

Research article

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**On the *Psammophis sibilans* group
(Serpentes, Lamprophiidae, Psammophiinae)
north of 12°S, with the description of a new species from West Africa**

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Abstract. Based on molecular, morphological and field data, the status and zoogeography of the taxa of the *Psammophis sibilans* group north of 12°S are reviewed. Molecular data including sequences from 20 of the 22 described species known to occur north of 12°S suggest that *P. sibilans* distribution is restricted to northeastern Africa, from Egypt to Ethiopia. Populations from West Africa are described as a new species, *P. afroccidentalis* sp. nov., and those from Chad, Cameroon and Central African Republic are assigned to *P. rukwae* which is also distributed from Tanzania to Ethiopia. Molecular data indicate the occurrence within this complex of three additional cryptic species in the Horn of Africa. Populations previously assigned to *P. phillipsi* in Central Africa north, south and east of the Congo forest block are assigned to *P. mossambicus* and the status of *P. occidentalis* is discussed. *P. phillipsi* is restricted to West Africa, with *P. irregularis* as junior synonym.

Key words. Reptilia, Ophidia; Psammophiinae, *Psammophis sibilans*, *Psammophis afroccidentalis* sp. nov., taxonomy, biogeography, Africa.

INTRODUCTION

According to Hughes (1999) *Psammophis sibilans* (Linnaeus, 1758) is the species “mostly widely and commonly reported from Africa and the most confused taxonomically of any African snake”. According to Broadley (1963)

“the *Psammophis sibilans* group has been a herpetologist’s nightmare for two centuries”. The nomen *sibilans* was based on several specimens, one of them is still extant and preserved at Uppsala University museum (Linnaeus coll. n° 42). It has been figured by Anderson (1898: fig. 12) and Brandstätter (1996: fig. 25), and its identi-

ty well established (Loveridge 1940). The type locality “Asia” (in error) was corrected to Africa (Anderson 1898, Flower 1933) then restricted to Egypt (Loveridge 1953). Loveridge (1940) revised the genus and grouped the following six taxa as subspecies of *P. sibilans*: *P. schokari* (Forskål, 1775), *P. phillipsi* (Hallowell, 1844), *P. notostictus* Peters, 1867, *P. trinasalis* Werner, 1902, *P. leightoni* Boulenger, 1902, and *P. sudanensis* Werner, 1919. He also synonymized *P. irregularis* Fisher, 1856, *P. brevirostris* Peters, 1881, *P. mossambicus* Peters, 1882 and *P. leopardinus* Bocage, 1887 with *P. sibilans*, and *P. regularis* Sternfeld, 1908 and *P. occidentalis* Werner, 1919 with *P. phillipsi*. Marx (1958) described *Psammophis aegyptius* and erected *P. schokari* as a full species. Broadley (1966) described *P. sibilans rukwae* from southwestern Tanzania. This taxon was distinguished from all other related southeastern forms of *Psammophis* by having the first five lower labials in contact with anterior sublinguals, an arrangement typical of Egyptian populations of *P. sibilans*. He also argued that *P. sibilans rukwae* was widely distributed north of the Equator from Tanzania to Senegal. Broadley (1977) recognized *P. phillipsi* as a full species ranging from Senegal to South Africa, *P. leopardinus* as a subspecies of *P. sibilans*, and *P. notostictus*, *P. leightoni* and latter (Broadley 2002) *P. trinasalis* and *brevirostris* as full species distributed in southern Africa. Spawls (1983) described *P. leucogaster* on the basis of a single specimen from Wa, Ghana. A revision of the genus *Psammophis* by Brandstätter (1995, 1996) was discussed by Hughes (1999) who provided an updated table of the nomenclatural changes in *Psammophis* over the past 100 years. Branch (1998) restricted *P. phillipsi* to West Africa and applied the name *P. mossambicus* for southern African populations. Hughes (1999), then Trape & Mané (2006), thought that *P. leucogaster* was conspecific with *P. sudanensis*, which they recognized as a full species, whereas Broadley (1977) previously synonymized *P. sudanensis* with *P. sibilans*, and Böhme (1986) treated it as conspecific with *P. rukwae*. Hughes & Wade (2002) described *P. zambiensis* from Zambia and southern Democratic Republic of the Congo, a species previously confounded with *P. leopardinus* from Angola that they erected as a full species. Broadley (2002) erected *P. orientalis* Broadley, 1977, from eastern and southern Africa as a full species. This taxon was initially described as a subspecies of *P. subtaeniatus* Peters, 1882, a species widely distributed south of 12°S (Broadley 2002). Hughes & Wade (2004) revived *P. occidentalis* from the synonymy of *P. phillipsi* and proposed to use this name for the populations of central Africa north of the Congo forest block previously assigned to *P. phillipsi*. Several *Psammophis* species were included in the phylogeny of the Lamprophiidae by Vidal *et al.* (2008). Kelly *et al.* (2008) published a phylogenetic study of *Psammophis* and allied genera including 39 species, but few specimens from West or Central Africa were included in these studies. Additional

species of the genus *Psammophis* currently recognized in Africa north of 12°S include *P. elegans* (Shaw, 1802), *P. praeornatus* (Schlegel, 1837), *P. lineatus* (Duméril, Bibron & Duméril, 1854), *P. punctulatus* Duméril, Bibron & Duméril, 1854, *P. angolensis* (Bocage, 1872), *P. biseriatus* Peters, 1881, *P. pulcher* Boulenger, 1895, *P. jallae* Perraca, 1896, and *P. tanganicus* Loveridge, 1940 (Wallach *et al.* 2014, Uetz & Hošek 2018). Here we present molecular and morphological data on the taxa of the *P. sibilans* group and review their status and zoogeography north of 12°S.

MATERIALS AND METHODS

Extensive field studies of snakes were conducted in West and Central Africa between 1980 and 2017 by one of the authors (JFT) who collected more than 4,000 specimens belonging to the genus *Psammophis*. The database of another author (DGB) included most of the *P. sibilans* group material available in American, European and southern African museums, totalling more than 3,000 specimens. Tissues from selected specimens of most taxa and colour variants of the *P. sibilans* group collected by JFT, MB and WB between 2006 and 2017, or originating from the BEV tissue collection in Montpellier, were used for the molecular study (see Table 1). We also obtained tissues from specimens of *P. sibilans* from Egypt (collected by MS), and of *P. mossambicus* from Gabon (provided by L. Chirio). We included in our phylogenetic tree data from GenBank, in particular those from Kelly *et al.* (2008) and Vidal *et al.* (2008) who sequenced most *Psammophis* taxa known from southern and eastern Africa. Sequences of *Malpolon monspessulanus* and *Psammophylax rhombeatus* downloaded from GenBank were used as outgroups.

Molecular studies were conducted independently in Montpellier (PS and PAC) and Marseille (OM and AK) with 3 mitochondrial DNA genes: ND4 (Montpellier), 16S (Marseille), and CytB (both Montpellier and Marseille, most samples duplicated). DNA from small pieces of snake tissue samples preserved in 80–96% ethanol was extracted using either the DNeasy Blood & Tissue Kit or the BioRobot MDx Workstation (Quiagen, Courtaboeuf, France), with customized extraction protocols following the manufacturer’s instructions and doing negative control with water. Whole DNA eluted in 200 µl AE Buffer was stored at 4°C until used in Polymerase chain reactions (PCR) amplifications. We amplified mitochondrial 16S rDNA with the universal vertebrate primers 16SA-2290, CGCCTGTTTACCAAAAACAT and 16SB-2860, CCGGTCTGAACTCAGATCACGT (Gatesy *et al.* 1997), NADH dehydrogenase subunit 4 with primers ND4, CACCTA TGACTACCAAAAAGCTCATGTAGAAGC and Leu CATTACTTTTACTTGGATTTCACCA (Arévalo *et al.* 1994) and Cytochrome b with primers

L14724, CGAAGCTTGATATGAAAAACCATCGTTG (Irwin *et al.* 1991) and H15547b AATAGGAAG TAT-CATTCTGGTTTAATG (Campbell 1997). Primers were manufactured by Eurogentec (Seraing, Belgium).

In Montpellier PCR amplification was carried out in 20 µL using REExtract-N-Amp PCR Reaction Mix, primers at 0.5 µM and 8 µL of DNA. Thermocycling conditions were an initial denaturation step of 2 minutes at 94°C, followed by 35 to 40 cycles of 94°C, 40 s; 53°C, 40 s; 72°C, 1 min and a final elongation step of 10 min at 72°C. Negative extraction and PCR controls with water were amplified to check absence of contamination by PCR products from previous amplifications in our amplicons. Approximately 150 ng of unpurified PCR products were sent to Eurofins Genomics (Ebersberg, Germany) for purification and sequencing with PCR primers and internal forward primer of Cytochrome b gene SNKP2b TGARGACAAATATCATTC (Kelly *et al.*, 2003).

In Marseille PCR was performed using a HotStar Taq DNA Polymerase Kit (Qiagen) with 1.0 µL MgCl₂, 0.2 µL HotStart Taq, 2.5 µL 10x PCR buffer, 2.5 µL dNTP (2 mM stock), 0.5 µL of a 10 µM solution of each primer, 12.8 µL sterile water and 5 µL of DNA. Cycling conditions were as follows: 94°C 2 minutes followed by 40 cycles of 94°C, 30 s; 53°C, 30 s; 72°C, 1 min.; the final elongation was at 72°C, 3 min. We did not use positive controls. Sterile water was used as negative control. PCR products were visualized by electrophoresis on a 1.5% agarose gel, stained with ethidium bromide and examined using an ultraviolet transilluminator. The PCR products were purified using a QIAquick Spin Purification Kit (Qiagen) according to the manufacturer's instructions. Sequencing of amplicons was performed using the Big-Dye Terminator Cycle Sequencing Kit (Perkin Elmer Applied Biosystems) with ABI automated sequencer (Applied Biosystems 3130 Genetic Analyzer).

We used Codon Code Aligner 4.2.5 (LI-COR, Inc) and MEGA 6.06 (Tamura *et al.* 2013) to check, assemble and align sequences. The phylogenetic tree was inferred using Maximum-likelihood with MEGA 6.06 using the following options: 1000 bootstrap replications, use all sites, and default settings for the other options. The best substitution model (HKY+G+I) was determined with MEGA using the BIC criterium for the whole alignment.

