

Diversity of Sand Snakes (Psammophiidae, *Psammophis*) in the Horn of Africa, with the description of a new species from Somalia

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Abstract

The biological diversity of the Horn of Africa is one of the least studied in the world. Yet the Horn supports rich communities of species that are mostly endemic to the region. Here we study the diversity of Sand Snakes (*Psammophis*) in East Africa, their phylogeny and systematics. Previous studies have unveiled several cryptic and potentially undescribed species of *Psammophis* that occur in the Horn and their taxonomic status has remained unclear to this day. We used sequence data from two mitochondrial and one nuclear genes to reconstruct the phylogeny of the genus, in which we included newly obtained samples of six different *Psammophis* species from Somalia, Ethiopia, Eritrea, Sudan, and Egypt. Our aim was to assess the status of some of the undescribed species, examine the level of intraspecific genetic variation within individual species, improve our understanding of the species distributions, and contribute to the taxonomy of the genus. Our results confirm the existence of two undescribed species, one in eastern Somalia, which we formally describe as new, and one in southern Ethiopia that we refer to as *Psammophis* cf. *sudanensis* in accordance with previous studies. Further, we provide first genetic data for the nominotypical subspecies of *P. punctulatus* and confirm the species status for its subspecies *P. trivirgatus*. In addition, we provide new genetic data for *P. tangericus* from Ethiopia and Somalia, and range extension records for *P. rukwae* from Eritrea and Ethiopia and for *P. aegyptius* from Somalia. Our findings contribute considerably to our understanding of the diversity and distribution of *Psammophis* in East Africa.

Key Words

East Africa, Eritrea, Ethiopia, phylogeny, reptilia, sand racers, Serpentes

Introduction

The Horn of Africa is the easternmost projection of the African continent that juts into the Indian Ocean. It supports a broad spectrum of habitats, from the Ethiopian Highlands that exceed 4500 m in elevation to the harsh lowland deserts of Somalia with barely any precipitation. The entire territory of the Horn is considered one of the global biodiversity hotspots, which are classified as regions of exceptionally high species richness and endemism while also suffering considerable habitat loss (Mittermeier et al. 2004). The Horn harbors a high diversity of squamate

reptiles, of which snakes with narrow distribution ranges stand out the most (Lewin et al. 2016), implying that the snake fauna is mostly endemic to the region. At the same time, however, large parts of the Horn remain virtually unexplored for their difficult accessibility, and the fauna of the Horn is vastly understudied, especially from a genetic perspective (Šmíd 2022).

Sand Snakes of the genus *Psammophis* are distributed primarily in Africa where there are 27 out of 33 currently recognized species. Six additional species occur strictly in Asia, and one stretches broadly across both continents (Uetz et al. 2023). They are slender and swift diurnal

hunters, with long heads and large eyes with round pupils, and relatively large, grooved rear fangs. The genus is typified by the unusually small male copulatory organs (hemipenes), which are short and thin and lack any ornamentation characteristic of other snakes (Steehouder 1984; de Haan 2003). As a result, the sex is almost impossible to determine externally in *Psammophis*.

Thirteen species of *Psammophis* occur in and around the Horn of Africa. Five range broadly across the Horn; these are *P. biseriatus* Peters, 1881; *P. pulcher* Boulenger, 1895; *P. punctulatus* Duméril, Bibron & Duméril, 1854 with two subspecies - *punctulatus* and *trivirgatus* Peters, 1878; *P. sibilans* (Linnaeus, 1758); and *P. tanganicus* Loveridge, 1940, although the distribution of *P. pulcher* is very limited as the species is known only from a handful of specimens. *Psammophis aegyptius* Marx, 1958 and *P. schokari* (Forskål, 1775) are distributed by the Red Sea along which they penetrate south to Eritrea and northern Somalia. The more marginal species to the Horn, but otherwise generally widespread in other parts of Africa, are *P. angolensis* (Bocage, 1872), *P. lineatus* (Duméril, Bibron & Duméril, 1854), *P. mossambicus* Peters, 1882, *P. orientalis* Broadley, 1977, *P. rukwae* Broadley, 1966, and *P. sudanensis* Werner, 1919 (Figs 1, 2; Lanza 1990; Largen and Spawls 2010; Spawls et al. 2018). This list is, however, apparently far from complete. The existence of additional phylogenetic lineages that may deserve the rank of species has been confirmed in several phylogenetic studies of the genus. For instance, *P. sibilans* has been found to represent two independent lineages unrelated to each other, the nominotypical one distributed in Egypt and western Ethiopia, the other one in central Ethiopia, and termed in this paper *P. sp. Ethiopia* (Trape et al. 2019). Similarly, *P. sudanensis* contains two lineages separated phylogenetically by many other species in between, with samples of the real *P. sudanensis* originating from Chad and those referred here to as *P. cf. sudanensis* from Kenya and Tanzania (Kelly et al. 2008; Trape et al. 2019). Trape et al. (2019) also recovered an isolated evolutionary entity in western Ethiopia (sample MBUR 8346; termed here *P. sp. Ethiopia 2*) that is related to the western African *P. phillipsii* (Hallowell, 1844) and the southern and eastern African *P. mossambicus*. And lastly, Vidal et al. (2008) included in their analysis a sample of an undetermined species from extreme eastern Somalia. Its taxonomy has remained unsolved to date (Keates 2021).

In this study we analyze new material from the Horn of Africa and adjoining countries to provide further insight into the phylogenetic relationships, distribution, and taxonomy of the *Psammophis* snakes of the region. The newly analyzed material originated from targeted herpetological fieldtrips to the Horn countries that were carried out between 2010 and 2022. We assembled a genetic dataset of two mitochondrial and one nuclear gene that was based on published data and which included all known *Psammophis* species, and we supplemented it by 14 newly analyzed specimens, including specimens that could not be determined with certainty on the basis of

morphology and which likely represented some of the putative new species. We inferred their phylogenetic position within the genus and investigated genetic variability of all *Psammophis* species to assess the taxonomic status of the putative new species in the context of a complete *Psammophis* phylogeny.

Methods

Data for genetic analyses

We assembled all genetic data that were available for the genus *Psammophis* on GenBank. To ensure sufficient overlap of loci we included only genes that were available for most of the Horn species. These were cytochrome b (cyt b) and NADH dehydrogenase subunit 4 (ND4) from the mitochondrial DNA, and oocyte maturation factor MOS (c-mos) from the nuclear DNA. Some species are represented in GenBank by many sequenced individuals. We pruned the dataset to contain only up to three samples per species, provided all the pruned species are monophyletic. It should be noted that the ND4 sequence of *P. biseriatus* (sample BK10724, GenBank accession [DQ486284](#)) and the c-mos sequence of *P. tanganicus* (sample CMRK87, GenBank accession [DQ486183](#)) contained too many ambiguous nucleotide positions to allow their inclusion in the dataset. Sequences of *Malpolon monspessulanus*, *Psammophylax variabilis*, *Psammophylax rhombeatus*, and *Rhamphiophis rostratus*, all of which belong to the Psammophiidae, were used to root the tree.

