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# Two new species of *Hemidactylus* Goldfuss, 1820 (Squamata: Gekkonidae) from the coastal areas of northern Somaliland

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The taxonomy of many *Hemidactylus* geckos from the Horn of Africa has recently been evaluated. However, the lack of fresh material for some species and also regions has led to the misidentification of some taxa and an underestimation of the true diversity in others. In this study we analyse new material of *Hemidactylus* collected from poorly known coastal areas of northern Somaliland. Our results support the existence of two yet undescribed species within the arid clade. One of the new species is small-sized and closely related to *H. afarensis* from the Afar Triangle in Ethiopia, and together with two other species (*H. foudaii, H. sinaitus*) forms the monophyletic group for which we propose here the name *sinaitus* species group. The other new species is medium to large-sized, known from only one locality, and belongs to the *macropholis* species group, where it is a sister species of *H. macropholis*. Both new endemic species from the northern coastal hyper-arid plains highlight the role of northern Somaliland as an important biodiversity hotspot. Furthermore, our results show pronounced genetic diversity within *H. macropholis*, and imply possible existence of cryptic taxa within the species. *Hemidactylus arnoldi* and *H. tropidolepis* have, for the first time, been sequenced and placed in a phylogenetic context in this study. Our results confirm that *H. tropidolepis* is nested within the African radiation and is most closely related to *H. funaiolii*. *Hemidactylus arnoldi* clustered within the Arabian radiation of *Hemidactylus* and it was recovered as a sister lineage to all other species of the radiation.

Keywords: Gekkota, Horn of Africa, lizards, morphology, reptiles, Somalia, taxonomy

Supplementary material: available online at https://doi.org/10.1080/15627020.2024.2376119

#### Zoobank registrations:

This article is registered in ZooBank under: https://zoobank.org/E2BECE23-F643-42AA-93B9-119C5469137D. These species are registered in ZooBank under: *Hemidactylus gubanensis*: https://zoobank.org/898FE504-7C3C-44AB-ADA7-691DD3FFC39F

Hemidactylus huluul: https://zoobank.org/A4ED38CF-B0BD-4197-A05B-F2789C028442

#### Introduction

The Horn of Africa (HoA), also known as the Somali Peninsula, is the easternmost projection of the African continent and is composed of Ethiopia, Eritrea, Djibouti, Kenya and Somalia. Although Somalia is officially recognised as a country, it is de facto divided into three different geo-political regions with independent governments (Bradbury 2008; Hoehne 2015). After the collapse of the former Somali Democratic Republic in 1991 and the onset of the Somali Civil War, the northern territory that was formerly a UK crown colony of British Somaliland declared independence and modern Somaliland was established (Supplementary Figure S1; Bradbury 2008; Mire 2008). The territories east of Somaliland declared their autonomy in 1998 as an autonomous state of Puntland (Mesfin 2009), and this is currently defined as a Federal Member State of the Republic of Somalia. The state of Somaliland, although unrecognised as an independent country by the United Nations, has been politically stable in contrast to the volatile Southern Somalia (Mire 2008; Jhazbhay 2009; Prunier 2021). It lies south of the Gulf of Aden, east of the Ethiopian highlands, north of the Somali Region of Ethiopia and west of Puntland. It is a geomorphologically complex country composed of three main geomorphological features (Supplementary Figure S1): Guban coastal plains; Ogo, mountainous areas south of Guban that reach up to 2 460 m in elevation; and the Haud, a flat plateau further south (Parker 1942; Pickering and Awale 2018). The geographic isolation of Somaliland from the regions adjacent to it — by the Gulf of Aden from the north, the high and vast Ethiopian Mountains from the west, and Puntland with the Indian Ocean from the east — has influenced the biogeography of plant and animal species that show a high degree of biodiversity endemism in the region (Balletto 1968; Burgess et al. 2004; Mittermeier et al. 2004; Friis et al. 2005; Lewin et al. 2016).

The first travelers, explorers and naturalists that explored the HoA accessed the region through important ports of Somaliland (Zeila, Berbera, Las Khorey). Thanks to these pioneer explorers, among which were Luigi Briccheti Robecchi, Vittorio Bottego, George Wyman Bury, Arthur Donaldson Smith, Carlo von Erlanger, Ethelbert Edward Lort-Phillips, Oscar Neumann, Georges Révoil, Eugenio Ruspoli and John Hanning Speke, Somaliland was fairly well studied in the first half of the 20th century, at least from a herpetological point of view (e.g. Vaillant 1882; Boulenger 1891, 1895a,b,c, 1898, 1901; Boettger 1893; Tornier 1905; Parker 1930, 1932, 1935, 1942, 1949).

Although our knowledge of the entire African herpetofauna has increased rapidly over the past years (Lewin et al. 2016; Tolley et al. 2016), recent studies that focus specifically on the Somaliland reptiles show that many groups remain largely understudied (Lanza and Nistri 2005; Wagner et al. 2013a,b; Petzold et al. 2014; Šmíd et al. 2015, 2020, 2023a; Mazuch et al. 2016, 2018; Bates and Broadley 2018; Burriel-Carranza et al. 2023). In addition, the entire territory of the HoA ranks among the least sampled regions of the world from a genetic perspective (Šmíd 2022).

The gecko genus Hemidactylus Goldfuss, 1820 is among the most diverse squamate taxa in Somaliland (Lanza 1990; Spawls et al. 2023; own unpublished data). With its currently recognised ~192 species (Uetz et al. 2024), Hemidactylus is the third-most speciesrich gecko genus globally and approximately half of this diversity is known from the African continent (Ceríaco et al. 2021; Uetz et al. 2024). The African and Arabian clades of the Hemidactylus geckos have been witnessing a species-description boom within the last decade (Sindaco et al. 2007. 2009: Busais and Joger 2011: Carranza and Arnold 2012; Šmíd et al. 2013b, 2015, 2017, 2020, 2023b; Malonza and Bauer 2014; Vasconcelos and Carranza 2014; Safaei-Mahroo et al. 2017). Adapted to semi-desert and dry savanna, these nocturnal geckos are represented in Somaliland by 20 currently described species, two of which are endemic (Lanza 1990; Šmíd et al. 2020; Spawls et al. 2023).

Hemidactylus is phylogenetically partitioned into four mostly allopatric clades (Carranza and Arnold 2006). Seventeen out of the twenty species that occur in Somaliland belong to the so-called arid clade (Smíd et al. 2013a. 2020). This clade is partitioned into three radiations: African, Arabian and Socotran (Garcia-Porta et al. 2016; Šmíd et al. 2020), which are further divided into several groups or subclades of closely related species (Busais and Joger 2011; Carranza and Arnold 2012; Šmíd et al. 2013a,b, 2015, 2017, 2020; Vasconcelos and Carranza 2014). All species of the African radiation are strictly African in their distribution (only H. sinaitus Boulenger, 1885 has an isolated population in Arabia, Figure 1); whilst the large Arabian radiation contains species that colonised Africa from Arabia and then radiated out (Šmíd et al. 2013a). The two radiations also differ in the ecology of their respective species. The African radiation comprises mostly small, ground-dwelling species with small adhesive lamellae (Šmíd et al. 2020), while the African species of the Arabian radiation are generally larger and better climbers, reflected in their relatively larger sized adhesive pads.

Within the Arabian radiation, Šmíd et al. (2017) delimited the so-called *yerburii* species group that includes *H. jumailiae* Busais & Joger, 2011; *H. montanus* Busais & Joger, 2011, *H. yerburii* Anderson, 1895 from Arabia; and *H. barodanus* Boulenger, 1901, *H. granchii* Lanza, 1978, *H. macropholis* Boulenger, 1896, and *H. pauciporosus* Lanza, 1978 from Africa. In this study, we focus on the African species of the *yerburii* group, which we for clarity refer to as the *macropholis* species group. They are mostly widespread in Somaliland, and preliminary morphological examinations have revealed that some show pronounced morphological differentiation across their ranges, possibly indicating the presence of species complexes (own unpublished data).

In this study, we analysed new material of *Hemidactylus* geckos obtained during four field trips in 2021–2023 to the coastal zones of northern Somaliland and to Djibouti in 2019. As a part of our ongoing project on the diversity of reptile and amphibian species of Somaliland, conducted in collaboration with Amoud University, Boorama, Somaliland, we surveyed some poorly visited and understudied areas in the coastal areas of the country that had previously been overlooked and which may potentially harbour some new species. We conducted a multilocus genetic analysis of two mitochondrial and four nuclear markers and examined morphological traits to compare the new specimens with previously available data.

#### Material and methods

#### Specimen collection

Fieldwork was conducted as part of a long-term project studying reptiles and amphibians in Somaliland, supported by the Ministry of Environment & Climate Change (MoECC) and Amoud University. Three field trips were completed in October 2021, January 2022 and November 2023. A total of 26 new Hemidactylus tissue samples and voucher specimens were collected for this study. Other comparative material was collected during previous field trips to Somaliland conducted by the first and the penultimate author between 2015-2019. A voucher specimen and tissue sample of H. arnoldi Lanza, 1978 from Djibouti was collected by AN during a survey carried out in 2019 by the Natural History Museum and the Department of Biology of the University of Florence (Italy). Genetic and morphological data for additional specimens and species were taken from previously published works (Lanza 1978; Loveridge 1947; Mazuch et al. 2016; Šmíd et al. 2017, 2020; Sindaco et al. 2009; Spawls et al. 2023).

The material used in this study is deposited in the following collections: CAS (California Academy of Sciences, San Francisco, USA), MNHN (Muséum National d'Histoire Naturelle, Paris, France), MSNG (Museo Civico di Storia Naturale «Giacomo Doria», Genova, Italy), MSNM (Museo Civico di Storia Naturale di Milano, Milano, Italy), MZUF



**Figure 1:** Geographic distribution of species of the *sinaitus* and *macropholis* groups of *Hemidactylus* in eastern Africa. Circles show localities of specimens used in the genetic analysis, morphological analysis or both, or published in Šmíd et al. (2020). The phylogeny to the left shows the position of the two groups in the arid clade of *Hemidactylus* and is similar to the tree detailed in Figure 2. The easternmost locality of *H. gubanensis* sp. nov. that is marked with a question mark in the map refers to a specimen only tentatively assigned to this species whose status needs to be confirmed

(Università di Firenze, Museo Zoologico «La Specola», Firenze, Italy), NHMUK (formerly BMNH; Natural History Museum, London, UK), NMP-P6V (National Museum Prague, Czech Republic), and TMHC (Tomas Mazuch private herpetological collection, Dříteč, Czech Republic).

# Material for phylogenetic analyses

For the phylogenetic analyses, we compiled a dataset of the 'arid' clade of *Hemidactylus* (Carranza and Arnold 2006) that comprises three main radiations: African, Arabian and Socotran.

The dataset contained 58 described species, two putative species from Ethiopia discovered in a previous study (Šmíd et al. 2023b; tentatively labeled *H.* sp. Etio2 and *H.* sp. Etio3), and two putative species from Somaliland that are the aim of this study. Most species were represented by one sample each; however, the putative species from Somaliland and their closely related taxa were sampled more thoroughly. The two intensively sampled groups were (1) the *sinaitus* group that contains *H. sinaitus*; *H. afarensis* Šmíd et al., 2020; *H. foudaii* Baha El Din, 2003; and one of the putative species, and (2) the *macropholis* group that contains *H. macropholis*; *H. barodanus*; *H. granchii*; *H. pauciporosus*; and the other putative species. Sampled localities of these species are shown in Figure 1. It should be mentioned that the *macropholis* group is

encompassed within the *yerburii* group as defined by Šmíd et al. (2017), which besides the above-listed species also includes *H. yerburii*, *H. montanus*, and *H. jumailiae* from the Arabian Peninsula.

In addition, included in the genetic analysis of *H. arnoldi* and *H. tropidolepis* Mocquard, 1888 were species that have not yet been placed in phylogenetic context. The tree was rooted with *H. flaviviridis* Rüppell, 1835; *H. mabouia* (Moreau de Jonnès, 1818), *H. ruspolii* Boulenger, 1896; *H. angulatus* Hallowell, 1854; and *H. platycephalus* Peters, 1854; that have been repeatedly shown to not belong to the *Hemidactylus* arid clade (e.g. Pyron et al. 2013; Zheng and Wiens 2016).

## Genetic data acquisition

New DNA sequence data for 23 recently collected samples belonging to eight species (Supplementary Tables S1,S2) were generated. Genomic DNA was extracted from ethanol-preserved tissue samples using Qiagen Blood and Tissue kit. We PCR-amplified two mitochondrial markers: 12SrRNA (12S, ~390 base pairs [bp]) and cytochrome b (cytb, up to 1137 bp) and four nuclear markers: the oocyte maturation factor MOS (cmos, 403 bp), melanocortin 1 receptor (mc1r, 668 bp), and recombination activating genes 1 and 2 (rag1, 1023 bp; rag2, 410 bp). Primers and PCR conditions are detailed in Šmíd et al. (2013a).

