

Six new species of viper within *Atheris* Cope, 1862 *sensu lato* from central Africa!

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ABSTRACT

An ongoing audit of the African herpetofauna has found seven further forms of previously unnamed viper from east Africa within the genus *Atheris* Cope, 1862 *sensu lato*. Five species were within *Atheris* and another in the associated genus *Montatheris* Broadley, 1996, as well as a subspecies within *Atheris*.

All are formally in accordance with the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999) based on consistent morphological divergence and/or allopatric distributions combined with identifiable geographical divergence. Previously published molecular evidence supports this action for some species, while the other newly named forms are separated by biogeographical barriers of significant antiquity (and in the absence of any molecular data), implying species-level divergence.

As all appear to be range-restricted forms in a region of rampant human population growth, the recognition of and conservation of these newly named taxa is critically important.

Taxonomic vandalism by way of pretending these forms are not unique, or by assigning them non-ICZN compliant duplicate names could hamper conservation to the degree that one or more may well become extinct as has already happened for other similarly affected taxa, including as detailed in Hoser (2019a, 2019b).

A new subgenus within *Atheris* comprising two divergent species is also formally named, as is a second monotypic one for another divergent member of the *Atheris* group.

Keywords: Viper; Africa; Kenya; Tanzania; Malawi; *Atheris*; *Woolfvipera*; *Montatheris*; *Adenorhinus*; *Poecilostolus*; *nitschei*; *desaixi*; *hindi*; *mabuensis*; *barbouri*; *matildae*; *rungweensis*; *woosnami*; new subgenus; *Piersonvipera*; *Kenyavipera*; new species; *piersoni*; *cummingae*; *euanedwardsi*; *ernestswilei*; *marleneswileae*; *josephburkei*; new subspecies; *divergans*.

INTRODUCTION

Snakes of the African genus *Atheris* Cope, 1862, were reviewed at the genus-level by Hoser in 2012 (Hoser 2012d). In that paper he divided the genus four ways into subgenera.

He did this using pre-existing and available names for three groups and erected the subgenus *Woolfvipera* Hoser, 2012 for the *Atheris nitschei* Tornier, 1902, species group.

Smid and Tolley (2019) confirmed a divergence of over 10 MYA for that trio of species from others in *Atheris*, thereby effectively supporting, the earlier taxonomic conclusion of Hoser (2012).

It was known that there were a number of unnamed species at the time Hoser (2012d) was published and I, Raymond Hoser deferred naming any on the basis that others claimed to be working on naming some of these.

Atheris matildae Menegon, Davenport and Howell, 2011 was named at the time Hoser (2012d) was being prepared and incorporated into that paper, although a second related unnamed species was not named by the same authors and prior to this paper, remained unnamed.

Following Hoser (2012d), two other species were formally named in 2020, being *Atheris hetfieldi* Ceriaco, Marques and Bauer, 2020 and *Atheris mongoensis* Collett and Trape, 2020.

Being aware of other yet unnamed taxa within the *Atheris* genus, including at least one species which is not known to occur within any formally protected areas, as well as the urgency in formally naming these forms increasing due to ongoing human population growth in the region, I have no hesitation in formally naming these six forms.

In addition one divergent subspecies with a divergence of about

700K years from the nominate form is also formally named.

In terms of these taxa, the only serious consideration was at what level (viz. species or subspecies), each should be formally named. In deciding ultimately to name each (bar one) as species, rather than subspecies, even though there was no molecular data available for four of these taxa, I made the decision based on likely divergences based on morphological differences and antiquity of barriers separating the relevant populations.

Smid and Tolley (2019) also found that *A. mabuensis* Branch and Bayliss, 2009 did not fit within any of the other subgeneric groups as outlined by Hoser (2012d), noting that Hoser (2012d) placed the species within *Adenorhinus* Marx and Rabb, 1965, a placement implied by the results of Smid and Tolley (2019) to be erroneous.

They found *A. mabuensis* diverged from the rest of *Atheris*, including the other species within *Adenorhinus* about 13 MYA.

Following on from that finding and the obvious divergence of *A. mabuensis* from the others, it only made sense to erect a subgenus for the species, which is done within this paper, because no one has seen fit to do so earlier and no alternative name is available.

As putative *A. mabuensis* has been found by myself to consist of two quite distinctive taxa, the type species is the newly named one and not *A. mabuensis*.

That act is intentional as the new subgenus and patronym named species is named in honour of a man, Charles Pierson, of Moss Vale, New South Wales, Australia who has made major life changing sacrifices for and contributions to, wildlife conservation globally, for which he has received relatively little recognition so far.

Another subgenus is formally named as *Kenyavipera subgen. nov.* to accommodate the similarly divergent species *Atheris desaixi* Ashe, 1968, believed to have diverged from all congeners about 12 MYA based on the findings of Smid and Tolley (2019).

Hoser (2012d) had placed that species in the subgenus *Woolfvipera* Hoser, 2012, type species *Atheris nitschei* Tornier, 1902, but the findings of Smid and Tolley (2019) showed this placement to be erroneous, necessitating the erection of a new genus for this divergent, range-restricted taxon.

In terms of the six species named in this paper, only one of them has been in in any way flagged as a new or unnamed species by anyone else, this being a species within *Adenorhinus* Marx and Rabb, 1965, that was identified as *Atheris cf ceratophora* by Menegon *et al.* (2014).

The single subspecies named in this paper has not been flagged as taxonomically distinct previously by anyone.

Again I emphasize the fact that none of those authors, who published Menegon *et al.* (2014), indicated any desire to name the taxon that was identified as *Atheris cf ceratophora*.

MATERIALS AND METHODS

As part of a wider audit of the African viperidae, all species and populations were assessed to see if there were any cryptic or otherwise unnamed species.

Previous papers naming new taxa of African vipers or relevant to the taxonomy and nomenclature of African species of Viperidae by myself, Raymond Hoser include Hoser (2012a, 2012b, 2012c, 2012d, 2013a, 2013c, 2013d, 2015g, 2022).

Naming species within *Atheris sensu lato* was deferred by myself in 2012, when I first identified a number of obviously unnamed forms, pending others naming those or other species, but ultimately only two species were named in the following decade and my earlier audit uncovered about 6 other candidate species.

Two people, Bill Branch of South Africa and Don Broadley sought to monopolize the genus *Atheris sensu-lato* and made unlawful threats against others who had an interest in the genus.

They even had people they saw as rivals raided by government authorities, including heavily armed police with guns, following their malicious complaints to them.

(These are the same Bill Branch and Don Broadley who were notorious for procuring young black boys for anal sex in the same way as done by Clergy (BBC World 2021, Bowcott and Sherwood

2020, Lauer and Hoyer 2019), and evading prosecution because of their senior positions at government-owned public museums). Broadley, a known thief, also engaged in taxonomic vandalism and acts of scientific fraud as detailed by Hoser (2012a).

In any event, Don Broadley died on 10 March 2016, and this was followed by Bill Branch dying on 14 October 2018.

As of 2022, there was no indication of anyone with any intent of naming any potential species within *Atheris sensu lato* and so the decision was made to revisit the group.

Some putative species, including, for example putative *Atheris (Atheris) chloroechis* (Pel, 1851) were found to contain more than one species, but in the main the generally unrecognized forms were found to already have available names.

They were effectively ignored in terms of the writing of this paper.

Although, for the record, I found *A. chloroechis* comprised two species. The type form (type locality of Bute, Ghana), occurs in Ghana and west Togo, mainly in the hills surrounding the lower Volta drainage. The specimens from Monts Nimba, western Ivory Coast and west of there, including within Liberia, Guinea and Sierra Leone are of a divergent species, for which the name *Atheris polylepis* Peters, 1864 is available.

The two taxa are widely allopatric as well.

Taxonomic vandalism as practiced by Kaiser *et al.* (2013) (and later incarnations), that is, the illegal renaming of previously named taxa and then promoting the illegally coined new name, is not the majority view of herpetologists or scientists in general, not my view either and was furthermore scathingly condemned by the ICZN in a ruling dated 30 April 2021 and again in an openly published editorial early 2023 (ICZN 2021, Ceriaco *et al.* 2023).

In terms of this paper, all putative species within *Atheris sensu lato* were investigated, including those within *Montatheris* Broadley, 1996 and *Proatheris* Broadley, 1996 for potentially unidentified and/or unnamed species or subspecies.

Known distributions were mapped, with barriers between populations investigated to determine if they were of recent and potentially "man made" form, or if they had been around for longer and if so, how long?

Living and dead animals from across the known ranges of each species were investigated and examined, as were quality photos of specimens with known locality data, all with a view to ascertaining any consistent or quantifiable differences between populations, that may warrant taxonomic division.

Where specimens appeared to be divergent, gaps in distribution were identified and a timeline put on this either by way of reference to previous molecular studies, biogeographical evidence, or both and if morphological divergence matched a dated divergence then it was determined to recognize the relevant taxa.

As already inferred, the relevant previously published literature on all of *Atheris sensu lato* and other African species groups known to have diverged because of the same biogeographical history, was checked to see if there were any available synonyms for these apparently unnamed forms and if there were, these would obviously be used in preference to any new name to be proposed.

However for five putative species in which divergent populations were found, no synonyms existed and these were the six ones identified to be formally named as done in this paper.