Morphological analysis included classical meristic data (numbers of dorsals, ventrals, subcaudals, oculars, temporals, supralabials and infralabials) and several coloration characters, with special attention to some characters that previous studies have shown to be of interest in the genus *Psammophis* (Hughes 1999, Broadley 2002, Hughes & Wade 2002): (1) the infralabials contact with anterior sublinguals, (2) the aspect of the cloacal scale (entire or divided), (3) the dorsal head pattern, (4) the occurrence and aspect of a vertebral chain (colour pattern of alternate pale and dark areas on the central row of dorsal

scales), and (5) the occurrence of pale longitudinal bands over body.

RESULTS AND DISCUSSION

Molecular analysis

We aligned 513-514 bp of 16S, 797 bp of cytochrome *b*, and 852-855 bp of ND4. Of the 2160 mitochondrial nucleotides, 776 are variable and 654 informative under the parsimony criterion. All sequences have been deposited with GenBank and accession numbers are given in Table 1 (Appendix I).

The phylogenetic tree (Fig. 1) includes sequences from our specimens and additional sequences from GenBank specimens. Only two taxa (*P. pulcher* and *P. zambiensis*) of the 22 *Psammophis* taxa currently known north of 12°S are missing in this tree which reveals eleven major lineages of *Psammophis* species, including nine lineages for the species (and unnamed cryptic species) distributed north of 12°S:

- Lineage 1 includes two clades, the first one (clade 1a) comprising the GenBank sequences of *P. rukwae* from Tanzania and Kenya, one of our sequences from Ethiopia, and sequences from Chad, with in particular all those from Baïbokoum at the tri-junction border of Chad, Cameroon and Central African Republic, some of them belonging to specimens with uniform dorsum (Fig. 2) and others with marked vertebral and dorsolateral stripes (Fig. 3). All these specimens are characterized by five infralabials in contact with the anterior sublinguals and a divided cloacal. The second clade 1b comprises all our sequences from West Africa, but also a sequence from Mao in Chad. As in clade 1a, some of them belong to specimens with uniform dorsum (Fig. 4) and others with marked vertebral and dorsolateral stripes (Fig. 5). As in clade 1a, all these specimens have also five infralabials in contact with the anterior sublinguals and a divided cloacal. Within clade 1a, there is very little divergence between *P. rukwae* from Tanzania and our specimens from Chad and Ethiopia, and less divergence between our specimens than between *P. rukwae* from Tanzania and *P. rukwae* from Kenya. Within clade 1b, two groups with close sequences are observed, one including specimens from Senegal, Mauritania, Guinea, Ivory Coast (data not shown, ND4 only), Mali (data not shown, ND4 only) and one of two specimens from Niger, the second group including specimens from Burkina Faso and Benin, the second specimen from Niger (data not shown, ND4 only) and a specimen from Mao in Chad. To our knowledge, there is no available name in the literature for these West African specimens of clade 1b that were previously confounded with *P. sibilans* or attributed either to *P. rukwae*, *P. cf. rukwae* or *P. cf. phillipsi* in the recent literature.

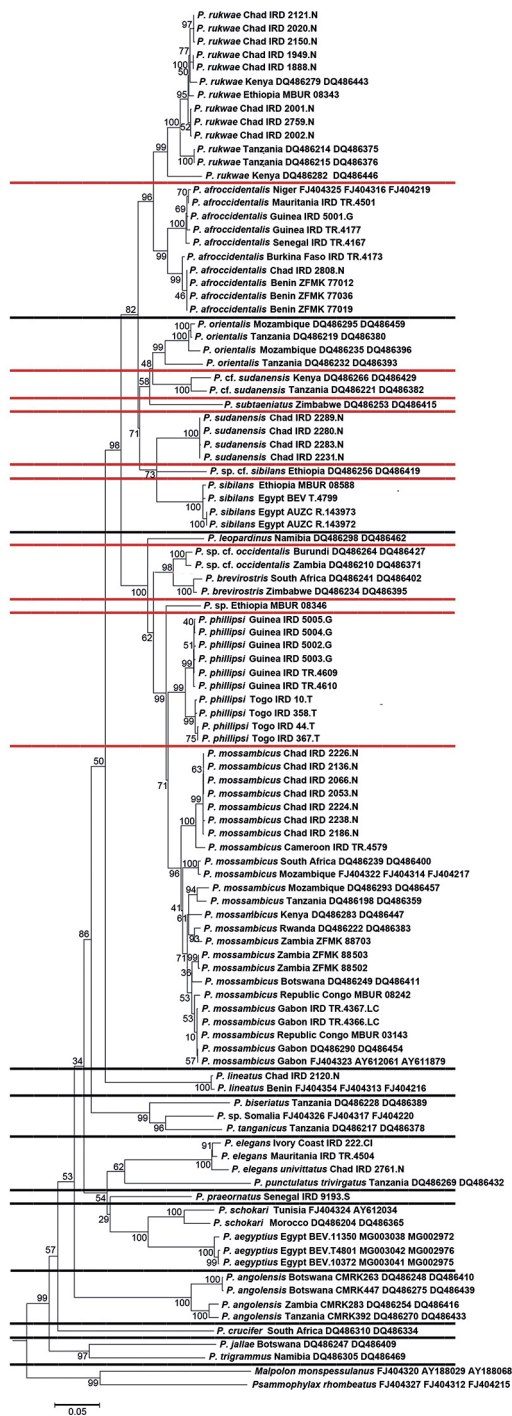


Fig. 1. Phylogenetic tree (16S, Cyt. B, ND4) of the African species of *Psammophis* inferred with maximum likelihood from a concatenated dataset. Numbers on branches are bootstrap support values. Black lines separate the major lineages, and red lines clades within lineages 1–3 which include most species of the *Psammophis sibilans* group.

They are described below as a new species, *Psammophis afroccidentalis* sp. nov.

• Lineage 2 includes six clades. Clade 2f comprises the three specimens of *P. sibilans* from Egypt and one specimen from Ethiopia, clade 2e a GenBank sequence from Ethiopia attributed to *P. cf. sibilans*, clade 2d our specimens of *P. sudanensis* from Chad, clade 2c GenBank sequences of Kenyan and Tanzanian specimens attributed to *P. sudanensis*, clade 2b *P. subtaeniatus* from Zimbabwe, and clade 2a *P. orientalis* from Tanzania and Mozambique. No sequence of *P. sibilans* from Egypt was available before the present study, and our results clearly show that most previous records of *P. sibilans* in the literature were erroneous, but also that *P. sibilans* distribution reach Ethiopia, likely with a continuous distribution through Sudan as previously proposed by Brandstätter (1995, 1996). Unfortunately, no specimen from Sudan was available for the molecular study.

• Lineage 3 corresponds to the *P. phillipsi* complex and includes five clades. All species belonging to these clades have four infralabials in contact with the anterior sublinguals. Clade 3a corresponds to *P. leopardinus* from Namibia, clade 3b comprises *P. brevirostris* from southern Africa and GenBank sequences from Burundi and Zambia of Kelly *et al.* (2008) labelled *P. phillipsi occidentalis* (see below), and clade 3c corresponds to a probably undescribed species from Ethiopia collected by one of us (MB). The two other clades include specimens of wet savannas and forest-savanna mosaics distributed either in West Africa (clade 3d), or north, east and south of the Congo forest block (clade 3e).

All specimens from West Africa (clade 3d) are almost identical genetically, but they include both typical *P. phillipsi* specimens (from Guinea and Togo, with entire cloacal scale) and two specimens from southern Togo characterized by black dorsal blotches and, for one specimen, by a divided cloacal scale, i.e., matching the characteristics of the holotype of *P. irregularis* that originated from the same area (Fig. 6). This supports the view that *P. irregularis* is a junior synonym of *P. phillipsi*, a species restricted to West Africa.

Around the Congo forest block (clade 3e), specimens from Chad and Cameroon selected for the molecular analysis also presented a variety of colour patterns, including unpatterned specimens, specimens with dorsal black blotches, specimens with orange supralabials (Fig. 7) that are common in Adamaoua mountains in Cameroon (*Psammophis* sp. 1 of Chirio & LeBreton 2007), and specimens with or without black spots on the supralabials, the throat and the ventrals. Despite these marked differences in colour patterns, sequences were all almost identical, and there was little difference between these specimens and those of *P. mossambicus* from south and east of the Congo forest block. All have four infralabials in contact with the anterior sublinguals and a divided cloacal. Hughes & Wade (2004) resurrect-

ed *P. occidentalis* Werner, 1919, for the populations of the *P. phillipsi* complex distributed north of the Congo forest block from Cameroon to Uganda. The lectotype of *P. occidentalis* (type locality: “Congo” without precision) has a vertebral chain, a dorsolateral light coloured stripe on body scales 4/5 and grey obfuscation of the ventral scales in the midline (Hughes & Wade 2004). This pattern was not observed in the specimens from Chad or Cameroon that we sequenced, but according to Hughes & Wade (2004) it is not rare north of the Congo forest block where various patterns are observed as previously highlighted by Roux-Estève (1965). However, the pattern with a vertebral chain and a dorso-lateral stripe is also common south of the Congo forest block, in particular in coastal savannas of Gabon, Republic of the Congo and Democratic Republic of the Congo (“*P. sibilans*” of Trape & Roux-Estève 1995, see Fig. 8). Our three specimens from coastal Gabon and Republic of the Congo with this pattern are very close molecularly to *P. mossambicus* specimens from Zambia, Rwanda, Tanzania, Kenya, Mozambique, Botswana and South Africa. Thus we follow Branch (1998) and Broadley (2002) in attributing all specimens of clade 3e to *P. mossambicus*, both north, east and south of the Congo forest block, and we treat *P. occidentalis* as synonym of *P. mossambicus*.

East and south of the Congo forest block, clade 3b includes *P. brevirostris* from Zimbabwe and South Africa, and two specimens from Burundi and Zambia doubted by Kelly *et al.* (2008) that were attributed with doubt by these authors to *P. phillipsi occidentalis*. According to Hughes & Wade (2004), who revived this taxon, *P. occidentalis* was attributable only to populations north of the Congo forest block from Cameroon to Uganda. However, as mentioned above, the specimens from this area that we sequenced match much better *P. mossambicus*. Kelly *et al.* (2008) sequences in clade 3b may correspond to *P. zambiensis* – a species known from Zambia – or to an undescribed cryptic species.

