



Description of a new and critically endangered species of *Atheris* (Serpentes: Viperidae) from the Southern Highlands of Tanzania, with an overview of the country's tree viper fauna

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Abstract

A new species of arboreal forest viper (Serpentes: Viperidae: *Atheris*) from a forest fragment in the Southern Highlands of Tanzania is described and named *Atheris matildae* **sp. nov.** The species resembles the forest horned viper, *Atheris ceratophora* Werner, by bearing horn-like supraciliary scales but it differs in size, body proportions, scalation, scale ultrastructure, and distribution. Genetic divergence is also assessed and the two species have an estimated divergence time of approximately 2.2 million years. An overview of the genus *Atheris* in Tanzania, including new distribution data, is presented and the conservation status of the new taxon is discussed.

Key words: Viperidae, *Atheris*, new species, Southern Highlands, Tanzania, Conservation

Introduction

Until recently Tanzania's Southern Highlands were largely unexplored biologically, the assumption being that they were of comparatively little significance. However, extensive work over the last decade by the Wildlife Conservation Society has shown that not only are the montane forests and grasslands north of Lake Nyasa extremely species rich, but they also demonstrate a high endemism and thus are as important for conservation as the Eastern Arc chain to the northeast (Davenport, 2005; 2006). New taxa discovered from this area include the chameleon *Kinyongia vanheygeni* (Necas, 2009) and most notably Africa's first new genus of monkey for 83 years, the kipunji *Rungecebus kipunji* (Davenport *et al.*, 2006). Furthermore, a number of novel vertebrates are currently being described of which the distinctive forest viper that is the subject of this work, is one.

The genus *Atheris* Cope, 1862 occurs across tropical Africa, south to Mozambique. Of the 14 recognised species, five occur in Tanzania. With one exception, all *Atheris* species are to some degree, arboreal and share a similar morphology; a relatively slender body, large broad head, and a prehensile tail. The only leaf litter-dwelling species, *Atheris barbouri* Loveridge, 1930 is a small heavy-bodied snake, with a short, blunt head, lacking the prehensile tail; and little is known about its biology (see Fig. 7). The conservative morphology of the arboreal *Atheris* species has, over the decades, led to a poor resolution of their taxonomy (Ernst & Rödel, 2002). Despite this and although the genus is still in need of full taxonomic revision (Broadley, 1998), several recent contributions have improved our understanding of its taxonomy, usually prompted by the discovery of new species (Broadley, 1998; Lawson & Ustach, 2000; Ernst & Rödel, 2002; Branch & Bayliss, 2009). Recent investigations in Tanzania's Southern Highlands have brought to light a new species of forest viper. The type series of this new taxon includes one subadult individual and three adult male specimens sufficiently distinctive to be taxonomically assessed and named. Along with *A. ceratophora*, it is the only *Atheris* species bearing horn-like scales above the eyes. Little is known yet about its ecology but it is likely to occur in only one or a very few isolated forest fragments and be of very considerable conservation concern.

Material and methods

Ventral and subcaudal scales were counted using standard techniques (Dowling, 1951). Scale rows were recorded at midbody (MSR). Interrictals are the scales on the dorsal surface of the head between the posterior supralabials, at the corners of the mouth (ricti). Supra- and infralabials were counted for both sides. Suprarostrals were defined as the only scales in contact with the upper edge of the rostral, excluding the bordering nasals; Total length (TL), snout-vent length (SVL) and tail length were recorded to the nearest millimetre. Comparative scale counts and character states for other *Atheris* species were based on data provided in Broadley (1998), supplemented with recent revisions (e.g. Lawson & Ustach, 2000; Lawson *et al.*, 2001) and new species descriptions (*A. broadleyi* Lawson, 1999; *A. hirsuta*, Ernst & Rödel, 2002) and specimens available in the herpetological collection of the Museo Tridentino di Scienze Naturali, Trento, Italy and University of Dar es Salaam, Tanzania. Total genomic DNA was extracted and a portion (about 1100 bp) of the cytochrome b was sequenced using the protocol described in Ursenbacher *et al.* (2006). SEM observations and photographs were performed at the Museo Tridentino di Scienze Naturali using a LEO XVP (Carl Zeiss SMT Ltd., Cambridge, U.K.) at high vacuum on gold-coated prepared material. GeneBank accession numbers for the specimens sequenced are as follow: sample MTSN 9344, accession number: [JF825389](#); sample MNHG 2667.45, accession number: [JF825388](#).

Label acronyms are as follow: MTSN: Museo Tridentino di Scienze Naturali, Trento, Italy; KMH: Kim M. Howell field tags; SHCP: Southern Highlands Conservation Programme herpetological Collection, Mbeya, Tanzania; MNHG: Museum d'histoire naturelle, Geneve; ZMB: Museum für Naturkunde, Berlin. Comparative material is listed in the cited publication and in the appendix.

Taxonomy

Within the Atherini tribe, the snakes found in the Southern Highlands are referred to the genus *Atheris* Cope, on the basis of the following diagnostic features: no enlarged supraocular shield (present in *Proatheris* Broadley, 1966), tail prehensile and subcaudals single (tail non-prehensile and subcaudals paired in *Montatheris* Broadley, 1996).

Atheris matildae Menegon, Davenport & Howell sp. nov.