Those species were as follows:

1/ A population of putative *Atheris mabuensis* Branch and Bayliss, 2009 from Mount Namuli, the highest peak in the Zambezia Province of Mozambique,

2/ A population of so-called *Atheris cf ceratophora* (subgenus *Adenorhinus* Marx and Rabb, 1965) as identified by Menegon *et al.* (2014), being from Kigogo Forest Reserve in southern Udzungwa, Tanzania,

3/ Putative *A. rungweensis* (subgenus *Woolfvipera* Hoser, 2012) from Mount Mtantwa, Tanzania, and a second population from isolated mountains further north.

4/ Putative *A. squamigera* Hallowell, 1854 (in the subgenus *Poecilostolus* Günther, 1863), from north-east of Lake Victoria,

mainly in Kenya.

5/ *Montatheris hindii* Boulenger, 1910 from Mt. Kirinyaga (AKA Mount Kenya) and area north-east of the main population of *M. hindii*.

Furthermore a subspecies of *Atheris barbouri* Loveridge, 1930 was also identified and is formally named herein.

Specimens of both the type forms and the divergent forms of each putative species and subspecies were closely inspected to see if there were consistent differences warranting separate taxonomic recognition of each form.

Literature relevant to the taxonomic conclusions with respect of the populations of the five or six above-mentioned putative species or species groups, which also included relevant publications about similarly biogeographically constrained taxa (e.g. *Crotaphopeltis* Fitzinger, 1843 *sensu lato* and *Dipsadoboa* Günther 1858 *sensu lato*), included the following: Akeret (2004, 2010), Angel (1925), Ashe (1968), Auerbach (1987), Barbour (1914), Barbour and Amaral (1927a, 1927b), Barbour and Loveridge (1928), Barnett (2001), Barnett and Emms (2005), Bates *et al.* (2014), Bayliss *et al.* (2014), Behangana *et al.* (2020), Beolens *et al.* (2011), Berkheimer (1996), Bittencourt-Silva (2019), Boettger (1887), Bogert (1940), Böhme (1987), Böhme *et al.* (2011), Boulenger (1896, 1897a, 1897b, 1901, 1906a, 1906b, 1907, 1910), Boycott (1992), Branch (1986, 1993), Branch and Bayliss (2009), Branch and Rödel (2003), Branch *et al.* (2005, 2019), Briscoe (1949), Broadley (1960, 1989, 1996, 1998), Broadley and Blaylock (2013), Broadley and Cotterill (2004), Broadley and Howell (1991), Broadley *et al.* (2003), Burger *et al.* (2004), Carlino and Pauwels (2015), Ceriaco *et al.* (2020), Chabanaud (1916, 1917), Chifundera (1990), Chippaux (2006), Chippaux and Jackson (2019), Chirio (2009), Chirio and Lebreton (2007), Chirio and Ineich (2006), Cimatti (2006), Collett and Trape (2020), Conradie *et al.* (2016, 2019, 2021), Capocaccia (1961), Cope (1860, 1862), Dehling and Dehling (2012), Demos *et al.* (2013), de Witte (see for Witte), Dobiey (2007), Dobiey and Vogel (2007), Dowling and Savage (1960), Duméril *et al.* (1854), Dunn (1946), Emmrich (1997), Engelbrecht (2017), Engelbrecht *et al.* (2020, 2021), Ernst and Rödel (2002), Ernst *et al.* (2020), Ferreira (1897), Fischer (1888), Fitzinger (1843), Fleck (2003), Gemel *et al.* (2019), Getreuer (2019), Goldberg *et al.* (2021), Gower *et al.* (2012), Gray (1858), Greenbaum (2017), Groen *et al.* (2009), Günther (1858, 1863a, 1863b, 1864, 1888, 1895, 1896), Gutsche (2014), Haagner *et al.* (2000), Hallermann (1998, 2007), Hallowell (1854), Harrington *et al.* (2018), Herrmann *et al.* (1999), Hirschmann (2008), Hoer (2013), Honess and Bearder (1991), Hörold (2014), Hoser (2012a, 2012b, 2012c, 2012d, 2013a, 2013c, 2013d, 2015g, 2022), Hughes (2013, 2017, 2018), Hughes and Barry (1969), ICZN (1991a, 1991b, 2001, 2021), Ionides and Pitman (1965), Jachan (2010), Jan (1863), Joger (1982), Joger and Courage (1999), Kielgast (2011), Koetze (2008), Kramer (1961), Krecsak (2007), Krecsak and Bohle (2008), Laita (2013), Lanoie and Branch (1991), Largen and Spawls (2010), Laurent (1955, 1956, 1958), Laurenti (1768), Lawson (1999), Lawson and Ustach (2000), Lawson *et al.* (2001), Lebreton (1999), Leaché *et al.* (2006), Lenk *et al.* (2001), Lillywhite (2014), LiVigni (2013), Love (2017), Loveridge (1929, 1930, 1932, 1933, 1936, 1938a, 1938b, 1946, 1957, 1957b), Lyakurwa (2017), Lyakurwa *et al.* (2019), Mallow *et al.* (2003), Malonza *et al.* (2006, 2017), Maritz *et al.* (2016), Marques *et al.* (2018), Marx and Rabb (1965), Marshall and Strine (2014), Masters *et al.* (2017), Mattison (1995, 2007), McDiarmid *et al.* (1999), Meek and Cory (1910), Meidinger (1998, 2000), Menegon *et al.* (2008, 2011, 2014), Menzies (1966), Mertens (1965), Meshack (2009), Milde (2019), Mocquard (1887), Monard (1931, 1940), Monzel (2012), Muchai and Malonza (2011), Müller (1910), Ota and Hikida (1987), Pauwels and Brecko (2020), Pauwels and Colyn (2023), Pauwels and David (2008), Pauwels and Vande Weghe (2008), Pauwels *et al.* (2002, 2016, 2019, 2022), Pel (1852), Penner *et al.* (2013), Perret (1961), Perret and Mertens (1957), Peters (1854, 1863, 1864), Pfeffer (1893), Phelps (2010), Pietersen *et al.* (2021), Pitman (1974), Portik *et al.* (2016), Pyron *et al.* (2013), Rasmussen (1981, 1985, 1986, 1989a, 1989b, 1993a, 1993b, 1997), Rasmussen and Howell (1982, 1999),

Razzetti and Msuya (2002), Reinhardt (1843), Reuss (1939), Ride *et al.* (1999), Robertson *et al.* (2003), Rochebrune (1885), Roelke and Smith (2010), Rovero *et al.* (2014), Sanchez-Vialas *et al.* (2022), Santos *et al.* (2021), Schlegel (1855), Schlüter and Hallermann (1997), Schmidt and Kunz (2005), Schmidt (1923), Segniabeto *et al.* (2011, 2022), Senter and Chippaux (2022), Spawls (1990), Spawls and Branch (1995), Spawls *et al.* (2011, 2018), Spranger (2002), Sternfeld (1908, 1917), Stevens (1973), Sweeney (1963), Timberlake *et al.* (2012), Tornier (1902), Trape and Balde (2014), Trape and Collet (2021), Trape and Mané (2000, 2004, 2006, 2015, 2017), Trape and Roux-Esteve (1995), Ullenbruch and Böhme (2017), Wagner (2018), Wallach *et al.* (2014), Wallach (2019), Werner (1895), Werning and Wolf (2007), Wirth (2011), Witte (1933), Wustrack (2002), Zassi-Boulou *et al.* (2020) and sources cited therein.

RESULTS

In terms of all the seven candidate taxa mentioned above, each were found to be divergent at the species level, bar one, with all being sufficiently morphologically divergent and allopatric, enabling relevant separation at the species or subspecies level.

The molecular evidence of Menegon *et al.* (2014), combined with the physical divergence of *Atheris cf. ceratophora* and one of the two populations of *A. rungweensis*, the one being from Mount Mtantwa was sufficient to warrant these two being regarded as full species.

The other population of putative *A. rungweensis* from further north is affected by the same biogeographical factors causing isolation and is presumably of the same antiquity in terms of divergence and so it too is regarded as a full species.

Putative *Atheris mabuensis* Branch and Bayliss, 2009 from Mount Namuli is only a short distance (about 60-70 km in a straight line) from Mount Mabu (including near slopes), but is separated by wholly unsuitable habitat and so the two populations have been disconnected for some time.

Significantly the divergence between the two forms of the same putative species are such that recognition of the unnamed form as merely a subspecies is not appropriate.

In any event, both populations are not interbreeding and clearly evolving as separate species.

A similar situation exists with *Montatheris hindii* Boulenger, 1910 from Mt. Kirinyaga (AKA Mount Kenya), the population of which is very close to that of the type form from Arberdare Range, with the higher slopes populated by the same putative species potentially just 20 km away.

Once again the morphological divergence of each population warrants full species-level recognition.

Putative *A. squamigera* Hallowell, 1854 (in the subgenus *Poecilostolus* Günther, 1863), from north-east of Lake Victoria, mainly in Kenya is also divergent from the previously named populations in the Democratic Republic of Congo and further west and is apparently allopatric, based on rifting in the intervening valley over the past 2 MYA and based on these factors is also of species-level divergence.