• Lineages 4–11 include species previously sequenced and discussed by Kelly *et al.* (2008) and some additional taxa. In the *P. sibilans* group, both *P. schokari* and *P. aegyptius* (lineage 8) belong to a lineage distant from those of *P. sibilans*, *P. rukwae* and *P. afroccidentalis* sp. nov. Lineage 5 comprises three species, all distributed in East Africa: *P. biseriatus*, *P. tanganicus* and a cryptic species from Somalia sequenced by Kelly *et al.* (2008). In the other lineages, no species belong to the *P. sibilans* group. There is little divergence between *P. elegans univittatus* Perret, 1961 from Cameroon and Chad and the nominate subspecies from West Africa (lineage 6). The colour patterns of these two taxa are distinct, with *univittatus* possessing a single vertebral brown line and lacking those present on the flanks in *elegans*. The *univittatus* pattern is rare in West Africa (Hughes unpublished, Trape & Mané 2015) but was observed in all specimens collected in Chad except two specimens from Mao (Trape unpub-

lished). Lineages 4, 7, 9 and 10 comprise each a single species, *P. lineatus*, *P. praeornatus*, *P. angolensis* and *P. crucifer*, respectively, with the later species restricted south of 12°S. Finally, lineage 11 comprises two species, *P. jallae* and *P. trigrammus*, which are also restricted south of 12°S (Broadley 2002).

SYSTEMATIC ACCOUNT

PSAMMOPHIS SIBILANS (Linnaeus, 1758)

Egyptian Hissing Sand Snake, *Psammophis rayé*, Schmuck-Sandrennmatter

Coluber sibilans Linnaeus, 1758, *Syst. Nat.*, ed. 10, 1: 222. Type locality: “Asia” & 1766, *Syst. Nat.*, ed. 12, 1: 383.

“Le Chapelet” Lacépède, 1789, *Hist. Nat. Serpens* 2: 246, pl. xii, fig. 1.

Coluber Gemmatus Shaw, 1802, *Gen. Zool.*, 3: 539. No locality.

Coluber moniliger Daudin, 1803, *Hist. Nat. Rept.* 7: 69. No locality.

Natrix sibilans Merrem, 1820: *Vers. Syst. Amphib.*: 114.

Coluber auritus Geoffroy Saint Hilaire, 1827, *Descr. Egypte*, 1, *Hist. Nat. Rept.*: 147, 151, pl. viii, fig. 4. Type locality: Egypt.

Psammophis sibilans Boie, 1827, in Oken, *Isis*, 20, col. 547; Günther, 1858: 136 (part); Jan & Sordelli, 1870: *Livr.* 34, Pl. iii, fig. 3 (Cairo); Boulenger, 1896: 161 (part); Anderson, 1898: 303, fig. 12, Pl. xliii; Boulenger, 1915c: 653 (part); Flower, 1933: 824; Corkill, 1935: 20 (part); Parker, 1949: 70 (part); Largen & Rasmussen, 1993: 366 (part); Brandstätter, 1995: 173 (part), Pl. 14; Schleich *et al.*, 1996: 517; Largen, 1997: 91 (part); Baha el Din, 2006: 266; Largen & Spawls, 2010: 564 (part); Geniez, 2015: 248.

Coluber lacrymans Reuss, 1834, *Mus. Senckenberg* 1: 139. Type locality: Tor District, Arabia (= Tor, Sinai Peninsula, Egypt).

Psammophis moniliger Peters, 1862: 274 (Egypt).

Psammophis sibilans sibilans Loveridge, 1940: 30 (part); Marx, 1956: 8; 1968: 198; Lanza, 1972: 178; 1983: 227 (part); 1990: 440 (part); Saleh, 1997: 156, Pl. 92.

Description. (325 specimens from Egypt and two specimens from Ethiopia examined) Nostril pierced between 2 nasals; preocular 1 (very rarely 2), in short contact with or separated from frontal; postoculars 2 (very rarely 3); temporals basically 2+2+3, but with frequent fusions; supralabials 8 (but often 9 in Upper Egypt), the 4th & 5th (or the 5th & 6th) entering orbit; infralabials usually 10 or 11 (rarely 9 or 12), the first 5 in contact with anterior sublinguals; dorsal scales in 17-17-13 rows; ventrals 154–178; cloacal divided; subcaudals 98–119 (lowest count 91 *fide*

Anderson 1898, but tip of the tail probably mutilated). Brandstätter (1995, fig. 68–70) has published SEM micrographs of a dorsal scale of an Egyptian specimen.

Dorsum brown, top of head often with a pale median stripe on the snout which either terminates at the frontal or continue up to two-thirds its length (Fig. 9), back of head often with pale transverse markings; labials immaculate yellow or with a few dark spots; dorsum plain (Fig. 10) or with a vertebral line with each scale yellow with black laterally or paler at base and pale dorsolateral stripes on scale rows 4 and 5 (Fig. 11); lower half of outer scale row and ventrals yellow; sometimes a pair of faint or broken black ventral hairlines.

Size. Largest specimen: 1,445 mm (Flower 1933).

Remarks. Here we follow the usage established by Loveridge (1953) in treating “Egypt” as the type locality of *P. sibilans*. However, to fulfil the requirements of the code of Zoological Nomenclature, a proper restriction of type locality would require designation of a lectotype and, if the origin of the lectotype cannot be traced and/or its identity cannot be ascertained, application to the commission to set aside the type and designate a neotype in accordance with Article 75.5 of the Code. Further studies are needed to establish the distribution of *P. sibilans* in north-eastern Africa. Sequences from Ethiopia and Somalia published by Kelly *et al.* (2008) and one additional sequence from our specimens suggest that at least three cryptic species of the *Psammophis sibilans* group occur in the Horn of Africa.

Habitat. Cultivated and other vegetated areas along the Nile in Egypt and Sudan, woodland savanna in Ethiopia.

Distribution. Egypt, Sudan and Ethiopia. Possibly extending in neighbouring areas of Eritrea and South Sudan. Figure 12 shows the geographic distribution of the *P. sibilans* specimens that we sequenced, and of other sequenced specimens of closely related species.

PSAMMOPHIS RUKWAE Broadley, 1966

Rukwa Whip Snake, *Psammophis* du Rukwa, Rukwa-Sandrennatter

Psammophis sibilans sibilans (not Linnaeus) Loveridge, 1940: 30 (part); 1956: 48 (part); Perret, 1961: 136; Roussel & Villiers, 1965: 1528; Graber, 1966: 141.

Psammophis sibilans (not Linnaeus) Boulenger, 1896: 161 (part); Sternfeld, 1908b: 218, 233; 1909a: 21; 1917: 478; Böhme, 1975: 40; Hughes, 1983: 353 (part); Chippaux, 2006: 175 (part); Chirio & Ineich, 2006: 52; Chirio & LeBreton, 2007: 534.

Psammophis subtaeniatus (not Peters) Loveridge, 1933: 254 (part).

Psammophis subtaeniatus sudanensis (not Werner) Veseley-FitzGerald, 1958: 62, Pl. 17; Robertson *et al.*, 1962: 428.

Psammophis sibilans rukwae Broadley, 1966: 3. Type locality: Kafukola, Rukwa valley, Tanzania. Holotype: NMZB 4212.

Psammophis rukwae Cadle, 1994: 119; Brandstätter, 1995: 151; Spawls *et al.*, 2002: 406.

Psammophis rukwae rukwae Broadley & Howell, 1991: 28.

Description. (127 specimens examined) Nostril pierced between 2 nasals; preocular 1 (very rarely 2), in short contact with or separated from frontal; postoculars 2; temporals basically 2+2+3, but with frequent fusions; supralabials 8 (very rarely 9), the 4th & 5th (very rarely 5th & 6th) entering orbit; infralabials usually 11 (rarely 10 or 12), the first 5 (very rarely 4) in contact with anterior sublinguals; dorsal scales in 17-17-13 rows; ventrals 160–184 (Rukwa type series 165–177; populations East of 25°E 160–184; Chad 169–177; up to 192 for Somalia, but probably a cryptic species); cloacal divided; subcaudals 71–102 (Rukwa type series 83–96; populations East of 25°E 71–100, Chad 84–102 (n=30). Brandstätter (1995, figs 63, 64) has published SEM micrographs of a dorsal scale of the holotype NMZB 4212.

Top of head with a pale median stripe which forks and then borders the frontal, but the head may become uniform yellow-brown in large adults; labials immaculate or with large brown spots; dorsum dark or light brown, rarely uniform, most specimens with at least a vertebral chain, each scale in vertebral row paler at base. Some specimens have ill-defined pale dorsolateral stripes on scale rows 4 and 5, which fade out in some adults, but many other specimens, including large adults, have both well contrasted vertebral chain, with black pigment on each side of the scales of the vertebral row, and well contrasted pale dorsolateral stripes on scale rows 4 and 5 with black pigment on each side. Lower half of outer scale row and ends of ventrals yellowish, separated or not by a pair of brown or blackish ventral lines from a yellow mid-ventral band.

Size. Largest specimen (TM 25301 – Kafukola, Rukwa, Tanzania) 1,090 + 388 = 1,478 mm.

Remarks. According to Broadley (1966) *P. rukwae* was a subspecies of *P. sibilans* distinguished by consistent ventral pattern of a pair of black lateral hairlines similar to that found in *P. subtaeniatus*. However our series of specimens from Chad show that many specimens lack black lateral hairlines.

Habitat. Flood plains and grasslands seem to be the preferred habitats in eastern Africa. In Chad this species is common in all types of savannas.

Distribution. East Africa from the Rukwa valley in Tanzania, north through Kenya, Uganda, Ethiopia, South Sudan and Sudan, then the western populations extend from the Central African Republic and Chad west to northern Cameroon.



Fig. 2. *Psammophis rukwae*. Plain phase. Sequenced specimen IRD 2002.N. N'Djaména (Chad).



Fig. 3. *Psammophis rukwae*. Lineated phase. Sequenced specimen IRD 2150.N. Baïbokoum (Chad)

PSAMMOPHIS AFROCCIDENTALIS Trape, Böhme & Mediannikov, sp. nov.

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West-African Whip Snake, *Psammophis ouest-africain*, Westafrikanische Sandrennmatter

Psammophis sibilans (not Linnaeus) Boettger, 1881: 395; Boulenger, 1896: 161 (part); Boulenger, 1906: 214; Sternfeld, 1908a: 412; Chabanaud, 1918: 165; Angel, 1933a: 69; 1933b: 162, fig. 61; Andersson, 1937: 8; Cansdale, 1949: 106; Hughes & Barry, 1969: 1023; Roman, 1980: 61; Chippaux, 2006: 175 (part); Trape & Mané, 2000: 26; 2002: 149; 2004: 21; 2015: 45; Villiers & Condamin, 2005: 144; Auliya *et al.*, 2012: 280; Hughes, 1983: 353 (part); 2012: 123; 125 (ZFMK 29365 from Tamanrasset); Chirio, 2012: 83; Trape & Baldé, 2014: 317.

Psammophis trinasalis (not Werner) Chabanaud, 1918: 166 (Senegal).

