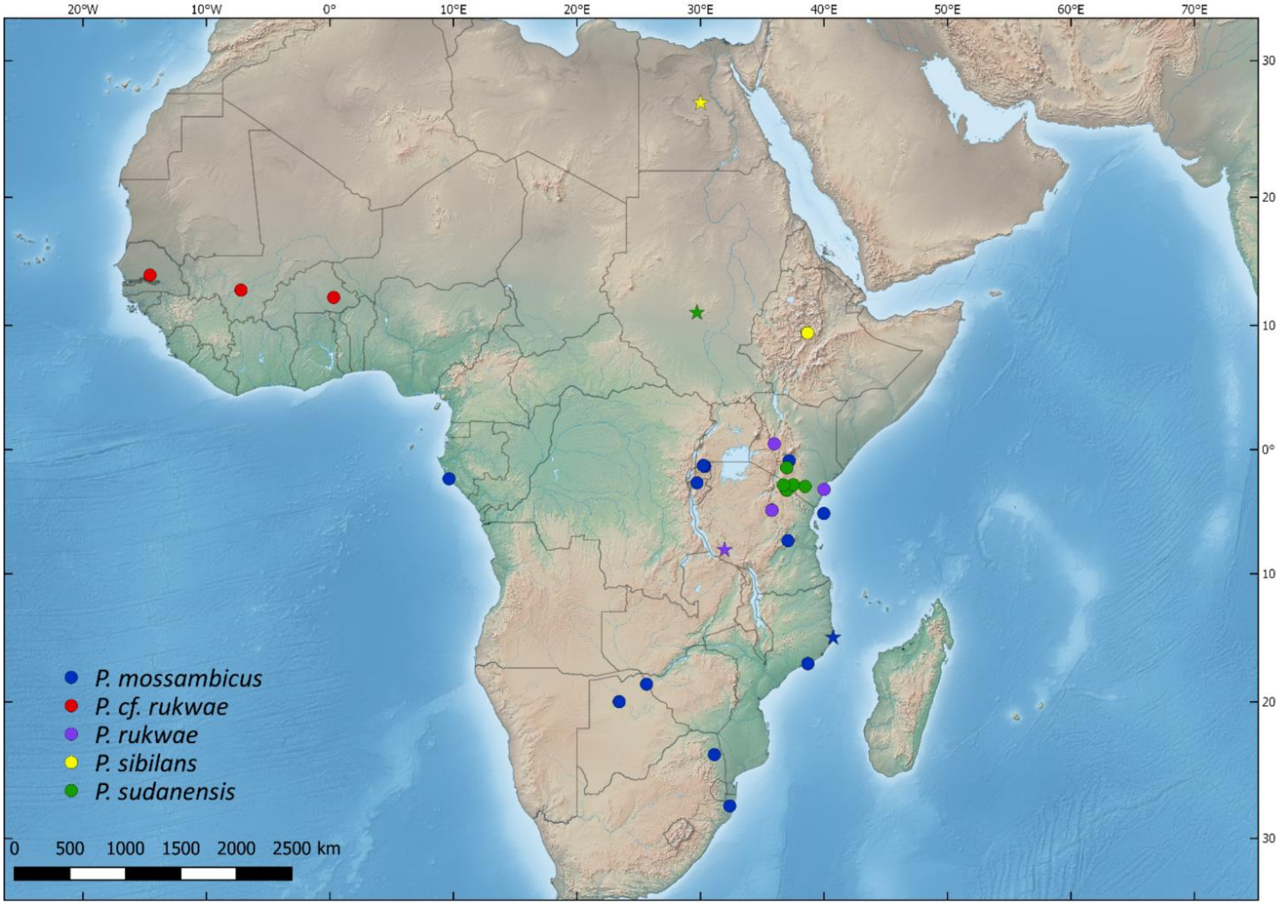

**Figure 30 –** Distribution of sequences used in phylogenetic analysis (circles) and respective type locality (stars).

**Table 6 –** Source of sequences used in phylogenetic analysis.

| Species | Country | Locality | Voucher specimen | Source | GenBank accession number (ND4 & tRNA) |
|---|---|---|---|---|---|
| ***P. mossambicus*** | Tanzania | Tanga | PEM R5679 | Kelly *et al*. (2008) | DQ486198 |
| ***P. mossambicus*** | Tanzania | Kingori | CMRK 81 | Kelly *et al*. (2008) | DQ486212 |
| ***P. mossambicus*** | Tanzania | Kingori | CMRK 82 | Kelly *et al*. (2008) | DQ486213 |
| ***P. mossambicus*** | Rwanda | Nyagatare | CMRK 125 | Kelly *et al*. (2008) | DQ486222 |
| ***P. mossambicus*** | Rwanda | Nyagatare | CMRK 126 | Kelly *et al*. (2008) | DQ486223 |
| ***P. mossambicus*** | Rwanda | Nyagatare | CMRK 127 | Kelly *et al*. (2008) | DQ486224 |
| ***P. mossambicus*** | Tanzania | Mikumi National Park | CMRK 175 | Kelly *et al*. (2008) | DQ486231 |
| ***P. mossambicus*** | South Africa | Sodwana Bay | CMRK 231 | Kelly *et al*. (2008) | DQ486239 |
| ***P. mossambicus*** | Botswana | Pandamatenga | CMRK 268 | Kelly *et al*. (2008) | DQ486249 |
| ***P. mossambicus*** | Rwanda | Butare | CMRK 376 | Kelly *et al*. (2008) | DQ486260 |
| ***P. mossambicus*** | Botswana | Maun | | Kelly *et al*. (2008) | DQ486278 |
| ***P. mossambicus*** | Kenya | Makuyu | BK 10357 | Kelly *et al*. (2008) | DQ486283 |
| ***P. mossambicus*** | Mozambique | Moebase | PEM R13258 | Kelly *et al*. (2008) | DQ486293 |
| ***P. mossambicus*** | Mozambique | Namagure | PEM R13217 | Kelly *et al*. (2008) | DQ486296 |
| ***P. mossambicus*** | South Africa | Palaborwa | TM 83688 | Kelly *et al*. (2008) | DQ486304 |
| ***P. mossambicus*** | Gabon | Loango National Park | PEM R5451 | Kelly *et al*. (2008) | DQ486290 |
