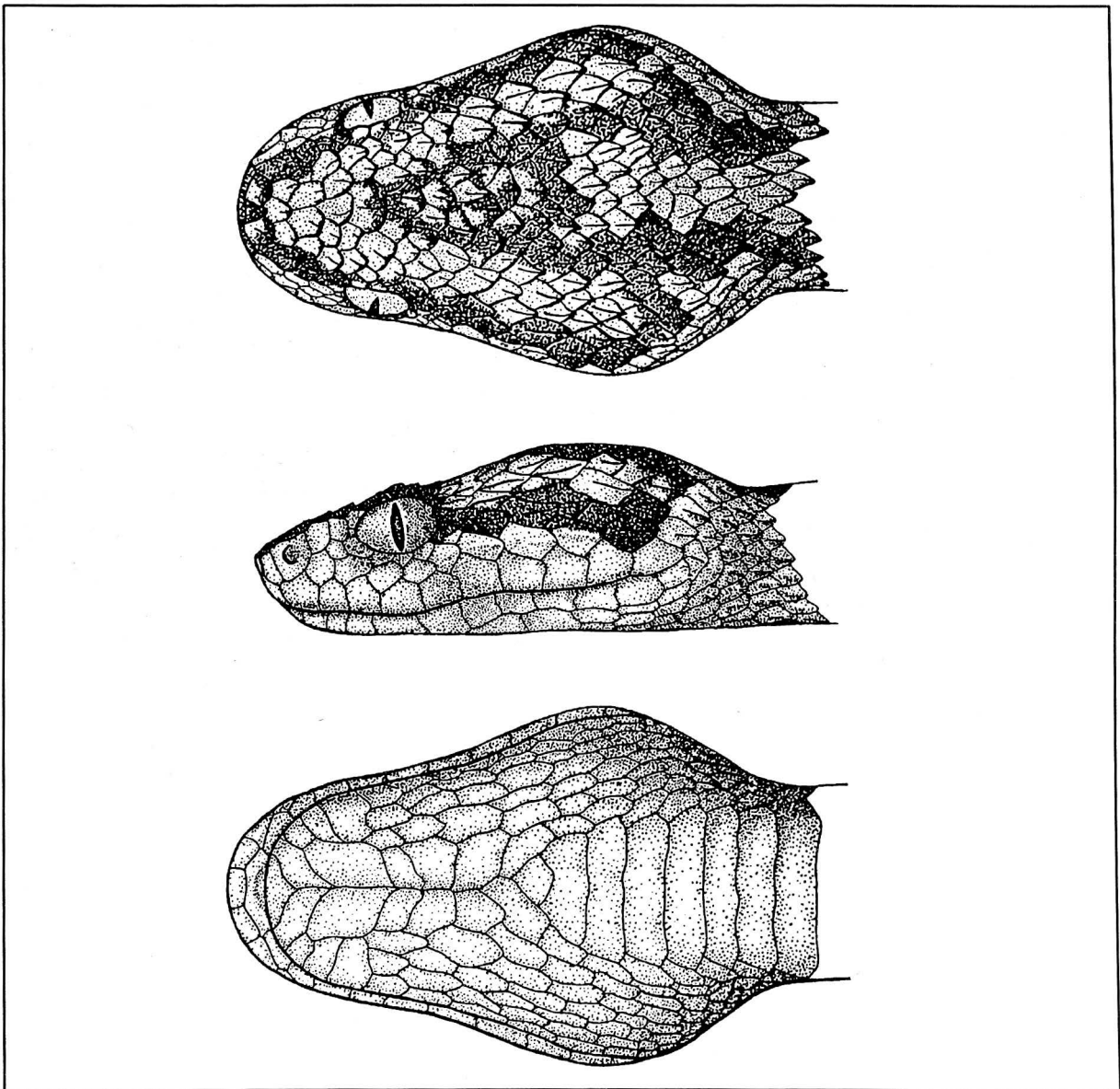


Volume 8, Number 3

July 1998

ISSN 0268-0130

THE HERPETOLOGICAL JOURNAL



Published by the
BRITISH HERPETOLOGICAL SOCIETY

Indexed in
Current Contents

A REVIEW OF THE GENUS *ATHERIS* COPE (SERPENTES: VIPERIDAE), WITH THE DESCRIPTION OF A NEW SPECIES FROM UGANDA

DONALD G. BROADLEY*

Natural History Museum of Zimbabwe, P.O. Box 240, Bulawayo, Zimbabwe

*Present address: The Biodiversity Foundation for Africa, P.O.Box FM 730, Famona, Bulawayo, Zimbabwe

The genus *Atheris* Cope [sensu stricto, after assignment of *superciliaris* (Peters) and *hindii* (Boulenger) to monotypic genera (Broadley, 1996)] is reviewed in order to determine the affinities of a distinctive new species, *Atheris acuminata*, described from a single specimen collected in western Uganda. A key is provided to the ten species recognized, and *A. anisolepis* Mocquard and *A. rungwensis* Bogert are recognized as full species.

INTRODUCTION

The genus *Atheris* Cope has never been fully revised. When discussing his new species *Atheris* (now *Adenorhinos*) *barbouri*, Loveridge (1933) recognized four other species (*ceratophora*, *nitschei*, *chlorechis* and *squamigera*). He did not recognize *A. laeviceps* Boettger, which Schmidt (1923) had revived for two specimens from the Lower Congo: Bogert (1940) subsequently pointed out that the name *anisolepis* Mocquard had priority and recognized it as a subspecies of *A. squamigera*. Bogert (1940) also described *A. nitschei rungwensis* from western Tanzania and two more species were later described from eastern Zaire: *katangensis* Witte 1953 and *hispida* Laurent 1955.

Marx & Rabb (1965) then reassigned to *Atheris* two terrestrial species, *superciliaris* (Peters) and *hindii* (Boulenger), both originally described in the palaearctic genus *Vipera* Laurenti. A generic name *Hindius* was proposed for the latter species by Reuss (1939), but this was not accompanied by a diagnosis and the name is therefore not available [ICZN Article 13 (a) (i)]. New monotypic genera have been erected for *superciliaris* and *hindii* (Broadley, 1996): they are not considered further in this paper. An additional species, *A. desaixi*, was described from Kenya by Ashe (1968).

In the past there has been some confusion about the gender of *Atheris*, but Cope (1862) treated it as feminine and this was confirmed by the ICZN in Opinion 1634 of 1991.

This review was prompted by the discovery of a new species in western Uganda. Unfortunately I do not have the time nor the facilities to undertake the full revision of the genus that is long overdue.

MATERIALS AND METHODS

This study is based on material in the Natural History Museum of Zimbabwe (Bulawayo), supplemented by a few specimens borrowed from other museums. Institutional acronyms follow Leviton *et al.* (1985). In addition: DCM = D.C. Moyer collection; KMH = K.M. Howell collection, University of Dar es Salaam; MUZM = Makerere University Zoological Museum, Kampala, Uganda; VW = Van Wallach collection.

The nomenclature of the scales on the snout requires clarification. Ashe (1968), in his diagnosis of *Atheris desaixi*, referred to the four scales surmounting the rostral as suprarostrals and Meirte (1992) uses the same terminology, but Groombridge (1987) refers to the outer ones as rostronasals. The situation is complicated by the new species from Uganda, which has only two large symmetrical shields above the rostral: should these be regarded as a divided suprarostrals or a pair of nasorostrals that meet above the rostral? It seems simplest to designate as suprarostrals all those shields on the vertical anterior face of the snout which are bordered below by the rostral, laterally by the nasals and above by the row of internasals (usually keeled) which indicates the beginning of the dorsal surface of the snout.

In order to keep the length of this paper within bounds, references are restricted to those used in the text, including the chresonymy (first reference to all nomenclatural combinations applicable to a taxon).

CHARACTER ANALYSIS

1. SUPRAROSTRALS (FIG. 1; TABLE 1)

The first author to draw attention to the suprarostrals arrangement in this genus was Ashe (1968), when he described *A. desaixi*. He suggested that the genus could be divided into two groups, which he thought might warrant subgeneric status. In *desaixi*, *chlorechis* and *ceratophora* the rostral had the highest point in the centre and there was an even number of suprarostrals, while in *katangensis*, *nitschei*, *squamigera* and *hispida* the rostral had a depressed centre and there was an odd number of suprarostrals. *A. ceratophora* actually has rather irregular scalation and is not readily assigned to either group.

The plesiomorphic condition within the tribe Atherini is shown only by *Proatheris superciliaris* (Fig. 1a), with an entire rostral in broad contact with the nasals and only 1-3 internasals. The remaining taxa have two or more suprarostrals separating the shallow rostral from the nasals, these being surmounted by a minimum of four internasals (usually five). The most primitive arrangement is probably three suprarostrals, the condition found in *Montatheris* Broadley, *Adenorhinos* Marx

TABLE 1. Variation in head scalation (rare variations in parentheses). COS, circumorbital scales; IL, infralabials; INS, internasals; IOL, interoculabials; ION, interocunasals; IOS, interorbitals; MTHS, maximum transverse head scales; PSL, pairs of sublinguals; SL, supralabials; SRO, suprarostrals.

Taxon	SRO	INS	IOS	MTHS	COS	IOL	ION	SL	IL	PSL
<i>Proatheris</i>	0	1-3	6-8	20-25	8-14	0(1)	2	8-11	10-13	1
<i>nitschei</i>	3-7	4-5	6-12	18-20	10-17	(0)1(2)	2-5	8-13	9-15	3-6
<i>rungwensis</i>	3-7	5-6	9-13	24-26	15-18	1-2	3-4	9-12	11-13	2-3
<i>desaixi</i>	6-7	5	8-11	22	14-17	1-2	2-3	10-12	11-14	4-6
<i>ceratophora</i>	5-9	4-5	7-11	19-20	13-19	0-1	2-4	7-11	8-12	1-3
<i>katangensis</i>	3-6	5-6	9-11	20-22	14-17	0-1	2-3	9-12	11	3
<i>chlorechis</i>	7-8	5	8-14	25-27	15-20	(0)1(2)	3-4	9-12	10-11	1-2
<i>squamigera</i>	3-7	3-5	5-11	15-22	10-18	0(1)	(1)2(3)	7-13	8-13	2-7
<i>anisolepis</i>	7-8	5	6-8	14-18	12-17	(0)1	2-4	10-13	10-14	3-8
<i>hispid</i>	3	4-6	6-10	12	9-15	0	2	9-10	8-10	1-2
<i>acuminata</i>	2	3	5	10	11-12	0	1	6	7-8	1

& Rabb and typical of the species *Atheris nitschei*, *rungwensis*, *katangensis*, *squamigera* and *hispid* (Figs 1 b, d, g, k & o). However, in the first two species and *A. squamigera* two small scales may be wedged in between the rostral and the outer suprarostrals on each

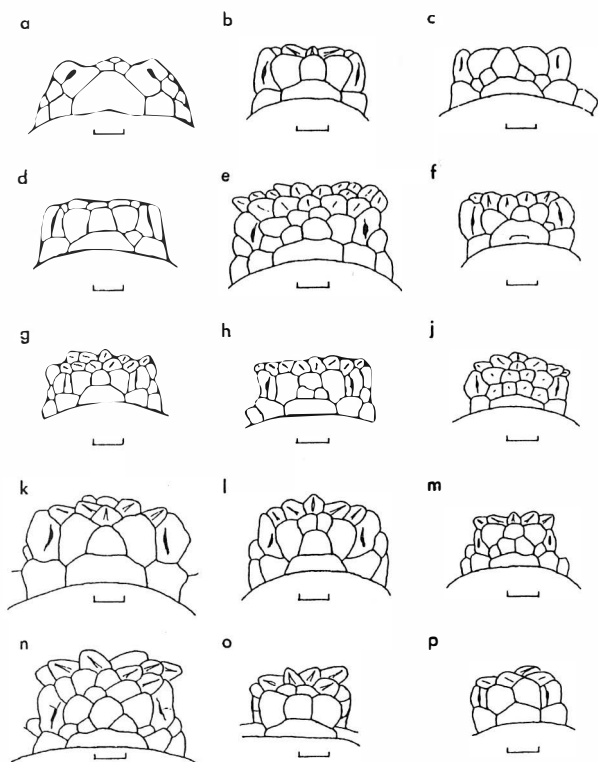


FIG. 1. Scalation of the snout: a, *Proatheris superciliaris* (NMZB-UM 27022 - Malawi); b, *Atheris nitschei* (NMZB 2557 - Uganda); c, *A. nitschei* (NMZB 1284 - Uganda); d, *A. rungwensis* (NMZB 11580 - Tanzania); e, *A. desaixi* (NMZB 13980 - Kenya); f, *A. ceratophora* (NMZB 7151 - Tanzania); g, *A. katangensis* (IRSNB 2209 - Zaïre); h, *A. katangensis* (IRSNB 2206 - Zaïre); j, *A. chlorechis* (ZMUC R6883 - Ghana); k, *A. squamigera* (CAS 197898 - Cameroon); l, *A. squamigera* (NMZB 3951 - Kenya); m, *A. anisolepis* (AMNH 11899 - Zaïre); n, *A. anisolepis* (MNHN 1886.242, lectotype - Congo); o, *A. hispid* (NMZB-UM 5317 - Kenya); p, *A. acuminata* sp. nov. (NMZB 13950, holotype - Uganda).

side, making a total of seven suprarostrals (Fig 1c). The middle suprarostal can also be split into three by a horizontal and a partial vertical sulcus, either dorsal (Fig 1i) or ventral (Fig 1h), making five suprarostrals.