We de-novo sequenced 14 samples from different localities across the Horn of Africa and neighboring countries and belonging to *P. aegyptius* (seven samples from Egypt [2], Sudan [1], Somaliland [4]), *P. punctulatus* (one sample from Ethiopia), *P. rukwae* (two samples from Ethiopia and Eritrea), *P. sudanensis* (one sample from Ethiopia), *P. tanganicus* (two samples from Ethiopia and Somaliland), and one sample from northern Somalia (central Somaliland) tentatively identified as *P. cf. tanganicus*. See Fig. 3 for the geographic origin of the samples and Suppl. material 1 for precise locality details.

DNA extraction, amplification, and sequencing

Genomic DNA was extracted from ethanol-preserved tissue samples using the DNA Mini Kit protocol. We PCR-amplified the three genes using primers and PCR conditions detailed in Šmíd et al. (2019). The PCR products were sequenced from both directions at Macrogen Europe (Amsterdam, the Netherlands). Quality of the raw sequences was inspected and contigs were assembled using the Geneious v. 11 software (Kearse et al. 2012). The tRNAs that flank the ND4 and that were amplified along with it were not included in the dataset because they may be problematic to align with certainty.



Figure 1. Sand Snakes of the Horn of Africa, part 1. **a.** *P. aegyptius* (Berbera, Somaliland); **b.** *P. angolensis* (South Africa); **c.** *P. biseriatus* (Voi, Kenya); **d.** *P. lineatus* (Nigeria); **e.** *P. mossambicus* (Baringo, Kenya); **f.** *P. orientalis* (Watamu, Kenya); **g.** *P. pulcher* (Bisanadi National Reserve, Kenya). Photo credit T. Mazuch (**a**); WR. Branch (**b**), S. Spawls (**c, e, f, g**), G. Dunger (**d**).



Figure 2. Sand Snakes of the Horn of Africa, part 2. **a.** *P. punctulatus* (Gewane, Ethiopia); **b.** *P. trivirgatus* (Mwingi, Kenya); **c.** *P. rukwae* (Asmara, Eritrea); **d.** *P. schokari* (Kasserine, Tunisia); **e.** *P. sibilans* (Debre Zeit, Ethiopia); **f.** *P. cf. sudanensis* (Yabelo, Ethiopia); **g.** *P. tanganicus* (Mado Gashi, Kenya). Photo credit T. Mazuch (**a, c, d, f, g**), S. Spawls (**b, e**).

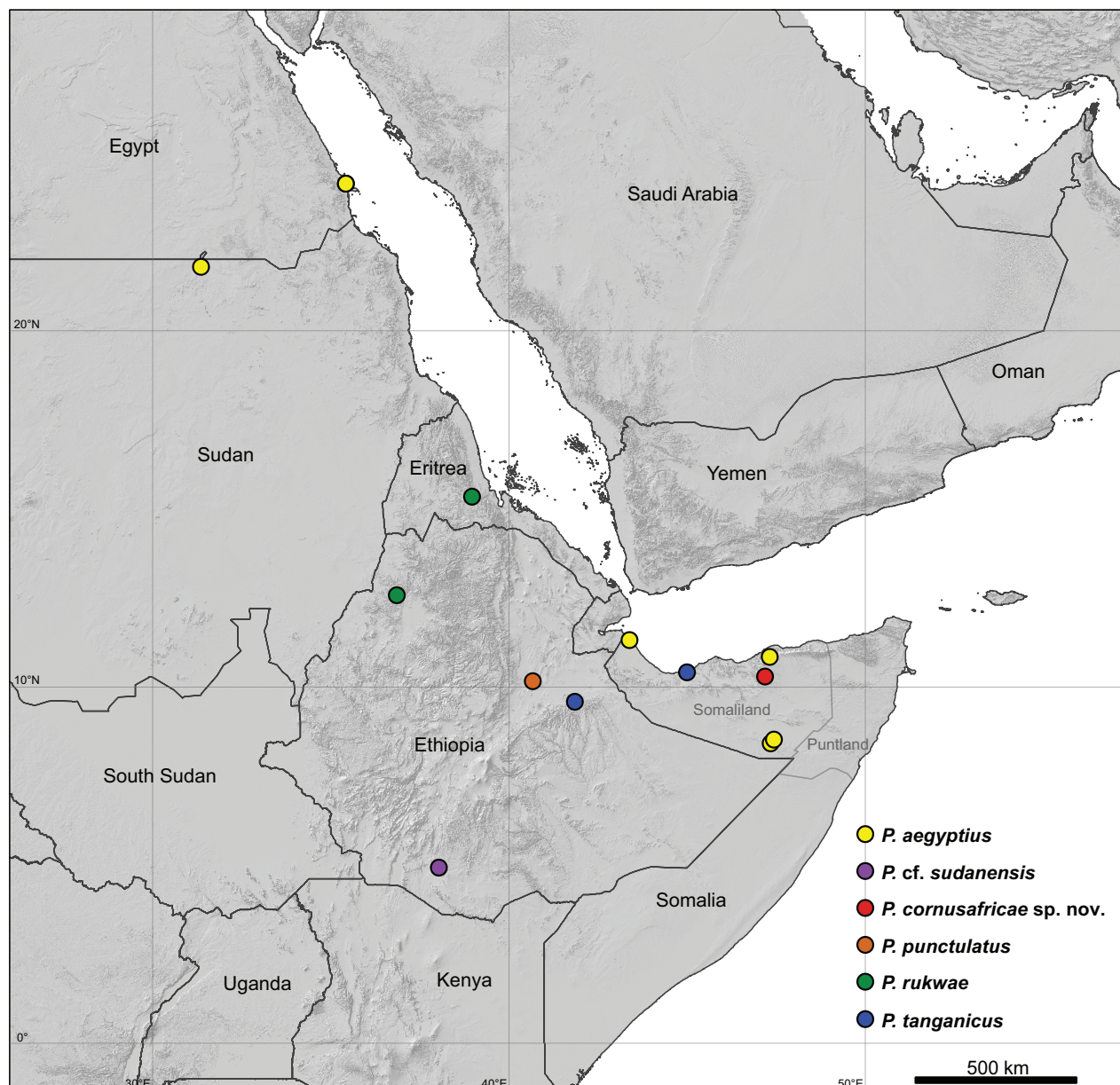


Figure 3. Geographic origin of the new material analyzed in this study. The background map shows the terrain surface. It was derived from the SRTM elevation data (Farr and Kobrick 2000) using the hillshade function of ArcMap.

All three genes were aligned with MAFFT (Katoh et al. 2019) using the auto strategy. The alignments were subsequently treated with Gblocks (Castresana 2000) to remove ragged ends. No stop codons were detected in the *cyt b* and ND4 alignments, indicating no nuclear mitochondrial pseudogenes were amplified. The final concatenated dataset contained 106 tips (102 ingroup + 4 outgroup) and was 2,149 base pairs (bp) long.

Phylogenetic analyses

The phylogenetic relationships within *Psammophis* were estimated by means of a Maximum Likelihood (ML) analysis and a Bayesian Inference (BI). The ML analysis was conducted in IQ-Tree (Nguyen et al. 2015) using the

online interface (Trifinopoulos et al. 2016). The dataset was partitioned by gene and the best-fit model of nucleotide substitution was selected automatically for each partition during the analysis. Branch support was assessed with 1,000 replicates of the Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT; Guindon et al. 2010), 1,000 replicates of ultrafast bootstrap (UFBoot; Hoang et al. 2018), and 100 standard bootstrap replicates (Felsenstein 1985).