(Fig. 1–3)

Holotype. Adult male, MTSN 9344, collected in a forest fragment in Southern Tanzania, at about 1995 m by Omari Kibure and Obadia Mwaipungu in February 2009; fixed in 70% EtOH, tissue fixed in 90% EtOH.

Paratypes. 2 adult males, MTSN 9399 and MTSN 9418 and an immature MTSN 9417 collected in February 2011 at the same locality as the holotype, by Michele Menegon, Tim Davenport and Sophy Machaga.

Additional material. 10 specimens collected at the type locality between March and April 2011 and being kept alive for conservation purposes. 4 are males, 5 are females and 2 are immatures. Among them there is the adult female individual shown in Fig. 3.

Type locality. Remote fragmented montane forest in Tanzania's Southern Highlands. Precise locality withheld until conservation insurance population secure. Additional information on the locality can be obtained for scientific purposes from the authors upon request. (www.atherismatildae.org)

Diagnosis. *Atheris matildae* sp. nov. is distinguished from all other members of the genus except *A. ceratophora* by the presence of two to three very enlarged erect, hornlike, supraciliary scales. It is distinguished from *A. ceratophora* by the combination of the following morphological and molecular features, based on the data from 69 specimens from all over the known range of *A. ceratophora*: (1) its larger size, TL of *A. matildae* type is 643mm (the biggest male *A. ceratophora* ever recorded does not exceed 510mm TL), (2) higher count of maximum transverse head scales (max. 20 in *A. ceratophora*, 28 in *A. matildae*), (3) four subequal suprarostal scales in *A. matildae*, the two central ones of the same size and the outer ones double in size in *A. ceratophora*, (4) marked difference in dorsal scale microdermatoglyphic pattern (irregular smooth surface in *A. ceratophora*, presence of papillae-like ridges in *A. matildae*), (5) in *A. matildae*, an extensive black marking across the frontal part of the mouth, including part of nasal, rostral, mental and few infralabial scales is often present, the above described

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colour feature has not been recorded in the examined *A. ceratophora* specimens and photographs. Genetic divergence of mitochondrial gene cytochrome b between *A. ceratophora* collected at type locality and *A. matildae* expressed as actual substitution difference is 3.18% based on uncorrected p-distance of 0.03180.

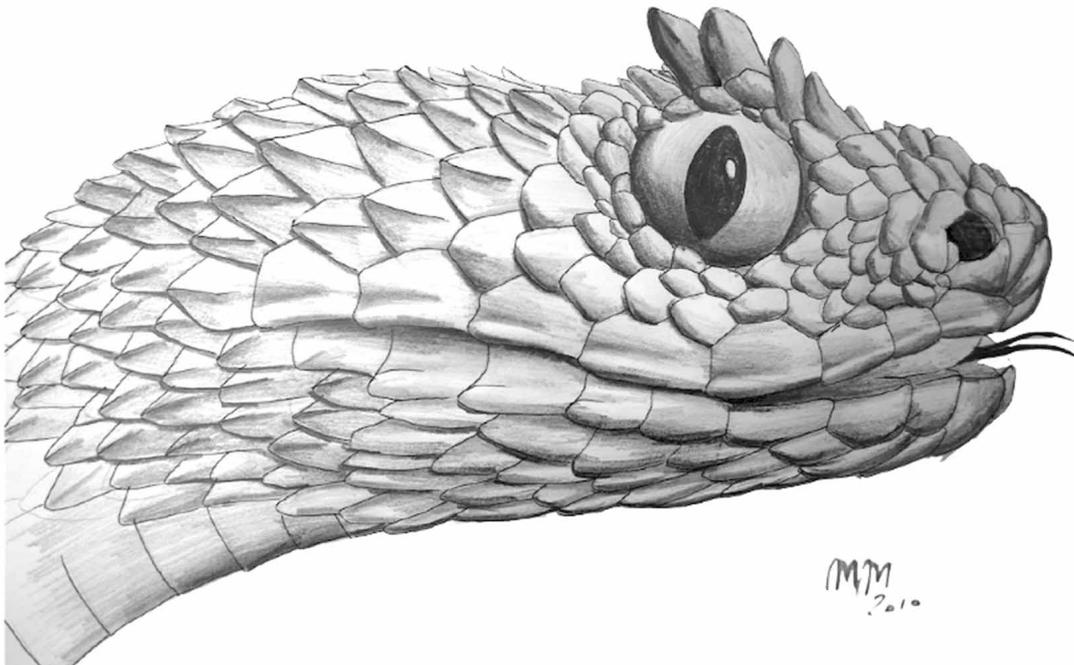


FIGURE 1. Comparison of general shape, size and body proportion between *A. matildae* holotype (left) and a fully grown specimen of *A. ceratophora* from Udzungwa (MTSN 7506, SVL=54.2) (right) and an illustration of lateral head scalation.

