

A division of the African Tree Viper genus *Atheris* Cope, 1860 into four subgenera (Serpentes:Viperidae).

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Received 15 February 2012, Accepted 2 April 2012, Published 30 April 2012.

ABSTRACT

The African Tree Viper genus *Atheris* has been of interest to taxonomists in recent years. Significant was the removal of the species *superciliaris* to the newly created monotypic genus *Proatheris* and the species *hindii* to the monotypic genus *Montatheris* both by Broadley in 1996 gaining widespread acceptance.

Marx and Rabb (1965), erected a monotypic genus *Adenorhinos* for the species *barbouri*, but this designation has not gained widespread support from other herpetologists, with a number of recent classifications continuing to place the taxon within *Atheris* (e.g. Menegon et. al. 2011).

Phylogenetic studies of the genus *Atheris sensu lato* using molecular methods (e.g. Pyron et. al. 2011) have upheld the validity of the creation of the monotypic genera *Proatheris* and *Montatheris* by Broadley.

These studies have also shown there to be at least four well-defined groups of species within the genus *Atheris* as recognized in early 2012, though not as divergent as seen for the snakes placed within *Proatheris* and *Montatheris*.

As a result, the genus is now subdivided into subgenera using available names for three, with the fourth one being named *Woolfvipera* subgen. nov.

Keywords: new genus; Viper; Africa; *Atheris*; *Poecilostolus*; *Adenorhinos*; *Woolfviper*; *Proatheris*; *Montatheris*.

INTRODUCTION

African Tree Vipers represent a significant case of convergent evolution when compared with Asian Pitvipers (*Trimeresurus* and related genera) and South American Pitvipers (*Bothrops* and related genera).

The majority of species have a derived body form superbly suited to an arboreal existence as a predator of other vertebrates.

African Tree Vipers as a group are fairly small snakes ranging in adult size from *Montatheris hindii* (20-36 cm total length) to *Atheris nitschei* and *A. squamigera* (some specimens may exceed 76 cm). They are characterized by having broad heads,

relatively large eyes, vertical pupils and narrow necks. Their bodies are usually slender and have strongly keeled and overlapping scales. These snakes come in a range of colours and patterns, sometimes within a single species. *Atheris ceratophora* and *A. squamigera* are particularly variable species. Most *Atheris* species are primarily arboreal, but may be frequently found on or near the ground. Snakes placed in the genera *Proatheris* and *Montatheris* are by notable contrast primarily terrestrial.

All *Atheris (sensu lato)* are characterized by normal slow and deliberate movements, relying on their cryptic coloration to avoid detection.

All these snakes are easily separated from the stout, heavily bodied terrestrial species of viper within the genus *Bitis sensu lato*.

African Tree Vipers are endemic to Africa. Many species have very limited ranges and it seems only exist in isolated populations, making them particularly vulnerable to human induced habitat modification. They range across equatorial Africa as far west as the rainforests of Guinea (*Atheris chlorechis*) and as far southeast as coastal Mozambique (*Proatheris superciliaris*). They occur at a wide range of elevations from lowland swamps (*P. superciliaris*) to high altitude montane moorland (*Montatheris hindii*). Rainforest, evergreen forest, montane forest, upland swamp, and lowland swamp bordering grassland are among the habitats utilized by African Tree Vipers.

There have been numerous studies into these snakes, both in terms of ecology and systematics. These have resulted in the publications of, Barbour and Loveridge (1928), Bartlett (1988), Bogert (1940), Boulenger (1906), Branch (2000), Broadley (1960, 1998), Broadley and Howell (1991), Broadley, et. al. (2003), Dobbie and Vogel (2007), Edwards (2000), Emmrich (1997), Ernst and Rödel (2002), Freed (1986), Günther (1863), Hallowell (1856), Ionides and Pitman (1965), Kramer (1961), Laurent (1955, 1956, 1960), Lawson (1993), Lawson (1999), Love (1988), Loveridge (1930, 1933, 1936, 1942, 1953 and 1957), Mallow et. al. (2003), McMahon (1990), Meidinger (1998, 2000), Menegon et. al. (2011), Morgan (1988), Pareti (1994), Pearson (1997), Pel (1851), Peters (1864), Phelps (2010), Pitman (1974), Pook (1990), Rasmussen and Howell (1982, 1998), Spawls (1990), Spawls and Branch (1995), Spawls et. al. (2001), Stevens (1973), Tornier (1902), Vesey-Fitzgerald (1958), Werner (1895) and Witte (1953).