Therefore in terms of the 6 previously identified candidate taxa, I have no hesitation in naming them as species in accordance with the rules of the *International Code of Zoological Nomenclature* (Ride *et al.* 1999).

As already mentioned in the introduction, two relevant species are also found to be sufficiently divergent from others in *Atheris sensu lato* as to warrant being named as within a separate newly named subgenus, as well as another separately divergent species to be moved to another newly erected subgenus.

Atheris barbouri Loveridge, 1930 is also split two ways, with the formal description of a new subspecies.

INFORMATION RELEVANT TO THE FORMAL DESCRIPTIONS THAT FOLLOW

There is no conflict of interest in terms of this paper or the conclusions arrived at herein.

Several people including anonymous peer reviewers who revised the manuscript prior to publication are also thanked as are relevant

staff at museums who made specimens and records available in line with international obligations.

In terms of the following formal descriptions, spelling of names should not be altered in any way for any purpose unless expressly and exclusively called for by the rules governing Zoological Nomenclature as administered by the International Commission of Zoological Nomenclature.

Material downloaded from the internet and cited anywhere in this paper was downloaded and checked most recently as of 20 April 2023, unless otherwise stated and were accurate in terms of the context cited herein as of that date.

Unless otherwise stated explicitly, colour descriptions apply to living adult male specimens of generally good health and not under any form of stress by means such as excessive cool, heat, dehydration or abnormal skin reaction to chemical or other input. It should be noted that in vipers in particular, juveniles can often appear quite different in colour to mature adults, as can be each sex in adults.

While numerous texts and references were consulted prior to publication of this paper, the criteria used to separate the relevant species has already been spelt out and/or is done so within each formal description and does not rely on material within publications not explicitly cited herein.

Delays in recognition of these species and subspecies could jeopardise the long-term survival of the taxa as outlined by Hoser (2019a, 2019b) and sources cited therein.

Therefore attempts by taxonomic vandals like the Wolfgang Wüster gang via Kaiser (2012a, 2012b, 2013, 2014a, 2014b) and Kaiser *et al.* (2013) (as frequently amended and embellished, e.g. Rhodin *et al.* 2015, Thiele *et al.* 2020, Hammer and Thiele 2021) to unlawfully suppress the recognition of these taxa on the basis they have a personal dislike for the person who formally named it should be resisted (e.g. Dubois *et al.* 2019 and Ceriaco *et al.* 2023).

Claims by the Wüster gang against this paper and the descriptions herein will no doubt be no different to those the gang have made previously, all of which were discredited long ago as outlined by Ceriaco *et al.* (2023), Cogger (2014), Cotton (2014), Dubois *et al.* (2019), Hawkeswood (2021), Hoser, (2007, 2009a, 2012a, 2012b, 2013, 2015a-f, 2019a, 2019b), ICZN (1991b, 2001, 2012, 2021), Mosyakin (2022), Wellington (2015) and sources cited therein.

Some material within descriptions is repeated to ensure each fully complies with the *International Code of Zoological Nomenclature* (Ride *et al.* 1999).

CONSERVATION THREATS TO THE NEWLY NAMED TAXA AND RELATIVES

There are no known significant immediate conservation threats to these newly named snake species and the subspecies, although the best part of the potential habitat for these taxa have been effectively erased by the creation of endless expanses human agriculture of ever increasing intensity throughout the region, brought about by the skyrocketing population of the region (East Africa) where women still as of 2022 have an average of more than 4 children per life time.

Alternatively, remaining populations in forest or habitat isolates, even if being formally preserved, as is happening in some cases, are now cut off from exits or spreading by way of human encroachment.

Small population sizes, in what are best seen as islands, are of course at higher risk of extinction due to some unforeseen calamity on a particularly small remnant population.

Unforeseen threats may include direct human activities (e.g. yet more land clearing for homes or farming activities), as well as potential threats caused by changed vegetation regimes.

The sub-Saharan African region is awash with introduced species from the northern hemisphere and Australia, introduced animal pests and potential pathogens, including those introduced via the legal importation of foreign reptiles and amphibians by government-owned zoos and other government backed commercial enterprises.

Denial of the existence of the relevant taxa *sensu* Wüster *et al.* as outlined by Hoser (2019a, 2019b), could ultimately cause extinction of these taxa in the same way it caused one or more earlier extinctions as documented by Hoser (2019a, 2019b), Mitchell (1948) and Peters (1863).

PIERSONVIPERA SUBGEN. NOV.

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Type species: *Piersonvipera piersoni* sp. nov.

Diagnosis: The subgenus *Piersonvipera* subgen. nov. includes species within the genus *Atheris* Cope, 1862 *sensu lato* that are about 13 MYA divergent from other members of the genus according to the evidence of Smid and Tolley (2019).

Snakes within *Piersonvipera* subgen. nov. are separated from all other species of *Atheris* (*sensu lato*) by the following suite of characters:

- (1) Small adult size, maximum length 384mm (all other *Atheris* exceed 580mm TL, with the exception of - *A. katangensis* De Witte, 1953, TL 397mm; *A. barbouri* Loveridge, 1930, TL 369 mm (Barbour and Howell, 1998); and the unique type of *A. acuminata* Broadley, 1998, TL 440mm);
 - (2) The lack of 'horns' (enlarged supraocular scales are present in *A. ceratophora* Werner, 1896);
 - (3) The lack of lanceolate or acuminate scales on top of the head (present in *A. hispida* Laurent, 1955 and *A. acuminata*);
 - (4) Having weakly keeled gular scales (smooth only in *A. nitschei* Tornier, 1902 and *A. woosnami* Boulenger, 1906; gulars moderately keeled in the eastern species, *A. rungweensis* Bogert, 1940, *A. desaixi* Ashe, 1968, *A. ceratophora* and *A. katangensis*, and strongly keeled in the remaining central and western species);
 - (5) Lacking interocularials (*sensu* Broadley, 1998, i.e. the supralabials are in contact with circumorbitals; 1 or 2 in *A. desaixi* and *A. rungweensis*);
 - (6) Having 19-21 transverse head scales (*sensu* Broadley, 1998, i.e. number of scales across head between posterior supralabials; these are reduced in highly arboreal species, e.g. *A. squamigera* Hallowell, 1854, 15-22, *A. hispida*, 12; and *A. acuminata*, 10);
 - (7) Having 21-23 Midbody scale rows, (MSR) (most species have 27+ MSR rows; reduced in highly arboreal species such as *A. squamigera*, 15-25, *A. hispida*, 15-19, and *A. acuminata*, 14);
 - (8) Lateral body scales not serrated (strongly serrated in *A. ceratophora*, *A. desaixi*, *A. nitschei* Tornier, 1902, *A. woosnami* and *A. rungweensis*, and weakly serrated in *A. katangensis*);
 - (9) Having 8-9 supralabials (six in *A. acuminata*, 10-12 in *A. desaixi*);
 - (10) Having low ventral counts 128-137 (this is the lowest in the genus; usually over 140 in both sexes in *A. nitschei*, *A. woosnami* Boulenger, 1906, *A. rungweensis*, *A. desaixi*, *A. chlorechis* (Pel, 1852), *A. hispida*, *A. mongoensis* Collet and Trape, 2020, *A. matildae* Menegon, Davenport and Howell, 2011 and *A. subocularis* Fischer, 1888, and in the only known males of *A. acuminata* (160) and *A. hirsuta* Ernst and Rödel, 2002 (160));
 - (11) Having low subcaudal counts - 39-47 (always higher than 45 in *A. rungweensis*, *A. ceratophora*, *A. chlorechis*, *A. squamigera* and *A. hispida*; and 54 and 58 in the only known males of *A. acuminata* and *A. hirsuta*, and 50 or more in *A. hetfieldi* respectively);
 - (12) Having a prehensile tail (non-prehensile in *A. barbouri*), and higher subcaudal (*A. barbouri* 15-21) and labial (*A. barbouri*, supralabials 5-6, infralabials 4-5) counts (modified from Branch and Bayliss 2009).
- Snakes in the genus *Atheris* Cope, 1862 including all subgenera are separated from all other African vipers by the following unique suite of characters:
- No single small horn above the eye; pupil vertical; many small scales on top of the head; head is not pear shaped; tail long; 38-65 single subcaudals; occurs in mid altitude woodland or forest; usually a mixture of black, yellow and/or green in life and arboreal in habit (excluding it seems *A. barbouri* which is largely terrestrial).
- Snakes in the closely related genus *Proatheris* Broadley, 1966 are

separated by the presence of an enlarged supraocular shield. Snakes in the other closely related genus *Montatheris* Broadley, 1996 are separated by the presence of paired subcaudals (versus single in *Atheris* Cope, 1862) and by having a tail that is not prehensile.

Distribution: Known only from Mount Namuli (*A. (Piersonvipera) piersoni* sp. nov.) and Mount Mabu (*A. (Piersonvipera) mabuensis* (Branch and Bayliss, 2009)), both locations in northern Mozambique, south-east Africa.

Etymology: The subgenus *Piersonvipera* subgen. nov. and species *Atheris (Piersonvipera) piersoni* sp. nov. (this paper) are both formally named in honour of Charles Pierson of Moss Vale, New South Wales, Australia in recognition of his amazing sacrifices and contributions to wildlife conservation in Australia.

For details see the account in Hoser (1996).