Of particular importance is the inclusion of paratype specimens of *H. pauciporosus* in the genetic analysis. We took muscle tissue samples of five out of 113 paratypes deposited in the MZUF collection that were collected in 1973 during an Italian expedition to Somalia ('Spedizione Biologica in Somalia del Centro di Studio per la Faunistica ed Ecologia Tropicali del C.N.R.'). DNA from these museum specimens was extracted using Invisorb Spin Forensic Kit (STRATEC) and concentrations were measured on a Qubit 1.0 fluorometer (Thermo Fisher Scientific). Using Illumina sequencing, we targeted a 148 bp-long fragment of the cytb gene using a modified mini-barcoding protocol (Galan et al. 2012). Library preparation included a three-step PCR; the first is a standard PCR, the second with modified primers uses the products of the first PCR as a template, and the third, the primers includes Illumina adaptors. Methodological details, primer combinations, PCR conditions and post-processing data treatment may be found in Šmíd et al. (2021).

Some phylogenetic studies on Hemidactylus (including this study) targeted a cytb fragment of 307 bp that does not overlap with the 148 bp generated for the H. pauciporosus paratypes. Therefore, to be able to infer the position of the paratypes within the *macropholis* group for the recently collected samples, we amplified the entire cytb gene with primers L14910 and H16064 (Burbrink et al. 2000; for PCR conditions see Šmíd et al. 2013a). When the complete cytb gene did not amplify, we targeted the same 148 bp fragment that was sequenced for the H. pauciporosus paratypes with primers L15411 and H15553 (Šmíd et al. 2021; PCR conditions: 94 °C for 15 min, followed by 25 cycles of 94 °C for 30 sec, 45 °C for 45 sec, 72 °C for 30 sec, with a final extension at 72 °C for 10 min). Thus, we achieved a complete sequence overlap for the recent and museum specimens.

The PCR products of the recent material were bidirectionally Sanger sequenced at Macrogen (Amsterdam, the Netherlands). Raw sequence data were edited and contigs were assembled in Geneious Prime 2023.2.1 (Kearse et al. 2012). Each gene was aligned independently using MAFFT (Katoh et al. 2019) using the auto strategy for all markers except the 12S, which was aligned with the Q-INS-i option that considers the secondary structure of the RNA. The 12S alignment contained regions that were difficult to align with confidence. The alignment was therefore treated with Gblocks (Castresana 2000) to remove these poorly aligned regions with gaps and ragged ends. Sequences of cytb were translated to amino acids and no stop codons were found, suggesting that no nuclear mitochondrial pseudogenes were amplified. Heterozygous positions in the nuclear markers were coded using the IUPAC ambiguity codes.

#### Phylogenetic analyses

We reconstructed the phylogenetic relationships at two different levels with two different datasets. Dataset 1 was a concatenation of all genes and contained all *Hemidactylus* species and specimens listed above except for the *H. pauciporosus* paratypes. Its total length was 3974 bp. We inferred the phylogeny using Maximum Likelihood (ML) and Bayesian Inference (BI). For the ML analysis,

we used IQTREE v. 1.6 (Nguyen et al. 2015) through its web interface (Trifinopoulos et al. 2016). The dataset was partitioned by gene and the best substitution models were selected automatically for each partition. Branch support was assessed with the Shimodaira-Hasegawalike approximate likelihood ratio test (SH-aLRT; Guindon et al. 2010) and the ultrafast bootstrap (UFBoot2; Hoang et al. 2018), both with 1 000 replicates.

The BI was run in MrBayes 3.2 (Ronquist et al. 2012). The dataset was again partitioned by gene and the best nucleotide substitution models were identified by PartitionFinder 1.1 (Lanfear et al. 2012). The best fitting models were: GTR+I+G for the 12S, cytb, mc1r, and rag2 genes; HKY+I+G for cmos; GTR+G for rag1. Character state frequencies, GTR substitution rates and Gamma shape parameters were unlinked across partitions. We did not include the + I parameter as it was substituted by the exponentially distributed + G. The analysis ran in three independent runs for 25 million generations. Posterior trees and parameter values were sampled every 5 000 generations. Stationarity was determined by the sequentially calculated standard deviations of the split frequencies being lower than 0.01. We used Tracer v.1.6 (Rambaut and Drummond 2007) to ensure that the runs had converged and mixed well, and to check the effective sample size of all estimated parameters. Instead of generating a consensus tree, which MrBayes does customarily, we used LogCombiner from the BEAST package (Rambaut and Drummond 2007) to remove the first 10% of trees as burnin, combined the output tree files, and then we used TreeAnnotator (also from the BEAST package) to identify the maximum clade credibility tree in the set of posterior trees.

Dataset 2 represented the 148 bp fragment of the cytb gene. It included species from the *macropholis* group for which this genetic region was available (*H. granchii*, *H. pauciporosus* including the MZUF paratypes, two of the three lineages of *H. macropholis*, and the putative species from Somaliland that clusters within this clade; see Results below). For this dataset, we constructed the haplotype network using the TCS algorithm (Clement et al. 2002) implemented in PopART (Leigh and Bryant 2015).

We also reconstructed allele networks for the four nuclear markers analysed to visualise the relationships between the studied *Hemidactylus* species at the level of individual nuclear markers. The alignments of the nuclear genes were phased for this analysis to resolve the heterozygous positions. We used SeqPHASE (Flot 2010) to prepare the data files and PHASE 2.1 (Stephens et al. 2001) to reconstruct the haplotypes. The phase probability threshold was set to 0.7 (Harrigan et al. 2008). The networks were also constructed in PopART.

#### Morphological data

New morphological data for 118 specimens were collected for the following species: *H. afarensis* (24 specimens), *H. barodanus* (15 specimens), *H. foudaii* (5 specimens), *H. granchii* (11 specimens), *H. macropholis* (18 specimens), *H. pauciporosus* (4 specimens), *H. sinaitus* (13 specimens) and the two putative species from Somaliland described herein (19 and 9 specimens, respectively). These data were complemented by measurements and scale counts that were published in earlier taxonomic studies on the genus (Lanza 1978; Šmíd et al. 2020). All measurements were taken by the same person (TM; except data taken from Lanza 1978). Completely new data are presented here for 49 specimens. Name-bearing type specimens were examined for all the studied species. except for *H. sinaitus*, for which only photographs of the holotype were available. For all newly studied specimens, we took high-resolution pictures, either in the field or after preservation. All photographs are publically available for downloading at MorphoBank (https://morphobank.org; Project number 5069; a total of 1 247 photographs). Photographs of most other specimens can be found in the same repository under the following project numbers: Project 3398 (H. afarensis, H. foudaii, H. sinaitus; Šmíd et al. 2020), Project 1069 (H. granchii; Šmíd et al. 2014) and Project 2227 (H. pauciporosus; Šmíd et al. 2017). MorphoBank accession numbers for each specimen are provided in Supplementary Table 1.

We scored the following metric and meristic characters for each specimen: snout-vent length (SVL; from the tip of snout to vent); tail length (TL; from vent to tip of original tail); head length (HL; from the tip of snout to retroarticular process of the jaw); head width (HW; at the widest part of the head); head depth (HD; maximum depth of head); horizontal eye diameter (EYE); axilla-groin distance (AG; distance from the insertion of the front limb to the insertion of the hind limb); number of infralabials (INF) and supralabials (SUP); number of nasals (NAS); contact of uppermost nasals (NASCON; none [0], point [1], broad [2]); number of internasal granulars (ING); contact of 1st supralabial with nostril (SUPNOS; broadly touching [0], barely touching [1], none - barely excluded [2], none - largely excluded [3]); number of infralabials in contact with anterior postmentals (MENINF); contact of anterior postmentals (MENCON; none [0], point [1], broad [2]): number of longitudinal rows of enlarged dorsal tubercles (TUBERCOUNT); number of small scales between enlarged dorsal tubercles, counted longitudinally (DORGRLONG) and transversely (DORGRTR); number of precloacal pores in males (PORES); number of lamellae under the 1st (FINGER1) and 4th finger (FINGER4); number of lamellae under the 1st (TOE1) and 4th toe (TOE4); ratio between the length of free distal phalanges of the 3rd toe and the proximal part of the toe (FDP/3TF; free distal phalanges were measured without claws, proximal part was measured from first distal lamella to the toe insertion); number of transverse rows of small scales separating 3rd and 4th ring of enlarged scales on the tail (WHORL); presence of enlarged subcaudal scales (SUBCAU; uniform [0], enlarged [1]). Except for minor modifications, the terminology and diagnostic characters follow Šmíd et al. (2020, 2023b). We used a digital caliper and dissecting microscope to take the measurements and scale counts. Original metric and meristic data are given in Supplementary Table S3.

The morphological data were used for comparisons between the recognised species and the putatively new species from the Guban coastal plain of Somaliland.

#### Results

#### Phylogenetic analyses

Both ML and BI analyses of Dataset 1 produced concordant topologies that differed only in a minority of nodes (Figure 2). General phylogeny could be matches that were recovered in previous studies (Šmíd et al. 2013a, 2020), with the new species added in this paper representing new branches in the tree.

Samples from coastal Somaliland, preliminarily identified in the field as *H.* cf. *afarensis*, clustered within the *sinaitus* group which was well supported (SH-aLRT support: 100/ UFBoot support: 100/ Bayesian posterior probability: 1.0; support values are given in the same order hereafter) and is part of the African radiation of *Hemidactylus*. Within this group, *H. foudaii* was basal to the remaining species (support 99.3/100/1.0), and then *H. sinaitus* was sister to the species pair *H. afarensis* and the new species described below (support 95.5/99/1.0). *Hemidactylus afarensis* forms two sister clades, one from northern Ethiopia (samples JS288, JS289; support 99.3/100/1.0), the other from central Ethiopia (samples JS216, JS217, JS230–233, JS351; support 98.3/88/1.0).

All samples from the village of Huluul in central Somaliland clustered within the macropholis group of Hemidactylus (group monophyly support 89.9/98/0.98), which belongs to the Arabian radiation of the genus. The relationships within the group differ slightly between the ML and BI analysis; however, in both of them H. macropholis was represented by three deeply divergent lineages. In the ML tree, one H. macropholis lineage from Kenya was in a sister clade to H. barodanus (support 88.8/73/ node not recovered in the BI analysis), and this clade was sister to the rest of the species of the macropholis group (support 95.2/74/ node not recovered in the BI analysis). These remaining species formed two sister lineages, one of H. pauciporosus and H. granchii (support 97.4/100/1.0), the other of the two H. macropholis lineages (one from southern Ethiopia, one from eastern Ethiopia and Somaliland) as sister clades (support 94.7/98/0.99), and the species from Huluul (support 95.9/76/ node not recovered in the BI analysis). The topology of the BI analysis differed in that all three H. macropholis lineages clustered together; however, the support for them being a clade was low (posterior probability: 0.60).

*Hemidactylus tropidolepis*, one of the two species included in the phylogeny for the first time here, clustered within the African radiation of *Hemidactylus* where it was sister to *H. funaiolii* Lanza, 1978 (support 87.8/98/0.99). The other species sequenced for the first time, *H. arnoldi*, belonged to the Arabian radiation of *Hemidactylus* where it formed a distinct branch that was sister to all the other species of that radiation (support 89.8/81/1.0).

The haplotype network constructed for the short fragment of cytb (Dataset 2; Figure 2) showed that two of the five analysed paratypes of *H. pauciporosus* (MZUF 6284, MZUF 6318) were identical in the cytb sequence to sample CAS 227511, and were only one substitution different from the other three paratypes (MZUF 6260, MZUF 6282, MZUF 6313). All species in the network represented well-isolated clusters that were separated from each other by 11–21

