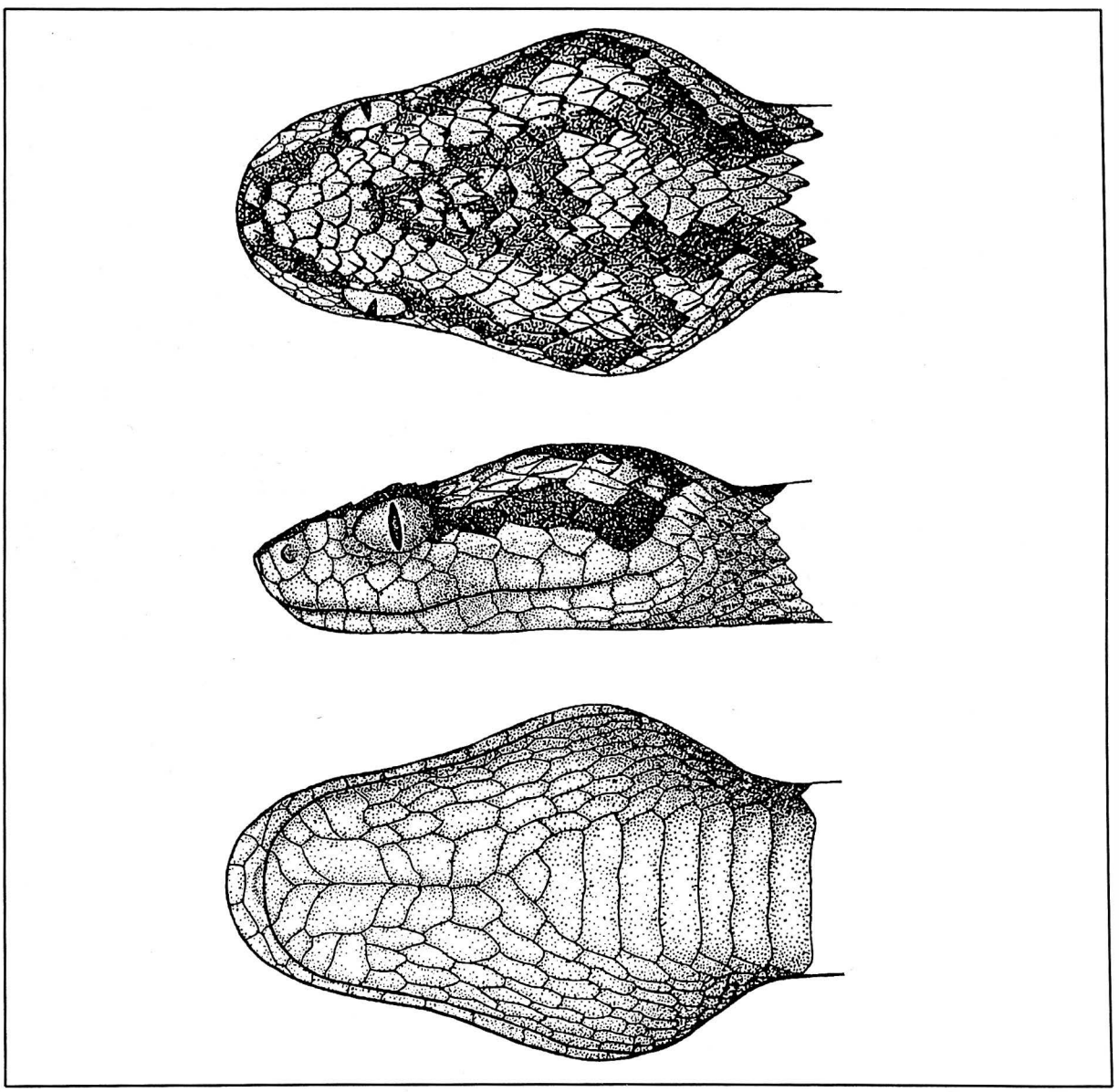
Volume 8, Number 3

July 1998
ISSN 0268-0130

THE HERPETOLOGICAL JOURNAL



Published by the
BRITISH HERPETOLOGICAL SOCIETY

Indexed in
Current Contents

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BRITISH HERPETOLOGICAL SOCIETY

FRONT COVER: *Atheris nitschei* (D. Broadley)

HERPETOLOGICAL JOURNAL, Vol. 8, pp. 117-135 (1998)

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

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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. rungweensis* 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 rungweensis* 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 suprarostral 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 suprarostral 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 warrent 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
Proatheris	0	1-3	6-8	20-25	8-14	0(1)	2	8-11	10-13	1
nitschei	3-7	4-5	6-12	18-20	10-17	(0)1(2)	2-5	8-13	9-15	3-6
rungweensis	3-7	5-6	9-13	24-26	15-18	1-2	3-4	9-12	11-13	2-3
desaixi	6-7	5	8-11	22	14-17	1-2	2-3	10-12	11-14	4-6
ceratophora	5-9	4-5	7-11	19-20	13-19	0-1	2-4	7-11	8-12	1-3
katangensis	3-6	5-6	9-11	20-22	14-17	0-1	2-3	9-12	11	3
chlorechis	7-8	5	8-14	25-27	15-20	(0)1(2)	3-4	9-12	10-11	1-2
squamigera	3-7	3-5	5-11	15-22	10-18	0(1)	(1)2(3)	7-13	8-13	2-7
anisolepis	7-8	5	6-8	14-18	12-17	(0)1	2-4	10-13	10-14	3-8
hispida	3	4-6	6-10	12	9-15	0	2	9-10	8-10	1-2
acuminata	2	3	5	10	11-12	0	1	6	7-8	1

& Rabb and typical of the species *Atheris nitschei, rungweensis, katangensis, squamigera* and *hispida* (Figs 1b, 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 side, making a total of seven suprarostrals (Fig 1c). The middle suprarostral can also be split into three by a horizontal and a partial vertical sulcus, either dorsal (Fig 1l) or ventral (Fig 1h), making five suprarostrals.

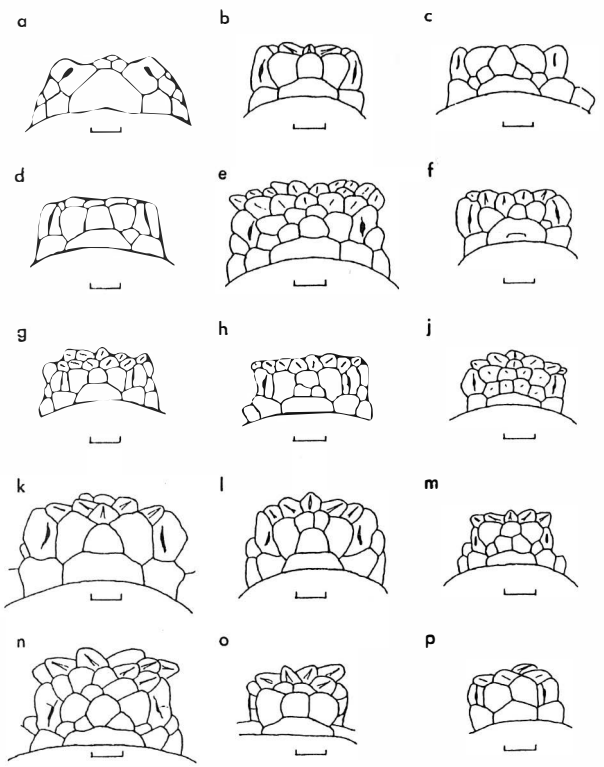

FIG. 1. Scalation of the snout: a, *Proatheris superciliaris* (NMZB-UM 27022 - Malawi); b, *Atheris nitschei* (NMZB 2557 - Uganda); c, *A. nitschei* (NMZB 1284 - Uganda); d, *A. rungweensis* (NMZB 11580 - Tanzania); e, *A. desaixi* (NMZB 13980 - Kenya); f, *A. ceratophora* (NMZB 7151 - Tanzania); g, *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. hispida* (NMZB-UM 5317 - Kenya); p, *A. acuminata* sp. nov. (NMZB 13950, holotype - Uganda).

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 suprarostral 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. hispida* by the loss of the median suprarostral.

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 *rungweensis* (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 (occuring 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 threat 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 *Dasypeltis* 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	
Proatheris	27-29	137-145	138-156	37-42	32-43	598
nitschei	23-34	140-160	141-162	41-59	35-54	750
rungweensis	23-33	154-162	150-165	54-58	46-53	642
desaixi	21-31	165	164-168	53-54	41-46	682
ceratophora	19-27	136-150	134-152	49-58	46-57	642
katangensis	23-31	140-144	133-141	45-49	38-42	397
chlorechis	25-37	151-165	153-165	55-63	48-58	585
squamigera	15-25	133-169	141-175	46-67	45-61	799
anisolepis	19-25	153-159	157-160	50-53	47-55	650
hispida	15-19	149-166	153-162	54-64	49-57	735
acuminata	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 (*rungweensis, 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 chloroechis* Schlegel 1855 [a junior subjective synonym of *Vipera chlorechis* Pel 1851], see Broadley, 1989: 264.

Poecilostolus Günther, 1863*a*: 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.

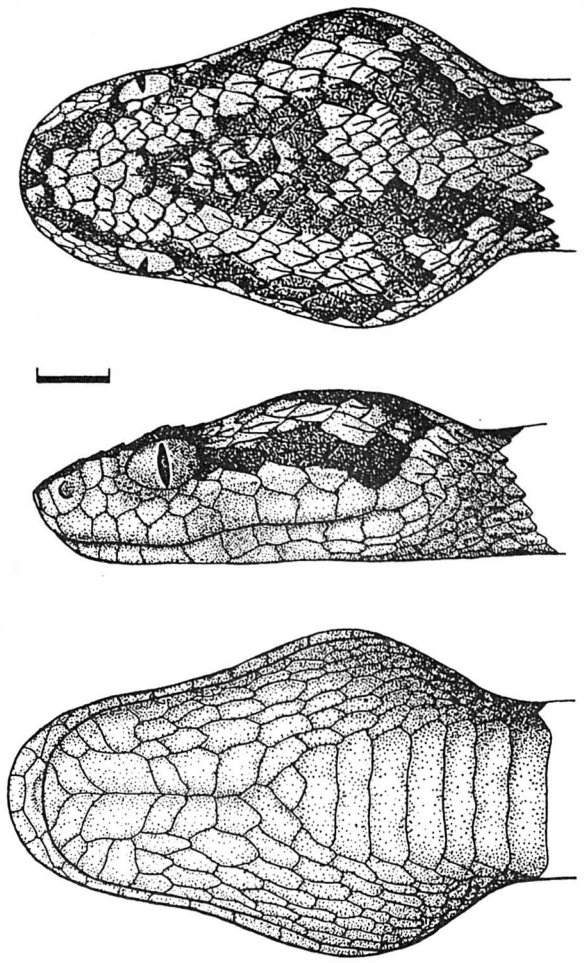

FIG. 2. *Atheris nitschei*: dorsal, lateral and ventral views of the head (after Witte, 1962: Fig. 93). The line indicates 5 mm to scale.

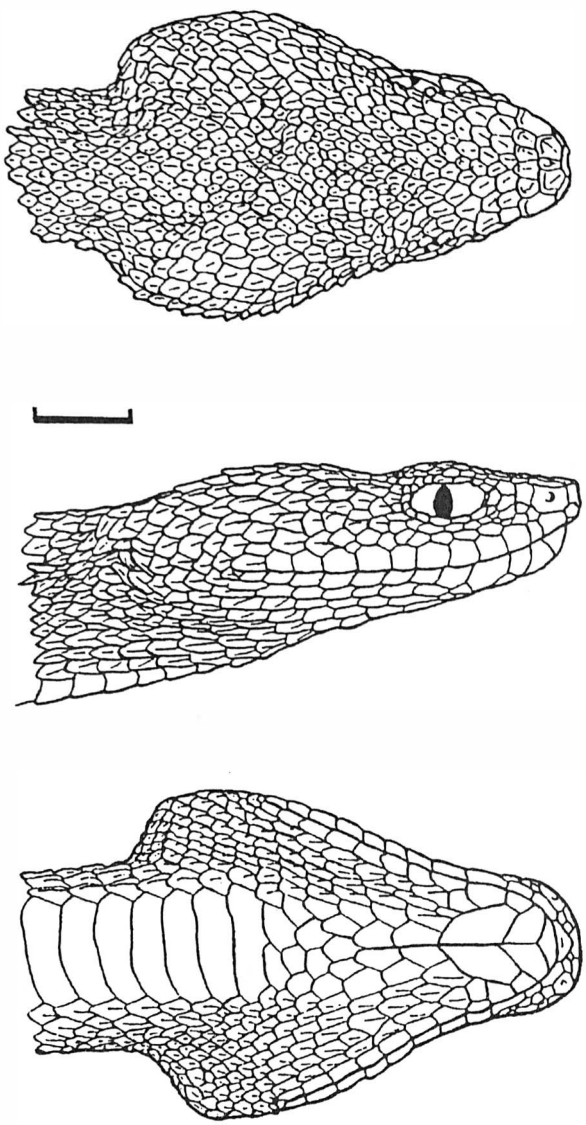

FIG. 3. *Atheris rungweensis*: dorsal, lateral and ventral views of the head (Holotype, AMNH 39186 - Rungwe Mountain, Tanzania: after Bogert, 1940: Fig. 18). The line indicates 5 mm to scale.

ATHERIS NITSCHEI 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 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 midbody, 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. Ventrum 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); 750mm (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 (*Leptosiaphos* 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 preventral.

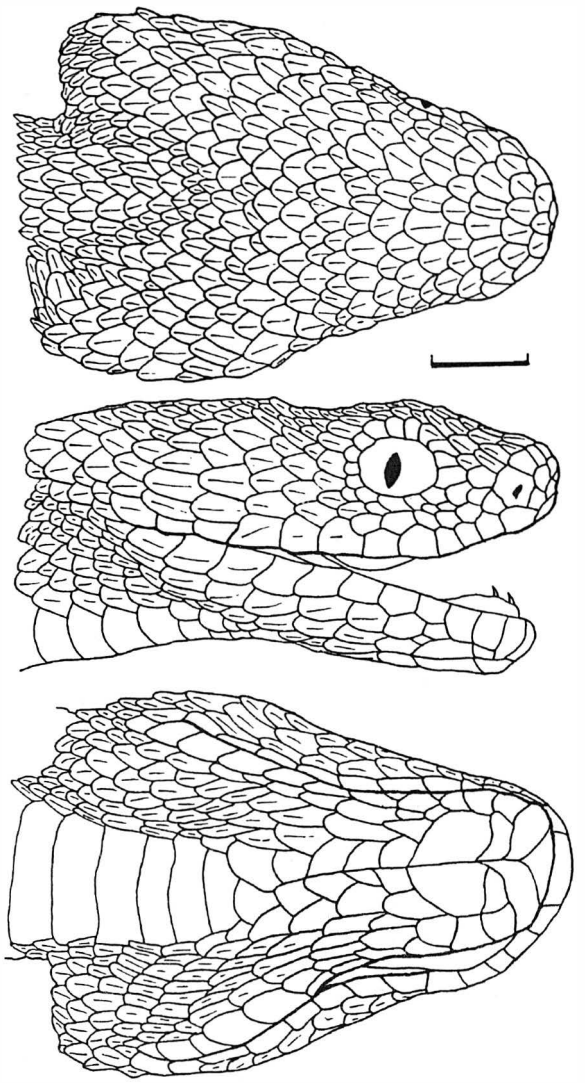

FIG. 4. *Atheris desaixi*: dorsal, lateral and ventral views of the head (NMZB 13980 - Meru, Kenya). The line indicates 5 mm to scale.

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;

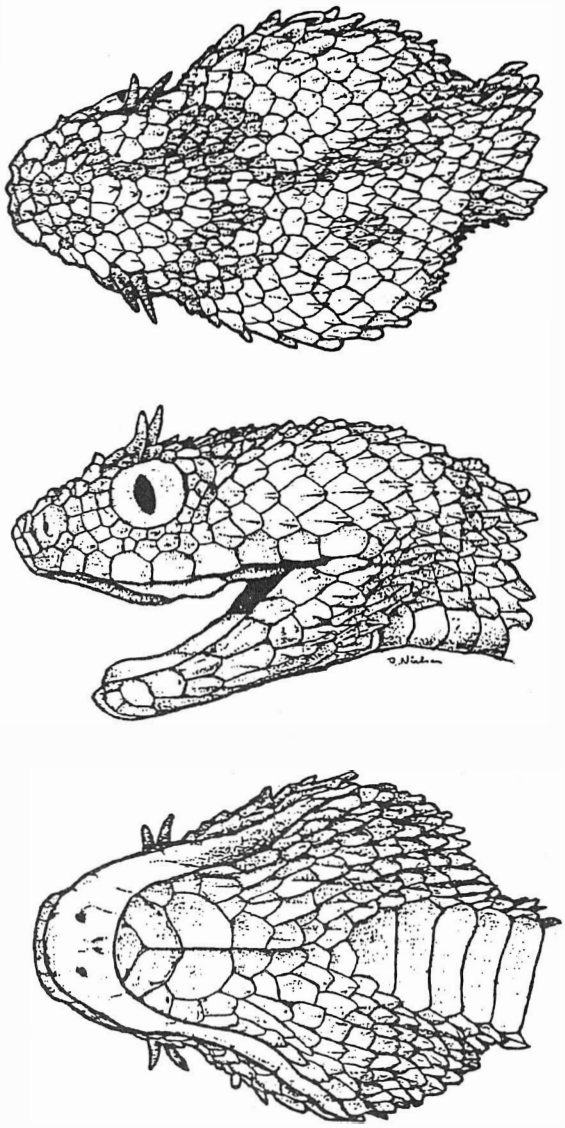

FIG. 5. *Atheris ceratophora*: dorsal, lateral and ventral views of the head (KMH 1893 - West Usambara Mts, Tanzania: after Rasmussen & Howell, 1982: Fig. 2).

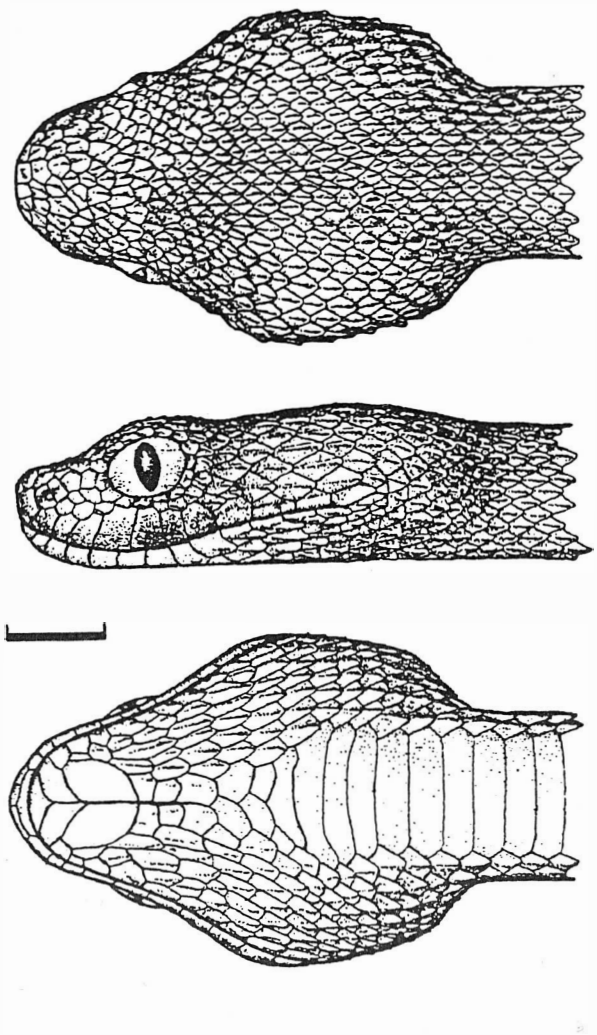

FIG. 6. *Atheris katangensis*: dorsal, lateral and ventral views of the head (Holotype, IRSNB 2207 - Mubale-Munte, Parc Nat. Upemba, Zaire: after Witte, 1953: Fig. 107). The line indicates 5 mm to scale.

Emmrich, 1997: colour plates). Ventrum 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 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 "Ukami") 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).