Paratypes and additional material variation. Details and meristics for the type series are summarized in Table 1. A total of 13 specimens have been observed, three of them are paratypes. The most significant differences between holotype and paratype specimens are in body colouration (see Fig. 2). The young specimen MTSN 9417 tends to be more greenish, the zigzag ornamentation is more conspicuous and the top of the head is marbled in green/yellow. The two adult individuals, both males, are similar in colouration to holotype, with a back dorsum and a bright yellow zigzag dorsolateral pattern. Ten additional specimens have been recently collected and are being kept alive for conservation purposes. 5 are males, 5 are females, and 2 are young. A black patch around nasal, rostral, mental and first infralabials is present in most of the observed males but also in few females and immature individuals. Males in general tend to be darker with belly suffused with black. Adult females tend to be more yellow, in some cases with immaculate throat and belly; horn-like scales are yellow with black outer edges. Side of the head can be completely yellow or with black patches at the tip of the scales. In preservation the specimen retains the original colouration (see Fig. 1).



FIGURE 2. *A. matildae* paratypes showing body shape, colouration and head details. Top - down: MTSN 9399; MTSN 9418 and MTSN 9417.



FIGURE 3. Illustration showing the variation in colour of the rostral and chin area, The black patches are present in many individuals of both sexes.

TABLE 1. Measurements and scalation of type-series of *A. matildae*, with data of *A. ceratophora* for comparison.

	<i>A. matildae</i>	<i>A. matildae</i>	<i>A. matildae</i>	<i>A. matildae</i>	<i>A. ceratophora</i>
Specimen number	MTSN 9344	MTSN 9417	MTSN 9418	MTSN 9399	n = 53
Type	Holotype	Paratype	Paratype	Paratype	N/A
Sex	Male	Immature	Male	Male	Males only
Head Lepidosis					
Suprarostrals (SRO)	4	4	4	4	5–9
Interorbitals (IOS)	12	12	121	12	7–11
Maximum transverse head scales (MTHS)	28	28	27	28	19–20
Circumorbital scales (COS)	16	16	16	162	13–19
Interoculabials (IOL)	1	1–2	1	1–2	0–1
Interocunasals (ION)	3–4	4	4	3–4	2–4
Supralabials (SL)	10	10	10	10	7–11
Infralabials (IL)	11	11	11	11	8–12
Body scalation					
Midbody Scale Rows (MSR)	26	27	26	26	19–25
Ventrals	150	142	149	150	136–150
Subcaudals	49	44	50	49	49–58
Max length (SVL+Tail) in mm	643 (547+96)	391 (334+57)	625 (532+93)	631 (538+93)	510 (416+94)
SVL/Tail	5.7	5.85	5.7	5.78	5.4 – 5.8 range

Description of holotype. Adult male preserved in 70% EtOH. Snout-vent length (SVL) 540.7 mm, tail 96.0 mm, rostral width 2.9 mm, rostral height 0.8 mm; eye diameter (vertical) 3.2 mm; snout to eye 3.3 mm. A heavy-bodied forest viper, sub-quadrangular in cross-section, with a rather thick prehensile tail (SVL/Tail approximately 5.7 times); head pear-shaped, with a very distinct neck, rounded snout and swollen supraorbital region that does

bear two/three elongated, horn-like scales; eyes relatively large, laterally placed, and with a horizontal diameter approximately 3/4 of the snout length. Crown of head covered in small scales, slightly larger over the temporal region (maximum transverse head scales—28); they bear a prominent keel and become mucronate over the head; the rostral is flattened, rectangular, about 3.5 times broader than high, contacting first supralabials and four small; unkeeled, roundish, subequal suprarostrals, nasal wider than high, with raised, embossed posterior edge, nostril circular and approximately in the centre of the nasal; internasals 5, all strongly keeled; interorbitals 9, keeled; circumoculars 16–16, not keeled but terminating in black blunt knobs; 1 row of suboculars present; circumoculars separated from nasals by two to three rows of feebly knobbed scales; a row of three irregular scales, bordering supralabials between nasal and lower circumoculars; supralabials 10–10, the first three smaller, and 6–8 with a swollen lower edge; infralabials 10–10, posteriormost with swollen upper edge and first in contact at the midline behind the mental; mental triangular, approximately twice as wide as deep; gulars bordering chin shields feebly-keeled, but prominently keeled towards the rictus; 2 preventrals, first largest; 150 ventrals; 49 undivided subcaudals (including spine); anal entire; 25 rows dorsal scales anteriorly, 26 rows at midbody, 19 rows posteriorly.

