Problems presented by geographical variation in the African vine snakes, genus *Thelotornis*

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Analysis of variation in 771 specimens of the genus *Thelotornis* A. Smith (Colubridae) confirms the absence of intergradation between the taxa *kirtlandii* (Hallowell) and *oatesii* (Günther) in northern Angola and southern Zaire, so *T. capensis* A. Smith is accepted as a full species. The western race *T. capensis oatesii* shows very little variation, but the eastern populations of *T. capensis* are extremely variable and it is convenient to revive the name *mossambicanus* (Bocage) for the populations which occur from central Mocambique northwards. *T. c. oatesii* hybridizes extensively with *T. c. capensis* and *T. c. mossambicanus* in southeastern Rhodesia and adjacent Mocambique. Northern populations of *T. c. mossambicanus* show features of *T. kirtlandii,* but these are apparently primitive characters retained since the original partition of *Thelotornis* into western and eastern forms. The highlands of Kenya and northern Tanzania isolate these northern *mossambicanus* from the nearest *kirtlandii* populations in Uganda.

S. Afr. J. Zool. 14: 125–131 (1979)

'n Analise van variasie in 771 voorbeelde van die genus *Thelotornis* A. Smith (Colubridae) bevestig die afwesigheid van intergradasie tussen die taxa *kirtlandii* (Hallowell) en *oatesii* (Günther) in noordelike Angola en suidelike Zaïre, en dus word *T. capensis* A. Smith as 'n volle spesie beskou. Baie min variasie kom voor in die westelike ras *T. capensis oatesii*, maar die oostelike populasie van *T. capensis* vertoon geweldig baie variasie en die hergebruik van die ou naam *mossambicanus* (Bocage) vir populasies wat van sentraal Mosambiek noordwaarts voorkom word aanbeveel. 'n Wye vermenging tussen *T. c. oatesii* en *T. c. capensis* en*T. c. mossambicanus* in suidoos Rhodesië en aangrensende dele van Mosambiek word aangetref. Noordelike populasies van *T. c. mossambicanus* vertoon eienskappe van *T. kirtlandii*, maar hierdie is blykbaar primitiewe kenmerke wat behoue gebly het na die oorspronklike skeiding van *Thelotornis* in westelike en oostelike vorms. Die hooglande van Kenia en noordelike Tanzanië sonder hierdie noordelike populasies van *mossambicanus* af van die naaste *kirtlandii* populasies in Uganda.

S.-Afr. Tydskr. Dierk. 14: 125–131 (1979)

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Accepted 12 February 1979

Leptophis kirtlandii was briefly described by Hallowell (1844) from a Liberian specimen, and *Thelotornis capensis* was described by Andrew Smith (1849) from 'Kaffirland and the country toward Port Natal'. *Dryiophis oatesii* was described and illustrated in colour by Günther (1881) from a Matabeleland snake.

The first review of the African vine snakes was provided by Bocage (1895), who distinguished three varieties of *Dryiophis kirtlandii.* The typical form, represented by specimens from Gabon and northern Angola, was characterized by the rostral and nasals recurved onto the top of the snout and the head uniform green above and rose-carmine below. Two specimens from Mocambique were described as a distinct variety, var. *mossambicana,* with the rostral and nasals more feebly recurved onto the top of the snout; a rose-coloured stripe speckled with black extends from the rostral through the eye and the temporal region, terminating on the neck; a speckled triangular marking covers the sixth labial and the edges of the labials and underside of the head are speckled with black. Angola specimens, excluding the specimen of the typical form from Duque de Braganca, were assigned to the variety *oatesi* Günther, having on top of the head a Y-shaped marking in rose-carmine speckled with black.

In his *Catalogue of Snakes* Boulenger (1896) divided material of *Thelotornis kirtlandii* into two groups. Group A comprised specimens from west and central Africa with the top and sides of the head uniform green and black crossbands on the neck, whereas Group B included specimens from eastern and southern Africa with black speckling on top and sides of the head and no crossbands on the neck.

Bogert (1940) noted that these differences in colouration were correlated with differences in scalation of the snout (as indicated by Bocage 1895), number of ventrals and length of hemipenis: he therefore recognized *T. capensis* (i.e. Boulenger's Group B) as a full species. However, Loveridge, in his 1944 revision of the genus, thought that intergradation between the two forms occurred in Tanzania and northern Angola and he consequently treated *capensis* as a southern race of *T. kirtlandii.* Bogert (1942) accepted Loveridge's findings and identified three snakes from south-eastern Kenya as *T. kirtlandii capensis,* although noting

that they had the top of the head immaculate like the typical form.