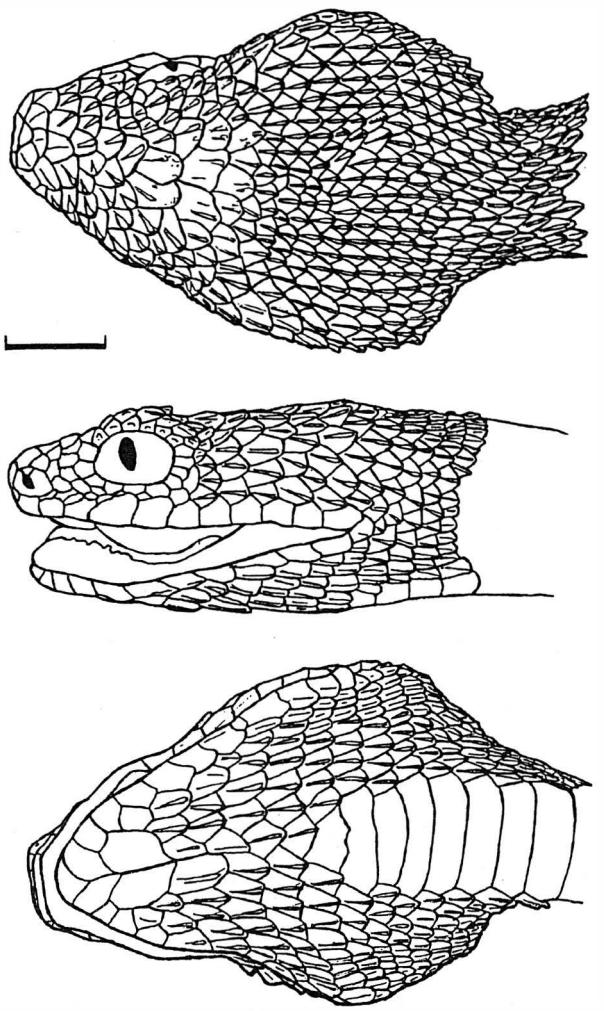

FIG. 7. *Atheris chlorechis*: dorsal, lateral and ventral views of the head (ZMUC R6883 - Bobiri Forest Reserve, Ghana). The line indicates 5 mm to scale.

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. 1h); 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. Ventrum 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, Zaire.

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, Zaire (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 preventrals.

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 crossbars on tail. Ventrum 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 Taï 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 70cm.

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 suprarostrals 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 preventrals.

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

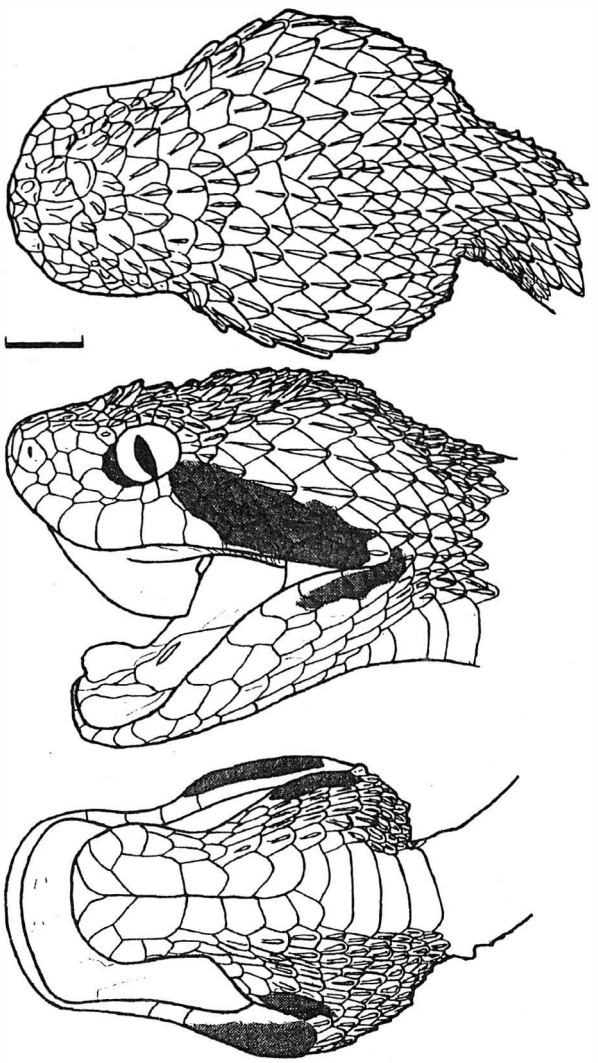

FIG. 8. *Atheris squamigera*: dorsal, lateral and ventral views of the head (CAS 197898 - Dja Forest Reserve, Cameroon). The line indicates 5 mm to scale.

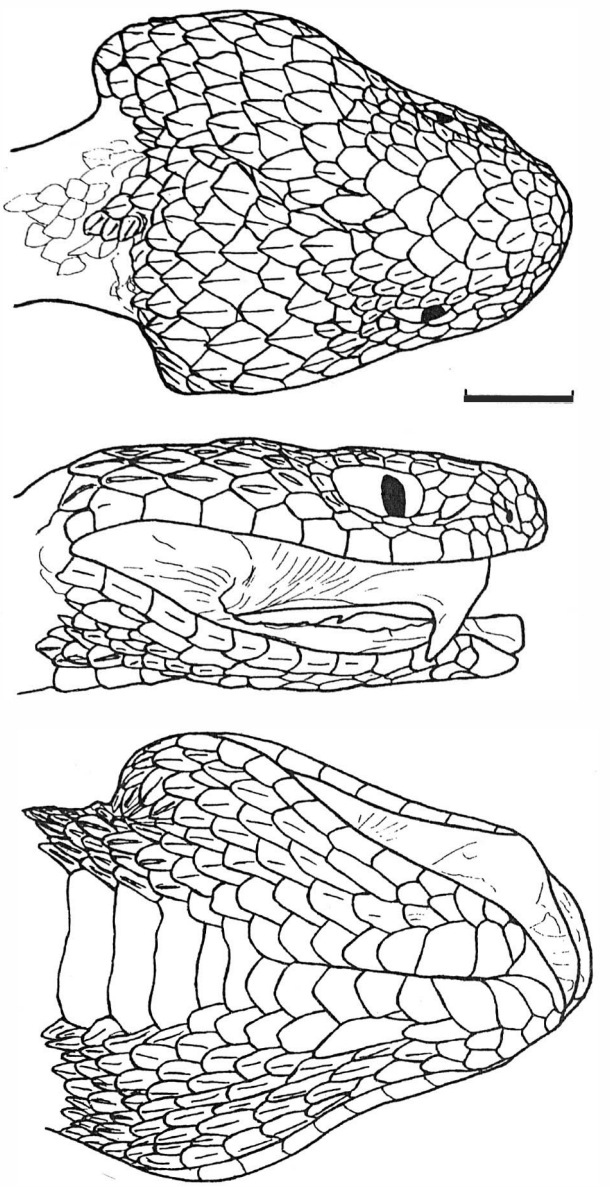

FIG. 9. *Atheris anisolepis*: dorsal, lateral and ventral views of the head (Lectotype, MNHN 1886.242 - Alima-Létéki, Congo). The line indicates 5 mm to scale.

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 preventrals.

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 Ménéngué, 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, Zaire) 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 [= Zaire]. 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 Zaire (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

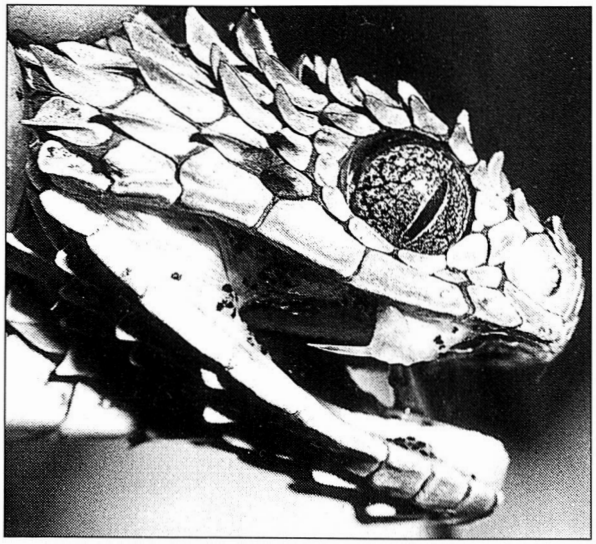

FIG. 10. *Atheris hispida*: lateral view of head, specimen from Kakamega Forest, Kenya (Photo by J.E. Cooper).

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. Ventrum 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).

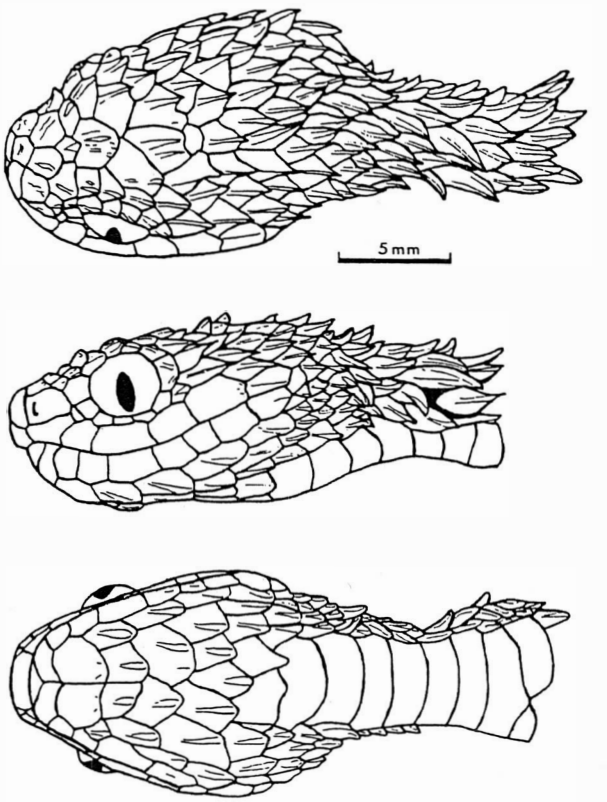

FIG. 11. *Atheris acuminata* sp. nov. dorsal, lateral and ventral views of head (Holotype, NMZB 13950 - Kyambura Game Reserve, Acholi, Uganda).

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') 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 suprarostral 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 anterior 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. Ventrum 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 abissinica* (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).

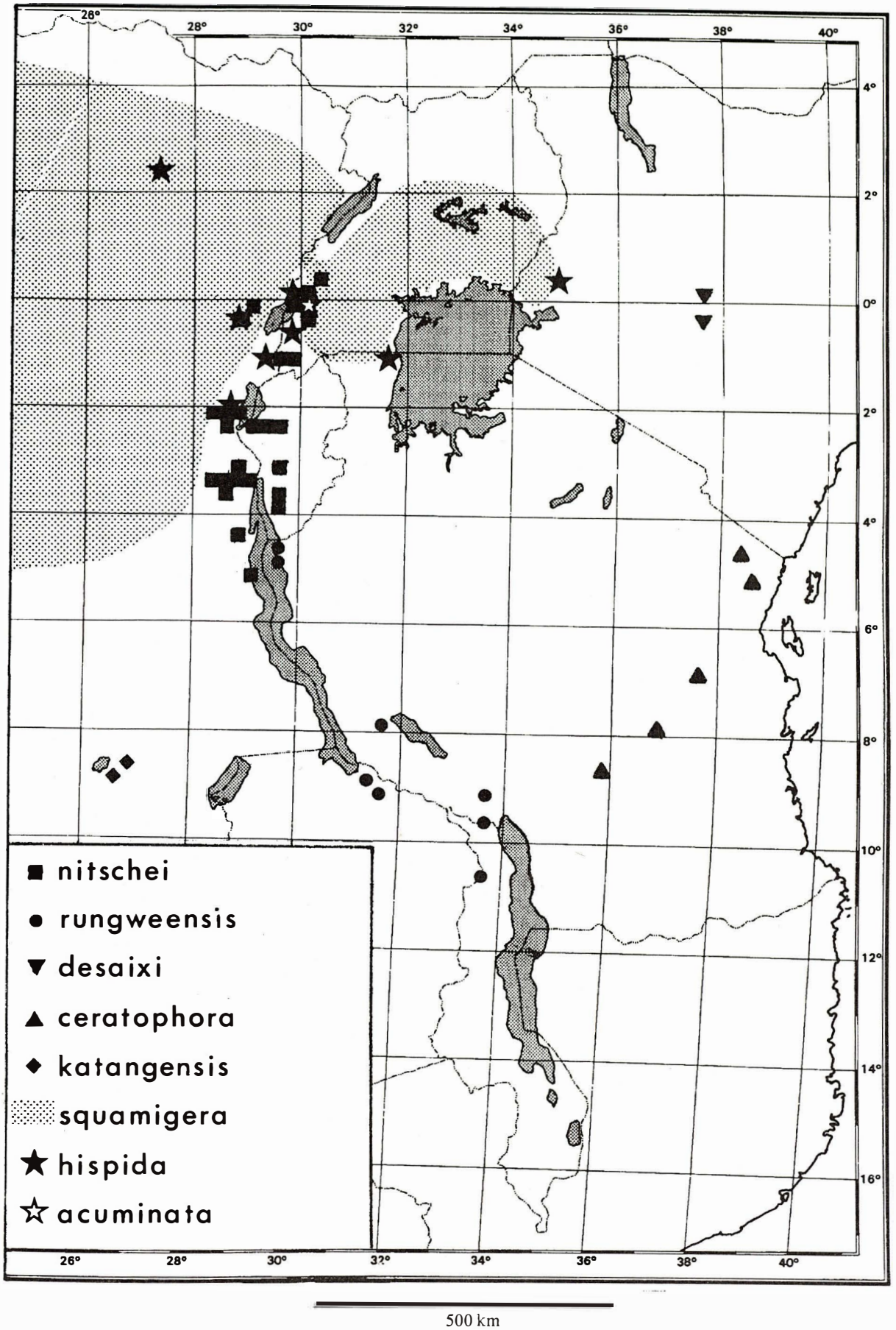

FIG. 13. Distribution of the *Atheris nitschei* and *A. hispida* species groups and the approximate distribution of eastern populations of *A. squamigera*.

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 suprarostral scales in first (or only) row; dorsals rounded at the apex; each dorsal scale tipped with yellow ..... *desaixi*
3b. Three to five suprarostrals 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 to of head between posterior supralabials 15-18 8
8a. Interorbital scales strongly keeled; interoculabials usually absent ..... *squamigera*
8b. Interorbital scales smooth or feebly keeled; usually one or two rows of interoculabials present ..... *anisolepis*
9a. Three large suprarostrals; 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 ..... *hispida*
9b. Two very large suprarostrals; 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, hispida* and *desaixi*) and they all showed closer affinities with *A. nitschei* than with *A. squamigera*. However, in a subsequent study (Herrmann & Joger, 1997), *A. hispida* 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 hispida* 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. hispida* 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 (MNHN) 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*.

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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 datasee 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 Ménéngué. 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

HERPETOLOGICAL JOURNAL, Vol. 8, pp. 137-143 (1998)

ON THE RICTAL GLANDS OF SOME ATRACTASPID SNAKES

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Structures around the corner of the mouth of atractaspid snakes are examined in serial sections. In addition one Madagascan and two African species of *Geodipsas* are reported. For *Atractaspis corpulenta* presence of a serous superior rictal gland is confirmed and the discovery of a hitherto unnoticed serous *inferior* rictal gland is reported. Inferior rictal glands are also reported for species of *Aparallactus, Chilorhinophis, Geodipsas, Poecilopholis* and *Polemon*. Neither superior nor inferior rictal glands are found in *Amblyodipsas, Hypoptophis, Macrelaps* or *Xenocalamus*. African species of "*Geodipsas*", now placed in the genus *Buhoma*, agree with aparallactines and differ from the Madagascan type species, *G. infralineata*, in the configuration of the rictal glands.

INTRODUCTION

Bourgeois (1961) was the first to propose a relationship between the burrowing asps, *Atractaspis*, and the aparallactine snakes, under the name Aparallactinae. Under the senior family group name Atractaspididae this has been followed by Heymans (1975), McDowell (1968) and Underwood & Kochva (1993). There has been agreement concerning most of the genera assigned to the group, but *Aparallactus* and *Macrelaps* were not included by McDowell (1968), and Underwood & Kochva (1993) included *Micrelaps* and *Brachyophis* with some doubts. Cadle (1994), however, finds no support for the association of *Atractaspis* with the aparallactines on the basis of albumin immunological distances.

Apart from the venom gland of *Atractaspis* and the mucous supralabial glands present in all snakes, Underwood & Kochva (1993) considered a gland associated with the posterior maxillary teeth. This was termed "glande parotide" by Phisalix & Caius (1918). Taub (1966), seeking to avoid confusion with the mammalian parotid gland, introduced the term "Duvernoy's" gland in reference to an early description by Duvernoy (1832). Phisalix & Caius (1918), however, point out that Duvernoy did not distinguish between the parotid and the supralabial glands. Leydig (1873) in a study of the head glands of some German snakes distinguishes between a yellow gland in the upper lip and the rest of the supralabial gland in *Natrix natrix*, *N. tessellata* and *Coronella austriaca*. He shows a difference in the staining reaction of the two glands. In plate 22, figure 1 he labels the yellow gland and adds, in parenthesis, "Homologon der Giftdrüse der Vipern". This homology has not been questioned since then. The term "Duvernoy's gland", associated with modified and often grooved posterior maxillary teeth, sets it apart from a "venom gland", associated with canaliculate fangs. In that many "Duvernoy's" glands have been shown to produce a toxin which, in some cases, functions as a venom, we regard this distinction as unfortunate. We therefore prefer Saint Girons' term "glande dentale" (1987), applicable to all glands associated with teeth.

Underwood & Kochva (1993) also paid attention to a gland of the upper lip opening into the corner of the mouth. This was originally called "glande temporale antérieure" by Phisalix & Caius (1918) but Underwood & Kochva (1993) preferred McDowell's (1968) term "rictal gland" on the grounds that although the position of the gland may vary it always opens into the corner of the mouth. Some of their observations were based on serial sections of the glands of the upper lip, some on dissections. They found that, as seen in dissection, the posterior end of the supralabial gland was sometimes slightly differentiated, but not sufficiently for presence of a rictal gland to be recorded with confidence. In sections a rictal gland can be distinguished from a supralabial gland by the presence of serous, as well as mucous cells, and by the duct which passes back to open into the corner of the mouth, as distinct from the margin of the lip.

Underwood & Kochva (1993) noted that in all but one previous report the rictal gland had been found to be mesial to the quadrato-maxillary ligament. In a survey by dissection of some lower snakes they found that with the exception of *Anilius*, a rictal structure, whether a gland or a pocket, lay mesial to the ligament.

Underwood (1996) has since verified in sections that *Anilius* has a large superior rictal gland, lateral to the quadrato-maxillary ligament, and also a large inferior rictal gland; they both open into the corner of the mouth.

Haas (1930, fig. 14) reported an anterior temporal gland in *Atractaspis corpulenta*; he interpreted its position lateral to the quadrato-maxillary ligament as a derived condition. Underwood & Kochva (1993) confirmed, by dissection, Haas's observation of a lateral rictal gland in *A. corpulenta* and found one in some other species of *Atractaspis* and other forms assigned to the Atractaspididae. For some, presence or absence was confirmed in serial sections. They further found, and confirmed in sections, that in *Polemon* and some other forms, the bulk of the supralabial gland is followed in sequence by compact dental and rictal glands overlapped only by a narrow strip of the supralabial gland (their figs 9 B & C). This compact condition was regarded as derived.

Kochva (1978, fig. 31) found a "posterior" gland, which we now interpret as rictal, lateral to the caudal end of the supralabial gland, in *Vipera palaestinae*. Ineich & Tellier (1992) and Saint Girons & Ineich (1993) report a gland in *Echis* which opens to the exterior within the margins of the posterior supralabial scale. It lies above the posterior end of the supralabial gland and shows evidence of a "séro-muqueux" secretion, here taken to be serous PAS positive. We interpret this as a rictal gland. Evidently *lateral* rictal glands are not confined to atractaspid snakes and *Anilius*.

MATERIALS AND METHODS

The present investigation was motivated by the wish to check in serial sections observations made by dissection. We started by making serial sections of the head of an *Atractaspis corpulenta*, half sagittal and half transverse. We confirmed the presence of a superior rictal gland but were surprised also to find an *inferior* rictal gland. This appears to be what Haas (1930) called "Mundwinkeldrüse"; apart from this, such a structure has not to our knowledge been previously reported. This observation turned our attention to the glands of the lower lip as well as the upper lip.

This investigation is largely based on specimens in the Natural History Museum, London. The specimens were of unspecified, and in some cases poor, fixation. Although histological detail could not be recognized in some, presence or absence of a rictal gland could be ascertained in nearly all specimens. Glands from the posterior half of the upper and lower lips were dissected out and serially sectioned. The choice of species was based on gaps in the histological survey already made. We noticed that the glands of the upper lip of *Geodipsas procterae*, as figured in dissection by Underwood (1967, fig. 6), bear a close resemblance to the glands of *Polemon bocourti* (Underwood & Kochva, 1993, fig. 9). Some African species then placed in *Geodipsas*, as well as the Madagascan type species *G. infralineata*, were therefore included in our survey.