A. desaixi has a first row of four suprarostrals, usually the centre pair smallest and surmounted by two more shields to make a total of six (Ashe, 1968: Fig. 1), or seven if an outer suprarostal is horizontally divided (Fig. 1e). However, G. Rilling (pers. comm.) noted that the specimens that he collected from the Nyambeni Range had three suprarostrals in the first row.

A. ceratophora has irregular scalation, with a first row of three or four large suprarostrals and additional smaller ones wedged in above or laterally, which may produce a total of up to nine.

A. chlorechis has a total of seven or eight suprarostrals, a lower row of four and an upper one of three or four (Fig. 1j).

A. anisolepis has a lower row of four or five suprarostrals, largest in the centre, and an upper row of three or four, the lateral ones largest (Fig. 1m & n).

The holotype of *A. acuminata* sp. nov. is unique in having only two large symmetrical suprarostrals (Fig. 1p), a pattern perhaps derived from that of *A. hispid* by the loss of the median suprarostal.

2. HEAD SCALES TRANSVERSELY (TABLE 1)

This has usually been recorded as an interorbital scale count (e.g. Marx & Rabb, 1965: 188; Meirte, 1992: 31), but there is too much intraspecific variation for it to be diagnostic. Hughes & Barry (1969) used the maximum transverse count at the widest point between the posterior supralabials to distinguish *A. chlorechis* from *A. squamigera* and it appears to be a much better character.

Using *Proatheris superciliaris* as an outgroup, the plesiomorphic condition is apparently 20-25, similar to *A. desaixi* (22) and *katangensis* (20-22). Slightly higher counts are found in *rungwensis* (24-26) and *chlorechis* (25-27), and slightly lower counts in

nitschei (18-20) and *ceratophora* (19-20). Enlarged dorsal head shields result in distinctly lower scale counts in *squamigera* (15-22), *anisolepis* (14-18), *hispida* (12) and *acuminata* (10).

3. CIRCUMORBITALS (TABLE 1)

The plesiomorphic condition is probably 8-14 circumorbitals as in *Proatheris*: only *A. hispida* (9-15) and *acuminata* (11-12) have similar counts. All other species have higher counts, the maximum attained by *chlorechis* (15-20).

4. INTEROCULABIALS (TABLE 1)

These are defined as scale rows inserted between the suboculars and the supralabials (Marx & Rabb, 1972: 50). This has been used as a diagnostic character to separate *chlorechis* and *anisolepis* (one row) from *squamigera* (absent), but is not very reliable. *A. squamigera* rarely has one row, or a labial may contact the eye (type of *A. subocularis* Fischer). *A. hispida* and *acuminata* (like *Proatheris*) have no interoculabials, *katangensis* and *ceratophora* may have one row or none, *nitschei* and *chlorechis* usually have one row, rarely none or two. *A. anisolepis* has one row (rarely none), *desaixi* and *rungweensis* have one or two.

5. INTEROCUNASALS (TABLE 1)

The plesiomorphic condition seems to be two scales between eye and nasal shield as in *Proatheris*. Most species tend to show an increase up to a maximum of five, but *acuminata* has only a single scale and this state may rarely occur in *squamigera*. Hughes & Barry (1969) found that in Ghana *A. squamigera* usually has two interocunasals and *A. chlorechis* three or more.

6. SUPRALABIALS (TABLE 1)

The plesiomorphic condition is probably 8-11 supralabials as in *Proatheris* and most *Atheris* show similar ranges. The only species showing a slight increase are *desaixi* (10-12) and *anisolepis* (11-13), while *acuminata* shows a marked decrease to six.

7. INFRALABIALS (TABLE 1)

The plesiomorphic condition is probably 10-13 infralabials as in *Proatheris* and most *Atheris* have similar counts. *A. hispida* (8-10) and *acuminata* (7-8) have lower counts.

8. PAIRS OF SUBLINGUALS AND GULARS (TABLE 1)

The plesiomorphic condition appears to be a single pair of sublinguals as in *Proatheris*. Most *Atheris* show multiple sublinguals + paired gulars, reaching a maximum in the lectotype of *A. anisolepis*, which attains a total of eight pairs due to the inner portions of the first infralabials being split off to form an additional pair anteriorly (Fig. 9). *A. hispida* (1-2) and *A. acuminata*

(one, Fig. 11) are the only species with low numbers of sublinguals; this is apparently a secondary synapomorphy.

9. GULAR SCALES

Only *A. nitschei* retains the plesiomorphic condition of smooth gular scales, all other species have more or less strongly keeled outer gulars, a synapomorphy otherwise found only in the terrestrial viperine genera *Cerastes* and *Eristicophis* (Marx & Rabb, 1972: 77). The gulars are moderately keeled in *rungweensis*, *desaixi*, *ceratophora* and *katangensis* and strongly keeled in *chlorechis*, *squamigera*, *anisolepis*, *hispida* and *acuminata*.

10. DORSAL SCALE ROWS AT MIDBODY (TABLE 2: MSR)

The plesiomorphic condition seems to be 27-29 rows both on the neck and at midbody as in *Proatheris*. Similar counts are found in *A. nitschei*, *rungweensis*, *katangensis* and *chlorechis*, reaching a maximum (25-36) in the last species, but there may be two fewer scale rows on the neck. The other species show a reduction in dorsal scale rows, especially *squamigera* (15-25), *hispida* (15-19) and *acuminata* (14).

In most species the lower lateral scales of individual transverse rows (usually rows 2-5) are frequently doubled, while entire transverse rows are sometimes duplicated (Groombridge, 1980, 1987). However, in *A. hispida* and *acuminata* there are frequent and regular fusions of transverse rows (occurring at rows 2-5), thus 7 vertebral scales may correspond to a section of 10 ventrals.

11. SERRATION OF KEELS ON LATERAL SCALES

Serrated keels (restricted to the posterior half of the keel) are present on the lateral scales of *A. nitschei*, *rungweensis*, *desaixi* and *ceratophora*, they are also found in a vestigial form in *katangensis* and also some scales of *chlorechis* (Groombridge, 1980). Stridulatory throat displays have been reported in *A. desaixi* (Ashe, 1968; Isemonger, 1968), and erroneously for *A. nitschei* (Goetz, 1975, based on Isemonger's remarks concerning *A. desaixi*!), but it is unclear whether such behaviour can be demonstrated when the snake is off the ground.

It would be illuminating to obtain scanning electron micrographs of the serrated lateral scales of *Atheris* spp. for comparison with those for *Echis*, *Cerastes* and *Dasypteltis* published by Gans & Baic (1974).

12. VENTRALS (TABLE 2)

The plesiomorphic condition, shown by *Proatheris*, is 137-156 ventrals, with weak sexual dimorphism (higher counts in females). The only *Atheris* species with counts within this range are *ceratophora* and *katangensis*. Most species have slightly higher counts,

TABLE 2. Variation in body scalation and maximum total length.

TAXON	MSR	VENTRALS		SUBCAUDALS		MAXIMUM LENGTH
		males	females	males	females	
<i>Proatheris</i>	27-29	137-145	138-156	37-42	32-43	598
<i>nitschei</i>	23-34	140-160	141-162	41-59	35-54	750
<i>rungwensis</i>	23-33	154-162	150-165	54-58	46-53	642
<i>desaixi</i>	21-31	165	164-168	53-54	41-46	682
<i>ceratophora</i>	19-27	136-150	134-152	49-58	46-57	642
<i>katangensis</i>	23-31	140-144	133-141	45-49	38-42	397
<i>chlorechis</i>	25-37	151-165	153-165	55-63	48-58	585
<i>squamigera</i>	15-25	133-169	141-175	46-67	45-61	799
<i>anisolepis</i>	19-25	153-159	157-160	50-53	47-55	650
<i>hispida</i>	15-19	149-166	153-162	54-64	49-57	735
<i>acuminata</i>	14	160	-	54	-	440

the greatest range being shown by the widely distributed *A. squamigera* (133-175) and the highest average counts by *A. desaixi* (165-168). There is no clear sexual dimorphism.

13. SUBCAUDALS (TABLE 2)

The plesiomorphic condition, shown by *Proatheris*, is 32-43 paired subcaudals with little sexual dimorphism. All *Atheris* have a more elongate prehensile tail with single subcaudals, the lowest counts being shown by *A. nitschei* (35-59) and *katangensis* (38-49) and the highest by *A. squamigera* (45-65). Males have higher average subcaudal counts and in some species (*rungwensis*, *desaixi* and *katangensis*) there is no overlap between the sexes.

14. MOLECULAR DATA

For albumin-immunological analyses Herrmann (1995) prepared antisera against *Proatheris superciliaris*, *Atheris nitschei* and *A. squamigera*.

A. nitschei showed the closer relationship to *Proatheris* (Herrmann & Joger, 1995), and the albumins of *A. chlorechis*, *hispida* and *desaixi* showed closer affinities with *A. nitschei* than with *A. squamigera*. However, subsequent analyses (Herrmann & Joger, 1997) placed *A. hispida* closer to *A. squamigera* in a Fitch-Margoliash dendrogram, but closest to *A. nitschei* in a UPGMA dendrogram.

SYSTEMATIC ACCOUNT

ATHERIS COPE 1862
AFRICAN BUSH-VIPERS

Chloroechis Bonaparte, 1849: 45 (footnote). A nomen dubium, with no species included in the genus, suppressed by the ICZN in 1991 (Opinion 1634).

Atheris Cope, 1862: 337. Type species, by subsequent designation of Loveridge (1957: 303) *Vipera chlorechis* Schlegel 1855 [a junior subjective synonym of *Vipera chlorechis* Pel 1851], see Broadley, 1989: 264.

Poecilostolus Günther, 1863a: 25. Type species by monotypy: *P. burtonii* Günther = *Echis squamigera* Hallowell.

Generic diagnosis. Habitus slender, body laterally compressed, with high ventral and subcaudal counts and a short square head. Dorsal head scales small to moderate, more or less keeled; rostral fragmented, so that a wide shallow rostral is surmounted by 2-8 suprarostrals between the nasals and below the transverse series of internasals that marks the beginning of the dorsal surface of the head; transverse dorsal scale rows with frequent duplications or fusions as one moves from ventrum to dorsum; subcaudals single. Palatine-pterygoid articulation a simple overlapping joint; intra-pulmonary bronchus short

Generic description. Skull: ectopterygoid without a lateral flange or anterior process; postorbital bone long and narrow; splenial absent, angular present.

Top of head with moderate to small more or less keeled scales, 5-14 interorbital scales; rostral surmounted by 2-9 suprarostrals; nasals entire, semidivided or divided, nostril centrally placed; no supranasal sac or subcutaneous nasal gland; a well-marked canthus rostralis; 1-4 scales between nasals and eye; eye moderate to large, vertical diameter equal to up to twice its distance from the lip, with a vertically elliptic pupil; 9-20 circumorbital scales; temporals keeled; supralabials 6-13; infralabials 7-14; a small triangular mental is usually separated from a series of 1-5 transversely enlarged sublinguals by a median suture of the first infralabials.

Dorsal scales in 14 to 36 rows at midbody, strongly keeled to acuminate and imbricate, with frequent duplication or fusion of lateral rows. Ventrals smooth, 133-173; anal entire; subcaudals smooth, 35-67, single.

Hemipenis with a naked zone on the medial face of each lobe, extending from the fork of the organ to the apical region, where there is a short calyculate zone. The rest of each lobe is covered with relatively short spines, largest proximal to the sulcus fork. There is no terminal awn nor basal hooks.

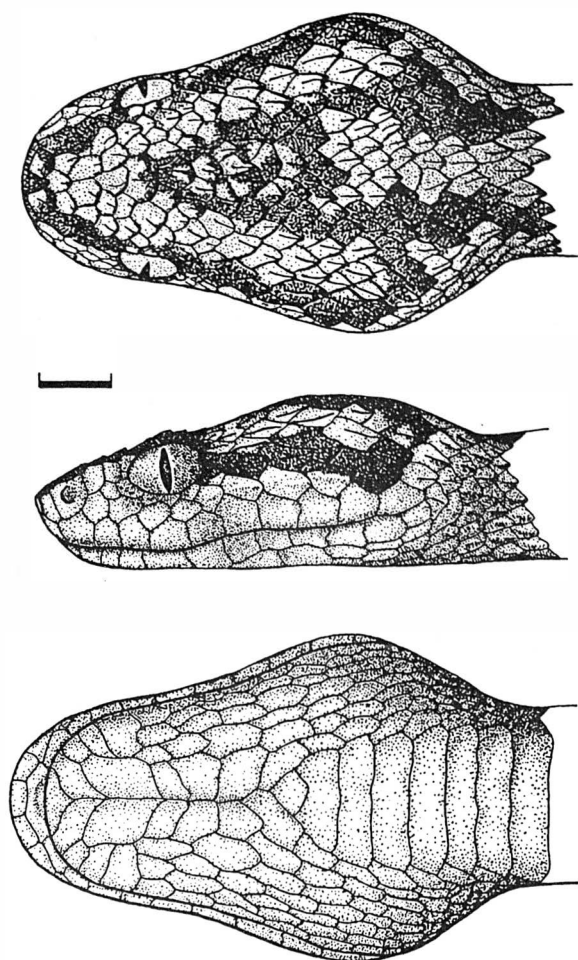


FIG. 2. *Atheris nitschei*: dorsal, lateral and ventral views of the head (after Witte, 1962: Fig. 93). The line indicates 5 mm to scale.

ATHERIS NITSCHERI TORNIER

GREAT LAKES BUSH-VIPER (FIG. 2)

Atheris nitschei Tornier, 1902: 589, fig. Type locality: Mpororo Swamp, Rwanda (on the border with Uganda: Loveridge, 1942), syntypes ZMB 17669.

Atheris woosnami Boulenger, 1906: 37. Type locality: "east side of Ruwenzori between 6000 & 6500 feet altitude", Uganda, syntypes BMNH 1946.1.19.60-63.

