

## African snake faunas

by

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### Introduction

A fauna is the totality of different animal species found in one place, be that anything in scale between a field and a continent. It is possible to speak of the African fauna — but meaningful only if one is making comparison with other continents. I am here concerned only with snakes and with associations of species which may constitute different and distinctive faunas in different parts of Africa. It has long been recognised that species found in tropical rain forest — hereafter referred to simply as forest, are almost totally different from those found in savanna, each biome has a distinctive fauna. Likewise one might expect other distinctive biomes — deserts, montane grassland, marshes, etc., to support equally distinctive faunas. In the case of African birds — whose systematics is better known than any other group, such faunas have been documented by Moreau (1966). The mammals, less well known systematically, have fared less well in their treatment (Bigalke 1968). But enough is known to show important differences between birds and mammals: for example, one cannot distinguish a montane forest fauna among mammals but forest birds are almost as sharply segregated between montane and lowland forest as between forest and savanna.

In the course of taxonomic work on African snakes, mostly yet unpublished, I have often encountered patterns of geographic distribution reminiscent of those found among birds (Hall & Moreau 1970, Snow 1978), mammals (Grubb 1978, Kingdon 1971, 1974, 1974 a), butterflies (Carcasson 1964), and even plants (Lebrun 1947). A study of distribution patterns has led in the past to zoogeographic classifications (eg. Chapin 1932 and Moreau 1966 for birds; Schmidt 1923 for reptiles) or, more recently, to studies of speciation (eg. Hall 1963, Grubb 1978). Since Schmidt's (1923) admirable work, there have been few attempts to establish the composition and extent of herpetological faunas. Laurent (1954) has analysed herp faunas in eastern Zaire; Schmidt & Inger (1959) the amphibians of Upemba National Park, Zaire; Poynton (1964) the amphibians of southern Africa; Schiøtz (1976) the East African treefrogs (Rhacophoridae). Balletto (1968) considered the reptiles of Africa, focussing his study on Somalia, but his source maps are extremely misleading eg. his fig.

4 where *Telescopus* is omitted from West Africa and fig. 12 where *Causus resimus* is shown extending down the east African coast to South Africa but not shown in the Sudan from where the type specimen originated! His analysis is, therefore, of little value. The few who have concerned themselves with snakes commonly identify zoogeographic "elements" eg. Dekeyser & Villiers, 1954, Papenfuss 1969; only Loveridge (1937), Uthmoeller (1937, 1941, 1941 a, 1942), Parker (1949) and Laurent (1954) dealing with actual faunas.

My own interest originates in a listing of Ghanaian snakes (Hughes & Barry 1968) and subsequent work to extend this to West Africa. As my own experience is West African it is possible that wide ranging species may differ in habits and habitats between West and East Africa and render generalisations based on West Africa invalid. In fact, experience has shown that where inconsistencies occur they are much more likely due to inadequacies of the taxonomy. Examples will be given in the following sections where it is proposed to deal with forest, savanna, and montane faunas. There is not space to deal on this occasion with the peculiar faunas of the Cape at the southern tip of Africa or the Maghreb on the Mediterranean coast, nor to compare the desert faunas of the Sahara — largely Palaearctic, Somalia and Namibia.

### Forest snakes

As indicated earlier, we are here using 'forest' as shorthand for "rain forest", in particular lowland rain forest, for the fauna of montane forest (above approx. 1500 m) will be considered separately.

The African forest fauna has always attracted interest because of its richness in number of species. Hamilton (1976) has most recently reviewed the distribution patterns of forest animals and plants but his paper has not been available to me and I have had to depend on a more recent paper on West African forest mammals (Robbins 1978) and older work, particularly by Moreau (1962, 1963, 1969).

The lowland rain forest extends from Sierra Leone (c. 13° W, Menzies 1966) to the Volta River, Ghana (0°), forming the Upper Guinea Forest Block and from the extreme east of Benin (2.30° E), across Cameroon and Zaire to the Uganda border (30° E), forming the Lower Guinea Forest Block (Fig. 1). It is useful to subdivide the Lower Guinea Block, as Carcasson (1964) has done (into Cameroons, Central, Congolese and Ugandan "zones") but we shall not consider snake distribution in such detail. Conspicuous outliers occur to the west along the Gambia (Håkansson 1981) and Casamance Rivers (Condamin & Villiers 1962) and to the east in Uganda and Kenya (eg. Kakamega Forest) and in Angola to the south (see Keay's 1959 map). Everywhere the forest extends along rivers as gallery forest (but see Swaine, Hall & Lock 1976 on the situation in Ghana) and this is obvious, even on a small scale map, in southern

Zaire. Many of the forest outliers are connected by a forest-savanna mosaic (Keay's 1959 designation) and this is so of the East African coastal forest outliers which occur from Kenya to South Africa and are otherwise quite separate from the main forest to the west.

Appendix A lists the species of snakes recorded from African Forest in selected countries. The snakes of the countries chosen are relatively well known

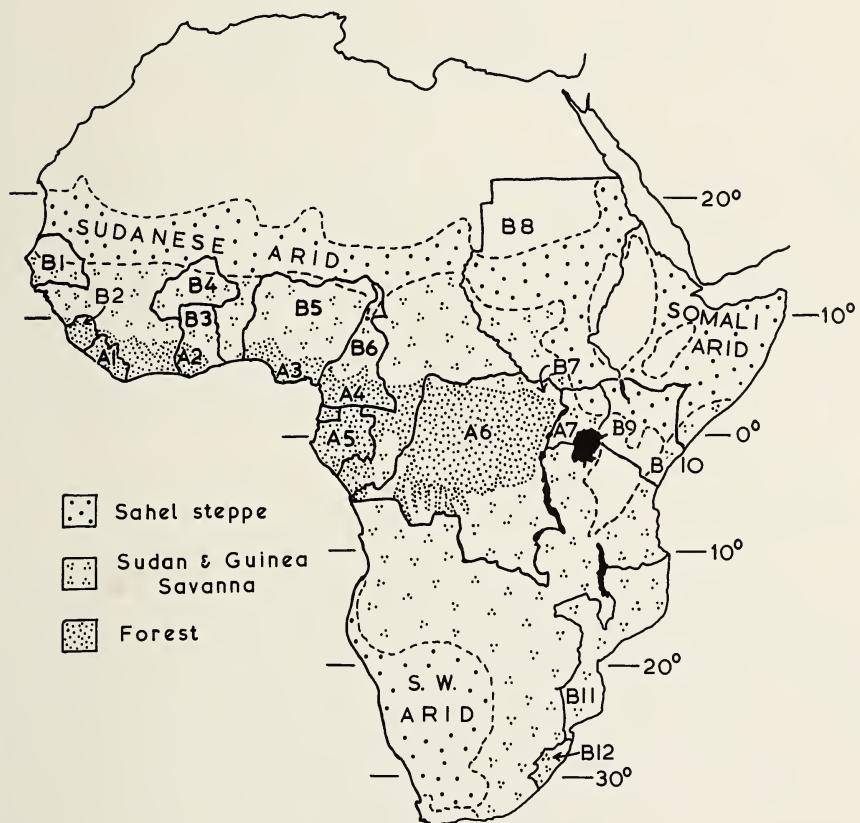


Fig. 1. African biotopes with location of territories from which derive snakes listed in appendix A (sites 1–7) and appendix B (sites 1–12). A1 Liberian forest, A2 Ghanaian forest, A3 Nigerian forest, A4 Cameroonian forest, A5 Gabon forest, A6 Zaire forest, A7 Ugandan forest outliers, A8 Kakamega Forest in Kenya (not shown); B1 Senegambian savanna, B2 degraded forest and Guinea savanna of Sierra Leone, B3 Ghanaian savanna, B4 savanna of Upper Volta, B5 savanna of Nigeria, B6 savanna of Cameroon, B7 savanna of Garamba National Park and environs, Zaire, B8 savanna of Sudan, B9 savanna and steppe of inland Kenya, B10 coastal lowland savanna of Kenya, B11 savanna of southern Mozambique, B12 savanna of Natal, South Africa. (From Davis 1962).

but the list suffers from under collection of rareties (eg. *Atractaspis r. reticulata* has been recently found in Ghana but is otherwise known only from the type from Cameroon) and taxonomic inadequacies (eg. *Dasypeltis atra*, validated subsequent to Gans' (1959) revision; *Atheris* spp.). Altogether there are 105 species but not more than 77 in any one country (Zaire). The widely different totals for each country reflect two different phenomena: one is the representation of more than one fauna, in Zaire due to the vast extent of the country, in Cameroon due to a 'suture zone' between east and west faunas; and secondly depauperisation of the fauna as one nears the extreme east (Uganda and Kenya) or west (Liberia). The similar total of species from Ghana (56), Nigeria (56) and Gabon (57) suggests that these faunas are almost completely known.

Fifteen species range from Liberia to Kenya but of these are six species known to occur also in savanna. All the Kenyan records are from the west of the country, from Kakamega Forest and environs, except for *Philothamnus nitidus* of which I have myself seen specimens from Lamu (Nairobi 64) and Yala River (Nairobi 65–69). *P. nitidus* is close to *P. punctatus*, a species restricted to the coastal plain, from Kenya to Mozambique, and previously confused with *P. semivariegatus* and the situation is reminiscent of Broadley's (1979) finding that in the same area *Thelotornis capensis mossambicanus*, a savanna species, shows affinities with *T. kirtlandii*, a West African forest species known no further east than in Uganda.

The number of species shared between territories decreases with increase of the distance between them (Table 1) but with certain exceptions. In every case Zaire has more species in common with West African territories than does Gabon. This is probably a result of Zaire being much larger and better collected than Gabon. The drastic reduction in common species when Uganda is reached, and even more so in Kenya, reflects the depauperisation of the fauna: all the forest species known from these countries are known also from Zaire except for *Atheris desaixi*, the only endemic. One might expect a sharp decrease in common species between Ghana and Nigeria or between Nigeria and Cameroon, reflecting the affect of the Dahomey Gap and transition from West Africa to Central Africa but this is not apparent. Robbins (1978) concluded that for forest mammals the Dahomey Gap was of little significance as a zoogeographic barrier compared to the Volta and, particularly, Niger River. Comparable statistics are difficult to extract as Robbins gives percentiles of the total fauna (57 species) under consideration but it would seem that about 82 % of those found in Ghana are to be found in Nigeria. The comparable snake figure is 91 %. The presence of 40 species of the Ghanaian fauna of 56 (ie. 71 %) in the Zaire fauna may be compared with the 157 of a total of 182 species of birds from Upper Guinea that Moreau (1966) found in the 212 species of N. E. Zaire (ie. 86 %). Zaire and Cameroons have the largest faunas and the greatest number of species in common (58) but this works out as no

more than 79 % of the Cameroon's total fauna, no doubt due to the presence of endemics and western species which swell the Cameroons total but are not found in Zaire.

Table 1

	1. Liberia	2. Ghana	3. Nigeria	4. Cameroon	5. Gabon	6. Zaire	7. Uganda	8. Kenya	
1. Liberia	44	93	91	82	70	75	57	57	Species in common as % smaller total compared
2. Ghana	41	56	91	82	70	71	52	70	
3. Nigeria	40	51	56	89	73	77	71	70	
4. Cameroon	36	46	50	73	98	79	81	78	
5. Gabon	31	39	41	56	57	93	78	74	
6. Zaire	33	40	43	58	53	77	100	100	
7. Uganda	25	29	30	34	33	42	42	100	
8. Kenya	13	16	16	18	18	23	23	23	
	Species in common								Total species

There are few forest endemics: *Typhlops manni* and *T. leucostictus* in Liberia, *T. caecus* in Ghana, *Mehelya egbensis* in Nigeria, *Poicilopholis camerunensis*, *Polemon gracilis*, and *Typhlops zenkeri* in Cameroon, and *Boulengerina christyi*, *Helophis schoutedeni*, *Lycodonomorphus subtaeniatus*, and *Polemon robustus* in Zaire, none in Uganda but montane forest species in Kenya (*Atheris desaixi*) and Tanzania (detailed later). *P. gracilis* was until recently assigned to an endemic, monotypic genus, *Elapocalamus*. *Poicilopholis* and *Helophis* remain monotypic and endemic genera. Most of these snakes are either water snakes or burrowers and it is not surprising, therefore, that the genus *Typhlops* is well represented.