We already had available serial sections of the heads of *Atractaspis engaddensis, Chilorhinophis gerardi* and *Micrelaps muelleri*. The further species examined are: *Amblyodipsas polylepis, Aparallactus capensis, A.modestus, "Geodipsas" depressiceps, "G". vauerocegae, G. infralineata, Hypoptophis wilsoni, Macrelaps microlepidotus, Poecilopholis cameronensis, Polemon gabonensis* and *Xenocalamus mechowi*.

Following the evidence of a lateral superior rictal gland in *Vipera* and *Echis*, a survey was made by dissection of the glands of the upper and lower lips of the following viperid and elapid snakes:

Viperidae – *Azemiops feae, Bothrops asper, Calloselasma rhodostoma, Hypnale hypnale, Trimeresurus monticola, Causus defilippi, C. lichtensteini, C. resimus, C. rhombeatus, Atheris nitschei, Bitis gabonica, Cerastes cerastes, C. vipera, Eristicophis mcmahoni, Vipera russeli* and *V. ursinii*.

Elapidae – *Aspidelaps lubricus, A. scutatus, Bungarus flaviceps, Elapsoidea guentheri, E.sundevalli, Naja mossambica, Ophiophagus hannah, Paranaja multifasciata* and *Walterinnesia aegyptia*.

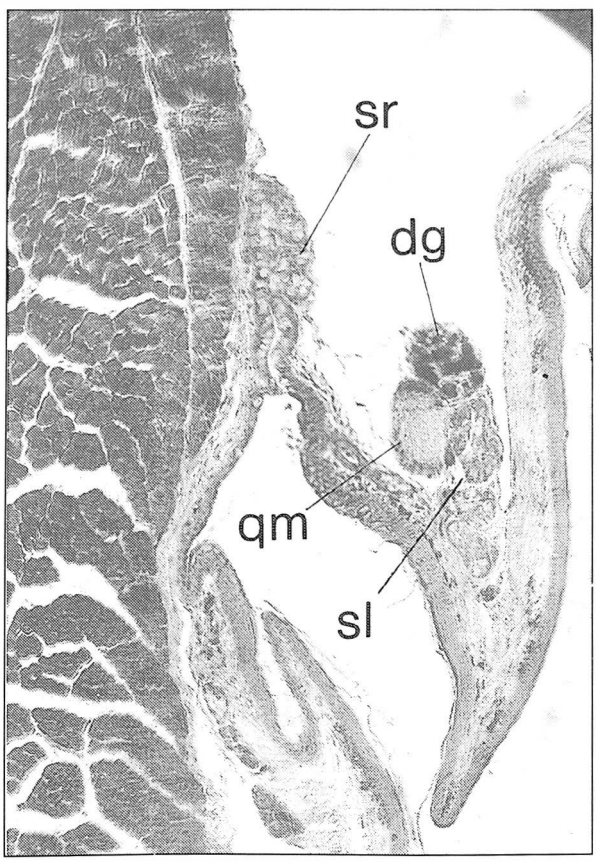

FIG. 1. Transverse section of corner of mouth of *Telescopus fallax*, to show relationships of superior rictal gland and duct opening into rictal groove, dental gland, quadrato-maxillary ligament and supralabial gland. dg, dental gland; hg, Harder's gland; il, infralabial gland; ir, inferior rictal gland; qm, quadrato-maxillary ligament; sl, supralabial gland; vg, venom gland.

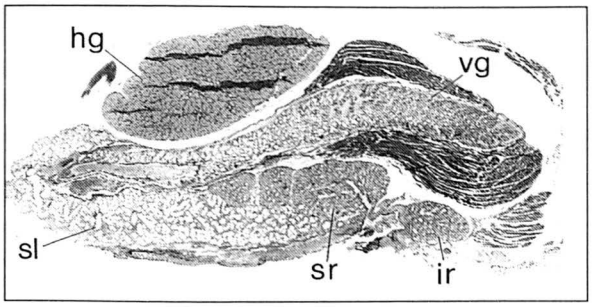

FIG. 2. Parasagittal section of head of *Atractaspis corpulenta* (BMNH 1916.5.29.3, Bitye, S.Cameroons) showing superior rictal gland, with duct opening backwards into corner of mouth, and inferior rictal gland. Abbreviations as Fig. 1.

RESULTS

We illustrate what is the most widespread condition in a transverse section of *Telescopus fallax* at the level of the opening of the superior rictal gland (Fig. 1). The superior rictal gland is mesial to the quadrato-maxillary ligament, and the duct opens into the groove between the upper and lower lips at the corner of the mouth. The dental and supralabial glands are lateral to the ligament. There is no evidence of an inferior rictal gland.

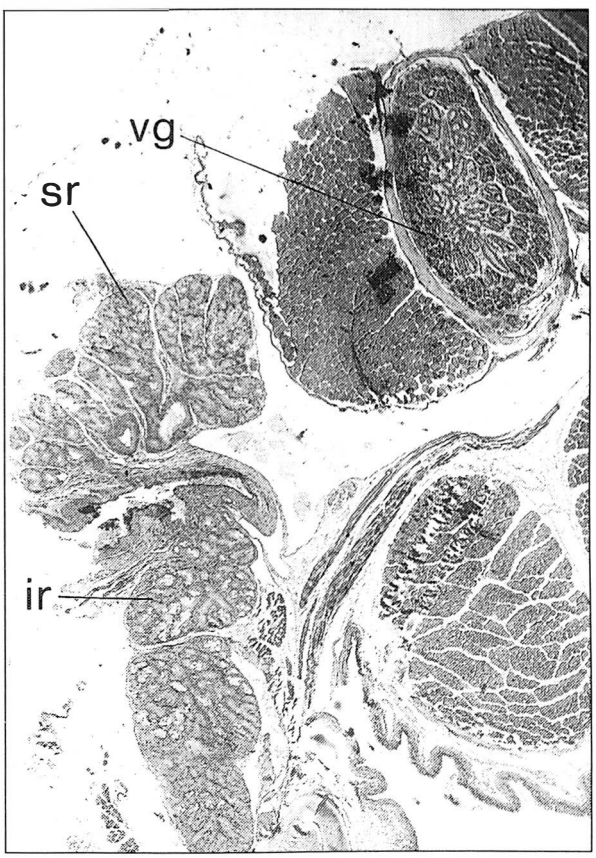

FIG. 3. Transverse section of head of *Atractaspis corpulenta* (same specimen), showing superior rictal gland with two ducts and inferior rictal gland, respectively above and below the rictal groove. Abbreviations as Fig. 1.

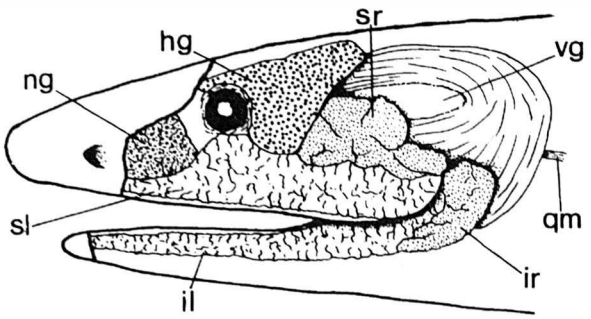

FIG. 4. Superficial dissection of *Atractaspis corpulenta* (BMNH 1909.12.3.15 & 1913.10.29.17, Bitye, S.Cameroon) to show relationships of superior and inferior rictal glands. Abbreviations as Fig. 1.

In *Atractaspis corpulenta* the superior rictal gland is more extensive than the inferior gland (Fig. 4). Both glands lie immediately beneath the skin (which has been peeled off, Fig. 3, transverse). The superior gland is lateral to the quadrato-maxillary ligament, as reported by Haas (1930). The superior gland is, vertically, much deeper than the supralabial gland, rising lateral to the venom gland. Staining with Masson's trichrome method shows that it is serous, except for the ducts which contain mucuous cells. A major duct runs through the gland and opens into the rictal fold. Two small additional ducts drain the posterior part of the gland and open somewhat caudal of the main duct. The inferior rictal gland is similar in structure (Fig. 2). No trace of rictal glands is found in *A. engaddensis*.

Aparallactus capensis has a lateral superior rictal gland with some mucous cells, mainly around the ducts. The compact dental and superior rictal glands, not overlapping one another but overlapped by a strip of the supralabial gland, are much as in *Polemon* (Underwood & Kochva, 1993, Fig. 9). *A. modestus* has a small gland at the posterior end of the supralabial gland which shows no goblet cells but nevertheless stains green, suggesting mucins. In this taxonomic con-

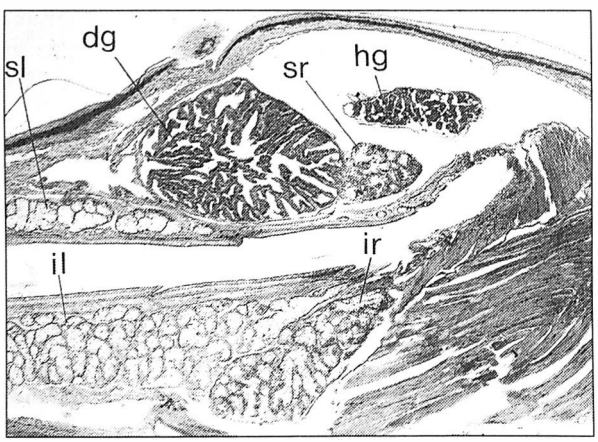

FIG. 5. Parasagittal section of corner of mouth of *Chilorhinophis gerardi*, showing superior and inferior rictal glands. Abbreviations as Fig. 1.

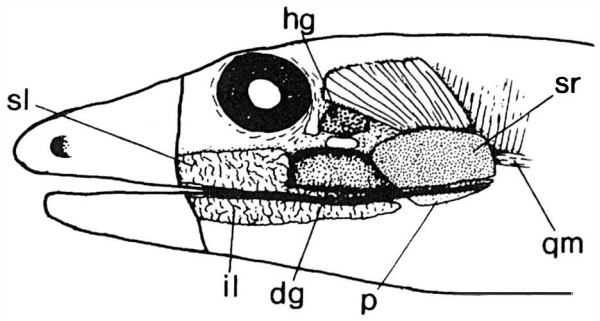

FIG. 6. Dissection of *Buhoma vauerocegae* (BMNH 1909.10.19.7, Usumbara, Tanzania) to show compact dental gland between anterior supralabial gland and large compact superior rictal gland. p, shallow pocket of buccal epithelium in lower corner of mouth. Between Harder's gland and the dental gland the anterior end of the ectopterygoid bone is visible. Abbreviations as Fig. 1.

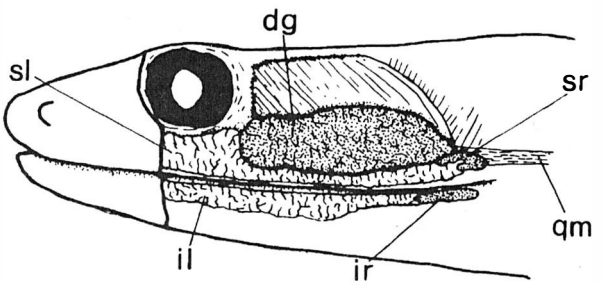

FIG. 7. Dissection of *Geodipsas infralineata* (BMNH 1930.2.2.14, Anamalagasta Forest, E. Madagascar) to show large dental gland followed by small, partly overlapping,rictal gland and inferred inferior rictal gland (subject to confirmation in sections). Abbreviations as Fig. 1.

text it seems likely that it is an atypical rictal gland but it could be a modified supralabial gland. *A. modestus* also differs from other members of the genus in the absence of grooves on the posterior maxillary teeth. An inferior rictal gland is also found.

Polemon gabonensis has a large superior rictal gland, as already reported. It also has a large inferior rictal gland. *Chilorhinophis* shows well developed superior and inferior rictal glands (Fig. 5). *Poecilopholis* has a very small serous gland in the superior rictal region and a more prominent inferior rictal gland.

The glands of the upper lip of *Buhoma vauerocegae* and *B. depressiceps*, which include a superior rictal gland, are similar to those of *Polemon* (Fig. 6). The infralabial gland of *B.vauerocegae* stops well short of the rictus; it is succeeded by a shallow pocket, the walls of which are not obviously glandular as seen by dissection. *B. depressiceps* has what we provisionally interpret as an inferior rictal gland. The condition of the *G. infralineata* is too poor for a histological report. However, in dissection it clearly has a large dental gland which extends nearly to the level of the rictus. There is also what appears to be a small discrete lateral superior rictal gland overlapping the posterior end of the dental gland and extending back to the level of the rictus. A narrow strip of supralabial gland overlaps both of these back to the rictus. The infralabial gland, just behind the level of the rictus, appears to separate naturally into two parts, suggesting that there is an inferior rictal gland (Fig. 7).

In *Macrelaps*, despite what looked in dissection like the orifice of a gland, we found no evidence of a superior rictal gland (two specimens); there was also no evidence of an inferior gland. In *Amblyodipsas, Hypoptophis, Micrelaps* and *Xenocalamus* we found no evidence of rictal glands, superior or inferior. In *Brachyophis* we could find no evidence, by dissection, of an inferior rictal gland, but this part was damaged; Underwood & Kochva (1993) have already reported absence of a superior gland.

In *Elapomorphus nasutus* we find a complex dental gland, in two parts, one mucous the other serous, on which insert some fibres of the adductor superficialis muscle. There is a lateral superior rictal gland which has some mucous cells, mainly around the ducts. The glands of the elapomorphine snakes are being investigated by Salomão & Ferrarezzi (1993). By dissection we find evidence of an inferior rictal gland in *E. nasutus* and *E. bilineatus*, but not in *E. quinquelineatus*.

Our reports on viperid and elapid snakes are based on dissection only, unless otherwise stated. They should therefore be read with the qualification "subject to confirmation in sections". The most convincing rictal glands are discrete bodies, which may differ in colour and texture, from the labial glands.

In *Cerastes cerastes* we find a lateral rictal gland and a small inferior rictal gland. In the African vipers *Atheris nitschei* and *Bitis gabonica* we find evidence of a lateral superior rictal gland but not of an inferior.

In *Vipera russeli* and *Eristicophis mcmahoni* we find no evidence of either superior or inferior rictal glands. In *Causus lichtensteini*, which has a short venom gland, we find a swollen body at the posterior end of the supralabial gland, with pigment on the mesial face. The infralabial gland passes back to the level of the rictus without evidence of an inferior rictal gland. In *C. defilippi*, also with a short venom gland, we find no evidence of a superior rictal gland but the infralabial gland extends beyond the rictus where it turns inwards but is not otherwise differentiated. In *C. rhombeatus*, with a long venom gland, we found evidence of a superior rictal gland but not of an inferior gland. In *C. resimus*, also with a long venom gland, we found no evidence of either superior or inferior rictal glands. In *Azemiops feae* and the pit-vipers *Bothrops atrox*, *Calloselasma rhodostoma, Hypnale hypnale* and *Trimeresurus monticola* we find no evidence of rictal glands.

Amongst the elapids we find the clearest evidence of rictal glands in *Paranaja multifasciata*. Mesial to the

last two supralabial scales is a discrete body, rising higher than the supralabial gland and lying immediately beneath the skin. Beyond the posterior end of the infralabial gland is a small oval body, presumably an inferior rictal gland.

In *Aspidelaps lubricus* and *A. scutatus* we find evidence of a lateral superior rictal gland, and in *A. lubricus* it turns downwards around the corner of the mouth. In *Elapsoidea guentheri* and *E. sundevalli* we find a lateral superior rictal gland but no indication of an inferior gland. In *Bungarus flaviceps, Naja mossambica, Ophiophagus hannah* and *Walterinnesia aegyptia* we found no evidence of rictal glands.

DISCUSSION

Within the Atractaspididae, Underwood & Kochva (1993) had already interpreted the sequence of compact, non-overlapping, dental and superior rictal glands of *Aparallactus, Polemon* and *Chilorhinophis* as a derived feature linking these three genera. The similar condition of "*Geodipsas*" *procterae*, "*G.*" *vauerocegae* and "*G.*" *depressiceps*, in contrast to the type species *G. infralineata*, suggests that they were not properly assigned to the genus. Cadle (1996) and Ziegler *et al.* (1997) have, on the the basis of other evidence, arrived at a similar conclusion and the latter authors have erected the new genus *Buhoma* for the African species formerly assigned to *Geodipsas*.

Of the remaining atractaspids, only *Atractaspis corpulenta* is known to have well-developed lateral superior *and* inferior rictal glands, but it is clear by dissection that several other species have at least a superior rictal gland. *Poecilopholis* has small superior and inferior rictal glands. On the other hand *Hypoptophis, Brachyophis, Micrelaps, Amblyodipsas, Xenocalamus, Macrelaps* and some *Atractaspis* show no evidence of rictal glands. This distribution suggests that rictal glands are retained by some *Atractaspis, Aparallactus, Chilorhinophis* and *Polemon*, are reduced in *Poecilopholis* and are lost in the others.

Amongst henophidian grade snakes only *Anilius* has a lateral superior rictal gland; it also has an inferior rictal gland (Underwood, 1996). All of the others which have differentiated rictal structures have mesial superior glands; in many these open into a rictal pocket (Cundall & Rossman 1993, Underwood in preparation) but an inferior rictal gland has been found only in *Cylindrophis* (*Anomochilus* not examined).

Some Caenophidia have a lateral superior rictal gland and an inferior gland. These include some atractaspids, probably elapomorphines, some viperids and some elapids. *Pareas* has a lateral superior gland but no inferior gland (correction to Underwood, 1996). A larger number of Caenophidia, including xenodermatines, have a mesial rictal gland; none of these is known to have an inferior gland. Many caenophidians appear to be without differentiated rictal structures. No caenophidian is known to have a structure comparable to the rictal pocket of many henophidians (McDowell, 1986; Underwood, 1996).

We notice that all of the caenophidians with a lateral superior gland appear to be members of low grade lineages of the radiation (Underwood & Kochva, 1993; Knight & Mindell, 1994). We note also a particular resemblance between *Anilius scytale* and *Atractaspis corpulenta* in respect of the rictal glands. On the other hand "higher" caenophidians have a mesial superior gland (albeit without a rictal pocket) and, as far as we know, no inferior gland; in this they resemble "boids". Kluge (1991, preliminary) and Cundall *et al.* (1993) have published analyses of henophidian grade snakes based on a variety of characters. Kluge has bolyerines, which are without differentiated rictal structures (Underwood, in preparation), as sister to Caenophidia; Cundall *et al.* (1993) have tropidophids, which have superior rictal glands, opening into a rictal pocket, as sister group. On either of these views, the Caenophidia derive from one of the higher branches of the henophidian radiation without an inferior rictal gland. Both analyses agree that *Anilius* is on one of the lower henophidian branches.

We see two alternative interpretations. The higher Caenophidia inherit from henophidian ancestors a primitive mesial condition of the superior rictal gland, with loss of rictal pocket, and the lower Caenophidia share a derived lateral condition in parallel with *Anilius*. On this view, tropidophines would fit better than bolyerines as sister group. Alternatively, the lateral condition is primitive for *Anilius* and for the Caenophidia, and the higher caenophidians share a derived mesial condition in parallel with most henophidians. This view would suggest that *Anilius* is sister to the Caenophidia. The Scolecophidia are so highly modified that they do not help this judgement. Underwood & Kochva (1993) included the South American *Elapomorphus* and *Apostolepis* in their investigation of the relationships of *Atractaspis*. They concluded that they are at about the same grade level but did not find clear evidence of affinity. The *lateral* condition of the superior rictal gland and the presence of an inferior rictal gland in *Elapomorphus* add to the grade resemblance.

We note a complex dental gland in one species of *Elapomorphus*. From the survey of the glands of elapomorphines by Salomão & Ferrarezzi (1993) it is evident that there is a considerable range of variation of the dental glands within the group. The interest of elapomophines is further enhanced by Lema's report (1978) that *Elapomorphus bilineatus* is dangerously venomous. Within South America, all of the other forms so far examined have a superior rictal gland mesial to the quadrato-maxillary ligament. These include representatives of *Alsophis, Clelia, Liophis, Lystrophis, Phimophis, Philodryas, Siphlophis, Pseudoboa, Thamnodynastes, Waglerophis* and *Xenodon* (Underwood, personal observations).

Cadle (1984) finds immunological evidence linking *Apostolepis* with South American xenodontines. This implies that a switch from lateral to mesial took place within the xenodontine lineage.