The BI analysis was conducted in MrBayes v. 3.2 (Ronquist et al. 2012). The dataset was partitioned by gene and the best models were estimated by Partition-Finder v. 2.1 (Lanfear et al. 2017). The best models were as follows: GTR+I+G for the *cyt b* and ND4, HKY+G for the *c-mos*. The proportion of invariable sites parameter (+I) was not included as it is accounted for by the +G

parameter. We ran three independent runs for 10 million generations, sampling every 10,000 generations. Stationarity was determined by the sequentially calculated standard deviations of the split frequencies being lower than 0.01. We discarded the initial 10% of trees as burnin and generated a 50 percent majority rule consensus tree. Branches with SH-aLRT \geq 80, UFBoot \geq 95, standard bootstrap \geq 70, and a Bayesian posterior probability (pp) \geq 0.95 were considered strongly supported.

Comparisons of genetic distances

We assessed whether the genetic distances that separate the samples of the unidentified species from eastern Somalia from its sister species *P. tanganicus* are similar to or deviate from distances between other sister species across the *Psammophis* tree following the method of Šmíd et al. (2018). Pairwise genetic distances between all samples were obtained from the ML tree and were categorized in the following groups: within species, between sister species, between non-sister species, between *tanganicus* and the new species. Zero genetic distances between identical haplotypes were removed. Species were considered sister only when the sister relationship was strongly supported in all the phylogenetic analyses. The four outgroup species were pruned from the tree. We tested for significance between the four groups by means of one-way ANOVA with the Tukey HSD post hoc test for pairwise significance using R (R Core Team 2013). We also calculated uncorrected patristic distances (*p*-distances) for the two mitochondrial markers in MEGA X v. 10.2 (Kumar et al. 2018) with the pairwise deletion option.

Sex identification

We used the method of Laopichienpong et al. (2017) that allows the identification of sex by using molecular markers located on the gametologous genes. The psammophiids possess the ZZ/ZW sex determination system where males are the homogametic sex (ZZ), and females are heterogametic (ZW) (e.g., Augstenová et al. 2018). We amplified the CTNNB1 gametologous gene using the primers Eq-CTNNB1-11-F1 and Eq-CTNNB1-13-R (Matsubara et al. 2016; Laopichienpong et al. 2017) and PCR conditions detailed in the latter paper. Males were identified based on the presence of a single band on gel electrophoresis (both alleles on the Z sex chromosomes are of the same length), females had two bands present (the allele on the W sex chromosome is shorter than that on the Z chromosome; Laopichienpong et al. 2017).

Morphological analyses

For morphological comparisons, we examined the two specimens of *P. tanganicus* that were used in the genetic analysis (NMP-P6V 76371–2) and three specimens

of the undescribed species from Somalia (NMP-P6V 76373, MVZ:Herp:242772, MVZ:Herp:242773), the former two of which were also included in the genetic analysis. Scale counts and color pattern of the *P. tanganicus* holotype (MCZ R-30380) were obtained from the photographs available at the MCZ collection database (<https://mczbase.mcz.harvard.edu/guid/MCZ:Herp:R-30380>). General morphological species characteristics of *P. biseriatus* and *P. tanganicus* were assembled from the literature (Largen and Spawls 2010; Spawls et al. 2018; Spawls et al. 2023). We measured snout-vent length (SVL), measured from the tip of the snout to the anterior margin of the cloaca, and tail length (TL), measured from the posterior margin of the cloaca to the tip of the tail. The following scale counts were recorded: supralabials; infralabials; dorsal scales at one head-length behind the head (termed anterior dorsals), at midbody (termed midbody dorsals), and one head-length anterior to the vent (termed posterior dorsals); ventrals; subcaudals. In addition, we collected data on the color and pattern of different body parts of all examined specimens. This dataset of color patterns was supplemented by photographs from throughout the distribution of *P. tanganicus* that were obtained from the literature (Bezy and Drewes 1985), provided by our colleagues (M. Beroneau, A. Childs, S. Kirchhoff, M. Menegon, D. Modrý, S. Spawls, A. Stein, E. Van Der Westhuizen) or downloaded from the iNaturalist online database (https://www.inaturalist.org/taxa/28961-Psammophis-tanganicus/browse_photos). Original high-resolution photographs of the examined specimens have been deposited in the MorphoBank (<https://morphobank.org/>) database where they are available for free download (346 photographs in total; Project No. 4527). MorphoBank accessions are provided in Suppl. material 1.

Due to a rather small number of specimens available for morphological examinations we did not carry out formal statistical analyses to compare the studied taxa. We nonetheless carried out informal comparisons between them to verify whether there are morphological differences consistent with the genetic results.

Museum acronyms

CAS – California Academy of Sciences, San Francisco, USA; **MCZ** – Museum of Comparative Zoology, Cambridge, USA; **MVZ** – Museum of Vertebrate Zoology, Berkeley, USA; **MSNG** – Museo Civico di Storia Naturale ‘Giacomo Doria’, Genova, Italy; **MZUF** – University di Firenze, Museo Zoologico ‘La Specola’, Firenze (Florence), Italy; **NHMUK** – Natural History Museum, London, UK; **NMP** – National Museum in Prague, Czech Republic; **TMHC** – Tomáš Mazuch herpetological collection, Dřítěč, Czech Republic; **UniMoRe** – Collezione Franchini nella Sezione Musei Anatomici del Dipartimento del Museo di Paleobiologia e dell’Orto Botanico dell’Università di Modena e Reggio Emilia, Modena, Italy.

Results

Phylogenetic analyses

The ML and BI analyses resulted in identical topologies, although some branches were not statistically supported in either of the analysis (Fig. 4). Given that the dataset for the genetic analysis relied mostly on previously published sequences, the relationships between the *Psammophis* species remained largely congruent with other recent studies on the genus' phylogeny (Branch et al. 2019; Chen et al. 2021; Kurniawan et al. 2021; Taft et al. 2022). The subtle topological differences resulted either from different composition of taxa across different studies or from low branch support.

As for the newly analyzed samples, the sample of *P. punctulatus punctulatus* (JIR513) was recovered as sister to *P. punctulatus trivirgatus* with a robust branch support (SH-aLRT: 100/UFBboot: 100/Standard bootstrap: 100/MrBayes pp: 1.0; support values are shown in the same order hereafter). The genetic distances between the two taxa are 8.0% in the cyt *b* and 9.06% in the ND4.

The newly analyzed samples of *P. rukwae* (JIR511, TMHC2012.12.148) clustered within other samples of the species from Chad and Kenya (support 97.4/100/96/1.0), with *p*-distances within the species ranging between 1.48–5.17% in the cyt *b* and 0.76–5.74% in the ND4.