Comment should be made on the only two published lists of forest snakes: one by Loveridge (1937) for East Africa, the other by Laurent (1954) limited to "la région des grands lacs" of Zaire, Rwanda and Burundi. Both authors recognise six (Loveridge) or seven (Laurent) snake faunas and although their categories differ Loveridge's "Rain Forest, usually Montane" clearly corresponds in composition to Laurent's "Forêt équatoriale", "Forêt de transition" and "Forêt de montagne". Loveridge lists 44 species (and another sub-

species) of which two (*Atractaspis bipostocularis* and *A. conradsi*) are synonyms (of *A. irregularis*) and 12 species are largely restricted to isolated mountains in Tanzania (Uluguru, Ukingu, Usambara, and Uzungwe — Barbour & Loveridge 1928, Broadley 1968).

These 12 are, with taxonomy updated:

<i>Adenorhinus barbouri</i>	— Ukingu and Uzungwe.
<i>Aparallactus werneri</i>	— Uluguru and Usambara.
<i>Atheris ceratophorus</i>	— Usambara.
<i>Atractaspis aterrima</i>	— Uluguru (the only specimen from Kenya or Tanzania).
<i>Crotaphopeltis tornieri</i>	— Uluguru and Usambara.
<i>Dipsadoboia werneri</i>	— Usambara.
<i>Elapsoidea nigra</i>	— Uluguru, Usambara and environs.
<i>Geodipsas procterae</i>	— Uluguru.
<i>Geodipsas vaueroceguae</i>	— Uluguru and Usambara.
<i>Philothamnus macrops</i>	— Usambara and environs.
<i>Typhlops gierrae</i>	— Usambara.
<i>Typhlops uluguruensis</i>	— Uluguru.

There remains from Loveridge's list a residue of 29 species which are restricted to forest and occur at low altitudes whether or not they also occur in montane forest. These are listed here under updated names (mostly available in Loveridge 1957), arranged alphabetically, and those which also occur in the Upper Guinea Forest Block are asterisked:

<i>Aparallactus guentheri</i>	* <i>Bothrophthalmus lineatus</i>
* <i>Aparallactus modestus</i>	* <i>Causus lichtensteini</i>
<i>Atheris nitschei</i>	* <i>Dendroaspis jamesoni</i>
* <i>Atheris squamigera</i>	* <i>Gastropyxis smaragdina</i>
* <i>Atractaspis irregularis</i>	* <i>Hapsidophrys lineatus</i>
* <i>Bitis gabonica</i>	* <i>Hormonotus modestus</i>
* <i>Bitis nasicornis</i>	<i>Lycophidion capense</i>
* <i>Boaedon olivaceus</i>	<i>Mehelya capensis</i>
* <i>Boiga blandingi</i>	* <i>Mehelya poenis</i>
* <i>Naja melanoleuca</i>	<i>Rhinotyphlops graueri</i>
* <i>Natriciteres variegata</i>	* <i>Thrasops aethiopissa</i>
* <i>Philothamnus carinatus</i>	<i>Thrasops jacksoni</i>
<i>Polemon christyi</i>	* <i>Typhlops angolensis</i>
<i>Polemon gabonensis</i>	* <i>Typhlops punctatus</i>
<i>Rhinotyphlops gracilis</i>	

Nineteen species (ie. 66 %) are common to the forests of the Upper Guinea Block and nineteen (66 %) are common to Laurent's list. The latter, totalling 38 species, includes *Grayia smythii*, *Philothamnus angolensis*, and *Thelotornis kirtlandii* which Loveridge excluded from his list on grounds of their not

being exclusively forest, but if these are excluded there are still 22 species which also occur in the Upper Guinea Forest Block, ie. 61 % of the 36 strictly forest species. This figure, lower than that for East Africa, results from Laurent's total including 8 species which reach Cameroon or are endemic to it.

### Species common to forest and savanna

The contrast between the faunas of forest and savanna has struck anyone who has concerned himself with the zoogeography of African animals. Thus Schmidt (1919, 1923) divided African reptiles between West African Forest and Savanna Provinces (of the Ethiopian Region), Carcasson (1964) attributed African butterflies to Sylvan or Open Formation Subregions. In the Appendices to this paper are listed 105 forest and 158 savanna snakes but each list is swollen by the addition of 16 species which occur in both habitats. It is possible that more than I have indicated are ubiquitous: Pitman (1974: 170) includes a table in which the habitats of Ugandan backfanged colubrids are classified as:

- a) savanna and woodland,
- b) forest,
- c) marsh or in or near water,
- d) dry to arid,

and he indicates that Boomslangs (*Dispholidus typus*) occur in a) and b) [and d) in case of *D. t. kivuensis*] and that *Amblyodipsas unicolor* occurs in b) alone. Loveridge (1937: 503) lists *D. typus* as one of 14 species (he lists 15 but "*Chlorophis neglectus*" is a synonym of *Philothamnus hoplogaster*), "-- which sometimes occur in rain forest, though not typical of its fauna having invaded it from the adjacent savanna", and he (Loveridge 1957: 281) says of "*Calamelaps u. unicolor*" (in coastal East Africa this is in fact *Amblyodipsas polylepis hildebrandi*, Broadley 1971 a: 654), "in the east they appear to be associated with the surviving montane or gallery forests --", an opinion followed by Broadley (op. cit.) who gives the habitat of this subspecies as, "Savanna, extending into montane evergreen forest in the Usambara Mts". Knoepfle (1966: 15) also cites *D. typus* from forest, this time in Gabon, but from the data he gives his specimen would appear to be a misidentified *Thrasops flavigularis*. *Dispholidus typus* and *Amblyodipsas polylepis* are common savanna snakes alleged to penetrate forest; this contradicts my West African experience and I have listed them as savanna snakes in Appendix B. On the other hand, I have listed two savanna snakes — *Leptotyphlops bicolor* and *Psammophis phillipsi*, as ubiquitous for in West Africa they occur in forest clearings and so penetrate the forest zone if not the actual forest biome.

The ubiquitous snakes so far considered have been savanna 'penetrants' of forest; there are as many examples of forest snakes occurring in savanna and

these constitute the majority of the species I have asterisked in the Appendices to indicate their occurrence in both biotopes:

- |                                  |                                      |
|----------------------------------|--------------------------------------|
| 1. <i>Afronatrix anoscopus</i> . | 9. <i>Leptotyphlops bicolor</i> .    |
| 2. <i>Atractaspis aterrima</i> . | 10. <i>Lycophidion irroratum</i> .   |
| 3. <i>A. irregularis</i> .       | 11. <i>L. ornatum</i> .              |
| 4. <i>Bitis gabonica</i> .       | 12. <i>Naja melanoleuca</i> .        |
| 5. <i>Causus maculatus</i> .     | 13. <i>Philothamnus angolensis</i> . |
| 6. <i>Dasypeltis fasciata</i> .  | 14. <i>Psammophis phillipsi</i> .    |
| 7. <i>Grayia ornata</i> .        | 15. <i>Typhlops angolensis</i> .     |
| 8. <i>G. smythii</i> .           | 16. <i>T. punctatus</i> .            |

This list may be subdivided as follows:

- i Savanna snakes of forest clearings (9, 14).
- ii Water snakes (1, 7, 8) associated primarily with water and therefore secondarily more commonly associated with forest.
- iii Forest snakes which occur extensively in savanna (5, 6, 12, 16). Some (eg. 6, 12, 16) have savanna races distinct enough to be recognised as subspecies whereas others (eg. 5) are morphologically, at least, undifferentiated.
- iv Forest snakes which occur sporadically in savanna (3, 4, 10, 13). These show no racial differences and are usually very rare.
- v Forest snakes in montane grassland (11, 15). *T. angolensis* is said by Roux-Estève (1974: 47) to occur in forest and wooded savanna in Angola, Zimbabwe and Cameroons but it has been listed only in Appendix A as it does not occur in savanna in any of the territories we consider here. *Lycophidion ornatum* occurs in lowland and montane forest and also in montane but not lowland savanna. The Nigerian record (from Obudu Plateau, Eastern Nigeria, now BM 1966.350) is the first from West Africa, Loveridge's (1957: 252) "Gold Coast" (= Ghana) specimen (MCZ 49606) having been referred to *L. irroratum* by Laurent (1968: 470).

### Savanna snakes

Loveridge (1937), Parker (1949) and Laurent (1954) have analysed the snake faunas of East Africa (Uganda, Kenya and Tanzania), Somalia, and eastern Zaire, Rwanda and Burundi respectively. The lists of forest snakes given by Loveridge and Laurent have been discussed above; Loveridge and Parker provide separate lists of lowland and upland savanna snakes and Parker divides his among six geographic areas: a northern coastal plain (Guban) of very dry steppe with 12 species, six of them of eremian origin; a much more extensive plain bordering the Indian Ocean with a fauna of 49 species, largely also found in the savanna of Kenya (34 species in common), and separating the two plains a range emanating from the Ethiopian highlands with its peculiar fauna (see later) but in the maritime mountains a fauna derived largely from

the neighbouring plains. The arid Guban fauna will be shown to resemble that of the West African Sudano-Sahel, the savanna fauna that of West African Guinea savanna.

Loveridge (1937) lists 51 coastal and 63 upland savanna forms from East Africa. The availability of a thorough checklist of Kenyan snakes (Spawls 1978), added to by Hoevers (1981), makes it expeditious to remove non-Kenyan snakes from Loveridge's list and recast his categories, first into inland and coastal forms, as in Appendix B, for many of his "upland" species do not occur above 1500 m or even less. And secondly to subdivide the inland species into those

- a) restricted to the extreme west, around Lake Victoria;
- b) occupying dry lowland across north and eastern Kenya, sometimes spreading down to the coast;
- c) with wider inland distribution, often (77 % of those listed) occurring in the Kenyan Highlands (above 1500 m).

The species constituting these groups are now listed together with the 21 (of a total of 48) coastal species which are largely restricted to the coastal plain (except for *Causus resimus*, *Natriciteres olivacea* and *Philothamnus heterolepidotus* which reappear in western Kenya). Species which also occur in forest are marked with an asterisk (\*) as is also done in Appendix B. A superscript ° indicates a species which also occurs on the coast.

#### S n a k e s o f i n l a n d K e n y a (61 species listed in Appendix B):

- a) Restricted to extreme west (9 species, numbers 4, 5, and 6 are associated with water, 7 found only at lower altitudes):
  1. *Atractaspis irregularis*\*
  2. *Causus resimus* — part, outlier on coast.
  3. *Crotaphopeltis degeni*.
  4. *Dromophis lineatus*.
  5. *Grayia smythii*\*
  6. *Grayia tholloni*.
  7. *Leptotyphlops emini*.
  8. *Natriciteres olivacea* — part, outlier on coast.
  9. *Philothamnus heterolepidotus* — part, outlier on coast.
- b) Occupying dry lowland (below 1500 m) of north and east (25 species):
  1. *Amblyodipsas unicolor* — known only from Kerio Valley (Broadley 1971a: other records from further east must be *A. polylepis*).
  2. *Aparallactus lunulatus*.
  3. *Atractaspis engdahli* — known only from Wajir Bor (Spawls 1978).
  4. *A. fallax*° — hitherto synonym of *A. microlepidota*.
  5. *Coluber keniensis* — Contra Spawls (1978), I have seen eight more

- specimens from Baringo and Kerio Valley.
6. *Coluber florulentus* (including *smithi*).
  7. *Dendroaspis polylepis* °.
  8. *Echis carinatus*.
  9. *Eryx colubrinus*.
  10. *Hemirhagerrhis nototaenia* °.
  11. *Leptotyphlops fieberi* — known only from Lokwa Kangole, Turkana, (Spawls 1978).
  12. *Micrelaps bicoloratus* °.
  13. *Micrelaps vaillanti*.
  14. *Naja haje* °.
  15. *N. pallida*.
  16. *Philothamnus semivariegatus*.
  17. *Prosymna ruspoli* — new Kenyan record from Broadley (1980).
  18. *Psammophis biseriatus* °.
  19. *P. pulcher*.
  20. *P. punctulatus* °.
  21. *Rhamphiophis rostratus* °.
  22. *R. rubropunctatus* °.
  23. *Rhinotyphlops unitaeniatus* °.
  24. *Telescopus dhara*.
- c) Occupying upland (over 1500 m) and in many cases widely distributed, some (°) reaching the coast; some not occurring above 1500 m:
1. *Aparallactus jacksoni*.
  2. *Bitis arietans* °.
  3. *B. worthingtoni*.
  4. *Causus rhombeatus* °.
  5. *Crotaphopeltis hotamboeia* °.
  6. *Dasypeltis scabra* °.
  7. *Dispholidus typus* °.
  8. *Duberria lutrix*.
  9. *Elapsoidea loveridgei*.
  10. *Hemirhagerrhis kelleri* °.
  11. *Lamprophis fuliginosus* °.
  12. *Leptotyphlops conjunctus* °.
  13. *Lycophidion capense*.
  14. *L. depressirostre* ° — below 1500 m.
  15. *Mehelya capensis* ° — below 1500 m.
  16. *Meizodon semiornatus* °.
  17. *Naja melanoleuca* \* °.
  18. *Naja nigricollis* — rare over 1200 m except Nairobi area.
  19. *Philothamnus battersbyi*.
  20. *Prosymna ambigua* — below 1500 m.