Content: *Atheris (Piersonvipera) piersoni* sp. nov. (type species); *A. (Piersonvipera) mabuensis* (Branch and Bayliss, 2009).

ATHERIS (PIERSONVIPERA) PIERSONI SP. NOV.

LSIDurn:lsid:zoobank.org:act:BB6E156D-A2FB-4BF6-AE8C-8BF89453166C

Holotype: A preserved specimen at the Port Elizabeth Museum Herpetology Collection, now known as Bayworld, Gqeberha, South Africa, Africa, specimen number PEM R17904, collected on a path at 1 PM in leaf litter in Khara Forest (lower end on Manho Forest), Mount Namuli, Zambezia Province, Mozambique, Africa, Latitude 15.24399 S., Longitude 37.02165 E. at about 1550 metres ASL by Colin Congdon on 26 November 2008.

This facility allows access to its holdings.

Diagnosis: The two species from this subgenus *Atheris (Piersonvipera) piersoni* sp. nov. and *A. (Piersonvipera) mabuensis* (Branch and Bayliss, 2009) are readily separated from one another as follows:

A. piersoni sp. nov. has a bluish tinge in colour, not seen in *A. mabuensis*, and has reddish scale tips on the body, vs yellowish in *A. mabuensis*.

A. piersoni sp. nov. has 128 ventrals, 22 mid body rows, 6 crown scales between crown oculars, 19 crown scales (n=1 male) vs 132-137 ventrals, 23-26 mid body rows 7-8 crown scales between crown oculars, 21-22 crown scales (n=4 both sexes).

A. mabuensis usually has a head pattern with a well-developed inverted 'V'-shape, but sometimes reduced to two isolated dark blotches at the back of the head in the holotype. This head pattern is virtually absent in *A. piersoni* sp. nov..

Both *A. piersoni* sp. nov. and *A. mabuensis* are depicted in life in Branch and Bayliss (2009), and identified effectively by their collection locality, with the specimen from Mount Namuli being *A. piersoni* sp. nov. and those from Mount Mabu being *A. mabuensis*.

The two preceding species, being the entirety of the subgenus *Piersonvipera* subgen. nov.

are separated from all other species of *Atheris (sensu lato)* by the following suite of characters:

- (1) Small adult size, maximum length 384mm (all other *Atheris* exceed 580mm TL, with the exception of - *A. katangensis* De Witte, 1953, TL 397mm; *A. barbouri* Loveridge, 1930, TL 369 mm (Barbour and Howell, 1998); and the unique type of *A. acuminata* Broadley, 1998, TL 440mm);
- (2) The lack of 'horns' (enlarged supraocular scales are present in *A. ceratophora* Werner, 1896);
- (3) The lack of lanceolate or acuminate scales on top of the head (present in *A. hispida* Laurent, 1955 and *A. acuminata*);
- (4) Having weakly keeled gular scales (smooth only in *A. nitschei* Tornier, 1902 and *A. woosnami* Boulenger, 1906; gulars moderately keeled in the eastern species, *A. rungweensis* Bogert, 1940, *A. desaixi* Ashe, 1968, *A. ceratophora* and *A. katangensis*, and strongly keeled in the remaining central and western species);
- (5) Lacking interoculars (*sensu* Broadley, 1998, i.e. the supralabials are in contact with circumorbitals; 1 or 2 in *A. desaixi* and *A. rungweensis*);
- (6) Having 19-21 transverse head scales (*sensu* Broadley, 1998, i.e. number of scales across head between posterior supralabials;

these are reduced in highly arboreal species, e.g. *A. squamigera* Hallowell, 1854, 15-22, *A. hispida*, 12; and *A. acuminata*, 10); (7) Having 21-23 mid-body scale rows (MSR) (most species have 27+ MSR rows; reduced in highly arboreal species such as *A. squamigera*, 15-25, *A. hispida*, 15-19, and *A. acuminata*, 14);

(8) Lateral body scales not serrated (strongly serrated in *A. ceratophora*, *A. desaixi*, *A. nitschei* Tornier, 1902 *A. woosnami* Boulenger, 1906 and *A. rungweensis*, and weakly serrated in *A. katangensis*);

(9) Having 8-9 supralabials (six in *A. acuminata*, 10-12 in *A. desaixi*);

(10) Having low ventral counts 128-137 (this is the lowest in the genus; usually over 140 in both sexes in *A. nitschei*, *A. woosnami*, *A. rungweensis*, *A. desaixi*, *A. chlorechis* (Pel, 1852), *A. hispida*, *A. mongoensis* Collet and Trape, 2020, *A. matildae* Menegon, Davenport and Howell, 2011 and *A. subocularis* Fischer, 1888, and in the only known males of *A. acuminata* (160) and *A. hirsuta* Ernst and Rödel, 2002 (160));

(11) Having low subcaudal counts - 39-47 (always higher than 45 in *A. rungweensis*, *A.*

ceratophora, *A. chlorechis*, *A. squamigera* and *A. hispida*; and 54 and 58 in the only known males of *A. acuminata* and *A. hirsuta*, and 50 or more in *A. hetfieldi* respectively);

(12) Having a prehensile tail (non-prehensile in *A. barbouri*), and higher subcaudal (*A. barbouri* 15-21) and labial (*A. barbouri*, supralabials 5-6, infralabials 4-5) counts (modified from Branch and Bayliss 2009).

Snakes in the genus *Atheris* Cope, 1862 including all subgenera are separated from all other African vipers by the following unique suite of characters:

No single small horn above the eye; pupil vertical; many small scales on top of the head; head is not pear shaped; tail long; 38-65 single subcaudals; occurs in mid altitude woodland or forest; usually a mixture of black, yellow and/or green in life and arboreal in habit (excluding it seems *A. barbouri*).

Snakes in the closely related genus *Proatheris* Broadley, 1966 are separated by the presence of an enlarged supraocular shield.

Snakes in the other closely related genus *Montatheris* Broadley, 1996 are separated by the presence of paired subcaudals (versus single in *Atheris* Cope, 1862) and by having a tail that is not prehensile.

Distribution: *Atheris (Piersonvipera) piersoni* sp. nov. is known only from Mount Namuli, the highest peak in the Zambezia Province of Mozambique.

Atheris (Piersonvipera) mabuensis (Branch and Bayliss, 2009) is from the Mount Mabu area.

Both locations are in northern Mozambique, south-east Africa.

Comment: While the collection locations of each species as diagnosed above are only about 80 km apart in a straight line, there appears to be generally unsuitable habitat of low elevation in between, prohibiting contact between the relevant populations..

Notwithstanding the lack of genetic evidence of separation, the obvious morphological divergence of the two forms implies long-term separation and on this basis I have chosen to formally name the previously unnamed form as a species rather than subspecies.

Etymology: The subgenus *Piersonvipera* subgen. nov. (this paper) and species *Atheris (Piersonvipera) piersoni* sp. nov. are both formally named in honour of Charles Pierson of Moss Vale, New South Wales, Australia in recognition of his amazing sacrifices and contributions to wildlife conservation in Australia. For details see the account in Hoser (1996).

KENYAVIPERA SUBGEN. NOV.

LSIDurn:lsid:zoobank.org:act:3CE632FF-B061-4362-A459-39E524B65D84

Type species: *Atheris desaixi* Ashe, 1968.

Diagnosis: The snake in this monotypic subgenus is separated from all other species within *Atheris* Cope, 1862 by the following unique combination of characters: A thick bodied snake with 41-54 subcaudals; the snake is not predominantly plain brown on top

with very prickly head scales or found west of Ghana; it has 160-174 ventrals; is found north of latitude 15 Deg. S. (only known from the northern Nyembi Range and the nearby Chuka area, at south-eastern Mount Kenya); lateral scales serrated; no supraocular "horns"; four suprarostrol scales in first (or only) row; dorsals rounded at the apex; each dorsal scale tipped with yellow.

Snakes in the genus *Atheris* Cope, 1862 including all subgenera are separated from all other African vipers by the following unique suite of characters:

No single small horn above the eye; pupil vertical; many small scales on top of the head; head is not pear shaped; tail long; 38-65 single subcaudals; occurs in mid altitude woodland or forest; usually a mixture of black, yellow and/or green in life and arboreal in habit (excluding it seems *A. barbouri*).

Snakes in the closely related genus *Proatheris* Broadley, 1966 are separated by the presence of an enlarged supraocular shield.

Snakes in the other closely related genus *Montatheris* Broadley, 1996 are separated by the presence of paired subcaudals (versus single in *Atheris* Cope, 1862) and by having a tail that is not prehensile.

Distribution: The sole species in the genus is only known from the northern Nyembi Range and the nearby Chuka area, at south-eastern Mount Kenya, both in Kenya, Africa.

Etymology: Named in reflection of the location this snake subgenus occurs, Kenya, as well as the fact that the snake is a viper.

Content: *Atheris (Kenyavipera) desaixi* Ashe, 1968 (Monotypic).

ATHERIS (ADENORHINUS) CUMMINGAE SP. NOV.

LSIDurn:lsid:zoobank.org:act:3CA33E5F-75A9-46B4-B0EF-A04D2F82701E

Holotype: A preserved specimen at the Museo Tridentino di Scienze Naturali, Trento, Italy, specimen number MTSN 5032, collected from the Kigogo Forest Reserve, Udzungwa Mountains, Tanzania, Latitude: -7.8000 S., Longitude: 36.6833 E. at an elevation of about 1,900 metres ASL.