The new sample of *P. sudanensis* from Ethiopia (TMHC2013.07.250) did not cluster with the other samples of the species included in the analyses, but actually with a lineage termed *P. cf. sudanensis* from Kenya and Tanzania that was first discovered by Trape et al. (2019) (support 96.4/98/91/1.0). Our new sample was sister to all the other samples of this undescribed species (support 92.3/100/92/1.0), with *p*-distances between our and the other samples ranging between 5.0–5.49% in the ND4 (cyt *b* sequence is not available for TMHC2013.07.250).

The samples of *P. aegyptius* from Egypt and Sudan clustered with other samples of the species available on GenBank from Egypt and Niger (support 100/100/100/1.0), and the four samples from Somaliland were sister to this clade (support 97.5/99/97/1.0). Mean *p*-distances between the Somali samples and those from the north (Egypt, Sudan, Niger) were 8.03% in the cyt *b* (range 4.92–10.42%) and 9.24% in the ND4 (range 8.61–10.27%).

The two samples of *P. tanganicus* and that from central Somaliland that we tentatively identified as *P. cf. tanganicus* all clustered in a clade with *P. biseriatus* that was well supported in all analyses (support 100/100/100/1.0). In this clade, the two samples of *P. tanganicus* from Ethiopia and Somalia JIR508–509 (vouchers NMP-P6V 76371–2) were recovered to form a clade (support 100/100/100/1.0) that was sister to the remaining samples of *P. tanganicus* from Tanzania (support 95.9/99/95/1.0). The sample JIR510 (voucher NMP-P6V 76373) from central Somaliland was closely related to a sample of an undescribed *Psammophis* species from eastern Somalia sequenced by Vidal et al. (2008; sample and voucher codes TP28431 and MVZ:Herp:242772, respectively; support 100/100/100/1.0). *Psammophis biseriatus* was then sister to the group of *P. tanganicus* and the

undescribed species (support 85.1/94/74/0.99). Uncorrected *p*-distances between *P. biseriatus*, *P. tanganicus* and the undescribed species are shown in Table 1.

Table 1. Mitochondrial genetic distances (uncorrected *p*-distances in %) between *P. biseriatus*, *P. tanganicus*, and *P. cornusafricae* sp. nov. Below the diagonal are values for the cyt *b* gene, above the diagonal for the ND4. For each comparison, the mean is shown with the min-max range in brackets.

	<i>P. biseriatus</i>	<i>P. tanganicus</i>	<i>P. cornusafricae</i> sp. nov.
<i>P. biseriatus</i>		10.18 (9.52–10.57)	12.04 (11.99–12.08)
<i>P. tanganicus</i>	10.78 (10.33–11.04)		9.74 (9.26–10.77)
<i>P. cornusafricae</i> sp. nov.	9.90 (9.75–10.06)	7.79 (7.2–8.58)	

Comparisons of genetic distances

The genus showed clear genetic structuring with significant differences in the genetic distances found between the examined categories: within species, between sister species, between non-sister species, and the distance between the *P. tanganicus* and the undescribed species from Somalia (ANOVA $F_{(3,5152)} = 575.4$, $p < 0.001$). The post hoc tests confirmed pairwise differences between all categories ($p < 0.01$), except for the comparison between the categories 'between sister species' and 'tanganicus-Somali species' ($p = 0.999$; Fig. 5), indicating that the genetic distance between *P. tanganicus* and this species is statistically comparable to the distance between other sister species pairs in the genus.

Taxonomic implications

Based on the combined evidence of the genetic and morphological differentiation we recognize the undescribed species from the northeastern Somali regions of Somaliland and Puntland as new and provide its formal description below.

Systematics

Psammophiidae Bourgeois, 1968

Psammophis Fitzinger, 1826

Psammophis cornusafricae sp. nov.

<https://zoobank.org/F1E4DC4C-D816-47A9-B9E1-1DAB56323E56>

English name: African Horn Sand Snake

Somali name: Subxaanyo [pronounced Subhanyo]; a term in the Somali language that refers to all *Psammophis* species that occur in the region. All Subxaanyo are believed to be harmless and friendly by the locals and are an important part of their folklore

Chresonymy. *Psammophis biseriatus* in Calabresi (1927; in part), Scortecci (1939a), Scortecci (1939b), Lanza (1983; in part), Regnoli et al. (2003; in part);