		sinaitus species	s group			macri	opholis species group		
Species (specimens examined)	H. gubanensis sp. nov.	H. afarensis	H. foudaii	H. sinaitus	H. huluul sp. nov.	H. macropholis	H. barodanus	H. granchii	H. pauciporosus
	( <i>n</i> = 19)	(n = 24)	(n = 5)	( <i>n</i> = 13)	(n = 9)	( <i>n</i> = 18)	( <i>n</i> = 15)	( <i>n</i> = 11)	( <i>n</i> = 4)
SVL (mm)	46 ± 4.3	42.7 ± 4.9	$41.5 \pm 5.4$	46.1 ± 5.0	56.2 ± 11.3	59.4 ± 12.6	61.2 ± 9.5	57.0 ± 4.8	58.5 ± 1.6
	(36.5–53.3)	(32.4–49.3)	(34.9–48.7)	(36.4–53.8)	(41.9–76.2)	(44.1–82.2)	(44.0–78.0)	(47.7–64.0)	(57.1–61)
Infralabials	$6.7 \pm 0.6$	7.1 ± 0.6	$6.8 \pm 0.7$	$7.0 \pm 0.6$	$7.9 \pm 0.5$	$7.1 \pm 0.5$	$7.9 \pm 0.4$	7.7 ± 1.0	$8.1 \pm 0.6$
	(6—8)	(6–9)	(6–8)	(6–8)	(62)	(8–8)	(26)	(69)	(6-2)
Supralabials	$8.5 \pm 0.6$	$8.5 \pm 0.7$	$8.5 \pm 0.9$	$8.3 \pm 0.8$	$11.2 \pm 0.4$	$9.9 \pm 0.6$	$10.5 \pm 0.4$	$10.3 \pm 1.1$	$11.6 \pm 0.5$
	(7–10)	(7–10)	(7–10)	(7–10)	(11–12)	(9–11)	(9–12)	(9–12)	(11–12)
Contact of uppermost nasals	Wide	Wide	Wide	Wide	Wide (in 56 %) /none	Wide (in 50 %) /none	Wide (in 50 %) /none	None	Usually none (in 63 %)
Contact of 1 <sup>st</sup> supralabial with nostril	Yes	NA	AN	NA	Yes (in 89 %)	Yes (in 97 %)	Yes	No	No
Number of infralabials in contact with anterior postmentals	1 (in 18 %) or 2	2	7	1 (in 38 %) or 2	Mostly 1 (in 78 %)	Mostly 1 (in 81 %)	1 (in 27 %) or 2	Usually 2 (in 86 %)	2
Rows of dorsal tubercles	149+10	165+11	14 4 + 0 R	152+10	144+08	144+11	14 8 + 1 0	143+11	133+00
	(14–16)	(14–18)	(14–16)	(14–16)	(14–16)	(12–16)	(13-16)	(12–16)	(12–14)
Dorsal tubercle shape	Conical	Conical	Subtrihedral	Conical	Trihedral	Subtrihedral / trihedral	Subtrihedral	Subtrihedral	Subtrihedral
DORGRLONG	$4.5 \pm 0.8$ (3-6)	$1.9 \pm 0.4$ (1.5-3)	$1.8 \pm 0.2$ (1.5-2)	3.3 ± 0.5 (2.5–4)	4.9 ± 0.5 (4−6)	$3.1 \pm 0.7$ (2-4)	$3.5 \pm 0.5$ (3-4)	3.0 ± 0.5 (2–4)	3.6 ± 0.8 (3−4)
DORGRTR	28+03	1 2 + 0 3	1 7 + 0 4	20+01	27+03	2 + 0 2	29+03	25+05	26+04
	(2-3)	(1-2)	(1-2)	(1.5–2)	(2-3)	(1-3)	(2.5–3.5)	(2-3)	(2-3)
Dorsal body	Indistinct	Six to seven	Eight to nine	Indistinct dark	Beige-brownish to	Mostly pinkish	Variable,	Yellowish-brown	Yellowish-brown
colour pattern	dark mottling	dark wide	dark narrow	mottling	grey with	orange to red, with	brownish-grey to	with four, darker	with four, darker
		transverse	transverse		four, irregular,	dark mottling or four	creamy-yellow, with	indistinct	X-shaped
		bands	bands		X-shaped	indistinct X-shaped	darker X-shaped	X-shaped	markings
Precloacal pores	$5.8 \pm 1.2$	$4.3 \pm 0.7$	$8.3 \pm 0.5$	$5 \pm 1.4$	$12 \pm 1.4$	8.1 ± 2.6	$8.5 \pm 0.8$	$5.8 \pm 1.1$	$6 \pm 1.0$
	(4-7)	(46)	(8–9)	(4-7)	(10–14)	(6–13)	(8-10)	(58)	(2-7)
Lamellae 1 <sup>st</sup> finger	$5.7 \pm 0.5$	$6.4 \pm 0.6$	$6.7 \pm 0.5$	$6.9 \pm 1.2$	8.0 ± 0.0	$9.0 \pm 1.0$	$7.7 \pm 0.5$	$7.1 \pm 0.6$	$7.3 \pm 0.5$
	(56)	(58)	(6–7)	(29)	(8–8)	(7–10)	(7–8)	(8–8)	(7–8)
Lamellae 4 <sup>th</sup> finger	$7.6 \pm 0.5$	$8.0 \pm 0.4$	$8.2 \pm 0.4$	8.1 ± 0.7	$9.2 \pm 0.4$	$10.1 \pm 1.0$	$9.1 \pm 0.7$	$8.3 \pm 0.5$	$8.7 \pm 0.5$
	(7–8)	(22)	(8–9)	(26)	(9–10)	(8–11)	(8–11)	(8–9)	(8–9)
Lamellae 1 <sup>st</sup> toe	$5.7 \pm 0.5$	$6.2 \pm 0.6$	$6.1 \pm 0.5$	$6.0 \pm 0.6$	$7.1 \pm 0.2$	$8.4 \pm 1.0$	$6.9 \pm 0.4$	$6.8 \pm 0.7$	$6.2 \pm 0.4$
	(9–6)	(/	(/-q)	(4-1)	(81)	(7-10)	(9-9)	(69)	(1-9)
Lamellae 4 <sup>th</sup> toe	$9.4 \pm 0.8$	$10 \pm 0.8$	$10.2 \pm 0.4$	$10.2 \pm 0.5$	$10.5 \pm 0.6$	$11.6 \pm 1.2$	9.8 ± 0.7	$10.2 \pm 0.5$	$10 \pm 0.0$
	(8-11)	(8-11)	(11-01)	(9–11)	(11-4)	(41–01)	(8–11)	(11-8)	(10-10)
FDP/3TF	$0.45 \pm 0.05$ (0.35-0.57)	0.24 ± 0.047 (0.12–0.34)	0.21 ± 0.04 (0.14–0.28)	0.33 ± 0.03 (0.29–0.38)	0.33 ± 0.06 (0.21−0.42)	$0.37 \pm 0.09$ (0.26-0.54)	$0.3 \pm 0.07$ (0.2-0.45)	$0.31 \pm 0.05$ (0.23-0.38)	$0.3 \pm 0.03$ ( $0.24-0.31$ )
Tail shape	Cylindrical, scarcely	Cylindrical,	Cylindrical,	Cylindrical,	Conical, not flattened	Cylindrical, moderately	Carrot-shaped,	Cylindrical,	Cylindrical, depressed
	depressed	scarcely depressed	scarcely depressed	scarcely depressed		depressed	strongly depressed	moderately depressed	
Tail basal constriction	No	No	No	No	No	No	Yes	No	No
WHORL	$3.3 \pm 0.5$	$2.5 \pm 0.4$	$3.0 \pm 0.0$	$2.9 \pm 0.6$	$4.6 \pm 0.5$	$3.7 \pm 0.6$	$4.95 \pm 0.7$	$5.0 \pm 0.5$	$4.8 \pm 0.8$
	(2-4)	(2–3)	(3–3)	(24)	(4–5.5)	(3–5)	(4–6)	(4–6)	(4–5.5)
Enlarged subcaudals present	Yes	Yes	Yes	No	Yes	Yes	Yes	Yes	Yes



**Figure 2:** (a) Maximum likelihood phylogeny of the arid clade of *Hemidactylus* which is composed of the African, Socotran and Arabian radiations highlighted in orange. The *sinaitus* group, part of the African radiation, and the *macropholis* group, part of the Arabian radiation, are delimited with dashed lines. Branch support values are given in this order: SH-aLRT/UFBoot/Bayesian posterior probability. The colour of the branches leading to the species of the *sinaitus* and *macropholis* groups match those in Figures 1 and 3. The branches that indicate the phylogenetic position of *H. tropidolepis* and *H. arnoldi* sequenced for the first time in this study are in red. Note that *H. macropholis* group showing the position of the paratypes of *H. pauciporosus* collected in 1973, which confirm that specimen CAS227511 has been determined correctly; for discussion on the specimen identification see Šmíd et al. (2017)

nucleotide substitutions. *Hemidactylus macropholis*, that was in this analysis represented by two of the three lineages, showed deep genetic separation between the lineages (21 substitutions), congruently to the results of the ML and BI phylogenetic analyses.

The allele networks reconstructed for the nuclear markers showed that species from both the *sinaitus* and *macropholis* groups had unique alleles that are not

shared with the other species of their groups (Figure 3). Exceptions to this were the rag2 gene in the *sinaitus* group where *H. afarensis* shared one allele with the new species from this group, and the cmos gene in the *macropholis* group where multiple species including *H. granchii*, *H. pauciporosus*, the lineage of *H. macropholis* from eastern Ethiopia and Somaliland, and the new species from this group, shared a common allele. *Hemidactylus barodanus* 



**Figure 3:** Allele networks for the four nuclear loci analysed in this study. The networks were drawn separately for the *sinaitus* and *macropholis* groups. Circle sizes are proportional to the number of specimens sharing that allele, and colours match those in Figures 1 and 2. Short transverse bars on the connecting lines = the number of mutational steps between alleles

and the lineage of *H. macropholis* from southern Ethiopia had their own unique alleles each in the cmos network. However, these private alleles were only one nucleotide position different from the allele shared amongst the four species, indicating a slow evolution of this marker within this group. It should be noted that the third lineage of *H. macropholis* from Kenya was included only in the analysis of the rag2 gene because sequences of the other markers were not available for it at the time. Nonetheless, the rag2 network showed a pronounced differentiation between all three *H. macropholis* lineages.

# Morphological comparisons

Comparisons of morphological characters of the species of the *sinaitus* and *macropholis* groups are provided in Table 1.

### **Taxonomic Implications**

Based on the combined evidence of the genetic and morphological differentiation we recognise the two putative species from northern Somaliland as new and provide their formal descriptions below.

# **Systematics**

#### Hemidactylus gubanensis sp. nov.

(Figures 4–6; Table 2) https://zoobank.org/898FE504-7C3C-44AB-ADA7-691DD3FFC39F

Proposed English name: Guban gecko [pronounced guban 'gekəʊ].

Somali name: Qoroto [pronounced Koroto]; a term in Somali language that refers to all *Hemidactylus* species and other similar geckos that occur in the region.

**Chresonymy:** *Hemidactylus sinaitus* in Parker (1942), Lanza (1983, 1990), Largen and Spawls (2006; in part), Largen and Spawls (2010; in part); *Hemidactylus turcicus turcicus* in Loveridge (1947; in part); *Hemidactylus afarensis* in Šmíd et al. (2020; in part), Spawls et al. (2023; in part).

**Holotype:** NMP-P6V 76683 (sample code TMHC\_998), adult male, Somaliland, Sahil Region, 1 km west of Girigoyan (or Gari Goan, Gorigaan) Mountain (10.297° N, 44.996° E; datum WGS84 hereafter, 261 m above sea level [asl]), collected by T. Mazuch on 27 January 2022 (Figures 4, 5, 6a).

**Paratypes (four):** NMP-P6V 76682 (sample code TMHC\_997), adult female, NMP-P6V 76684 (sample code TMHC\_999), adult male; same collection data as the holotype. NMP-P6V 76680 (sample code S22-03), juvenile (Figure 6b), NMP-P6V 76681 (sample code TMHC\_996), adult male; Somaliland, Sahil Region, 1 km north-west of Girigoyan (or Gari Goan) Mountain (10.309° N, 45.0° E, 241 m asl), collected by T. Mazuch on 25 January 2022.

Other material (16): TMHC 2024.01.1036, TMHC 2024.01.1038-1039, adult males, TMHC 2024.01.1037, adult female; Somaliland, Awdal Region, 3.5 km north-west of Jidhi village (10.636° N, 43.043° E, 468 m asl), collected by T. Mazuch, D. Hlaváč, P. Konečný, H. Sh. A. Elmi on



Figure 4: Male holotype of Hemidactylus gubanensis sp. nov. (NMP-P6V 76683), general body habitus from dorsal (a) and ventral (b) sides

15 November 2023. TMHC 2024.01.1040-1041, adult females; Somaliland, Awdal Region, 1 km north-west of Gargara Galbeed (10.774° N, 43.031° E, 350 m asl), collected by T. Mazuch, D. Hlaváč, P. Konečný, H. Sh. A. Elmi on 15 November 2023. TMHC 2024.01.1042, TMHC 2024.01.1044, TMHC 2024.01.1047, adult males, TMHC 2024.01.1043, TMHC 2024.01.1045-1046, adult females; Somaliland, Sahil Region, 6 km east-southeast of Xagal village, (10.235° N, 45.793° E, 185 m asl), collected by T. Mazuch, D. Hlaváč, P. Konečný, H. Sh. A. Elmi on 22 November 2023. TMHC 2017.12.872-873, adult females (Figure 6c); Somaliland, Awdal Region, Geerissa village (10.629° N, 43.441° E, 223 m asl), collected by T. Mazuch on 11 September 2017. NHMUK 1937.12.5.293, adult male; Somaliland, Awdal Region, ca. 25 km south-western of Geerissa (10.5° N, 43.25° E, 485 m asl), collected by R.H.R. Taylor on 18 April 1933. NHMUK 1937.12.5.294, juvenile male; Somaliland, Awdal Region, ca. 25 km west of Zeila (11.416667° N, 43.25° E, 29 m asl), collected by R.H.R. Taylor on 9 January 1934. The NHMUK specimens were compared based on photographs but were not included in the morphological analysis.

**Diagnosis:** A species of the African radiation of the arid clade of *Hemidactylus* (sensu Šmíd et al. 2013a, 2020) with the following combination of morphological traits: (1) small size, SVL 41.5–53.3 mm in males, 36.5–52.9 mm

in females; (2) large and robust head, head depth 32-50% of head length, head width 58-82% of head length; (3) relatively short tail, tail length 94.0-111.3 % of SVL; (4) uppermost nasals in broad contact: (5) large anterior postmentals usually in wide contact (in 84% specimens) or in one point (16% specimens); (6) large anterior postmentals usually in contact with the first and second infralabials (in 82% specimens, with the first infralabial only in 18% specimens); (7) 7-10 supralabials; (8) 6-8 infralabials; (9) dorsum with 14-16 rows of enlarged, strongly keeled, conical tubercles; (10) other dorsal scales smooth, juxtaposed, and rather homogeneous; (11) 3-6 (counted longitudinally) and 2-3 (transversely) small smooth dorsal scales between dorsal tubercles; (12) 22-27 tail segments; (13) 2-4 rows of small scales between tail tubercles of two adjacent tail segments: (14) subcaudals enlarged; (15) rather long free distal phalanges of digits (relative length of free distal phalanges and proximal parts with lamellae on the 3rd toe 0.35-0.57, mean  $0.45 \pm 0.05$ ); (16) 5-6 lamellae under the 1st finger, 7-8 lamellae under the 4th finger, 5-6 lamellae under the 1st toe, and 8-11 lamellae under the 4th toe; (17) 4-7 precloacal pores in males; (18) presence of lateral postanal tubercles; (19) in life, body colour light beige-brownish with irregular and indistinct dark mottling, some tubercles whitish and some dark; tail with similar colouration and pattern like body or with very slightly marked light and dark irregular bands



Figure 5: Male holotype of *Hemidactylus gubanensis* sp. nov. (NMP-P6V 76683), lateral (a), dorsal (b), ventral (c) views of the head; precloacal area (d) showing four precloacal pores; detail of dorsal scalation (e); and left foot showing the structure of the lamellae and length of free distal phalanges

especially in the anterior half; head paler with darker brown snout and rather irregular pale brownish-yellow stripe running from posterior margin of eye to above the ear (Figure 6a,b,c).