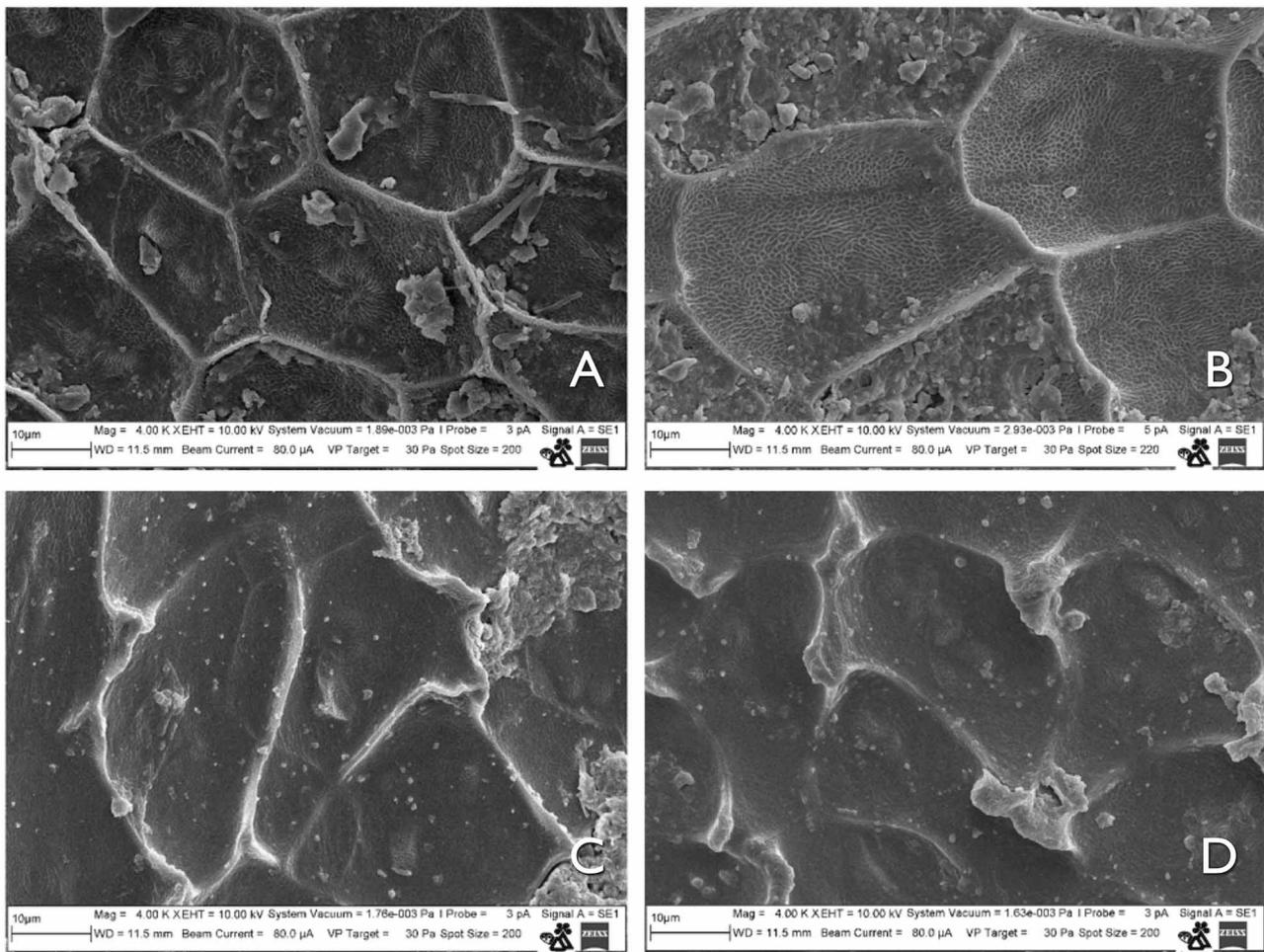


FIGURE 4. Dorsal scale microdermatoglyphic pattern of *A. matildae* (A–B) and *A. ceratophora*: (C–D). Note in B the papillae-like ridges covering the keratin layers on the scale of *A. matildae*.

Hemipenes. Both hemipenes are only partially everted. They resemble the *A. ceratophora* one as described by Emmrich (1997). The sulcus is bifurcate on a typically divided organ. The extreme basal area is naked, followed by an area with enlarged proximal spines, most prominently on the outer side of each lobe. Towards the apex, on the inner side of the sulcus, there are a few smaller scattered spines, while the distal area seems to be characterized by the lack of clearly differentiated ornamentation. A more detailed description of hemipenial morphology will be possible when a fully everted hemipenis becomes available for examination.