In 1953 Loveridge revived *oatesii* (Günther) as a subspecies of *T. kirtlandii*, after finding that in Malawi this large lowland form with a speckled 'Y' dorsal head marking and high ventral counts was readily separable from the smaller speckle-headed *capensis* (= *mossambicanus*) inhabiting the montane forests. De Witte (1953) pointed out that *kirtlandii* and *capensis* (= *oatesii*) were sympatric in Katanga (= Shaba Province of Zaire) and he treated them as separate species.

After examining 771 specimens of *Thelotornis*, I recognize two species: *T. kirtlandii* restricted to evergreen forest and *T. capensis* which is widespread in savannas but also occurs in East African forests. Provisionally the savanna vine snake may be divided into three races: the typical form described from Natal by Andrew Smith (1849), the western race *oatesii* described from Matabeleland by Günther (1881) and a variable northeastern race *mossambicanus* described from the Manica Province of Mocambique by Bocage (1895). Microfilm copies of most of the relevant data sheets are deposited in the Transvaal

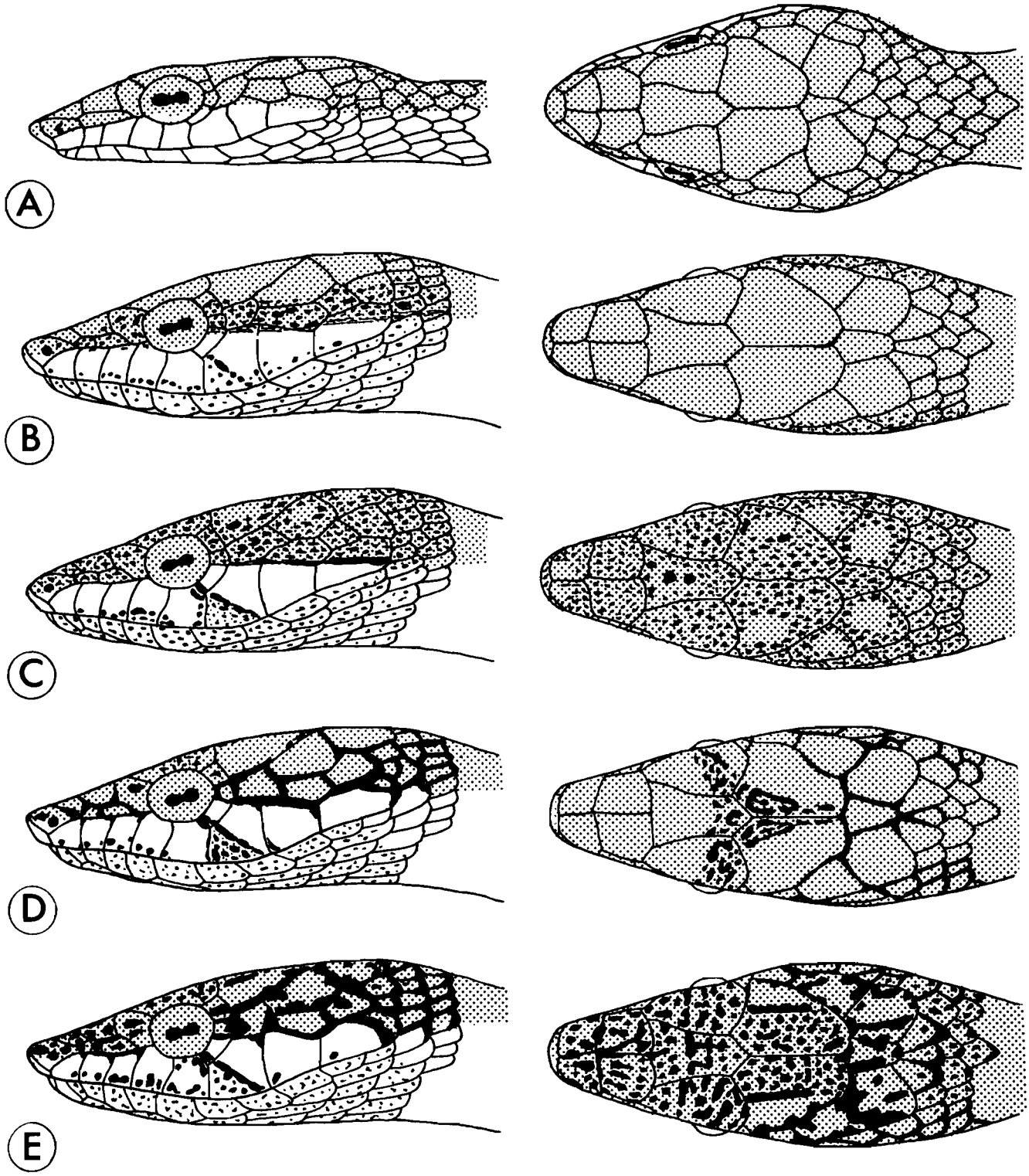

Fig. 1 *Thelotornis:* variation in head markings (lateral and dorsal views), semi-diagrammatic. A. *T. kirtlandii* UM 20596 Mushafi, Zaire. B. *T. capensis mossambicanus* (typical) UM 9067 Goonda, Mocambique. C. *T. c. mossambicanus* (fully speckled) NMSR 1563 Ugalla, Tabora, Tanzania. D. *T. c. oatesii* NMSR 3828 Mtorashanga, Rhodesia. E. *T. c. capensis* (fully speckled) UM 17530 Sinkukwe, Rhodesia. All specimens in the Umtali Museum.

Museum, the British Museum (Nat. Hist.) and the Smithsonian Institution.

Geographical variation

Colour markings of head and neck

In *T. kirtlandii* the top and sides of the head are uniform dull green and the supralabials uniform white or pink (Fig. 1A). The neck has black crossbars or chevrons, well illustrated in Pitman (1974).

In the typical *T. capensis mossambicanus* the top of the head is uniform emerald green. The temporal region is brown, speckled with black; the supralabials have black speckling, in particular a triangle with its base on the lower border of the sixth labial and its apex entering the lower posterior margin of the eye (Fig. 1B and C). The dark chevrons on the neck are suppressed and replaced by a series of black lateral blotches, which may be confluent.

The geographical variation in *T.c. mossambicanus* may be summarized as follows:

Somalia: Top of head uniform green; temporals brown marbled with black; some black labial speckling.