Radovanovic (1935) comments on a special gland of *Coluber najadum* and *C. gemonensis,* mesial to the ligament, which he regarded as undoubtedly homologous with the "anterior temporal gland". By dissection Smith & Bellairs (1947) found a rictal gland in some colubrine snakes of the genera *Coluber, Elaphe, Lytorhynchus* and *Ptyas.* They note that it is "partly overlapped by the posterior end of the supralabial gland and the ligamentum zygomaticum" (quadrato-maxillary ligament), i.e. it is mesial. Gabe & Saint Girons (1969) find a mesial rictal gland in the genera *Coronella* and *Oligodon.*

On the basis of dissection, McDowell (1986) reports a rictal gland, mesial to the quadrato-maxillary ligament, in species of many genera, including: *Alsophis, Calamaria, Carphophis, Coniophanes, Diadophis, Duberria, Heterodon, Hydrops, Manolepis, Nerodia, Oxyrhopus, Pseudoxenodon, Rhadinaea* and *Tantalophis.* He comments on the large size of the gland in *Rhadinaea multilineata.*

Cadle (1994) made an extensive immunological survey of African "colubrid" snakes. Relevant to the present investigation are *Amblyodipsas polylepis, A. unicolor, Aparallactus capensis, A. lunulatus, Atractaspis bibroni and Macrelaps microlepidotus.* Two analytical procedures found distant links between *Atractaspis, Amblyodipsas* and Madagascan *Leioheterodon*, (Cadle, 1994: Fig. 1). His overall conclusion is however that *Atractaspis, Amblyodipsas* and *Leioheterodon* represent separate lineages deriving from the "basal radiation" with no more than the "marginal association" noted above. Cadle (1994) considers the bearing of his data on the group which we treat as atractaspids. He finds "no significant association" of *Atractaspis* with "aparallactines" and at best a very distant relationship of *Aparallactus* with either *Atractaspis* or *Amblyodipsas.* On the other hand, affinity of *Macrelaps* with *Amblyodipsas* is clear. If presence of a lateral superior rictal gland plus an inferior gland are derived features within the Caenophidia then our new data would give further support to a link between *Atractaspis* and *Aparallactus*; otherwise they suggest a shared low grade level. If, as we suspect, the absence of rictal glands is derived then this would add weak support to the link between *Macrelaps* and *Amblyodipsas.*

It is already clear that rictal glands occur in many snake lineages and that their distribution is far from completely surveyed. That they persist in many lineages suggests that they have some functional significance notwithstanding their usual small size. That they have been lost from some lineages suggests that they are not important to all lifestyles. Study of the secretion was begun by Phisalix and Caius in 1918, but does not appear to have been taken further in the following 80 years!

ACKNOWLEDGEMENTS

We are indebted to Miguel Vences for correspondence about the proposal to erect a new genus for the African species of *Geodipsas*, a proposal which we supported.

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Accepted: 17.9.97

HERPETOLOGICAL JOURNAL, Vol. 8, pp. 145-148 (1998)

IDENTIFICATION OF *BUFO* LARVAE BY MOLECULAR METHODS

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We have characterized two molecular techniques, protein typing and RAPD analysis, for the identification of two species of European *Bufo* larvae (*Bufo bufo* and *B. calamita*). These tadpoles are very difficult to distinguish on morphological grounds. Protein typing was improved by the use of a sensitive (silver-based) staining method, and replacement of low temperatures with ethanol submergence for tissue storage. Both techniques reliably resolved the two species and required very small amounts (<2 mg) of tissue, which could be obtained easily and without sacrificing the animals.

INTRODUCTION

Amphibians are replete with examples of problematical identification during early developmental stages, and there are many instances where morphological differentiation is impossible or highly unreliable. For many ecological studies, however, accurate identification of amphibian larvae is essential. In Britain, for example, there are two species of *Bufo* (*B. bufo* and *B. calamita*) which sometimes compete during larval development (e.g. Heusser, 1972; Banks & Beebee, 1987), and the tadpoles of these toads are very difficult to distinguish from one another. Both species are uniformly black in colour, though relative sizes, ratios of inter-ocular distance: mouth width, tooth row arrangement and chin patch coloration have been invoked as suitable methods for identification (Smith, 1951; Beebee, 1977; Davis, 1985). All, however, are time-consuming, unreliable, and often damage or kill the subjects of study. Beebee (1990) developed a protein typing method which distinguished spawn jelly proteins, embryos and large tadpoles which (except in the case of embryos) did not require killing the subjects. This approach required relatively large amounts of tissue and was thus impractical for small larvae; furthermore, it required inconvenient cold storage facilities (liquid nitrogen or dry-ice flasks) in the field.

In this study we report on modifications to the protein typing method which render it useful with small larvae and removes the need for cold storage. The development of a simple DNA-based (RAPD) technique (Williams *et al.*, 1990) that achieves the same end is also described. RAPD analysis is useful over a wide range of taxonomic levels, and has been used successfully with amphibians to quantify genetic variation at individual, population and species levels (e.g. Masters & Forester, 1995; Masters, 1995; Kimberling *et al.*, 1996).

MATERIALS AND METHODS

SAMPLING OF TADPOLES

Larvae of both species were sampled at widely different geographic locations within the UK. *B. calamita* and *B. bufo* samples were obtained from Birkdale sand dunes (Merseyside); *B. calamita* were also obtained from Haverigg dunes (Cumbria) and *B. bufo* from a field pond near Brighton (Sussex) . In some cases animals of known parentage (and thus species) were used, in others a preliminary classification was made based on morphological characters. From each larva a 2 mm section of tail tip (< 2 mg) was removed by scalpel and stored immediately in an eppendorf tube containing 0.5-1.0 ml pure ethanol. These samples were kept for at least six months, at environmental temperatures, prior to analysis.

Standard reagents for protein electrophoresis and silver-staining, including molecular weight markers, were purchased from Sigma Chemicals, Poole, UK. Molecular biology grade agarose and DNA molecular weight markers (1 kb ladder) were from Gibco-BRL (UK), *Taq* DNA polymerase was from Genpak (UK), and 10-mer oligonucleotide primers were generated by the University of Sussex DNA synthesizer. Chelex 100 resin was from Bio-Rad, Richmond, California.

PROTEIN TYPING

Each tail tip was heated at 65°C for 10 min in 60 µl loading buffer (50 mM Tris-HCl pH 8, 0.15 M b-mercaptoethanol, 1% sodium dodecyl sulphate [SDS], 10% glycerol, 0.01% phenol red), homogenized by gentle pipetting, and immersed in a boiling water bath for 2 min. Solid debris was removed by centrifugation at 1000 x g for 25 seconds, and 40 µl supernatant then loaded into each gel well.

A stacking gel of 4% acrylamide, 0.2% bisacrylamide and 10% glycerol in 125 mM Tris-HCl pH 6.8, 0.1% SDS was used with a separating gel of 7.5% acrylamide, 0.2% biscarylamide in 0.38 M Tris-HCl pH 8.8, 0.1% SDS. Electrophoresis was for about 5 hr, at 50 v through the stacking gel and 100 v through the separating gel. Proteins were then fixed by immersing the gel in 50% (v/v) methanol, 10% (v/v) glacial acetic acid for 2 hours, then overnight in 50% methanol alone.

Proteins were silver-stained (Switzer *et al.*, 1979) by immersing the gel for 15-20 min in saturated ammoniacal silver nitrate solution (0.8% silver nitrate made up in 0.08% NaOH and 0.035% ammonium hydroxide). Excess silver nitrate was removed by washing in dis-

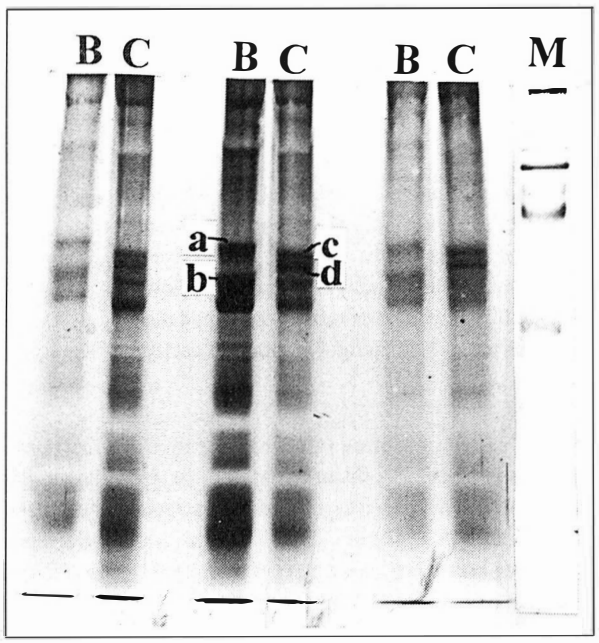

FIG. 1. Identification of *Bufo* larvae by protein fingerprinting. Larval tail tip proteins from three individuals of each species were electrophoresed and stained as described in Methods. B: *Bufo bufo*; C: *Bufo calamita;* M: Molecular weight markers; a, b: distinctive *B. bufo* bands; c, d: distinctive *B. calamita* bands. Molecular weight markers visible on this gel (a composite photo with the marker lane cut and moved next to the samples) were egg albumin (45,000), bovine plasma albumen (66,000), phosphorylase B subunit (97,400) and b-galactosidase subunit (116,000).

tilled water for 5-10 min, and stain developed by the addition of 0.0046% citric acid, 0.00185% formaldehyde. The reaction was stopped by immersing the gel in 50% methanol.

RAPD ANALYSIS

DNA was extracted from tail tips by incubating each at 55°C overnight in 160 µl sterile distilled water (SDW) with 40 µl of a Chelex 100 resin suspension made up in SDW. Each sample was then briefly vortex-mixed, immersed in a boiling water bath for 8 min, vortexed again and centrifuged at 8000 x g for 3 min. 1 µl aliquots of the supernatants were then used in polymerase chain reactions (PCRs).

Each PCR was in a final volume of 20 µl and included 1 µl DNA extract, 50 mM Tris-HCl pH 8.5, 16 mM ammonium sulphate, 0.15 mg/ml bovine serum albumin, 3.5 mM $MgCl_2$, 0.1 mM dATP, dGTP, dCTP and dTTP, 0.2 mM oligonucleotide and 0.4 units Genpak *Taq* polymerase. An initial denaturation cycle (94°C x 4 min) was followed by 35 cycles each of: 94°C x 1 min, 40°C x 1 min, 72°C x 2 min, followed by a final extension cycle of 72°C x 4 min.

Each sample was mixed with 5 µl loading buffer (60% w/v sucrose, 2.5 mg/ml bromophenol blue, in 2 x RB; RB [running buffer] = 13.5 mM Tris-acetate pH 8.3, 0.3 mM EDTA) and electrophoresed through 1.5 % agarose in RB containing 1 µg/ml ethidium bromide. After electrophoresis at 60 v for 2-3 hours the gel was examined by UV transillumination and photographed.

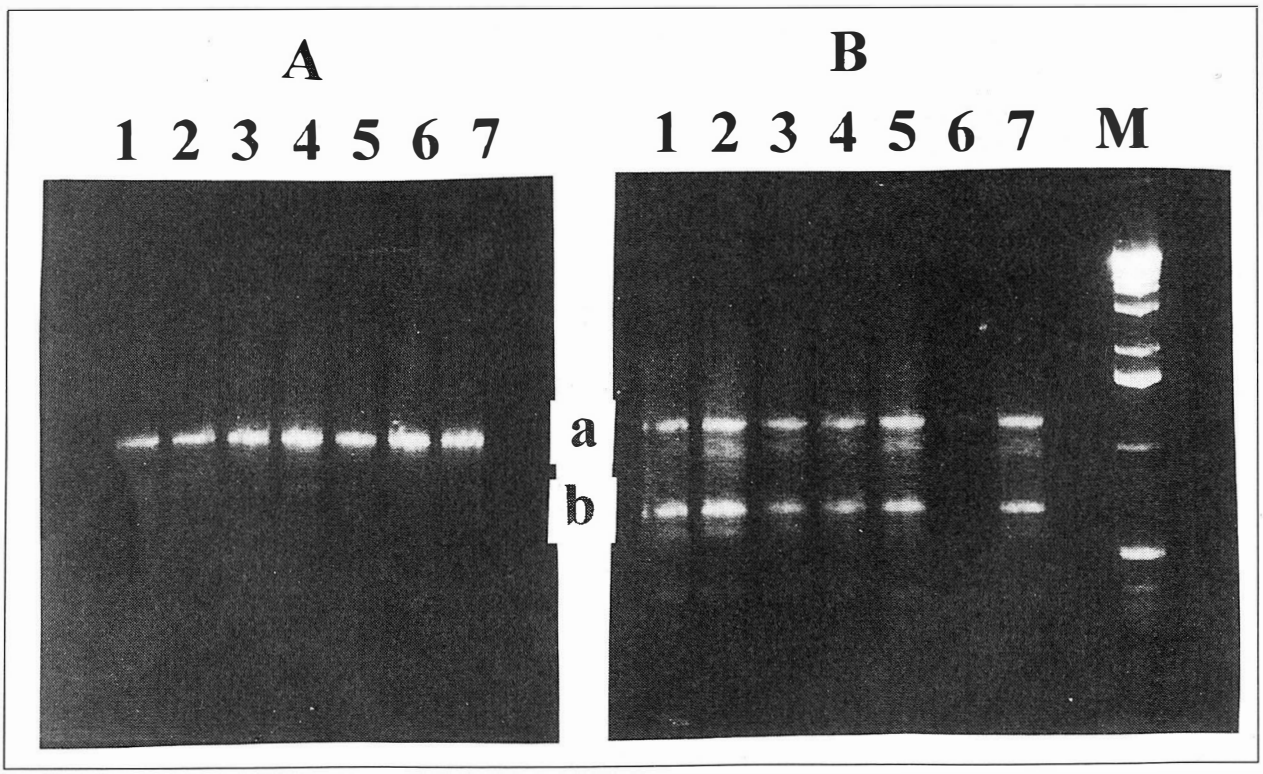

FIG. 2. Identification of *Bufo* larvae by RAPD analysis. Larval tail tip DNA from seven individuals of each species was amplified by PCR using primer PR4 and products identified by ethidium bromide staining after electrophoresis, all as described in methods. A: *B. calamita*; B: *B. bufo*; a: common PCR product; b: *B. bufo*-specific PCR product; M: 1 kb ladder molecular size markers.

RESULTS

PROTEIN TYPING

A representative sample of three *B. bufo* and three *B. calamita* tail tip protein profiles is shown in Fig. 1. The kinetics of silver-staining were highly sensitive to protein concentration, and the inevitable small variations between samples generated different optimal "stop times" for the reactions in the various gel lanes. Good quality photography of such gels is therefore difficult. Nevertheless, because the gels were observed carefully during the staining reaction, it was possible to score each individual at its optimum staining point. *B. bufo* larval tail tips exhibited a distinctive band pair (Fig. 1a,b) of approximate molecular weights 58 900 and 50 100, while *B calamita* larvae had an intermediate pair (Fig. 1c,d) of about 57 500 and 53 700 daltons. The relative gap sizes between these bands were very distinctive and quickly recognizable during stain development.

Reliability of the procedure was ascertained in two ways. Firstly, screening many tens of individuals of known parentage from geographically distant populations never revealed a single anomalous individual. Secondly, a blind test was carried out: three individual tail tips of each species, of known parentage, were ascribed random numbers by one of us and analysed by another. All six were correctly identified by the experimenter.

A sample of 400 larval tail tips from ponds where competition between the two species was under study was then subjected to protein analysis, after individual tadpoles were given a preliminary identification on morphological grounds. The results are shown in Table 1. Only 1% did not yield gel banding patterns clear enough to score; however, the data suggest that 11.4% of putative *B. bufo* and 13.4% of putative *B. calamita* were misclassified on morphological criteria (mainly relative size and chin patch occurrence).

RAPD ANALYSIS

Eight 10-mer primers were screened initially with DNA samples from *B. bufo, B. calamita* and *Rana temporaria* larvae. One of these primers (PN4, 5'-GCAAGTAGCT-3') yielded simple and apparently species-specific electrophoretic phenotypes. This primer was tested with DNA from seven individuals of each species, again taken from different populations. The results are shown in Fig. 2, in which only one individual (*B. bufo* no. 6) failed to yield amplification products. PN4 yielded two main products, one of about 1.24 kb common to both species (band a), and one of about 0.79 kb found only in *B. bufo* samples.

DISCUSSION

In this study we have developed two molecular methods for the identification of larvae of two species of *Bufo*. Both seem to be equally sensitive and take similar amounts of time. Tail tips can be taken from the smallest tadpoles (Gosner stage 26: Gosner, 1960) with very low risk of mortality. Except for the smallest (immediately post-hatch) *B. calamita* larvae, which experienced death rates higher than controls after tail-tip amputation, survivorship was unaffected by the excision when larvae were subsequently reared in the laboratory (data not shown). In the field, larvae were normally retained for a few hours prior to release to allow wound healing and thus minimize the danger from predators responding to olfactory cues arising from tissue damage. Protein typing benefited from greatly increased sensitivity using silver stain compared with coomassie blue (Beebee, 1990), and from the demonstration that tissue for protein analyses of this kind can be preserved conveniently in ethanol rather than at low temperatures. Protein typing requirements are therefore less stringent than those for allozyme studies, in which enzyme activity must be retained and the proteins preserved in a non-denatured state.

We expect these techniques to be useful for fieldworkers studying *B. bufo* and *B. calamita*, and that they will be readily extrapolated to other species combinations. We have, for example, subsequently shown that RAPD primer PN4 also distinguishes larvae of *B. viridis* from those of *B. bufo* and *B. calamita,* and is thus a specific indicator for all three European *Bufo* (data not shown). Tail tips can be collected quickly from large numbers of larvae, permitting retrospective identification after subsequent laboratory analysis. It is of course important always to run control samples of known species on every gel, but each gel can (depending on mould size) also take 10-20 unknowns simultaneously. Protein typing is cheaper than PCR-based methods and requires less specialised equipment; conversely, ethidium bromide staining is simpler than silver staining and DNA extracts can be used for other purposes, such as amplification and sequencing of specific genes of interest. The choice between them will therefore usually be dictated by available facilities and the details of particular research objectives.

TABLE 1. Comparative identification of *Bufo* larvae by morphology and protein fingerprinting.

Species predicted from morphology	No. identified as *B. bufo* by fingerprinting	No. identified as *B. calamita* by fingerprinting	No. indistinguishable by fingerprinting
Bufo bufo	225	19	2
Bufo calamita	29	123	2

ACKNOWLEDGMENTS

We thank David Simpson and Paul Rooney for help at fieldwork sites, Dr Susan Hitchings for provision of some *B. bufo* larvae, Dr Sandy MacGillivray for advice about silver staining, and the Leverhulme Trust for financial support.

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Accepted: 14.11.97

HERPETOLOGICAL JOURNAL, Vol. 8, pp. 149-159 (1998)

A NEW *MANTIDACTYLUS* FROM SOUTH-EASTERN MADAGASCAR, WITH A REVIEW OF *MANTIDACTYLUS PERACCAE* (RANIDAE: MANTELLINAE)

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In the course of a herpetological survey in southern Malagasy rainforest, a new species of the endemic genus *Mantidactylus* was discovered and is here described as *M. brunae* n. sp. This frog is similar to *M. peraccae* for which a redescription, new locality records, and natural history notes are provided. The examined *M. peraccae* specimens are slightly warty dorsally, with small, dark protruding dots surrounding brown rounded patches on the light brown dorsum. *Mantidactylus peraccae* has a wide distribution in eastern Madagascar, occurring at elevations between 900 and 1800 m. *M. brunae* n. sp. inhabits the low-altitude rainforest of Andohahela and differs from *M. peraccae* in its slender form and smoother skin. In contrast to *M. peraccae* (which is arboreal), *M. brunae* n. sp. was found on the ground in crevices along rocky forest brooks. Its acoustic repertoire consists of a rapid trill-like series of 3-4 click notes with a frequency ranging from about 1.4 to 6.7 kHz, whereas *M. peraccae* emits metallic sounds, single or in series, from elevated positions. Morphological and bioacoustic differences between populations attributed to *M. peraccae* indicate that they may constitute more than one species, but available data are insufficient to corroborate taxonomic conclusions. A redescription of *M. elegans*, phenetically similar to *M. brunae* n. sp. and *M. peraccae*, is provided based on specimens from Andringitra, together with a diagnostic key to the currently known species of the subgenus *Spinomantis*.

INTRODUCTION

The ranid subfamily Mantellinae currently contains two genera, *Mantella* and *Mantidactylus* (Glaw & Vences, 1994). The genus *Mantella* is phylogenetically a well defined unit which is characterized by several autapomorphies such as hyoid structure, presence of skin alkaloids and loss of maxillary teeth (pers. obs.; Daly *et al.* 1996). Some *Mantidactylus* of the subgenus *Chonomantis* (e.g. *M. opiparis* and *M. albofrenatus*) superficially resemble some *Mantella* (especially *M. betsileo*). However, this is probably due to convergence since these species are characterized by a derived femoral gland structure which is shared with other *Mantidactylus* (but not with *Mantella*), and by a unique tadpole morphology (Glaw & Vences, 1994; pers. obs.). At present, relationships between *Mantella* and *Mantidactylus* remain unresolved and no evidence is known to support the monophyly of *Mantidactylus*. Basic data on morphology, variability and natural history of many *Mantidactylus* are still unknown, even though the Malagasy herpetofauna has been intensively studied during recent years.