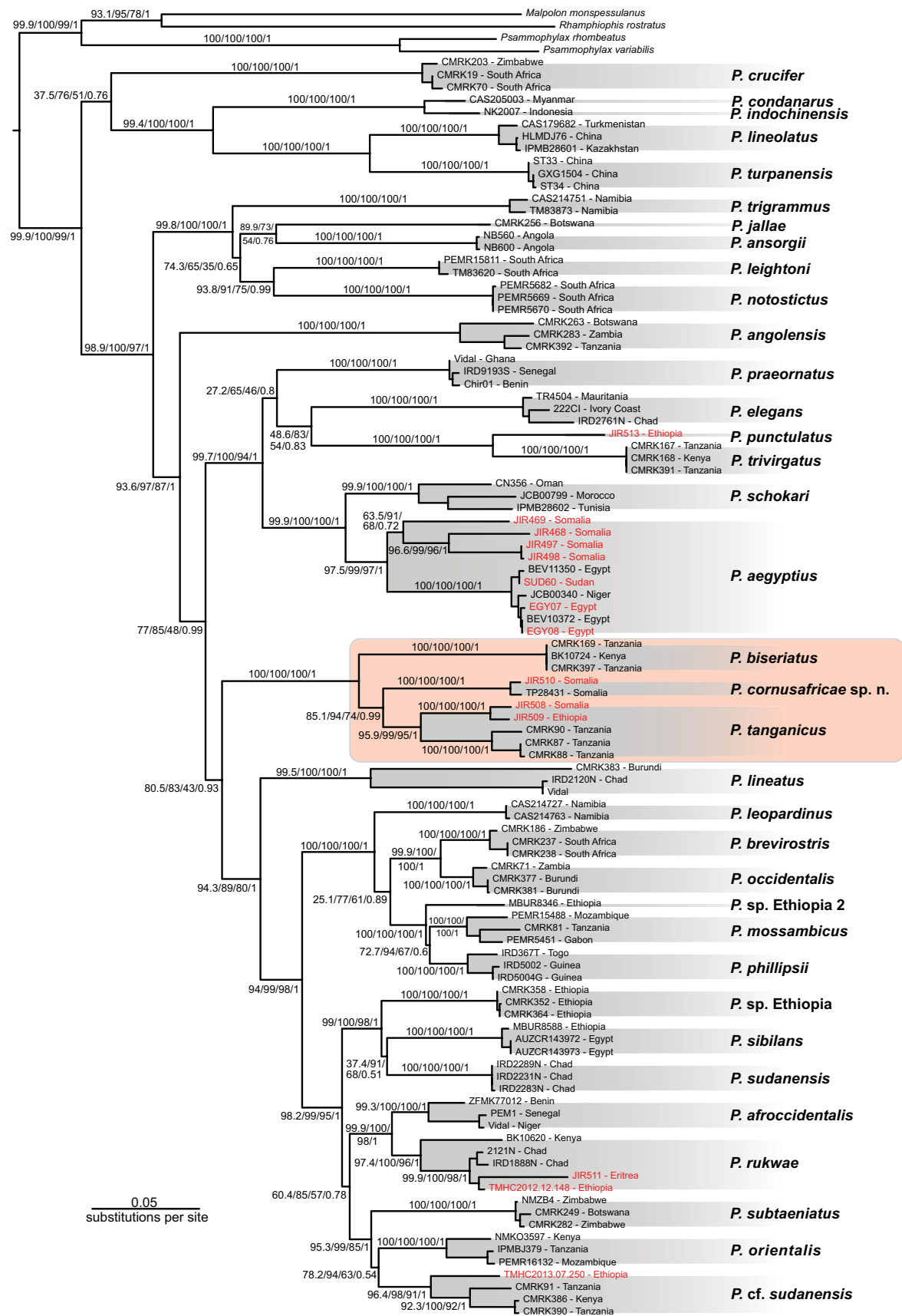


Figure 4. Maximum Likelihood phylogeny of the genus *Psammophis* based on a concatenated alignment of the cyt *b*, ND4 and c-mos genes (2,149 bp in total). The clade containing *P. biseriatus*, *P. tanganicus* and *P. cornusafricae* sp. nov. is highlighted in pink. Codes of samples newly sequenced for this study are in red. Locality details and original references of all samples are given in Suppl. material 1. Branch support is given in the order SH-aLRT/UFBoot/Standard bootstrap/MrBayes posterior probability.

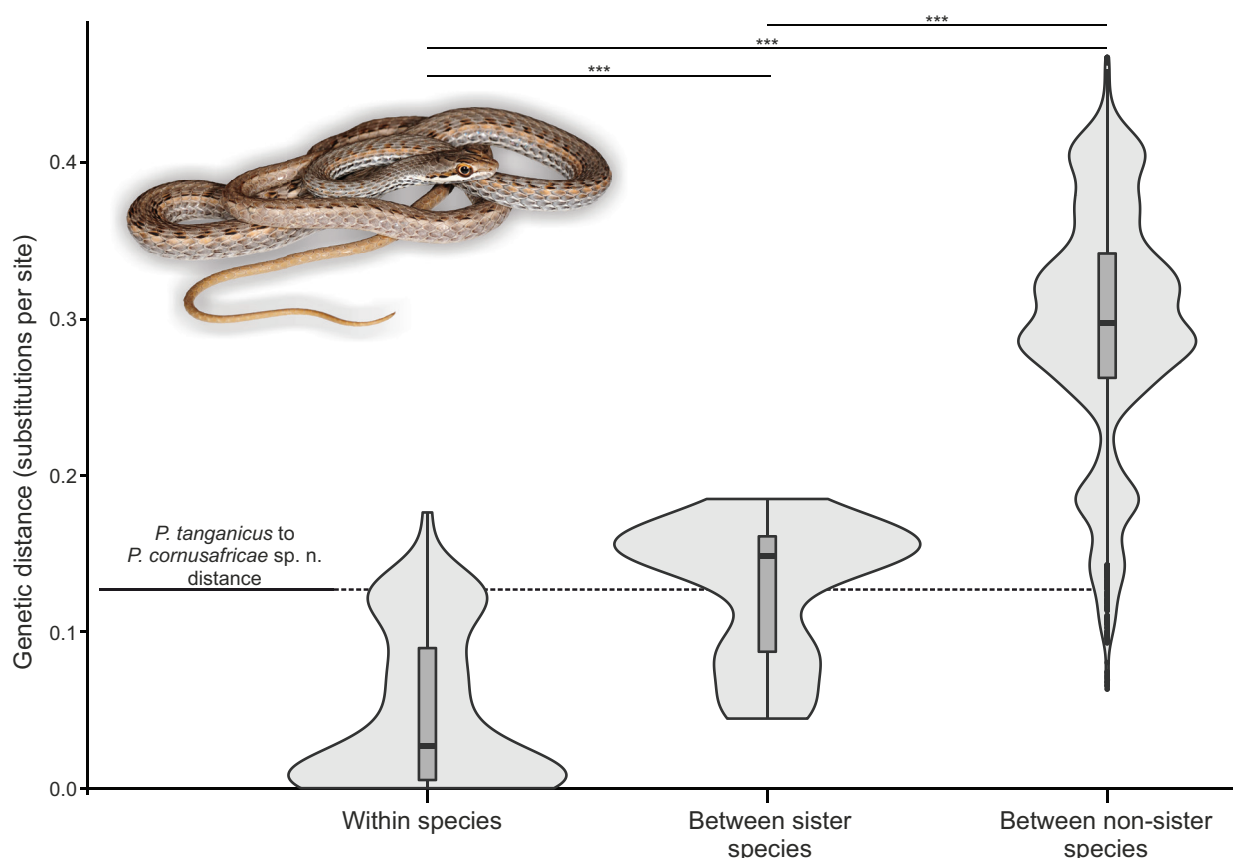


Figure 5. Comparison of genetic distances within the *Psammophis* species, between sister species pairs, between non-sister species. The distances (y axis) are based on the ML tree. Horizontal bars with asterisks on top of the graph indicate significant differences in the observed genetic distances ($p < 0.001$; tested by the Tukey HSD post hoc test of ANOVA). The average distance between *P. tanganicus* and *P. cornusafricae* sp. nov. (0.127 subst. per site) is shown by the dashed line. The animal depicted is specimen NMP-P6V 76373 (sample JIR510) of *P. cornusafricae* sp. nov.

Psammophis biseriatus tanganicus in Loveridge (1940; in part), Lanza (1990; in part);

Psammophis tanganicus Largen and Ramussen (1993; in part), Brandstätter (1996; in part), Largen and Spawls (2010; in part), Wallach et al. (2014; in part), Boundy (2020; in part);

Psammophis sp. in Vidal et al. (2008), Trape et al. (2019), Keates (2021).

Type material. *Holotype*: MVZ:Herp:242772 (sample code TP28431; Fig. 6), subadult, sex unknown; Somalia, Bari Region, Heela Spring, 11 km NW (by road) of Baargaal (11.371°N, 51.0412°E), elevation 77 m above sea level; collected by T. J. Papenfuss on June 29, 2003.

Paratype: MVZ:Herp:242773, adult, sex unknown; same collection data as holotype.

Other material. NMP-P6V 76373 (sample JIR510; Fig. 7; MorphoBank accessions: M851260–M851339), subadult female (sex confirmed by genetics); Somaliland, 8.5 km S of Yuffleh (10.3°N, 47.182778°E), elevation 1758 m above sea level; collected by T. Mazuch on September 5, 2017.

Diagnosis. A *Psammophis* species sister to *P. tanganicus*, with the following combination of morphological characters: 11 infralabials; 9 supralabials, three of which are in contact with the eye; nostril pierced between two

equal sized nasals; 15 anterior dorsals; 14–15 midbody dorsals; 11 posterior dorsals; 146–158 ventrals; 95–100 subcaudals. Body brown, grey or beige with only a faintly visible pale vertebral stripe but with well pronounced dorsolateral orange stripes on each side of the body. Tail with only a slight trace of or completely lacking any dark vertebral stripe; the posterior half of the tail uniformly pale yellow. Venter white to yellowish with a conspicuous stipple of irregular dark smears. Head dorsally with a symmetrical pattern of brown markings outlined by black margins which contrast with the grey or beige background coloration. Labials white with dark margins forming a black lip. Dark brown temporal stripe outlined by black blotches and stretching from the eye to the posterior end of the head.