Psammophis sibilans sibilans (not Linnaeus) Loveridge, 1940: 30 (part); Leston 1950: 84; Villiers, 1950: 93; 1951: 827; 1952: 892; 1953: 1119; 1954: 1242; 1956a: 880; 1956b: 158; 1963: 1372; 1975: 138; Condamin, 1958: 255; Doucet, 1963: 306.

Psammophis phillipsii (not Hallowell) Böhme, 1978: 398, Fig. 16, 17 (right); 2000: 71.

Psammophis rukwae (not Broadley) Böhme, 1978: 401; 1987: 259; Brandstätter, 1995: 151 (part); Chirio, 2009: 30.

Psammophis cf. *rukwae* (not Broadley) Joger, 1981: 332; 1982: 332; Gruschwitz *et al.*, 1991: 30.

Psammophis cf. *phillipsii* (not Hallowell) Schätti, 1986: 771; Böhme *et al.*, 1996: 21; Rödel *et al.*, 1995: 7; 1999: 170; Ullenbruch *et al.*, 2010: 43.

Psammophis sudanensis (not Werner) Ullenbruch *et al.*, 2010: 44; Chirio, 2012: 83.

Psammophis aff. *sibilans* (not Linnaeus) Trape & Mané, 2017: 120.

Holotype. MNHN 2018.0013 (formerly IRD 7631.S, a male from Dakar Hann, Senegal (14°43'N, 17°26'W) collected by J.-F. Trape on December 10th, 2005 (Figs. 13 & 14).

Diagnosis. Distinguishable from other species of the *P. sibilans* group by the combination of the following characters: 17 scale rows around midbody, 156–185 ventrals, 96–120 subcaudals (rarely less than 100), cloacal divided, 5 infralabials in contact with anterior sublinguals (very rarely 4). Dorsum pale brown, dark brown or greenish-brown, rarely uniform, usually a vertebral chain with the scale of vertebral row paler at base, but this chain often restricted to part of the dorsum, ill-defined and occasionally totally absent; pale dorsolateral stripes on the 4th row of dorsals, but often ill-defined or absent; top of head with a pale median stripe on the snout

which forks when reaching the frontal and then borders the frontal, but often ill defined or absent in adults. Genetically diagnosable through possession of unique mitochondrial haplotypes. *Psammophis afroccidentalis* sp. nov. can be distinguished from *P. rukwae* by a higher number of subcaudals (*P. rukwae* 70–100, exceptionnaly up to 105), from *P. sibilans* by major differences in mitochondrial haplotypes, a pale median stripe that borders the frontal (not bordering the frontal in *P. sibilans*) and a more uniform dorsal colouration in most specimens, from *P. schokari* and *P. aegyptius* by a lower number of sublabials (8 versus 9) and a different head pattern, and from *P. sudanensis*, *P. phillipsi*, *P. occidentalis*, *P. mosambicus*, *P. leopardinus*, *P. zambiensis* and *P. subtaeniatus* by a higher number of infralabials in contact with the anterior sublinguals (5 versus 4) and by different head and dorsal patterns.

Description of holotype. A male specimen, snout-vent length 745 mm, tail length 345 mm, total length 1090 mm, ratio total length: tail length 3.16. Supralabials 8/8 supralabials, 4th & 5th entering orbit (Fig. 15); 11/11 infralabials, first 5 contact anterior sublinguals; 1/1 preocular contacting frontal; 2/2 postoculars; 2/2 anterior temporals (the lower one on right side divided); 2+3/2+3 posterior temporals. Scale rows 17 around hood, 17 around midbody, 13 one head length ahead of the vent, all smooth and oblique. Dorsal scales smooth, oblique. Vertebral row not enlarged. Ventrals 168 (Dowling: 167), subcaudals 104, all divided, cloacal divided.

Top of head with a pale median stripe on the snout which forks and then borders the frontal; labials pale brown and yellowish. Dorsum uniform brown except pale dorsolateral stripes on scale rows 4 and adjacent parts of rows 3 and 5. No vertebral chain. Belly yellowish, limit with dorsal colouration on the first row of dorsals; traces of broken brown hairlines on part of the ventrals.

Etymology. The name is derived from the contraction of Africa and occidentalis, the region of Africa where this species is distributed.

Variation. (924 specimens examined) Nostril pierced between 2 nasals; preocular 1, in contact with or separated from frontal; postoculars 2; temporals basically 2+2+3 with occasional fusions or divisions, supralabials 8, the 4th & 5th entering orbit; infralabials usually 11 (rarely 9 or 10), the first 5 (very rarely 4, 2% of specimens only) in contact with anterior sublinguals; dorsal scales in 17-17-13 rows; ventrals 156-165.9-180 in males; 160-173.2-185 in females, cloacal divided; subcaudals 98-108.0-121 in males, 96-106.2-120 in females.

Colouration variable (Figs 4, 5, 16, 17). Top of head pale brown with a pale median stripe on the snout which forks and then borders the frontal, but the head often becomes uniform brown in adults; labials immaculate or with brown spots; dorsum from light brown to dark brown; a vertebral chain rarely absent but often ill-defined, with most scale in vertebral row paler at base and



Fig. 4. *Psammophis afroccidentalis* sp. nov. Plain phase. Sequenced specimen IRD TR.4501. Matmata (Mauritania).



Fig. 5. *Psammophis afroccidentalis* sp. nov. Lineated phase. Dakar (Senegal).

rarely black edged; pale dorsolateral stripes on scale row 4 either well contrasted, ill-defined or absent; belly light yellowish, often immaculate but occasionally with hair-lines.

Size. Largest intact specimen (IRD 3538.S – Matam, Senegal) 1,145 + 460 = 1,505 mm, but largest SVL = 1,260 mm in two specimens with truncated tails (IRD 3345.S – Jalalawy, Senegal, and IRD 3345.S – Matam, Senegal).

Remarks. There are limited molecular differences between a mainly western group of specimens (Senegal, Mauritania, Mali, Guinea, Ivory Coast and one of the two specimens from Niger) and those from Burkina Faso, Benin, Niger, and Mao in Chad. They are not correlated to differences in colour patterns nor in meristic data.

Habitat. Sahel and Sudan savanna in West Africa. Penetrates in Guinea savanna and relict populations in sahelo-saharan wetlands.

Distribution. Mauritania (northernmost record: Tidra island 19°44'N, 16°24'W), Senegal, Gambia, Guinea Bissau, Guinea, Mali (northernmost record: Tinjemban 16°44'N, 02°50'W and along the Niger River), Ivory Coast, Burkina Faso, Ghana, Togo, Benin, Niger (northernmost record: Azzel 17°03'N, 08°03'E), Nigeria and Chad (Mao). Possibly a relict population in southern Algeria (ZFMK 29365 from 200 km north of Tamanrasset, a damaged specimen previously assigned to *P. rukwae* by Böhme 1986 and to *P. sibilans* by Hughes 2012).

***PSAMMOPHIS SUBTAENIATUS* Peters, 1882**

Western Stripe-bellied Sand Snake, *Psammophis* à ventre ligné, Gelbbauch-Sandrennnatter

Psammophis sibilans var. *subtaeniata* Peters, 1882: 121 (part). Type locality: Tete, Mozambique. Lectotype: ZMB 9992A designated by Broadley, 1977:13.

Psammophis bocagii Boulenger, 1895: 538. Type locality: “Angola”, subsequently given as Benguela (Boulenger 1896). Lectotype: BMNH 67.7.23.22.

Psammophis subtaeniatus Broadley, 2002: 93.

One specimen examined by DGB from north of Latitude 12° S, MBL 1772 from Rio Bengo near Luanda in Angola (8°43'S, 13°24'E), one of the syntypes of *P. bocagii* destroyed by fire in the Museu Bocage. Full data for this taxon have been published in Broadley (2002).

***PSAMMOPHIS ORIENTALIS* Broadley, 1977**

Eastern Stripe-bellied Sand Snake, *Psammophis* oriental, Östliche Sandrennnatter

Psammophis subtaeniatus orientalis Broadley, 1977, *Arnoldia Rhod.* **8**, No, 12: 17. Type locality: Morogoro,

Tanzania. Holotype: MCZ 146965; Broadley & Howell, 1991: 27; Brandstätter, 1995: 194 (part).

Psammophis orientalis Broadley, 2002: 94; Spawls *et al.*, 2002: 405.

Description. (147 specimens examined) Nostril pierced between 2 nasals; preocular 1 (very rarely 2), in short contact with or separated from frontal; postoculars 2; temporals basically 2+2+3, but with frequent fusions; supralabials 8 (very rarely 7 or 9), the 4th & 5th (rarely 3rd & 4th, 4th, 5th & 6th or 5th & 6th) entering orbit; infralabials usually 10 (rarely 9 or 11), the first 4 (very rarely 3 or 5) in contact with anterior sublinguals; dorsal scales in 17-17-13 rows; ventrals 148–170; cloacal divided; subcaudals 95–117. Brandstätter (1995, figs 74–75) has published SEM micrographs of a dorsal scale of NMZB 23336 from Mutare, Zimbabwe.

Dorsum dark brown, top of head uniform; each scale in vertebral row paler at base, an ill-defined pale dorso-lateral stripe on scale row 4 and 5; a dark stripe across rostral, anterior nasal and upper portions of supralabials 1–4; labials white speckled with black; lower half of outer scale row and ends of ventrals white, separated by a pair of well defined black ventral lines from a yellow mid-ventral band.

Size. Largest male (NMZB 11267 – Mafia Island, Tanzania) 790 + 395 = 1,185 mm; largest female (USNM 72471 – Dodoma, Tanzania) 730 = 350 = 1,080 mm.

Remarks. This form was originally assigned to *P. subtaeniatus sudanensis* (Loveridge, 1940; Broadley, 1966), but was later described from Morogoro, Tanzania, where it is sympatric with *P. sudanensis*.

Habitat. Dry savannas on the east coast from Kenya south to about Latitude 23°S in Mozambique, sometimes sympatric with *P. subtaeniatus* in southeastern Zimbabwe.

Distribution. East Africa from coastal Kenya, south through Tanzania, Malawi, eastern Zimbabwe and Mozambique to the Bazaruto archipelago and adjacent mainland.

***PSAMMOPHIS SUDANENSIS* Werner, 1919**

Northern Stripe-bellied Sand Snake, *Psammophis* sudanien, Sudanesische Sandrennnatter

Psammophis subtaeniatus (not Peters) Boulenger, 1896: 161 (part); Tornier, 1896: 82 (part, Arusha); Corkill, 1935: 22; Loveridge, 1936a: 38, 193; Uthmoller, 1937: 119; Pitman 1938: 155, Pl. K, fig. 2; Böhme, 1975: 39 (Makolo); Hedges 1983: 30, fig. 39; Chippaux, 1999: 166; 2006: 179.