**Comparisons:** The new species is most similar to the two closest relatives from the *sinaitus* group: *H. afarensis* and *H. sinaitus*. It can be distinguished from *H. afarensis* by having anterior postmentals in contact with 1 or 2

infralabials (v. always with 2 infralabials in *H. afarensis*); fewer dorsal tubercles, mean 14.9, range 14–16 (v. mean 16.5, range 14–18); wider spacings between dorsal tubercles, counted longitudinally (3–6 small scales v. 1–2 scales); fewer lamellae on first digits, 5–6 on fingers and toes (v. 6–8 on fingers and 6–7 on toes); longer free distal phalanges; rings of tail tubercles separated by 3–4 transverse rows of small scales (v. with 2–3 rows); by larger size (SVL 36.5–53.3 mm, v. 32.4–49.3 mm); and



**Figure 6:** Live specimens of *Hemidactylus gubanensis* sp. nov. and the species' localities. (a) adult male, holotype (NMP-P6V 76683); (b) juvenile, paratype (NMP-P6V 76680); (c) adult female (TMHC 2017.12.872); (d) the type locality 1 km west of Girigoyan Mountain (or Gari Goan, Gorigaan, 261 m asl), seen in the background of the photo, Sahil region, Somaliland; (e) vicinity of Geerissa village (223 m asl), Awdal region, Somaliland

by different colouration (irregular dark mottling on the body and tail (*v.* dark-brown transverse bands). It can be distinguished from *H. sinaitus* by having distinctly enlarged subcaudal scales (*v.* scales on the ventral surface of tail uniform in size); wider spacings between dorsal tubercles (3–6 small scales *v.* 2–4 scales, counted longitudinally; 2–3 scales *v.* 1.5–2 scales, counted transversely); and fewer lamellae on first digits (5–6 on fingers and toes *v.* mostly 6–8 on fingers and 6–7 on toes).

Morphological differences (the most prominent morphological characters given for each species) between *H. gubanensis* sp. nov. and the other species of the African radiation of the arid clade of *Hemidactylus* are the following: from *H. albopunctatus* (Loveridge, 1947), *H. barbouri* Loveridge, 1942, *H. curlei* Parker, 1942, *H. fragilis* Calabresi, 1915, *H. funaiolii, H. isolepis* Boulenger, 1895, *H. klauberi* Scortecci, 1848, *H. laevis* Boulenger, 1901, *H. lanzai* Šmíd et al. 2020, *H. megalops* Parker, 1932,

H. modestus (Günther, 1894), H. ophiolepis Boulenger, 1903, H. ophiolepoides Lanza, 1978, H. puccionii Calabresi, 1927 and H. somalicus Parker, 1932 by the presence of strongly keeled dorsal tubercles (v. keeled tubercles absent); from H. barbierii Sindaco, Razzetti & Ziliani, 2007 by a lower number of precloacal pores in males (4-5 v, 8), and by its different colouration (dark dorsal bands clearly bordered with black in adult specimens of H. barbierii); from H. bavazzanoi Lanza, 1978 by wider spacings between dorsal tubercles, counted longitudinally (3-6 small scales v. 2 scales) and different colouration (three well-delineated dark bands in H. bavazzanoi); from H. citernii Boulenger, 1912 by its larger size (SVL 42.0-48.9 mm v. 29.6-39.9 mm) and longer free distal phalanges of digits; from H. foudaii by longer free distal phalanges of digits, lower number of preanal pores (4-5 v. 8-9), different colouration (usually eight narrow transverse bands of dark brown tubercles in H. foudaii); from H. floweri Werner, 1908,

Species		Hemidac	ctylus gubanensis	sp. nov.			Hemi	dactylus huluul sp	. nov.	
Specimen No.	NMP-P6V 76683	NMP-P6V 76680	NMP-P6V 76681	NMP-P6V 76682	NMP-P6V 76684	NMP-P6V 76688	NMP-P6V 76685	NMP-P6V 76686	NMP-P6V 76687	NMP-P6V 76689
Type Status	Holotype	Paratype	Paratype	Paratype	Paratype	Holotype	Paratype	Paratype	Paratype	Paratype
Sex	Male	Juvenile	Male	Female	Male	Male	Male	Female	Male	Male
SVL	46.7	24.28	47.9	48.9	42	60.2	41.9	45.7	47.5	61.7
ТL	48.8	24.26	50.4	49	45.3	71.4	47	49.2	55.1	*
НL	13.5	7.87	14.01	14.27	12.7	17.64	13.38	14.72	14.87	18.69
HW	8.38	5.16	9.95	8.91	8.6	13.41	9.7	9.44	10.14	12.92
HD	5.04	3.54	5.85	6.67	5.52	8.34	6.05	6.48	6.81	8.79
EYE	3.11	2.13	3.44	3.04	3.21	4.6	3.63	3.71	3.89	4.67
AG	19.7	10.25	20.82	20.61	15.3	24	17.4	18.26	17.65	24.4
INF (R/L)	8/8	2/6	8/8	2/2	2/2	9/8	8/7	8/7	8/8	8/8
SUP (R/L)	6/6	8/8	6/6	8/9	8/8	11/12	11/11	11/11	12/12	11/11
NAS	с	ო	ო	က	2	က	e	ო	ო	e
NASCON	2	2	2	2	2	~	0	2	2	2
ING	0	0	0	0	0	2	2	0	0	0
SUPNOS	0	0	0	0	0	0	0	0	0	0
MENINF	2	1.5	1.5	2	2	2	-	-	-	<del>.</del>
MENCON	2	2	-	1.5	-	2	2	2	2	2
TUBERCOUNT	16	16	14	16	14	14	16	16	14	14
DORGRLONG	5	4	9	5	9	5	5.5	5	5	9
DORGRTR	ю	ო	с	ю	ო	ю	ი	2.5	ю	ю
PORES	4	NA	5		4	12	NA		10	14
FINGER1 (R/L)	6/6	5/5	5/6	5/5	6/6	8/8	8/8	8/8	8/8	8/8
FINGER4 (R/L)	8/8	8/8	<i>L</i> / <i>L</i>	8/8	8/8	10/10	6/6	10/10	6/6	6/6
TEO1 (R/L)	5/6	5/5	5/5	5/5	6/6	<i>L</i> / <i>L</i>	7/7	Z/7	7/7	<i>L</i> / <i>L</i>
TOE4 (R/L)	10/10	8/8	10/10	6/6	11/11	11/11	10/10	11/10	11/11	11/11
FDP/3TF (R/L)	0.52/0.43	0.47/0.46	0.48/0.51	0.44/0.46	0.42/0.37	0.32/0.42	0.29/0.33	0.35/0.36	0.42/0.39	0.34/0.33
WHORL	ю	ი	4	ю	3.5	5	5.5	4.5	4.5	4.5
SUBCAU	1	1	1	-	1	1	1	1	-	-

**Table 2:** Metric (in mm) and meristic data for the type series of *Hemidactylus gubanensis* sp. nov. and *H. huluul* sp. nov. Abbreviations as in Materials and Methods, except: \* indicates tail reconnected R/I = richt/left NA = data not available.

*H. squamulatus* Tornier, 1896 and *H. tropidolepis* by the presence of tail segments (*v.* tail segments absent).

Compared to H. robustus Heyden, 1827, a species of the Arabian radiation with which H. gubanensis sp. nov. geographically overlaps, the new species has uppermost nasals in contact (v. usually separated); fewer preanal pores (4-5 v. 5-8); lateral tail tubercles protruding when viewed from above (v. not showing from the tail outline). All other Hemidactylus species in the region, namely H. angulatus, H. arnoldi, H. awashensis Šmíd et al., 2015, H. barodanus, H. flaviviridis, H. frenatus Duméril & Bibron, 1836, H. granchii, H. jubensis Boulenger, 1895, H. laticaudatus Andersson, 1910, H. mabouia, H. macropholis, H. pauciporosus, H. platycephalus, H. ruspolii, H. smithi Boulenger, 1895 and H. taylori Parker, 1932 have well-developed dorsal trihedral or subtrihedral keeled tubercles or have larger size (SVL 57-95 mm). A comparison of metric and meristic variables with closely related species is given in Table 1.

Description of holotype: Adult male (Figures 4, 5), SVL 46.7 mm, head length 13.5 mm, head width 8.4 mm, head depth 5.0 mm, eye diameter 3.1 mm, axilla-groin distance 19.7 mm, tail length 48.8 mm. Head and body depressed, separated by a distinct and fairly narrow neck. Head pointed, relatively flat (HD = 37% of HL). Eyes rather large and prominent (horizontal eve diameter = 23% of HL). Supralabials (left/right) 9/9, infralabials 8/8. Ear opening vertically oval with slightly pointed ends. Head covered with small round scales intermixed with larger round tubercles at a rather regular spacing in the temporal and parietal region. Nostril surrounded by the rostral scale and three nasals. Uppermost nasals large, in broad contact. Middle nasals small. First supralabial largely (left) or barely (right) excluded from the nostril. Mental large, pentagonal, slightly wider than long, deeply wedged between anterior postmentals. Anterior postmentals large, longer than wide, longer than the mental scale, in broad contact with the first and second infralabials. Posterior postmentals smaller, in contact with the second infralabials. Digits slightly dilated, proximal phalanges rather short. Lamellae small, not exceeding the outline of the fingers, slightly wider than long, under the 1st finger 6/6, under the 4th finger 8/8, under the 1st toe 6/5, under the 4th toe 10/10. Rather long free distal phalanges of digits; relative length of free distal phalange to proximal part with lamellae on the 3rd toe 0.43/0.52. Dorsal tubercles large, distinctly keeled (not trihedral), oval at the back and round on the sides, slightly posteriorly pointed, and arranged in 16 longitudinal rows at midbody. 8 between hind-limbs. Dorsal scales other than tubercles smooth, juxtaposed, rather homogeneous in size, usually in 5 and 3 rows between dorsal tubercles, counted longitudinally and transversely, respectively. Posterior sides of forearms and thighs with pointy tubercles. Tail original, cylindrical, without basal constriction, with 25 whorls bearing 6 moderately raised, moderately protruding and fairly smaller round tubercles. Tail tubercles separated longitudinally by usually 3 rows of small scales. Subcaudals enlarged, starting from the first whorl. Hemipenial bulges well developed with two small lateral postanal tubercles. Four precloacal pores.

In life (Figure 6a), light beige-brownish, yellowish on lower flanks, with irregular and indistinct dark mottling, some tubercles whitish and some dark, the whitish ones tend to merge into six to seven transverse very faint and narrow bands; tail similarly mottled with 12-13 indistinct narrow whitish bands on the dorsal side; light brown irregular markings on head: rather irregular pale brownishvellow stripe running from posterior margion of eye to above the ear; supralabials and infralabials creamy white with faint dark stipple; iris sandy yellow with a complex pattern of brown reticulated veins. Ventral side of head, limbs and anterior half of tail pinkish white; body white; posterior half of tail light whitish-yellow and darker toward the tip. The colour pattern had slightly faded after fixation. Original high-resolution photographs of the holotype may be accessed in Morphobank, Project 5069, accession numbers: M901314-M901336.

Variation: While the holotype has 8 infralabials, all other specimens have 6-7. Most specimens have between 8-9 supralabials, except for two individuals with 7 or 10 supralabials unilaterally. In specimens TMHC 2017.12.873 and TMHC 2024.01.1036 on both sides, and in NMP-P6V 76680-81 and TMHC 2024.01.1043 unilaterally, 1st postmental is in contact only with the 1st supralabial. In 16% of specimens, the contact between the 1st pair of postmentals is narrow, in others it is wide. In 53% of the examined specimens there are 14 rows of dorsal tubercles, the others have 16, and one specimen has 15. Number of small intermixed scales between enlarged tubercles, counted longitudinally, varies between 3-6 (most frequently 4–5). Half of the examined specimens have three scale rows between enlarged tubercles on tail, counted longitudinally, the rest have four scale rows. In TMHC 2024.01.1046 the subcaudal scales are almost uniform, only a few scales are slightly larger. The holotype and specimen NMP-P6V 76684 have four pores, which is the lowest number among all examined males. One other male has five, two have six and three have seven pores. There is a slight variation in the numbers of lamellae on 1st (5-6) and 4th (7-8) fingers and 1st (5-6) and 4th (9-10, exceptionally 8 or 11) toes. Relative length of free distal phalange and proximal part with lamellae on the 3rd toe varies between 0.37-0.57. Some specimens (NMP-P6V 76681 and NMP-P6V 76684) had creamy white supralabials and infralabials without faint dark stipple in life. In TMHC 2017.12.873 there are six dark faintly visible X-shaped blotches on the back. Juvenile specimen TMHC 2023.07.1034 differs in its background dorsal colouration in that it is light pinkish-brown, with enlarged tubercles vellowish and distinct, while the smaller darker scales are inconspicuous. Original measurements and meristic data are provided in Table 2 and Supplementary Table S3.