This facility allows access to its holdings.

Paratype: A preserved specimen at the Museo Tridentino di Scienze Naturali, Trento, Italy, specimen number MTSN 5033, collected from the Kigogo Forest Reserve, Udzungwa Mountains, Tanzania, Latitude: -7.8000 S., Longitude: 36.6833 E. at an elevation of about 1,900 metres ASL.

Diagnosis: *Atheris (Adenorhinus) cummingae sp. nov.* known only from the Kigogo Forest Reserve, Udzungwa Mountains, Tanzania has until now been treated as a population of either, *Atheris ceratophora* Werner, 1896, type locality of Usambara Mountains and occurring in suitable habitat blocks between there and the north-east Udzungwa Mountains, all in Tanzania, or more recently as *A. matildae* Menegon, Davenport and Howell, 2011, known from the Rungwe, Ukinga and Misuki blocks near the Tanzania, Malawi border, but based on sequences in Genbank of all three taxa, is clearly of a separate geographically isolated and allopatric species, likely to have diverged from the other two at least 1.5 MYA.

Recent published molecular phylogenies have placed the population herein identified as *Atheris cummingae sp. nov.* as being most closely related to the nepotistically patronym named species *A. matildae* (named after Tim Devenport's then recently born child, aged 5 YO at the time she was honoured, with the spurious claim she was a great herpetologist), with an estimated divergence of 1.5 MYA, rather than *Atheris ceratophora*, from which it diverged about 2.2 MYA, although I note that Menegon *et al.* (2011) identify this taxon as *A. ceratophora*. Elsewhere in the past 15 years it has been identified as either "*Atheris cf. ceratophora*" or "*A. cf. ceratophora*".

The three species are separated from one another by the following three unique combinations of characters:

A. cummingae sp. nov. has a dorsum and flanks that are mainly yellow, rather than blackish and the dark markings are in the form of distinctive brownish-black spots of irregular shape and small to medium on size, some of which may join to form elongated and even more irregularly-shaped dark markings. There are no lines as

such running along the lateral edges of the dorsum as seen in *A. matildae*. The upper surface of the head is mainly yellow, but with some black markings of irregular nature and/or peppering. The supraciliary spines above the eye are all or mainly yellow.

Separating *A. cummingae sp. nov.* from the other two species (*A. ceratophora* and *A. matildae*) is a distinctive dark-brown to black line that starts above the eye and runs to the back of the temple on either side of the head. Because the entirety of the top of the head is blackish in *A. matildae* (see below), this line is not seen in that species. The same line is either absent, broken or faded in *A. ceratophora*. Sides of the head are mainly yellow, save for limited dark pigment at the very edges of some scales.

A. ceratophora has a dorsum and flanks that are mainly yellow, rather than blackish and the dark markings are in the form of distinctive brownish-black spots of irregular shape and small to medium on size, some of which may join to form elongated and even more irregularly-shaped dark markings, but those on the mid dorsum are more prominent than ones on the upper and mid flanks, versus of similar size and intensity in *A. cummingae sp. nov.*. There are no lines as such running along the lateral edges of the dorsum as seen in *A. matildae*. The upper surface of the head is mainly yellow, but with some black markings of irregular nature and/or peppering and in particular at the rear of the head. The supraciliary spines above the eye are all or mainly yellow.

Atheris matildae has a dorsum that is a pattern of mainly black, over a yellow back ground, being mainly black on the mid dorsum and on the upper flanks yellow, intruding in and out of the broader medial line, forming a distinct reticulated pattern, or alternatively tending to be of one. The upper surface of the head is blackish all over (separating this species from *A. cummingae sp. nov.* and *A. ceratophora*) as are the supraciliary spines above the eye. Sides of the head, including labials are yellow; marked brown or peppered brown on edges.

The three species, *A. cummingae sp. nov.*, *A. ceratophora*, *A. matildae* are separated from all other species of *Atheris* Cope, 1862 *sensu lato* by the presence of two or three supraciliary spines above the eye, each composed of a single supraciliary scale, in turn surrounded a series of smaller raised scales.

Snakes in the genus *Atheris* Cope, 1862 including all subgenera are separated from all other African vipers by the following unique suite of characters:

No single small horn above the eye; pupil vertical; many small scales on top of the head; head is not pear shaped; tail long; 38-65 single subcaudals; occurs in mid altitude woodland or forest; usually a mixture of black, yellow and/or green in life and arboreal in habit (excluding it seems *A. barbouri*).

Snakes in the closely related genus *Proatheris* Broadley, 1966 are separated by the presence of an enlarged supraocular shield.

Snakes in the other closely related genus *Montatheris* Broadley, 1996 are separated by the presence of paired subcaudals (versus single in *Atheris* Cope, 1862) and by having a tail that is not prehensile.

A. matildae in life is depicted in Menegon *et al.* (2011), and online at:

<http://novataxa.blogspot.com/2011/12/atheris-matildae-2011-tanzania.html>

and

<https://news.mongabay.com/2011/12/new-large-horned-viper-discovered-but-biologists-keep-location-quiet/>

A. cummingae sp. nov. in life is depicted online at:

<https://www.inaturalist.org/observations/1648208>

A. ceratophora in life is depicted online at:

<https://www.inaturalist.org/observations/22379210>

and

<https://www.inaturalist.org/observations/22378990>

and

<https://www.inaturalist.org/observations/112048989>

and

<https://www.inaturalist.org/observations/22378907>

Conservation of this taxon: Meshack (2009), noted that the Mufindi forests, of which Kigogo Forest Reserve is an important fragment, is presently known to include the most range restricted species of any location in the Udzungwas, highlighting the conservation significance of this remnant patch, still under threat from encroachment and harvesting from outside.

A. cummingae sp. nov. is a range-restricted endemic only known from the type locality. Other specimens morphologically similar to this snake from other parts of the Udzungwa Mountains area are morphologically and genetically most similar to *A. ceratophora* and therefore referred to that species.

A. cummingae sp. nov. should therefore be formally identified as highly threatened and in a legislative sense, "critically endangered" would be the appropriate legal designation.

This species needs a management plan and appropriate implementation as a matter of urgency.

Included should be the need for multiple captive populations as insurance against extinction. These captives should be held in multiple countries and both within and outside the government sector.

The collection location of the species has not been withheld as to do so is in my view counter-productive to the long-term conservation of the species, noting that this is best achieved by identification of the habitat and ecosystem, making it well-known to people, including the local inhabitants and the subsequent preservation of it as a whole.

I note the recent upsurge of herpetological tourism, where enthusiasts travel to find, catch, photograph and release target species in their natural habitats and this species lends itself to be a target for such eco-tourism.

Distribution: *A. cummingae* sp. nov. is only known from the Kigogo Forest Reserve, within the Mufindi forests within the Udzungwa Mountains area. Specimens that are morphologically and genetically similar to *A. ceratophora* from other parts of the Udzungwa Mountains are referred to that taxon.

Etymology: *A. cummingae* sp. nov. is named in honour of wildlife conservation icon and journalist Fia Cumming of Lyons, Canberra, ACT, Australia, previously of Chatswood, NSW, Australia, in recognition of major contributions and sacrifices for wildlife conservation globally.

See Hoser (1996) for details.

ATHERIS (WOOLFVIPERA) EUANEDWARDSI SP. NOV.

LSIDDurn:lsid:zoobank.org:act:0ED02F11-6C3E-4C4F-838A-82657F304765

Holotype: A preserved specimen at the K.M. Howell collection, University of Dar es Salaam, Dar es Salaam, Tanzania, Africa, specimen number KMH 6150 collected from the Gombe National Park, Tanzania, Latitude 4.6983 S., Longitude 29.6446 E.

This facility allows access to its holdings.

Paratype: A preserved specimen at the Museum of Natural History, London, UK, specimen number BMNH 1 979.982 collected from Kigoma, Tanzania, Africa, Latitude 4.8824 S., Longitude 29.6615 E.

Diagnosis: Until now, both *Atheris euanedwardsi* sp. nov. from Gombe National Park, Tanzania and immediately south of there in the Kigoma area and *A. ernestswilei* sp. nov. from the Ufipa Plateau, Tanzania have been treated as outlier populations of *A. rungweensis* (Bogert, 1940), type locality Rungwe Mountains (southern highlands), Tanzania, a species found in this immediate region only, including immediately adjacent Ukinga uplands and in north-east Malawi in the Misuki uplands.

They are all readily separated from the morphologically similar species *A. nitschei* Tornier, 1902, type locality of Mpororo Swamp, Tanzania, and found in this general region, (as well as the allopatric and divergent *Atheris woosnami* Boulenger, 1906 with a type locality of Mount Ruwenzori, Uganda, herein formally resurrected from the synonymy of *A. nitschei*) by the absence of a black arrowhead marking on top of the head, this being bold, distinct and sometimes fragmented in (*A. nitschei* and *A. woosnami*), as well as the absence of a massive preponderance

of dark pigmentation along a broad mid-dorsal line (broken by light interspaces in *A. woosnami*), combined with generally lighter (green) pigment on the lateral edges of the dorsum and flanks, with only limited amounts of dark, dark spotting, or similar.