Psammophis sibilans (not Linnaeus) Hedges 1983: 30, fig. 29.

- Psammophis subtaeniatus* var. *sudanensis* Werner, 1919: 504. Type locality: Kadugli, Sudan. Lectotype NMW 19086.
- Psammophis sibilans sibilans* (not Linnaeus) Bogert, 1940: 79 (part); 1942: 3 (Voi); Villiers 1951: 827 (part), Fig. 3; Broadley & Howell, 1991: 28.
- Psammophis subtaeniatus sudanensis* Loveridge, 1940: 50 (part); 1956: 49 (part); 1957: 280 (part); Mertens, 1955: 59; Broadley, 1966: 5 (part); Spawls, 1978: 8 (part).
- Psammophis* cf. *rukuae* (not Broadley) Böhme, 1978: 402, fig. 17 (left); Joger, 1982: 332, fig. 8.
- Psammophis leucogaster* Spawls, 1983: 11. Type locality: Wa, Ghana. Holotype BMNH 1980.261.
- Psammophis rukuae* (not Broadley) Böhme, 1986: 172 (part); Böhme & Schneider, 1987: 259.
- Psammophis subtaeniatus* subsp. Böhme, 1987: 85 (Darfur).
- Psammophis subtaeniatus orientalis* (not Broadley) Brandstätter, 1995: 194 (part).
- Psammophis sudanensis* Hughes 1999: 67; Spawls, et al., 2002: 407; Trape & Mané, 2002: 149, 2015: 45; Trape, 2005: 142; Villiers & Condamin, 2005: 144; Trape & Baldé, 2014: 323.
- Psammophis sudanensis leucogaster* Trape & Mané, 2006: 156.

Description. (114 specimens examined) Nostril pierced between 2 nasals; preocular 1, in short contact with or separated from frontal; postoculars 2 (very rarely 1 or 3); temporals basically 2+2+3, but with frequent fusions; supralabials 8 (very rarely 7 or 9), the 4th & 5th (rarely 3rd & 4th or 4th, 5th & 6th) entering orbit; infralabials usually 10 (rarely 9 or 11), the first 4 (very rarely 3 or 5) in contact with anterior sublinguals; dorsal scales in 17-17-13 rows; ventrals 150–180; cloacal divided (entire in type of *leucogaster*); subcaudals 93–122. Dorsum dark brown, top of head with a black-bordered pale median stripe extending far back on the frontal before forking (Fig. 18), transverse pale markings on back of head; labials immaculate white or speckled with black; vertebral stripe ill-defined in the east, strongly marked in the west, broadening on the nape; pale dorsolateral stripes on scale rows 4 and 5; lower half of outer scale row and ends of ventrals whitish, often separated by a pair of well defined black ventral lines (occasionally ill-defined or absent in West and Central Africa) from a yellow mid-ventral band.

Size. Largest male (MCZ 53449 – Torit, South Sudan) 820 + 390 = 1210 mm; largest female (FMNH 58389 – Torit, South Sudan) 920 + 405 = 1325 mm.

Remarks. The type of *P. leucogaster* from Ghana appears to be a highly aberrant specimen of *P. sudanensis*. Populations from Chad are probably similar genetically to those in Kordofan, the type locality, which is close geographically and ecologically. The sequences of *P. sudanensis* from Tanzania and Kenya of Kelly *et al.* (2008)

belong to a distinct clade, suggesting that they may belong to a cryptic species. However, the pattern of a Kenyan specimen illustrated by Spawls *et al.* (2002) is similar to those of our specimens from West Africa and Chad (Fig 19). Some rare specimens from Chad are uniformly beige dorsally (e.g. IRD 2871.N and 2884.N).

Habitat. In eastern Africa, coastal thicket, moist and dry savanna and high grassland, from sea level to 2,700 m (Spawls *et al.* 2002). In Chad it was the most common colubrid snake that JFT collected in almost all moist and dry savanna areas of the country (17% of 1,010 colubrids collected between 7°N and 14°N). In West Africa, it is a very rare species: only three specimens out of 9,000 snakes in Senegal, all in the Sahel north of 14°N (Trape & Mané unpublished), one specimen out of 1,714 in Niger (Trape & Mané 2015), none out of 4,906 in Guinea (Trape & Baldé 2014), and none out of 5,224 in Mali (Trape & Mané 2017). A single specimen of *P. sudanensis* was present in Roman's collection of 5,000 snakes from Burkina Faso (Trape 2005). *Psammophis sudanensis* reports from Sangaredi area (Guinea) by Chirio (2012) and from southern Benin by Ullenbruch *et al.* (2010, see Figs 16 & 17 p. 44) are in fact attributable to specimens belonging to the lineated phase of *P. afroccidentalis* sp. nov.

Distribution. East Africa from southern Sudan, south through eastern Uganda and Kenya to northern Tanzania, west through the Central African Republic, Cameroon, Nigeria, Niger, Burkina Faso, Ghana, Senegal. Sympatric with *P. orientalis* at Morogoro in Tanzania, with *P. rukuae* in Chad and Cameroon, and with *P. afroccidentalis* sp. nov. in West Africa.

PSAMMOPHIS PHILLIPSI (Hallowell, 1844)

Phillips' Whip Snake, *Psammophis* de Phillips, Phillips-Sandrennatter

Coluber Phillipsii Hallowell, 1844, *Proc. Acad. Nat. Sci. Phil.*: 169. Type locality: Liberia. Lectotype: ANSP 5112, designated by Broadley 1977: 24.

Psammophis Phillipsii Hallowell, 1854: 100 & 1887: 69.

Psammophis irregularis Fischer, 1856: 92. Type locality: Peki, Ghana; Günther, 1858: 137. Holotype apparently lost according to Hughes & Wade 2004. Duméril, 1860: 208, Pl. xvii, fig. 9; Jan & Sordelli, 1870: livr. 34, Pl. iv, fig. 1–2; Matschie, 1893: 212.

Psammophis sibilans (not Linnaeus) Werner, 1902: 338 (Togo); Klaptoz, 1913: 286; Aylmer, 1922: 21; Barbour & Loveridge, 1930a: 773 (Liberia); Monard, 1940: 177.

Psammophis notosticta (not Peters) Matschie, 1893: 212 (Togo).

Psammophis regularis Sternfeld, 1908a: 412, 428 (Togo); 1909b: 20 (Togo); Chabanaud, 1916: 377; 1917: 12 (Benin).

Psammophis sibilans phillipsi Loveridge, 1938: 59; 1940: 41 (part); 1946: 246; Leston, 1950: 84; Villiers, 1950: 98; 1954: 1242; Angel *et al.*, 1954: 396; Condamin, 1958: 255; 1959: 1359; Taylor & Weyer, 1958: 1217; Doucet, 1963: 307; Menzies, 1966: 175; Roux-Estève, 1969: 121; Balletto *et al.*, 1973: 101; Villiers, 1975: 140.

Psammophis sibilans sibilans (not Linnaeus) Loveridge, 1940: 30 (part); Villiers, 1956: 158; 1966: 1765; Doucet, 1963: 306 (part).

Psammophis sibilans var. *phillipsi* Cansdale, 1949: 106 (Ghana).

Psammophis phillipsi Leston & Hughes, 1968: 754; Hughes & Barry, 1969: 1023; Böhme, 1978: 398 (part); Joger, 1981: 331, fig. 16; Hughes, 1983: 346, 353 (part); Roman, 1984: 23; Butler & Reid, 1990: 32 (part); Gruschwitz *et al.*, 1991: 30 (Gambia); Cadle, 1994: 119; Brandstätter, 1995: 75 (part); Böhme, 2000: 71; Ineich, 2003: 619; Luiselli *et al.*, 2004: 415 (part); Villiers & Condamin, 2005: 144; Trape & Mané, 2006: 150; Chippaux, 2006: 178 (part); Ullénbruch *et al.*, 2010: 43; Hughes, 2012: 123; Trape & Baldé, 2014: 316; Trape & Mané, 2017: 120.

Psammophis cf. *phillipsii* Rödel *et al.*, 1995: 7; 1999: 170.

Description. (180 specimens examined) Nostril pierced between 2 (rarely 3) nasals; preocular 1, usually widely separated from frontal; postoculars 2; temporals usually 2+2 or 2+3; supralabials 8 (very rarely 7), the 4th & 5th entering orbit; infralabials usually 10 (rarely 9 or 11), the first 4 (very rarely 5) in contact with anterior sublinguals; dorsal scales in 17-17-13 rows; ventrals 161–183; cloacal usually entire (9% divided); subcaudals 89–115. Brandstätter (1995: Fig. 56–57) illustrated photomicrographs of a mid-dorsal scale of SMF 20067 from Ghana.

Dorsum olive brown, uniform in most specimens (Fig. 20), rarely with black-edged mid-dorsal scales forming black lines (Fig. 21), or with irregularly scattered black scales on the body anteriorly (Fig. 6). Top of head usually uniform, but reticulations may be present, including a double pale line on the frontal (Fig. 6). Each labial and sublingual is usually adorned with a dark spot. Venter yellow or white, uniform or with lateral rows of black spots or short streaks or irregular black speckling.

Size. Largest specimen (MCZ 53726 – Achimota, Ghana) 1,280 + 533 = 1,813 mm,

Remarks. Brandstätter (1995) and Hughes (1999) first restricted the name *P. phillipsi* to the uniform olive form with an entire cloacal shield in West Africa, where it occupies forest clearings and moist savanna. Our molecular data also support this view for the occasional West Af-



Fig. 6. *Psammophis phillipsi* “irregularis”. Sequenced specimen IRD 44.T. Vicinity of Kpalimé (Togo).

rican specimens with a divided cloacal shield and black dorsal blotches (*P. irregularis* Fisher).

Habitat. Moist savannas and deforested rainforest areas of West Africa from coastal Gambia to Nigeria.

Distribution. Gambia, Senegal, Guinea Bissau, Guinea, Sierra Leone, Liberia, southern Mali, Ivory Coast, Ghana, Togo, Benin, Nigeria.

PSAMMOPHIS MOSSAMBICUS (Peters, 1882)

Olive Whip Snake, *Psammophis olivâtre*, Olivenfarbige Sandrennnatter

Psammophis sibilans (not Linnaeus) Mocquard, 1887: 78 (Brazzaville); Bocage, 1895: 114 (part, var. C); Tornier, 1896: 82; Boulenger, 1905: 113; 1906: 214 (part, Fernand Vaz); Sternfeld, 1911: 250; Boulenger, 1915a: 213; 1915b: 631; Loveridge, 1916: 85; 1918: 328; Sternfeld, 1917: 478; Schmidt, 1923: 111; Loveridge, 1923: 886; Loveridge, 1928: 39; 1933: 255; Witte, 1933a: 123; 1933b: 93; Corkill, 1935: 20 (part); Loveridge, 1936a: 38; 1936b: 262; Uthmoller, 1937: 119; Mertens, 1955: 59; Laurent, 1960: 55; Trape & Roux-Estève, 1995: 41.