One of these poorly known species is *Mantidactylus peraccae,* which was originally described by G. A. Boulenger in 1896 as *Rhacophorus Peraccae.* Boulenger named this new frog based upon a single specimen (BM 1947.2.9.7) captured by C. J Forsyth Major at "*Ivohimanita*", and he dedicated it to his Italian colleague M. G. Peracca. The type locality was located in NW Madagascar by Blommers-Schlösser (1985), but most likely it corresponds to Ivohimanitra (Tanala region, Fianarantsoa Province) in central-eastern Madagascar (Blommers-Schlösser & Blanc, 1991). The species was transferred to the genus *Mantidactylus* by Blommers-Schlösser (1978). This author examined two further specimens from "Tampoketsa d'Ankazobe" in central Madagascar. At least one of them was found within the axil of a *Pandanus* screw palm at an altitude of 1600 m, this representing the first information on *M. peraccae* ecology. The species was more formally transferred to the genus *Mantidactylus* by Blommers-Schlösser (1979) who, in her monographic contribution on mantellines, included *Mantidactylus peraccae* in the *Mantidactylus depressiceps* group together with *M. depressiceps* and *M. tornieri.*

In the first volume of "Faune de Madagascar" dedicated to the amphibians, Blommers-Schlösser & Blanc (1991) reported further localities for *M. peraccae*: Tsaratanana Massif (northern Madagascar) and Anosy Mountains (SE Madagascar). The *Mantidactylus depressiceps* group then increased by addition of *M. elegans.* The *depressiceps* group was later treated as a *Mantidactylus* subgenus, *Guibemantis,* by Dubois (1992).

In the second edition of their field guide, Glaw & Vences (1994) published a black-and-white photograph (Fig. 289, p. 142) and a colour plate (Pl. 84) of a

M. peraccae specimen from Ankeniheny (forest south of Moramanga, central-eastern Madagascar). The ecology and presence of distinct femoral glands, as well as morphochromatic and bioacoustic data led them to transfer the species to the subgenus *Spinomantis*, which presently includes *Mantidactylus aglavei*, *M. fimbriatus*, *M. massi, M. phantasticus* and *M. peraccae* (Glaw & Vences, 1997*b*).

Recent field observations of *Mantidactylus peraccae* have been carried out by F. Andreone on the western slopes of the Anjanaharibe chain (NE Madagascar), by F. Glaw at Vohiparara (Ranomafana National Park), and by D. Vallan in the rainforest of Ambohitantely, a locality which corresponds to Tampoketsa d'Ankazobe, already quoted by Blommers-Schlösser (1978). Our observations, together with the re-examination of all specimens previously attributed to *M. peraccae,* allows the clarification of some aspects of the ecology and distribution of this species. Furthermore, one specimen captured in a low-altitude rainforest in SE Madagascar which has been tentatively assigned to *M. peraccae*, turned out to be a new species. The aim of the present paper is therefore to describe this new taxon and to review *M. peraccae* based on our recent studies.

MATERIALS AND METHODS

Specimens were captured during the night with the aid of electric torches by locating calling males. Advertisement calls were recorded with a variety of tape recorders and microphones, and were analysed with the sound system Voxys 3.0. Specimens were fixed in 10% formalin or in 90% ethanol, with successive preservation in 65% ethanol. All morphological measurements were taken by the senior author to the nearest 0.1 mm on the following parameters (Table 1): A, snout vent length (SVL); B, head width at the maxillary commissure; C, head length from the maxillary commissure to the tip of the snout; D, eye commissure - nostril distance; E, nostril - tip of snout; F, horizontal eye diameter; G, horizontal tympanum diameter; H, forearm length to the tip of the longest finger; I, hand length to the tip of the longest finger; J, tibia length; K, foot length (including the tarsus) to the longest toe. Some other morphological data such as the tibiotarsal articulation extension, size of femoral glands and inner metatarsal tubercle length were also recorded. The webbing formula described by Blommers-Schlösser (1979) and Glaw & Vences (1994), provides the range of the free unwebbed phalanges at each side of the fingers and toes. Museum acronyms used are as follows: BM, Natural History Museum, London; MNHN, Muséum national d'Histoire naturelle, Paris; MRSN, Museo Regionale di Scienze Naturali, Torino; NMBE, Naturhistorisches Museum, Bern; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn. The location of the sites of *M. peraccae* and the new species is given in Fig. 1. Latitudes and longitudes were given according to GPS prospecting, bibliography analysis and IUCN/UNEP/WWF (1987).

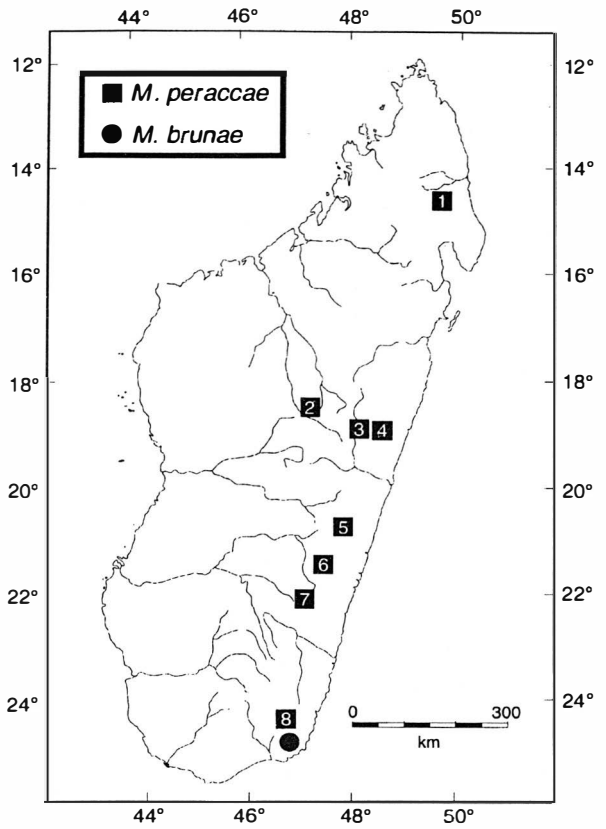

FIG. 1. Provenance localities of *Mantidactylus peraccae* [1, Anjanaharibe-Sud; 2, Tampoketsa d'Ankazobe (= Ambohitantely); 3, Ankeniheny; 4, Andasibe; 5, Ivohimanitra; 6, Vohiparara; 7, Andringitra (after Raxworthy & Nussbaum, 1996); 8, Anosy Chain], and *M. brunae* n. sp. between Eminiminy and Isaka-Ivondro (Andohahela Strict Nature Reserve).

RESULTS

REVIEW OF *MANTIDACTYLUS PERACCAE*

Mantidactylus peraccae (Boulenger, 1896) [Figs. 2-4]

Rhacophorus Peraccae - Boulenger, 1896: 420-421.

Rhacophorus peraccae - Mocquard, 1909: 60; Ahl, 1931: 191; Guibé, 1978: 67

Mantidactylus peraccae - Blommers-Schlösser, 1978: 32, Fig. 14; Blommers-Schlösser, 1979: 43; Blommers-Schlösser, 1985: 438; Blommers-Schlösser & Blanc, 1991: 153-154; Glaw & Vences, 1992 a: 108-109, 117, Figs. 135-136; Blommers-Schlösser & Blanc, 1993: Pl. 15 (Fig. 53); Raxworthy & Nussbaum , 1996: 162, 169.

Mantidactylus (*Guibemantis*) *peraccae* - Dubois, 1992: 312

Mantidactylus (*Spinomantis*) *peraccae* - Glaw & Vences, 1994: 124-125, 144.

Mantidactylus (*Spinomantis*) cf. *peraccae* - Glaw & Vences, 1997b: 243-258.

Diagnosis. A medium-sized arboreal and nocturnal *Mantidactylus* (SVL 30-45 mm). Dorsally brownish-greenish with darker blotches; dorsum rather warty with small dark protruding dots. Measurements of the

TABLE 1. Biometric measurements (to the nearest 0.1 mm) of the specimens analysed in the present paper and belonging to *Mantidactylus brunae* n.sp. and to *M. peraccae*. Holotypes are marked with an asterisk. M, males; F, females; Locality, capture locality of the specimens (T. d'Ankazobe = Tampoketsa d'Ankazobe); A, snout-vent length; B, head width at the maxillary commissure; C, head length from the maxillary commissure to the tip of snout; D, eye - nostril distance; E, nostril - tip of snout distance; F, eye diameter; G, horizontal tympanum diameter; H, forearm length at the tip of the longest finger; I, hand length at the tip of the longest finger; J, tibia length; K, foot length (including the tarsus) at the longest toe; L, length of the femoral gland; M, width of the femoral gland; N, tibiotarsal articulation reaching (1) eye, (2) beyond eye, (3) nostrils, (4) snout tip. Range and mean of females was calculated from the positively sexed specimens (ZFMK 62270 and ZMA 6869/704) whereas possibly immature individuals (ZMA 6869/703 and BM 1947.2.9.7) were not included.

Species	Sex	Locality	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Mantidactylus brunae n.sp.																
MRSN A1649*	M	Andohahela	32.3	11.5	13.4	2.5	3.8	5.4	2.8	17.2	10.5	18.0	23.6	8.6	3.2	(4)
Mantidactylus peraccae (males)																
MRSN A1861	M	Anjanaharibe (Analabe Valley)	43.9	15.9	17.1	4.4	3.3	6.2	3.3	22.9	16.0	23.6	35.9	10.5	4.0	(2)
MRSN A1862	M	Anjanaharibe (Analabe Valley)	44.3	17.3	17.2	4.3	3.1	5.8	3.4	23.6	15.3	23.0	34.8	9.7	3.8	(3)
MRSN A1863	M	Anjanaharibe (Analabe Valley)	40.9	16.1	16.9	4.5	3.9	5.6	3.1	25.2	16.1	24.2	33.9	9.0	3.3	(3)
MRSN A1864	M	Anjanaharibe (Analabe Valley)	34.1	13.2	14.4	3.1	3.3	5.5	2.4	20.1	14.9	19.2	25.9	8.8	3.5	(3)
NMBE 1035196	M	Ambohitantely	41.3	16.2	17.1	4.4	3.8	5.2	2.8	22.8	15.0	19.9	32.6	9.3	4.2	(2)
ZFMK 57452	M	Ankeniheny	37.7	14.2	14.7	2.9	3.6	4.6	2.5	20.1	12.5	17.9	26.9	10.0	4.0	(2)
ZFMK 62269	M	Vohiparara	38.7	14.9	15.4	3.7	4.8	5.7	3.0	22.1	13.3	20.4	29.8	9.8	4.9	(4)
MNHN 1975-753	M	Anosy Chain	43.1	16.6	18.1	3.6	3.9	6.5	2.8	23.1	14.9	22.4	32.7	7.5	3.2	(4)
Range			34.1-44.3	13.2-17.3	14.4-18.1	2.9-4.5	3.1-4.8	4.6-6.5	2.4-3.4	20.1-25.2	12.5-16.1	17.9-24.2	25.9-35.9	7.5-10.5	3.2-4.9	
Mean			40.5	15.6	16.4	3.9	3.7	5.6	2.9	22.5	14.8	21.3	31.6	9.3	3.9	
Mantidactylus peraccae (females)																
ZFMK 62270	F	Vohiparara	39.4	15.6	16.5	3.7	3.5	5.5	3.1	23.2	14.3	20.9	31.2	/	/	(3)
ZMA 6869/704	F	T. d'Ankazobe	45.0	15.4	17.7	3.5	4.5	5.6	2.7	23.2	14.7	23.3	33.5	/	/	(1)
ZMA 6869/703	F?	T. d'Ankazobe	34.7	12.9	14.9	3.2	2.9	5.2	2.5	18.6	12.5	18.5	25.2	/	/	(1)
BM 1947.2.9.7*	F?	Ivohimanitra	31.9	12.1	13.4	3.7	3.2	5.4	2.4	18.1	10.8	12.0	23.9	/	/	(2)
Range			39.4-45.0	15.4-15.6	16.5-17.7	3.5-3.7	3.5-4.5	5.5-5.6	2.7-3.1	23.2-	14.3-14.7	20.9-23.3	31.2-33.5	/	/	
Mean			42.2	15.5	17.1	3.6	4.0	5.6	2.9	23.2	14.5	22.1	32.4	/	/	

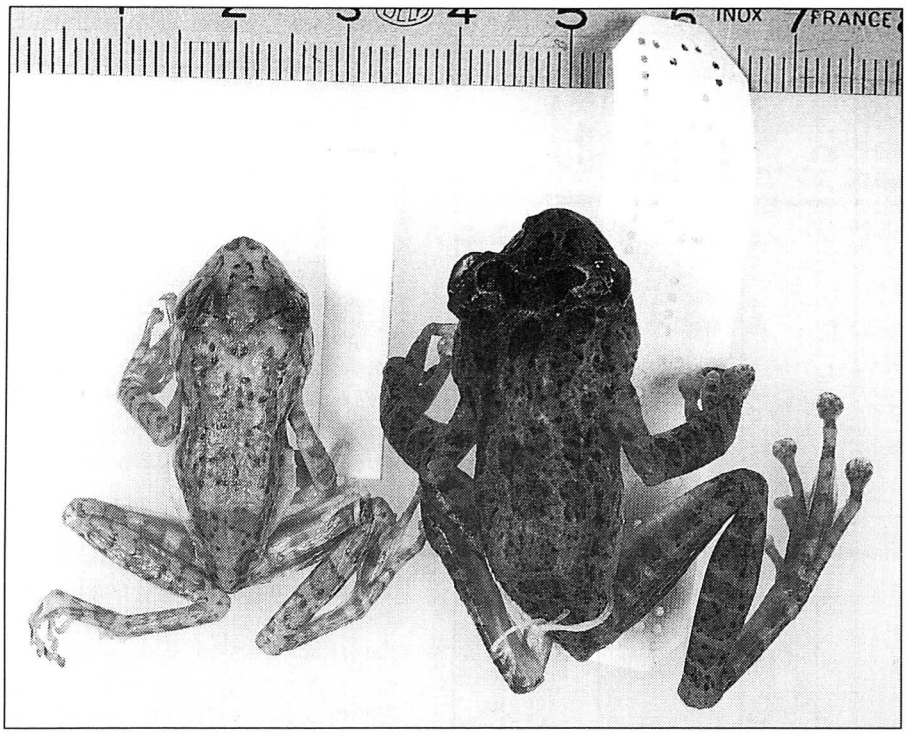

FIG. 2. Dorsal view of preserved specimens of *Mantidactylus peraccae*. Left: Holotype (female?) from Ivohimanitra (BM 1947.2.9.7). Right: comparative specimen (male) from Anosy Chain (MNHN 1975-753).

holotype and comparative specimens are given in Table 1. Distinguishable from the other species of the subgenus *Spinomantis* (*M. aglavei*, *M. fimbriatus*, *M. massi* and *M. phantasticus*) by the absence of dermal flaps and fringes on the legs; from *M. elegans* by the presence of an outer metatarsal tubercle and large femoral glands, and by the relative length of the 3rd toe. Quite similar to *M. brunae* n. sp.: for distinctive characters see the diagnosis of this new species.

Redescription of the holotype. BM 1947.2.9.7, Ivohimanitra, Tanala region, Fianarantsoa Province, collected by C. J. Forsyth Major. Specimen in rather good condition, with a longitudinal cut on the belly. As indicated by the lack of femoral glands, the specimen is not an adult male; it may be a female or a subadult specimen. Head slightly longer than wide; snout rounded, not projecting and as long as the diameter of the orbit. Canthus rostralis obtuse, loreal region concave; nostrils interposed midway between the eye and the tip of the snout. Interorbital space as broad as the upper eyelid; tympanum distinct, about half the diameter of the eye. Vomerine teeth in two slightly oblique oval groups just behind choanae. Hind legs overlap about 3 mm when curved at right angle; tibiotarsal articulation reaches the nostril when appressed to the body. Finger length: 1 < 2 < 4 < 3. Fingers without webbing; finger tips with well developed expansions about half of the tympanum diameter. Subarticular tubercles and the tubercle at the basis of the pollex are visible. Toe length: 1 < 2 < 5 < 3 < 4. Foot webbing: 1(1), 2i(1), 2e(0.5), 3i(1), 3e(0.5), 4i(2), 4e(2), 5(1). Inner metatarsal tubercle 1.3 mm long; outer metatarsal tubercle reduced. Lateral metatarsalia separated. Expansions of toes smaller than those of fingers. Small warts on the head, dorsum and upper surface of tibiae. Foreleg and upper femur surfaces rather smooth. A prominent fold extends above the tympanum. Throat smooth; belly and ventral side of thighs slightly warty. Femoral glands absent. The colouration is still in accordance with the original description i.e. pale brown above with dark brown, light-edged markings forming a cross on the head, the horizontal branches on the upper eyelids, and regular bars on the limbs (see Fig. 2). Small protruding blackish dots on the dorsum, especially at the borders of the dark markings. The belly and lower parts of the body are whitish except for a few dark spots on the throat.

Comparative specimens. MNHN 1975.753, Anosy Chain, Toliara (Tuléar) Province, Camp VI, approximately 24°25'S / 47°00' E, 1800 m, 12 December 1971, Ch.P. Blanc leg.; ZMA 6869/703, Tampoketsa d'Ankazobe, Antananarivo (Tananarive) Province, approximately 18°08'-18°13'S / 47°18'-47°21'E, 1500-1600 m, 9 April 1972, A. Peyrieras leg.; ZMA 6869/704, Tampoketsa d'Ankazobe, Antananarivo (Tananarive) Province, approximately 18°08'-18°13'S / 47°18'-47°21'E, 1500-1600 m, 9 April 1972, A. Peyrieras leg.; ZFMK 57452, Ankeniheny, Toamasina (Tamatave) Province, 19°10'S / 48°2'E, about 1000 m, 20 February 1994, F. Glaw, N. Rabibisoa and O. Ramilison leg.; NMBE 1035196, Ambohitantely (Ankazobe), Antananarivo (Tananarive) Province, 18°06,4'S / 47°15,0'E; 1475 m, 7 February 1996, D. Vallan leg.; MRSN A1861, Analabe Valley, Anjanaharibe Chain, Mahajanga (Majunga) Province, Camp 1, 14° 47'S / 49° 27'E, 1050 m, 25 January 1996,

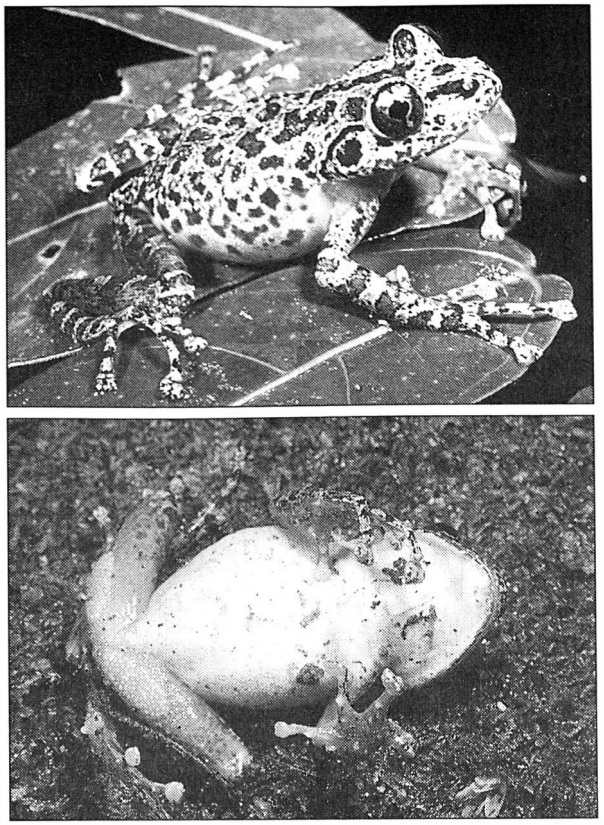

FIG. 3. *Mantidactylus peraccae*. MRSN A1862, live male from Analabe Valley, Anjanaharibe Chain. Dorsal (a) and ventral (b) views.

F. Andreone, H. Randriamahazo and J.E. Randrianirina leg.; MRSN A1862, Analabe Valley, Anjanaharibe Chain, Mahajanga (Majunga) Province, Camp 1, 14°47'S / 49°27'E, 1050 m, 26 January 1996, F. Andreone, H. Randriamahazo and J.E. Randrianirina leg.; MRSN A1863, Analabe Valley, Anjanaharibe Chain, Mahajanga (Majunga) Province, Camp 2, 14°46'S / 49°26'E, 1200 m, 5 February 1996, F. Andreone, H. Randriamahazo and J.E. Randrianirina leg.; MRSN A1864, Analabe Valley, Anjanaharibe Chain, Mahajanga (Majunga) Province, Camp 2, 14°46'S / 49°26'E, 1200 m, 6 February 1996, F. Andreone, H. Randriamahazo and J.E. Randrianirina leg.; ZFMK 62269 and 62270, Vohiparara Forest, Ranomafana National Park, Fianarantsoa Province, 21°13'S / 47°22'E, 1000 m, 27 February 1996, F. Glaw, D. Rakotomalala and F. Ranaivojaona leg.