(*A. woosnami* is further separated from *A. nitschei* by the reduced size of the arrowmark on the head, with it commencing behind the line between the eyes, versus in front in *A. nitschei*.)

The three species, *Atheris euanedwardsi* sp. nov., *A. ernestswilei* sp. nov. and *A. rungweensis* are readily separated from each other by the following combinations of characters:

Atheris euanedwardsi sp. nov. is generally lime green above, with light yellow fadings forming an indistinct and ill defined reticulatum over the body. Along the mid dorsal line across a moderately broad diameter from the head down is a light grey peppering. Anterior of the upper surface of the head is green, with grey peppering posteriorly. Upper labials are bright yellow at the bottom, becoming green above and this green is then including most of the upper side of the head.

There are no markings of any sort on the labials.

A. ernestswilei sp. nov. is generally greenish on top, but without the faded yellow indistinct and ill defined reticulatum on the body or the flanks as seen in *A. euanedwardsi* sp. nov.. Along the mid-dorsal line is a very slight grey tinge, from the back of the head, where it is reasonably prominent as a marking from the bridge of the eyes backwards, noting it is blunt edged anteriorly and not arrow-shaped as seen in *A. nitschei* or *A. woosnami*. On the dorsum along the mid dorsal line, but positioned alternately along it and away from it, are small dark, blackish blotches of irregular shape, but tending to be triangular, with apex pointing to the midline (laterally), each bounded on the midline sides by lighter yellowish-green, this bright border not on the lower "base" of each triangle.

The labials are generally whitish with dark grey bars or patches, although this is sometimes obscured by peppering of the labials in some specimens, this being the only one of the three relevant species to have labials marked in this way.

A. rungweensis is mainly dark grey on top and the flanks, with a series of bold thin green markings on either side of the midline, on the border of the lateral surfaces, being about 1 scale wide, from head to tail, these being broken on the neck, becoming entire on the upper body and to the tail.

The head is generally even in colour, but a greenish-grey colour, rarely with minor peppering or spots, dark or light. Labials are slightly lighter than above (the top of the head), but there is no obvious markings or colour changes on the labials in any way, with only a gradual change in colour intensity on different parts of the head.

A. nitschei and *A. woosnami* are further separated from *A. euanedwardsi* sp. nov., *A. ernestswilei* sp. nov. and *A. rungweensis* by having scales on top of the head anteriorly smooth or feebly keeled; 18-20 scales across the back of the head between posterior supralabials; dorsal body scales with keels extending to the tip; dorsum yellowish green with an intense and sometimes variable black marking along a well-defined midline.

In turn *A. euanedwardsi* sp. nov., *A. ernestswilei* sp. nov. and *A. rungweensis* have scales on top of the head anteriorly strongly keeled; 24-26 scales across the back of the head between posterior supralabials; dorsal body scales with keels not extending to the tip; dorsum light lime green to blackish, often with symmetrical yellow markings on back of head and dorsolateral yellow zig-zag lines in a reticulatum, or irregularly-shaped triangles or spots or a generally dark colour with generally well defined yellow-green lines crossing on either side of the dorsolateral edge (as a single line on each side) (modified from Loveridge, 1942).

The five preceding species are separated from all other species within *Atheris* Cope, 1862 by the following combination of characters: 39-59 subcaudals; does not have a predominantly brown colour, with very prickly head scales or is found west of Democratic Republic of Congo; 150-165 ventrals; occurs north of 15 Deg. South; lateral scales serrated; no supraciliary "horns"; three to five suprarostrals in first (or only) row; dorsals pointed at

apex; dorsal scales not tipped with yellow; gular scales smooth or feebly keeled; lateral scale rows 2-6 or -8 strongly keeled; dorsum green with irregular black markings or green to blackish with symmetrical yellow markings and/or lines, sometimes indistinct or faded.

Snakes in the genus *Atheris* Cope, 1862 including all subgenera are separated from all other African vipers by the following unique suite of characters:

No single small horn above the eye; pupil vertical; many small scales on top of the head; head is not pear shaped; tail long; 38-65 single subcaudals; occurs in mid altitude woodland or forest; usually a mixture of black, yellow and/or green in life and arboreal in habit (excluding it seems *A. barbouri*).

Snakes in the closely related genus *Proatheris* Broadley, 1966 are separated by the presence of an enlarged supraocular shield.

Snakes in the other closely related genus *Montatheris* Broadley, 1996 are separated by the presence of paired subcaudals (versus single in *Atheris* Cope, 1862) and by having a tail that is not prehensile.

A. euanedwardsi sp. nov. is depicted online at:

<https://storymaps.arcgis.com/stories/4530ed5edb924a2d991d2b6ef4bf2b53>

A. rungweensis in life is depicted in Menegon *et al.* (2011) in figure 7, middle left and online at:

<https://www.inaturalist.org/observations/120811957>

and

<https://www.inaturalist.org/observations/112271362>

and

<https://www.inaturalist.org/observations/120811991>

A. nitschei is depicted in life in Menegon *et al.* (2011) in figure 7, bottom right and online:

<https://www.inaturalist.org/observations/151711653>

and

<https://www.inaturalist.org/observations/95084667>

A. woosnami in life is depicted online at:

<https://www.inaturalist.org/observations/125589156>

and

<https://www.inaturalist.org/observations/136743961>

Menegon *et al.* (2014) found that *Atheris ernestswilei* sp. nov. and *A. rungweensis* diverged 2.5 MYA which is self-evidently species-level divergence noting no known sympatry or co-existence of the relevant forms. They had no data for *A. euanedwardsi* sp. nov.

They also found that the type form of *A. rungweensis* diverged from the type form of *A. nitschei* 5.4 MYA.

Distribution: *Atheris euanedwardsi* sp. nov. is known only from Gombe National Park, Tanzania and immediately south of there in the Kigoma area and so should be regarded as a range-restricted endemic that is vulnerable to extinction.

Etymology: Named in honour of Euan Edwards, of the Gold Coast, Queensland, Australia, in recognition of his many contributions to herpetology over many decades, including some serious fieldwork in most parts of Africa, including east Africa.

ATHERIS (WOOLFVIPERA) ERNESTSWILEI SP. NOV.

LSIDDurn:lsid:zoobank.org:act:48D2EC86-EA61-4873-87D7-5C8CF81EBE71

Holotype: A specimen lodged at the Southern Highlands Conservation Programme herpetological Collection, Mbeya, Tanzania, specimen number SHCP 07-R-02 collected from Nkasi/Ntantwa, Tanzania, Africa.

This facility allows access to its holdings.

Diagnosis: Until now, both *A. ernestswilei* sp. nov. from the Ufipa Plateau, Tanzania and *Atheris euanedwardsi* sp. nov. found further north in the Gombe National Park, Tanzania and immediately south of there in the Kigoma area have been treated as outlier populations of *A. rungweensis* (Bogert, 1940), type locality Rungwe Mountains (southern highlands), Tanzania, a species found in this immediate region only, including immediately adjacent

Ukinga uplands and in north-east Malawi in the Misuki uplands.

They are all readily separated from the morphologically similar species *A. nitschei* Tornier, 1902, type locality of Mpororo Swamp, Tanzania, and found in this general region, as well as the allopatric and divergent *Atheris woosnami* Boulenger, 1906 with a type locality of Mount Ruwenzori, Uganda, herein formally resurrected from the synonymy of *A. nitschei* by the absence of a black arrowhead marking on top of the head, this being bold, distinct and sometimes fragmented; as well as the absence of a massive preponderance of dark pigmentation along a broad mid-dorsal line (broken by light interspaces in *A. woosnami*), combined with generally lighter (green) pigment on the lateral edges of the dorsum and flanks, with only limited amounts of dark, dark spotting, or similar.

A. woosnami is further separated from *A. nitschei* by the reduced size of the arrowmark on the head, with it commencing behind the line between the eyes, versus in front in *A. nitschei*.

The three species, *Atheris euanedwardsi* sp. nov., *A. ernestswilei* sp. nov. and *A. rungweensis* are readily separated from each other by the following combinations of characters:

Atheris euanedwardsi sp. nov. is generally lime green above, with light yellow fadings forming an indistinct and ill defined reticulatum over the body. Along the mid dorsal line across a moderately broad diameter from the head down is a light grey peppering. Anterior of the upper surface of the head is green, with grey peppering posteriorly. Upper labials are bright yellow at the bottom, becoming green above and this green is then including most of the upper side of the head.

There are no markings of any sort on the labials.

A. ernestswilei sp. nov. is generally greenish on top, but without the faded yellow indistinct and ill defined reticulatum on the body, or the flanks seen in *A. euanedwardsi* sp. nov.. Along the mid-dorsal line is a very slight grey tinge, from the back of the head, where it is reasonably prominent as a marking from the bridge of the eyes backwards, noting it is blunt edged anteriorly and not arrow-shaped as seen in *A. nitschei* or *A. woosnami*. On the dorsum along the mid dorsal line, but positioned alternately along it and away from it, are small dark, blackish blotches of irregular shape, but tending to be triangular, with apex pointing to the midline (laterally), each bounded on the midline sides by lighter yellowish-green, this bright border not on the lower "base" of each triangle.