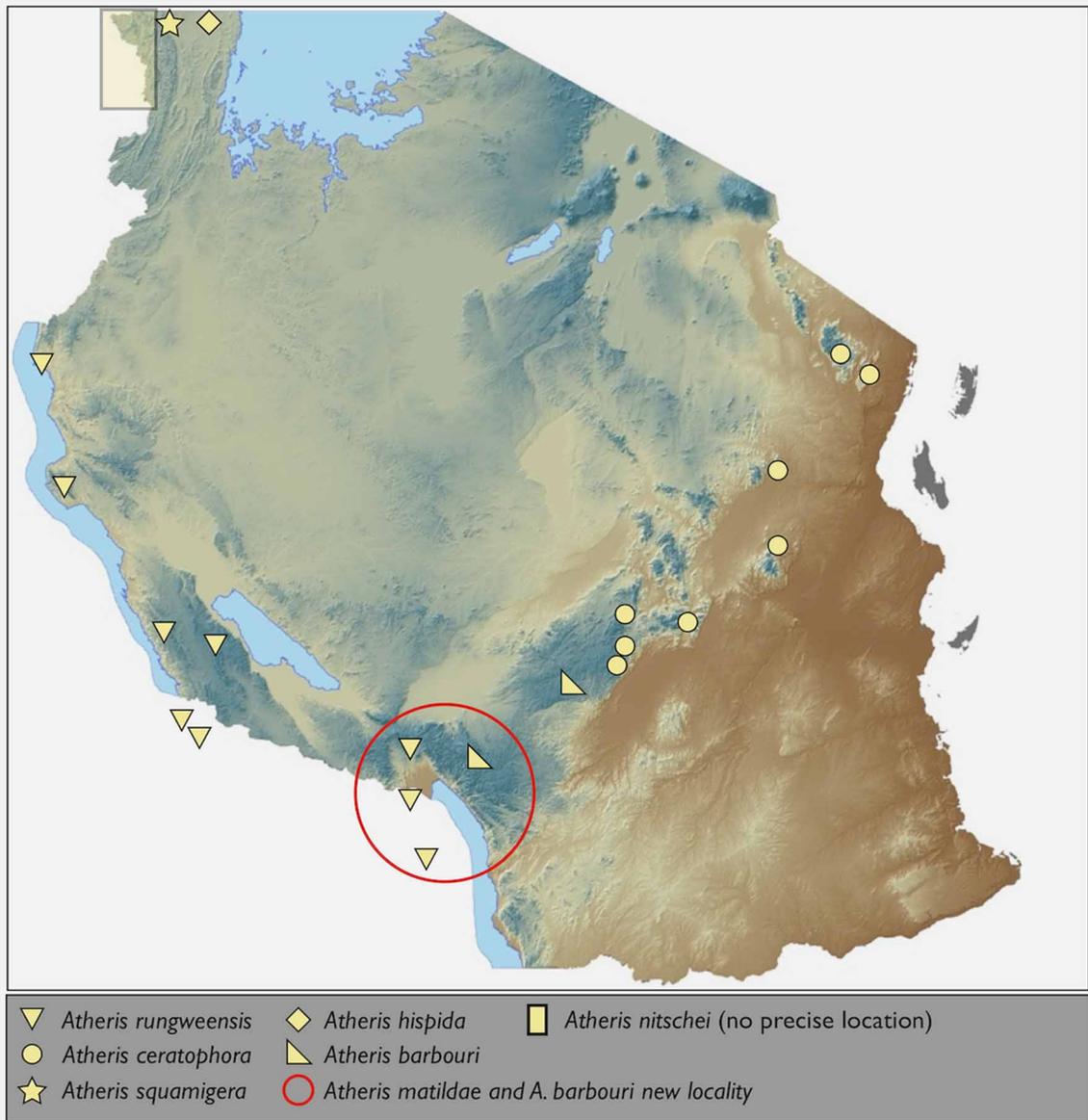


FIGURE 5. Map of the *Atheris* species occurring in Tanzania (the occurrence of *A. nitschei* within Tanzania borders still need confirmation).



FIGURE 6. The forest fragment in the Southern Highlands of Tanzania where *A. matildae* was collected, and a detail of the forest canopy.

Colouration. Dorsally it appears as a black snake with bright yellow dorso-lateral zig-zag lines. Flanks are marbled in yellow. Dorsum of the head is almost entirely black with scattered yellow scales or groups of scales, sides of the head are mainly yellow with an irregular longitudinal black marking. An extensive black marking across the frontal part of the mouth, including part of nasal, rostral, mental and few infralabial scales is present, by contrast it delimitates an inverted pale triangle. Eyes are light olive green (in life). Throat is yellow; belly is pale yellow to greyish-green, suffused by black speckling; horn-like scales are yellow with black outer edges. In preservation the specimen retains the original colouration (see Fig. 1).

Dorsal scale microdermatoglyphics. The surface microstructure of several scales from midbody and the last third of the body of two specimens of *A. matildae* (MTSN 9344, 9417) and three specimens of *A. ceratophora* from Usambara Mountains (MTSN 5117, 5118, 5121) were examined by scanning electron microscopy, in order to evaluate the intra- and inter-specific differences. Two-dimensional classes of microdermatoglyphics were identified; the coarser one consists of juxtaposed or imbricated layers of keratin with a raised edge, forming a 'scaly background'. This layer is shared by both *A. ceratophora* and *A. matildae*. At greater magnification (4000x) a further pattern of microdermatoglyphics is visible in *A. matildae*, where papillae-like ridges cover the entire surface of the keratin layer. The latter ornamentation is absent in *A. ceratophora* specimens from type locality.

Distribution and conservation. *Atheris matildae* is currently known only from the type series and a few other individuals of both sexes, all collected in a remote montane forest fragment in the Southern Highlands. The site probably represents the remnants of a wider forested landscape, interspersed with plateau grasslands and possibly naturally isolated from other Southern Highland forest blocks. For this reason the forests are of great biological value and now the focus of further exploration and conservation intervention. During the last decade the Southern Highlands have been the subject of extensive biological investigation by the Wildlife Conservation Society. However, this species has not been detected in any other areas. It is therefore probable that *A. matildae* is a range-restricted forest species, now relying on just a few forest fragments. *A. matildae* has an extent of occurrence smaller than 100 km² with extent of occurrence, area of occupancy and quality of habitat in continuing decline. According to IUCN guidelines (IUCN 2010) therefore, we propose to list *A. matildae* as 'Critically Endangered' CR B1b(i,ii,iii). Further investigations are being carried out in order to collect more information on this magnificent snake, and a small breeding programme has been established (see www.atherismatildae.org).

Etymology. *Atheris matildae* is named for TRBD's daughter Matilda Davenport, one of the next generation of herpetologists. We suggest the common name 'Matilda's Horned Viper'.