Atheris nitschei nitschei Bogert, 1940: 104.

Description. Rostral two and a half times as broad as deep, surmounted by three suprarostrals, the outer ones largest (sometimes with two small scales wedged in between the rostral and the outer suprarostrals on each side) followed by 5 (rarely 4) rugose internasals. Nasals separated from eye by 2 - 5 scales. Anterior dorsal head scales smooth to weakly keeled, posterior dorsal and lateral head scales strongly keeled, not mucronate, interorbitals 6-12 and 18-20 across back of head between posterior supralabials. Eye moderate, its vertical diameter subequal to its distance from the lip. Circumorbitals 10-17, separated from the supralabials by one (rarely two or none) row of scales. Supralabials

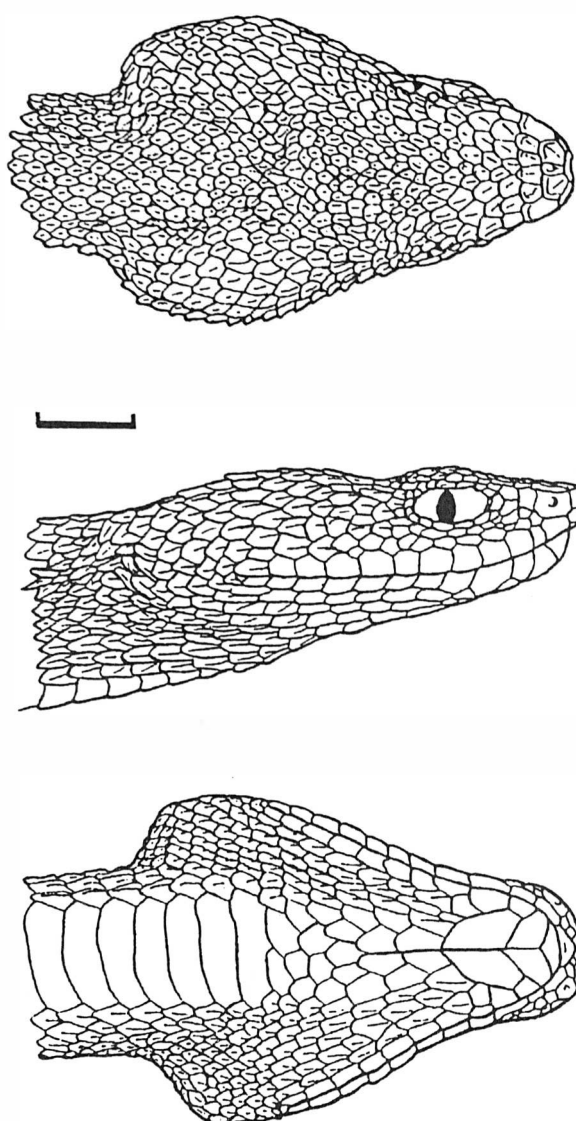


FIG. 3. *Atheris rungweensis*: dorsal, lateral and ventral views of the head (Holotype, AMNH 39186 - Rungwe Mountain, Tanzania: after Bogert, 1940: Fig. 18). The line indicates 5 mm to scale.

8-13, usually third and fourth or fourth and fifth below the eye. Mental twice as wide as long; 9-15 infralabials, first pair in contact behind the mental, followed by 3 to 6 pairs of smooth sublinguals and 1 to 3 preventrals; lateral gulars smooth (feebly keeled in some juveniles).

Dorsal scales strongly keeled and pointed, with the keels reaching the tip, 23-34 transverse rows at mid-body, lateral rows 2 to 8 strongly serrated and frequently duplicated; ventrals 140-162; subcaudals 35-59.

Colouration. Green above, with a black arrowhead marking on top of the head (often fragmented) and often a black lateral stripe from the tip of the snout through the eye. A series of irregular black dorsal blotches which may fuse to form a zig-zag pattern, many dorsal scales tipped or bordered black, tail tip blackish. Ventrals uniform lighter green to yellow-green or with a dark median streak. Juveniles dull

grey-green to almost black, with or without black markings, tail tip white.

Size. Maximum total length: 745 mm (Kaniamagufa Ravine); 750 mm (Tshumba), both in the Virunga National Park, Kivu, Zaire (Witte, 1941).

Habitat. Abundant in *Papyrus* and *Phragmites* swamps and riparian elephant grass (*Pennisetum*), also found in bushes and montane forest up to the bamboo zone (Pitman, 1974). Altitudinal range about 1600 to 2700 metres.

Behaviour. Basks in the sun, forming a flat coil on top of *Papyrus* stems or tangled creepers smothering elephant grass up to 3 metres from the ground.

Diet. Presumably feeds mainly at night, juveniles taking amphibians, adults rodents and shrews (Loveridge, 1942). A few lizards (*Leptosiphos* spp.; *Chamaeleo* cf. *bitaeniatus*) are also taken (Laurent, 1956).

Breeding. Pook (1990) records 13 viable young born in captivity from a wild-caught gravid female.

Distribution. Eastern Zaire (eastern Kivu and extreme northeast Shaba Provinces), southwestern Uganda (Kigezi and Toro Districts) and western Rwanda and Burundi (Fig. 13).

ATHERIS RUNGWEENSIS BOGERT
RUNGWE BUSH-VIPER (FIG. 3)

Atheris nitschei rungweensis Bogert, 1940: 104, fig. 18. Type locality: Rungwe Mountain, Tanzania, holotype AMNH 39186.

Atheris squamiger (not Hallowell) Hedges, 1983: fig. 52.

Description. Rostral twice as broad as deep, surmounted by three suprarostrals, the outer ones largest (sometimes with two small scales wedged in between the rostral and the outer suprarostrals on each side), followed by five rugose internasals. Nasals separated from eye by 3 or 4 scales. Dorsal and lateral head shields strongly keeled, some mucronate, 9-13 interorbitals and 24-26 scales across back of head between posterior supralabials. Eye moderate, its vertical diameter slightly less than its distance from the lip. Circumorbitals 15-18, separated from the supralabials by one row of scales. Supralabials 9-12, usually the fifth and sixth below the eye. Mental slightly wider than long, 11-13 infralabials, first pair in contact behind the mental, followed by two pairs of smooth sublinguals and five rows of gulars (outer ones feebly keeled) before the first ventral.

Dorsals keeled and pointed, but with keels ending before the tip, 23-33 rows at midbody, lateral rows 2-6 strongly serrated and frequently duplicated; ventrals 150-165; subcaudals 46-58.

Colouration. Bright green to blackish above, often with a yellow pattern on the back of the head, a pair of yellow dorsolateral zig-zag lines and/or a row of yellow lateral spots on the edges of the ventrals; ventrum uniform yellow to grey-green. The bright green and yellow specimen illustrated by Skinner (1973) and

Hedges (1983) was one of six from Gombe Stream National Park received at the Nairobi Snake Park in 1970 (S. Spawls, *in litt.*). The type was slaty black above and below, except for a whitish tail tip (Bogert, 1940) and seems to be unique in this respect.

Size. Largest (NMZB 11580 - Mbizi Forest Reserve, Sumbawanga District, Tanzania) 585 (485 + 100) mm; largest (MCZ 51615 - Matipa Forest, Misuku Hills, Malawi) 642 (550 + 92) mm.

Taxonomic discussion. This form was originally described as a subspecies of *A. nitschei*, but it has smaller cephalic scales which are more strongly keeled anteriorly, while its usual colour pattern is green and yellow rather than green and black. There is no sign of intergradation between the two taxa, so *rungweensis* is here considered a valid species.

Habitat. Usually found in bushes or on the ground at the edge of montane forest. In Gombe N.P. they occur along streams in bushes at heights from one to three metres (Rilling, pers. comm.). Altitudinal range about 800 to 2000 metres.

Diet. Two small frogs (*Phrynobatrachus ukingensis*) in a Malawi snake (Loveridge, 1953).

Distribution. Western Tanzania from the Gombe National Park south to Rungwe Mountain, northwestern Zambia from the Mbala area south to the Nyika Plateau and northern Malawi (Misuku Hills) (Fig. 13).

Recorded localities. TANZANIA. Gombe National Park (Broadley & Howell, 1991) KMH 6150; SDSU --- (VW 3069); Kigoma (Rasmussen & Howell, 1982) BMNH 1979.982; Mbizi Forest Reserve NMZB 11580; Nsangu Montane Forest KMH 3136; Rungwe Mountain (Bogert, 1940) AMNH 39189. ZAMBIA. Mbala to Mpulungu (Vesey-FitzGerald, 1958); Mbala to Mbeya (Broadley & Pitman, 1960) IRSNB 18284; Nyika Plateau (Wilson, 1965) NMZB-UM 3151. MALAWI. Misuku Hills (Loveridge, 1953) MCZ 51614-7.

ATHERIS DESAIXI ASHE
MOUNT KENYA BUSH-VIPER (FIG. 4)

Atheris desaixi Ashe, 1968: 53, fig. 1-2. Type locality: near Chuka, Mount Kenya, holotype BMNH 1969.338.

Description. Rostral twice as broad as deep, deepest mesially and surmounted by 5 to 7 irregular suprarostrals, 3 or 4 in the lower row and 2 or 3 in the upper, followed by five rugose internasals. Nasals separated from eye by two or three scales. Dorsal and lateral head scales strongly keeled, but keels do not reach the tip of the scale; 8 to 11 interorbital scales and 22 across back of head between posterior supralabials. Eye moderate, its vertical diameter subequal to its distance from the lip. Circumorbitals 14-17, separated by one or two rows of scales from the 10-12 supralabials, the fourth to sixth below the eye. Mental about twice as wide as long; 11-14 infralabials, the first pair in contact behind the mental, followed by a pair of large smooth sublinguals and 3 to 5 rows of gulars (the outer ones feebly keeled) and a prefrontal.

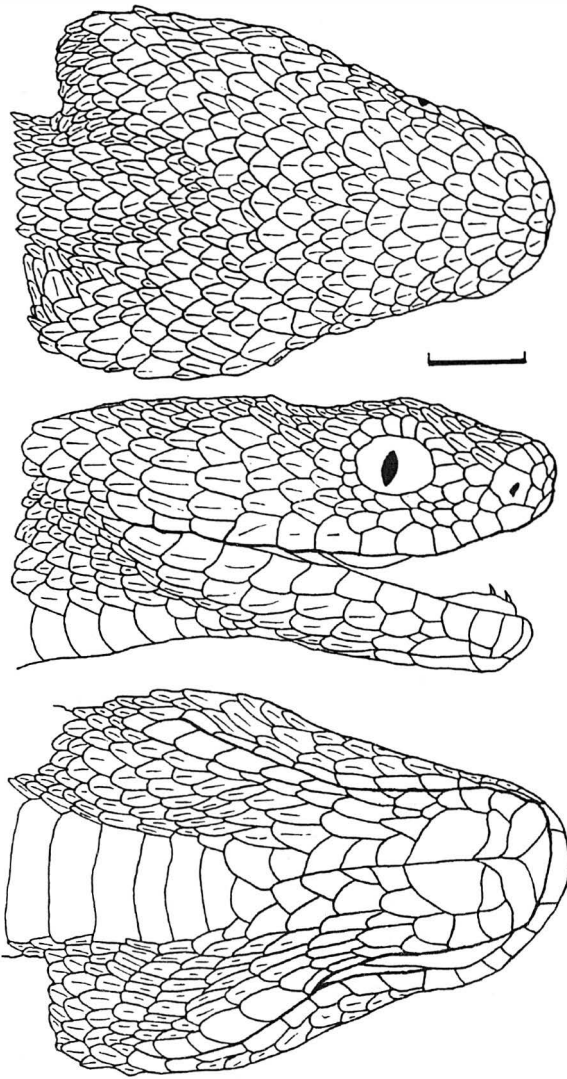


FIG. 4. *Atheris desaixi*: dorsal, lateral and ventral views of the head (NMZB 13980 - Meru, Kenya). The line indicates 5 mm to scale.

Dorsals rounded at the apex, the strong keels ending before the tip, 21-31 rows at midbody, lateral rows 2-6 strongly serrated and frequently duplicated; ventrals 164-168; subcaudals 41-54.

Colouration. Black above, each scale tipped with yellow, poorly defined yellow dorsolateral and ventrolateral zig-zag stripes become more distinct caudad; ventrum yellow anteriorly, suffused with black after midbody, becoming uniform black posteriorly and beneath tail. Hatchlings are predominantly yellow with a white tail tip, but gradually darken to attain adult colouration at a length of ca. 30 cm (Spawls & Branch, 1995).

Size. Allotype (BMNH 1969.339) 555 (465 + 90) mm; largest (NMK 1628) 682 (597 + 85) mm, both from near Chuka, Kenya.

Habitat. Montane forest at an altitude of ca. 1600 metres in trees and bushes about 1.5 to 3 metres from the ground. A pair were observed resting in the canopy 15 m above ground at the type locality (Emmrich, 1997). Specimens from the Nyambeni Hills came from

in or near yam plantations at about 1700 m (Rilling, 1972).

Behaviour. When captive specimens were alarmed, they went into a display resembling that of *Echis*, forming the body into loops which countermarched upon themselves, producing a hissing sound (Ashe, 1968). Spawls (*in litt.*) found them very irascible in captivity, more so than *A. rungweensis*, but Emmrich (*in litt.*) found that they soon settled down in captivity and were easy to handle, like *A. nitschei* and *A. ceratophora*.

Breeding. A female from the Nyambeni Range gave birth to 13 young which varied between 175 and 211 mm in total length (Spawls & Branch, 1995).