Psammophis sibilans var. *mossambica* Peters, 1882, *Reise nach Mossambique...3*: 122. Type locality: Mozambique Island. Lectotype: ZMB 2468A.

Psammophis sibilans var. *tettensis* Peters, 1882, *Reise nach Mossambique...3*: 122. Type locality: Tete, Mozambique.

Psammophis sibilans var. *intermedius* Fischer, 1884: 14 (Arusha, Tanzania).

Psammophis irregularis (not Fischer) Sauvage, 1884: 201.

Psammophis sibilans var. *occidentalis* Werner, 1919: 504. Type locality: Congo. Holotype NMW 19245:2.

Psammophis notostictus (not Peters) Witte, 1933a: 123; 1933b: 93.

Psammophis brevirostris (not Peters) Witte, 1933a: 123; 1933b: 93.

Psammophis sibilans phillipsii Loveridge, 1940: 41 (part); Witte 1962: 117 (part); Perret 1961: 136; Böhme 1975: 40; Stucki-Stirn, 1979: 434.

Psammophis subtaeniatus (not Peters) Witte, 1941: 212 (part, Bitshumbi, P.N. Virunga); Joger, 1990: 97, Fig. 6 (Bangui, CAR).

Psammophis sibilans sibilans (not Linnaeus) Bogert, 1940: 79 (part); Loveridge, 1940: 30 (part); 1942a: 110; 1942b: 8; 1956: 48 (part); Witte, 1941: 213; 1955: 220; 1962: 117; 1975: 87; Laurent, 1950: 8; 1954: 59; 1956: 249, Pl. xxiv, fig. 1; 1964: 113; Monard, 1951: 164; Villiers, 1966: 1765; Vesey-FitzGerald, 1958: 60; Robertson *et al.*, 1962: 428; Bourgeois, 1964: 81; Roux-Estève, 1965: 72; Thys van den Audenaerde, 1965: 381 (Kinshasa); Broadley, 1971: 88 (Zambia);

Pitman, 1974: 156; Stucki-Stirn, 1979: 430; Pakenham, 1983: 26; Spawls, 1978: 8; Rasmussen, 1991: 177.

Psammophis subtaeniatus sudanensis (not Werner) Laurent, 1956: 248, Pl. xxiv, fig. 2 (part, Bitshumbi); Perret, 1961: 136; Witte, 1962: 117; 1975: 88.

Psammophis phillipsi Joger, 1982: 331, 1990: 97; Hughes, 1983: 346, 353 (part); Butler & Reid, 1990: 32 (part); Broadley, 1991: 530; Broadley & Howell, 1991: 28; Rasmussen, 1991: 177; Brandstätter, 1995: 75 (part), 1996: 55 (part); Trape & Roux-Estève, 1995: 41; Chippaux, 1999: 164 (part); Luiselli *et al.*, 2004: 415 (part); Chirio & Ineich, 2006: 52; Jackson *et al.*, 2007:77.

Psammophis mossambicus Branch, 1998: 92; Haagner *et al.*, 2000: 15; Hughes & Wade, 2002: 77; Spawls *et al.*, 2002: 405; Broadley *et al.*, 2003: 167, Pl. 110–1; Marais, 2004: 153; Bates *et al.*, 2014: 377.

Psammophis phillipsi occidentalis Hughes & Wade, 2004: 129, Fig. 1.

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

Psammophis sp.1 Chirio & LeBreton, 2007: 538.

Psammophis cf. *phillipsi* Pauwels & Vande weghe, 2008: 220.

Description. (431 specimens examined) Nostril pierced between 2 (rarely 3) nasals; preocular 1, usually widely separated from frontal; postoculars 2 (rarely 1 or 3); temporals usually 2+2/3 but fusions or partial fusions frequent; supralabials 8 (very rarely 6, 7 or 9), the fourth and fifth & (rarely third & fourth or fifth and sixth) entering orbit; infralabials usually 10 (rarely 9 or 11), the first 4 (rarely 5, e.g. sequenced specimen IRD 2226.N) in contact with anterior sublinguals; dorsal scales in 17-17-13 rows; ventrals 154–188; cloacal divided (rarely entire); subcaudals 84–122.

Dorsum brown or greenish brown often uniform (Fig. 22), sometimes yellowish posteriorly, sometimes with scattered black scales (rarely more black scales than olive ones). Other specimens have black-edged dorsal scales, a vertebral chain and a yellow or whitish dorsolateral stripe on scale rows 4 and 5 (Fig. 23), this pattern almost constant in specimens from coastal areas of Gabon, Republic of the Congo and Democratic Republic of the Congo. Top of head uniform or reticulated, which fades out in adults. Supralabials uniform or speckled with black. Venter yellow or whitish, uniform or with lateral rows of black spots or short streaks or irregular black speckling, sometimes delimiting a mid-ventral band of grey ofuscation. A specimen from coastal Gabon with a contrasted head and body pattern is illustrated in Pauwels & Vande weghe (2008, Figs 333–334), and a specimen from Kenya with uniform dorsum is illustrated in Spawls *et al.* (2002: 405). Roux-Estève (1965) provided a detailed description of the two types of patterns of the populations of southern Central African Republic.



Fig. 7. *Psammophis mossambicus*. Orange throat phase. Sequenced specimen 2186.N. Baïbokoum (Chad).



Fig. 8. *Psammophis mossambicus*. Typical specimen from Pointe Noire area (Republic of Congo) with a head reticulated pattern, a vertebral chain and a pale dorso-lateral stripe (MNHN 1988.2316).

De Witte (1966) provided scale counts of specimens of Garamba National Park in northern Democratic Republic of the Congo.

Size. Largest specimens for the species, including south of 12°S: NMK 3233/1 – Kassa B, Sennar, Sudan, 1,320 + 460 = 1,780 mm; IRD 2226.N – Baïbokoum, Chad, 1,227 + 508 = 1,735 mm; IRD 2136.N – Baïbokoum, Chad, 1,235 + 515 = 1,750 mm; NMZB 16031 – Ndaou School, Western Province, Zambia, 1,260 + 500 = 1,760 mm.

Remarks. (Broadley, 1977, 1983) first applied the name *P. phillipsi* to populations in eastern Africa, but Brandstätter (1995) and Hughes (1999) restricted the name to the uniform olive form with an entire cloacal shield in West Africa, and our molecular data support this view. Branch (1998) first used the name *P. mossambicus* Peters for the southern African populations after Broadley selected a lectotype in Berlin. Hughes & Wade (2004) used the name *P. occidentalis* for populations from Cameroon to Uganda with a divided cloacal, but our data show little molecular divergence between southern African populations and those from north of the Congo forest block, despite a great variety of colour patterns in both regions. Another available name for this species was *P. irregularis* Fischer, 1856, based on a specimen from Peki in former German Togo with a divided cloacal and extensive black dorsal patches on the anterior third of the body, decreasing posteriorly, but our molecular study show that such specimens from Togo are molecularly identical to typical *P. phillipsi* from West Africa. Data for specimens south of 12°S were published by Broadley (2002). Further molecular studies are needed to investigate if additional species of this complex occur around the Congo forest block (e.g. sequencing specimens with a grey mid-ventral band from Central African Republic and other areas), and to clarify the situation in Nigeria where both *P. phillipsi* and *P. mossambicus* occur, possibly in sympatry.

Habitat. Moist savannas and grasslands, especially riparian habitats, swamps, reed beds and cultivated areas from sea level to 1,500 metres.

Distribution. Southeastern Nigeria, Cameroon, southern Chad, Central African Republic, Sudan, South Sudan, Gabon, Republic of Congo, Democratic Republic of Congo, Rwanda, Burundi, Uganda, Kenya, Tanzania, Angola, Zambia, Mozambique, Malawi, northeastern Namibia, northern Botswana, Zimbabwe and the Northern, Mpumalanga and KwaZulu-Natal provinces of South Africa.

PSAMMOPHIS LEOPARDINUS Bocage, 1887

Leopard Whip Snake, *Psammophis léopard*, Leoparden-Sandrennnatter

Psammophis sibilans var. *leopardinus* Bocage, 1887: 206. Type locality: Catumbela, Angola. Lectotype MBL 1798, destroyed by fire in the Museu Bocage.

Psammophis sibilans var. C (part) & D Bocage, 1895: 117; Ferreira 1905: 116.

Psammophis sibilans leopardinus Broadley, 1977: 18, Pl. ii; 1983: 143

Psammophis brevirostris leopardinus Brandstätter, 1995: 53.

Psammophis leopardinus Broadley, 2002: 95.

Description. Two specimens examined by DGB from the Angolan coast north of Latitude 12° S: USNM 20132 from Luanda and TM 45751 from Quiçama National Park. Nostril pierced between 2 or 3 nasals; preocular 1, widely separated from frontal; postoculars 2; temporals usually 2 + 3; supralabials 8, 4th & 5th entering orbit; infralabials 10, the first 4 in contact with anterior sublinguals; dorsal scales in 17-17-13 rows; ventrals 163–167; cloacal divided; subcaudals 104–106.

Both specimens have *P. leopardinus* head markings, but the dorsum is uniform except for a yellow dotted vertebral line in USNM 20132 and pale dorsolateral stripes on scale row 4 in TM 45751.

Ferreira (1905) recorded three specimens from northern Angola (Cazengo; Chingo) and Cabinda, which were presumably destroyed by fire in the Museu Bocage. Further data on this taxon were published by Broadley (2002) and Hughes & Wade (2002).

PSAMMOPHIS ZAMBIENSIS Hughes & Wade, 2002

Zambian Whip Snake, *Psammophis zambien*, Sambische Sandrennnatter

Psammophis sibilans (not Linnaeus) Pitman, 1934: 297 (part, ‘Chimikombe’ specimens only).

Dromophis lineatus (not Dumèril & Bibron) Laurent, 1956: 247 (Kundelungu, DRC).

Psammophis ? *sibilans* Broadley & Pitman, 1960: 445.

Psammophis brevirostris leopardinus (not Bocage) Broadley, 1971: 88; Brandstätter, 1955: 53, Pl. 39 & 1966: 48 (Zambia only); Haagner *et al.*, 2000: 16.