21. *Psammophis phillipsi*.
22. *P. sibilans* °.
23. *Psammophylax variabilis*.
24. *Pseudaspis cana*.
25. *Python sebae* °.
26. *Scaphiophis albomaculatus* — below 1000 m.
27. *Typhlops lineolatus*.

S n a k e s o f t h e c o a s t a l l o w l a n d s — 48 species listed in Appendix B, those found elsewhere marked with superscript ° in those lists, following r e s t r i c t e d to coast except nos. 6, 15 and 16 which also occur in extreme west but not between:

1. *Amblyodipsas teitana*.
2. *Aparallactus guentheri*.
3. *A. turneri*.
4. *Atractaspis bibronii*.
5. *Causus defilippi*.
6. *Causus resimus*.
7. *Dasypeltis medici*.
8. *Dendroaspis angusticeps*.
9. *Dipsadoboa aulicus*.
10. *Leptotyphlops boulengeri*.
11. *L. longicauda*.
12. *Lycophidion capense*.
13. *Mehelya nyassae*.
14. *Meizodon coronatus*.
15. *Natriciteres olivacea*.
16. *Philothamnus heterolepidotus*.
17. *P. hoplogaster*.
18. *P. punctatus*.
19. *Rhinotyphlops pallidus*.
20. *R. schlegeli*.
21. *Thelotornis capensis*.

Section c) could be subdivided according to the range of the component species but my aim is not analysis into faunal 'elements' but establishment of what constitutes a total fauna.

From Appendix B it is possible to record the number of species shared by any two areas (Table 2). The Kenyan coastal fauna has 27 out of 48 (or 56 %) species in common with the inland faunas which is very low for two neighbouring territories, only the pair Coastal Kenya / Southern Mozambique being lower (54 %) and no other less than 72 % (Inland Kenya / Sudan pair). This reflects coastal Kenya being a watershed between faunas of Southern and Northern African savannas.

Two of the three species with a discontinuous distribution in Kenya — found on the coast and near Lake Victoria, are West African species (*Natriciteres olivacea* and *Philothamnus heterolepidotus*). Southern African species are found amongst the coastal fauna — *Atractaspis bibronii* (of which, however, there is a single specimen from Garamba, northern Zaire — see Schmidt 1923, contra Laurent 1945, 1950), *Causus defilippi*, *Dendroaspis angusticeps* (but misapplied to inland *polylepis* by Loveridge 1937: 496), *Dipsadoboa aulicus*, *Philothamnus hoplogaster*, *Telescopus semiannulatus*; and amongst the inland fauna, at higher (1500 m) altitudes — *Duberria lutrix* and *Pseudaspis*

Table 2

	1. Senegambia	2. Sierra Leone	3. Ghana	4. Upper Volta	5. Nigeria	6. Cameroon (inland)	7. Garamba N.P., Zaire	8. Sudan	9. Kenya inland	10. Kenya coast	11. southern Mozambique	12. Natal, S. Africa	Species in common as % smaller total compared
1. Senegambia	43	87	77	81	88	74	49	51	40	26	28	26	
2. Sierra Leone	20	23	96	74	96	83	61	65	52	39	35	35	
3. Ghana	33	22	55	89	87	78	66	50	36	27	22	20	
4. Upper Volta	35	17	41	46	91	74	51	46	35	24	22	17	
5. Nigeria	38	22	48	42	58	83	66	59	41	31	24	24	
6. Cameroon (inland)	32	19	42	34	44	53	83	62	45	33	26	27	
7. Garamba N.P., Zaire	17	14	23	18	23	29	35	67	60	40	37	37	
8. Sudan	22	15	27	21	32	33	26	54	72	46	33	26	
9. Kenya inland	17	12	20	16	24	24	21	36	61	56	34	33	
10. Kenya coast	11	9	13	11	15	16	14	22	27	48	54	42	
11. southern Mozambique	12	8	12	10	13	14	13	18	19	26	55	71	
12. Natal, S. Africa	11	8	10	8	12	14	13	13	17	20	36	51	
													Total species
													Species in common

cana. The importance of the coastal 'tropical corridor' has been recognised as the route south for tropical species entering South Africa (Broadley 1962 a) but it also functions as a northward route into Kenya and Somalia (eg. *Philothamnus punctatus* and *Rhinotyphlops schlegeli*).

Comparing Kenya with territories to the west (Table 2) faunal similarity increases to 72 and 74 % between the pairs Inland Kenya/Sudan and Sudan/Garamba National Park (Northern Savanna of Zaire) and then jumps to 83 % between Garamba/Cameroun and continues high into West Africa, reflecting the range of many species throughout the Sudanese Subprovince (Table 3).

The figures tend to be misleadingly high when the number of species known from one territory is small eg. only 23 from Sierra Leone, leading to a 96 % similarity with Ghana whose fauna (of 54 species) is much better known and therefore more likely to include the commoner species of Sierra Leone. One

Botanic areas		Faunal areas				
Engler 1910 in Schmidt 1923:399	Keay 1959	Latitude north at approx. longitude 2°W (Ghana/Up- per Volta)	Schmidt 1923:7	Noble 1924:152 , 'convenient areas'	Carcasson 1964:134 ,"faunistic division"	Davis 1962 in Bigalke 1968:276 ,"biotic zones",
Desert Region	desert	19	Saharan Subregion	(omitted)	Schmidt & Inger 1959:194 ,"faunal division"	Moreau 1952:889 ,"biotic divisions"
Sudanese savanna Subprovince	subdesert steppe	17½	Sudanese Subprovince	Sudanese open formation	(omitted)	(omitted)
	wooded steppe (Sahel savanna)	14	Sudanese Subprovince	Sudanese semi-arid grassland	Sudanese arid	Sudanese Arid
	dry savanna (Sudan savanna)	10½	Sudanese Subprovince	Senegambian Sudan	N/W Sudan grassland savanna	Northern savanna
	moist savanna (Guinea savanna)	8+	Sudanese Subprovince	Western Lowland Forest		
	forest/ savanna mixture	8-	West African Forest Province	Portuguese Guinea— Nigerian forest	Liberia— Ivory Coast rainforest	lowland forest
	Western Forest Province (forest indicated on map)	forest	coastline			lowland forest

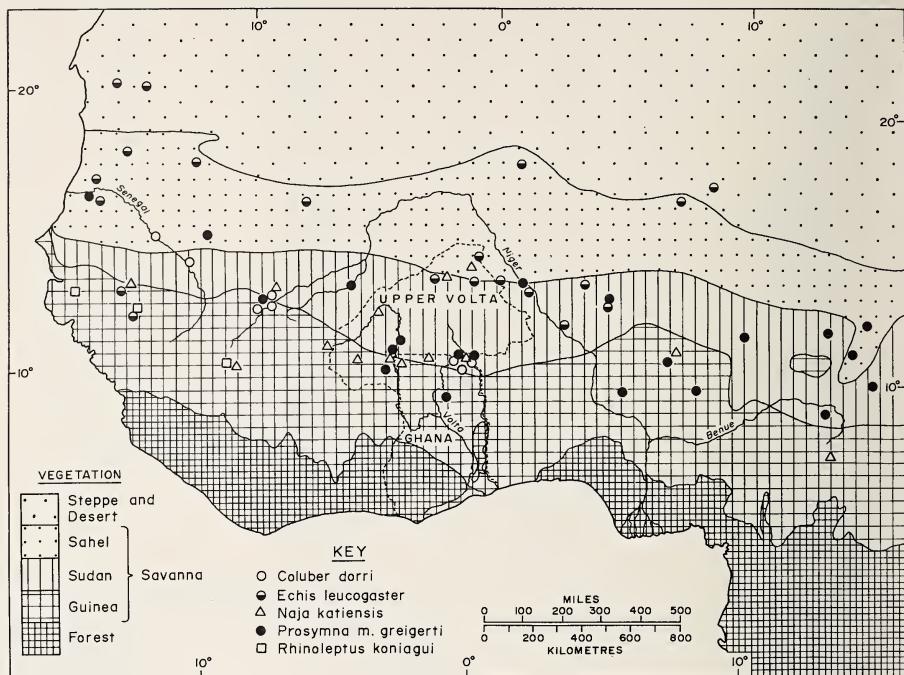


Fig. 2. Distribution of West African savanna snakes: West African endemics.

should also bear in mind the disparity in the areas considered cf. for example territories B 2 and B 8 (Fig. 1). Apart from these sampling complications, reference to Fig. 1 shows territories B 1, B 4, B 6 and B 8 to span both Sudanese Arid and Northern Savanna Zones and perhaps, therefore, to include slightly different faunas. This is the subject of the next section.

#### Sudanese arid and northern savanna faunas

Figure 1 shows the extent of Northern Savanna — between the coastal forest on the one hand and the subdesert steppe of the Sudanese Arid on the other. The extent of these zones and the equivalence of terms used by other authors is shown in Table 3. Some authors (eg. Schmidt 1923, Carcasson 1964) have not differentiated the savanna/steppe of West Africa (Schmidt's "Sudanese Subprovince") but division into Sudanese Arid steppe and subdesert on the one hand and Northern Savanna on the other (eg. Davis 1962) has had wide acceptance. The boundary between these plant-based, ecogeographic zones approximates 14° N in the Ghana/Upper Volta transect (about 2° W) and reference to Figs. 5 and 6 shows the boundary to coincide with the northernmost limit of many Guinea Savanna snakes. But a more important

boundary as regards the distribution of savanna snakes seems to be that between Guinea and Sudan savannas, at about  $11^{\circ}$  N at the Ghana/Upper Volta longitude. Reference to Figs. 3, and 5 (right column) will show that no desert snakes pass south of this boundary and the inland range of many coastal, Guinea Savanna snakes (Fig. 5, left column) terminate about this point. Indeed, considering snakes alone, it would seem that the greatest faunal change in the savanna is the fading out of southern species, commencing coincident roughly with the Guinea/Sudan vegetational boundary, not with the Sudan/Sahel boundary. Villiers (1975: 55) has stated this earlier, but without supporting documentation: "In fact, both the Sahel and Sudan Zones are of mixed character due to the intrusion of external elements: the Sahel Zone by penetration of forms from the Sahara Desert and absence of forms of the Guinea Savanna, the Sudan Zone by the presence of certain Guinea forms and the absence of Saharan forms." (my translation).