Kenya: Specimens from Taveta (BM), Voi (AMNH) and Tana River USNM) resemble *T. kirtlandii* in lacking black speckling on top of head and temporal region, but have black stippling on the labials; a Kilibassi specimen (AMNH 61657) has three black vertical bars on the neck, but AMNH 61640-1 from Voi have horizontal black bars on the neck. Specimens from Mt Mbololo (MCZ) and Loitokitok (MCZ) have top of head and temporal region uniform speckled.

Tanzania: Fifteen specimens from the Usambara Mountains (MCZ; BM) and one from Vituri, Uluguru Mts (MCZV) have top of head and temporal region uniform green but have black stippling on the labials, including the stripe on the sixth supralabial. All other specimens have speckled temporals, but uniform green heads are found in specimens from Uleia, Rondo Plateau and Mikindani. A speckled 'Y' pattern is found in specimens from Tendaguru, Liwale, Newala and Rondo Plateau. The head is uniform speckled in specimens from the south shore of Victoria Nyanza; Kibondo; Zengeragusu; Ugalla; Gulwe; Mpwapwa; Nyange, Uluguru Mts; Mahali Peninsula; Kitungulu; Rungwe Mtn; Newala and Kitaya.

Specimens from southeastern Zaire, northeastern Zambia and northern Malawi (Misuku Hills) have top of head and temporal region red-brown with dark stippling.

Specimens from southern Malawi have head stippling more or less restricted to 'Y' marking, often much reduced.

In all Mocambique material head is uniform green except for a series of five specimens from Mitacué Mountain which have uniformly speckled heads.

Specimens from eastern Rhodesia have head uniform green or with speckling restricted to a 'Y' marking.

In *T. capensis oatesii* the top of head is blue-green with coarse pink and black speckling restricted to a 'Y' marking, with its stem lying along the parietal suture and its arms extending across the supraoculars. The temporals are pink with the sutures outlined in black (Fig. 1D). The supralabial and neck markings are similar to those of *T. c. mossambicanus*, except that dark neck chevrons derived from the forest form are often discernible.

Zululand specimens of *T. c. capensis* have head markings similar to *T. c. oatesii*, but the temporal markings may be broken up by black spots. Specimens from Botswana, Rhodesia and the Transvaal usually have the coarse black speckling expanded to form a triangle with its base linking the anterior edges of the orbits and its apex on the occiput, speckling often extends forward to the end of the snout, but lateral parts of parietals are free from speckling (Fig. 1E). Head markings are poorly developed in juveniles of all taxa.