Compared to the holotype, the male MNHN 1975.753 (Anosy Chain) is larger, with nostrils protruding, equidistant between the tip of snout and the eye commissure. The finger tip expansions are of about the same size of the tympanum. Foot webbing: 1(0.5), 2i(1), 2e(0), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1). The femoral glands are ovoidal, whitish, their internal distance being 3.2 mm. Dorsal colouration brownish with irregular darker spots. Small protruding warts are distributed almost uniformly on the upper surfaces of the dorsum as well as on the femurs and the forelegs. They are blackish when within the dark markings, lighter in the areas between them. The belly is whitish with scattered dark spots on the anterior chest.

ZMA 6869/704 (Tampoketsa d'Ankazobe) is probably an adult female. Foot webbing: 1(1), 2i(1), 2e(0), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1). The other specimen from the same locality (ZMA 6869/703) is similar, but smaller. Both the specimens are beige with dark spots and small warts. NMBE 1035196, a male captured from the same area, has well developed femoral glands. Its dorsum is rather smooth while the belly is warty. Foot webbing: 1(0.5), 2i(1), 2e(0), 3i(1), 3e(0.5), 4i(2), 4e(1.5), 5(1).

ZFMK 57452 (Ankeniheny) is a male with a blunted, non-projecting, snout. Nostrils situated nearer to the tip of the snout than to the eye. Tibiotarsal articulation reaches between the eye and the nostril. Foot webbing: 1(1), 2i(1.5), 2e(0.5), 3i(2), 3e(1), 4i(2), 4e(2), 5(0.5). Small dark spots (not visible in life) are present in the areas between the larger dark blotches of the dorsum. The belly is almost completely white. Head and dorsum do not show warts, but these were recognizable in the live specimen.

ZFMK 62269 (Vohiparara) is a male with a rather contrasting dorsal colouration and large, brownish spots. Foot webbing: 1(1), 2i(1), 2e(0), 3i(1), 3e(1), 4i(2), 4e(2), 5(1). The whitish-yellow belly has a few scattered dark dots on the chest. ZFMK 62270 from the same locality is a female of 39.4 mm. The colouration and general morphology is as in the male. Foot webbing: 1 (0.5), 2i(1), 2e(0), 3i(1), 3e(0.5), 4i(2), 4e(2), 5(0.5).

The specimens from Analabe Valley, western slope of the Anjanaharibe Massif, are rather homogeneous in morphology and colouration. MRSN A1861 (male) has large femoral glands, but these are not pronounced and not protruding in preservative. Its dorsum is slightly granular with blackish warts. The finger tips are large, about the same size as the tympanum. The throat is immaculate, while the thorax has some isolated black spots. The lower surfaces of thighs are brownish. Foot webbing: 1(0.5), 2i(1), 2e(0), 3i(1.5), 3e(0), 4i(1.5), 4e(1.5), 5(1). MRSN A1862 (male) has a warty dorsum and a rather enlarged head (Fig. 3a). The finger-tips expansions are smaller than the tympanum. The head is rather flattened, and the throat is smooth, while the belly is relatively warty. The femoral glands are visible and well developed. The belly is whitish with some dark spots (Fig. 3b). Foot webbing: 1(1), 2i(1.5), 2e(0.5), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1.5). MRSN A1863 (male) has a warty dorsum, the belly is rather smooth and the femoral glands are large. The finger-tips are enlarged and of the same size as the tympanum diameter. The dorsum is rather dark with large dark spots. Foot webbing: 1(0.5), 2i(1), 2e(0), 3i(1), 3e(1), 4i(2), 4e(2), 5(1). MRSN A1864 (most likely a subadult male) is rather small. Its body, compared to that of the other examined specimens from the same locality, is also less flattened. The snout is rather pointed. The eyes are large. The dorsum, belly and throat are smooth.

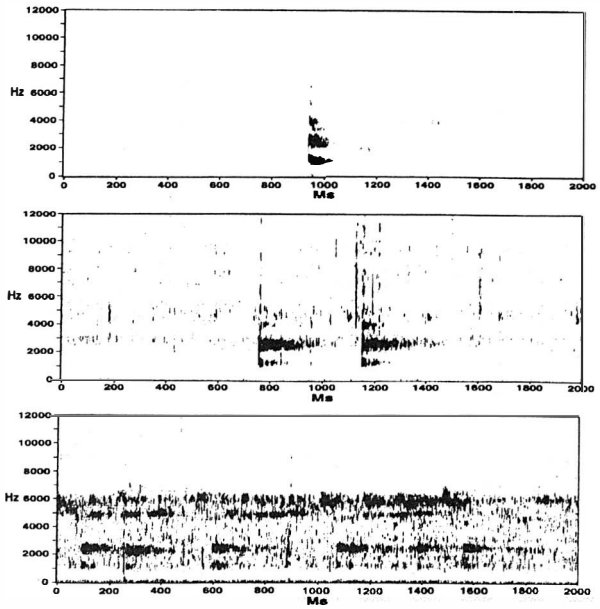

FIG. 4. Sonagrams of *Mantidactylus peraccae:* (a) isolated note from Ankeniheny, central-eastern Madagascar; temperature, 19°C; (b) note pair from Vohiparara, Ranomafana National Park, central-eastern Madagascar; temperature, 21°C; (c) note series from Analabe Valley, Anjanaharibe Chain, north-eastern Madagascar; temperature, 20 °C.

Femoral glands are pronounced and whitish. A few large and contrasting spots are present on the dorsum. Belly whitish, without dark spots. Foot webbing: 1(1), 2i(1), 2e(0), 3i(1.5), 3e(1), 4i(2), 4e(2), 5(1).

Colouration in life. Data are available for specimens from Ankeniheny, Vohiparara, Anjanaharibe, and Ambohitantely. These had a similar dorsal colour pattern, i.e. light brown with large irregular brown markings. The markings were oblong at the centre of the dorsum, becoming more rounded dorsolaterally. In ZFMK 57452 from Ankeniheny (colour photograph in Glaw & Vences, 1994), greenish shading was present as a thin line around the dark markings; the flanks were whitish to green; the throat and anterior part of belly were white; the posterior part of the belly and the ventral side of the arms and legs were translucent green; the femoral glands were bright yellow and the bones were greenish; the tympanum was brownish and the iris yellowish with an irregular brownish outer border. Specimens from Vohiparara corresponded well with the above description, also sharing the greenish shade of the ventral side, and the bright yellow of the femoral glands in the males. In MRSN A1862 from Analabe Valley (Anjahaheribe), the greenish colour was less developed when compared to the Ankeniheny specimen. The posterior part of the belly and the femoral glands were more whitish.

Habitat and habits. The studied specimens of *M. peraccae* were found in mid-altitude rainforests. At Anjanaharibe (Analabe Valley) the habitat is a patchwork of pristine and altered forest, with most of the unaltered forest occurring on the ridges and steepest slopes. In the degraded patches, the original vegetation has been replaced by ferns and grasses. Trunks along the forests streams are usually covered by lichens and mosses. *Mantidactylus peraccae* appears to be mainly an arboreal species. A high density of males was usually observed overnight at Campsite 1 (altitude of about 1050 m) on the mossy trees at an elevation of 2-4 m. At Vohiparara one male was found in February at night, 2-3 m high on a tree. A fresh clutch of eggs, possibly belonging to *M. peraccae* and similar to clutches of *M. aglavei* as described in Glaw & Vences (1992), was hanging from a leaf near the female.

Acoustic repertoire. The advertisement call of *M. peraccae* is composed of one note type which often has a rather "metallic" sound. Some differences regarding note arrangements exist in the different tape recordings which may be ascribed to intraspecific geographical variation or to the varied motivational states of the calling specimens.

At Ankeniheny (Fig. 4a), only single, explosive and isolated notes were noticed (see also Glaw & Vences, 1994). Note duration (recorded 20 February 1994, 21:30, 19°C) was 132-273 ms (mean 212 ± 51 ms, n = 5). Intervals between two notes were 20-70 s (mean 37 ± 20 s, n = 5). Fundamental frequency was between 1.05 and 1.45 kHz, dominant frequency 2.25-2.85 kHz, additional (lower emphasized) frequency bands at 3.80-4.20, 4.95-5.50, 6.25-6.55 and 7.65-7.80 kHz.

At Vohiparara (Fig. 4b), calls consisted mostly of note pairs (temperature = 21°C). Note duration was 195-250 ms (mean 221 ± 17 ms, n = 10), and duration of intervals between the notes of a note pair was 248-336 ms (mean 278 ± 30 ms, n = 10). To guard against presenting subjective measurements, we also state the period from the start of the first note until the start of the second note. This time period, which could be accurately measured, was 340-360 ms (mean 352 ± 9 ms, n = 5). Two dominant frequency bands were present at 1.2-1.5 kHz and 2.4-2.9 kHz, and an additional low intensity frequency band is present at 3.9-4.2 kHz. Besides the note pairs, several isolated notes were recorded which were similar to those from Ankeniheny. Duration of these notes was 52-85 ms (mean 69 ± 14 ms, n = 4). Two three-note calls were also recorded. These resemble note pairs but contain an additional short note (duration 9 and 22 ms).

At Anjanaharibe, Analabe Valley, calls usually consisted of note pairs. Sometimes the call series was followed by a "croaking" note. This additional note has a frequency ranging from 1.1-1.9 kHz. In a few cases the calls were repeated in a series of up to 5 notes (Fig. 4c). Temperature during time of recording was 20°C. Frequency ranged between about 0.9-9.0 kHz, with a maximum of emission at 2.5-2.8 kHz. Note duration was 53-349 ms (mean 140 ± 76 ms, n = 27) and duration of intervals between the starts of notes within one series was 419-727 ms (mean = 624 ± 98 ms, n = 7).

At Ambohitantely (temperature = 19°C) the recorded calls ranged from typical double notes up to five notes. The spectral structure is very similar to that of other localities: the maximum intensity of emission is at

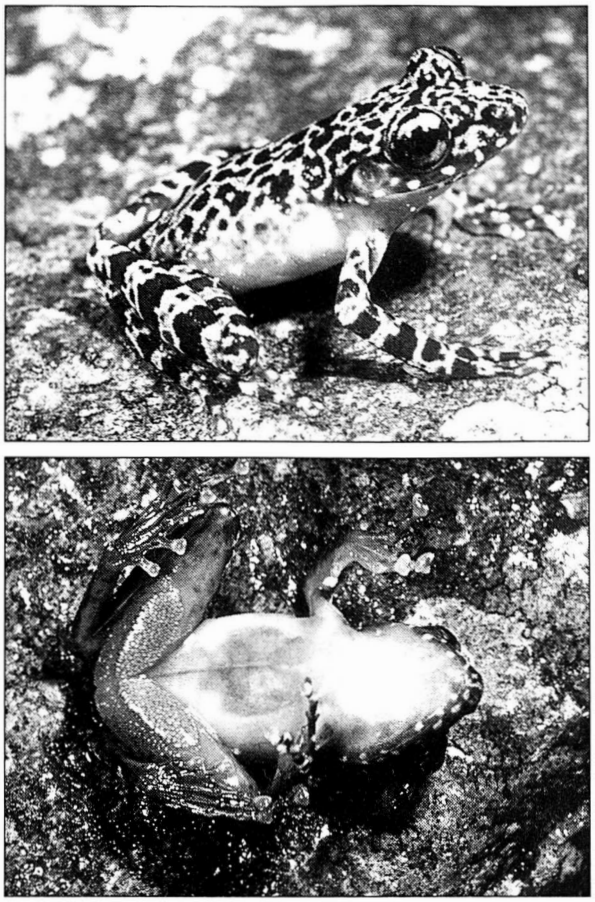

FIG. 5. *Mantidactylus brunae* n. sp. MRSN A1649, live holotype (male) from Andohahela low altitude rainforest, southern Madagascar. Dorsal (a) and ventral (b) views.

about 2.2-3.0 kHz, with other components at 1.2 and 4.0 kHz and highest frequency at 9.0 kHz. Note duration was 137-228-ms (mean = 175 ± 28 ms, n = 10), duration of intervals between the starts of notes within one series was 376-544 ms (mean = 458 ± 61 ms, n = 8).

Remarks. ZMA 6869/703 was identified as a male by Blommers-Schlösser (1979). Femoral glands are not evident in this specimen, whereas they are visible in MNHN 1975-753 (Fig. 2; also depicted by Blommers-Schlösser & Blanc, 1991 and by Glaw & Vences, 1992*a*: Figs. 135-136, p. 116). Gonads are not recognizable, but the presence of eggs can be excluded. For this reason it might be an immature individual; it was probably upon the analysis of this specimen that Blommers-Schlösser & Blanc (1991) concluded that the femoral glands of *Mantidactylus peraccae* males are not visible.

Other specimens held at Paris were attributed to *M. peraccae,* but most likely do not belong to this species: they all have the fifth toe longer than the third, a feature distinctive of *M. elegans* and *M. brunae* n. sp. (see below). MNHN 1975.752 (from Anjaridilava, Andringitra, Fianarantsoa Province; presumably collected by Ch.P. Blanc, 15 January 1971), SVL 37.9 mm, colouration similar to that of *M. peraccae*: the dorsum is brownish with irregular darker spots, not large as

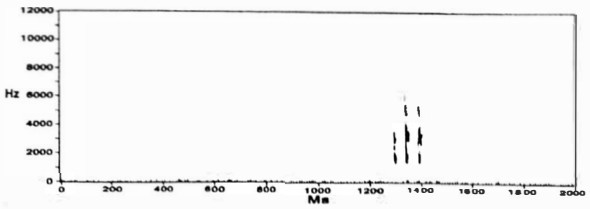

FIG. 6. Sonagram of the advertisement call of *Mantidactylus brunae* n. sp. from Andohahela low altitude rainforest; temperature, 18°C.

in other *M. elegans* specimens (e.g. Fig. 268 and plate 85 in Glaw & Vences, 1994). The belly is whitish with blackish spots on the chest forming a network on the throat. The dorsum and throat are smooth while the belly and under-surface of hindlegs are slightly granular. The snout is rather rounded and the nostrils do not protrude. An inner metatarsal tubercle is present (length = 1.5 mm) as well as a small wart-like protuberance similar to the external tubercles observed in the "typical" *M. peraccae.*

MNHN 1975.754 (same collecting data as MNHN 1975.752) lacks the outer metatarsal tubercle (inner metatarsal tubercle length = 1.9 mm). The tibiotarsal articulation reaches beyond the tip of snout. Femoral glands are absent. The dorsum colouration is greyish with large dark spots, the throat is dark. The SVL of 33.1 mm is comparable to that of a newly metamorphosed *M. elegans* found at Andringitra (shown by Glaw & Vences, 1994, plate 85) which measured 34 mm.

MNHN 1975.751, from Andilabe, Tsaratanana Massif, Antsiranana (Diégo-Suarez) Province, 1700 m, aproximately 13°49'-14°05'S / 48°44'-59' E, February 1951, unknown collector, labelled as "Rhacophorinae sp.", is here tentatively regarded as a juvenile of *M. elegans*, as already noted in the old catalogues. Snout - vent length is 23.5 mm. The preservation conditions are poor, but it is still possible to discern a dorsum colour patterning very similar to that of *M. elegans*. The belly is "dirty" and dark spots are not visible, neither are femoral glands. The inner metatarsal tubercle is evident (length = 1.1 mm), while the outer one is lacking.

A NEW *MANTIDACTYLUS* FROM SOUTHERN MADAGASCAR

Mantidactylus brunae new species [Figs. 5-6]

Mantidactylus cf. *peraccae* - Andreone, 1995: 35; Andreone, 1996*a*: 307, 402; Andreone & Randriamahazo, 1997: 112-113, 126, Figs. 51-52.

Holotype. MRSN A1649, adult male from the low altitude rainforest between the villages of Isaka-Ivondro and Eminiminy, Andohahela Strict Nature Reserve, Toliara (Tuléar) Province, 24°45'30"S / 46°51'15"E, elevation of about 600 m, 17 November 1994, F. Andreone & D. Vallan leg.

Diagnosis. A medium-sized slender frog belonging to the genus *Mantidactylus* as is evident from the presence of femoral glands in the male (females unknown).

It differs from the other known *Mantidactylus* species as follows: from the species of the subgenera *Mantidactylus, Brygoomantis, Chonomantis, Ochthomantis*, and *Hylobatrachus* by the lack of a visible porus in the femoral glands; from the species of the subgenera *Laurentomantis* and *Pandanusicola,* as well as the species of the *M. boulengeri* group (subgenus *Gephyromantis*), by separated lateral metatarsalia; from the *M. asper* group (subgenus *Gephyromantis*) by the lack of distinct folds on the shoulder region and shorter hindlimbs; from most species of the subgenus *Phylacomantis (M. pseudoasper, M. corvus, M, granulatus, M. leucomaculatus*) by the lack of a paired vocal sac; from *M. redimitus* and *M. cornutus* (subgenus *Phylacomantis*) by the lack of two tubercles between the eyes; from the subgenus *Guibemantis* (*M. depressiceps, M. tornieri, M. liber*) by the presence of distinctly visible femoral glands; from the *M. wittei* complex (subgenus *Blommersia*) by the larger size; from *M. argenteus* (subgenus *Blommersia*) by the smaller tympanum; from *M. guibei* and *M. bertini* (subgenus *Blommersia*) by separated metatarsalia; from *M. aglavei, M. fimbriatus, M. massi,* and *M. phantasticus* (subgenus *Spinomantis*) by the complete lack of dermal flaps and fringes, and relative toe lengths. Externally *M. brunae* mostly resembles *M. peraccae,* from which it differs in the relative third and fifth toe length, trilled calls, terrestrial/scansorial habits, slender form, rather pointed snout, lack of dorsal warts, and the dorsal pattern arranged to form a dark reticulation. Another *Mantidactylus* of uncertain subgeneric attribution, the high-mountain species *M. elegans,* has a similar relative toe length, colour pattern, and, according to Glaw & Vences (1994), also habitat preferences. However, it differs by larger size, lack of outer metatarsal tubercle, and, as far as is known, by lack of femoral glands. A re-description of this species is given later (see *Remarks*).

Subgeneric attribution. The species cannot unequivocally be assigned to any subgenus. Based on its phenetic similarity with *Mantidactylus peraccae* it is tentatively included in the subgenus *Spinomantis.*

DESCRIPTION OF THE HOLOTYPE

Morphology. Male in excellent preservative condition. SVL 32.3 mm. Snout pointed, head longer than wide. Loreal region rather concave, nostrils not distinctly projecting, situated nearer to the eyes than to the tip of snout. Tympanum distinct, half the diameter of the eye. Vomerine teeth arranged in two slightly oblique oval groups behind the choanae. Hind legs overlap about 2 mm when curved at right angles; the tibiotarsal articulation reaches the tip of the snout. Finger length: 1 < 2 < 4 < 3. Unwebbed fingers with digital expansions about the same size as the tympanum. Subarticular tubercles, as well as the tubercle at the basis of the pollex, visible. Lateral metatarsalia separated. Toe length: 1 < 2 < 3 < 5 < 4. Foot webbing: 1(1), 2i(0.75), 2e(0), 3i(1), 3e(0.75), 4i(2), 4e(2), 5(0.5). Inner metatarsal tubercle length = 1.7 mm; wart-like outer metatarsal tubercle. Dorsum and belly rather smooth. Femoral glands distinct, 8.6*3.2 mm, distance between inner margins of glands on opposite femurs = 1.5 mm.

Colouration in life. The dorsum has a yellowish - light brownish ground colour. Several black blotches are present on the dorsum, coalescing to form a reticulation on the head and loreal region. Upper surface of humerus and forearm smooth, of the same colouration of the dorsum with dark transverse bands. Fingers and toes with dark and whitish transverse bands; fingertips whitish. Flanks, as well as the area between the foreleg insertion and the jaw, are pink; the yellowish dorsum colouration continues onto the pink flanks with isolated yellowish spots. Upper jaw dark with yellow spots. Iris yellowish: lower part darker; upper part lighter; dark outer ring encircling the eye. Belly pink and throat brownish. A few light spots were visible on the dark area of throat, especially at its anterior part. Femoral glands reddish.

Colouration in preservative. The dorsum colour has changed from yellowish to greyish. The eyes are greyish-blackish. The belly is whitish and the throat greyish with some whitish spots. Femoral glands are greyish, having lost their reddish colouration.

Etymology. The specific name is a personal noun in the genitive case. F. Andreone wishes to dedicate this new species to his mother Bruna Cugnetto, for her enthusiastic support and continuous help.