The recognition of two savanna faunas has two immediate consequences: one is the realisation that many of the savanna sample areas shown in Fig. 1 not only transgress the traditional boundary between Sudanese Arid and Northern Savanna zones but also the newly recognised Guinea/Sudan savanna faunal boundary. Applied to Ghana and Upper Volta — from where we have most data, this means that the snake fauna of the extreme north of Ghana (north of  $10^{\circ}.30$  N) resembles that of most of Upper Volta whereas that of the southwest corner of Upper Volta is more like that of the greater part of Ghanaian savanna. Those species restricted to southwest Upper Volta in fact range further north than the Guinea/Sudan savanna boundary (at about  $11.00^{\circ}$  N) and may be listed according to northward range:

*Dendroaspis polylepis* (no. 40 in Appendix B and C

and Fig. 5)

$9^{\circ}.54'$  N

<i>Afronatrix anoscopus</i> (no. 1)	$10^{\circ}.50'$ N
<i>Natriciteres olivacea</i> (no. 106)	$11^{\circ}.06'$ N
<i>Grayia smythii</i> (no. 59)	$11^{\circ}.51'$ N
<i>Gonionotophis granti</i> (no. 57)	$12^{\circ}.23'$ N
<i>Dispholidus typus</i> (no. 42)	$12^{\circ}.25'$ N
<i>Meizodon coronatus</i> (no. 95)	$12^{\circ}.25'$ N
<i>Atractaspis dahomeyensis</i> (no. 18)	$12^{\circ}.28'$ N
<i>Naja melanoleuca</i> (no. 102)	$12^{\circ}.28'$ N

The Black Mamba (*Dendroaspis polylepis*) is known from a single specimen so its range is unknown, but *Afronatrix*, *Grayia smythii* and perhaps to some extent *Natriciteres olivacea* are water snakes apparently associated with the Comoe and Black Volta Rivers. The remaining show a remarkable coincidence of northward limiting latitude although without obvious reason. These are all, with the exception of the Black Mamba, southern species of Guinea savanna whereas the species confined within Ghana to its northernmost Upper Region are invaders of or endemic to the drier, more northern Sudan-Sahel

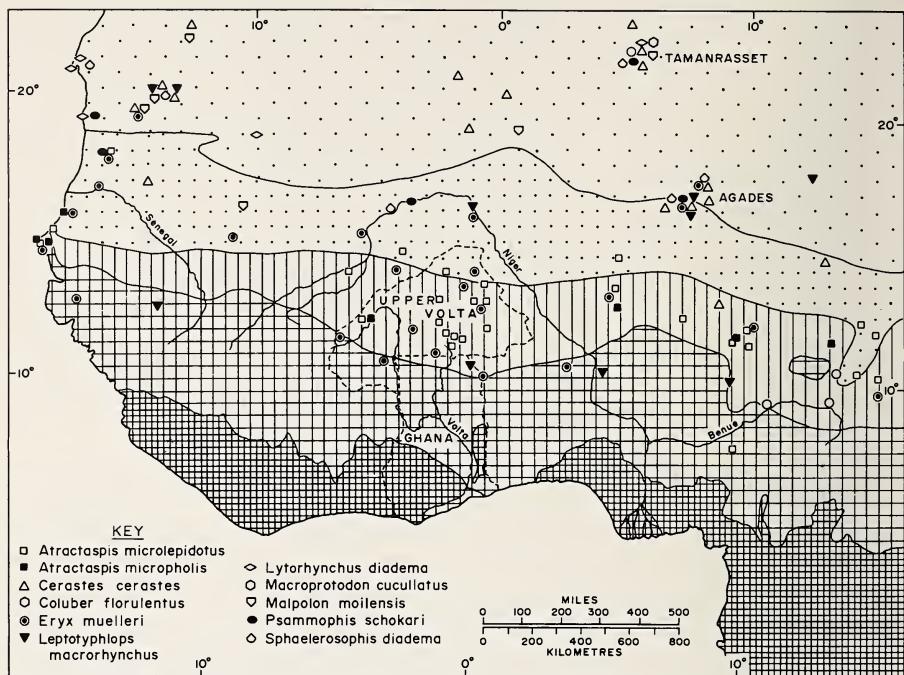


Fig. 3. Distribution of West African savanna snakes: the desert invaders.

savanna as now indicated:

- Aparallactus lunulatus* — East African invader,
- Coluber dorri* — endemic to West Africa,
- Leptotyphlops macrorhynchus* — desert invader,
- Naja haje* — East African invader,
- Naja katiensis* — endemic to West Africa.

The two East African invaders (*Aparallactus lunulatus* and *Naja haje*) occur widely in West African Sudan-Sahel savanna and are representatives of a larger group (Fig. 4) which penetrate West Africa to differing extent. Some (group "a" below) are known only from eastern Nigeria and do not penetrate further into West Africa; others (group "b" below) are known from well inside West Africa but often from few localities and as their identification too has frequently been in doubt it may be as well to document their occurrence:

a) East African non-penetrants of West African savanna.

*Causus resimus* — not known further west than Garoua Boulai (5.53 N 14.33 E), Cameroon but very likely occurring in Sudan-Sahel savanna of northeastern Nigeria (Hughes, 1978) and possibly present among the 633 specimens of „*Causus maculatus*” of which Roman (1973 a) has examined only 112.

*Causus rhombeatus* — definitely known from Dilli in Nigerian Sudan savanna (Johnsen 1962, cited in Hughes 1978).

*Eryx colubrinus* — documented only from Tabello and Agades in subdesert or wooded (Sahel) steppe (Villiers 1950: 338).

*Naja pallida* — two specimens from Irabellaben, Air (Villiers 1950 c) in subdesert steppe, greatly extend the range of this species from Garamba and Faradje in Zaire (Schmidt 1923) towards West Africa and if a specimen from "Deutsch-Kamerun" in the Naturhistorisches Museum, Vienna is correctly attributed this species may reach West Africa.

b) East African penetrants of West African savanna.

*Aparallactus lunulatus* (no. 12 in Fig. 5) is not known west of Bobo-Dioulasso (11.11 N 04.18 W) in Upper Volta (Roman 1969) or south of Binaparba (09.14 N 00.46 E) in Togo (Hulselmans, de Roo & de Vree 1970), ranging from Sudan to Guinea savanna.

*Dendroaspis polylepis* (no. 40 in Fig. 5) — twice recorded from Senegal (Villiers 1954, 1956) in Sudan savanna, once in Upper Volta (Roman 1973 a), surprisingly from Mangodara (9.54 N 4.21 W) in Guinea savanna.

*Elapsoidea semiannulata* (no. 53 in Fig. 5) — widely present in Sudan and northern Guinea savanna (Broadley 1971).

*Grayia tholloni* — unpublished specimens in the British Museum, 1955.1.4.70 from Kotu stream, south of Bathurst, Gambia and 1937.12.4.47 from Makurdi, Nigeria together with another in the University of Zaria collection from Mubi in Nigeria (mapped Fig. 4). I am indebted to Miss Grandison for first drawing my attention to the Gambian specimen.

*Hemirhagerrhis nototaenia* — a single specimen has been mentioned from Togo (Hulselmans, de Vree & van der Straeten 1971) but without further details, even of locality.

*Lycophidion capense* — misidentification of West African specimens as *L. capense* (eg. by Loveridge 1957: 253) has been so prevalent that Laurent (1968: 464) discounts previous identifications. However, *L. capense* does occur in eastern Nigeria (Fig. 4) and Roman's (1973 a) specimen from Upper Volta (without locality) is substantiated by his photograph (Roman 1969). Nigerian records are in Sudan and Guinea savanna.

*Naja haje* (no. 100 on Fig. 5) — widespread and long known (eg. Villiers 1950 c) from West African Sudano-Sahel savanna.

*Philothamnus angolensis* (Fig. 3) is the correct name for what has long been known in East and Southern Africa as *P. i. irregularis*, the latter being restricted to West Africa (Cameroon and west). *P. angolensis* is not to be expected in West Africa but two specimens purport to be from Senegal: one, without further locality, was collected by Dr. Audeoud and is in the Muséum d'Histoire Naturelle, Genève (744.05); the other was collected by R. P. Ber-

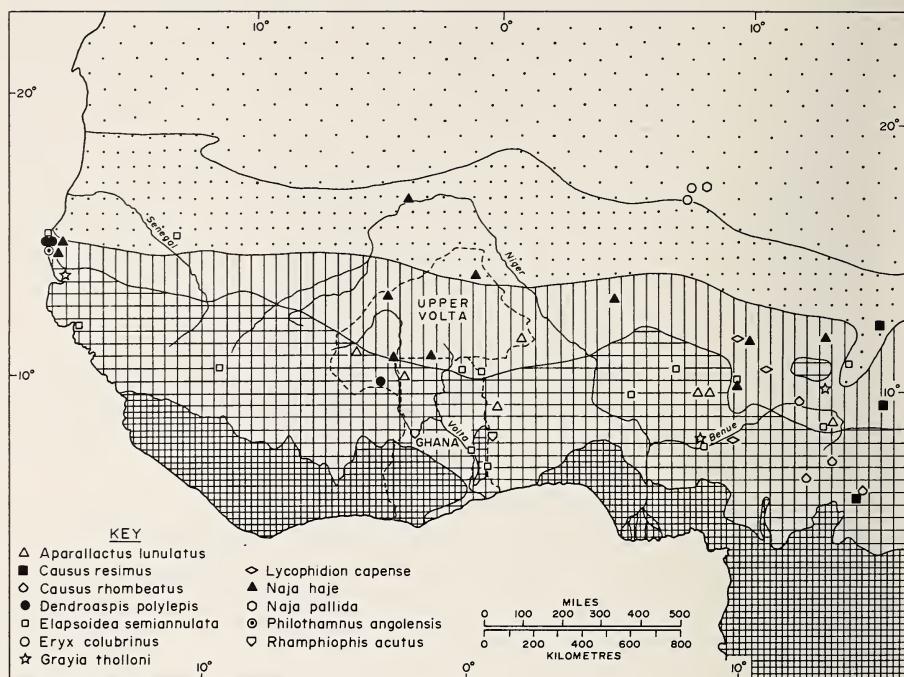
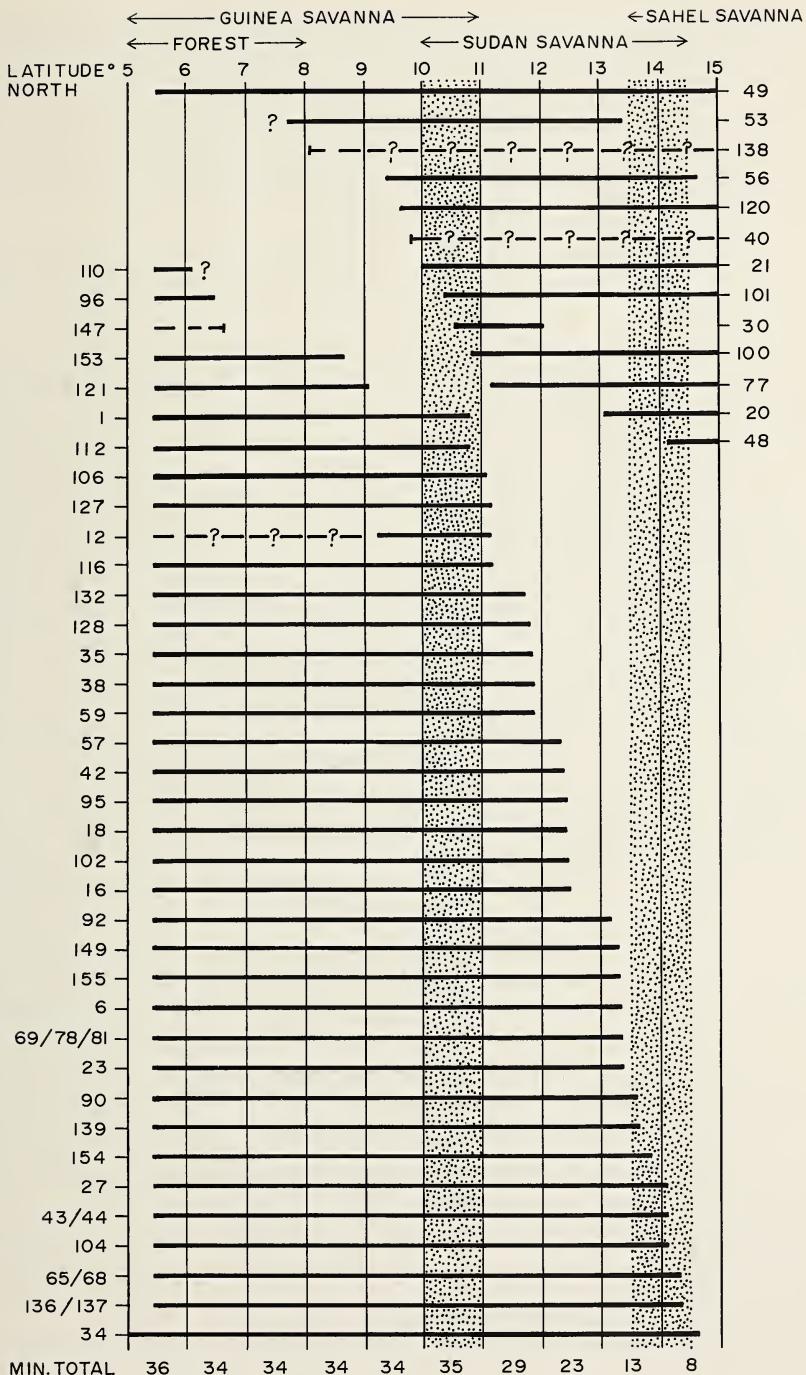


Fig. 4. Distribution of West African savanna snakes: the East African invaders.