Loreals (Table 1)

Populations of *T. kirtlandii* west of Benin normally have two loreals in tandem. As one proceeds eastwards, an increasing proportion of specimens shows fusion of these two shields, so that in Zaire, Uganda and southern Sudan nearly all snakes have a single elongate loreal. In *T. capensis* two loreals is usual in all populations. If the number is reduced, it is often due to fusion of a loreal with an internasal or a prefrontal rather than with the other loreal.

Infralabial counts (Table 1)

The two species are clearly distinguishable on this character. In *T. kirtlandii* the range is 7 — 11, with a mode of 9, whereas in *T. capensis* the range is 9 — 13 with a mode of 11.

Ventral counts (Fig. 2)

Females usually have slightly higher counts than males. *T. kirtlandii* has the highest ventral counts (162-189). In *T. capensis*, relatively high counts are found in the western race *oatesii* (158-177), while in the east the counts decrease from north to south.

Subcaudal counts (Fig. 2)

These snakes have long slender tails with a high subcaudal count that may exceed the ventral count. Males have higher average counts than females. Only 47% of *T. kirtlandii* and 59% *T. capensis* had complete tails, so the samples available for analysis were small. The highest sample means occur in *T. kirtlandii* and the Usambara sample of *T. c. mossambicanus*. *T. c. oatesii* and *capensis* x *oatesii* hybrids have higher sample means than *T. c. capensis* or southern populations of *T. c. mossambicanus*.

Snout-vent length (Fig. 3)

Loveridge (1953), when distinguishing the taxa *capensis* and *oatesii* in Malawi, noted that *oatesii* attained a total length in excess of 1 400 mm, whereas *capensis* (= *mossambicanus*) did not exceed 1 250 mm.

Because of the high proportion of damaged tails, snout-vent length is a more practical indicator of size in this genus.

Thelotornis c. oatesii is the largest form and this is emphasized by the fact that it is also the most robust taxon. Typical *T. capensis* is relatively robust, but *T. c. mossambicanus* tends to be slender like *T. kirtlandii*.

Habitat

All authors have regarded *T. kirtlandii* as an evergreen forest species throughout its range and its distribution (Fig. 4) substantiates this view.

T. capensis mossambicanus is a versatile form which

Table 1 *Thelotornis:* variation in loreals and infralabials

Taxon and geographical sample	Loreals						Infralabials							
	N	0	1	2	3	$\bar{X}$	7	8	9	10	11	12	13	$\bar{X}$
kirtlandii (Hallowell)														
1. Sierra Leone to Ghana	21	—	2	38	—	1,95	—	—	21	14	3	—	—	9,53
2. Nigeria	9	—	6	12	—	1,67	—	9	9	—	—	—	—	8,50
3. Cameroun; Gabon; Congo	15	—	14	16	—	1,53	—	9	12	6	1	—	—	8,96
4. Zaire; north Angola	33	—	58	8	—	1,12	—	7	25	31	3	—	—	9,45
5. Uganda; south Sudan	12	—	24	—	—	1,00	1	5	6	10	—	—	—	9,14
capensis mossambicanus (Bocage)														
6. Somalia; Kenya	15	—	15	11	—	1,42	—	—	1	5	11	8	1	11,12
7. Usambara Mts; Tanzania	15	—	7	23	—	1,77	—	—	—	4	21	5	—	11,03
8. Rest of Tanzania	37	—	13	65	1*	1,88	—	—	—	14	52	10	2	11,00
9. Malawi; north Zambia; south-east Zaire	53	—	10	60	—	1,86	—	—	8	25	58	14	1	10,75
10. Mocambique; Rhodesia	97	1	18	157	2	1,90	—	—	2	23	122	34	9	11,13
capensis oatesii (Günther)														
11. Angola; South West Africa; Botswana	42	—	4	70	—	1,95	—	—	1	17	59	7	—	10,86
12. Zaire; Zambia; Malawi	116	3	20	158	—	1,86	—	—	7	32	147	34	2	10,96
13. Rhodesia	70	3	25	103	1	1,77	—	—	1	24	88	22	1	11,00
capensis hybrids														
14. Rhodesia; Mocambique	91	4	24	143	1	1,82	—	—	1	23	87	23	4	11,03
capensis capensis A. Smith														
15. Botswana; Rhodesia	24	—	5	39	2	1,93	—	—	—	5	30	12	1	11,19
16. Transvaal; Swaziland; Mocambique	64	1	8	117	2	1,94	—	—	4	23	77	20	—	10,91
17. Zululand; Natal	57	2	13	91	—	1,84	—	—	—	22	80	4	2	10,87

*Four loreals on one side of one snake.