Distribution. Central Kenya: forests on the eastern slopes of Mount Kenya near Chuka and Meru, and around Igembe on the north-east slope of the Nyambeni Range to the north-east of Mount Kenya (Rilling, 1972; Spawls, 1990: Fig. 13).

ATHERIS CERATOPHORA WERNER
HORNED BUSH-VIPER (FIG. 5)

Atheris ceratophora Werner, 1895: 194, pl. v, fig. 1. Type locality: Usambara Mts, Tanzania, holotype BMNH 1946.1.18.23.

Description. Rostral twice as broad as deep, surmounted by 3 or 4 suprarostrals, the outer ones largest, and additional smaller ones wedged in above or laterally; 4 or 5 feebly keeled internasals. Nasal separated from eye by 2 to 4 scales. Dorsal and lateral head shields strongly keeled and mucronate, 7 to 11 interorbitals and 19 to 20 scales across back of head between posterior supralabials. Eye rather large, the vertical diameter one and a third times its distance from the lip. The eye is separated from the supralabials by one or two rows of scales, including the circumorbitals, which number 13 to 19, the one to five above the eye forming moderate to elongate "horns" (Fig. 5). Supralabials 7 to 11, usually third to fifth below eye. Mental about one and a third times as wide as long, infralabials 8 to 12, the first pair in contact behind the mental, followed by a pair of elongate smooth sublinguals and about five irregular rows of more or less keeled gulars before the first ventral.

Dorsals pointed, keeled and mucronate, 19-27 rows at midbody, lateral rows 2 to 6 strongly serrated and frequently duplicated; ventrals 134-152; subcaudals 46-58. Data for the discrete populations are analysed by Emmrich (1997).

The hemipenis is illustrated by Emmrich (1997) and is similar to those of other *Atheris* (Groombridge, 1980).

Colouration. Yellow, olive green or grey above, with a bold pattern in black (sometimes bordered with yellow), consisting of a series of irregular chevrons on the head, a zig-zag vertebral stripe and a lateral series of crescents or circles, the tail tip is yellow (Böhme, 1987; Emmrich, 1997: colour plates). This pattern becomes fragmented in some adults, others become uniform olive green or uniform black (Spawls & Branch, 1995;

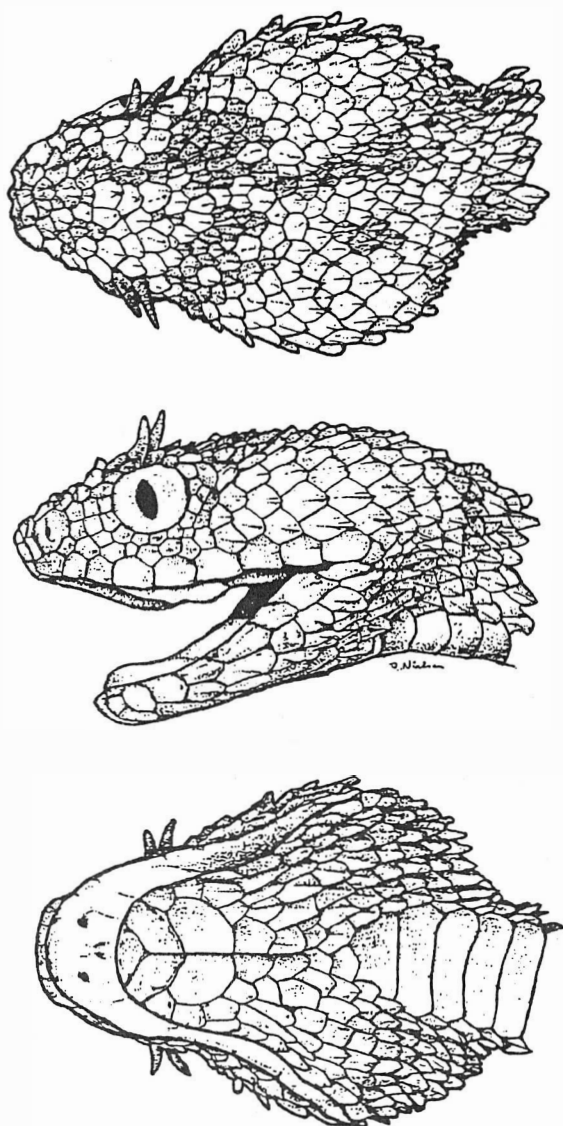


FIG. 5. *Atheris ceratophora*: dorsal, lateral and ventral views of the head (KMH 1893 - West Usambara Mts, Tanzania: after Rasmussen & Howell, 1982: Fig. 2).

Emmrich, 1997: colour plates). Ventrums olive green, grey, dull orange or almost black, with or without black speckling. Emmrich (1997) found that embryos and neonates were always uniform black with 10 mm bright yellow tail tips, which are probably used for caudal luring of small frogs and lizards.

Size. Total length, largest (ZMB 48129) 510 (416 + 94) mm, largest (ZMB 48120) 550 (458 + 92) mm, both from Mazumbai Forest Reserve, West Usambara Mts., Tanzania (Emmrich, 1997).

Habitat. Barbour & Loveridge (1928) reported that Usambara residents said that *A. ceratophora* was found in grass or low bushes about a metre above ground. Rasmussen and Howell (1982) collected five specimens on paths in montane forest, usually at about 0900 hrs. D.C. Moyer's Luhega specimens were collected in leaf litter on the floor of secondary montane forest near Ihambwi stream at 1400-1425 metres. In Mazumbai Forest Reserve in the western Usambaras, most were on

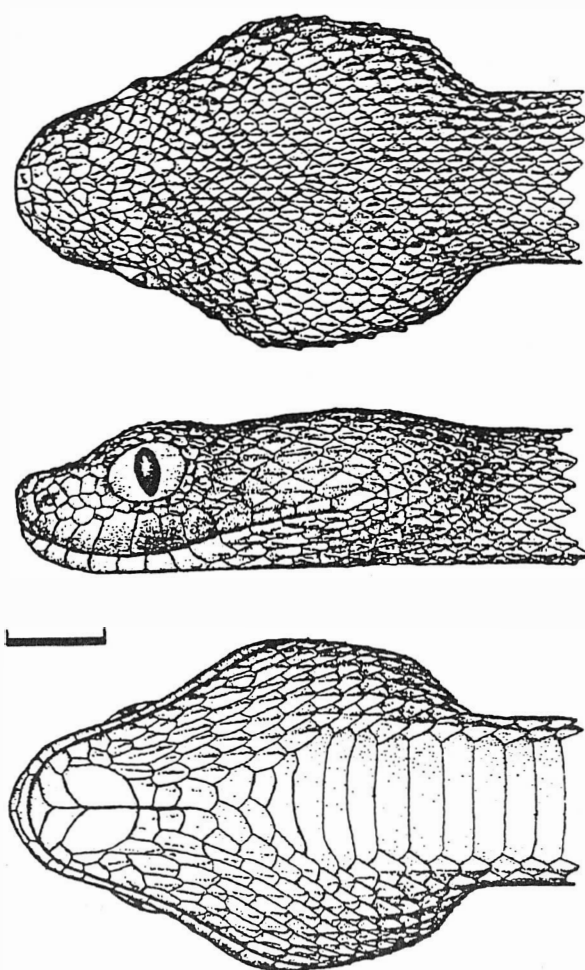


FIG. 6. *Atheris katangensis*: dorsal, lateral and ventral views of the head (Holotype, IRSNB 2207 - Mubale-Munte, Parc Nat. Upemba, Zaire: after Witte, 1953: Fig. 107). The line indicates 5 mm to scale.

the ground, some resting on stumps 1 to 1.5 m above ground; none were recorded below 1400 m (Emmrich, 1997).

Diet. A frog (*Hyperolius* sp.) in the stomach of a specimen from the East Usambaras (Barbour & Loveridge, 1928). In captivity they will take frogs, geckos, nestling birds and small rodents (Emmrich, 1997).

Distribution. West and East Usambara Mountains, ? Uluguru Mountains (NHMG 1610 from "Ukumi") and Udzungwa Mountains, Tanzania (Fig. 13).

Localities. Subsequent to Rasmussen & Howell (1982), the following additional material has been collected in the southern Udzungwa Mountains: near Mufindi (Böhme, 1987) ZFMK 44846-7; Luhega Forest Reserve, Mufindi District LSUS/DCM 463-4, NMZB 11588-9. Emmrich (1997) has collected 21 additional specimens in the West Usambaras (ZMB 48110-29, 48551).

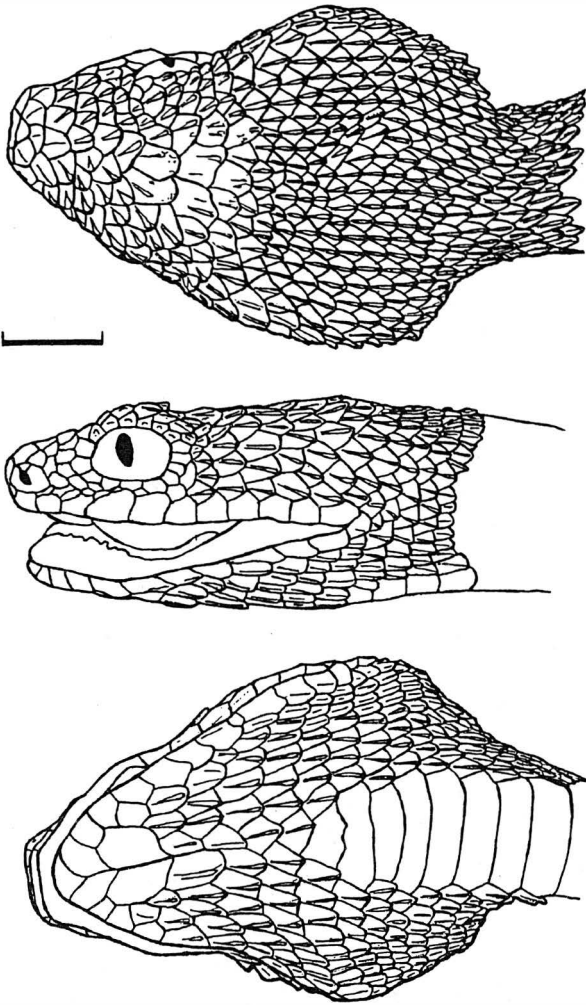


FIG. 7. *Atheris chlorechis*: dorsal, lateral and ventral views of the head (ZMUC R6883 - Bobiri Forest Reserve, Ghana). The line indicates 5 mm to scale.

ATHERIS KATANGENSIS WITTE
UPEMBA BUSH-VIPER (FIG. 6)

Atheris katangensis Witte, 1953: 301, Fig. 107, Col. Pl. iii, Fig. 4, pl. xxi, Fig. 2. Type locality: Mubale-Munte, Upemba National Park, Zaïre, holotype IRSNB 2207.

Description. Rostral three times as broad as deep, surmounted by three suprarostrals, the outer ones largest (the middle one may be split into three, two small ones below a larger one: Fig. 1 h); 5 or 6 slightly rugose internasals. Nasals separated from eye by 2 or 3 scales. Dorsal and lateral head shields strongly keeled, keels terminating in a knob, 9-11 interorbital scales and 20-22 across back of head between posterior supralabials. Eye moderate, its vertical diameter subequal to its distance from the lip, usually separated from the 9-12 supralabials only by the 14-17 circumorbitals. Mental about one and a half times as wide as long, infralabials 11, the first pair in contact behind the mental, followed by a pair of large sublinguals and five rows of gulars (the outer ones keeled) anterior to the first ventral.

Dorsals keeled and pointed, the keel terminating at the tip, 23-31 rows at midbody, lateral rows often duplicated and rows 4-6 very feebly serrated; ventrals 133-144; subcaudals 38-49.

Colouration. Pale brown to olive or purple brown above, with a vertebral series of dark-bordered and dark-centred yellowish rhombic markings, tail tip yellow. Ventrums yellow anteriorly, sometimes becoming grey-green posteriorly, about every third ventral with a yellow lateral spot and a few ventrals with short black transverse bars.

Size. Largest (Holotype, IRSNB 2207) 397 (335 + 62) mm, largest (Paratype, IRSNB 2206) 364 (310 + 54) mm, both from Mubale-Munte, Upemba National Park, Zaïre.

Habitat. Gallery forests at an altitude of 1250 to 1480 metres.

Diet. IRSNB 2206 contained the foot of a frog (*Ptychadena* sp.).

Distribution. Known only from a restricted area in the northeastern sector of the Parc National de l'Upemba, Shaba Province, Zaïre (Fig. 13).

ATHERIS CHLORECHIS (PEL)
WESTERN BUSH-VIPER (FIG. 7)

Vipera chlorechis Pel, 1851: 172. Type locality: Butre, Ghana (by designation of Hughes & Barry, 1969), lectotype RMNH 1648.

Vipera chloroechis Schlegel, 1855: 317.

Toxicoa chloroechis Cope, 1860: 341.

Echis chlorechis Jan, 1863: 122.

Atheris polylepis Peters, 1864: 642. Type locality: Liberia, holotype ZMB 5131.

Atheris chloroechis Peters, 1864: 645.

Atheris chlorechis Boulenger, 1896: 508.

Description. Rostral four times as long as deep, surmounted by two rows of three or four rugose suprarostrals and five keeled internasals. Nasal separated from eye by three or four scales. Dorsal and lateral head shields strongly keeled, each keel ending in a knob, 8-14 interorbital scales and 25-27 across back of head between posterior supralabials. Eye moderate, its vertical diameter slightly greater than its distance from the lip. An incipient row of scales partially separates the 14-20 circumorbitals from the 9-12 supralabials, third to fifth below the eye. Mental twice as wide as long, infralabials 10-11, the first pair in contact behind the mental, followed by a pair of elongate feebly keeled sublinguals, four rows of keeled gulars and two prementals.