Fig. 5. Latitudinal ranges of the savanna snakes of Ghana and Upper Volta: to the left snakes which reach the coast (except no. 12: *Aparallactus lunulatus* and perhaps no. 147: *Scaphiophis albomaculatus*) and are primarily snakes of Guinea savanna, to the right snakes which do not reach the coast (except 49 — *Echis ocellatus*) and are primarily snakes of Sudan and Sahel savanna. The latter include some of the invaders and endemics whose distribution is mapped in Figs. 2 to 4. The numbers are those used in Appendix B. Key to species: 1 *Afronatrix anoscopus*, 6 *Amblyodipsas unicolor*, 12 *Aparallactus lunulatus*, 16 *Atractaspis aterrima*, 18 *Atractaspis dahomeyensis*, 21 *Atractaspis microlepidota*, 22 *Atractaspis micropholis*, 23 *Bitis arietans*, 27 *Causus maculatus*, 30 *Coluber dorri*, 34 *Crotaphopeltis hotamboeia*, 35 *Dasypeltis fasciata*, 38 *Dasypeltis scabra*, 40 *Dendroaspis polylepis*, 42 *Dispholidus typus*, 43 *Dromophis lineatus*, 44 *Dromophis praeornatus*, 48 *Echis leucogaster*, 49 *Echis ocellatus*, 53 *Elapsoidea semiannulata*, 56 *Eryx muelleri*, 57 *Gonionotophis granti*, 59 *Grayia smythii*, 65 *Lamprophis fuliginosus*, 68 *Lamprophis lineatus*, 69 *Leptotyphlops bicolor*, 77 *Leptotyphlops macrorhynchus*, 78 *Leptotyphlops nirostris*, 81 *Leptotyphlops sundevalli*, 90 *Lycophidion semicinctum*, 92 *Mehelya crossi*, 95 *Meizodon coronata*, 96 *Meizodon regularis*, 100 *Naja haje*, 101 *Naja katiensis*, 102 *Naja melanoleuca*, 104 *Naja nigricollis*, 106 *Natriciteres olivacea*, 110 *Philothamnus heterolepidotus*, 112 *Philothamnus irregularis*, 115 *Philothamnus semivariegatus*, 116 *Polemon neuwiedi*, 120 *Prosymna meleagris greigerti*, 121 *Prosymna m. meleagris*, 127 *Psammophis elegans*, 128 *Psammophis phillipsi*, 132 *Psammophis sibilans*, 136 *Python regius*, 137 *Python sebae*, 138 *Rhamphiophis acutus*, 139 *Rhamphiophis oxyrhynchus*, 147 *Scaphiophis albomaculatus*, 149 *Telescopus variegatus*, 153 *Typhlops lineolatus*, 154 *Typhlops punctatus*.



haut at Sebikotané, Senegal, was published by Villiers (1963) as „*Philothamnus irregularis* subsp. *irregularis*“ and is in the Muséum National d'Histoire Naturelle, Paris (1964: 144) where I have seen it. Either occurrence alone would be considered in error, together and in the light of the other records from the environs of Dakar (Fig. 3) it begins to look as though another East African species (unknown in Kenya but common in Uganda) may extend far beyond its known western limit in Cameroon.

*Rhamphiophis acutus* (no. 138 in Fig. 5) — known in West Africa from three Togolese and one Ghanaian specimen (Fig. 4), all from Guinea savanna (Broadley 1971).

It can be seen that East African savanna species penetrate West Africa at various latitudes, in different vegetation zones, and to varying degree. Other species found only in the extreme north of Ghana are either endemic to West Africa or are associated with desertification of the Sahara and range into Asia. The endemics (Fig. 2) are largely confined to the Sudanosahel zone and their restriction to West Africa can be accounted for only in historical terms — a matter to be discussed elsewhere. The desert invaders (Fig. 3) are represented in Ghana by only *Leptotyphlops macrorhynchus* but it should be emphasized that other species may have originated in this way (eg. *Echis ocellatus*) but are excluded from our list because they reach the coast. *Leptotyphlops macrorhynchus* might also be excluded on these grounds for there is a specimen from Achimota, near Accra (Villiers 1950 c) but although I have checked the specimen and can confirm its identification the lack of confirmatory specimens from such a well-collected area (Achimota School) suggests incorrect origin of the specimen. From elsewhere in West Africa desert invaders penetrate southwards to varying degrees (Fig. 3). *Cerastes vipera*, *Lytorhynchus*, *Macroprotodon*, *Malpolon*, *Psammophis schokari*, *Spalerosophis*, and *Telescopus dhara* are confined to desert and subdesert steppe and are not part of the Ethiopian fauna, representing a Palaearctic fauna which extends with the desert into Asia and in many cases (eg. *Leptotyphlops macrorhynchus*, *Spalerosophis diadema*, *Psammophis schokari*) reaching as far as Pakistan (Minton 1962). *Cerastes cerastes* is also virtually confined to the same habitats but a record from Dungas (13.04 N 9.20 E) in Nigerian Sudan savanna seems well documented (Pellegrin 1909). Other desert invaders — listed on Fig. 3, range into Sudan savanna (eg. *Coluber florulentus*) or even Guinea savanna (eg. one record of *Atractaspis microlepidota* from Wukari, 7.51 N 9.47 E, well south of other records), and some are largely confined to the Sudanosahel (eg. *Atractaspis microlepidota* and *A. micropholis*, and *Eryx muelleri*).

If comparison is now made with East Africa (Tables 2 and 4, Appendix B and lists in chapter on savanna snakes) we find that of the snakes restricted to the Kenyan coast only four are known from West Africa and these are all species with a discontinuous distribution, being found near Lake Victoria in the extreme west of Kenya as well as on the coast. These species are:

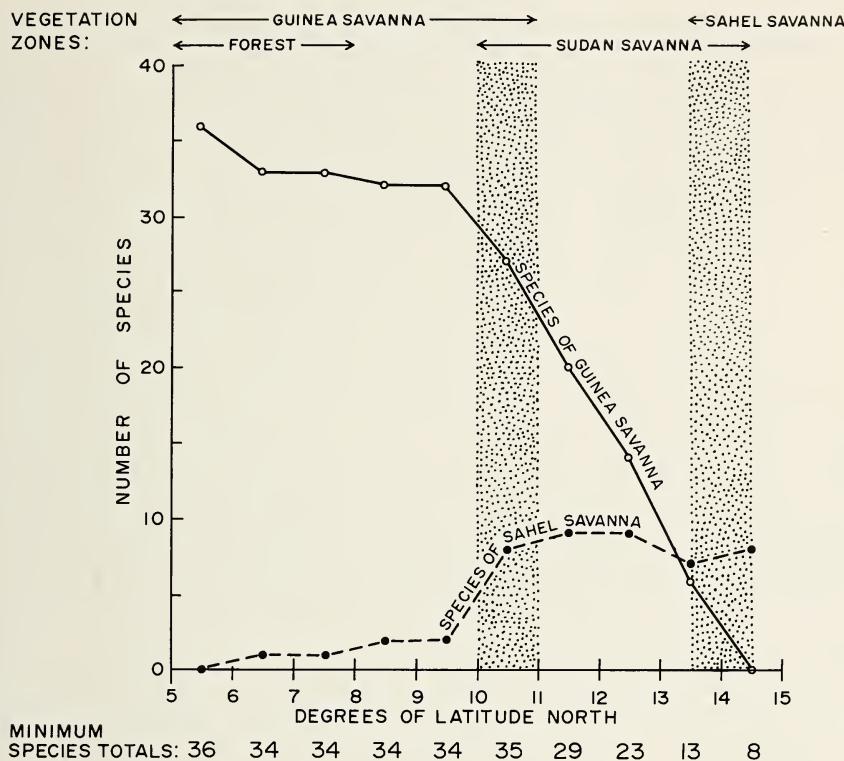


Fig. 6. Changes in the numbers of species of Guinea or Sudanosahel savanna snakes at different latitudes in Ghana and Upper Volta, centred about longitude 2° W. Compare with Fig. 5 from which data derived. Shaded latitudes indicate approximate extent of transition from one vegetation type to another.

*Causus resimus* — non-penetrant in West Africa,

*Meizodon coronatus*

*Natriciteres olivacea*

*Philothamnus heterolepidotus*

} West African penetrants.

But the total snake fauna of the Kenyan coast amounts to 48 species (Appendix B and Table 4) and of these 17 (or 35 %) reach West Africa. The Kenyan inland fauna (of 61 species) includes 30 (or 49 %) West African species. Most of the species also found in West Africa occur there throughout Guinea savanna but others get no further than eastern Nigeria or Niger and are considered non-penetrant whilst others are penetrant but restricted to the Sudanosahel:

*Causus rhombeatus*

*Eryx colubrinus*

*Naja pallida*

*Telescopus dhara*

} non-penetrant species.

*Aparallactus lunulatus*      |      penetrant but restricted to Sudanosahel zone.  
*Naja haje*

All the non-penetrants and the two Sudanosahel penetrants are, in Kenya, snakes of the dry lowland and it is with this biotope that the West African Sudanosahel fauna seems to have affinity. The dry lowland fauna includes five penetrants of West African Guinea savanna but these are mostly rare and of recent discovery (*Coluber florulentus*, *Dendroaspis polylepis*, *Hemirhagerrhis nototaenia*), only two (*Amblyodipsas unicolor* and *Philothamnus semivariegatus*) occurring commonly. The fauna of the dry coastal (Guban) plain of Somalia which was mentioned earlier has several species in common with the Kenyan lowland dry fauna and West African steppe and Sudanosahel savanna viz. *Coluber florulentus*, *Eryx colubrinus*, *Naja pallida*, *Psammophis schokari*, and *Telescopus dhara*. Some of these are considered 'desert invaders' of West Africa (Fig. 3) and their number increases if comparison is made with a fauna from further north: In an Egyptian checklist Marx (1968) includes *Cerastes cerastes* and *C. vipera*, *Leptotyphlops macrorhynchus*, *Lytorhynchus diadema*, *Macroprotodon cucullatus*, *Malpolon moiensis*, *Psammophis schokari*, *Spalerosophis diadema*, and *Telescopus dhara*. This is clearly the Saharan fauna which in West Africa dies away in the Sudan zone.

Table 4

Kenyan territory	Number of species	Number of West African species present —		
		total	non-penetrant	as % total fauna
coast	48	17	2	35
inland (excepting dry lowland)	37	20	2	54
dry lowland	24	10	3	42

### Montane faunas

The existence of a distinctive montane forest bird fauna was mentioned in the introduction. Not only is this fauna distinct from the fauna of the forest below about 1500 m but related birds occur on isolated montane forest outliers in East Africa, southern Sudan, Ethiopia, Cameroon and even as far west as Mt Nimba, Guinea (Moreau 1966, Forbes-Watson 1967). Mountains and highland above 1500 m may be occupied by grassland — "montane savanna", often derived from montane forest by human destructiveness. Above about 3500 to 4000 m there occurs an "Afroalpine moorland" which is again open

country. The only snake associated with the latter known to me is *Atheris hindii*, endemic to the Aberdare and Kenya Mountains at over 2833 m (Ionides & Pitman 1965, Spawls 1978). Two other montane vipers are endemic to Kenya: *Bitis worthingtoni* which occurs from the western flank of the Aberdare Range, across the Rift Valley to Eldoret, everywhere above 1500 m; and *Atheris desaixi*, known only from forest on Mt Kenya (at 1600 m, Ashe 1968) and the Nyembeni Range (Spawls 1978). Several other Kenyan snakes occur above 1500 m, to the heights indicated in parentheses (Spawls 1978):

- Dasypeltis "scabra"* (including *D. atra*, 3000 m).  
*Dispholidus typus* (2000 m).  
*Duberria lutrix* (1500 m plus).  
*Mehelya capensis* (2000 m).  
*Meizodon semiornatus* (2500 m).  
*Psammophis phillipsi* (2500 m).  
*P. sibilans* (2000 m).  
*Psammophylax variabilis* (3500 m, Broadley 1977).