The labials are generally whitish with dark grey bars or patches, although this is sometimes obscured by peppering of the labials in some specimens, this being the only one of the three relevant species to have labials marked in this way.

A. rungweensis is mainly dark grey on top and the flanks, with a series of bold thin green markings on either side of the midline, on the border of the lateral surfaces, being about 1 scale wide, from head to tail, these being broken on the neck, becoming entire on the upper body and to the tail.

The head is generally even in colour, but a greenish-grey colour, rarely with minor peppering or spots, dark or light. Labials are slightly lighter than above (the top of the head), but there is no obvious markings or colour changes on the labials in any way, with only a gradual change in colour intensity on different parts of the head.

A. nitschei and *A. woosnami* are further separated from *A. euanedwardsi* sp. nov., *A. ernestswilei* sp. nov. and *A. rungweensis* by having scales on top of the head anteriorly smooth or feebly keeled; 18-20 scales across the back of the head between posterior supralabials; dorsal body scales with keels extending to the tip; dorsum yellowish green with intense and sometimes variable black marking along a well-defined midline.

In turn *A. euanedwardsi* sp. nov., *A. ernestswilei* sp. nov. and *A. rungweensis* have scales on top of the head anteriorly strongly keeled; 24-26 scales across the back of the head between posterior supralabials; dorsal body scales with keels not extending to the tip; dorsum light lime green to blackish, often with symmetrical yellow markings on back of head and dorsolateral yellow zig-zag lines in a reticulatum, or irregularly-shaped triangles

or spots or a generally dark colour with generally well defined yellow-green lines crossing on either side of the dorsolateral edge (as a single line on each side) (modified from Loveridge, 1942).

The five preceding species are separated from all other species within *Atheris* Cope, 1862 by the following combination of characters: 39-59 subcaudals; does not have a predominantly brown colour, with very prickly head scales or is found west of Democratic Republic of Congo; 150-165 ventrals; occurs north of 15 Deg. South; lateral scales serrated; no supraciliary "horns"; three to five suprarostrals in first (or only) row; dorsals pointed at apex; dorsal scales not tipped with yellow; gular scales smooth or feebly keeled; lateral scale rows 2-6 or -8 strongly keeled; dorsum green with irregular black markings or green to blackish with symmetrical yellow markings and/or lines, sometimes indistinct or faded.

Snakes in the genus *Atheris* Cope, 1862 including all subgenera are separated from all other African vipers by the following unique suite of characters:

No single small horn above the eye; pupil vertical; many small scales on top of the head; head is not pear shaped; tail long; 38-65 single subcaudals; occurs in mid altitude woodland or forest; usually a mixture of black, yellow and/or green in life and arboreal in habit (excluding it seems *A. barbouri*).

Snakes in the closely related genus *Proatheris* Broadley, 1966 are separated by the presence of an enlarged supraocular shield.

Snakes in the other closely related genus *Montatheris* Broadley, 1996 are separated by the presence of paired subcaudals (versus single in *Atheris* Cope, 1862) and by having a tail that is not prehensile.

A. euanedwardsi sp. nov. is depicted online at:

<https://storymaps.arcgis.com/stories/4530ed5edb924a2d991d2b6ef4bf2b53>

A. rungweensis in life is depicted in Menegon *et al.* (2011) in figure 7, middle left and online at:

<https://www.inaturalist.org/observations/120811957>

and

<https://www.inaturalist.org/observations/112271362>

and

<https://www.inaturalist.org/observations/120811991>

A. nitschei is depicted in life in Menegon *et al.* (2011) in figure 7, bottom right and online at:

<https://www.inaturalist.org/observations/151711653>

and

<https://www.inaturalist.org/observations/95084667>

A. woosnami in life is depicted online at:

<https://www.inaturalist.org/observations/125589156>

and

<https://www.inaturalist.org/observations/136743961>

Menegon *et al.* (2014) found that *Atheris ernestswilei* sp. nov. and *A. rungweensis* diverged 2.5 MYA which is self-evidently species-level divergence noting no known sympatry or co-existence of the relevant forms. They had no data for *A. euanedwardsi* sp. nov.

They also found that the type form of *A. rungweensis* diverged from the type form of *A. nitschei* 5.4 MYA.

Distribution: *Atheris ernestswilei* sp. nov. is known only from the Ufipa Plateau region of Tanzania (west of Lake Rukwa). It should be regarded as a range-restricted endemic that is vulnerable to extinction.

Etymology: Named in honour of Ernest Swile of Athlone (Cape Town), South Africa, in recognition of his assistance's with herpetological fieldwork across Africa.

ATHERIS (POECILOSTOLUS) MARLENESWILEAE SP. NOV.

LSIDDurn:lsid:zoobank.org:act:FB7C9598-6553-42B2-A9AA-8BD7AFAF6662

Holotype: A preserved specimen at the Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe, specimen number NMZB-UM 5393 collected from Kakamega Forest, Kenya, Africa, Latitude

0.2913 N., Longitude 34.8565 E.

This facility allows access to its holdings.

Paratypes: 1/ Two preserved specimens at the Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe, specimen numbers NMZB-UM 6518-9 collected from Kakamega Forest, Kenya, Africa, Latitude 0.2913 N., Longitude 34.8565 E.

2/ 64 preserved specimens at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA, specimen numbers MCZ Herp R-40797, 40799, 40800, 40805, 40806, 40807, 40808, 40810, 40812, 40815, 40818, 40820, 40821, 40823, 40824, 40825, 40826, 40827, 40828, 40829, 40830, 40831, 40833, 40834, 40835, 40836, 40838, 40841, 40796, 40798, 40801, 40802, 40803, 40804, 40809, 40811, 40813, 40814, 40816, 40817, 40819, 40822, 40832, 40837, 40839, 40840, all collected at Kaimosa, Kakamega, Kenya, Africa, Latitude .2055555 N., Longitude 34.491667 E.

Diagnosis: Until now *Atheris marleneswileae* sp. nov. has been treated as a population of

A. squamigera Hallowell, 1854 (in the subgenus *Poecilostolus* Günther, 1863).

There are several populations of *A. squamigera* Hallowell, 1854 type location Gabon, Guinea, that have been described as other species and subspecies, but all have been previously listed and synonymised by Loveridge (1957) and Broadley (1998).

Notwithstanding the preceding, there is clear evidence of regional divergence and allopatry between the populations, implying species-level divisions.

At the barest minimum, this includes "*Atheris squamigera robusta* Laurent, 1956" with a type locality of Ituru, Democratic Republic of Congo (DRC), which is morphologically divergent to the type form and formally recognised as a separate species.

A. robusta as recognized herein occurs in the region of east DRC and nearby Uganda, west of Lake Victoria and including western Tanzania further south. *A. marleneswileae* sp. nov. occurs east of Lake Victoria and Lake Kyoga in the forested areas around Kakamega, Kenya. *A. squamigera* occupies the rest of the range for the putative taxon, being most of the DRC, Congo (Brazzaville), Equatorial Guinea, Gabon, Cameroon, Central African Republic, east Nigeria and Angola.

The three species, *A. squamigera*, *A. robusta* and *A. marleneswileae* sp. nov. are separated from one another by the following unique character combinations:

A. squamigera has a dorsal pattern characterised by a greenish dorsum with distinctive whitish, creamish, or lighter green semi-irregular narrow crossbands, often broken and with scale tips on the dorsum either green, light green, or sometimes whitish tipped, or otherwise as just detailed but yellowish instead. Under the chin, the scales are green. There are 12-13 scales around (and) entering the eye. Iris is green.

A. robusta has a greenish-brown dorsum with the crossbands reduced, with each being simply 3-5 yellowish or yellow tipped scales, as well as a separate layer of dull yellowish brown scales (or parts thereof) on the dorsum or flanks. Most scale tips on the dorsum and flanks are slightly yellow tipped. Under the chin the scales are yellow. There are 13-14 scales around (and) entering the eye. Iris is bluish-grey.

A. marleneswileae sp. nov. is similar in colour to *A. robusta*, but is separated from that taxon by having a strong reddish or brown tinge over the dorsum and flanks, scale tips are yellowish-brown, this extending back onto the mid scales giving the snake are more brownish colour, being a greenish-purplish-brown snake instead. Lower labials are green, with other chin shields yellow in colour. There are usually 15 scales around (and) entering the eye. Iris is brown to golden in colour.

The three preceding species are separated from all others in the genus *Atheris* Cope, 1862, *sensu lato* by the following unique combination of characters:

Lateral scales not, or but feebly and irregularly serrated; no supraocular horns. Rostral three times as wide as deep, surmounted by 3-5 suprarostrals and 5 keeled internasals. Nasals

entire, separated from the eye by 1-3 scales (usually 2); one or two scales between eye and nasal. Dorsal and lateral head shields strongly keeled, 5-11 interorbitals and 15-22 scales across back of head between the posterior supralabials. Eye moderate, its vertical diameter is slightly greater than its distance from the lip. There is rarely a row of scales between the 10-18 circumorbitals and the 7-13 supralabials, usually fourth to sixth below the eye. Midbody scale rows 15-25; scales on neck are lanceolate or acuminate; 2-5 lateral scale rows, frequently duplicated; interorbital scales strongly keeled; interoculabials usually absent (modified from Broadley 1998).