Description of the holotype (Fig. 6). SVL 42.6 mm, TL 20.3 mm (the very tip of the tail is missing; the original tail was hence probably a few millimeters longer), total length 62.9 mm.

Head flattened dorsoventrally, separated from the body by a distinct neck; nostril pierced between two nasals, major sector-shaped (‘pac-man’-like shape); eyes large, with a round pupil; rostral roughly heptagonal, with a distinct groove at the base for flicking the tongue out; rostral visible from above and followed dorsally by one



Figure 6. Holotype of *Psammophis cornusafricae* sp. nov. (MVZ:Herp:242772).

pair of internasals, one pair of prefrontals, a long and narrow frontal with nearly equally as long supraoculars to its side; preoculars in narrow contact with the frontal and wedged between the prefrontals and supraoculars; large pair of parietals contacted laterally by large anterior temporals, posterior temporals and enlarged postparietals. The temporal formula of the anterior temporal + posterior temporal scales is 1+3. Laterally, rostral followed by two consecutive nasals, an elongated loreal and a large preocular that forms the anterior margin of the eye. Two postoculars at the posterior eye margin, the upper of which being contacted by the parietal and the lower by the anterior temporal. Nine supralabials, of which the 4th, 5th and 6th are in contact with the eye; 11 infralabials, five of which are in contact with the anterior pair of chin shields. Two pairs of chin shields. Four (right side) and five (left side) gulars in a longitudinal row between chin shields and prementals. Anterior dorsals 15, midbody dorsals 14, posterior dorsals 11; 158 ventrals; 85 subcaudals.

Coloration in preservation: body brownish beige, dorsum darker than the flanks, with dark sets of three to five dorsolateral scales separated by two to three paler scale rows. The frontal and supraoculars with dark pigment patches at their anterior sides, posterior margins pale. Parietals with dark oblong blotches by the medial line and at the anterior margin of the scales. Internasals and prefrontals dark to the sides and paler medially, which forms a narrow white-yellowish stripe at the nose tip. Supral-

abials white with contrasting dark brown upper and lower margins. The white of the supralabials continues onto the sides of the neck. Throat with extensive dark spots arranged in longitudinal stripes – one on each side of the mouth on the lower side of the infralabials up to the 6th infralabial, one at the mid-line running through the chin shields and gulars further on the belly.

Comparisons. *Psammophis cornusafricae* sp. nov. can be differentiated from other congeners that occur in the Horn of Africa as follows: from its sister species *P. tanganicus* (character in brackets) by having 3–5 gulars in a longitudinal row between chin shields and prementals (*versus* 2–3), posterior tip of the frontal moderately pointed (*versus* rounded), by lacking a clear orange or brownish dorsal stripe along the body and tail (*versus* orange vertebral stripe present), tail lacking a stripe, or having only a weakly developed dark vertebral stripe (*versus* tail with a clear dark vertebral stripe), having a clearly demarcated narrow temporal stripe on the head (*versus* broad stripe without clear demarcation), dark markings on the head dorsum paired and not fused (*versus* dark marking on the back of the head fused into a ‘W’ shape); from *P. biseriatus* (character in brackets) by having three supralabials in contact with the eye (*versus* two), usually one large anterior temporal (*versus* two), gular region strongly pigmented with dark longitudinal stripes (*versus* weakly pigmented with small dark spots), head ornately patterned above (*versus* uniformly colored), tail with



Figure 7. *Psammophis cornusafricae* sp. nov. in life (specimen NMP-P6V 76373, sample JIR510), with a close-up of the head in the upper left corner, and the habitat at the locality where the specimen was found (8.5 km S of Yuffleh, Somaliland) at the bottom.

absent or only a weakly developed dark vertebral stripe (*versus* tail with a clear dark vertebral stripe). Further morphological comparisons between *P. cornusafricae* sp. nov., *P. tanganicus*, and *P. biseriatus* are summarized in Table 2.

From the other Horn species *P. cornusafricae* sp. nov. differs by having a lower number of midbody dorsals (14–15 *versus* 17 or 19 in *P. aegyptius*, *P. lineatus*, *P. mossambicus*, *P. orientalis*, *P. punctulatus*, *P. rukwae*, *P. schokari*, *P. sudanensis* a *P. cf. sudanensis*, *P. trivirgatus*), or a higher number of midbody dorsals (11 in *P. angolensis*, 13 in *P. pulcher*).

Variation. The studied specimens of *P. cornusafricae* sp. nov. show some degree of morphological variation (Table 2). Namely, the number of infralabials varies between 10–11 and the number of supralabials between 8–9. The 3rd–5th supralabials are in contact with the eye in specimen NMP-P6V 76373 (the one with 8 supralabials); in the other two specimens it is the 4th–6th supralabials that touch the eye. Specimen NMP-P6V 76373 has three postoculars at the posterior eye margin and two anterior temporals (*versus* two postoculars and one anterior temporal in the other two specimens). Specimens MVZ:Herp:242773 and NMP-P6V 76373 (unilaterally) have two posterior tem-

Table 2. Morphological comparisons of *P. biseriatus*, *P. tanganicus* and *P. cornusafricae* sp. nov. Superscript letters refer to the original references from which the data was obtained as follows: ^a - Spawls et al. (2023); ^b - Largen and Spawls (2010); ^c - Bezy and Drewes (1985). *NA** indicates characters unavailable due to incomplete tail.

	<i>P. biseriatus</i>	<i>P. tanganicus</i>				<i>P. cornusafricae</i> sp. nov.		
	General	General	MCZ R-30380 Holotype	NMP-P6V 76371	NMP-P6V 76372	NMP-P6V 76373	MVZ:Herp:242772 Holotype	MVZ:Herp:242773 Paratype
Total length (cm)	~ 50–80 (max 100) ^a	~ 50–80 (max 100) ^a	63	90.8	NA *	58.8	62.9	73.8
SVL (cm)			40.6	61.5	47.4	39.7	42.6	49.7
TL (cm)			22.4	29.3	NA *	19.1	20.3	24.1
SVL/Total length (×100)	61.7 (56–66) ^c	66.7 (64–81) ^c	64.4	67.7		67.5	67.7	67.3
Infralabials	10–11 ^c	9–11	11	11	10	10/11 (right/left)	11	10
Supralabials	9 ^c	9 ^c	9	9	9	8	9	9
Supralabial in contact with eye	Two ^a (5 th –6 th)	Three (4 th –6 th)	Three (4 th –6 th)	Three (4 th –6 th)	Three (4 th –6 th)	Three (3 rd –5 th)	Three (4 th –6 th)	Three (4 th –6 th)
Midbody dorsals	15 ^a	15 ^a	15	15	15	15	14	15
Ventrals	138–168 ^a	143–169 ^a	151	159 (+2 preventrals)	150 (+1 preventral)	151 (+1 preventral)	158	146 (+1 preventral)
Subcaudals	97–134 ^a	81–123 ^a	114	110	NA *	95	85	100

porals (*versus* three in the holotype). There are 14 mid-body dorsals in the holotype, while the other two specimens have 15. The number of ventrals and subcaudals varies between 146–158 and 85–100, respectively. The two specimens examined genetically are closely related (Fig. 4). They are 99.35% identical in the *cyt b* sequence (different in 7 out of 1087 bp), 98.63% identical in the ND4 (different in 9 out of 662 bp), and 99.75% identical in the *c-mos* (different in 1 out of 400 bp).