Discussion

The genus *Atheris* includes 14 recognised species and occurs across tropical Africa, south to Mozambique. It is part of the Atherini tribe as morphologically defined by Broadley (1996). This originally included four genera: the genus *Atheris*, the two monotypic genera *Proatheris* and *Montatheris* and the enigmatic genus *Adenorhinos*. Recent molecular investigations on vipers revealed the presence of five major monophyletic groups within the family (with *Causus* used as outgroup), where the Atherini tribe represents a major monophyletic group along with the genera *Bitis*, *Echis*, *Cerastes* and the Eurasian viperines (Lenk *et al.*, 2001). Within the tribe, *Proatheris* is basal and the genus *Adenorhinos* clusters with *Atheris* and is here considered belonging to the latter genus, agreeing with Lenk *et al.* (2001) and Branch & Bayliss (2009).

Atheris squamigera (Hallowell, 1854) is the most wide-ranging and variable species within the genus, and occurs from Nigeria in the West, across the Congolian forest belt to Kakamega forest in western Kenya in the East (Phelps, 2008). A few species have relatively wide distributions within a specific region, two species occur in the Upper Guinea forests *A. chlorechis* (Pel, 1851) and *A. hirsuta* Ernst & Rödel, 2002. *A. broadleyi* Lawson, 1999, once confused with *A. squamigera* and only recently recognised as a separate species by Lawson (1999) is known from the forested parts of Cameroon, Congo, Central African Republic and Gabon (Chirio & LeBreton, 2007). Several species are apparently restricted to a few localities and further investigations are needed to assess their actual distribution and conservation status. *A. subocularis* Fischer, 1888 is known only from two localities in western Cameroon (Lawson *et al.*, 2001). *A. katangensis* De Witte, 1953 is known from the northeast sector of Upemba National Park in the Shaba Province of southeastern Democratic Republic of Congo. *A. hispida* Laurent, 1955 is known to occur in isolated populations in western Kenya, western Tanzania, southwestern Uganda, and eastern

Democratic Republic of Congo (Spawls *et al.*, 2002). The Kenyan endemic *A. desaixi* Ashe, 1968 is known from only a few localities on Mt. Kenya and the Nyambeni Hills (Broadley, 1998; Spawls *et al.*, 2002). The poorly known *A. acuminata* Broadley, 1998 is known only from the Kyambura (also known as Chambura) Game Reserve, in Uganda (Broadley, 1998). The recently described *A. mabuensis* Branch & Bayliss, 2009 is known from two isolated mountains in northern Mozambique, Mt. Mabu and Mt. Namuli (Branch & Bayliss, 2009). The latter species represents the southernmost limit of the entire genus.

The genus *Atheris* in Tanzania. Recent collections throughout the country, together with an examination of material deposited in international institutions, have provided new data on the occurrence and distribution of the genus *Atheris* in Tanzania. Along with *A. squamigera* and *A. hispida* in the northwestern part of the country, Tanzanian forests and woodlands harbour another four *Atheris* species. The Eastern Arc Endemic *Atheris ceratophora* was described by Werner (1896) for the East Usambara mountains, to which it had been considered endemic until new records extended the known range of the species to the West Usambara, Udzungwa and possibly Uluguru mountains (Rasmussen & Howell, 1982). The presence of the species in the Ulugurus was based on a specimen donated by F. Werner to the Museum of Gothenburg, and the label of this specimen was reported to read "Ukami, East Africa". Ukami is identified as a geographical area in East Tanzania from app. 6°30'–7°20'S and 37°50' to 38°30'E, and the Uluguru Mountains are the only large areas of rain forest in this area, another possibility is that the location refers to the Ukami village in the Udzungwa and to the neighbouring forest patches. In 2005, subsequent field collections carried out in the Ulugurus by Frontier Tanzania, included two specimens of *A. ceratophora* identified by D. G. Broadley. The two specimens (field labels KMH 26230 and 26631) were found in the Uluguru North Forest reserve at two different sites, at 1300 and 1700 m respectively. Menegon *et al.* (2008) further expanded the known range of the species on the basis of two specimens collected in the Kanga Forest Reserve in the Nguru South Mountains (see Fig. 5 for the current distribution).

The rare and enigmatic *Atheris barbouri*, probably one of the world's least known snakes, was originally collected and described by Loveridge (1930) from two widely separated localities in the Udzungwa and Ukinga ranges. The eight specimens originally collected have been the only ones known for over 65 years, until Rasmussen & Howell (1998) published a review of the species based on a further 13 specimens collected by local residents in the Southern Udzungwa Mountains. Basic ecological information was also provided. More recently a gravid female was collected in March 2007 by L. Mahler in the vicinity of fields of agricultural crops in the Bomalang'ombe village. This represents a range extension within the southern Udzungwa plateau. Between 2009 and 2010 two other specimens were found. One adult male (Fig. 7), by D. Moyer at Kidabaga Forest Reserve (the type locality) and one adult female in Madehani Forest (Fig. 7) in a clearing surrounded by bamboo forest, representing the first specimen in the Ukinga mountains since A. Loveridge's collection (see appendix for details). Four additional specimens were also recently collected by MM and TRBD in the same forest as *A. matildae*, in a *Hagenia abissinica* dominated forest habitat. This new record represents a major range extension southward and indicates that *A. barbouri* and *A. matildae* are sympatric.