Habitat and habits. The holotype was found in a small shaded spring, a tributary of the Ampasy stream, within the primary low altitude rainforest of Andohahela. The water source was covered by large rocks which constituted a cave-like formation. The specimen vocalized in these crevices at about 18.00 hr whilst clinging onto a wet rock a few centimetres above the water flow. Thus it appears to be a terrestrial-scansorial species, although it is also possible that it may be arboreal or semi-arboreal during certain periods.

Acoustic repertoire. The analysis of nine calls (temperature, 19-20° C) is presented in Table 2. The call is a trill consisting of 3-4 click notes; the duration of each note series ranges from 106-155 ms. The duration of single notes ranges from 4-25 ms, the first note being distinctly shorter than the successive ones. Inter-note intervals (within a note series) vary from 17-38 ms, being longest between the first two notes. The frequency (Fig. 6) ranges from 1.4-6.7 kHz, dominant frequency is 3.1-3.6 kHz. Other components are visible at about 1.5-1.7 and 5.0-5.2 kHz. Usually the beginning and end of the calls are less intense.

Remarks. Since the new species *M. brunae* is rather similar to *M. elegans*, we here give a detailed description of specimens attributed to *M. elegans* collected at Andringitra. It must be stated, however, that specimens currently considered as *M. elegans* may in fact belong to different species. The most problematic point is that

TABLE 2. Analysis of nine calls of *Mantidactylus brunae* n. sp. Each call consists of 3-4 short clicks, here called notes. Note duration and duration of intervals between notes is given separately for successive notes of a call. Recording temperature, 19-20°C.

Call number	*N*	range	mean	SD
Number of notes	9	3-4	3.4	0.5
Call duration (ms)	9	106-155	125.1	20.3
Note duration (1) (ms)	9	4-19	10.0	4.7
Note duration (2) (ms)	9	14-25	19.2	4.1
Note duration (3) (ms)	9	12-23	18.6	4.3
Note duration (4) (ms)	4	14-19	16.5	2.4
Interval duration 1 (ms)	9	31-38	34.3	2.3
Interval duration 2 (ms)	9	25-34	28.9	3.7
Interval duration 3 (ms)	4	17-30	22.0	5.9

up to now no reproducing specimens of *M. elegans* have been found; it is therefore not possible to draw definite conclusions on the adult morphology of the species. Lack of femoral glands in *M. elegans* is probable (despite the contrary mention in Guibé, 1978:31 which probably referred to *M. peraccae* specimens), but not yet definitely ascertained in live adult males. Specimens of the type series of *M. elegans*, however, are distinctly larger than *M. brunae* (52-60 mm SVL; Blommers-Schlösser & Blanc, 1991), and easily distinguished from that species by a number of external features.

ZFMK 57453 (Fig. 7) is a specimen in good state of preservation coming from Pic Boby (Andringitra Massif; Fianarantsoa Province, approximately 22°07'-21'S / 46°47'-47°02'E, 18 January 1994, F. Glaw & M. Vences leg. SVL of 34.7 mm. Snout rather rounded, head clearly longer than wide. Loreal region rather straight, nostrils not projecting, situated nearer to tip of snout than to eye. Tympanum rather indistinct, about half the diameter of the eye. Vomerine teeth arranged in two small, indistinct groups between the choanae. Hind legs overlap about 2 mm when curved at right angles; the tibiotarsal articulation reaches nearly the tip of the snout. Finger length: 1 < 2 < 4 < 3. Unwebbed fingers with digital expansions slightly larger than tympanum diameter. Subarticular tubercles visible. Lateral metatarsalia more or less separated. Toe length: 1 < 2 < 3 < 5 < 4. Foot webbing: 1(0.5), 2i(1), 2e(0.5), 3i(1.25), 3e(1), 4i(2), 4e(2), 5(0.5). Inner metatarsal tubercle length = 1 mm; no distinct outer metatarsal tubercle. Dorsum smooth, venter slightly granular. No distinct, prominent femoral glands visible; a granular thigh patch (see Daly *et al.* 1996) extends from the anus onto about 2/3 of the ventral femur surface.

No definite conclusion as to the sex of this specimen is possible; it is most probably a subadult, since a specimen of similar size (ZFMK 57454; SVL 34.3 mm) is newly metamorphosed, as indicated by presence of a tail remnant. ZFMK 57453, together with other individuals of similar size, was collected under stones on rocky ground in high-mountain habitat, together with

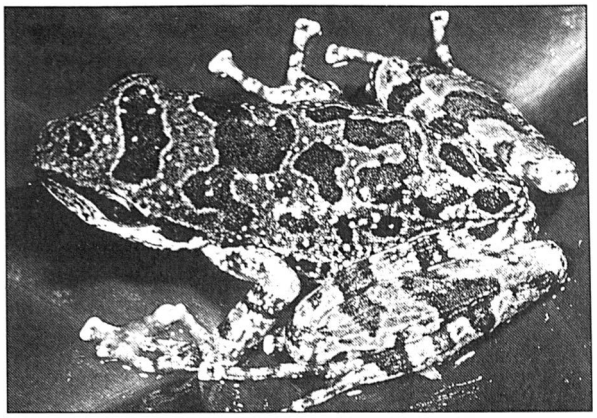

FIG. 7. *Mantidactylus elegans*. ZFMK 57453, live subadult from Pic Boby (Andringitra Massif). Dorsal view.

specimens of *Anodonthyla montana* (see Glaw & Vences, 1994). This indicates that the species is largely not arboreal.

DISCUSSION

According to present knowledge, *M. peraccae* has a wide distribution which extends from northern Madagascar (Anjanaharibe Chain), through the central-eastern escarpment (Vohiparara, Andasibe, Ankeniheny), Andringitra Massif (Raxworthy & Nussbaum, 1996), to the Anosy Chain in the south. It appears to be a mid-high altitude rainforest species, the lowest records being Andasibe (about 900 m), Ankeniheny (about 1000 m) and Analabe, Anjanaharibe Chain, Camp 1 (about 1050 m), whereas the highest locality is the Anosy Chain at 1800 m. Since this species is present on some high altitude massifs (e.g. Andringitra, Anosy Chain) which may constitute biogeographic refuges (Raxworthy & Nussbaum, 1996), it is quite likely that some of the populations presently included in *M. peraccae* may in fact belong to different taxa. If so, this might explain the observed variability in morpho-chromatic and acoustic traits. The existence of previously unrecognised cryptic species which differ bioacoustically has already been pointed out for other Malagasy frogs, e.g. those belonging to the *Boophis luteus* group (Andreone, 1996*b*), *B. goudoti* group (Glaw & Vences, 1997*a*) and some recently described *Mantidactylus* species (*M. fimbriatus, M. phantasticus*) of the subgenus *Spinomantis* which resemble *M. aglavei* (Glaw & Vences, 1994; 1997*b*). However, the small number of analysed *M. peraccae* specimens and populations, as well as the lack of knowledge of the extent of motivational call differences, currently do not allow for further statements on a possible taxonomic differentiation.

The new species herein described, *Mantidactylus brunae*, may represent a southern relative of *M. peraccae*, being currently known only from the Andohahela rainforests. Its tentative inclusion within the subgenus *Spinomantis* makes it necessary to provide a new diagnosis of this subgenus. The following

TABLE 3. Key to the *Mantidactylus* species currently included in the subgenus *Spinomantis*, and to *Mantidactylus elegans*.

1a. Large inner and distinct outer metatarsal tubercle present. One distinct femoral gland on each femur in males (ovoid, well defined and generally prominent, without median porus, each gland consisting of generally more than 60 single granules of similar size) subgenus *Spinomantis* 2
1b. Small inner metatarsal tubercle present; no distinct outer metatarsal tubercle. Prominent femoral glands probably absent in males and females ..... *Mantidactylus elegans*
2a. Dermal tubercles and fringes present, especially on hindleg; Ratio tympanum diameter/eye diameter < 0.5 3
2b. Dermal tubercles and fringes absent; Ratio tympanum diameter/eye diameter 0.5 6
3a. Small dermal tubercles on hindleg; belly greenish ..... *Mantidactylus massi*
3b. Larger dermal extensions and fringes, some of which generally reach a length of 1 mm; venter white or greenish 4
4a. Distinct tubercles and fringes on head and dorsum; belly greenish; call consisting of double-click series ..... *Mantidactylus phantasticus*
4b. No fringes on head and dorsum; belly whitish; calls without double-click series 5
5a. SVL < 40 mm; generally one single (sometimes incomplete) row of lateral dermal fringes on foot and tarsus..... *Mantidactylus fimbriatus*
5b. SVL > 40 mm; generally smaller tubercles or fringes interposed between row of primary lateral dermal fringes on foot and tarsus ..... *Mantidactylus aglavei*
6a. SVL of adult male 32 mm; head narrow; toe 3 < toe 5; belly pinkish; terrestrial habits; trill call ..... *Mantidactylus brunae*
6b. SVL of adult males generally > 34 mm; head broad; toe 5 < toe 3; belly greenish or whitish-pinkish; arboreal habits; no trill call ..... *Mantidactylus peraccae*

characters seem to apply to *Spinomantis* species, and their combination allows for a distinction from all other *Mantidactylus*: medium sized frogs (SVL 31-52 mm), tympanum diameter less than 2/3 of eye diameter, tympanum not distinctly larger in males than in females (known only in *M. aglavei, M. fimbriatus* and *M. peraccae*), lateral metatarsalia separated, inner and outer metatarsal tubercle present, finger disks distinctly enlarged, dorsum often with large, rounded, dark brown markings, femoral glands distinct and prominent in males, ovoid and well defined without median pores, consisting of a large number (generally > 60) of densely arranged, clearly discernible small granules of similar size which often (except *M. aglavei* and *M. fimbriatus*) are of different colour to the surrounding integument, absent in females. Since none of these characters is an exclusive feature of the subgenus, its monophyly can not be currently ascertained.

The morphochromatic similarity of *M. brunae* with other representatives of *Spinomantis* in relation to its alternative ecology raises interesting questions regarding the subgeneric attribution and relationships within *Mantidactylus*. If *M. brunae* is really closely related to the other *Spinomantis* species it would be the first scansorial representative of this otherwise strictly arboreal subgenus, although it cannot be excluded (since only one specimen is known thus far) that it is at least partially arboreal. Another *Mantidactylus* species which may have relationships with *M. brunae* is *M. elegans*. The few available observations (e.g., Glaw & Vences, 1994) suggest that it is a terrestrial-scansorial frog living in high-mountain rocky habitats. In general appearance and ecology it is similar to *M. brunae,* differing in larger size, absence of an outer metatarsal tubercle and probably absence of femoral glands. Although little is known on morphological variation between the populations of Malagasy anuran species, we provide an updated diagnostic key which summarizes current knowledge on morphological differentiation within the subgenus *Spinomantis* (Table 3).

Considering the incomplete knowledge about Malagasy herpetofauna, it is likely that *M. brunae* and *M. elegans* represent key species in the understanding of relationships within *Mantidactylus* and between the subgenera as currently defined. Further data are therefore needed to determine the distribution and ecology of *M. brunae* and *M. elegans*, as well as to establish the variability within *M. peraccae*.

ACKNOWLEDGEMENTS

We are indebted to the Direction des Eaux et Forêts at Nanisana (Antananarivo), particularly to C. Ravoarinoromanga, for permission to visit the protected areas, and for collecting and exportation permits. The work of F. Andreone was carried out in collaboration with the Parc Botanique et Zoologique de Tsimbazaza (Antananarivo). He acknowledges A. Randrianjafy (Antananarivo) for assistance in getting the necessary authorizations, J. E. Randrianirina and H. Randriamahazo (Antananarivo) for help in the field. F. Glaw made his work on the basis of an accord between the Zoological Institute of the University of Antananarivo and the Zoologisches Forschungsinstitut und Museum A. Koenig (Bonn) and was financially supported by the "Deutscher Akademischer Austauschdienst". D. Vallan's work was made possible by scientific co-operation between the University of Antananarivo and the Zoologisches Institut (Universität Bern) and by the financial support of the Swiss Academy of Natural Sciences. Thanks are also due to A. Dubois and A. Ohler (Paris), W. Böhme (Bonn), B. T. Clarke (London), K. Grossenbacher (Berne) and L. Van Tuijl (Amsterdam) for the loan of comparative specimens. M. Burger (Grahamstown) reviewed the English style. R. A. Griffiths

(Canterbury) and three anonymous referees made useful comments on an earlier draft of this paper.

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Accepted: 24.11.97

HERPETOLOGICAL JOURNAL, Vol. 8, pp. 161-165 (1998)

SEXUAL AND SIZE-RELATED DIFFERENCES IN THE DIET OF THE SNAKE *NATRIX MAURA* FROM THE EBRO DELTA, SPAIN

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The Ebro Delta is a wetland area partially covered by rice fields. The viperine snake *Natrix maura*, is a common colubrid snake in this ecosystem. Males delayed feeding activity by one month, and foraged for a shorter time, compared to females. Diet consisted mainly of fish and frogs, although size-related and sexual differences were found: immature snakes had a more diverse diet than adults, and adult females ate more frogs than adult males. Males captured larger numbers of smaller fish than females. Like other water snakes, large viperine snakes avoid small prey. The biomass ingested is higher in large females, providing supplementary resources for reproduction. These dietary differences may be related to the ecological needs of each category of snakes and reflect the influence of the rice cycle on diet dynamics.

INTRODUCTION

Aquatic snakes of the genus *Natrix* are mainly found in temperate climates and often occur at high densities, allowing the collection of large enough samples for carrying out very detailed dietary studies. Indeed, the diet of the viperine snake, *Natrix maura*, has been described in several previous studies (e.g. Duguy & Saint Girons, 1966; Valverde, 1967; Alberch & González, 1973; Hopkins, 1974; Vericad & Escarre, 1976; Schätti, 1982; Hailey & Davies, 1986; Galan, 1988; Jaén, 1988; Pleguezuelos & Moreno, 1989).

Wetlands in the Ebro Delta Natural Park are highly productive areas with a high diversity and biomass of vertebrate fauna (Martínez-Vilalta, 1989). The natural vegetation has partially been supplanted by rice fields, which constitute temporary aquatic and highly dynamic ecosystems as a result of rapid changes in water levels (Fasola & Ruiz, 1996). These unusual environmental characteristics cause seasonal disturbances to the biology of semi-aquatic species, such as the viperine snake, which is the most common snake in the Ebro Delta ecosystem. Here we provide detailed data on the trophic ecology of *N. maura* in this area, highlighting sexual and size-related differences as well as the influence of the seasonal flooding of rice fields on the diet of this species.

MATERIAL AND METHODS

STUDY AREA

The Ebro Delta (40° 42'N, 0° 51'E) is a coastal plain of about 28 000 ha located in the north-east of the Iberian Peninsula. It is one of the most important wetland areas in the Mediterranean basin, and is protected by Spanish law.

More than 40% of the Ebro Delta surface is covered by rice fields, with a dense network of channels. The rest of the surface consists of natural wetlands and other field crops. The rice growing cycle is seasonal: the channels and rice fields are dry from December to April. By April the channels overflow and become colonized by a varied fauna including *Gambusia holbrooki*, *Cyprinus carpio* and *Rana perezi*. The rice grows until September, when it is harvested. After that, the fields and channels are drained again.

SAMPLING AND DATA RECORDING

Rice fields were searched for viperine snakes on at least two consecutive days per month between February 1990 and October 1991, by two observers. Every snake collected was induced to regurgitate following the method of Fitch (1987), and the prey items obtained in this way were preserved in 70% alcohol. No specimens were induced to regurgitate more than once during the study. Additional food samples consisted of the stomach contents of fresh specimens found killed on roads and of specimens sampled for histological studies. All the snakes were measured (snout-vent length, SVL in mm) and weighed. Adults were sexed by observation of gonads in dead specimens, and by tail shape and the number of subcaudal scales in live snakes (Feriche, Pleguezuelos & Cerro, 1993).

Prey items were measured (furcal length in fish and snout-vent length in frogs and tadpoles) and identified to species level, distinguishing between adult and larval forms of amphibians. Dry weight (biomass) of prey was estimated using linear regression of length against dry weight established using individuals collected in the Ebro Delta (González-Solís, Bernardí & Ruiz, 1996).

STATISTICAL PROCEDURES

The diet descriptors used were abundance (%*P*), occurrence (%*N*) and the resource use index (*IU*) (Jover, 1989). *IU* is a good descriptor of the diet because it combines in a single index (standardized as a percentage) the three diet components: (1) abundance, (2) occurrence and (3) homogeneity, which is estimated by calculating the diversity as a measure of variance of the animals consuming a resource.

To establish sexual and size-related differences in the diet, comparisons of (1) number of prey, (2) prey size, and (3) prey biomass were performed by ANCOVA analysis using SVL as a covariate. Sheffé *post hoc* tests were used after obtaining a significant result in the ANCOVA. Normality was assessed in all variables and log transformation was performed on the variables prior to ANCOVA tests. All means are reported ± 1 SE. All tests were two-tailed, and α was set at 5%.

Margalef's diversity index (Brillouin's index for diet) was used according to Pielou (1966, 1975) and Hurtubia (1973). Mean individual diversity (*Hi*), population diversity (*Hp*) (estimated by the jack-knife technique, see Jover, 1989) and total accumulated diversity (*Hz*) were calculated. Population diversities were compared by *t*-tests, instead of using the analysis of variance, because of their non-additivity. Evenness (*E*) was calculated using the Shannon-Weaver Diversity Index (Pielou, 1969; Magurran, 1989).

RESULTS

A total of 343 snakes were examined for food. Prey items were found only in 13.4% of individuals, all belonging to samples collected from March to October: 15 males (SVL= 322.3±13.4 mm), 15 females (SVL= 411.2±27.8 mm), 15 immatures (SVL= 163.7±8.2 mm) and one undetermined adult. The proportion of stomachs containing prey did not vary between sexes (χ^2=0.07, df=1, *P*=0.79). Adults (15.0%) contained food more frequently than immatures (10.9%), though differences were not significant (χ^2=0.92, df=1, *P*=0.34). Males only fed from April to July, while females fed for a longer period, i.e. from March to October. During August both sexes avoided feeding. Immatures showed the same foraging activity period as females.

NUMBER OF PREY PER STOMACH

The mean number of prey per stomach was 2.44±0.74 (mean±SE). Sixty-three percent of the examined snakes had only one prey item in the stomach, but the maximum number of prey found in a single stomach was 33 fish (a male, 392 mm SVL, captured in May 1990).

Male stomachs contained a higher number of prey (4.87±2.12) than females (1.46±0.17). Immatures contained only one prey item per stomach (Table 1). The differences in the number of consumed prey were significant among males, females and immatures (Kruskal-Wallis test: $H_{2,45}$ = 15.36, *P*<0.001). Dunn's *post hoc* test showed significant differences only between males and immatures.

There was no correlation between SVL and the number of prey items when all snakes were pooled (r_s=0.27, *n*=45, *P*=0.07), or when males and females were considered separately (males: r_s=-0.18, *n*=15, *P*=0.52; females: r_s=-0.11, *n*=15, *P*=0.68).

TABLE 1. Mean and standard error of the number of prey per stomach and of the prey size. Ranges are given in parentheses.

	Prey per stomach	Prey size (mm)
Males	4.87±2.12 (1-33)	19.91±0.66 (11-37)
Females	1.46±0.17 (1-3)	36.70±3.34 (18.7-84)
Adults	3.17±1.09 (1-33)	23.18±1.11 (11-84)
Immatures	1±0.00 (1)	26.34±2.36 (15-42)
Total	2.44±0.74 (1-33)	23.51±1.02 (11-84)

The mean number of fish per stomach did not differ from the mean number of frogs per stomach (Mann-Whitney *U*=136.5, *P*=0.15). The mean number of frogs per stomach did not differ between males and females (Mann-Whitney *U*=12.0, *P*=0.3), whilst the mean number of fish per stomach was significantly higher in males than in females (Mann-Whitney *U*=19.5, *P*= 0.04).

PREY TYPE AND SIZE

Only five prey types were detected in the stomachs: two fish (*Cyprinus carpio* and *Gambusia holbrooki*), adults and tadpoles of *Rana perezi*, and earthworms. None of the stomachs contained more than one kind of prey. Table 2 shows the diet descriptors for male, female and immature snakes. Frogs and carp were the prey most frequently eaten by adults. Mosquito fish, tadpoles and earthworms were sporadically preyed upon and consumed mainly by young snakes.

There were sexual differences in the prey type: males fed mainly on carp, with frogs as a secondary prey (*IU*=96.2% and 3.8%, respectively); whereas females fed on both these prey types without significant differences (*IU*=55.2% and 44.8%, respectively).