Psammophis zambiensis Hughes & Wade, 2002: 75. Type locality: “Abercorn”, probably = Mweru-Wantipa, Zambia. Holotype: BM 1959.1.1.81; Broadley *et al.*, 2003: 170.

Description. (23 specimens examined) Nostril pierced between 2 nasals; preocular 1, separated from frontal; postoculars 2; temporals usually 2+2/3; supralabials 8 (rarely 7 or 9), the 4th & 5th (rarely 3rd & 4th) entering orbit; infralabials 9 or 10, the first 4 in contact with anterior sublinguals; dorsal scales in 17-17-13 rows; ventrals 147–161; cloacal divided (entire in NMZB 16601); subcaudals 72–83. Brandstätter (1995, fig. 39) has published



Fig. 9. *Psammophis sibilans*. Dorsal view of the head of BM 1897.10.28.603 from Abassiyeh near Cairo, Egypt (A), MNHN 2001.0601 from Ain Ghossair near Ismailia, Egypt (B), and AUZC.R02262 from Qalubiya near Cairo, Egypt (C). Note the black edged yellow median line starting from the snout which is not forking then bordering the frontal as observed in *Psammophis afro-cidentalis* sp. nov. and *P. rukwae*.



Fig. 10. *Psammophis sibilans*. Plain phase. Specimen from Faiyum (Egypt).



Fig. 11. *Psammophis sibilans*. Lineated phase. Specimen from Aïn Ghossair near Ismailia, Egypt (MNHN 2001.0601).

a SEM micrograph of a dorsal scale of NMZB 10636 from Ikelenge, Zambia.

Dorsum greenish-brown, top of head with complex pale markings; labials yellowish speckled with black; a pale double chain marking covers the dorsal nine scale rows anteriorly, dorsal scales heavily edged in black (more extensive in juveniles and subadults), a pale dorso-lateral stripe on scale row 4 and 5 continues caudad; lower half of outer scale row and ventrals greenish, free edges of ventral irregularly bordered with black (more extensive in subadults). Two specimens from Sakeji School (Haagner *et al.* 2000), and all those from the Muchinga escarpment and Malawi, lack the distinctive dorsal and ventral markings, but are still distinguishable from sympatric / parapatric *P. mossambicus* by their low ventral and subcaudal counts.

Size. Largest male (PEM 6237 – Sakeji School, Zambia) 770 + 275 = 1,045 mm; largest female (PEM 6224 – Sakeji School, Zambia) 740 + 180+ mm (tail truncated).

Remarks. This taxon was originally assigned to *P. leopardinus*, which it resembles in dorsal colour pattern, but it differs in its much lower mandibular tooth counts and also lower ventral and subcaudal counts. In addition there seems to be no connection across eastern Angola and the two forms occupy very different habitats. The sequences of “*P. occidentalis*” from Zambia and Burundi in Kelly *et al.* (2008) and Fig. 1 may correspond to this species. See Hughes & Wade (2002) for further data.

Habitat. Apparently inhabiting swampy areas in moist miombo woodland in Zambia and Katanga or montane grassland in Malawi.

Distribution. Northern Zambia and adjacent Katanga Province of the DRC, extending into montane areas of northern and central Malawi.

**TENTATIVE KEY TO THE SPECIES OF
PSAMMOPHIS NORTH OF LATITUDE 12°S**

(excluding the cryptic species only known by their sequences)

- 1a. Dorsal scales in 17 or 19 rows at midbody 2
- 1b. Dorsal scales in less than 17 rows at midbody 14
- 2a. Supralabials usually 8 (occasionally 9 for *P. sibilans*), with fourth and fifth, or four, fifth and sixth entering the orbit (occasionally fifth and sixth for *P. sibilans*). Dorsal scales in 17 rows..... 3
- 2b. Supralabials usually 9, with fifth and sixth, or four, fifth and sixth entering the orbit. Dorsal scales in 17 row (rarely 19)..... 10
- 3a. Temporals 1+2, rarely two anterior temporals. Ventrals 138–167, subcaudals 73–107. Dorsum brown or olive, uniform or with a fine yellow vertebral line and a yellow dorsolateral stripe. Belly yellowish, often with short transverse black marks at the outer edges *Psammophis lineatus*

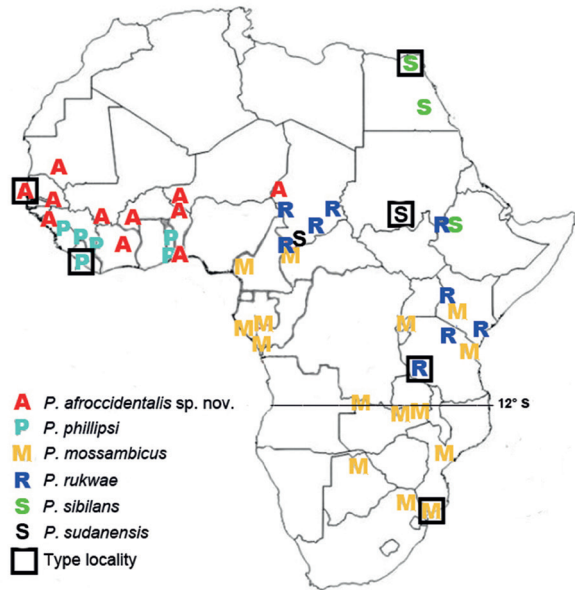


Fig. 13. *Psammophis afroccidentalis* sp. nov. General view of the holotype MNHN 2018.0013 (formerly IRD 7631.S) from Dakar, Senegal.

Fig. 12. Geographic distribution of the sequenced specimens of *P. sibilans* and other species frequently confounded with *P. sibilans*: *P. phillipsi*, *P. mossambicus*, *P. rukwae*, *P. sudanensis*, and *P. afroccidentalis* sp. nov. One symbol may correspond to several specimens from neighbouring localities. Location of type locality is approximate for *P. sibilans* (“Egypt”), *P. phillipsi* (“Liberia”) and *P. mossambicus* (“insel Mossambique”).

- 3b. Temporals basically 2+2, fusions and/or divisions frequent 4
- 4a. Usually the first five infralabials in contact with the anterior sublinguals 5
- 4b. Usually the first four infralabials in contact with the anterior sublinguals 6
- 5a. Subcaudals 71–102, ventrals 160–184. Dorsum brown, often with a black and white vertebral chain, the black pigment either covering the edges or the hindermost part of the scale. A pale dorsolateral stripe absent or present. Top of head often with a pale median stripe on the snout which forks when reaching the frontal and then borders the frontal. Sahel and Sudan savanna from Cameroon to Ethiopia and Tanzania..... *Psammophis rukwae*
- 5b. Subcaudals 98–119, ventrals 154–178. Dorsum uniform or strongly striped with a black and white vertebral chain, the black pigment covering the edges of the scale, and a pale dorsolateral stripe. Top of head often with a pale median stripe on the snout which is interrupted before the frontal or forks only after the middle of the frontal. Northeastern Africa from Egypt and Sudan to Ethiopia *Psammophis sibilans*

- 5c. Subcaudals 96–120, ventrals 156–185. Dorsum brown with a black and white vertebral chain, the black pigment covering the hindermost part of the scale. A pale dorsolateral stripe absent or present. Top of head often with a pale median stripe on the snout which forks when reaching the frontal and then borders the frontal. Sahel, Sudan and Guinean savannas of West Africa *Psammophis afroccidentalis* sp. nov.
- 6a. Cloacal scale usually entire. Dorsum and top of head usually uniform. If present, reticulations on the top of the head may form a complex network, but never with a pale median stripe on the snout which forks and then borders the frontal. Moist savannas of West Africa *Psammophis phillipsi*
- 6b. Cloacal scale divided 7
- 7a. Ventrums yellowish usually with a pair of well-defined black lines 8
- 7b. Ventrums uniform or with ill-defined black lines or dashes 9
- 8a. Top of head with a yellow median stripe on the snout and the frontal. A yellow vertebral line bordered by two pairs of brown and one pair of yellow dorsolateral stripes. Ventrals 148–180, subcaudals 90–129. Dry savannas of West, Central and East Africa *Psammophis sudanensis*
- 8b. No median stripe on the top of the head. Dorsum brown uniform. Ventrals 148–170, subcaudals 95–117. Coastal areas of East Africa *Psammophis orientalis*



Fig. 14. *Psammophis afroccidentalis* sp. nov. Ventral view of the holotype MNHN 2018.0013 from Dakar, Senegal.



Fig. 15. *Psammophis afroccidentalis* sp. nov. Lateral (A), dorsal (B) and ventral (C) view of the head of the holotype MNHN 2018.0013 from Dakar, Senegal.

- 9a. Subcaudals 84–122, ventrals 154–188. Dorsum olive to yellow-brown, uniform or with black-edged scales forming narrow black longitudinal lines, or with scattered black scales (rarely largely black), or with a black and white vertebral line and a pale dorsolateral stripe. Top of head uniform or with complex pale markings. Ventrums yellow or whitish, uniform or with rows of black lateral spots or irregular black speckling, some specimens with a mid-ventral band of grey obfuscation. Moist savannas and forest clearings from southeastern Nigeria to eastern and southern Africa *Psammophis mossambicus*
- 9b. Subcaudals 75–90, ventrals 148–165. Dorsum greenish-brown with scales often heavily edged in black and the nine median rows with black and white markings. Top of head reticulated. Free edges of ventrals irregularly edged in black. Zambia, Malawi and southern Democratic Republic of Congo *Psammophis zambiensis*
- 9c. Subcaudals 79–106, ventrals 151–167. Colour pattern variable, a pale dorsal chain pattern usually changes posteriorly to paired dorsolateral stripes. Pale transverse and reticulated markings often present on back of head. Chin and throat speckled and sometimes bands of grey flecking on ventrum. Angola and northern Namibia *Psammophis leopardinus*



Fig. 16. *Psammophis afroccidentalis* sp. nov. General view of a specimen with a typical dorsal head pattern, ill-defined vertebral chain and lacking pale dorsal stripes. Dielmo, Senegal.