The type of the Rungwe bush viper, *Atheris rungweensis* Bogert, 1940 was found on Mt. Rungwe and described as a southern race of *A. nitschei* (Bogert, 1940). It was subsequently elevated to a full species due to differences in lepidosis, colour pattern and because of the lack of signs of intergradation between the two forms (Broadley, 1998). Recent findings obtained during fieldwork by WCS in the Southern Highlands have added a few localities for *A. rungweensis* to those reported by Broadley (1998). A specimen collected in Mahale National Park and two more specimens from the eastern shore of the southern half of Lake Tanganyika at Nkasi/Ntantwa in Rukwa region, suggest that the species probably occurs in woodland and forest patches, from Gombe Stream National Park in the North, all the way along the eastern shore of the lake, down to Mbizi Forest in Sumbawanga and Mt. Rungwe in the South (see Fig. 5 for the updated distribution).

The occurrence of *A. nitschei* Tornier, 1902 in Tanzania is still debated. The only verifiable records are represented by the type specimens (syntypes ZMB 16834, ZMB 17669), collected from a locality originally given as: 'Mpororosumpf, zwischen Papyrusstauden, Deutsch-Ost-Afrika'. During colonial times the Mpororo region was situated in the so-called "Zwischenseengebiet" (in-between lakes region), between Lake Victoria, Lake Kivu and Lake Tanganyika. Today this region comprises parts of northwest Tanzania, Rwanda and Burundi. The collection locality could have been situated in the region of today's border between Tanzania and Rwanda (as mentioned by McDiarmid *et al.*, 1999). Suitable habitat for the species occurs in the system of swamps along Kagera River that borders the two countries; however, the presence of *A. nitschei* within Tanzania has not been confirmed.



FIGURE 7. *Atheris* species in Tanzania (from left to right): *Atheris barbouri* from Udzungwa Mts.; *Atheris barbouri* from Ukinga Mts.; *Atheris rungweensis* from Mt. Rungwe; *Atheris rungweensis* from Mbizi Forest in the Ufipa range; *Atheris ceratophora* from Udzungwa Mts.; *Atheris nitschei* from Nyungwe National Park, Rwanda (the occurrence of the latter species in Tanzania still needs confirmation).

Tanzania's biodiversity is unparalleled on mainland Africa, and nowhere is this more evident than in its forest herpetofauna. However, the endemics for which the nation is so renowned are seriously threatened by habitat loss, disease and overexploitation for the wildlife trade. The latter is largely unmanaged, often illegal and increasingly pervasive. Collection from the wild is mostly unsustainable and has reached a level whereby it represents perhaps the biggest threat to Tanzania's amphibians and reptiles. And yet with political will, a scientifically-derived quota system and trade that focuses on captive breeding rather than wild capture, the threat could be turned into a conservation opportunity.

Unfortunately however, that scenario is for the future and in the meantime great care is needed to avoid the loss of many of Tanzania's rarest and most charismatic animals, especially those most recently discovered. Against this background, we have initiated a breeding programme for *A. matildae* in Tanzania. This is intended not only as an

'insurance population' to protect the new species from overexploitation, but also to begin the conservation of its threatened habitat so that this unique animal can persist in the wild (see www.atherismatildae.org).

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References

- Barbour, T. & Loveridge, A. (1928) A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory with descriptions of new species. *Memoirs of the Museum of Comparative Zoology*, 50, 85–265.
- Branch, W.R. & Bayliss, J. (2009) A new species of *Atheris* (Serpentes: Viperidae) from northern Mozambique. *Zootaxa*, 2113, 41–54.
- Bogert, C.M. (1940) Herpetological results of the Vernay Angola Expedition. I. Snakes, including an arrangement of the African Colubridae. *Bulletin of the American Museum of Natural History*, 77, 1–107.
- Broadley, D.G. (1996) A review of the tribe Atherini (Serpentes: Viperidae), with the description of two new genera. *African Journal of Herpetology*, 45, 40–48.
- Broadley, D.G. (1998) A review of the genus *Atheris* Cope (Serpentes: Viperidae), with the description of a new species from Uganda. *Herpetological Journal*, 8, 117–135.
- Chirio, L. & LeBreton, M. (2007) Atlas des reptiles du Cameroun. Publications Scientifiques du Muséum national d'Histoire naturelle, vol. 67, Paris: 1–686.
- Davenport, T.R.B. (2005) Merely 'Other forested mountains'? Biodiversity, biogeography and conservation in Tanzania's Southern Highlands. Proceedings of the Fifth Annual Scientific Conference. Tanzania Wildlife Research Institute, Arusha, 1–3 December 2005, 152–156.
- Davenport, T.R.B. (2006) Plants, primates and people: Conservation in the Southern Highlands of Tanzania. *Miombo*, 28, 7–8.
- Davenport, T.R.B., Stanley, W.T., Sargis, E.J., De Luca, D.W., Mpunga, N.E., Machaga, S.J. & Olson, L.E. (2006) A new genus of African monkey, *Rungwecebus*: morphology, ecology and molecular phylogenetics. *Science*, 312, 1378–1381.
- Dowling, H.G. (1951) A proposed standard system of counting ventral scales in snakes. *British Journal of Herpetology*, 5, 97–99.
- Ernst, R. & Rödel, M.-O. (2002) A new *Atheris* species (Serpentes: Viperidae), from Tai National Park, Ivory Coast. *Herpetological Journal*, 12, 55–61.
- IUCN Standards and Petitions Subcommittee. (2010) Guidelines for Using the IUCN Red List Categories and Criteria. Version 8.1. Prepared by the Standards and Petitions Subcommittee in March 2010. Available at: <http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf>.
- Lawson, D.P. (1999) A new species of arboreal viper (Serpentes: Viperidae: *Atheris*) from Cameroon, Africa. *Proceedings of the Biological Society of Washington*, 112, 793–803.
- Lawson, D.P. & Ustach, P.C. (2000) A redescription of *Atheris squamigera* (Serpentes: Viperidae) with comments on the validity of *Atheris anisolepis*. *Journal of Herpetology*, 34, 386–389.
- Lawson, D.P., Noonan, B.P. & Ustach, P.C. (2001) *Atheris subocularis* (Serpentes: Viperidae) revisited: Molecular and morphological evidence for the resurrection of an enigmatic taxon. *Copeia*, 2001, 737–744.
- Lenk, P., Kalyabina, S., Wink, M. & Joger, U. (2001) Evolutionary relationships among the true vipers (Reptilia: Viperidae) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 19, 94–104.
- Loveridge, A. (1930) Preliminary description of a new tree viper of the genus *Atheris* from Tanganyika Territory. *Proceedings*