**Etymology:** The species epithet is an adjective referring to Guban, a hot coastal plain in northern Somaliland where all specimens have been collected and where it is one of the most abundant ground-dwelling gecko species. The word Guban translates as 'burnt' in Somali language, referring to the torrid weather conditions that prevail in the region throughout most of the year (March–September).

**Distribution**, habitat and ecology: Hemidactylus gubanensis sp. nov. inhabits coastal areas of northern Somaliland from the border with Djibouti to Senag and Dabaje plains around Xagal (or Hagal) village (Figure 1). Two specimens from close to the border between Somaliland and Djibouti, one adult male (NHMUK 1937.12.5.293) and one juvenile male (NHMUK 1937.12.5.294) from 10.5° N; 43.25° E (= ca. 25 km SW of Geerissa) and 11.416667° N; 43.25° E (ca. 25 km W of Zeila, Figure 1), respectively, that were originally attributed to H. sinaitus (Parker 1942) have since been described as belonging to H. gubanensis sp. nov. (MorphoBank accessions: Project 483, M100639-M100657 and M100658-M100674). Of interest would be to explore the adjacent part of the Djiboutian territory around the northern border with Somaliland, as the specimen NHMUK 1937.12.5.294 was collected just 1.7 kilometres east of the border. There is a specimen deposited in the MNHN collection (voucher code MNHN-RA-0.5852) from Las Khorey, eastern Guban, originally identified as H. verruculatus (Cuvier, 1829) (Vaillant 1882) and later redetermined by Lanza (1978) to H. sinaitus. Given that the range of *H. sinaitus* does not reach this far east, we believe this specimen to represent *H. gubanensis* sp. nov. However, we could not examine this specimen personally and did not see any pictures of it. If the specimen turns out to be *H. gubanensis* sp. nov. then the distribution of this species can be expanded by another 280 km east.

The Guban is mostly a sandy coastal plain that runs along the Gulf of Aden from extreme north-western Somaliland to northern Puntland, about 80 km wide at its widest point in the west and only a few hundred meters wide at its narrowest point in the east. Its total length is about 750 km. South of the flat coastal plains are low coastal hills, which rise to about 500 m and are still considered to be a part of Guban. The climate is hot, with daily average temperatures 25–36 °C with summer maxima up to 49 °C, and with about 50 mm of annual precipitation (Muchiri 2007; Pickering and Awale 2018). This area is one of the hottest places in the HoA. Vegetation is sparse with semi-desert to steppe supporting low growing, drought tolerant species.

The type specimens were collected in the vicinity of Girigoyan Hill about 15 km south of Berbera (Figure 6d) at elevations of 240-270 m. The locality is characterised by flat plains covered with a mantle of stoney, sandy calcareous soils and gravels of mixed origin from the Pleistocene to the present (Pickering and Awale 2018; Billi 2022). The vegetation is composed mainly of scattered, dwarf, woody plants with dominant tree species Senegalia hamulosa (Benth.) Boatwr; Vachellia edgeworthii (Anderson) Kyal. & Boatwr.; V. horrida subsp. benadirensis (Harms ex Y. Sjöstedt) Kyal. & Boatwr; stunted V. tortilis (Forssk.) Galasso & Banfi (Mimosaceae) and Balanites orbicularis Sprague, (Balanitaceae). Shrubs and herbs are represented by Iphiona rotundifolia Oliv. & Hiern. (Asteraceae) and Indigofera sparteola Chiov (Leguminosae). One adult male was found during the day hiding under an old rusty canister; other specimens were found hiding under large stones. It should be noted that three adult individuals (NMP-P6V 76682-84) were found together under one shelter. The species is terrestrial. Two specimens (Figure 6c) from the vicinity of Geerissa (Figure 6e) were found to be active at night (18:30-20:00) on the sand at the edge of a large wadi with slightly denser vegetation dominated by taller acacia trees Vachellia tortilis and almost devoid of any herbs. Night temperatures on this collection site ranged between 29.9 °C and 32.7 °C and the relative air humidity between 47% and 58%. Ten specimens from the vicinity of the Jidhi and Xagal villages were collected during the day in similar habitats, hiding under small boulders on a sandy plain devoid of any vegetation. The plain was bordered by plant-rich biotopes with many low shrubs and acacia trees where the geckos were not found. Thus, sparsely vegetated biotopes with sandy soil and scattered boulders appear to be a suitable habitat for this species. Other gecko species found syntopic with H. gubanensis sp. nov. in the vicinity of Girigoyan Hill were: Hemidactylus citernii; Pristurus crucifer (Valenciennes, 1861); P. flavipunctatus Rüppell, 1835; P. somalicus Parker, 1932 (Sphaerodactylidae); and Tarentola annularis (Geoffroy Saint-Hilaire, 1827) (Phyllodactylidae); in Geerissa, species were Hemidactylus robustus, Pristurus flavipunctatus and Tarentola annularis.

**Conservation status:** The extent of occurences (EOO) of *H. gubanensis* sp. nov. is 735.82 km<sup>2</sup>, and the area of occupancy (AOO) is 36 km<sup>2</sup> according to the IUCN red-listing criteria (IUCN 2022). Such low numbers are because the species is known from only nine unique localities (Figure 1). The size of the Guban plain in combination with the low habitat requirements of the species suggest that it is likely more widespread in the coastal area of Somaliland. Given that Guban has a very low human population density, we do not assume the species to be under human-induced pressure. Unfortunately, this is not entirely true for the type locality, where works on a new and extensive Berbera Special Economic Zone that will result in disturbance to the nearby natural environment are currently underway.

*Hemidactylus huluul* sp. nov. (Figures 7–9; Table 2) https://zoobank.org/A4ED38CF-B0BD-4197-A05B-F2789C028442

Proposed English name: Huluul gecko [pronounced hulu:1 'gekəʊ].

Somali name: Qoroto [pronounced Koroto]; a term in Somali language that refers to all *Hemidactylus* species and other similar geckos that occur in the region.

**Holotype:** NMP-P6V 76688 (sample code TMHC\_994), adult male, Somaliland, Sanaag Region, Huluul (9.974° N; 46.698° E; 829 m asl), collected by T. Mazuch on 10 October 2021 (Figures 7, 8, 9a, 9b).

**Paratypes (four):** NMP-P6V 76685 (sample code TMHC\_991), adult male; NMP-P6V 76686 (sample code TMHC\_992), adult female; NMP-P6V 76687 (sample code TMHC\_993), adult male; NMP-P6V 76689 (sample code TMHC\_995), adult male. All paratypes have the same collection data as the holotype.



Figure 7: Male holotype of Hemidactylus huluul sp. nov. (NMP-P6V 76688), general body habitus from dorsal (a) and ventral (b) sides

**Other material (4):** TMHC 2024.01.1051, adult male, Somaliland, Sanaag Region, Huluul (9.974° N; 46.698° E; 829 m asl), collected by T. Mazuch on 10 October 2021; TMHC 2024.01.1048, juvenile, TMHC 2024.01.1049, TMHC 2024.01.1050, adult females, Somaliland, Sanaag Region, Huluul (9.974° N; 46.698° E; 829 m asl), collected by T. Mazuch, D. Hlaváč and P. Konečný on 23 November 2023.

Diagnosis: A species of the Arabian radiation of Hemidactylus (sensu Šmíd et al. 2013a, 2020), a member of the macropholis group characterised by the following combination of morphological traits: (1) medium to large size, SVL 41.9-61.7 mm in males, 45.7-76.2 mm in females; (2) head robust, short and high, head depth 44-51% of head length, head width 64-78% of head length; (3) relatively long tail, tail length 104.9-118.6% of SVL; (4) uppermost nasals frequently in broad contact, less frequently in a narrow or no contact; (5) 1st supralabial in broad contact with nostril; (6) large anterior postmentals in a wide contact; (7) anterior postmentals usually in contact with only the first infralabials (in 78% of specimens); (8) 11-12 supralabials; (9) 7-9 infralabials (9 only in 6% of specimens, otherwise 7-8); (10) dorsum with 14-16 rows (16 in 22% of specimens, otherwise 14) of large, prominent, trihedral, strongly keeled, round tubercles; (11) other

dorsal scales smooth (or less usually with a feeble keel), subimbricate, homogeneous; (12) 4-6 (mostly 5, counted longitudinally) and 2-3 (mostly 3, transversely) small dorsal scales between dorsal tubercles; (13) 22-26 tail segments; (14) 4-5 rows of small scales between tail tubercles of two adjacent tail segments; (15) subcaudals enlarged; (16) moderately long free distal phalanges of digits (relative length of free distal phalanges and proximal parts with lamellae on the 3rd toes 0.21-0.42, mean  $0.33 \pm 0.06$  mm); (17) 8 lamellae under the 1st finger, 9-10 lamellae under the 4th finger, 7-8 lamellae under the 1st toe, and 9-11 lamellae under the 4th toe; (18) 10-14 precloacal pores in males; (19) presence of small lateral postanal tubercles; (20) in life, body colour beige-brownish to grey with four irregular X-shaped markings across the body, additional similar marking in the pelvic area or the base of tail. Brown stripe from nostril to anterior margin of eye continues from posterior eye margin to above the ear, then interrupted to continue above the shoulder, additional stripe from the upper posterior eye margin runs in temporo-parietal region, U-shaped or curved crossbar on the nape visible in adult specimens. Tail banded with five to eight broad bands, the black and white bands become more prominent down the tail end (when original). Body pinkish-white ventrally, posterior half of tail with four to six blackish bands ventrally (Figure 9a,b).



Figure 8: Male holotype of *Hemidactylus huluul* sp. nov. (NMP-P6V 76688), lateral (a), dorsal (b), ventral (c) views of the head; precloacal area (d) showing twelve precloacal pores; detail of dorsal scalation (e); and left foot showing the structure of the lamellae and length of free distal phalanges

**Comparisons:** The new species can be distinguished from its sister species, *H. macropholis*, by the following characters: smaller size (SVL 41.9-76.2 mm v. 44.1-82.2 mm); higher numbers of infralabials (7–9, mostly 8 v. 6–8, mostly 7); higher numbers of supralabials (11–12 v. 9–11); wider spacings between dorsal tubercles (4–6 small scales v. 2–4 scales); higher number of preanal pores (10–14 v. 6–13); fewer lamellae on first digits (8 on fingers

and mostly 7 on toes v. mostly 8–10 on fingers and 7–10 on toes); rings of tail tubercles separated by 4–5 transverse rows of small scales (v. 3–4); different overall colouration (beige-brownish to grey v. mostly pinkish orange to red, less frequently brownish); and tail colouration (prominent black and white bands down the tail end v. bands completely missing or indistinct). It must, however, be kept in mind that the results of the phylogenetic analyses point



Figure 9: Live specimens of *Hemidactylus huluul* sp. nov. and the species' type locality: (a) general body habitus of male holotype (NMP-P6V 76688), (b) detail of its head, (c) type locality Huluul (829 m asl), Sanaag region, Somaliland

towards the presence of several species under what is currently called *H. macropholis* and that these differences may not apply to all of its distinct lineages.

Morphological differences between *H. huluul* sp. nov. and the rest of the species of the African radiation of the arid clade and particularly of the *macropholis* group that occur in the same general area are as follows (the most prominent morphological characters given for each species): from *H. barodanus* by smaller maximum size (61.7 mm v. 78 mm), conical tail (v. distinctly carrot-shaped) with barely protruding lateral tubercles (v. strongly protruding lateral tubercles); from *H. granchii* by higher numbers of supralabials (11–12 v. 9–10) and infralabials (7–9 v. 6–7), having a broad contact of the 1st supralabial with nostril (v. none), a higher number of preanal pores in males (10–14 v. 5); from *H. pauciporosus* by having a broad contact of the 1st supralabial with nostril (v. none, barely or largely exluded), a higher number of preanal pores in males (10–14 v. 4–8), having a contact of anterior postmentals with only one infralabial (most frequently v. always two infralabials), by different colouration of the posterior half of tail (clearly black and white banded in adults v. beige and brown banded). *Hemidactylus huluul* sp. nov. differs from other congeners that occur in the same region (the most prominent morphological characters given for each species) as follows: from *H. albopunctatus*, H. barbouri, H. curlei, H. flaviviridis, H. fragilis, H. funaiolii, H. isolepis, H. klauberi, H. laevis, H. lanzai, H. megalops, H. modestus, H. ophiolepis, H. ophiolepoides, H. puccionii and *H. somalicus* by the presence of strongly keeled dorsal tubercles (v. keeled tubercles absent); from H. afarensis, H. gubanensis sp. nov. by a higher number of preanal pores (10-14 v. 4-5), different colouration of the posterior half of tail (clearly black and white banded in adults v. beige and brown banded or mottled); from H. barbierii by a higher number of precloacal pores in males (10-14 v. 8), and by its different colouration (dark dorsal bands clearly bordered with black in adult specimens of H. barbierii); from H. bavazzanoi by its larger size (SVL 41.9-76.2 mm v. 40.0 mm) and different colouration (three well-delineated dark dorsal bands in H. bavazzanoi); from H. citernii by its larger size (SVL 41.9-76.2 mm v. 29.6-39.9 mm), longer free distal phalanges of digits (v. short phalanges); from H. floweri, H. squamulatus and H. tropidolepis by the presence of tail segments (v. tail segments absent): from H. foudaii by longer free distal phalanges of digits (v. phalanges short); a higher number of preanal pores in males (10-14 v. 8-9), different colouration (usually eight narrow transverse bands of dark brown tubercles in H. foudaii); from H. laticaudatus, H. ruspolii, and H. taylori by conical tail (v. strongly depressed, carrot-like shaped tail); from H. mabouia, H. platycephalus, H. robustus, and H. smithi by the presence of large strongly keeled trihedral dorsal tubercles (v. flat, granular or conical smooth or weakly keeled); from H. sinaitus by the size of subcaudal scales (enlarged v. uniform).