Publications of relevance to the taxonomic placements within this paper include those of Ashe (1968), Boulenger (1910), Broadley (1989), Broadley (1996), Broadley (1998), Cope (1859), Fischer (1888), ICZN (1991), Lawson (1999), Lawson and Ustach (2000), Lawson et. al. (2001), Loveridge (1930), Marx and Rabb (1965), Pyron et. al. (2011) and Werner (1895).

As mentioned in the abstract, recent studies of the phylogeny of these and related snakes have shown clearly that the monotypic genera *Proatheris* and *Montatheris* are more than sufficiently divergent to be valid.

The results of a molecular study published by Pyron et. al. (2011) were somewhat ambiguous in terms of any further divisions within *Atheris* as currently known.

The species placed in the monotypic genus *Adenorhinus* by Marx and Rabb in 1965, namely *A. barbouri*, was found by Pyron et. al. to be closest to *Atheris ceratophora*. In fact both species were found to be closer to one another than any other of the remaining four *Atheris* species tested by Pyron et. al.

Because these two species formed a well defined group separate from other *Atheris* tested and by a significant amount, there is a strong argument that could be mounted for not only retaining the genus *Adenorhinus*, but furthermore it's expansion to include those species closely related to the type species *A. barbouri*, namely *Atheris ceratophora* and *A. katangensis*, as well as *A. mabuensis*, and the recently described species *A. matildae*.

Rather than recognize *Adenorhinus* as a genus, I have taken the conservative position and recognized it within *Atheris* as a subgenus.

Based on the molecular results of Pyron et. al. (2011) and the obvious morphological affinities of the rest of *Atheris*, it is clear that the remainder of *Atheris* also forms three other well-defined species group clades. As a matter of consistency with *Adenorhinus*, these too should be assigned to subgenera.

This is fairly straight forward with those species associated with *Atheris squamigera* being placed in the genus *Poecilostolus* Günther, 1863.

These other species are, *A. hispida*, *A. acuminata*, *A. subocularis*, *A. broadleyi* and *A. hirsuta*.

A. chlorechis remains within *Atheris*, noting that the ICZN has ruled this the type species for the genus. This is a monotypic group.

The remaining species, namely *A. desauxi*, *A. nitschei* and *A. rungweensis*, are herein placed in a new subgenus, namely *Woolfvipera* gen. nov. as defined below.

GENUS *ATHERIS* *SENSU LATO* (DIAGNOSIS)

These snakes are characterized by the characters already mentioned. In addition they have a broadly triangular head, distinct from the neck, thickly covered with small keeled imbricate scales, with small scales separating the labials from the eye. The mouth appears grotesquely wide, the eye is large and the pupil vertically elliptical. The nostrils are laterally oriented, the body is somewhat vertically compressed and the body scales are keeled (not serrated) with apical pits. The laterals are more-or-less oblique, smaller than dorsals and last lateral row is larger, ventrals are rounded, the tail is moderately short but prehensile (the degree of which varies between subgenera), subcaudals are single. Most adults are less than 700 mm in total length and most species appear to move about mostly at night.

They are live-bearing.

SUBGENUS *WOOLFVIPERA* SUBGEN. NOV.

Type species: *Atheris nitschei* Tornier, 1902

Diagnosis: Separated from other species within the genus *Atheris* by the following suite of characters: Their head is broad, flat and angular, conspicuously distinct from the neck, covered above with strongly keeled imbricate scales; the last four upper labials are slightly keeled, the scales below the head to the end of the gape are not keeled.

By contrast snakes in the subgenera *Adenorhinus* and *Poecilostolus* have heads that have a shaggy spiked appearance or if not, then with more strongly keeled scales than seen in *Woolfvipera* subgen. nov. forming three or four distinct rows of ridges on each side of the head running from behind the eyes to the beginning of the neck, with the ridges running down the centre of each scale. In *Woolfvipera* subgen. nov. such ridges are either absent, or if present, barely discernable.

Atheris is separated from this subgenus by the considerably longer and more prehensile tail, noting that *Atheris* (subgenus) tends to have smaller and more imbricate head shields than seen in *Adenorhinus* and *Poecilostolus*.