Most are species which range widely throughout African savanna and occur commonly down to sea level but some (eg. *Duberria lutrix*, *Mehelya capensis*, *Meizodon semiornatus*, and *Psammophylax variabilis*) are southern African species which range north at higher altitudes. Other South African snakes exhibit this phenomenon: *Amplorhinus multimaculatus*, *Bitis atropos*, *Hemachatus haemachatus*, and *Psammophis crucifer* occur as relict populations in montane grassland at about 2000 m in Inyangana National Park, eastern Zimbabwe (Broadley 1962); and Laurent (1956) has described new races of *Duberria lutrix*, *Lycodonomorphus whytei*, *Psammophylax tritaeniata* and *Pseudaspis cana* from above 1500 m in eastern Zaire, Rwanda and Burundi.

Endemic montane species are also found in Ethiopia (*Bitis parviocula*, *Coluber taylori*, *Pseudoboodon lemniscatus*) and on Uzungwe (*Adenorhinus barbouri*), Uluguru (*Aparallactus werneri*, *Crotaphopeltis tornieri*, *Geodipsas procterae*, *G. vauerocegae*, *Prosymna ornatissima*, *Typhlops uluguruensis*), and Usambara Mts (*Atheris ceratophorus*, *Aparallactus werneri*, *Crotaphopeltis tornieri*, *Geodipsas vauerocegae*, *Philothamnus macrops*, *Typhlops gierrai*) in Tanzania (Barbour & Loveridge 1928, Loveridge 1957). These mountains harbour peculiar, endemic amphibians (eg. *Bufo* and *Nectophrynoides* spp. — Grandison 1972, 1978) and Amiet (1976) has described many new amphibians from the mountains of Cameroon but the latter lacks a peculiar snake fauna. The only snake species which may prove peculiar to the Cameroon Mts is *Lycophidion ornatum* of which there is a specimen in the British Museum (1966: 351) from Obudu, immediately across the border in Nigeria. This species is known from montane forest in Kenya (Spawls 1978), eastern Zaire (Laurent 1956), and Angola (Parker 1936): the Nigerian specimen is from montane grassland.

Only three of the 24 snakes listed by Mertens (1964) from Fernando Po occur above 1000 m and these (*Atheris squamigera*, *Thrasops aethiopissa* and *T. flavigularis*) are found elsewhere at lower altitudes. In the Usambara Mts (Barbour & Loveridge 1928), of the 26 snake species listed from forest or forest edge between 900 and 2400 m, at most 12 are in fact forest snakes and perhaps 7 not found at lower altitudes. Likewise, on Kilimandjaro, Meru and Hanang Mts, Tanzania, Uthmöller (1942) found 11 species above 1700 m, all in forest or forest edge but three also occurring in steppe, but none being species usually associated with forest and all occurring in savanna at lower altitudes. These were:

*Aparallactus capensis,*  
*Bitis arietans,*  
*Boaedon lineatus,*  
*Crotaphopeltis hotamboeia,*  
*Dispholidus typus,*  
*Duberria lutrix,*

*Lycophidion capense,*  
*Natriciteres olivacea,*  
*Psammophis angolensis,*  
*P. phillipsi,*  
*Psammophylax tritaeniatus.*

### Summary

African snakes are mostly found in forest or savanna, not in both. The occurrence of species in selected areas of Africa has been documented in Appendixes A and B and comparison made in Tables 1 and 2. About 70 % of the species range throughout the forest and the number of species shared by neighbouring sample areas is usually more than 90 %. There is no marked difference between areas within or without West Africa, nor on either side of the Dahomey Gap, contrary to what might be expected. Species and generic endemism is greatest in Cameroon and Zaire. Very few snakes are limited to montane forest, this biome being largely populated by species which occur in lowland forest. Some of the montane species, perhaps originally forest, now survive in montane grassland.

About 25 to 30 % savanna snakes occur widespread in African savanna and the proportion shared by neighbouring sample areas is high — 83 to 96 % except for the inland and coastal Kenya whose index of similarity is only 56 %. This reflects the faunal break between Northern and Southern Savanna. An attempt is made to further divide Kenyan inland snake faunas into i extreme western, ii dry lowland, and iii upland.

Sixteen species which occur in forest and savanna are listed and classified according to their pattern of occurrence in the two very different biomes.

The latitudinal ranges of West African savanna snakes are shown by means of maps (Figs. 2—4) and diagrams (Figs. 5 & 6) to indicate a major faunal change at the Guinea/Sudan Savanna boundary with most of the desert species not extending south of this point and Guinea savanna species decreasing in number to the north of it until none is known beyond the Sudan/Sahel boundary. Villiers (1975) has earlier recognised a faunal change within the savanna but has identified the Sudan/Sahel boundary as the transition point whereas, in fact, it seems the Guinea/Sudan boundary is of greater importance. Examination of the northward range limits of species restricted to the southwest of Upper Volta, — all but one species of Guinea Savanna, shows most to extend to a point midway between Guinea/Sudan and Sudan/Sahel boundaries. Clearly much

more needs to be known, especially as to the environmental physiology of African snakes before we can understand what limits their geographic distribution. The recent discovery of many East African species in West African savanna (Fig. 4, Tables 2 and 4) — some reported here for the first time, invites comparison of the West African Guinea Savanna fauna with the Upland fauna of inland Kenya and of the Sudano-Sahel fauna with the fauna of dry, lowland Kenya and the Somalian Juban.

### Zusammenfassung

Die meisten afrikanischen Schlangenarten findet man entweder im Wald oder in der Savanne, nicht aber in beiden Großlebensräumen. Das Auftreten von Arten in ausgewählten Gebieten Afrikas wurde in den Anhängen A und B zusammengestellt und in den Tabellen 1 und 2 verglichen. Ungefähr 70 % der Arten kommen durch das ganze Waldgebiet hindurch vor, und die mit benachbarten Stichprobengebieten gemeinsame Artenzahl beträgt gewöhnlich über 90 %. Es gibt keinen deutlichen Unterschied zwischen Gebieten inner- und außerhalb Westafrikas, nicht einmal beiderseits der „Dahomey Gap“, was man eigentlich hätte erwarten sollen. Art- und Gattungsendemismen sind in Kamerun und Zaire am beträchtlichsten. Sehr wenige Schlangenarten sind in ihrer Verbreitung auf den Montanwald beschränkt; dieser Lebensraum wird größtenteils von Niederungswald bewohnenden Arten mit eingenommen. Einige der montanen Arten, ursprünglich wohl Waldarten, überleben heute in der montanen Grassavanne.

Ungefähr 25–30 % savanicoler Schlangen kommen weitverbreitet in der afrikanischen Savanne vor, und der Prozentsatz, der mit Nachbargebieten gemeinsam ist, liegt hoch: 83–96 %; eine Ausnahme sind die Inland- und Küstengebiete Kenias, deren Ähnlichkeitsindex nur 56 % beträgt. Dies spiegelt die Faunenscheide zwischen nördlicher und südlicher Savanne wider. Es wird versucht, die kenianischen Inland-Schlangenfaunen weiter zu untergliedern, nämlich in (1) den äußersten Westen, (2) die trockenen Tiefländer und (3) die Hochländer.

Sechzehn Arten, die sowohl im Wald als auch in der Savanne vorkommen, werden aufgelistet und nach ihrem Verbreitungsmuster in den beiden so verschiedenen Biomen klassifiziert.

Die Nord-Süd-Erstreckungen der westafrikanischen Savannenschlangen werden mit Hilfe von Karten (Abb. 2–4) und Diagrammen (Abb. 5 und 6) dargestellt, um einen beträchtlichen Faunenwechsel an der Guinea-/Sudan-Savannengrenze darzustellen; dabei erreichen die allermeisten Wüstenarten nach Süden diesen Bereich nicht, während die für die Guinea-Savanne typischen Arten in ihrer Zahl nördlich dieses Bereiches abnehmen und keine von ihnen die Sudan-/Sahel-Savannengrenze überschreitet. Villiers (1975) hat bereits früher auf einen Faunenwechsel innerhalb der Savanne hingewiesen, dabei aber die Sudan-/Sahel-Grenze als Übergangsbereich identifiziert, während es den Tatsachen besser zu entsprechen scheint, der Guinea-/Sudan-Grenze hier größere Bedeutung zuzumessen. Die Prüfung der Nordgrenzen von Arten, die auf den Südwesten Obervoltas beschränkt sind (mit einer Ausnahme sind es sämtlich Guinea-Arten), zeigt, daß die meisten von ihnen ein Gebiet erreichen, das auf halber Strecke zwischen den Grenzlinien Guinea-/Sudansavanne und Sudan-/Sahelsavanne liegt. Selbstverständlich müssen noch viel mehr Kenntnisse erarbeitet werden, speziell über die umweltbezogene Physiologie der Schlangen Afrikas, bevor man zu einem Verständnis dessen kommt, was die geographische Verbreitung limitiert. Die erst kürzlichen Entdeckungen vieler ostafrikanischer Arten in den Savannengebieten Westafrikas — einige davon werden hier zum ersten Male mitgeteilt — fordern zu einem Vergleich auf zwischen der westafrikanischen Savannenfauna einerseits und der Hochlandfauna des inneren Kenia so-

wie des Sudanosahel andererseits, einschließlich der Fauna der trockenen kenianischen Niederungsgebiete und des somalischen Guban.

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Appendix A. Distribution of forest snakes (including snakes also found in savanna and marked by an asterisk).

Sources: Taxonomic works are cited after the genus to which they apply; Hughes in prep. refers to manuscript work as yet unpublished and often at variance with published accounts. For particular countries the following have been utilised: Senegambia — Böhme 1978, Håkansson 1981; Sierra Leone — Menzies 1966; Liberia — Loveridge 1938, Taylor & Weyer 1958; Ghana — Hughes & Barry 1969; Upper Volta — Roman 1969, 1973, 1975; Nigeria — Dunger 1971, 1971a, 1972, 1973, 1973a; Cameroon — Perret 1961; Gabon — Knoepffler 1966; Zaire — Witte 1962, 1966; Sudan — Loveridge 1956; Uganda — Pitman 1974; Kenya — Spawls 1978; Mozambique and South Africa — Fitz Simons 1962. Bogert 1940, Loveridge 1957, and Parker 1949 are indispensable sources of information.

species (information source)	territories							
	1	2	3	4	5	6	7	8
	Liberia	Ghana	Nigeria	Cameroon	Gabon	Zaire	Uganda	Kenya
<i>Afronatrix</i> (Rossman & Eberle 1967)								
1. <i>anoscopus</i> * .....	x	x	x	x				
<i>Aparallactus</i> (Witte & Laurent 1947)								
2. <i>lineatus</i> .....	x	x						
3. <i>modestus</i> .....	x	x	x	x	x	x	x	
4. <i>niger</i> .....	?	x						

## Appendix A (cont'd)

## Appendix A (cont'd)

species (information source)	territories							
	1 Liberia	2 Ghana	3 Nigeria	4 Cameroon	5 Gabon	6 Zaire	7 Uganda	8 Kenya
25. <i>maculatus</i> * .....	x	x	x	x	?	x	x	
<i>Chamaelycus</i> (Witte 1963; Hughes in prep.)								
26. <i>christyi</i> .....						x		
27. <i>fasciatus</i> .....	x	x	x	x	x	x		
28. <i>parkeri</i> .....						x		
29. <i>werneri</i> .....				x	x			
<i>Chilorhinophis</i> (Witte & Laurent 1947)								
30. <i>gerardi</i> .....						x		
<i>Dasypeltis</i> (Gans 1959, 1964; Hughes in prep.)								
31. <i>atra</i> .....						x	x	x
32. <i>fasciata</i> * .....	x	x	x	x	x	x	x	
<i>Dendroaspis</i>								
33. <i>jamesoni</i> .....	x	x	x	x	x	x	x	x
34. <i>viridis</i> .....	x	x	x					
<i>Dendrolycus</i> (Hughes in prep.)								
35. <i>elapoides</i> .....		x	x	?	x			
<i>Dipsadoboaa</i> (Rasmussen 1979; Hughes in prep.)								
36. <i>duchesnei</i> .....	x	x	x	x	x	x	x	
37. <i>unicolor</i> .....	x	x	x	x	x	x	x	x
<i>Gastropyxis</i>								
38. <i>smaragdina</i> .....	x	x	x	x	x	x	x	
<i>Geodipsas</i>								
39. <i>depressiceps</i> .....				x	x	x	x	
<i>Gonionotophis</i> (Loveridge 1939; Hughes in prep.)								
40. <i>brussauxi</i> .....				x	x			
41. <i>kingi</i> .....	x	x						
<i>Grayia</i> (Boulenger 1915)								
42. <i>caesar</i> .....				x	?			
43. <i>ornata</i> .....				x	x	x		