The new species is the most similar in overall apperance (moderately sized, greyish-brown coloured strongly tuberculated gecko with X-shaped markings at the back and strikingly black and white banded tail) to *Hemidactylus inintellectus* Sindaco et al. 2009, which is an endemic species of Socotra and a member of the Socotran radiation within the arid clade of *Hemidactylus*. It can, however, be easily distinguished from *H. huluul* sp. nov. by having a higher number of infralabials (8–11, mean 9.22 ± 0.66 v. 7–9, mean 7.9 ± 0.5); contact of anterior postmentals with two infralabials (v. with one infralabial, in seven of nine known specimens); and fewer preanal pores (6–10 v. 10–14).

A comparison of all examined metric and meristic variables with other closely related *Hemidactylus* species is given in Table 1.

**Description of holotype:** Adult male (Figures 7, 8) SVL 60.2 mm, head length 17.6 mm, head width 13.4 mm, head depth 8.3 mm, eye diameter 4.6 mm, axilla-groin distance 24 mm, tail length 71.4 mm. Head and body slightly depressed. Head pointed, relatively wide (HW = 76% of HL) and high (HD = 47% of HL), separated by a rather short neck. Eyes large (horizontal eye diameter = 26% of HL), prominent. Supralabials (left/right) 12/11, infralabials 8/9. Ear opening elongated, bean-shaped. Head covered with small round scales intermixed with larger round tubercles that are much smaller in the frontal region. Nostril surrounded by the rostral scale and three nasals. Uppermost nasals large, in narrow contact with two granular scales inserted from below and above. Middle nasals small. First supralabials largely touching the nostril. Mental large, pentagonal, slightly wider

than long, deeply wedged between anterior postmentals. Anterior postmentals large, longer than wide, shorter than the mental scale, in broad contact. Anterior postmentals in contact with the first and second infralabials. Posterior postmentals smaller, in contact with the second infralabials. Digits distinctly dilated, proximal phalanges moderately long. Lamellae well developed, exceeding the outline of the fingers, about twice as wide as long, under the 1st finger 8/8, under the 4th finger 10/10, under the 1st toe 7/7, under the 4th toe 11/11. Rather long free distal phalanges of digits; relative length of the free distal phalange and proximal part with lamellae on the 3rd toe 0.42/0.32. Dorsal tubercles large, prominent, round or slightly longer than wide, trihedral, with distinct medial keels in 12 longitudinal rows at midbody, 6 between hind-limbs. Dorsal scales other than tubercles smooth (or less usually with a feeble keel). subimbricate, rather homogeneous in size, usually in 5 and 3 rows between each dorsal tubercle, counted longitudinally and transversely, respectively. Posterior sides of forearms and thighs with pointy tubercles. Tail original, conical and not flattened, without basal constriction, with 20 whorls bearing 6 moderately raised, little protruding, and rather short round tubercles. Tail tubercles separated longitudinally by 5 rows of small scales. Subcaudals enlarged, starting from the fourth whorl; subcaudals on the first four whorls mostly paired. Hemipenial bulges not well developed. Twelve precloacal pores.

In life (Figure 9a,b), beige-brownish to grey with four brown, irregular, X-shaped markings across the body; additional similar marking at the base of tail. Dorsal side of tail distinctly banded with three broad light brown bands, one dark brown and four blackish bands towards the tip; background colour of dorsal side of tail light beige-brown in anterior half, white posteriorly. Brown stripe from nostril to anterior margin of eye continues from posterior eye margin to above the ear, then it continues interrupted above the shoulder; additional stripe from the upper posterior eye margin runs in temporo-parietal region; U-shaped or curved crossbar on the nape visible; supralabials and infralabials creamy white or yellowish with numerous brownish stipples; iris sandy yellow with a complex pattern of brown reticulated veins. Upper sides of lower arms and lower legs with indistinct darker markings. Ventral side of head, body, limbs and anterior half of tail pinkish white, slightly brown stippled on the edges; ventral side of posterior half of tail with five dark bands that get darker towards the tail tip. Original high-resolution photographs of the holotype may be accessed in Morphobank, Project 5069, accession numbers: M901170-M901191.

**Variation:** All paratypes have 7–8 infralabials (8 in 75% of specimens). In three paratypes the contact between the uppermost nasals is wide, only in one (NMP-P6V 76685) the nasals do not touch. While the holotype has the 1st postmentals in contact with both 1st and 2nd infralabials, all paratypes have contact only with the 1st infralabials; in four additional specimens the variation is similar. The number of rows of dorsal tubercles is 14 (in six of eight examined specimens). The number of small intermixed scales between enlarged tubercles varies between 4–6 (six only

in one specimen, counted longitudinally), and 2-3 (counted transversely). Males have either 10 (NMP-P6V 76687), 12 (NMP-P6V 76688, TMHC 2024.01.1051) or 14 (NMP-P6V 76689) preanal pores. There is a slight variation in the number of lamellae under the 4th finger (9-10; 9 in 88% of specimens) and the 4th toe (9-11; 9 only in one specimen, all other specimens have 10-11). Relative length of free distal phalange and proximal part with lamellae on the 3rd toe varies between 0.21-0.42. Tail tubercles separated longitudinally by 4–6 (mostly 4–5, in 88% of specimens) rows of small scales. Colouration in life of three vounger paratypes (NMP-P6V 76685-87) and TMHC 2024.01.1049 is light pinkish-brown. The U-shaped or curved crossbar is well visible only in the largest paratype (NMP-P6V 76689) and another two large specimens (TMHC 2024.01.1050-1051). The number of dark bands on the dorsal side of the tail varies; NMP-P6V 76686 has two light brown, one dark brown and four blackish bands, NMP-P6V 76687 has two light brown, one dark brown and five blackish bands, TMHC 2024.01.1050 has five light brown, one dark brown and two blackish bands. The largest paratype (NMP-P6V 76689) has a regenerated tail, which is light beige-brown with a few irregular darker markings; two other adult specimens (TMHC 2024.01.1051 and TMHC 2024.01.1048) have tails that are more pale yellowish beige-brown with fewer darker markings. Ventral sides of paratypes generally agree with colouration of the holotype, only the three smallest paratypes are without any brown stipple. The number of dark bands on the ventral side of the tail varies between 4-6. Original measurements and meristic data are provided in Table 2 and Supplementary Table S3.

**Etymology:** The species epithet refers to the village of Huluul, in the vicinity of which all specimens have been collected. It is a noun in apposition.

Distribution, habitat and ecology: Hemidactylus huluul sp. nov. is so far known from a single locality at a mid-elevation (829 m asl) on the southern edge of the Guban plains and low coastal hills of north-central Somaliland (Figure 1). The area where it was recorded is poorly visited and understudied, and therefore it is likely that its distribution in the surrounding area is much wider. At present, it can be declared as endemic to Somaliland. Specimens were found in the vicinity of the Huluul village (Figure 9c), which is located on a wide open plain geologically formed by the so-called Taleh formation consisting of massive gypsumanhydrite (evaporites) layers on whose edges are multiple parallel mountain ridges, Dhukukulo (1261 m asl), Dhuuro (1122 m asl), and Suugaale (ca. 1310 m asl), which are of Auradu formation that includes marine limestones (Abbate et al. 1994; Petrucci 2022; Quiroga et al. 2022). The immediate area where the type series of *H. huluul* sp. nov. was collected is formed by flat limestone stones with a mantle of a brownish-beige sandy soil or limestone gravel, occasionally with gypsum crusts, characterised as Haplic Solonchaks and Eutric Leptosols (Jones et al. 2013). The vegetation is composed mainly of dwarf, scrubby and herbaceous plants, dominated by a few scattered acacia trees (Vachellia tortilis, Mimosaceae), and the very densely growing shrub Melocarpum hildebrandtii (Engl.) Beier & Thulin (Zygophyllaceae, Figure 9c). Specimens were found active after dusk between ca. 18:30 and 23:00. Four individuals were collected while running on the ground among low bushes, others were on the walls of two brick buildings on the outskirts of the village; one specimen was found during the day hiding under a large stone. The geckos were fast and alert. Other gecko species found sympatric with *H. huluul* sp. nov. were *Hemidactylus somalicus*; *Holodactylus africanus* Boettger, 1893 (Eublepharidae); and *Tarentola annularis*.

**Conservation status:** *Hemidactylus huluul* sp. nov. is at present known only from the type locality (Figure 1). We found the species in natural as well as synanthropic habitats. The area around the type locality is very sparsely populated, and is one of the least populated places in Somaliland. The species is likely more widespread in the area and has been overlooked to date due to the lack of field work in the area. Besides the limited distribution, we are not aware of any possible threats and thus suggest it to be listed as Data Deficient (DD) according to IUCN red-listing criteria (IUCN 2022).

#### Discussion

The HoA is a globally recognised biodiversity hotspot that hosts high numbers of endemics (Mittermeier et al. 2004; Friis et al. 2005; Lewin et al. 2016). The genus Hemidactylus is the most species rich reptile genus in the HoA, with most species endemic to the region (Šmíd et al. 2015, 2020; Spawls et al. 2023; Uetz et al. 2024). In Somaliland alone, twenty species have been confirmed to occur within its borders to date (Spawls et al. 2023). In this study, we provide new genetic and morphological data for several Hemidactylus species, which update our knowledge of the phylogenetic relationships and species diversity within the arid clade of the genus. The arid clade of Hemidactylus has witnessed a species description boom within the last decade. While most of the species were described from Arabia (Sindaco et al. 2009; Busais and Joger 2011; Carranza and Arnold 2012; Šmíd et al. 2013b, 2015, 2017, 2023b; Vasconcelos and Carranza 2014), proportionally fewer were discovered in the HoA (Smid et al. 2015, 2020). The descriptions of the two new species presented herein thus strengthen the position of Hemidactylus as the most diversified reptile genus in the HoA.

*Hemidactylus gubanensis* sp. nov., described here as a new species, is most closely related and morphologically similar to *H. sinaitus* and *H. afarensis*, both of which also occur in the HoA. The distinctiveness of *H. gubanensis* sp. nov. from its sister species *H. afarensis* was already noted by Šmíd et al. (2020), who analysed morphological data for two Somaliland specimens (TMHC 2017.12.872–873) and found differences in colouration and several morphological traits. With new material available for this study, we were able to show that the populations from Somaliland are indeed genetically and morphologically distinct from *H. afarensis* and should be treated as a separate species. This removes *H. afarensis* from the list of Somaliland *Hemidactylus* and confines its distribution to the Afar Triangle of Ethiopia and Eritrea. *Hemidactylus* 

gubanensis sp. nov. appears widespread in the Guban plain of Somaliland. Considering how thoroughly this area was surveyed in the past (e.g. Boulenger 1891, 1895a,b,c, 1898, 1901, 1907; Boettger 1893; Meek and Elliot 1897; Parker 1932, 1942, 1949; Loveridge 1947; Gans et al. 1965; Lanza 1990) it is thus surprising that specimens of the species are not more frequent in herpetological collections, especially in museums that hold rich collections from Somaliland (e.g. NHMUK, MSNG, MZUF).

We only found a handful of specimens that may represent H. gubanensis sp. nov. in two collections. The MNHN collection possesses a specimen from eastern coastal Somaliland (Figure 1; Las Khorey, Sanaag Region; MNHN-RA-0.5852) that was originally identified as H. verruculatus (Vaillant 1882) and later re-determined to H. sinaitus by Lanza (1978). With our current knowledge on the distribution of the species of the sinaitus group, this specimen may represent the easternmost record of H. gubanensis sp. nov. which it resembles morphologically (Figure 28A in Lanza 1978). However, we were not able to personally examine the specimen and we thus assign it only tentatively to the species . One specimen was reported by Boulenger (1895b) from Boholgarshan [= Boholgashin, 9.91667°N, 44.33333°E, 894 m asl] and one specimen from Garowe, Puntland, is deposited in the MZUF collection (MZUF 10814; MorphoBank M902041-M902057). Both were identified as *H. sinaitus*, however, both were likely misidentified. We examined detailed photographs of both specimens and we conclude that they both resemble H. citernii. Šmíd et al. (2020) identified several clades within the African radiation of the arid clade of Hemidactylus, one of which included H. afarensis, H. foudaii and H. sinaitus. We now add the newly described H. gubanensis sp. nov. to this clade and define herewith the sinaitus group as a clade of these four species.