Dorsals bluntly pointed, keels terminating in a knob, 25-37 at midbody, lateral rows frequently duplicated, rarely some scales with faint serration (Groombridge, 1980); ventrals 151-165; subcaudals 48-64.

Colouration. Green with irregular small yellow spots forming paravertebral series, vague black cross-bars on tail. Ventrums yellow-green, blue-green below tail, with some black speckling distally. Doucet (1963)

records a melanistic specimen and also a uniform citron yellow snake from the Tai region. Neonates are tan-brown in colour, but within 24 hours change to yellow-green with irregular dark green mottling, the tail tip is sulphur yellow (Spawls & Branch, 1995). Cansdale (1961) describes juveniles as yellowish with green spots.

Size. Largest, unsexed (IFAN 48-1-6 Tchien, Liberia) 585 (497 + 88) mm (Villiers, 1950). Spawls & Branch (1995) state that this species occasionally reaches 70 cm.

Habitat. In Liberia this species is found in low vines or bushes 1-2 metres from the ground (G. Allen in Barbour & Loveridge, 1930).

Diet. A multimammate mouse (*Praomys*) and a shrew (*Crocidura*) in the stomachs of Liberian snakes (Barbour & Loveridge, 1930).

Distribution. Forests of West Africa from Guinea to Gabon at altitudes of up to 560 metres (Mount Nimba).

ATHERIS SQUAMIGERA HALLOWELL
VARIABLE BUSH-VIPER (FIG. 8)

Echis squamigera Hallowell, 1856: 193. Type locality: "near the River Gaboon, Guinea", holotype ANSP 6949.

Toxicoa squamigera Cope, 1860: 341.

Atheris squamatus [sic] Cope, 1862: 337.

Poicilostolus burtonii Günther, 1863a: 25. Type locality: Cameroons, holotype BMNH 1946.1.20.83.

Atheris burtonii Günther, 1863b: 16, pl. iii.

Atheris squamigera Peters, 1864: 645.

Atheris squamiger Peters, 1876: 120.

Atheris Lucani Rochebrune, 1885: 89. Type locality: Landana, Cabinda ("in Museo Bouvieri").

Atheris proximus Rochebrune, 1885: 90. Type locality: (?) Bissarié, Casamance, Senegal. ("in Museo Bouvieri").

Atheris subocularis Fischer, 1888: 5, pl. i, fig. 2 & pl. ii, fig. 11. Type locality: Cameroon, holotype BMNH 1946.1.20.80.

Atheris squamigera squamigera Bogert, 1940: 103.

Atheris squamigera robusta Laurent, 1956: 332, 383, pl. xxviii, fig. 2. Type locality: Nioka, Ituri District, Zaïre, holotype MRAC 16836.

Atheris squamigera ssp. Perret, 1961: 137.

Description. Rostral three times as wide as deep, surmounted by 3-5 suprarostals and 5 keeled internasals. Nasals entire, separated from eye by 1-3 scales (usually 2). Dorsal and lateral head shields strongly keeled, 5-11 interorbitals and 15-22 scales across back of head between posterior supralabials. Eye moderate, its vertical diameter 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. Fischer (1888) described the synonym *subocularis*, based on a single specimen from Cameroon. It seems to be the only *Atheris* recorded with the fourth labial entering the orbit, although

Boulenger (1919) recorded the fifth labial entering the orbit in one of eight specimens from Medje, Ituri Forest. Mental one and a half times as wide as long; infralabials 8-13, the first pair in contact behind the mental, followed by 2-5 pairs of sublinguals (the last three may be replaced by keeled gulars) and about two prementals.

Dorsals strongly keeled and pointed, laterals often acuminate, 15-25 at midbody, lateral rows frequently duplicated: Boulenger (1919) pointed out that females tend to average two more scale rows than males from the same area; ventrals 133-175; subcaudals 45-67.

Laurent (1956) described *A. squamigera robusta* on the basis of the holotype and paratype from Nioka, Kivu Province and a paratype from Blukwa. He based this montane forest race on large size and robust build, fewer subcaudals in females and a tendency for the second infralabials to be separated from the anterior sublinguals. Witte (1975) found evidence of intergradation in the northern sector of the Virunga National Park and synonymized *A. s. robusta* with *A. squamigera*.

Colouration. Usually dark green to olive brown above, uniform or with vague narrow yellow crossbands, more pronounced caudad; ventrum paler and often with a series of white or yellow blotches along outer ends of ventrals. Wallach (1980) recorded the following colour combinations in specimens collected from Kinshasa and Mbanza-Ngungu, Zaïre: (1) dorsum uniform bright orange with bright yellow ventrum; (2) dorsum dark to bright orange with yellow crossbars and ventrum; (3) dorsum yellow with reddish brown to black crossbars and yellow ventrum; (4) dorsum uniform reddish brown to brown with pale yellow ventrum. On 21 Jan 1980 a female gave birth to eight young. Six of the neonates were orange with yellow crossbars like their mother, but one had a yellow dorsum with green crossbars and another had a green dorsum with black crossbars. Pitman (1974) describes Ugandan neonates as dark olive with paler wavy crossbars.

An interesting colour phase occurs in southern Cameroon on the upper reaches of the Dja River and its tributaries. These snakes are olive brown above, darkening caudad, where there are faint traces of irregular pale crossbands. Sides of head and neck yellowish, with a broad black stripe extending from the eye to the commissure of the mouth and terminating on the posterior infralabials (Fig. 8). Chin and throat uniform white, rest of ventrum heavily mottled black. This colour phase has only been reported in the literature by Perret & Mertens (1957), who examined two specimens from Foulassi. It was presumably this population that Perret (1961) listed as *A. squamigera* ssp. for "Sud forestier oriental" in his checklist for Cameroun. It is strange that Boulenger (1919) did not mention the lateral eye stripe in the long series in the BMNH collected by G.L. Bates in this area when he published the scale counts. B. Hughes (in litt.) reports that a few specimens from this

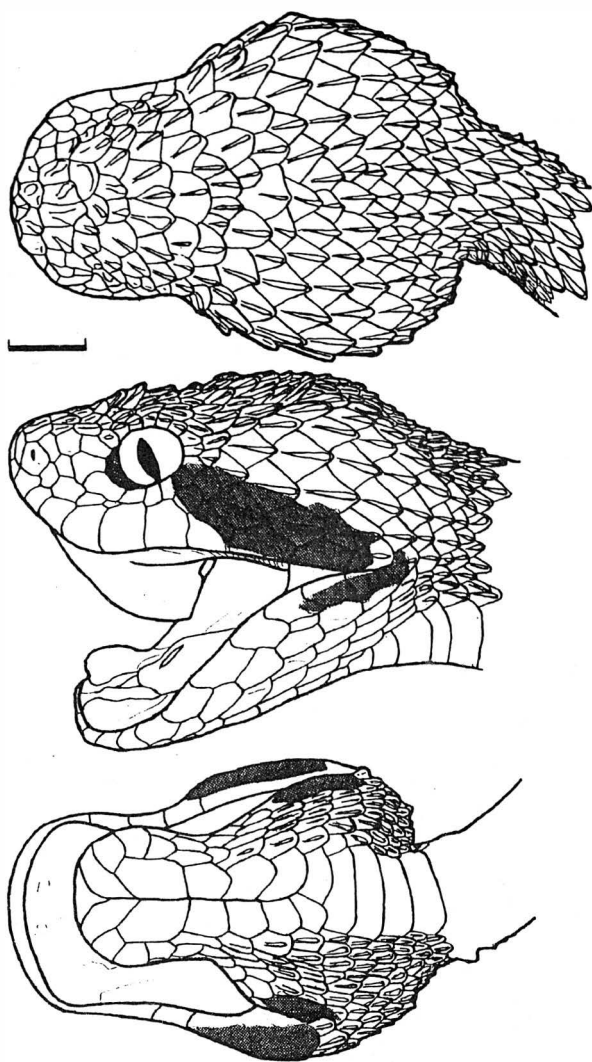


FIG. 8. *Atheris squamigera*: dorsal, lateral and ventral views of the head (CAS 197898 - Dja Forest Reserve, Cameroon). The line indicates 5 mm to scale.

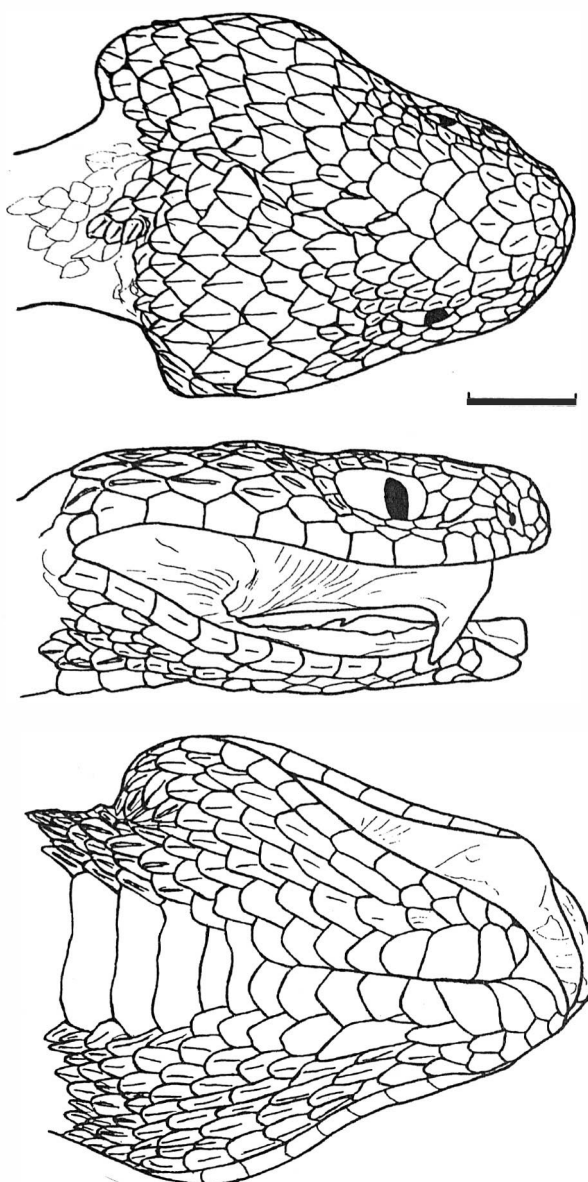


FIG. 9. *Atheris anisolepis*: dorsal, lateral and ventral views of the head (Lectotype, MNHN 1886.242 - Alima-Létéki, Congo). The line indicates 5 mm to scale.

region lack the postocular stripe or retain only vestiges. The only specimen from outside Cameroon for which he recorded a postocular stripe was ANSP 20334 from Nola, C.A.R.

Size. Largest (AMNH 11877 - Niapu, Ituri Forest, Zaire) 657 (547 + 110) mm, largest (MNHN 1964-553 - La Maboké/Boukoko, C.A.R.) 799 (664 + 135) mm (Roux-Estève, 1965).

Habitat. A forest species found at heights of up to 6 metres in trees, but also common at the forest edge in low bushes, descending to the ground to hunt its mammalian prey at night. Altitudinal range from sea level to 1900 metres (Kakamega Forest, Kenya).

Diet. A Togo specimen had a gecko (*Hemidactylus* sp.) in its stomach (Werner, 1897). Rodent remains were recorded from five Ituri Forest snakes (Schmidt, 1923). Specimens from Kaimosi, Kenya, contained rodents (1 *Dendromus*, 1 *Praomys*, 2 *Leggada*, rodent fur) and a frog (*Hyperolius*) (Loveridge, 1936). A pigmy mouse (*Leggada*) in a Ugandan snake

(Loveridge, 1942). Ionides only recorded rodents, some surprisingly large (Kakamega Forest), and Pitman (1974) found rodents, exceptionally lizards and amphibians. Two specimens from northwestern Tanzania both contained small rodents (Broadley, 1995). Cannibalism and predation on other snakes (*Bitis arietans* juv., 2 *Natriciteres olivacea*) has been observed in captivity in Zaire (Wallach, 1980). This species typically bites and holds on to its prey until it is dead before swallowing it (Wallach, 1980).

Breeding. Mating observed in Uganda during September-October (Pitman, 1974). Females give birth to three to nine young 180-200mm in length.

Distribution. Forests from Ghana (Hughes & Barry, 1969) east to western Kenya (Kakamega Forest) and north - Dr Indraneil Das, western Tanzania (Rumanyika

Game Reserve: Broadley, 1995), south to Angola (Laurent, 1964). Also Bioko Island.

ATHERIS ANISOLEPIS MOCQUARD
MAYOMBE BUSH-VIPER (FIG. 9)

Atheris anisolepis Mocquard, 1887: 89. Type locality: Alima [River]-Leketi, Congo, lectotype MNHN 1886.242.

Atheris laeviceps Boettger, 1887: 651 & 1888: 92, pl. ii, fig. 7. Type locality: Povo Netonna, near Banana, Zaïre, lectotype SM 21065.

Atheris squamigera (not Hallowell) Bocage, 1895: 152 (part, see footnote, p. 153).

Atheris squamiger (not Hallowell) Werner, 1902: 348 (part). *Atheris squamiger anisolepis* Bogert, 1940: 104.

Atheris squamiger squamiger (not Hallowell) Laurent, 1964: 128 (part).