## Appendix A (cont'd)

species (information source)	territories							
	1	2	3	4	5	6	7	8
Liberia	Ghana	Nigeria	Cameroon	Gabon	Zaire	Uganda	Kenya	
44. <i>smythii</i> * .....	x	x	x	x	x	x	x	x
<i>Hapsidophrys</i>								
45. <i>lineata</i> .....	x	x	x	x	x	x	x	x
<i>Helophis</i>								
46. <i>schoutedeni</i> .....						x		
<i>Hormonotus</i>								
47. <i>modestus</i> .....	x	x	x	x	x	x	x	x
<i>Hydraethiops</i>								
48. <i>laevis</i> .....					x			
49. <i>melanogaster</i> .....					x	x	x	
<i>Lamprophis</i> (including <i>Boaedon</i> : Roux-Estève & Guibé 1965)								
50. <i>olivaceus</i> .....	x	x	x	x	x	x	x	x
51. <i>virgatus</i> .....	x	x	x	x	x	x	x	
<i>Leptotyphlops</i> (Broadley & Watson 1976; Hahn 1978; Roux-Estève 1979)								
52. <i>bicolor</i> * .....		x						
53. <i>narirostris</i> .....	x	x	x					
54. <i>perreti</i> .....				x				
55. <i>sundevalli</i> .....	x	x	x					
<i>Limnophis</i>								
56. <i>bicolor</i> .....					x			
<i>Lycodonomorphus</i> (Loveridge 1953; Laurent 1964; Broadley 1967)								
57. <i>bicolor</i> .....					x			
58. <i>subtaeniatus</i> .....					x			
59. <i>whytei</i> .....					x			
<i>Lycophidion</i> (Laurent 1968; Guibé & Roux-Estève 1972; Hughes in prep.)								
60. <i>irroratum</i> * .....	x	x	x	x	x			
61. <i>laterale</i> .....	x	x	x	x	x	x		
62. <i>nigromaculatum</i> ...	x	x	x					
63. <i>ornatum</i> * .....				?	x	x	x	x

## Appendix A (cont'd)

species (information source)	territories							
	1 Liberia	2 Ghana	3 Nigeria	4 Cameroon	5 Gabon	6 Zaire	7 Uganda	8 Kenya
<i>Mehelya</i> (Loveridge 1939; Dunger 1966)								
64. <i>egbensis</i> .....			x					
65. <i>guirali</i> .....	x	x	x	x	?	x		
66. <i>poensis</i> .....	x	x	x	x	x	x	x	
67. <i>capensis</i> .....				x	x	x	x	x
68. <i>stenophthalmus</i> ....	x	x	x	x	x	x	x	
<i>Naja</i> (Broadley 1968; Hughes in prep.)								
69. <i>melanoleuca</i> * .....	x	x	x	x	x	x	x	x
<i>Natriciteres</i> (Broadley 1966)								
70. <i>fuliginoides</i> .....	x	x	x	x	x	x	?	
71. <i>variegata</i> .....	x	x	x	x		x	?	?
<i>Paranaja</i> (Perret 1960)								
72. <i>multifasciata</i> .....				x	x	x		
<i>Philothamnus</i> (Hughes in prep.)								
73. <i>angolensis</i> .....				x	x	x	x	
74. <i>carinatus</i> .....	x	x	x	x	x	x	x	x
75. <i>dorsalis</i> .....					x	x		
76. <i>heterodermus</i> .....	x	x	x	x	x	x	x	
77. <i>nitidus</i> .....	x	x	x	x	x	x		
78. <i>ruandae</i> .....						x	x	
<i>Poicilopholis</i>								
79. <i>camerunensis</i> .....				x				
<i>Polemon</i> (including <i>Chlorhinophis</i> , <i>Cynodontophis</i> and <i>Miodon</i> :								
Witte & Laurent 1947; Resetar & Marx 1981, Hughes in prep.)								
80. <i>acanthias</i> .....	x	x	x					
81. <i>barthi</i> .....	x	x						
82. <i>bocourti</i> .....				x	x	x		
83. <i>christyi</i> .....						x	x	x
84. <i>fulvicollis</i> .....						x	x	

## Appendix A (cont'd)

species (information source)	territories							
	1	2	3	4	5	6	7	8
	Liberia	Ghana	Nigeria	Cameroon	Gabon	Zaire	Uganda	Kenya
85. <i>gabonensis</i> .....			x	x	x	x	x	
86. <i>gracilis</i> .....				x				
87. <i>notatus</i> .....				x	x	x		
88. <i>robustus</i> .....						x		
<i>Psammophis</i> (Broadley 1977)								
89. <i>phillipsi</i> * .....	x	x	x	x	x	x	x	
<i>Pseudohaje</i> (Hughes 1977; Courtois 1979)								
90. <i>goldii</i> .....		x	x	x	x	x	x	x
91. <i>nigra</i> .....	x	x	x					
<i>Rhinotyphlops</i> (Roux-Estève 1974)								
92. <i>caecus</i> .....	?	?	?	x	x	x		
<i>Thelotornis</i> (Broadley 1981)								
93. <i>kirtlandii</i> .....	x	x	x	x	x	x	x	
<i>Thrasops</i> (Loveridge 1944)								
94. <i>aethiopissa</i> .....	x	x	x	x	x	x	x	x
95. <i>batesii</i> .....				x	x	x		
96. <i>flavigularis</i> .....			x	x	x	x		
97. <i>jacksoni</i> .....						x	x	x
98. <i>occidentalis</i> .....	x	x	x					
<i>Typhlops</i> (Roux-Estève 1974)								
99. <i>angolensis</i> * .....				x	x	x	x	x
100. <i>caecatus</i> .....		x						
101. <i>leucostictus</i> .....	x							
102. <i>manni</i> .....	x							
103. <i>punctatus</i> * .....	x	x	x	x	x	x	x	x
104. <i>steinhausi</i> .....			x	x				
105. <i>zenkeri</i> .....				x				
Totals:	44	56	56	73	57	77	42	23

Sources: see Appendix A.

## Appendix B (cont'd)

species (information source)	territories											
	1	2	3	4	5	6	7	8	9	10	11	12
Senegambia												
Sierra Leone												
Ghana												
Upper Volta												
Nigeria												
Cameroon (inland)												
Garamba N.P., Zaire												
Sudan												
Kenya (inland)												
Kenya (coast)												
southern Mozambique												
Natal, S.Afr.												
<i>19. fallax</i> ....								?	x	x		
<i>20. irregularis*</i> ....	?	x	?	x	x	x	x	x	x			
<i>21. microlepidota</i> ....	x			x	x	x	?	x				
<i>22. micropholis</i> ....	x	?	x	x	?	?	x					
<i>Bitis</i>												
<i>23. arietans</i> ....	x	x	x	x	x	x	x	x	x	x	x	x
<i>24. gabonica*</i> ....			x									?
<i>25. worthingtoni</i> ...									x			
<i>Causus</i> (Hughes 1978)												
<i>26. defilippi</i> ....									x	x	x	
<i>27. maculatus*</i> ....	x	x	x	x	x	x	x	x	x			
<i>28. resimus</i> ....					x	x		x	x	x		
<i>29. rhombeatus</i> ....					x	x	x	x	x	x	x	x
<i>Coluber</i> (Bons 1962)												
<i>30. dorri</i> ....	x		x	x	?							
<i>31. florulentus</i> ....				?	x	x	?	x	x			
<i>32. keniensis</i> ....									x			
<i>Crotaphopeltis</i> (Broadley 1968; Rasmussen 1979)												
<i>33. degeneri</i> ....								x	x			
<i>34. hotamboeia</i> ....	x	x	x	x	x	x	x	x	x	x	x	x
<i>Dasypeltis</i> (Gans 1959, 1964; Hughes in prep.)												
<i>35. fasciata*</i> ....	x		x	x	x	x						
<i>36. inornata</i> ....										x		
<i>37. medici</i> ....									x	x		
<i>38. scabra</i> ....	x	x	x	x	x	x	x	x	x	x	x	x
<i>Dendroaspis</i>												
<i>39. angusticeps</i> ....								x	x	x		

## Appendix B (cont'd)

species (information source)	territories											
	1 Senegambia	2 Sierra Leone	3 Ghana	4 Upper Volta	5 Nigeria	6 Cameroon (inland)	7 Garamba N.P., Zaire	8 Sudan	9 Kenya (inland)	10 Kenya (coast)	11 southern Mozambique	12 Natal, S.Afr.
40. <i>polylepis</i> .....	x							x	x	x	x	
<i>Dipsadoboaa</i> (Rasmussen 1979; Hughes in prep.)												
41. <i>aulicus</i> .....									x	x	x	x
<i>Dispholidus</i> (Hughes in prep.)												
42. <i>typus</i> .....	x	x	x	x	x	x	x	x	x	x	x	x
<i>Dromophis</i> (Loveridge 1940)												
43. <i>lineatus</i> .....	x	x	x	x	x	x	x	x	x			
44. <i>praeornatus</i> ....	x		x	x	x	x						
<i>Duberria</i>												
45. <i>lutrix</i> .....								x		x	x	
46. <i>variegata</i> .....									x	x		
<i>Echis</i> (Hughes 1976)												
47. <i>leakeyi</i> .....								x				
48. <i>leucogaster</i> ....	x				x	x						
49. <i>ocellatus</i> .....	x		x	x	x	x						
<i>Elaps</i>												
50. <i>lacteus</i> .....										x		
<i>Elapsoidea</i> (Broadley 1971)												
51. <i>laticincta</i> .....							x	x				
52. <i>loveridgei</i> .....									x			
53. <i>semiannulata</i> ...	x		x	x	x	x				x		
54. <i>sundevalli</i> .....										x	x	
<i>Eryx</i>												
55. <i>colubrinus</i> ....								x	x			
56. <i>muelleri</i> .....	x		x	x	x			x				
<i>Gonionotophis</i> (Hughes in prep.)												
57. <i>granti</i> .....		x	x	x	x							

## Appendix B (cont'd)

species (information source)	territories											
	1 Senegambia	2 Sierra Leone	3 Ghana	4 Upper Volta	5 Nigeria	6 Cameroon (inland)	7 Garamba N.P., Zaire	8 Sudan	9 Kenya (inland)	10 Kenya (coast)	11 southern Mozambique	12 Natal, S Afr.
<i>Grayia</i> (Boulenger 1915)												
58. <i>ornata</i> * .....								x				
59. <i>smythii</i> * .....	x	x	x	x	x	x	x	x	x	x		
60. <i>tholloni</i> .....	x		?	?	x			x				
<i>Hemachatus</i>												x
61. <i>haemachatus</i> ...												x
<i>Hemirhagerrhis</i>												
62. <i>kellери</i> .....								x	x			
63. <i>nototaenia</i> .....							?	x	?	x	x	
<i>Lamprophis</i> (including <i>Boaedon</i> : Roux-Estève & Guibé 1965)												
64. <i>aurora</i> .....												x
65. <i>fuliginosus</i> .....	x	x	x	x	x	x	x	x	x	x	x	x
66. <i>guttatus</i> .....												x
67. <i>inornatus</i> .....												x
68. <i>lineatus</i> .....	x	?	x	x	x	?	?	?				
<i>Leptotyphlops</i> (Broadley & Watson 1976; Hahn 1978)												
69. <i>bicolor</i> * .....			x	x	x		?					
70. <i>boulengeri</i> .....										x		
71. <i>cairi</i> .....									x			
72. <i>conjuncta</i> .....									x	x	x	x
73. <i>distanti</i> .....										x	x	
74. <i>emini</i> .....									x			
75. <i>fiechteri</i> .....									x			
76. <i>longicauda</i> .....										x		
77. <i>macrorhynchus</i> ?			x	?	x		?					
78. <i>narirostris</i> * .....	x		x	x	x		?					
79. <i>nigricans</i> .....										x		