Snakes in the genus *Atheris* Cope, 1862 including all subgenera are separated from all other African vipers by the following unique suite of characters:

No single small horn above the eye; pupil vertical; many small scales on top of the head; head is not pear shaped; tail long; 38-65 single subcaudals; occurs in mid altitude woodland or forest; usually a mixture of black, yellow and/or green in life and arboreal in habit (excluding it seems *A. barbouri*).

Snakes in the closely related genus *Proatheris* Broadley, 1966 are separated by the presence of an enlarged supraocular shield.

Snakes in the other closely related genus *Montatheris* Broadley, 1996 are separated by the presence of paired subcaudals (versus single in *Atheris* Cope, 1862) and by having a tail that is not prehensile.

A. squamigera in life is depicted online at:

<https://www.inaturalist.org/observations/35974716>

and

<https://www.inaturalist.org/observations/3971446>

and

<https://www.inaturalist.org/observations/97472250>

A. robusta in life is depicted online at:

<https://www.inaturalist.org/observations/26674315>

and

<https://www.inaturalist.org/observations/137163256>

A. marleneswilae sp. nov. in life is depicted online at:

<https://www.flickr.com/photos/mp7/51102635468/>

and

<https://www.flickr.com/photos/mp7/51044740618/>

and

<https://www.inaturalist.org/observations/125373213>

and

<https://www.inaturalist.org/observations/69927141>

and

<https://www.inaturalist.org/observations/102132834>

Distribution: *Atheris marleneswilae* sp. nov. is known only from the region of the type locality, Kakamega Forest, Kenya, Africa, being immediately east of Lake Victoria, Kenya. It should be regarded as a range-restricted taxon that is vulnerable to extinction.

Etymology: Named in honour of Marlene Swile of Mitchell's Plain (Cape Town), South Africa, in recognition of her assistance with herpetological fieldwork across Africa.

ATHERIS BARBOURI DIVERGANS SUBSP. NOV.

LSIDurn:lsid:zoobank.org:act:4D11B56C-052E-4158-B18B-B560E6918C15

Holotype: A preserved specimen at the Museo Tridentino di Scienze Naturali, Trento, Italy, specimen number MTSN 7299 collected from Madehani, Ukinga Mountains, Tanzania, Africa, Latitude 9.3342 S., Longitude 34.0633 E.

This facility allows access to its holdings.

Paratype: A preserved specimen at the Natural History Museum, London, UK, specimen number BMNH 1931.6.6.9 collected from Madehani, Ukinga Mountains, Tanzania, Africa, Latitude 9.3342 S., Longitude 34.0633 E.

Diagnosis: The subspecies *Atheris barbouri divergens* subsp. nov. is confined to the Ukinga Mountains, Tanzania, while the

morphologically similar nominate form *Atheris barbouri* Loveridge, 1930 has a type locality of "Dabaga, Uzungwa Mountains, southeast of Iringa" Tanzania and also occurs in the Southern Highlands of Tanzania.

The two subspecies are separated as follows:

A. barbouri of the nominate form has beige to white rear upper labials and the second and third upper labials past the nostril are of similar size, versus yellowish, sometimes with a greenish tinge rear upper labials and the third upper labial past the nostril is usually much larger than the second in *A. divergens* subsp. nov..

Atheris barbouri (both subspecies) is the only member of the genus *Atheris* Cope, 1862, including all subgenera, to have less than 22 subcaudals and be generally a ground dweller.

Snakes in the genus *Atheris* Cope, 1862 including all subgenera are separated from all other African vipers by the following unique suite of characters:

No single small horn above the eye; pupil vertical; many small scales on top of the head; head is not pear shaped; tail long; 38-65 single subcaudals; occurs in mid altitude woodland or forest; usually a mixture of black, yellow and/or green in life and arboreal in habit (excluding it seems *A. barbouri*).

Snakes in the closely related genus *Proatheris* Broadley, 1966 are separated by the presence of an enlarged supraocular shield.

Snakes in the other closely related genus *Montatheris* Broadley, 1996 are separated by the presence of paired subcaudals (versus single in *Atheris* Cope, 1862) and by having a tail that is not prehensile.

The type form of *Atheris barbouri* is depicted in Menegon *et al.* (2011) on page 52 in Fig 7, top left.

Atheris barbouri divergens subsp. nov. is depicted in Menegon *et al.* (2011) on page 52 in Fig. 7, at top right or online at: <https://www.inaturalist.org/observations/1790296>

Menegon *et al.* (2014) found that *Atheris barbouri divergens* subsp. nov. diverged from *A. barbouri* about 700 thousand YBP. Combined with limited morphological divergence and allopatry supported by a barrier not penetrable by either population, subspecies-level recognition of the newly named taxon is appropriate.

Distribution: The subspecies *Atheris barbouri divergens* subsp. nov. is confined to the Ukinga Mountains, Tanzania, while the morphologically similar nominate form *Atheris barbouri* Loveridge, 1930 has a type locality of "Dabaga, Uzungwa Mountains, southeast of Iringa" Tanzania and also occurs in the Southern Highlands of Tanzania.

Etymology: *A. barbouri divergens* subsp. nov. is named in reflection of the fact that it is a divergent subspecies. The spelling of the subspecies name "*divergens*" is intentional and should not be changed.

MONTATHERIS JOSEPHBURKEI SP. NOV.

LSIDurn:lsid:zoobank.org:act:D316CED9-4540-4318-BC56-484CBE75B850

Holotype: A preserved specimen in the collection of the Natural History Museum, London, UK, specimen number NHMUK ZOO 1950.1.2.69 collected from 1 mile west of Rutundu, Mount Kenya, (about 20 km North East of Mount Kenya), Kenya, Africa, Latitude 0.0412 S., Longitude 37.4635 E.

This facility allows access to its holdings.

Diagnosis: Until now, *Montatheris josephburkei* sp. nov. known only from the high altitude slopes of Mount Kenya has been treated as an isolated population of *Montatheris hindii* Boulenger, 1910.

That taxon has a given type locality of "Fort Hall, Kenya". Based on Boulenger's original description of the specimen's colouration, it is self-evidently of the Aderdare Range form, this range also being proximal to Fort Hall.

Fort Hall does however sit between both areas putative "*Montatheris hindii*" occurs.

While the ranges of each of *M. josephburkei* sp. nov. and *M. hindii* are proximal and potentially within 10 km of each other, based on

potential habitat, the altitude barrier dividing the two populations is sufficient to have maintained long term isolation.

However to date specimens of each taxon have not been found within 20 km of each other.

The divergence of the two populations of what has until now been treated as one species, is confirmed by the substantial consistent morphological divergence between the two species.

The two species are separated by the following character suites:

M. hindii is grey or brown in overall colour (grey/beige overlay) usually and has well defined dark shapes running along either side of the dorsolateral edge, being mainly more-or-less triangular in shape and with whitish borders on the outer edges (*sensu* Boulenger 1910) and has 12-13 scales around the eye, versus reddish (usually, poorly defined dark shapes running along either side of the dorsolateral edge, usually without obvious whitish borders on the outer edges and 14-16 scales around the eye in *M. josephburkei* sp. nov. (versus 12-13 scales in *M. hindii*).

The two preceding species, being the entirety of the genus *Montatheris* Broadley, 1998 are separated from the closely related genus *Atheris* Cope, 1862 by the presence of paired subcaudals (versus single in *Atheris*) and by having a tail that is not prehensile. Snakes in the closely related genus *Proatheris* Broadley, 1966 are separated by the presence of an enlarged supraocular shield.

Snakes in the genus *Atheris*, as well as the genera *Montatheris* and *Proatheris* including all subgenera within *Atheris*, are separated from all other African vipers by the following unique suite of characters:

No single small horn above the eye; pupil vertical; many small scales on top of the head; head is not pear shaped; tail long; 38-65 single subcaudals; occurs in mid altitude woodland or forest; usually a mixture of black, yellow and/or green in life and arboreal in habit (excluding it seems *A. barbouri*).

M. josephburkei sp. nov. in life is depicted online at: <https://www.inaturalist.org/observations/142676665>

M. hindii in life is depicted in Spawls *et al.* (2011) on page 495 at top right and online at: <https://www.inaturalist.org/observations/155358086>

and <https://www.inaturalist.org/observations/69810726>

Distribution: *Montatheris josephburkei* sp. nov. is known only from the high altitude slopes of Mount Kenya (between 2700 to 3800 metres ASL). *Montatheris hindii* Boulenger, 1910 is herein confined to the Aberdare Mountains, Kenya at similar altitude (Spawls *et al.* 2011), although Boulenger's type specimen was taken from about 4000 feet ASL (about 1,333 metres). Both species appear to be confined to treeless moorland and fortunately are known only from areas that are protected. While both are range restricted endemics, they appear to be relatively secure as compared to many other reptile taxa and should at the present time be listed as "vulnerable" species.

Etymology: *M. josephburkei* sp. nov. is named in honour of Joseph Burke of (Fairfield), Melbourne, Victoria, Australia, a highly regarded criminal defence lawyer for services to the legal profession in Australia, including fighting the endemic police corruption in the State of Victoria and (mostly) successfully defending in court, people maliciously charged with fake offences by corrupt police.

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CONFLICT OF INTEREST

None.

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