Description. Rostral three times as wide as high, surmounted by seven or eight suprarostrals (the two middle ones in the lower row and the two outer ones in the upper row largest) and five keeled internasals. Nasals entire, separated from eye by 2-4 scales. Dorsal and lateral head scales strongly keeled, except for a group in the frontal/parietal region which are smooth or feebly keeled, 6-8 interorbitals and 14-18 scales across back of head between posterior supralabials. Eye moderate, its vertical diameter nearly one and a half times its distance from the lip. A row of scales usually separates the 12-17 circumorbitals from the 10-13 supralabials, fourth to seventh below the eye. Mental one and a half times as wide as long, infralabials 10-14, the first pair in contact behind the mental, followed by a pair of large rugose or feebly keeled sublinguals, 4 or 5 rows of keeled gulars and one or two prementals.

Dorsals pointed, strongly keeled (not mucronate or knobbed), 19-25 at midbody, lateral rows frequently duplicated; ventrals 153-160; subcaudals 47-55.

Colouration. Most adults are similar to *A. squamigera*: dull green above, uniform or with faint yellow crossbands posteriorly and black interstitial skin, yellowish-green below. The paratype of *A. laeviceps* was reddish yellow, suffused with olive green laterally, and with irregular broad olive green crossbars on posterior body and tail, tail tip blackish, ventrum chrome yellow with a few large green blotches on the posterior ventrals and anterior subcaudals (Boettger, 1888). Two specimens from Banana (AMNH 11898-9) are yellow with small green spots or mottling above, ventrum yellow, uniform or with a few small green spots. ZMUC R.68269 from Ménégué, Congo, is yellow with a few scattered blackish dorsal scales.

Size. Largest (Lectotype, MNHN 1886.242 - Leketi, Congo) 650 (543 + 107)mm; larger examined (AMNH 11898 - Banana, Zaïre) 435 (370 + 65) mm.

Taxonomic discussion. Mocquard (1887) described *Atheris anisolepis* on the basis of two specimens from Alima [River]-Leketi, Congo and a third from

Franceville [Gabon]. The larger of the Leketi specimens (MNHN 1886.242) is here nominated lectotype (Fig. 9) and the smaller (MNHN 1886.243) and the Franceville specimen (MNHN 1886.368) paralectotypes. The name was placed in the synonymy of *A. squamigera* by Boulenger (1896), but was revived as a subspecies by Bogert (1940) and is here reinstated as a full species, although its status needs to be confirmed by the examination of all available material from the Congo, Gabon, western Zaïre and northern Angola.

Boettger (1887) described *A. laeviceps* on the basis of two specimens from Povo Netonna, near Banana, Congo [= Zaïre]. He emphasized the lack of keels on about ten median scales on the crown of the head and two rows of infraorbital scales between eye and supralabials. He recorded 23-25 dorsal scale rows, 154-157 ventrals and 49-54 subcaudals. Mertens (1967) listed SMF 21065 as lectotype. The species was listed in the synonymy of *A. squamigera* by Boulenger (1896), but was revived by Schmidt (1923). Bogert (1940) pointed out that the name *A. anisolepis* Mocquard had priority, but *A. laeviceps* was again reinstated as a full species by Trape & Roux-Estève (1995), using the same diagnostic characters as Boettger. They did not mention *A. anisolepis*, although listing the Leketi syntypes among the Congo material in Paris.

Habitat. Forest at low and medium altitude (0 to 800 metres) and forest-savanna mosaic.

Distribution. Southern Gabon, southern Congo, western Zaïre (Mayombe) and (?) northern Angola.

ATHERIS HISPIDA LAURENT
BRISTLY BUSH-VIPER (FIG. 10)

Atheris squamigera (part, not Hallowell) Schmidt, 1923: 144;

Atheris squamiger (part, not Hallowell) Witte, 1933: 98.

Atheris squamigera squamigera (part, not Hallowell) Witte, 1941: 229. *Atheris hispida* Laurent, 1955: 138, 1956: 333 & 383, fig. 48B, pl. xxix, fig. 3-4. Type locality: Lutunguru, Kivu Province, Zaïre, holotype MRAC 15841.

Atheris squamiger squamiger (not Hallowell) Pitman, 1974: pl. 3, fig. 3.

Description. Rostral two and a half times as wide as high, surmounted by three suprarostrals (outer ones largest) and 4 to 6 smooth to feebly keeled internasals. Nasals large, separated from the eye by two scales. Dorsal and lateral head shields very strongly keeled, those on back of head mucronate to lanceolate (not in hatchlings: Pitman, 1974), 6-10 interorbital scales and 12 across back of head between posterior supralabials. Eye very large, the vertical diameter about twice its distance from the lip. The 9-15 circumorbitals are in contact with the 7-10 supralabials, the third and fourth or third to fifth below the eye. Mental two and a half times as wide as long, infralabials 8-10, the first pair in

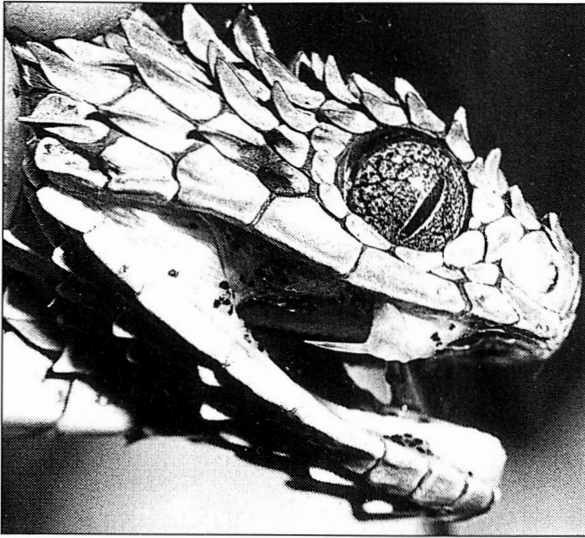


FIG. 10. *Atheris hispida*: lateral view of head, specimen from Kakamega Forest, Kenya (Photo by J.E. Cooper).

contact behind the mental, followed by a pair of small sublinguals and three rows of keeled gulars.

Dorsals strongly keeled and mucronate, those on the neck lanceolate, 15-19 rows at midbody, the laterals with frequent and regular fusions from rows 2-5; ventrals 149-166; subcaudals 49-64.

Colouration. Yellow-green to olive-brown or blackish above, darkening posteriorly, with a black marking on the back of the head that may take the form of a chevron, a W, an H or a pair of black blotches, often also a black temporal band extending diagonally from the eye to the commissure of the mouth (Spawls & Branch, 1995: colour photo); irregular dark dorsal blotches may coalesce to form crossbars or a zig-zag pattern, there may be a row of yellow lateral spots on the outer dorsal scale row. Ventrums green or yellow-green, becoming bluish caudad, more or less blotched with black, subcaudals almost entirely black, sometimes ventrum entirely black.

Size. Largest (Paratype, MRAC 4393 - Medje, Uele, Zaire) 735 (584 + 151) mm; largest (Paratype, IRSNB 2435 - Rutshuru, Virunga National Park, Kivu, Zaire) 578 (478 + 100) mm.

Habitat. A series from the Kivu Province of Zaire was taken in shrubs that were generally very thick with dark foliage, at a height of 1.5 to 2 metres above the ground (Laurent, 1960). In Kakamega Forest *A. hispida* seems to prefer tall dry thorn bushes, rarely more than 2-3 metres above the ground, whereas sympatric *A. squamigera* inhabits the more lush vegetation (Pitman, 1974).

Diet. A snail was found in the stomach of the holotype (Laurent, 1956). Small mammals and frogs in Kakamega Forest (Spawls & Branch, 1995).

Breeding. Females gave birth to 5-12 young in captivity, neonates measuring up to 170 mm in total length (Spawls & Branch, 1995).

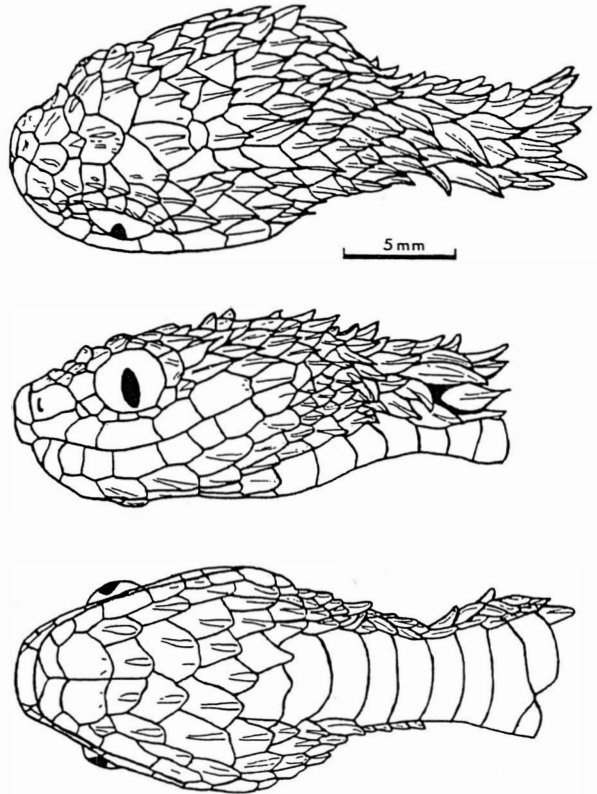


FIG. 11. *Atheris acuminata* sp. nov. dorsal, lateral and ventral views of head (Holotype, NMZB 13950 - Kyambura Game Reserve, Acholi, Uganda).

Distribution. Equatorial forest and gallery forests at altitudes between 800 m (Medje, Ituri Forest) and 1900 m (Kakamega Forest), i.e. northeastern Zaire (Orientale and Kivu Provinces), southwestern Uganda (southwest Ruwenzori and Kayonza, western Kigezi), northwestern Tanzania (Minziro Forest) and western Kenya (Kakamega Forest) (Fig. 13).

ATHERIS ACUMINATA SP. NOV.

ACUMINATE BUSH-VIPER (FIG. 11 & 12).

Holotype: NMZB 13950, a male from forest near Nsere Lodge, Kyambura Game Reserve, Ankole District, western Uganda (00°09'S: 30°08'E) at an altitude of ca. 950 m. Collected by Ms C. Allen on 3 May 1994.

This specimen was collected on the Frontier-Uganda UG12 Game Reserves Project, which is a collaborative project between the Society for Environmental Exploration (U.K.) and the Uganda Game Department.

Diagnosis. Closely related to *A. hispida*, but distinguished therefrom by the pentagonal rostral shield surmounted by two large suprarostrals (three in *hispida*); an enlarged weakly keeled frontal shield present, so that there are only five interorbitals (6-10 strongly keeled interorbital scales in *hispida*); only six supralabials (7-10 in *hispida*); mid-dorsal scales to beyond midbody with elongate recurved acuminate



FIG. 12. *Atheris acuminata* sp. nov. (Holotype, NMZB 13950) dorsolateral view of entire snake. (Photo by F.P.D. Cotterill).

spines (such spines restricted to the head and neck region in *hispida*).

Etymology. The name *acuminata* refers to the elongate dorsal scales on the back of the head and anterior body, which taper in long hollow curves to a sharp point.

Description. Rostral pentagonal, one and a half times as broad as deep, surmounted by two large smooth suprarrostral shields covering the anterior face of the snout, followed by three keeled internasals.

Nasals large, undivided and in contact with the largest anterior scale of the circumorbital ring. The anterior and lateral head scales are strongly keeled, but there is a large frontal and two pairs of "pseudoparietal" shields which are weakly keeled and consequently there are only five interorbital shields. Eye very large, the vertical diameter nearly twice its distance from the lip. The 11-12 circumorbital scales are in contact with the 6 supralabials, the third and fourth below the eye. Temporals and scales on back of head strongly keeled and acuminate, 10 between posterior supralabials. Mental two and a half times as wide as long, 7-8 infralabials, the first pair in broad contact behind the mental, followed by a pair of large, smooth, sublinguals and four rows of large, more or less keeled gulars ante-

rior to the first ventral.

Dorsal scales strongly keeled and acuminate, the median rows with elongate spines which decrease in size posteriorly, 13 rows on neck, 14 at midbody, 11 just before the vent, frequent fusions of lateral scale rows from rows 2 and 3, no lateral serration; ventrals 160; subcaudals 54.

Colouration. Yellow-green above, with a vague black H-shaped marking on back of head, a short black stripe extending from eye along lower temporals and black blotches on tail; interstitial skin black; eye mottled green with a gold border to the pupil in life. Ventrums pale greenish-yellow with black blotches posteriorly and on tail.

Size. Length 440 (359 + 81) mm. Mass 15 g.

Habitat. The holotype was found on a path in gallery forest fringing a small lake (ca. 1 km in diameter) and its feeder river just south of Lake George. The dominant trees in this forest are *Diospyros abyssinica* (50-75% of total cover), *Blighia unjugata* (25-50%), *Euclea schimperi* (25-50%), *Cola gigantea* (12-25%) and *Turrea robusta* (5-12%) (Zandri & Viskanic, 1992).

Distribution. Known only from the type locality, which is close to the Ugandan localities for *A. hispida* (Fig. 13).