## Appendix B (cont'd)

species (information source)	territories											
	1 Senegambia	2 Sierra Leone	3 Ghana	4 Upper Volta	5 Nigeria	6 Cameroon (inland)	7 Garamba N.P., Zaire	8 Sudan	9 Kenya (inland)	10 Kenya (coast)	11 southern Mozambique	12 Natal, S.Afr.
80. <i>scutifrons</i> .....										x	x	
81. <i>sundevalli</i> .....	x	?	x	?								
82. <i>telloi</i> .....										x		
<i>Lycodonomorphus</i> (Loveridge 1953; Laurent 1964; Broadley 1967)												
83. <i>laevisimus</i> .....										x		
84. <i>rufulus</i> .....										x	x	
<i>Lycophidion</i> (Laurent 1968; Guibé & Roux-Estève 1972; Hughes in prep.)												
85. <i>capense</i> .....	x	x	x	x	x	x	x	x	x	x	x	x
86. <i>depressirostre</i> ...							?	x	x	x		
87. <i>irroratum</i> * .. ?	x	x		x	x	x						
88. <i>ornatum</i> * .....			x						?			
89. <i>semiannule</i> .....										x		
90. <i>semicinctum</i> .... x x x x x x												
<i>Macrelaps</i>												
91. <i>microlepidotus</i> ..										x		
<i>Mehelya</i> (Loveridge 1939; Dunger 1966)												
92. <i>crossi</i> ..... x ? x x x x ?												
93. <i>nyassae</i> .....							x			x	x	x
94. <i>capensis</i> .....					x	x	x	x	x	x	x	x
<i>Meizodon</i> (Roux-Estève 1969)												
95. <i>coronatus</i> .... x x x x x x x x										x		
96. <i>regularis</i> .....	?	x	?	x	x	x	x	x				
97. <i>semiornatus</i> ....							x	x	x	x		
<i>Micrelaps</i>												
98. <i>bicoloratus</i> .....								x	x			
99. <i>vaillanti</i> .....								x				

## Appendix B (cont'd)

species (information source)	territories											
	1	2	3	4	5	6	7	8	9	10	11	12
Senegambia												
Sierra Leone												
Ghana												
Upper Volta												
Nigeria												
Cameroon (inland)												
Garamba N.P., Zaire												
Sudan												
Kenya (inland)												
Kenya (coast)												
southern Mozambique												
Natal, S.Afr.												
<i>Naja</i> (Broadley 1968; Hughes in prep.)												
100. <i>haje</i> .....	x		x	x	x	x	x	x	x	x	x	x
101. <i>katiensis</i> .....	x		x	x	x	x						
102. <i>melanoleuca</i> * ...	x		x	x	x	x		x	x	x	?	?
103. <i>mossambica</i> ....										x	x	
104. <i>nigricollis</i> .....	x	x	x	x	x	x	x		x			
105. <i>pallida</i> .....								x	x			
<i>Natriciteres</i> (Broadley 1966)												
106. <i>olivacea</i> .....		?	x	x	x	x	x	x	x	x	x	x
<i>Philothamnus</i> (Hughes in prep.)												
107. <i>angolensis</i> * .....	x					x		x		x	x	x
108. <i>battersbyi</i> .....						x	x	x	x			
109. <i>bequaerti</i> .....						x	x	x				
110. <i>heterolepidotus</i> .	x	x		x	x	x	x	x		x		
111. <i>hoplogaster</i> ....										x	x	x
112. <i>irregularis</i> .....	x	x	x	x	x	x	x					
113. <i>natalensis</i> .....										x	x	
114. <i>punctatus</i> .....										x	x	
115. <i>semivariegatus</i> ..	x	x	x	?	x	x	x	x	x	x	x	x
<i>Polemon</i> (including <i>Miodon</i> and <i>Cynodontophis</i> : Witte & Laurent 1947; Hughes in prep.)												
116. <i>neuwiedi</i> .....			x	x								
<i>Prosymna</i> (Broadley 1980)												
117. <i>ambigua</i> .....						x	x	x	x	x	x	
118. <i>frontalis</i> .....											x	
119. <i>jainii</i> .....											x	x
120. <i>m. greigerti</i> .....	x		x	x	x	x	x	x	x			

## Appendix B (cont'd)

species (information source)	territories											
	1 Senegambia	2 Sierra Leone	3 Ghana	4 Upper Volta	5 Nigeria	6 Cameroon (inland)	7 Garamba N.P., Zaire	8 Sudan	9 Kenya (inland)	10 Kenya (coast)	11 Southern Mozambique	12 Natal, S.Afr.
121. <i>m. meleagris</i> ....	x	x	x	x	x							
122. <i>ruspolii</i> .....									x			
123. <i>sundevalli</i> .....										x	x	
<i>Psammophis</i> (Loveridge 1940; Broadley 1975, 1977)												
124. <i>angolensis</i> .....										x		
125. <i>biseriatus</i> .....								x	x	x		
126. <i>crucifer</i> .....											x	
127. <i>elegans</i> .....	x	x	x	x	x	x						
128. <i>phillipsi</i> * .....	x	x	x	?	x	x	?	x	x	?	x	x
129. <i>pulcher</i> .....									x			
130. <i>punctulatus</i> ....								x	x	x		
131. <i>schokari</i> .....								x				
132. <i>sibilans</i> .....	x	?	x	x	x	x	?	x	x	x		x
<i>Psammophylax</i> (Broadley 1977)												
133. <i>tritaeniatus</i> .....									x			
134. <i>variabilis</i> .....								x				
<i>Pseudaspis</i>												
135. <i>cana</i> .....								x		x	x	
<i>Python</i>												
136. <i>regius</i> .....	x	x	x	x	x	x	x	x	x			
137. <i>sebae</i> .....	x	x	x	x	x	x	x	x	x	x	x	x
<i>Rhamphiophis</i> (Broadley 1971)												
138. <i>acutus</i> .....		x	?	?	x							
139. <i>oxyrhynchus</i> ....	x		x	x	x	x	?	?				
140. <i>rostratus</i> .....								x	x	x		
141. <i>rubropunctatus</i> .								x	x	x		

## Appendix B (cont'd)

species (information source)	territories											
	1	2	3	4	5	6	7	8	9	10	11	12
Senegambia												
Sierra Leone												
Ghana												
Upper Volta												
Nigeria												
Cameroon (inland)												
Garamba N.P., Zaire												
Sudan												
Kenya (inland)												
Kenya (coast)												
southern Mozambique												
Natal, S.Afr.												
<i>Rhinoleptus</i> (Orejas-Miranda et al. 1970)												
142. <i>koniagui</i> ..... x												
<i>Rhinotyphlops</i> (Roux-Estève 1974)												
143. <i>pallidus</i> .....										x		
144. <i>schlegeli</i> * .....									x	x	x	
145. <i>sudanensis</i> .....								x				
146. <i>unitaeniatus</i> ....									x	x		
<i>Scaphiophis</i> (Parker 1949)												
147. <i>albopunctatus</i> .. x ? x x x x x x												
<i>Telescopus</i> (Kramer & Schnurrenberger 1963; Rasmussen 1979)												
148. <i>dhara</i> .....								x	x			
149. <i>semiannulatus</i> ..									x	x	x	
150. <i>variegatus</i> ..... x x x ? x x												
<i>Thelotornis</i> (Broadley 1981)												
151. <i>capensis</i> .....									x	x	x	
<i>Typhlops</i> (Roux-Estève 1974)												
152. <i>bibronii</i> .....											x	
153. <i>fornasinii</i> .....									x	x		
154. <i>lineolatus</i> ..... x x x ? x x x x x												
155. <i>punctatus</i> * ..... x ? x x x x ?												
<i>Atheris</i>												
156. <i>hindii</i> .....									x			
<i>Xenocalamus</i> (Broadley 1971)												
157. <i>bicolor</i> .....										x		
158. <i>transvaalensis</i> ...										x		
Totals:	43	23	55	46	58	53	35	54	61	48	55	51

## Appendix C. Data base for Figure 5

Species listing in Appendix B	Limiting locality:			Source
	Place	Country	Latitude: °      'N	
1	Toussiana	Upper Volta	10.50	Villiers 1953, Roman 1973
6	Kongoussi	Upper Volta	13.19	Roman 1969
12	Bobo-Dioulasso	Upper Volta	11.12	Roman 1969 as <i>A. modestus</i>
16	Pabré	Upper Volta	12.30	Roman collection, per. obs.
18	Dedougou	Upper Volta	12.28	Roman 1973a
21	South of Kampty	Upper Volta	10.00	Roman 1973a
22	Bomborokuy	Upper Volta	13.04	Roman 1973a
23	Bani	Upper Volta	13.22	Roman 1969
27	Djibo	Upper Volta	14.06	Roman 1973a
30	Diapaga	Upper Volta	12.04	Roman 1969
34	Markoye	Upper Volta	14.39	Roman 1969
35	Tenkodogo	Upper Volta	11.47	Villiers 1965 and pers. obs.
38	Garango	Upper Volta	11.48	Villiers 1965 and pers. obs.

*Daspeltis scabra* is known from Diafarabé (14.09N) in Mali and Agades (17.00N) in Niger and many of Roman's (1969) records may be of this species.

40	Mangodara	Upper Volta	9.54	Roman 1973a and pers. obs.
42	Tassila	Upper Volta	12.25	Roman 1969
43/44	Djibo	Upper Volta	14.06	Roman 1969
48	Djibo	Upper Volta	14.06	Roman 1973
49	Accra	Ghana	5.33	pers. obs.
53	Ketekrachi	Ghana	7.46	Broadley 1971
	Gorom-gorom	Upper Volta	14.26	Roman 1973a
56	Markoye	Upper Volta	14.39	Roman 1969
57	Barlavé	Upper Volta	12.23	Roman 1969
59	Bondoukuy	Upper Volta	11.51	Roman 1969
65/68	Gorom-Gorom	Upper Volta	14.26	Roman 1969
69/78/81	Kongoussi	Upper Volta	13.19	Roman 1969
77	Bawku	Ghana	11.03	Papenfuss 1969 (as <i>L. brevicauda</i> )

## Appendix C (cont'd)

Species listing in Appendix B	Limiting locality:			Source
	Place	Country	Latitude: ° 'N	
90	Garango	Upper Volta	11.45	Villiers 1965 (as <i>L. irroratum</i> )
92	near Barani	Upper Volta	13.10	Roman 1969
95	?Sanaba	Upper Volta	12.25	Roman 1969
96	Peki	Ghana	6.32	Roux-Estève 1969
100	Tumu	Ghana	10.52	Papenfuss 1969
101	Garoua	Upper Volta	10.20	Roman 1973a
102	Dédougou	Upper Volta	12.28	Roman 1969
104	Djibo	Upper Volta	14.06	Roman 1969
106	Dianlé	Upper Volta	11.06	Roman 1969
110	Akuse	Ghana	6.06	pers. obs.

*Natriciteres olivacea* is largely coastal in occurrence but is known from Poli (8.31N), Cameroon and could well occur inland along the Niger River.

112	Toussiana	Upper Volta	10.50	Villiers 1953 and pers. obs.
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*Philothamnus irregularis* occurs much further north in Mali, at Lobi (16.15N) on River Niger.

115	Tikaré	Upper Volta	13.17	Roman 1969
116	Bobo-Dioulasso	Upper Volta	11.12	Roman 1969 (as <i>Miodon gabonensis</i> )
120	Pong Tamale	Ghana	9.41	Broadley 1980
121	Mole Nat. Park	Ghana	9.05	Broadley 1980
127	Dano	Upper Volta	11.09	Villiers 1950, 1951
128	near Dano	Upper Volta	c.11.09	Paris 1965.81—2, pers. obs.
132	Garango	Upper Volta	11.45	Viliers 1965 and pers. obs.
136/137	Gorom-Gorom	Upper Volta	14.26	Roman 1969
138	Banda Hills	Ghana	8.10	Broadley 1971b
139	Ouahigouya	Upper Volta	13.35	Roman 1969
147	Ho	Ghana	6.36	pers. obs.
149	Tougouri	Upper Volta	13.18	Roman 1969, 1974
153	Sheribong River	Ghana	8.40	Roux-Estève 1974
154	Birni N'konni	Niger	13.48	Roux-Estève 1974

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