The total accumulated diversity was 0.43 in males, 0.88 in females and 1.61 in immatures. The population

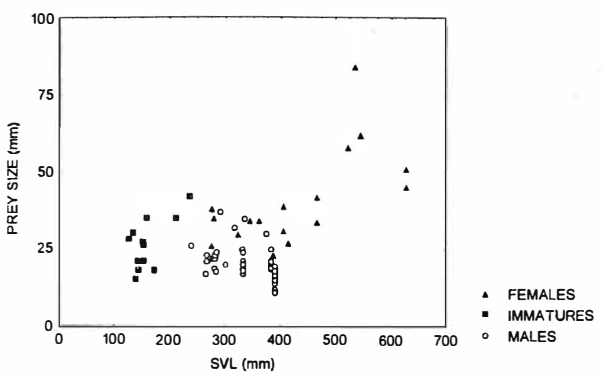

FIG. 1. Relationship between prey size and SVL for male, female and immature *Natrix maura* in the Ebro Delta.

TABLE 2. Diet descriptors. *N*, snake sample size; *n*, number of prey captured, %*P*, occurrence of each prey type; %*N*, abundance of each prey type. *IU*, Resource Use Index (Jover, 1989). *C.c, Cyprinus carpio, Gh. Gambusia holbrooki, Rp, Rana perezi* adults (ad) and larvae (l). Ew, earthworms. *One unsexed adult is included.

	N	*n*	%P					%N					IU				
			Cc	*Gh*	*Rp* ad	*Rp* l	Ew	*Cc*	*Gh*	*Rp* ad	*Rp* l	Ew	*Cc*	*Gh*	*Rp* ad	*Rp* l	Ew
Males	15	73	73.3	-	20.0	6.7	-	91.8	-	4.1	4.1	-	96.2	-	3.8	-	-
Females	15	22	53.3	-	46.7	-	-	54.5	-	45.5	-	-	55.2	-	44.8	-	-
Adults*	31	104	64.5	-	32.3	3.2	-	84.6	-	12.5	2.9	-	84.2	-	15.8	-	-
Immatures	15	15	13.3	40.0	26.7	13.3	6.7	13.3	40.0	26.7	13.3	6.7	7.3	56.4	29.1	7.3	-
Total*	46	119	47.8	13.0	30.4	6.5	2.2	75.6	5.0	14.3	4.2	0.8	73.2	5.0	19.9	1.9	-

diversity and variance calculated by the jack-knife technique was 0.44 (v=1.50) in males, 1.02 (v=0.03) in females and 2.07 (v=0.69) in immatures. The comparisons between groups showed that the population diversity was higher in immatures than in both males (t=4.28, df=28, P=0.0002) and females (t=4.81, df=28, P<0.0001). There were no differences between males and females (t=1.82, df=28, P=0.08). Although the accumulated diversity cannot be compared between groups, the similar tendency of accumulated and population diversity values corroborates evidence that the samples used are representative of the diet spectrum (Jover, 1989). The evenness of diet was E=0.218 in males, E=0.994 in females and E=0.892 in immatures.

The larger snakes selected against smaller prey sizes (Fig. 1), as the minimum prey size increases directly with snake size (r_s=0.33, n=41, P=0.03). However, this correlation was significant only for females (r_s=0.63, n=15, P=0.01), but not for males (r_s=-0.05, n=14, P=0.87) or immatures (r_s=0.38, n=12, P=0.22).

Females fed on larger prey than males and immatures (Table 1; ANCOVA: $F_{2,37}$= 6.04, P=0.005). Moreover, females fed on larger fish than males when only fish-eating snakes were compared (Mann-Whitney U=13.0, P=0.01), but both sexes fed on similarly sized frogs (Mann-Whitney U=7.0, P=1.0).

There was a positive correlation between snake size and biomass eaten (r_s= 0.63, n = 41, P<0.001), especially in the case of females (r_s= 0.75, n = 15, P = 0.001). The contribution of frogs to biomass was higher than the other prey types (ANCOVA: $F_{3,36}$ = 6.56, P< 0.001).

DISCUSSION

The percentage of snakes containing prey in the stomach was higher when rice fields were flooded (19.3% wet and 6.4% dry, χ^2=9.56, df=1, P=0.002), suggesting that feeding frequency increased with prey availability. These results suggest that the seasonal flooding of this ecosystem (and the resulting dramatic shifts in water availability) can be an important factor regulating the trophic ecology of *Natrix maura* in the Ebro Delta.

In August, the feeding frequency was very low (4.3%). A reduction in feeding activity during the warmest month of the year has already been reported for *Vipera aspis* in Mediterranean central Italy (Luiselli & Agrimi, 1991). In both cases high temperatures during summer could be the determining factor.

Based on the proportions of specimens containing food in the stomachs, immature viperine snakes fed less frequently than adults, as in conspecific populations (Hailey & Davies, 1987; Pleguezuelos & Moreno, 1989) and in other species (e.g. Shine, 1987; Luiselli & Agrimi, 1991; Agrimi & Luiselli, 1994; Luiselli, 1996).

Males foraged from April to July, while females showed a longer feeding period, starting their foraging activity in March and finishing it in October. A similar delay in the commencement of feeding activity in males has been reported for other conspecific populations (Duguy & Saint-Girons, 1966; Pleguezuelos & Moreno, 1989), as well as for other snakes, such as *Nerodia sipedon* (Feaver, 1977; King, 1986) and *Morelia s. spilota* (Slip & Shine, 1988). This suggests that sexual activity reduces male feeding activity, as reported in vipers (i.e. Luiselli & Agrimi, 1991).

Gravid females were found in the field from June to August and, except for August, they fed even more frequently than in the other months. Females with very enlarged follicles contained prey in the stomach, while females with oviductal eggs did not. This contrasts with other studies where a reduction in food intake during gestation has been observed (Keenlyne, 1972; Keenlyne & Beer, 1974; Shine, 1979, 1980, 1986, 1987). A reduction in locomotive ability of gravid females could increase the risk of predation and could decrease foraging success in some snake populations (Shine, 1980; Seigel, Huggins & Ford, 1987). However, we hypothesize that the coincidence between gestation and flooding, when prey biomass abundance in the field is very high (González-Solís *et al.*, 1996), might induce females to maintain their feeding activity, even if it could involve a reduction in activity and an increase in predation risk.

The fact that males consumed more fish relative to females or immatures is similar to the pattern observed in *Acrochordus arafurae* (Houston & Shine, 1993). Indeed, only the males and the small females frequently contained more than one prey item in the stomachs. The low number of fish found in the stomachs of the largest females suggests that they spent less time foraging.

If only May-July is considered, sexual differences in the diet decreased (*IU*: 98.4% carp and 1.6% frogs for males; 77.4% carp and 22.6% frogs for females), and in both cases the diet consisted mainly of fish. The increase in frogs in the diet of females occurred in spring (March-April) when rice fields were dry, and autumn (September-October), after rice harvesting. In spring, drought led to a lack of fish, while in autumn, the fish population declined (although drought was not so marked as in spring), probably due to the influence of harvesting on the availability of this prey (González-Solís *et al.*, 1996).

Despite an increase in frogs in the diet of the largest snakes, a size-related change in the type of fish consumed was observed with increases in snake size (from *Gambusia* to *Cyprinus*). Furthermore, immatures eat more earthworms and tadpoles than adults, as previously reported in other studies (Schätti, 1982; Hailey & Davies, 1986; Pleguezuelos & Moreno, 1989). Size-related changes in diet composition have also been observed in other water snakes: e.g. *Natrix natrix* (Luiselli, Capula & Shine, 1997), *Nerodia rhombifera*, *N. cyclopion*, *N. fasciata* and *N. erythrogaster* (Mushinsky, Hebrard & Vodopich, 1982), and *N. rhombifera* studied in a fish hatchery in Arkansas (Plummer & Goy, 1984).

The evenness values of the diet showed that males fed on a dominant prey type (carp) whereas female diet consists of two different and equally abundant prey (carp and green frogs). Immatures fed on a wider range of prey (five taxa) than adults, and none of them were dominant as shown by the evenness value.

A size-related shift in the lower size limit of prey was observed when all the individuals were considered. However, only snakes larger than 400 mm SVL (all females) tended to select against smaller prey sizes. This pattern, characteristic of fish-eating snakes (see Plummer & Goy, 1984; Jayne, Voris & Heang, 1988), corresponds to the concept of "ontogenetic shift in lower size limit" and has been qualified as "enigmatic" by Arnold (1993). In the range of prey sizes consumed, only the smaller females overlap with males and immatures. This apparent resource partitioning might be relevant for reducing intraspecific competition.

Only females showed a positive correlation between biomass ingested and SVL. In many snake species, including *N. maura* (Santos & Llorente, unpublished data), large females have a higher clutch mass (Seigel & Ford, 1987). If females need more food for reproductive output (Houston & Shine, 1993; Shine, 1989), sexual dietary differences in food consumption can be explained in terms of the additional food needed for reproduction, as has been previously shown in *Natrix natrix* (Luiselli *et al.*, 1997) and *Coronella austriaca* (Luiselli, Capula & Shine, 1996).

ACKNOWLEDGMENTS

We thank M. Pascual for helping with the field work; X. Ruiz and M. A. Carretero for valuable comments on early versions of the manuscript; and the authorities of the Ebro Delta Natural Park for logistic help. The research was conducted under the hunting permits [Nos. 6539 (26.10.1990) and No. 537 (29.01.1991)] of the "Direcció General del Medi Natural". Dr. L. Luiselli and an anonymous reviewer made useful comments on the manuscript.

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Accepted: 17.2.98

BOOK REVIEWS

Monitor Lizards: Natural History, Biology and Husbandry. Daniel Bennett (1998). Edited by T. Wilms and B. Bartholomew. 352 pp. Edition Chimaira: Frankfurt-am-Main (paper).

Several years ago Daniel Bennett produced *A Little Book of Monitor Lizards*, a hefty piece of work containing around 200 pages and assorted illustrations. This tome, published in Aberdeen and marketed by Mr. Bennett himself, proved very successful. So successful, in fact, that a German edition, with improved illustrations and colour photographs, was developed by the German publisher Edition Chimaira and translator Thomas Wilms. To avoid the exclusion of other audiences, the revised format was then translated back into English to produce *Monitor Lizards: Natural History, Biology and Husbandry.*

This book summarises what is known about monitor lizards in their natural habitat, and applies that knowledge towards captive maintenance and propagation. The first eight chapters cover topics such as basic biology, evolution, lifestyle, interactions with man and maintenance and propagation, including behavioural and climatological aspects which should be catered for in captivity.

Although it could be argued that this is yet another "care and breeding in captivity" manual, this is one of the few books I have come across where herpetoculture and herpetofauna ecology are happily married. Following the detailed captive care sections are natural history accounts of 45 species with distribution maps. These accounts detail current distribution and status, species descriptions, behaviour, diet and captive status. This is then followed by climatological data for each region where these species are found, and a fully comprehensive 32 page bibliography. The book concludes with conservation considerations, striking a balance between their ecological requirements and commercial use of monitors in the trade as pets and for skins.

There are over 100 high quality photographs, both black and white and in colour. While many of the photos appear to be of captive specimens, there are also illustrations of behavioural aspects, typical habitat and of monitors in their natural environment.

This book has been written by someone with a deep admiration, appreciation and extensive first-hand field experience of these species. Mr. Bennett also has a great sense of humour, the presence of which was not lost in the translation. Aimed at a non-scientific audience, avoiding the use of jargon, but sufficiently informative to be of use to scientists, the book maintains a balance between science, natural history and anecdote to sustain interest throughout. It also contains some interesting typographical errors (missed by the German editors?), the best one being the *Varanus albigularis* which is 41 mm SVL and weighs 2430 g. That's one startlingly heavy lizard!

The photographs are fantastic, the narrative is compelling, the typos are entertaining, but the book itself is just a little bit flimsy. I was worried as I was reading it that the pages might start falling out, and was loathe to remove it to other locations without suitable protection. Some books are deserving of careful treatment, but this one should, by its nature, be a bit more robust.

A field guide it is not, but rather a catalogue of the monitors useful not only to those interested in keeping these fascinating lizards as pets, but also to scientists. It provides a good basis for comparison of basic ecology between the species and the extent of previous work, and new researchers will find it worth having for the bibliography alone.

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Canterbury Christ Church College

The Clawed Salamanders of Asia. Sergius L. Kuzmin (1995). 108 pp. Die Neue Brehm-Bücheri, Westarp Wissenschaften (paper).

The Hynobiidae is a rather primitive family of salamanders that rarely gets more than a cursory treatment in amphibian biology books. Particularly neglected, at least within the western literature, are an intriguing group that lack lungs, and develop claws on their digits as a secondary sexual character. These comprise just two species belonging to a single genus, *Onychodactylus*, and are known as the clawed salamanders.

The book starts with a fascinating historical account of the use of clawed salamanders in traditional medicines and scientific research. Apparently, smoke-dried specimens are still sought after as aphrodisiacs to the present day! A short section on the distribution and systematics of the genus *Onychodactylus* follows, with particular emphasis on its relationships with the six other genera of Hynobiid salamanders. The bulk of the book consists of a detailed natural history of each of the two species of *Onychodactylus*, the Japanese clawed salamander (*O. japonicus*) and the long-toed clawed salamander (*O. fischeri*). These accounts are comprehensive treatments, encompassing classification, morphology, karyology, distribution, physiology, reproduction, ecology and behaviour. The two species have much in common, and the staging table and accompanying illustrations, which run to some 13 pages, will prove useful to any worker studying the development of these salamanders. As one of the leading players in the study of salamander trophic ecology, Kuzmin is particularly lavish in his treatment of the feeding biology of the two species. A short section near the end of the book deals with keeping and breeding in captivity. Hynobiid salamanders are not the easiest of animals to breed in captivity, but Kuzmin summarises the successes and failures achieved to date.

Before reading this book, I believed that the Hynobiid salamanders were poorly studied. This is not the case. The reference list of this book runs to well over 200 citations, the majority of which are published in Russian, Chinese or Japanese journals. The linguistic barrier has made much of this work inaccessible to many researchers, and Kuzmin has provided a valuable service to western herpetologists by bringing this literature to their attention, and synthesizing it such a concise and readable format. This little book is attractively presented with numerous photographs, maps, figures and a colour plate section. Die Neue Brehm-Bücheri are filling a much-needed niche by publishing high-quality books on specialist herpetological topics. *The Clawed Salamanders of Asia* maintains the high standard, and salamander-philes everwhere should find this a valuable and unique addition to their personal libraries.

Richard Griffiths
University of Kent

ANNOUNCEMENTS

9TH O.G.M. OF SOCIETAS EUROPAEA HERPETOLOGICA

The 9th Ordinary General Meeting of the Societas Europaea Herpetologica will be held at the Université de Savoie in France from 25-29 August 1998. The main topics covered by the meeting will be systematic biogeography, ecology, conservation management, ethology, physiology, toxicology, evolution and genetics. Further information from: Département de Biologie, Université de Savoie, C.I.S.M., Campus Scientifique, F-73378 Le Bourget du Lac, France. Fax: +33 (0) 4 79 75 8880; http://www.biop7.jussieu.fr/SHF/.

NEW (XVIII) INTERNATIONAL CONGRESS OF ZOOLOGY

The date of the New Congress has been set for 4-9 September 2000 in the Faculty of Philosophy, University of Athens, Greece, under the auspices of the Hellenic Zoological Society. Further information from: Dr Rosa Polymeni, University of Athens, Dept. of Biology, Section of Zoology and Marine Biology, 15784 Athens, Greece. Tel: 30 1 7264364; Fax: 30 1 7284604; email: rpolymeni@biology.db.uoa.gr. First circular is also available at http://www.york.biosis.org/zrdocs/new_icz.

EDITOR'S NOTE

The Editor is grateful to the following for reviewing manuscripts submitted to the *Herpetological Journal:*

K. Adler, R. Altig, B. Arano, P. Arntzen, R. Avery, E. Baard, R. Ballinger, D. Bauwens, A. Bauer, T. Beebee, D. Bennett, K. Berven, W. Branch, G. Brown, M. Bruford, T. Burton, J. Castanet, A. Castilla, A. Channing, B. Clarke, P. Daszak, J. Davenport, C. Diaz-Paniagua, J. Dixon, C. K. Dodd, M. Dyson, D. Frost, D. Galbraith, A. Gardner, M. Geach, T. Gent, R. Gibson, L. Gillett, L. Guillette, A. Hailey, T. Halliday, P. Harris, C. Herman, J. Holman, W. Holt, M. Hoogmoed, J. Jackson, J. Jeffers, U. Joger, J. Just, M. Kalezic, R. King, J. Kuhn, M. Klemens, J. Loman, C. Lowe, L. Luiselli, C. McCarthy, J.-C. Monney, C. Miaud, A. Milner, P. Narins, D. Nicholls, G. Nilson, R. Oldham, M. Olsson, M. O'Shea, V. Perez-Mellado, G. Packard, J. Petranka, R. Platenberg, J. Pleguezuelos, J. Poynton, J. Phillips, C. Raxworthy, C. Reading, C. Richards, J. Schall, A. Schiotz, G. Shea, U. Sinsch, F. Slater, G. Smith, M. Sparreboom, J. Stewart, D. Stiffler, H. Strijbosch, Z. Szyndlar, M. Tejedo, F. Tiedemann, R. Tinsley, D. Toews, C. Tracy, L. Trueb, G. Underwood, N. Scott, M. Van Sluys, J. Van Wyk, P. Verrell, M. Veith, M. Vences, M. Walkey, V. Wallach, E. Werner, M. Wilkinson, W. Wüster.

ERRATUM

In *Herpetological Journal* 7(4), p. 156, line 3 of Table 2 should be amended as follows: the Mean±SD for 'Scales around midbody' for *V. v. ornatus* should read 162±8.7 instead of 90±4.5.

THE HERPETOLOGICAL JOURNAL

INSTRUCTIONS TO AUTHORS

(revised January 1998)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: *Full Papers* (no length limit); *Reviews* and *Mini-reviews* (generally solicited by a member of the editorial board); *Short Notes*; controversies, under *Forum* (details available from the Editor); and *Book Reviews*. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance. Authors should bear in mind that the *Herpetological Journal* is read by a wide range of herpetologists from different scientific disciplines. The work should therefore appeal to a general herpetological audience and have a solid grounding in natural history.

2. *Three* copies of all submissions, and illustrations, should be sent to the Editor. All papers will be subject to peer review by at least two referees. Authors are invited to suggest the names of up to three referees, although the editor may choose alternative referees to those suggested. Papers will be judged on the basis of the reports supplied by referees, scientific rigour, and the degree of general interest in the subject matter. The Editor's decision will be final.

3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer (at least near-letter quality, avoid worn ribbons), and double-spaced with wide margins all round. The journal is typeset direct from the author's computer diskette, so all manuscripts should be prepared using a wordprocessor (preferably on a PC-compatible microcomputer). It is not necessary to submit a computer diskette with the initial manuscript, but this will be required in the event of the manuscript being accepted for publication.

4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of 5 words or less, and no more than 5 keywords for abstracting purposes. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted. *Short Notes* (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text.

5. The usual rules of zoological nomenclature apply.

6. Tables are numbered in arabic numerals, e.g. TABLE 1; they should be typed double spaced on separate sheets with a title/short explanatory paragraph above the table. Horizontal and vertical lines should be avoided.

7. Line drawings and photographs are numbered in sequence in arabic numerals, e.g. FIG. 1. Colour photographs can only be included at cost to the author. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied camera-ready for uniform reduction of one-half on A4 size paper. Line drawings should be drawn and fully labelled in Indian ink, dry-print lettering or laser printed. Illustrations produced using other types of computer printer are not usually of suitable quality. A metric scale must be inserted in micrographs etc. Legends for illustrations should be typed on a separate sheet.

8. References in the text should be given as in the following examples: "Smith (1964) stated —"; "—as observed by Smith & Jones (1963)." "—as previously observed (Smith, 1963; Jones, 1964; Smith & Jones, 1965)". For three or more authors, the complete reference should be given at the first mention, e.g. (Smith, Jones & Brown, 1972), and *et al.* used thereafter (Smith *et al.*, 1972). For the list of references the full title or standard abbreviations of the journal should be given. The following examples will serve to illustrate the style and presentation used by the Journal.

   Bellairs, A. d'A. (1957). *Reptiles.* London: Hutchinson.

   Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* **2**, 206–210.

   Dunson, W. A. (1969*a*). Reptilian salt glands. In *Exocrine glands*, 83–101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.

   Dunson, W. A. (1969*b*). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* **216**, 995–1002.

9. Final acceptance of a paper will depend upon the production by the author of a typescript, illustrations and computer diskette ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.

10. Proofs should be returned to the Editor by return of post. Alterations should be kept to the correction of errors; more extensive alterations will be charged to the author.

11. Twenty-five offprints and one complimentary copy of the Journal are provided free of charge. Further copies (minimum of twenty-five) may be purchased provided that they are ordered at the time the proofs are returned.

12. All submissions are liable to assessment by the editorial board for ethical considerations, and publication may be refused on the recommendation of this committee. Contributors may therefore need to justify killing or the use of other animal procedures, if these have been involved in the execution of the work. Likewise, work that has involved the collection of endangered species or disturbance to their habitat(s) will require full justification.

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Herpetological Journal vol. 8, no. 2 was published on 10 May 1998