Hemidactylus huluul sp. nov. is presently known only from the type locality in the vicinity of the Huluul village, north-western Sanaag Region. The area is sparsely populated with no main roads. It lies on the southern edge of the coastal Guban strip, wedged between the mountainous Wagar Mountain range in the west and Cal Madow Mountain range in the east (Figure S1). This part of Somaliland has been historically poorly visited and reptile collections from here are scarce, which contrasts with the relatively well-sampled mountain ranges to the west and east of the type locality. *Hemidactylus huluul* sp. nov. seems to be a rare species; all nine known specimens were collected after spending 140 days in the field, that were spread over more than ten years.

Hemidactylus huluul sp. nov. is genetically related to *H. macropholis*. It has been previously shown that *H. macropholis* represents a complex of several species (Šmíd et al. 2017). The new material analysed in this study shows that the lineages termed as *H. macropholis* do not form a clade; samples from Kenya cluster with *H. barodanus*, samples from southern Ethiopia cluster with those from eastern Ethiopia and Somaliland, but the two lineages are strongly genetically differentiated. This implies that *H. macropholis* is in need of taxonomic revision with the aim of resolving its currently polyphyletic status, likely resulting in descriptions of new taxa. For such revision, it will be essential to either obtain genetic data from the type specimens or at least include material from the species' type locality in Dolo, Somalia in the triangle between Ethiopia, Somalia and Kenya.

Besides the new species described in this study, we provide two important additions to the phylogeny of *Hemidactylus*. For the first time, we infer the phylogenetic position of *H. tropidolepis* and *H. arnoldi* within the genus. *Hemidactylus tropidolepis* is known from two disjunct regions in northern Somaliland and adjacent parts of Ethiopia and Puntland, and from southern Somalia and Kenya (Spawls et al. 2023). Its phylogenetic position was estimated on the basis of phylogenetically informative morphological characters by Šmíd et al. (2020), who preliminarily identified it as closely related to either *H. modestus*, *H. ophiolepis* or *H. funaiolii*. We here confirm that *H. tropidolepis* is nested in the African radiation of *Hemidactylus* and is indeed sister to *H. funaiolii* from Kenya.

Hemidactylus arnoldi is a little known species with a confined distribution. Until recently, it was known only from the type locality in north-western Somaliland near the border with Djibouti. Recently, it has also been confirmed from Djibouti (Nistri 2019). The phylogenetic position of H. arnoldi within Hemidactylus is curious. The results of the phylogenetic analyses show that it clusters within the Arabian radiation of the genus and that it is a sister lineage to all the other species of the Arabian radiation. As has been mentioned, there are other Hemidactylus species of the Arabian radiation that occur in Africa (e.g. the macropholis group, H. awashensis). These are all deeply nested within the Arabian radiation and they most likely colonised Africa from Arabia by a transmarine dispersal after the continents were separated by the Red Sea and the Gulf of Aden (Šmíd et al. 2013a). However, the phylogenetic position of H. arnoldi implies that its presence in Africa may either be a result of vicariance caused by the separating African and Arabian landmasses, or an early dispersal at the onset of diversification within the Arabian radiation. In any case, the long isolated branch that connects H. arnoldi with the rest of the tree, the lack of species closely related to it, and its extremely limited distribution range all suggest that *H. arnoldi* is a relictual lineage within the Arabian radiation of Hemidactylus.

By using Illumina sequencing and a mini-barcoding protocol (Galan et al. 2012) we were able to obtain a short fragment of the mitochondrial cytb gene for five paratype specimens of *H. pauciporosus* collected in 1973 (Lanza 1978). Even such a short DNA fragment sufficed to show that the paratypes match genetically to one other specimen of *H. pauciporosus* present in our dataset (CAS227511), the only specimen of the species that has until now been available for phylogenetic analyses. This provides solid evidence that despite some historical confusion with the specimen determination (for discussion see Šmíd et al. 2017), the specimen has been determined correctly and does belong to *H. pauciporosus*.

Another species worth commenting on is *H. granchii*. The species was known only from its type series from central and southern Somalia until Šmíd et al. (2014) reported another specimen from Somaliland that morphologically matched the type series (Lanza 1978). We here report five additional

specimens from Somaliland that genetically cluster with the specimen from 2014. However, this and previous studies (Lanza 1978; Mazuch et al. 2016; Šmíd et al. 2017, 2020) have shown that morphological characters may be confounding when identifying many Hemidactylus species in the HoA. Moreover, recent findings have repeatedly confirmed the existence of a biogeographic boundary between Somaliland and southern Somalia, implying that the two regions do not share as many species as was previously thought (Schätti and Lanza 1989; Cherlin 1990; Lanza and Nistri 2005: Zimkus and Larson 2011: Petzold et al. 2014: Bates and Broadley 2018; Spawls et al. 2023, Šmíd et al. 2023a). As a result, although we refer to these specimens as H. granchii, it may be that our samples are not conspecific with real H. granchii and that the true position of the species in the Hemidactylus tree will need to be confirmed with genetic data either from the type locality in central Somalia (roughly 6.0° N; 48.5° E; Lanza 1978) or preferably from the type specimens themselves.

The Guban Plain hosts several endemic reptile taxa not found elsewhere. These are *Tropiocolotes somalicus* Parker, 1942 and *Hemidactylus arnoldi* (Gekkonidae); *Agama lanzai* Wagner et al., 2013b and *Uromastyx macfadyeni* Parker, 1932 (Agamidae); *Latastia doriai scorteccii* Arillo, Balletto & Spano, 1967 (Lacertidae); and *Eryx borrii* Lanza & Nistri, 2005 (Erycidae). *Hemidactylus gubanensis* sp. nov. and *H. huluul* sp. nov. described here add to the list of Guban endemics, making it a place of biodiversity significance. The high levels of climatic and biogeographic isolation of Guban from the neighbouring regions make it an island-like ecosystem for species that have adapted to the harsh climate of the coastal plain and which have high conservation potential, and the area should be included in future conservation plans of the country.

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#### References

- Abbate E, Sagri M, Sassi FP. 1994. Geological map of Somalia. Mohadishu: Somali National University.
- Balletto E. 1968. Contributo alla biogeografia della Somalia. Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova 36: 191–280.
- Bates MF, Broadley DG. 2018. A revision of the egg-eating snakes of the genus *Dasypeltis* Wagler (Squamata: Colubridae: Colubrinae) in north-eastern Africa and south-western Arabia, with descriptions of three new species. *Indago* 34: 1–95.
- Billi P. 2022. Fluvial landscape of the Dabaan Basin, Northern Somalia. In: Billi P. (ed), Landscapes and landforms of the Horn of Africa. World Geomorphological Landscapes. Cham: Springer Nature Switzerlang AG. pp 265–280. https://doi. org/10.1007/978-3-031-05487-7\_12.
- Boettger 0. 1893. Übersicht der von Prof. C. Keller anlässlich der Ruspoli'schen Expedition nach den Somaliländern gesammelten Reptilien und Batrachier. *Zoologischer Anzeiger, Leipzig* 16: 113–119. https://biostor.org/reference/71372.
- Boulenger GA. 1891. On some reptiles collected by Sig. L. Brichetti Robecchi in Somaliland. *Annali del Museo Civico di Storia Naturale Giacomo Doria* 32: 5–15.
- Boulenger GA. 1895a. On the reptiles and batrachians obtained by Mr. E. Lort-Phillips in Somaliland. *Annals and Magazine of Natural History* 16: 165–169. https://doi. org/10.1080/00222939508680248.
- Boulenger GA. 1895b. An account of the reptiles and batrachians collected by Dr. A. Donaldson-Smith in western Somali-land and the Galla Country. *Proceedings of the Zoological Society of London* 1895: 530–540.
- Boulenger GA. 1895c. Esplorazione del Giuba e dei suoi affluenti compiuta dal Cap. V. Bottego durante gli anni 1892-93 sotto gli auspicii della Società Geografica Italiana. Risultati zoologici.
  II. Rettili e Batraci. Annali del Museo Civico di Storia Naturale Giacomo Doria 35: 9–18.
- Boulenger GA. 1898. On a second collection of reptiles made by Mr. E. Lort-Phillips in Somaliland. *Annals and Magazine of Natural History* 2: 130–133. https://doi.org/10.1080/00222939808678026.
- Boulenger GA. 1901. A list of the batrachians and reptiles obtained by Dr. Donaldson Smith in Somaliland in 1899. Proceedings of the Zoological Society of London 1901: 47–49.
- Boulenger GA. 1907. XLVII.—Descriptions of two new African lizards of the genus *Latastia*. *Annals and Magazine of Natural History* 19: 392–394.
- Bradbury M. 2008. *Becoming Somaliland*. London: Progressio/ James Currey.
- Burbrink FT, Lawson R, Slowinski JB. 2000. Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. *Evolution* 54: 2107–2118.
- Burgess N, Hales JA, Underwood E, Dinerstein E, Olson D, et al. 2004. *Terrestrial ecoregions of Africa and Madagascar: a conservation assessment*. Washington: Island Press.
- Burriel-Carranza B, Mazuch T, Estarellas M, Talavera A, Riaño G, et al. 2023. Pristurus guweirensis Haas, 1943 (Gekkota: Sphaerodactylidae): the most abundant and widely distributed species of Pristurus previously referred to as Pristurus sp. 1. Zootaxa 5297: 594–599. https://doi.org/10.11646/zootaxa.5297.4.9.
- Busais S, Joger U. 2011. Three new species and one new subspecies of *Hemidactylus* OKEN, 1817 from Yemen (Squamata, Gekkonidae). *Vertebrate Zoology* 61: 267–280. https://doi.org/10.3897/vz.61.e31151.

- Carranza S, Arnold EN. 2006. Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 38: 531–545. https://doi. org/10.1016/j.ympev.2005.07.012.
- Carranza S, Arnold EN. 2012. A review of the geckos of the genus *Hemidactylus* (Squamata: Gekkonidae) from Oman based on morphology, mitochondrial and nuclear data, with descriptions of eight new species. *Zootaxa* 3378: 1–95. https:// doi.org/10.11646/zootaxa.3378.1.1.
- Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17: 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334.
- Ceríaco LM, Bauer AM, Kusamba C, Agarwal I, Greenbaum E. 2021. A new species of ground-dwelling *Hemidactylus* (Squamata: Gekkonidae) from southwestern Democratic Republic of the Congo. *Journal of Herpetology* 55: 105–111. https://doi.org/10.1670/20-094.
- Cherlin VA. 1990. Taxonomic review of the snake genus *Echis* (Viperidae). II. An analysis of taxonomy and descriptions of new forms. *Proceedings of the Zoological Institute, Leningrad* 207: 193–223. (in Russian, with English abstract)
- Clement M, Snell Q, Walker P, Posada D, Crandall K. 2002. TCS: estimating gene genealogies. In: Proceedings of the 16th International Parallel and Distributed Processing Symposium, 15–19 April, Fort Lauderdale, Florida. https://doi.org/10.1109/ IPDPS.2002.1016585.
- Flot JF. 2010. Seqphase: a web tool for interconverting phase input/output files and fasta sequence alignments. *Molecular Ecology Resources* 10: 162–166. https://doi. org/10.1111/j.1755-0998.2009.02732.x.
- Friis I, Thulin M, Adsersen H, Bürger AM. 2005. Patterns of plant biodiversity and endemism in the Horn of Africa. *Biologiske Skrifter* 55: 289–314.
- Galan M, Pages M, Cosson JF. 2012. Next-generation sequencing for rodent barcoding: species identification from fresh, degraded and environmental samples. PLoS ONE 7: e48374 https://doi. org/10.1371/journal.pone.0048374.
- Gans C, Laurent RF, Pandit H. 1965. Notes on a herpetological collection from the Somali Republic. *Annales du Musée Royal de l'Afrique Centrale. Série in Octavo, Science Zoologique* 134: 1–93.
- Garcia-Porta J, Šmíd J, Sol D, Fasola M, Carranza S. 2016. Testing the island effect on phenotypic diversification: insights from the *Hemidactylus* geckos of the Socotra Archipelago. *Scientific Reports* 6: 23729. https://doi.org/10.1038/srep23729.
- Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic Biology 59: 307–321. https://doi. org/10.1093/sysbio/syq010.
- Harrigan RJ, Mazza ME, Sorenson MD. 2008. Computation vs. cloning: evaluation of two methods for haplotype determination. *Molecular Ecology Resources* 8: 1239–1248. https://doi. org/10.1111/j.1755-0998.2008.02241.x.
- Hoang DT, Chernomor O, Von Haeseler A, Minh BQ, Vinh LS. 2018. UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35: 518–522. https://doi. org/10.1093/molbev/msx281.
- Hoehne MV. 2015. Between Somaliland and Puntland: marginalization, militarization and conflictiong political visions. London-Nairobi: Rift Valley Institute.
- IUCN (Standards and Petitions Committee). 2022. Guidelines for using the IUCN Red list categories and criteria. Version 15.1. Available at https://www.iucnredlist.org/documents/ RedListGuidelines.pdf. [accessed 17 February 2024]