Etymology. The species epithet indicates the geographic origin of the species and translates as “The Sand Snake of the Africa’s Horn”. It is a noun in the genitive case that is derived from the Latin words for horn (*cornu-us*) and Africa (*Africa-ae*).

Distribution. Our knowledge on the distribution of *P. cornusafricae* sp. nov. is very limited because it has so far been confirmed only from two localities. They are both located in Somalia; the type locality is at the very tip of the Horn of Africa (Puntland), the locality of specimen NMP-P6V 76373 lies in central Somaliland, some 440 km west-southwest from the type locality (Fig. 8). Puntland and the eastern part of Somaliland are the driest parts of the Horn of Africa. They receive less than 200 mm of precipitation annually (Muchiri 2007), and are covered by sparse vegetation (ESA CCI Team 2017) and geologically formed by the so-called Karkar and Taleh formations that include limestones, dolomites, and gypsum (Schreiber 1993; Quiroga et al. 2022). We assume *P. cornusafricae* sp. nov. to roughly match the extent of the Karkar and Taleh formations and adjoin the range of *P. tanganicus* from the east. This distribution pattern with central Somaliland being a contact zone of closely related taxa has already been confirmed for other taxa, e.g. *Tomopterna* (Pyxicephalidae), *Hemidactylus* (Gekkonidae), *Heliobolus*, *Latastia*, *Pseuderemias* (Lacertidae), *Uromastix*, *Xenagama* (Agamidae), *Echis* (Viperidae)

(Arillo et al. 1965; Lanza 1990; Zimkus and Larson 2011; Wagner et al. 2013; Tamar et al. 2018; Spawls and Branch 2020; Šmíd et al. 2020; Spawls et al. 2023).

Discussion

Sand Snakes represent an important element of the snake fauna of Africa and Asia. Their diurnal habits, active foraging for prey and a relatively large size make them conspicuous and frequently encountered by naturalists (e.g., 2008 observations on iNaturalist as of April 27, 2023). This may be the reason why tissue samples are not that difficult to obtain for genetic analyses and why our understanding of their phylogenetic relationships is fairly complete, at least from the taxon sampling perspective. Of the 33 currently recognized species (Wallach et al. 2014; Uetz et al. 2023), 30 have been placed in the phylogenetic context. The phylogenetic studies have not only untangled the evolutionary history of the genus, but also identified several distinct genetic lineages that may represent yet undescribed species (Kelly et al. 2008; Branch et al. 2019; Chen et al. 2021; Keates 2021; Kurniawan et al. 2021; Taft et al. 2022). Coincidentally, samples of all these undescribed species came from the Horn of Africa and the nearest adjacent regions, suggesting that the fauna of this forsaken region is still overlooked and that it needs further attention of researchers.

This study is the first to target the Sand Snakes of the Horn of Africa specifically. We analyze 14 newly obtained samples of six species and provide new insights into their distribution, genetic variability, and taxonomy. The phylogenetic reconstruction of the broader relationships between the *Psammophis* species confirmed previous findings (Kelly et al. 2008; Branch et al. 2019; Chen et al. 2021; Keates 2021; Taft et al. 2022), which is not surprising given their largely overlapping genetic data

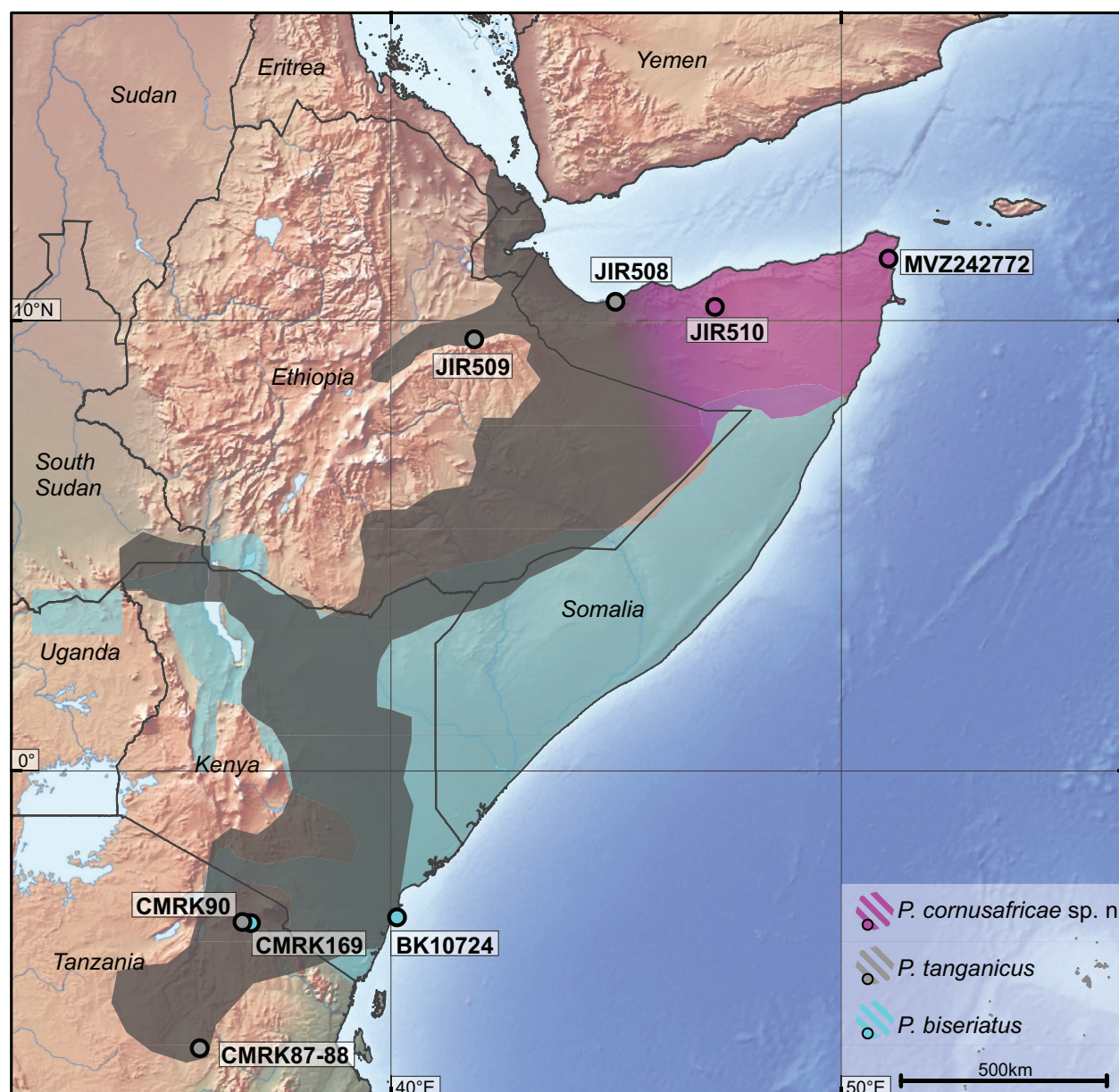


Figure 8. Distribution of *P. biseriatus*, *P. tanganicus* and *P. cornusafricae* sp. nov. in the Horn of Africa. Localities sampled for the genetic analysis are shown along with sample codes. The background layer shows shaded relief and water bodies and drainages and was made with Natural Earth (www.naturalearthdata.com). The species range maps were derived from Roll et al. (2017, 2021), Spawls et al. (2023), and the findings presented in this study.

matrices. The general structure of the tree and its potential implications for evolutionary origins of the genus are not new findings and we will not comment on them here. We will rather focus on the individual species analyzed by us, their intraspecific variation, closest phylogenetic relationships, and novel findings on their distribution.