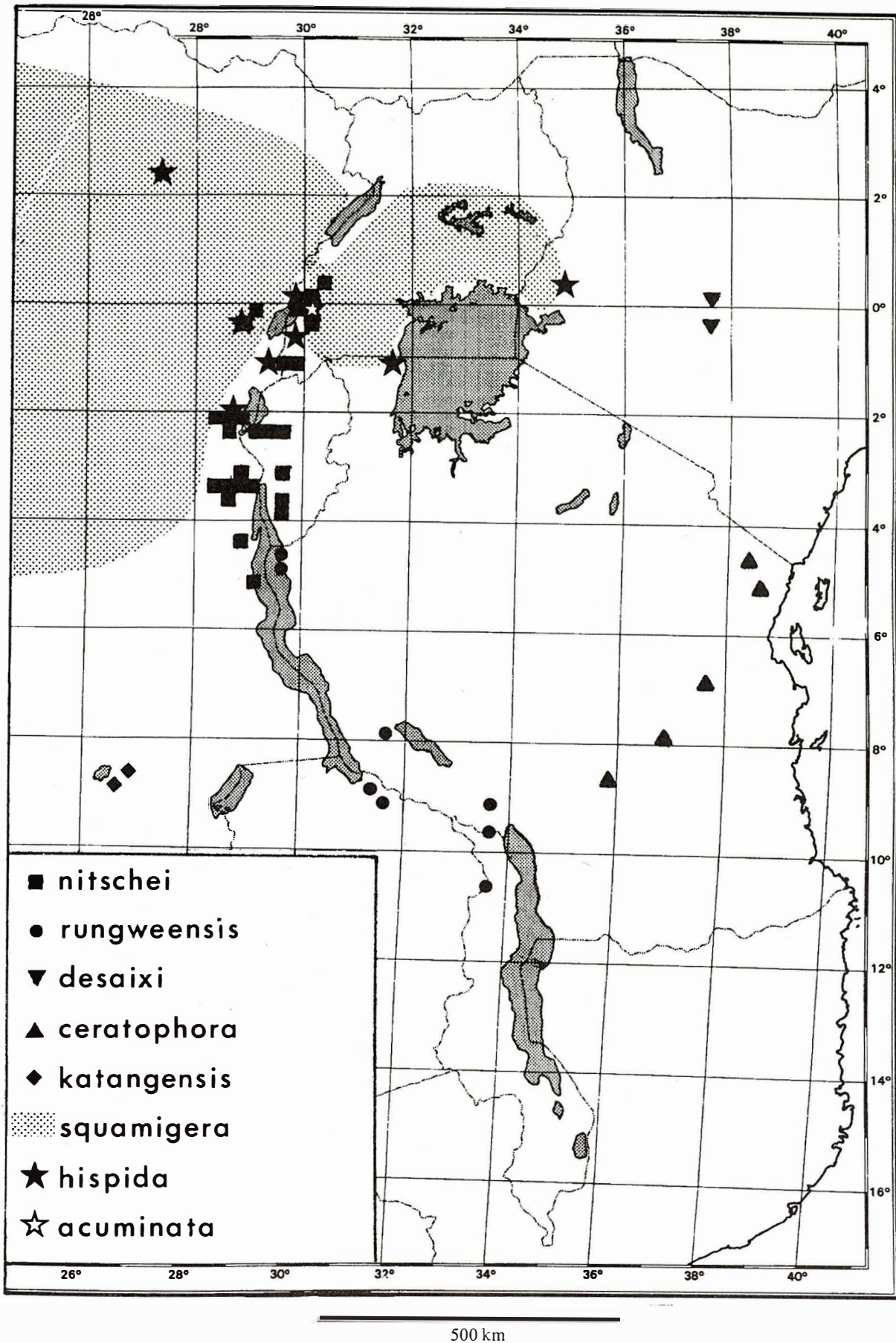


FIG. 13. Distribution of the *Atheris nitschei* and *A. hispida* species groups and the approximate distribution of eastern populations of *A. squamigera*.

KEY TO THE GENUS *ATHERIS*

- 1a. Lateral scales serrated.....2
- 1b. Lateral scales not, or but feebly and irregularly serrated.....6
- 2a. Supraocular scales forming elongate "horns" (Fig. 5) *ceratophora*
- 2b. No supraocular "horns" 3
- 3a. Four suprarostrol scales in first (or only) row; dorsals rounded at the apex; each dorsal scale tipped with yellow *desaixi*
- 3b. Three to five suprarostrols in first (or only) row; dorsals pointed at apex; dorsal scales not tipped with yellow 4
- 4a. Gular scales smooth or feebly keeled; lateral scale rows 2 to 6 or 8 strongly serrated; dorsum green with irregular black markings or green to blackish with symmetrical yellow markings 5
- 4b. Gular scales strongly keeled; lateral scale rows 4 to 6 weakly serrated; dorsum yellow-brown to purple-brown with dark-centred pale yellowish rhombic vertebral markings *katangensis*
- 5a. Scales on top of head anteriorly smooth or feebly keeled; 18-20 scales across back of head between posterior supralabials; dorsal body scales with keels extending to the tip; dorsum yellowish green with variable black markings (See Loveridge, 1942: pl. 3, fig. 3); habitat upland swamps and forests *nitschei*
- 5b. Scales on top of head anteriorly strongly keeled; 24-26 scales across back of head between posterior supralabials; dorsal body scales with keels not extending to the tip; dorsum dark green to blackish, often with symmetrical yellow markings on back of head and dorsolateral yellow zig-zag lines and spots (See Loveridge, 1953: pl. 5, fig. 1); habitat montane forest *rungweensis*
- 6a. Scales across top of head between posterior supralabials usually more than 23; three or more scales between eye and nasal; midbody scale rows 25-36 *chlorechis*
- 6b. Scales across top of head between posterior supralabials less than 23; one or two scales between eye and nasal; midbody scale rows 14-25 7
- 7a. Scales on neck lanceolate or acuminate; lateral scale rows 2-5 frequently fused; scales across top of head between posterior supralabials 10-12 9
- 7b. Scales neck not lanceolate or acuminate; lateral scale rows 2-5 frequently duplicated; scales across top of head between posterior supralabials 15-18 8
- 8a. Interorbital scales strongly keeled; interoculars usually absent *squamigera*
- 8b. Interorbital scales smooth or feebly keeled; usually one or two rows of interoculars present *anisolepis*
- 9a. Three large suprarostrols; interorbitals 6-10, strongly keeled; two scales between eye and nasal; supralabials 9-10; midbody scale rows 15-18; lanceolate dorsal scales do not extend beyond midbody *hispidia*
- 9b. Two very large suprarostrols; interorbitals 5, median ones feebly keeled; a single scale between eye and nasal; supralabials 6; midbody scale rows 14; lanceolate dorsal scales extend beyond midbody *acuminata* sp. nov.

PHYLOGENY

The albumin-immunological data of Herrmann (1995) confirm that the species *superciliaris* constitutes a sister group to all other members of the tribe Atherini and consequently it has been assigned to the new genus *Proatheris* (Broadley, 1996). *Proatheris superciliaris* can therefore be used as an outgroup for the investigation of the phylogeny of *Atheris* sensu stricto.

Herrmann (1995) prepared antisera against the albumins of *P. superciliaris*, *A. nitschei* and *A. squamigera*, in addition to seven species of *Bitis*, two species of *Cerastes*, *Echis leucogaster*, *Macrovipera deserti*, *Daboia russelli*, *Causus rhombeatus* and *Boulengerina annulata*. His reciprocal matrix of albumin-immunological distances indicates that *A. nitschei* has closer affinities with *Proatheris* than does *A. squamigera*. Unidirectional comparisons were then made with albumins from three additional species of *Atheris* (*chlorechis*, *hispidia* and *desaixi*) and they all showed closer affinities with *A. nitschei* than with *A. squamigera*. However, in a subsequent study (Herrmann & Joger, 1997), *A. hispidia* came closer to *A. squamigera* in a Fitch-Margoliash dendrogram, so the phylogeny of the genus remains unsettled.

On the basis of its serrated keels on the lateral scales, *nitschei* can head a species group including the eastern species *rungweensis*, *desaixi*, *ceratophora* and *katangensis*. This character is not present in *Proatheris*, so it seems that these *Atheris* do not share a common ancestry with the other vipers with serrated lateral scales (*Echis* and *Cerastes*), whose spectacular stridulatory threat displays are in any case shared by the totally unrelated genus *Dasypeltis* (Groombridge, 1980). *A. chlorechis*, the westernmost species in the genus, perhaps represents a peripheral member of the *nitschei* group, as it may sometimes show slight serration on some lateral scales (Groombridge, 1980).

Atheris squamigera is the most wide-ranging and variable species in the genus, apparently with a sibling species, *A. anisolepis*, sympatric in the Mayombe region. Better understanding of this species group will require re-examination of all available museum material.

The *Atheris hispidia* group is readily distinguished by the development of lanceolate or acuminate dorsal scales and the fusion of lateral scale rows rather than their duplication as in the other species groups. There is also a reduction in the number of head shields and dorsal scale rows. It is interesting to note that although *A. hispidia* has frequently been confused with *A. squamigera*, on the basis of albumin-immunological data it is closer to *A. nitschei*. *A. acuminata* shares with *A. anisolepis* the development of an interorbital patch of smooth or weakly keeled scales, but it differs in that some have fused to form the equivalent of a colubrid frontal and two pairs of parietal shields.

ACKNOWLEDGEMENTS

I am indebted to the following colleagues for the loan of comparative material: Charles Myers (AMNH); Robert Drewes and Jens Vindum (CAS); G. Lenglet (IRSNB); Ivan Ineich (MNH) and Jens Rasmussen (ZMUC). I also thank Kim Howell for the donation of Tanzanian material and for facilities provided when I examined his collection at the University of Dar es Salaam and Robert Kityo for assistance when I examined the reptile collection in the Makerere University Zoological Museum. I am grateful to Damaris Rotich (NMK), who provided a specimen of *Atheris desaixi* in an exchange. Barry Hughes and Van Wallach kindly supplied basic data for many specimens of *Atheris squamigera* and *A. nitschei* personally examined. I am particularly indebted to Hans-Werner Herrmann, who presented me with a copy of his thesis at the Fourth Herpetological Association of Africa Symposium at St. Lucia in October, 1995, and also to Colin McCarthy (BMNH), who provided me with a photocopy of the relevant sections of Brian Groombridge's 1980 PhD thesis. I am grateful to Dietmar Emmrich and Aaron Bauer for several translations from the German. I thank Ms Christie Allen for providing details of the habitat for the holotype of *Atheris acuminata* and Gerald Rilling for habitat data for *A. rungweensis*.

REFERENCES

- Ashe, J. (1968). A new bush viper. *J. E. Afr. nat. Hist. Soc. natn. Mus.* **27**, 53-59.
- 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. *Mem. Mus. comp. Zool. Harv.* **50**, 87-265.
- Barbour, T. & Loveridge, A. (1930). Reptiles and amphibians from Liberia. In Strong, R., *Report of the Harvard-African Expedition upon the African Republic of Liberia and the Belgian Congo* **2**, 769-786.
- Bocage, J. V. Barboza du (1895). *Hérpétologie d'Angola et du Congo*. Lisbonne: Imprimerie Nationale.
- Boettger, O. (1887). Diagnoses Reptilium Novorum ab ill. viro Paul Hesse in finibus fluminis Congo reptorum. *Zool. Anz.* **10**, 649-651.
- Boettger, O. (1888). Materialien zur Fauna des unteren Congo. II. Reptilien und Batrachier. *Ber. Senckenberg Naturf. Ges.* 3-108.
- Bogert, C. M. (1940). Herpetological results of the Vernay Angola Expedition, with notes on African reptiles in other collections. Part I. Snakes, including an arrangement of African Colubridae. *Bull. Amer. Mus. nat. Hist.* **77**, 1-107.
- Böhme, W. (1987). Seltene Reptilien aus dem Uzungwe-Gebirge, Süd-Tansania. *Herpetofauna* **9** (48), 27-34.
- Bonaparte, C. L. (1849). On the Lorine genus of parrots, *Eclectus*, with the description of a new species, *Eclectus cornelia*. *Proc. zool. Soc. Lond.* 142-146.
- Boulenger, G. A. (1896). *Catalogue of the snakes in the British Museum (Natural History)*. **3**. London: British Museum (Natural History)
- Boulenger, G. A. (1906). Description of a new Tree-Viper from Mount Ruwenzori. *Ann. Mag. nat. Hist.* (7) **18**, 37-38.
- Boulenger, G. A. (1919). Batraciens et Reptiles recueillis par le Dr. C. Christy au Congo Belge, dans les districts de Stanleyville, Haut-Uelé et Ituri en 1912-1914. *Rev. Zool. Afr.* **7**, 1-29.
- Broadley, D. G. (1989). Case 2691: *Atheris* Cope, 1862 (Reptilia, Serpentes): proposed conservation, and proposed confirmation of *Vipera chlorechis* Pel, [1851] as the valid name of the type species. *Bull. zool. Nomencl.* **46**, 264-266.
- Broadley, D. G. (1995). Geographical distribution: *Atheris squamigera squamigera*. *Afr. Herp. News* No. **23**, 49.
- Broadley, D. G. (1996). A review of the tribe Atherini (Serpentes: Viperidae), with the descriptions of two new genera. *Afr. J. Herpetol.* **45**, 40-48.
- Broadley, D. G. & Howell, K. M. (1991). A checklist of the reptiles of Tanzania, with synoptic keys. *Syntarsus* No. **1**, 1-70.
- Broadley, D. G. & Pitman, C. R. S. (1960). On a collection of snakes taken in Northern Rhodesia by Monsieur H. J. Bredo. *Occ. Pap. natn. Mus. S. Rhod.* Ser. B, **24**, 437-451.
- Cansdale, G. S. (1961). *West African Snakes*. 74 pp. London: Longmans.
- Cope, E. D. (1860). Catalogue of the venomous serpents in the Museum of the Academy of Natural Sciences of Philadelphia, with notes on the families, genera and species. *Proc. Acad. nat. Sci. Philad.* **1859**, 332-347.
- Cope, E. D. (1862). Notes on some reptiles of the Old World. *Proc. Acad. nat. Sci. Philad.* **1862**, 337-344.
- Doucet, J. (1963). Les Serpents de la République de Côte d'Ivoire. *Acta Tropica* **20**, 200-340.
- Emmrich, D. (1997). Further remarks on the rare Usambara Forest-Viper, *Atheris ceratophora*, Werner, 1895. *Mitt. Zool. Mus. Berlin* **73**, 131-151.
- Fischer, J. G. (1888). Über zwei neue Schlangen und einen neuen Laubfrosch von Kamerun. *Jb. hamb. wiss. Anst.* **5**, 1-10.
- Gans, C. & Baic, D. (1974). Convergent surface structures in the sound producing scales of some snakes (Reptilia: Serpentes). In L. Arvy (ed.) *Recherches Biologiques Contemporaines*: 265-272. Nancy: Vagner.
- Goetz, J. C. (1975). The vipers of Africa south of the Sahara. *Bull. New York Herpetol. Soc.* **12**, 3-11.
- Groombridge, B. C. (1980). *A phyletic analysis of viperine snakes*. Unpub. PhD thesis, Council for National Academic Awards
- Groombridge, B. C. (1987). Phyletic relationships among viperine snakes. In Rocek, Z. (ed.) *Studies in Herpetology*, 219-222. Prague: Proceedings of the Third Ordinary General Meeting of the Societas Europaea Herpetologica, 1985.