- Jhazbhay ID. 2009. Somaliland: an African struggle for nationhood and international recognition. Midrand: Institute for Global Dialogue & Johannesburg: South African Institute of International Affairs.
- Jones A, Breuning-Madsen H, Brossard M, Dampha A, Deckers J, et al. (eds). 2013. *Soil Atlas of Africa*. Luxembourg: European Commission, Publications Office of the European Union.
- Katoh K, Rozewicki J, Yamada KD. 2019. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20: 1160–1166. https://doi.org/10.1093/bib/bbx108.
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, et al. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649. https://doi.org/10.1093/ bioinformatics/bts199.
- Lanfear R, Calcott B, Ho SYW, Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29: 1695–1701. https://doi.org/10.1093/molbev/ mss020.
- Lanza B. 1978. On some new or interesting East African amphibians and reptiles. *Monitore Zoologico Italiano Supplemento, Nuova Serie* 14: 229–297.
- Lanza B. 1983. A list of the Somali amphibians and reptiles. Monitore Zoologico Italiano Supplemento, Nuova Serie 18: 193–247.
- Lanza B. 1990. Amphibians and reptiles of the Somali Democratic Republic: check list and biogeography. *Biogeographia* 14: 407–465. https://doi.org/10.21426/B614110318.
- Lanza B, Nistri A. 2005. Somali Boidae (genus *Eryx* Daudin 1803) and Pythonidae (genus *Python* Daudin 1803) (Reptilia Serpentes). *Tropical Zoology* 18: 67–136. https://doi.org/10.108 0/03946975.2005.10531215.
- Largen M, Spawls S. 2006. Lizards of Ethiopia (Reptilia Sauria): an annotated checklist, bibliography, gazetteer and identification key. *Tropical Zoology* 19: 21–109.
- Largen M, Spawls S. 2010. *The amphibians and reptiles of Ethiopia and Eritrea.* Frankfurt am Main: Edition Chimaira.
- Leigh JW, Bryant D. 2015. PopART: full-feature software for haplotype network construction. *Methods in Ecology and Evolution* 6: 1110–1116. https://doi. org/10.1111/2041-210X.12410.
- Lewin A, Feldman A, Bauer AM, Belmaker J, Broadley DG, et al. 2016. Patterns of species richness, endemism and environmental gradients of African reptiles. *Journal of Biogeography* 43: 2380–2390. https://doi.org/10.1111/jbi.12848.
- Loveridge A. 1947. Revision of the African lizards of the family Gekkonidae. *Bulletin of the Museum of Comparative Zoology* 98: 1–469.
- Malonza PK, Bauer AM. 2014. A new species of arboreal forestdwelling gecko (*Hemidactylus*: Squamata: Gekkonidae) from coastal Kenya, East Africa. *Zootaxa* 3786: 192–200. https://doi. org/10.11646/zootaxa.3786.2.7.
- Mazuch T, Šmíd J. Bauer A. 2016. Rediscovery and a new record of *Hemidactylus laevis* (Reptilia: Gekkonidae) from Somaliland, with notes on and resurrection of *Hemidactylus fragilis*. *Zootaxa* 4117: 529–542. https://doi.org/10.11646/zootaxa.4117.4.5.
- Mazuch T, Šmíd J, Price T, Frýdlová P, Awale AI, Elmi H.ShA., Frynta D. 2018. New records of one of the least known snakes, *Telescopus pulcher* (Squamata: Colubridae) from the Horn of Africa. *Zootaxa* 4462: 483–496. https://doi.org/10.11646/ zootaxa.4462.4.2.
- Meek SE, Elliot DG. 1897. List of fishes and reptiles obtained by Field Columbian Museum East African expedition to Somali-land in 1896. *Field Museum of Natural History Publication, Zoological Series* 1: 163–184.

- Mesfin B. 2009. The political development of Somaliland and its conflict with Puntland. *Institute for Security Studies* September: ISS Paper 200. https://www.files.ethz.ch/isn/111689/p200.pdf
- Mire S. 2008. The Republic of Somaliland, stability, international recognition and economic development. *The Middle East in Europe* April/May: 12–13.
- Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T, et al. 2004. Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions. Mexico City: CEMEX.
- Muchiri PW. 2007. Climate of Somalia. Technical Report No. W-01. FAO-SWALIM, Nairobi.
- Nguyen LT, Schmidt HA, Von Haeseler A, Minh BQ. 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. https://doi.org/10.1093/molbev/msu300.
- Nistri A. 2019. New data on *Hemidactylus arnoldi* Lanza 1978 in the Horn of Africa. SEH 2019, 20th European Congress of Herpetology, 2–6 September 2019, Milan, Italy.
- Parker HW. 1930. Three new reptiles from Somaliland. Annals and Magazine of Natural History 6: 603–606. https://doi. org/10.1080/00222933008673259.
- Parker HW. 1932. Two collections of amphibians and reptiles from British Somaliland. *Proceedings of the Zoological Society of London* 1932: 335–367. https://doi. org/10.1111/j.1096-3642.1932.tb01080.x.
- Parker HW. 1935. Two new lizards from Somaliland. Annals and Magazine of Natural History 16: 525–529. https://doi. org/10.1080/00222933508655079.
- Parker HW. 1942. The lizards of British Somaliland. Bulletin of the Museum of Comparative Zoology 91: 1–101.
- Parker HW. 1949. The snakes of Somaliland and the Sokotra islands. *Zoologische Verhandelingen* 6: 1–115.
- Petrucci B. 2022. Lanscape and landforms of Northern Somalia. In: Billi P. (ed), *Lanscapes and landforms of the Horn of Africa. World geomorphological landscapes*. Cham: Springer Nature Switzerlang AG. pp 233–247. https://doi. org/10.1007/978-3-031-05487-7\_10.
- Petzold A, Vargas-Ramírez M, Kehlmaier Ch, Vamberger M, Branch WR, et al. 2014. A revision of African helmeted terrapins (Testudines: Pelomedusidae: *Pelomedusa*), with descriptions of six new species. *Zootaxa* 3795: 523–548. https://doi. org/10.11646/zootaxa.3795.5.2.
- Pickering H, Awale Al. 2018. *Introduction to plants in Central Somaliland*. Hargeysa: Ponte Invisible (Redsea Cultural Foundation).
- Prunier G. 2021. The country that does not exist: a history of Somaliland. London: C. Hurst & Co. (Publishers) Ltd.
- Pyron RA, Burbrink F, Wiens J. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13: 93.https://doi. org/10.1186/1471-2148-13-93.
- Quiroga E, Bertoni C, Van Goethem M, Blazevic LA, Ruden F. 2022. A 3D geological model of the horn of Africa: new insights for hydrogeological simulations of deep groundwater systems. *Journal of Hydrology. Regional Studies* 42: 101166. https://doi. org/10.1016/j.ejrh.2022.101166.
- Rambaut A, Drummond A. 2007. Tracer v1.4. Available at http://beast.bio.ed.ac.uk/Tracer.
- Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, et al. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systemtic Biology* 61: 539–542. https://doi.org/10.1093/sysbio/sys029.
- Safaei-Mahroo B, Ghaffari H, Ghafoor A, Amini S. 2017. A new species of *Hemidactylus* (Squamata: Gekkota: Gekkonidae) from Qara Dagh Mountains, Kurdistan Region, with a key to the genus in Iraq. *Zootaxa* 4363: 377–392. https://doi.org/10.11646/ zootaxa.4363.3.4.

- Schätti B, Lanza B. 1989. Coluber messanai, a new species of snake from Northern Somalia (Reptilia, Serpentes). Bolletino del Museo Regionale di Scienze Naturali, Torino 7: 413–421.
- Sindaco R, Razzetti E, Ziliani U, Wasonga V, Carugati C, Fasola M. 2007. A new species of *Hemidactylus* from Lake Turkana, Northern Kenya (Squamata: Gekkonidae). *Acta Herpetologica* 2: 37–48.
- Sindaco R, Ziliani U, Razzetti E, Carugati C, Grieco C, et al. 2009. A misunderstood new gecko for the genus *Hemidactylus* from Socotra Island, Yemen (Reptilia: Squamata: Gekkonidae). *Acta Herpetologica* 4: 83–98.
- Spawls S, Mazuch T, Mohammad A. 2023. *Handbook of amphibians and reptiles of North-east Africa*. London: Bloomsbury.
- Stephens M, Smith NJ, Donnelly P. 2001. A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics* 68: 978–989. https://doi. org/10.1086/319501.
- Šmíd J, Carranza S, Kratochvíl L, Gvoždík V, Nasher AK, Moravec J. 2013a. Out of Arabia: a complex biogeographic history of multiple vicariance and dispersal events in the gecko genus *Hemidactylus* (Reptilia: Gekkonidae). *PLoS One* 8: e64018. https://doi.org/10.1371/journal.pone.0064018.
- Šmíd J, Moravec J, Kratochvíl L, Gvoždík V, Nasher AK et al. 2013b. Two newly recognized species of *Hemidactylus* (Squamata, Gekkonidae) from the Arabian Peninsula and Sinai, Egypt. *ZooKeys* 355: 79–107. https://doi.org/10.3897/ zookeys.355.6190.
- Šmíd J, Mazuch T., Sindaco R. 2014. An additional record of the little known gecko *Hemidactylus granchii* Lanza, 1978 (Reptilia: Gekkonidae) from Somalia. In: Capula M, Corti C (eds), *Scripta Herpetologica. Studies on amphibians and reptiles in honour of Benedetto Lanza.* Latina: Societas Herpetologica Italica. pp 165–169.
- Šmíd J, Moravec J, Kratochvíl L, Nasher AK, Mazuch T, Gvoždík V, Carranza S. 2015. Multilocus phylogeny and taxonomic revision of the *Hemidactylus robustus* species group (Reptilia, Gekkonidae) with descriptions of three new species from Yemen and Ethiopia. *Systematics and Biodiversity* 13: 346–368. https://doi.org/10.1080/14772000.2014.996264.
- Šmíd J, Shobrak M, Wilms T, Joger U, Carranza S. 2017. Endemic diversification in the mountains: genetic, morphological, and geographical differentiation of the *Hemidactylus* geckos in southwestern Arabia. *Organisms Diversity & Evolution:* 17: 267–285. https://doi.org/10.1007/s13127-016-0293-3.
- Šmíd J, Mazuch T, Nováková L, Modrý D, Malonza PK, et al. 2020. Phylogeny and systematic revision of the gecko genus *Hemidactylus* from the Horn of Africa (Squamata: Gekkonidae). *Herpetological Monographs* 33: 26–47. https://doi.org/10.1655/ HERPMONOGRAPHS-D-19-00010.1.
- Šmíd J, Sindaco R, Shobrak R, Busais S, Tamar K, et al. 2021. Diversity patterns and evolutionary history of Arabian squamates. *Journal of Biogeography* 48: 1183–1199. https://doi. org/10.1111/jbi.14070.
- Šmíd J. 2022. Geographic and taxonomic biases in the vertebrate tree of life. *Journal of Biogeography* 49: 2120–2129. https://doi. org/10.1111/jbi.14070.
- Šmíd J, Fernández SM, Elmi HShA, Mazuch T. 2023a. Diversity of sand snakes (Psammophiidae, *Psammophis*) in the Horn of Africa, with the description of a new species from Somalia. *Zoosystematics and Evolution* 99: 345–361. https://doi. org/10.1111/jbi.14070.
- Šmíd J, Uvizl M, Shobrak M, Busais S, Ali Salim AF, et al. 2023b. Diversification of *Hemidactylus* geckos (Squamata: Gekkonidae) in coastal plains and islands of southwestern Arabia with descriptions and complete mitochondrial genomes of two endemic species to Saudi Arabia. *Organisms Diversity & Evolution* 23: 185–207.

- Tolley KA, Alexander GJ, Branch WR, Bowles P, Maritz B. 2016. Conservation status and threats for African reptiles. *Biological Conservation* 204: 63–71. https://doi.org/10.1016/j. biocon.2016.04.006.
- Tornier G. 1905. Schildkröten und Eidechsen aus Nordost-Afrika und Arabien. Aus Carlo v. Erlager's und Oscar Neumann's Forschungsreise. *Zoologische Jahrbücher* 22: 365–388.
- Trifinopoulos J, Nguyen LT, von Haeseler A, Minh BQ. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44: W232–W235. https://doi.org/10.1093/nar/gkw256.
- Uetz P, Freed P, Aguilar F, Reyes F, Hošek J. 2024. The Reptile database. Available at http://www.reptile-database.org. [accessed 8 May 2024]
- Vaillant L. 1882. Reptiles et Batraciens. In: Révoil G. (ed), Faune et flore des Pays Comalis (Afrique orientale). Paris: Challamel Ainé. pp 25.
- Vasconcelos R, Carranza S. 2014. Systematics and biogeography of *Hemidactylus homoeolepis* Blanford, 1881 (Squamata:

Gekkonidae), with the description of a new species from Arabia. *Zootaxa* 3835: 501–527. https://doi.org/10.11646/zootaxa.3835.4.4.

- Wagner P, Leaché A, Mazuch T, Böhme W. 2013b. Additions to the lizard diversity of the Horn of Africa: two new species in the Agama spinosa group. Amphibia-Reptilia 34: 363–387. https:// doi.org/10.1163/15685381-00002897.
- Wagner P, Mazuch T, Bauer AM. 2013a. An extraordinary tailintegrative review of the agamid genus *Xenagama*. *Journal of Zoological Systematics and Evolutionary Research* 51: 144–164. https://doi.org/10.1111/jzs.12016.
- Zheng Y, Wiens JJ. 2016. Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular Phylogenetics and Evolution* 94: 537–547. https://doi.org/10.1016/j.ympev.2015.10.009.
- Zimkus BM, Larson G. 2011. Examination of the molecular relationships of sand frogs (Anura: Pyxicephalidae: *Tomopterna*) and ressurection of two species from the Horn of Africa. *Zootaxa* 2933: 27–45. https://doi.org/10.11646/zootaxa.2933.1.2.