The description of *P. cornusafricae* sp. nov. adds one more species to the list of snakes endemic to Puntland and eastern Somaliland (e.g., *Platycephalus brevis* and *P. messanai* (Schätti and Lanza 1989; Schätti and Charvet 2003), *Spalerosophis josephscortecii* (Lanza 1964), *Telescopus pulcher* (Mazuch et al. 2018), *Echis hughesi* (Cherlin 1990; Spawls et al. 2023), *Rhinotyphlops leucocephalus* (Roux-Estève 1974)). When first analyzed by Vidal et

al. (2008), the phylogenetic relationships of this, at that time undescribed, species could not be inferred with certainty because there were only nine *Psammophis* species included in their study. Only more recent studies with a broader sampling of taxa enabled the identification of its closest relatives – *P. tanganicus* and *P. biseriatus*. *Psammophis tanganicus* has consistently been recovered as a sister species to *P. cornusafricae* sp. nov. (Trape et al. 2019; Keates 2021; this study). Precise delineation of the distribution ranges of *P. tanganicus* and *P. cornusafricae* sp. nov. and their potential contact zone is difficult to make at this point. The two closest confirmed localities of both species are in Somaliland and about 240 km apart. We assume the ranges of the two species meet some-

where in central Somaliland as observed in other taxa (see the Distribution section above). Ideally, other specimens from across Somaliland and Puntland that are deposited in herpetology collections worldwide and either catalogued as *P. tanganicus* or *P. biseriatus* (e.g., CAS, NHMUK, presumably MSNG, MZUF, UniMoRe; Calabresi 1927; Scortecci 1939b; Regnoli et al. 2003) and which were unfortunately not available to us should be examined to assess the distribution limits of both species. The new samples of *P. tanganicus* from Ethiopia and Somalia are slightly genetically different from those from Tanzania, which indicates that there is some level of intraspecific variation across its range. This genetic differentiation is, however, not mirrored by the morphological variation as the specimens from the northern part of the distribution are morphologically identical to other *P. tanganicus* populations from other parts of its range, including the holotype (MCZ R-30380) from central Tanzania.

Besides the description of the new species we also analyzed new specimens of other Horn taxa to shed light on their diversity and distributions. The two newly analyzed samples of *P. rukwae* from Ethiopia and Eritrea cluster with other samples of the species from Chad and Kenya. This broadly distributed species ranges from Senegal in the West through the Sahel to East Africa (Trape and Mané 2006; Spawls et al. 2018). *Psammophis rukwae* has only been confirmed recently from Ethiopia (Trape et al. 2019), and there are no records yet from Eritrea (Largen and Spawls 2010). The genotyped sample from Eritrea presented here is thus the first record of *P. rukwae* for the country.

The existence of the cryptic species referred to as *P. cf. sudanensis* that morphologically resembles *P. sudanensis* is well established (Trape et al. 2019; Keates 2021; Taft et al. 2022). Quite surprisingly, the two species are not closely related. While the real *P. sudanensis* forms a clade with *P. sibilans* and an undescribed species from Ethiopia (termed '*P. sp. Ethiopia*'), *P. cf. sudanensis* clusters with the East African *P. orientalis* and *P. subtaeniatus* from southern Africa. The new sample from Ethiopia included here that we originally identified as *P. sudanensis*, and which in fact turned out to belong to *P. cf. sudanensis*, proves that the two species are indeed phenotypically similar. Until detailed examinations of specimens of both species are carried out, and a formal description of the cryptic species is presented together with a differential diagnosis, it seems impossible to distinguish them without having to use DNA genotyping. We refrained from attempting to sort out the taxonomy of *P. cf. sudanensis* here due to the lack of comparative material.

The species with the most newly analyzed samples was *P. aegyptius*. The new samples from Egypt and Sudan are genetically very similar to other conspecific samples from the same region. The four samples from Somaliland, on the other hand, show marked genetic differences from the North African samples, as well as within themselves. The range of *P. aegyptius* covers the eastern part of the Sahara and has until now not been known to occur this far south (Largen and Spawls 2010; Geniez 2018). The new

localities from Somaliland thus present a considerable range extension for the species.

Lastly, the sample of *P. punctulatus punctulatus* included in our analysis is the first of the taxon to have been analyzed. Previous material of the species belonged to the subspecies *P. p. trivirgatus* (Kelly et al. 2008) and the two taxa cluster together in the phylogeny. *Psammophis p. punctulatus* extends from southeastern Egypt to the extreme northwest of Somaliland; *P. p. trivirgatus* is distributed from northern Somaliland to Uganda, South Sudan (Ilemi Triangle) and Tanzania (Largen and Rasmussen 1993; Spawls et al. 2023). The two taxa show considerable and stable morphological differences, with *P. p. trivirgatus* having a lower number of subcaudals than *P. p. punctulatus* (143–163 in the former and 158–178 in the latter) and a bright orange head and three black dorsal stripes, compared to a grey head and one dorsal stripe in the latter (Fig. 2a, b). On the basis of their apparently partially overlapping ranges Lanza (1990) concluded that they represent different species. Based on the evidence of profound genetic diversification between the two taxa laid out here, in combination with the above mentioned morphological and geographical differences between them we follow Lanza's (1990) conclusion and recognize them as two distinct species, *Psammophis punctulatus* Duméril, Bibron & Duméril, 1854 and *Psammophis trivirgatus* Peters, 1878.

Sand Snakes rank among the most studied African snakes from the phylogenetic perspective. Yet, as evidenced by the number of cryptic or undescribed species, we are still far from fully comprehending their diversity. With the currently available sampling it is obvious that East Africa, and the Horn of Africa in particular, supports the highest diversity of undescribed species of *Psammophis*. Once their taxonomy is resolved, the diversity in the Horn may surpass that of the currently richest hotspot of the genus in southern Africa.

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Supplementary material 1

List of *Psammophis* species and samples included in the phylogenetic analysis

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Data type: Genetic data matrix

Explanation note: List of *Psammophis* species and samples included in the phylogenetic analysis, with their sample/voucher number, country and locality of origin (datum WGS84), GenBank accession numbers, MorphoBank accessions (MorphoBank Project No. 4527), and original reference. Samples newly sequenced for this study are in bold. The GPS coordinates of *P. tanzanicus* from Tanzania that are marked with asterisks are only approximate.

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