New England Zoological Club, 11, 107–108.

- McDiarmid, R.W., Campbell, J.A. & Touré, T.A. (1999) *Snake Species of the World: A Taxonomic and Geographical Reference, vol. 1*. The Herpetologists' League, Washington, DC., pages?
- Menegon, M., Daggart, N. & Owen, N. (2008) The Nguru Mountains of Tanzania, an outstanding hotspot of herpetofaunal diversity. *Acta Herpetologica*, 3, 107–127.
- Necas, P. (2009) Ein neues Chamäleon der Gattung *Kinyongia* Tilbury, Tolley & Branch 2006 aus den Poroto-Bergen, Süd-Tansania (Reptilia: Sauria: Chamaeleonidae). *Sauria* 31 (2), 41–48
- Phelps, T. (2008) *Old World Vipers. A Natural History of the Azemiopinae and Viperinae*. Chimaira, Frankfurt am Main.
- Rasmussen, J.B. & Howell, K.M. (1982) The current status of the rare Usambara mountain forest-viper, *Atheris ceratophorus* Werner, 1895, including a probable new record of *Atheris nitschei rungweensis* Bogert, 1940, and a discussion of its validity (Reptilia, Serpentes, Viperidae). *Amphibia-Reptilia*, 3, 269–277.
- Rasmussen, J.B. & Howell, K.M. (1998) A review of Barbour's Short-headed Viper, *Adenorhinus barbouri* (Serpentes: Viperidae). *African Journal of Herpetology*, 47, 69–75.
- Spawls, S. & Branch, W.R. (1995) *Dangerous snakes of Africa*. Southern Books Publ., Johannesburg, 192 pp.
- Spawls, S., Howell, K.M., Drewes, R. & Ashe, J. (2004) *A field guide to the reptiles of East Africa*. Academic Press, San Diego, pages.
- Ursenbacher S, Carlsson M, Helfer V & Tegelström H, (2006) Phylogeography and Pleistocene refugia of the adder (*Vipera berus*) as inferred from mitochondrial DNA sequence data. *Molecular Ecology*, 15, 3425–3437.
- Wüster, W., Salomão, M.G., Quijada-Mascareñas, J.A. & Thorpe, R.S. (2002) Origin and evolution of the South American pit-viper fauna: evidence from mitochondrial DNA sequence analysis. In: Schuett, G.W., Höggren, M., Douglas, M.E. & Greene, H.W. (Eds.) *Biology of the Vipers*. (Eagle Mountain Publishing, Eagle Mountain, Utah, 111–128.

APPENDIX

Additional material included. In addition to the records obtained from literature the following material was included in the analysis.

- Atheris ceratophora*: KMH 26230 and 26631, Uluguru North Forest Reserve; MTSN 8874, Kigogo Forest Reserve, Udzungwa Mountains; MTSN 5032 and 5033, Udzungwa Scarp forest Reserve, Udzungwa Mountains; KMH 23977 and 35468 Kanga Forest Reserve – Nguru Mountains, MTSN 5117, 5118 and 5121 from Usambara Mountains, MNHG 2667.45 from Usambara Mountains.
- Atheris barbouri*: MTSN7311 Edge of New Dabaga Forest Reserve, Udzungwa Mountains; MTSN 9177 Bomalang'ombe, Udzungwa Mountains; MTSN 7299 Madehani forest, Ukinga Mountains; MTSN 9500, 7400 and 7399 from Livingstone Mountains.
- Atheris rungweensis*: MTSN 8993 Mahale National Park; SHCP 07-R-02 Nkasi/Ntantwa, Rukwa Region.
- Atheris hispida*: KMH 7940 Minziro Forest Reserve.
- Atheris squamigera* KMH 7757 and 7758 Rumanyika Forest Reserve.