Ventrally *Woolfvipera* subgen. nov. are immaculate yellow or creamish in colour, versus mottled, patterned or otherwise dark in the other three subgenera *Atheris*, *Adenorhinus* and *Poecilostolus*.

Woolfvipera subgen. nov. are characterized by a somewhat more stout build than the snakes in the other subgenera and due to their attaining a length in line with those of the other subgenera, these snakes are in fact considerably heavier. Their tails are also generally shorter than seen in the other subgenera, except for *Adenorhinus*.

Scale counts for ventrals, subcaudals, mid-body rows, labials and the like are variable and overlap with species in the other subgenera.

The subgenus *Adenorhinus* are separated from other *Atheris* by their smaller adult size (average maximum total length of 45 cm) and non-prehensile tails.

The Green Bush Viper, *Atheris chlorechis*, monotypic for the subgenus *Atheris* is diagnosed by the following suite of characters: Adults large, often 45-60 cm (18-24 inches) in total length. Some specimens occasionally reach 70 cm (28 inches). The keeled body scales are smaller than other members of the genus giving it a smoother appearance. Its tail is long and strongly prehensile with a yellow tip. Not nearly as variable as other *Atheris* species with most adult specimens overwhelmingly

green. Western bush vipers are light green with a pale green or bluish venter and pale yellowish paired dorsal spots. The 15-19 cm (6-7 1/2 inch) babies may be tan or light brown and change to yellowish green with dark green markings within 24 hours (Freed, 1986, Spawls and Branch, 1995).

The snakes in the subgenus *Poecilostolus* are separated from other *Atheris* by the following suite of characters: prehensile tail, shaggy or spinose head, alternatively not such, but with heavily ridged neck and body scales dark, mottled or patterned venter.

Montatheris is separated from all other *Atheris* and *Proatheris* by the following suite of characters: It is a very small viper only 20-36 cm (8-14 inches) in total length. Greyish or brown with pairs of black triangles with light edges on the dorsum. Head is brownish with a dark brown 'V' or arrow mark. Venter is greyish with darker speckling.

Proatheris is separated from all other *Atheris* and *Montatheris* by a pair of large supraocular shields, that none of the others have. It is a heavy bodied viper with a greyish brown dorsum with three rows of dark spots separated by yellowish bars that form a broken lateral line on either side of the body. The unusually elongated head has three blackish chevrons. Venter is whitish with dark blotches, underside of tail is orange or yellow. Adult size is usually 42-60 cm (16-24 inches).

Distribution: *Woolfvipera* gen. nov. is found in Central Africa.

Etymology: *Woolfvipera* subgen. nov. is named in honour Australian herpetologist, Paul Woolf, in recognition of his many decades valuable contribution to Australian herpetology, including as founder president of the Herpetological Society of Queensland.

Content of Subgenus *Woolfvipera* subgen. nov.

Atheris (Woolfvipera) nitschei Tornier, 1902 (Type species)

Atheris (Woolfvipera) desauxi Ashe, 1968

Atheris (Woolfvipera) rungweensis Bogert, 1940

Content of Subgenus *Atheris* Cope, 1860

Atheris (Atheris) chlorenchis (designated type species)

Content of Subgenus *Adenorhinus* Marx and Rabb, 1965

Atheris (Adenorhinus) barbouri Loveridge, 1930 (Type species)

Atheris (Adenorhinus) ceratophora Werner, 1895

Atheris (Adenorhinus) katangensis Witte, 1953

Atheris (Adenorhinus) mabuensis Branch and Bayliss, 2009

Atheris (Adenorhinus) matildae Menegon et. al., 2011

Content of Subgenus *Poecilostolus* Günther, 1863

Atheris (Poecilostolus) squamigera (Hallowell, 1854) (Type species)

Atheris (Poecilostolus) acuminata Broadley, 1998

Atheris (Poecilostolus) broadleyi Lawson, 1999

Atheris (Poecilostolus) hirsuta Ernst and Rödel, 2002

Atheris (Poecilostolus) hispida Laurent, 1955

Atheris (Poecilostolus) subocularis Fischer, 1888

The genus *Montatheris* Broadley (1996) is monotypic for the species *M. hindii*

(Boulenger, 1910). The genus *Proatheris* Broadley (1996) is monotypic for the species *Proatheris superciliaris* (Peters, 1854).

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ISSN 1836-5698 (Print)
ISSN 1836-5779 (Online)