- Günther, A. (1863a). On new species of snakes in the collection of the British Museum. *Ann. Mag. nat. Hist.* **11**, 20-25.
- Günther, A. (1863b). On *Atheris burtonii*, a new snake from West Africa. *Proc. zool. Soc. Lond.* 16-17.
- Hallowell, E. (1856). Descriptions of new reptiles from Guinea. *Proc. Acad. nat. Sci. Philad.* **1854**, 193-194.
- Hedges, N. G. (1983). *Reptiles and amphibians of East Africa*. Nairobi: Kenya Literature Bureau.
- Herrmann, H.-W. (1995). *Zur Phylogenie Afrikanischer Vipern (Reptilia: Serpentes: Viperidae)*. Unpub. DSc thesis, Philipps-Universität Marburg
- Herrmann, H.-W. & Joger, U. (1995). Molecular data on the phylogeny of African vipers. Preliminary results. In: Llorente, G.A. et al. (Eds). *Scientia Herpetologica*, 92-97.
- Herrmann, H.-W. & Joger, U. (1997). Evolution of viperine snakes. In: Thorpe, R. S. et al. (Eds) *Venomous Snakes: Ecology, evolution and snakebite. Symp. zool. Soc. Lond.* **70**, 43-61.
- Hughes, B. & Barry, D. H. (1969). The snakes of Ghana: a checklist and key. *Bull. Inst. fond. Afr. noire sér. A*, **31**, 1004-1041.
- Isemonger, R. M. (1968). *Snakes of Africa*. Cape Town: Books of Africa.
- Jan, G. (1863). *Elenco Sistimatico degli Ofidi descritti e disegnati per l'Iconographie generale*. Milano.
- Laurent, R. F. (1955). Diagnoses préliminaires de quelques Serpents venimeux. *Rev. Zool. Bot. Afr.* **51**, 127-139.
- Laurent, R. F. (1956). Contribution à l'Herpétologie de la Région des Grands Lacs de l'Afrique centrale. *Ann. Mus. roy. Congo belge, sér. in 8vo, Sci. Zool.* **48**, 1-390.
- Laurent, R. F. (1960). Notes complémentaires sur les Chéloniens et les Ophidiens du Congo oriental. *Ann. Mus. roy. Congo belge, sér. in 8vo, Sci. Zool.* **84**, 1-86.
- Laurent, R. F. (1964). Reptiles et Ophidiens de l'Angola (Troisième contribution). *Publçoes cult. Co. Diam. Angola No.* **67**, 1-165.
- Leviton, A. E., Gibbs, R. H. Jr., Heal, E. & Dawson, C. E. (1985). Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* **1985**, 802-832.
- Loveridge, A. (1933). Reports on the scientific results of an expedition to the south-western highlands of Tanganyika Territory. VII. Herpetology. *Bull. Mus. comp. Zool. Harv.* **74**, 197-416.
- Loveridge, A. (1936). Scientific results of an expedition to rain forest regions in eastern Africa. V. Reptiles. *Bull. Mus. comp. Zool. Harv.* **79**, 209-337.
- Loveridge, A. (1942). Scientific results of a fourth expedition to forested areas in east and central Africa. IV Reptiles. *Bull. Mus. comp. Zool. Harv.* **91**, 237-373.
- Loveridge, A. (1953). Zoological results of a fifth expedition to East Africa. III Reptiles from Nyasaland and Tete. *Bull. Mus. comp. Zool. Harv.* **110**, 141-322.
- Loveridge, A. (1957). Check list of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). *Bull. Mus. comp. Zool. Harv.* **117**, 151-362 + i-xxxvi.
- Marx, H. & Rabb, G. B. (1965). Relationships and zoogeography of the Viperine snakes (Family Viperidae). *Fieldiana: Zool.* **44**, 161-206.
- Marx, H. & Rabb, G. B. (1972). Phyletic analysis of fifty characters of advanced snakes. *Fieldiana: Zool.* **63**, i-vii, 1-321.
- Meirte, D. (1992). Cles de détermination des serpents d'Afrique. *Ann. Mus. roy. Afr. cent. sér. 8vo, Sci. Zool.* **267**, 1-161.
- Mertens, R. (1967). Die herpetologische Sektion des Natur-Museums und Forschungs-Institutes Senckenberg in Frankfurt a. M. nebst einem Verzeichnis ihrer Typen. *Senckenb. biol.* **48**, 1-106.
- Mocquard, M. F. (1887). Sur les ophidiens rapportés du Congo par la mission de Brazza. *Bull. Soc. philom. Paris* **11**, 62-92.
- Pel, H. S. (1851). Over de jagt aan de Goudkust, volgens een tienjarige eigene ondervinding. *Ned. Tijdschr. Jagtkunde* **1**, 149-173.
- Perret, J.-L. (1961). Études herpétologiques Africains III. *Bull. Soc. neuchâteloise Sci. nat.* **84**, 133-138.
- Perret, J.-L. & Mertens, R. (1957). Étude d'une collection herpétologique faite au Cameroun de 1952 à 1955. *Bull. Inst. fond. Afr. noire, sér. A*, **19**: 548-601.
- Peters, W. C. H. (1864). Eine neue Art der Baumvipern, *Atheris polylepis* aus Liberia. *Mber. Königl. Akad. Wiss. Berl.* **1864**, 642-645.
- Peters, W. C. H. (1876) Eine zweite Mittheilung über die von Hrn. Professor Dr. R. Bucholz in Westafrika gesammelten Amphibien. *Monatsber. Akad. Wiss. Berlin*: 117-1323, pl. i.
- Pitman, C. R. S. (1974). *A guide to the snakes of Uganda*. Revised Edition. xxii + 290 pp. Codicote: Wheldon & Wesley.
- Pook, C. E. (1990). Notes on the genus *Atheris* (Family Viperidae). *Br. herpetol. Soc. Bull.* **32**, 31-36.
- 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 *A. nitschei rungweensis* Bogert, 1940, and a discussion of its validity (Reptilia, Serpentes, Viperidae). *Amphibia-Reptilia* **3**, 269-277.
- Reuss, T. (1939). Berichtigungen und Ergänzungen zu meinen Arbeiten über Toxicophidier, 1938. *Z. Aquar.-u. Terrar. Ver.* **1**, 14.
- Rilling, G. (1972). Records from the Nyambeni Hills. *Bull. E. Afr. nat. Hist. Soc.*: 202.
- Rochebrune, A. T. de (1885). Vertébratons nouveaux vel minus cognitorum orae Africae occidentalis in colarum. *Bull. Soc. philom. Paris* **9**, 86-99.
- Roux-Estève, R. (1965). Les Serpents de la région de La Maboké-Boukoko. *Cahiers de la Maboké* **3**, 51-92.
- Schlegel, H. (1855). Over eenige nieuwe soorten van vergiftige slangen van de Goudkust. *Versl. Meded. K. Akad. wet. Amst.* **3**, 312-317.

- Schmidt, K. P. (1923). Contributions to the herpetology of the Belgian Congo based on the collection of the American Congo Expedition, 1909-1915 Part II. Snakes. *Bull. Am. Mus. nat. Hist.* **49**, 1-146.
- Skinner, H. A. (1973). *Snakes and us*. Nairobi: East African Literature Bureau.
- Spawls, S. (1990). Further comments on *Atheris*. *Br. herpetol. Soc. Bull.* **34**, 44-45.
- Spawls, S. & Branch, W. R. (1995). *The dangerous snakes of Africa*. Halfway House: Southern Book Publishers.
- Tornier, G. (1902). Herpetologische Neues aus Deutsch-Ost-Afrika. *Zool. Jahrb.* **16**, 578-590.: 578-590.
- Trape, J. F. & Roux-Estève, R. (1995). Les Serpents du Congo: Liste commentée at clé de détermination. *J. Afr. Zool.* **109**, 31-50.
- Vesey-FitzGerald, D. F. (1958). The snakes of Northern Rhodesia and the Tanganyika borderlands. *Proc. Trans. Rhodesia sci. Assoc.* **46**, 17-102.
- Villiers, A. (1950). La collection de Serpents de l'IFAN. *Inst. fr. Afr. noire, Catalogues* **6**, 1-155.
- Wallach, V. (1980). Interspecific and intraspecific predation in captive bush-vipers (*Atheris squamiger* Hallowell, 1854), with notes on different colour phases. *J. Herpetol. Assoc. Afr.* **24**, 2-3.
- Werner, F. (1897). Ueber Reptilien und Batrachier aus Togoland, Kamerum und Tunis aus dem Kgl. Museum für Naturkunde in Berlin. *Verh. zool.-bot. Ges. Wien* **47**, 395-408.
- Werner, F. (1902). Ueber westafrikanische Reptilien. *Verh. zool.- bot. Ges. Wien* **52**, 332-348.
- Wilson, V. J. (1965) The snakes of the Eastern Province of Zambia. *Puku* **3**, 149-170.
- Witte, G.-F. de (1933). Reptiles récoltés au Congo Belge par le Dr. H. Schouteden et par M. G.-F. de Witte. *Ann. Mus. Congo Belge Zool.*, sér. 1, **3**, 55-98.
- Witte, G.-F. de (1941). Batraciens et Reptiles. *Explor. Parc natn. Albert Miss. G.-F. de Witte* **33**, 1-xvii + 1-261.
- Witte, G.-F. de (1953). Reptiles. *Explor. Parc natn. Upemba Miss. G.-F. de Witte* **6**, 1-322.
- Witte, G.-F. de (1962). Genera des Serpents du Congo et du Ruanda-Urundi. *Annls Mus. r. Afr. Cent.*, Sér. 8vo, Sci. Zool., **104**, 1-203.
- Witte, G.-F. de (1975). Serpents: Boidae, Colubridae, Elapidae et Viperidae. In: *Explor. Parc. natn. Virunga*, sér. 2, **24**, 62-121.
- Zandri, E. & Viskanac, P. (1992). *Vegetation survey and mapping in the Queen Elizabeth National Park, Kyambura Game Reserve and Kigezi Game Reserve*. [Uganda] Rome: FAO

APPENDIX

Comparative material examined:

Atheris nitschei

UGANDA: NMZB 1282, NMZB-UM 211 Kishasha Valley, Kigezi; NMZB 1283-4 Muko, Lake Bunyonyi, Kigezi. RWANDA: KMH 6148 Beza Forest.

Atheris rungweensis

TANZANIA: KMH 3136, 6150; NMZB 11580. ZAMBIA: IRSNB 18284, NMZB-UM 3151. (For locality data see species account)

Atheris desaixi

KENYA: BMNH 1969.2419 (holotype) near Chuka; NMZB 13980 Meru area.

Atheris ceratophora

TANZANIA: BMNH 1960.1.6.54, 1971.223 Amani, East Usambaras; NMZB 7151 West Usambaras; LSUS/DCM 463-4, NMZB 11588-9 Luhega Forest Reserve, Udzungwa Mountains.

Atheris katangensis

ZAIRE: IRSNB 2206, 2209 Parc National Upemba

Atheris chlorechis

GHANA: ZMUC R6883 Bobiri Forest Reserve. SIERRA LEONE: ZMUC R6884 Gola Forest

Atheris squamigera

CAMEROON: CAS 103164 34km N of Lolodorf; CAS 197898-9 Boumir Camp, Dja Forest Reserve; NMZB 1278 Metet; ZMUC R68270 Tchissanga.

KINSHASA: AMNH 11857-8 Avakubi; AMNH 11859-60, 11862-3 Medje; AMNH 11865-6 Rungu; AMNH 11867 Nola; AMNH 11868-9 Akenge; AMNH 11870-2, 11874-7 Niapu; NMZB-UM 33612 Mbanza-Ngungu, Kinshasa; NMZB-UM 33613 Kinsuka, Kinshasa. UGANDA: MUZM 110-2, 117 Itwara Forest; NMZB 1279 Kajansi Forest; NMZB 1280 Kasiriye, Kyagwe; NMZB 1281 Mabira Forest.

KENYA: NMZB 3610, 3722, 3753, 3951-2, NMZB-UM 5393, 6518-9 Kakamega Forest. TANZANIA: NMZB 11501-2 Rumanyika Game Reserve. Basic data was also provided by Barry Hughes (54 specimens) and Van Wallach (85 specimens).

Atheris anisolepis

CONGO: MNHN 1886.42 (Lectotype) Leketi; ZMUC R68269 Ménégué. ZAIRE: AMNH 11898-9 Banana

Atheris hispida

UGANDA: BMNH 1934.12.15.630 S.W. Ruwenzori; NMZB-UM 2558 Kayonza, S.W. Kigezi. KENYA: BMNH 1969.2866; NMZB-UM 5317 Kakamega Forest. TANZANIA: KMH --- Minziro Forest.

Accepted: 5.6.97