| ***P.* cf. *rukwae*** | Burkina Faso | Fada N'Gourma-Bogande | | Rato *et al*. (2007) | EF128028 |
| ***P.* cf. *rukwae*** | Mali | Fama, Segou Bamako | | Rato *et al*. (2007) | EF128029 |
| ***P.* cf. *rukwae*** | Senegal | | MNHN | Kelly *et al*. (2008) | DQ486288 |
| ***P. sibilans*** | Ethiopia | Keriyo Hamlet | CMRK 352 | Kelly *et al*. (2008) | DQ486256 |
| ***P. sibilans*** | Ethiopia | Keriyo Hamlet | CMRK 358 | Kelly *et al*. (2008) | DQ486257 |
| ***P. sibilans*** | Ethiopia | Keriyo Hamlet | CMRK 364 | Kelly *et al*. (2008) | DQ486259 |
| ***P. sibilans*** | Ethiopia | Derba | | Kelly *et al*. (2008) | DQ486285 |
| ***P. rukwae*** | Tanzania | Kondoa Region | CMRK 83 | Kelly *et al*. (2008) | DQ486214 |
| ***P. rukwae*** | Tanzania | Kondoa Region | CMRK 85 | Kelly *et al*. (2008) | DQ486215 |

**Table 6** (Continued).

| Species | Country | Locality | Voucher specimen | Source | GenBank accession number (ND4 & tRNA) |
|---|---|---|---|---|---|
| ***P. rukwae*** | Kenya | Lake Baringo | BK 10358 | Kelly *et al*. (2008) | DQ486279 |
| ***P. rukwae*** | Kenya | Kakuyuni | BK 10620 | Kelly *et al*. (2008) | DQ486282 |
| ***P. sudanensis*** | Tanzania | Kingori | CMRK 91 | Kelly *et al*. (2008) | DQ486221 |
| ***P. sudanensis*** | Kenya | Loitokitok | CMRK 334 | Kelly *et al*. (2008) | DQ486307 |
| ***P. sudanensis*** | Kenya | Athi River | CMRK 385 | Kelly *et al*. (2008) | DQ486266 |
| ***P. sudanensis*** | Kenya | Athi River | CMRK 386 | Kelly *et al*. (2008) | DQ486267 |
| ***P. sudanensis*** | Tanzania | Namanga | CMRK 390 | Kelly *et al*. (2008) | DQ486268 |
| ***P. sudanensis*** | Kenya | Tsavo National Park | BK 10603 | Kelly *et al*. (2008) | DQ486280 |
| ***M. monspessulanus*** | | | | Kelly *et al*. (2008) | AY058989 |
| ***R. rostratus*** | Tanzania | Dodoma Region | CMRK 80 | Kelly *et al*. (2008) | DQ486312 |