- | | | | |
|---|--------------------------------|--|------------------------------------|
| 10a. Subcaudals more than 140 | 11 | 14a. Dorsal scales in 11 rows at mid-body | <i>Psammophis angolensis</i> |
| 10b. Subcaudales less than 135 | 12 | 14b. Dorsal scales in 13 rows at mid-body..... | <i>Psammophis pulcher</i> |
| 11a. Ventrals 170–198, subcaudals 143–178. Flanks and belly heavily speckled with black. Semi-desert and arid savannas from southeastern Egypt to Somalia and northern Tanzania | <i>Psammophis punctulatus</i> | 14c. Dorsal scales in 15 rows at mid-body | 15 |
| 11b. Ventrals 186–211, subcaudals 142–172. Flanks not speckled with black, belly with a large median grey band. Sahel and sudano-guinean savannas from Senegal to Chad and Central African Republic..... | <i>Psammophis elegans</i> | 15a. Two upper labials, usually fourth and fifth, entering orbit. Ventrals 161–191, subcaudals 107–133. Top of head with transverse black bars. West and Central Africa..... | <i>Psammophis praeornatus</i> |
| 12a. Usually three supralabials entering the orbit. Ventrals 155–181, subcaudals 106–132. Angola and southern Africa..... | <i>Psammophis subtaeniatus</i> | 15b. Two upper labials, usually fifth and sixth, entering orbit. Ventrals 138–156, subcaudals 102–134. Top of head more or less uniform. East Africa..... | <i>Psammophis biseriatus</i> |
| 12b. Usually two supralabials entering the orbit. North Africa and Sahel..... | 13 | 15c. Three upper labials, usually the fourth, fifth and sixth, entering orbit. Ventrals 142–169, subcaudals 81–123. Top of head with dark bordered tan blotches and a light longitudinal stripe along the junctions of infranasals and prefrontals. East Africa | <i>Psammophis tanganicus</i> |
| 13a. Ventrals 167–181. Dorsal scales in 17 rows at mid-body..... | <i>Psammophis schokari</i> | | |
| 13b. Ventrals 183–203. Dorsal scales in 17 or 19 rows at mid-body..... | <i>Psammophis aegyptius</i> | | |



Fig. 17. *Psammophis afroccidentalis* sp. nov. Juvenile specimen with a vertebral chain and pale dorso-lateral stripes. Dakar, Senegal.



Fig. 18. *Psammophis sudanensis*. Jos (Nigeria). Specimen with a typical head and dorsal pattern.



Fig. 19. *Psammophis sudanensis*. Bitea (Chad). Specimen with a typical head and dorsal pattern.



Fig. 20. *Psammophis phillipsi*. Mt Nimba (Guinea).



Fig. 21. *Psammophis phillipsi*. Sequenced specimen IRD 5002.G. Kindia (Guinea).



Fig. 22. *Psammophis mossambicus*. Sequenced specimen IRD 2238.N. Baïbokoum (Chad).



Fig. 23. *Psammophis mossambicus*. Sequenced specimen LC.4366. Gamba (Gabon).

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APPENDIX I

Table 1. Localities and GenBank numbers of sequenced specimens.

Species & collection N°	Country & locality	Coordinates	Cyt B	ND4	16S
<i>P. rukwae</i> IRD 2121.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997939	MK032650	MK005696
<i>P. rukwae</i> IRD 2150.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997941	MK032652	MK005698
<i>P. rukwae</i> IRD 2020.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997931	MK032646	MK005692
<i>P. rukwae</i> IRD 1888.N	Chad Mahargal	12°07'N / 21°22'E	MH997936	MK032643	MK005689
<i>P. rukwae</i> IRD 1949.N	Chad Bon Amdaoud	10°41'N / 19°28'E	MH997937	MK032644	
<i>P. rukwae</i> MBUR 08343	Ethiopia near Kutaworke	10°36'N / 34°24'E	MH997968	MK032678	MK005726
<i>P. rukwae</i> IRD 2001.N	Chad N'Djaména	12°04'N / 15°07'E	MH997929		MK005690
<i>P. rukwae</i> IRD 2002.N	Chad N'Djaména	12°04'N / 15°07'E	MH997930	MK032645	MK005691
<i>P. rukwae</i> IRD 2759.N	Chad Kiéké	10°33'N / 19°48'E	MH997951	MK032658	MK005706
<i>P. afroccidentalis</i> sp. nov. ZFMK 77019	Benin Za-Kpota	07°13'N / 02°12'E	MH997972	MK032682	
<i>P. afroccidentalis</i> sp. nov. ZFMK 77012	Benin Djidja	07°20'N / 01°56'E	MH997971	MK032681	

Species & collection N°	Country & locality	Coordinates	Cyt B	ND4	16S
<i>P. afroccidentalis</i> sp. nov. ZFMK 77036	Benin Bohicon	07°11'N / 02°04'E	MH997973	MK032683	
<i>P. afroccidentalis</i> sp. nov. IRD 370.N	Niger Toundi Farkia	14°02'N / 01°32'E		MK032663	
<i>P. afroccidentalis</i> sp. nov. IRD TR.4173	Burkina Faso Pâ	11°32'N / 03°18'W	MH997961	MK032677	MK005718
<i>P. afroccidentalis</i> sp. nov. IRD TR.4167	Senegal Dar Salam	13°12'N / 13°06'W	MH997960		MK005717
<i>P. afroccidentalis</i> sp. nov. IRD 328.CI	Ivory Coast Niagnon	09°31'N / 06°26'W		MK032660	
<i>P. afroccidentalis</i> sp. nov. IRD 115.M	Mali Doussoudiana	11°09'N / 07°48'W		MK032642	
<i>P. afroccidentalis</i> sp. nov. IRD TR.4177	Guinea near Tiva	10°16'N / 14°11'W	MH997962	MK032671	MK005719
<i>P. afroccidentalis</i> sp. nov. IRD 5001.G	Guinea near Sangaredi	11°10'N / 13°50'W	MH997954	MK032665	MK005711
<i>P. afroccidentalis</i> sp. nov. IRD TR.4501	Mauritania near Matmata	17°51'N / 12°09'W	MH997965	MK032674	MK005721
<i>P. afroccidentalis</i> sp. nov. IRD 2808.N	Chad Mao	14°08'N / 15°18'E	MK005683		MK005708
<i>P. sibilans</i> BEV T4799	Egypt near Edfu	25°01'N / 32°58'E	MH997935	MK032641	
<i>P. sibilans</i> AUZC R.143972	Egypt Faiyum	29°25'N / 30°54'E	MH997928	MK032639	MK005687
<i>P. sibilans</i> AUZC R.143973	Egypt Faiyum	29°25'N / 30°54'E	MH997934	MK032640	MK005688
<i>P. sibilans</i> MBUR 08588	Ethiopia near Kutaworke	10°35'N / 34°21'E	MH997970	MK032680	MK005727
<i>P. sudanensis</i> IRD 2280.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997948		MK005703
<i>P. sudanensis</i> IRD 2283.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997949	MK032657	MK005704
<i>P. sudanensis</i> IRD 2231.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997946	MK032655	
<i>P. sudanensis</i> IRD 2289.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997950		MK005705
<i>Psammophis</i> sp. MBUR 08346	Ethiopia NE of Kutaworke	10°40'N / 34°25'E	MH997969	MK032679	
<i>P. phillipsi</i> IRD 5002.G	Guinea Kindia	10°03'N / 12°51'W	MH997955	MK032666	MK005712
<i>P. phillipsi</i> IRD 5003.G	Guinea Kindia	10°03'N / 12°51'W	MH997956	MK032667	
<i>P. phillipsi</i> IRD 5004.G	Guinea Kissidougou	09°14'N / 10°03'W	MH997957	MK032668	MK005713
<i>P. phillipsi</i> IRD 5005.G	Guinea Kissidougou	09°14'N / 10°03'W	MH997958	MK032669	MK005714
<i>P. phillipsi</i> IRD TR.4609	Guinea Ziéla	07°43'N / 08°21'W	MK005681		MK005715

Species & collection N°	Country & locality	Coordinates	Cyt B	ND4	16S
<i>P. phillipsi</i> IRD TR.4610	Guinea Païa	08°01'N / 09°02'W	MK005682		MK005716
<i>P. phillipsi</i> IRD 358.T	Togo Djiguengué	08°05'N / 00°38'E	MK005680	MK032661	MK005709
<i>P. phillipsi</i> IRD 367.T	Togo Djiguengué	08°05'N / 00°38'E	MH997952	MK032662	MK005710
<i>P. phillipsi</i> IRD 10.T	Togo Sodo	07°19'N / 00°48'E	MK005686		
<i>P. phillipsi</i> IRD 44.T	Togo Kpalimé	06°54'N / 00°37'E	MH997953	MK032664	
<i>P. mossambicus</i> IRD 2136.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997940	MK032651	MK005697
<i>P. mossambicus</i> IRD 2186.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997942		MK005699
<i>P. mossambicus</i> IRD 2226.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997945	MK032654	MK005701
<i>P. mossambicus</i> IRD 2053.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997932	MK032647	MK005693
<i>P. mossambicus</i> IRD 2066.N	Chad Baïbokoum	07°44'N / 15°41'E	MK032648	MK032648	MK005694
<i>P. mossambicus</i> IRD 2224.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997944	MK032653	MK005700
<i>P. mossambicus</i> IRD 2238.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997947	MK032656	MK005702
<i>P. mossambicus</i> IRD TR.4579	Cameroon Foumban	05°43'N / 10°55'E	MH997967	MK032676	MK005723
<i>P. mossambicus</i> ZFMK 88703	Zambia Luambe Nat. Park	12°20'S / 32°15'E	MH997976	MK032686	
<i>P. mossambicus</i> ZFMK 88502	Zambia Ikelenge Nchila	11°14'S / 24°16'E	MH997974	MK0326684	
<i>P. mossambicus</i> ZFMK 88503	Zambia Ikelenge Nchila	11°14'S / 24°16'E	MH997975	MK032685	
<i>P. mossambicus</i> IRD TR.4366.LC	Gabon Gamba	02°43'S / 10°01'E	MH997963	MK032672	MK005720
<i>P. mossambicus</i> IRD TR.4367.LC	Gabon Gamba	02°43'S / 10°01'E	MH997964	MK032673	
<i>P. mossambicus</i> MBUR 08242	Republic of Congo Hinda	04°32'S / 12°04'E	MK005684		MK005725
<i>P. mossambicus</i> MBUR 03143	Republic of Congo Lake Fony	04°29'S / 11°46'E	MK005684		MK005724
<i>P. lineatus</i> IRD 2120.N	Chad Baïbokoum	07°44'N / 15°41'E	MH997938	MK032649	MK005695
<i>P. elegans</i> IRD TR.4504	Mauritania 35 km E Rosso	16°33'N / 15°31'W	MH997966	MK032675	MK005722
<i>P. elegans</i> IRD 222.CI	Ivory Coast Drekro	07°00'N / 05°17'W	MH997943		MK005728
<i>P. elegans univittatus</i> IRD 2761.N	Chad Bon Amdaoud	10°41'N / 19°28'E	MK005679	MK032659	MK005707
<i>P. praeornatus</i> IRD 9193.S	Senegal Fafakourou	13°04'N / 14°33'W	MH997959	MK032670	

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