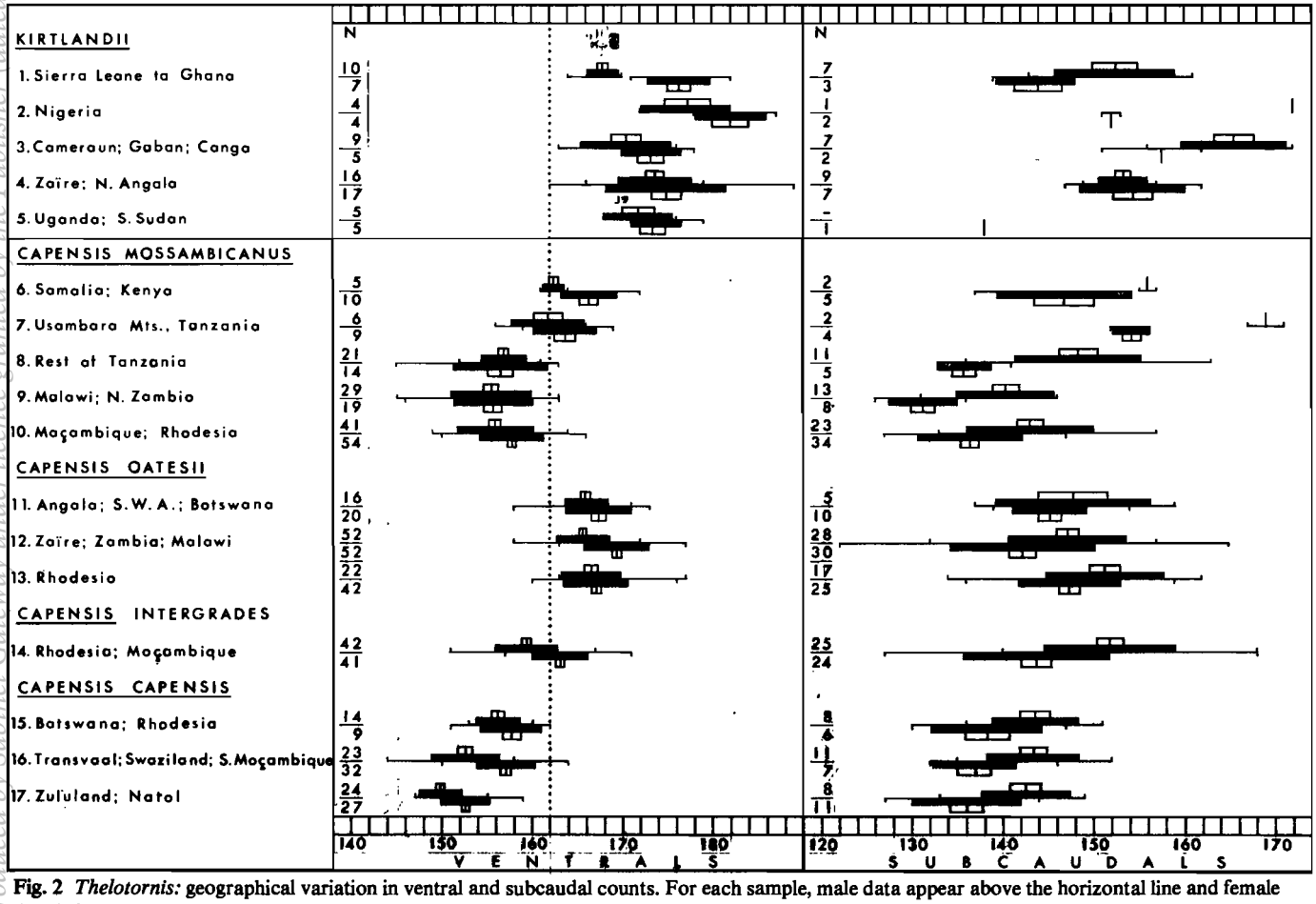

Fig. 2 *Thelotornis:* geographical variation in ventral and subcaudal counts. For each sample, male data appear above the horizontal line and female data below it. The horizontal line indicates the ranges; the vertical lines indicate the means; the solid rectangles indicate one standard deviation on each side of the mean and the hollow rectangles indicate one standard error on each side of the mean. Numbers indicate populations mapped in Fig. 4.

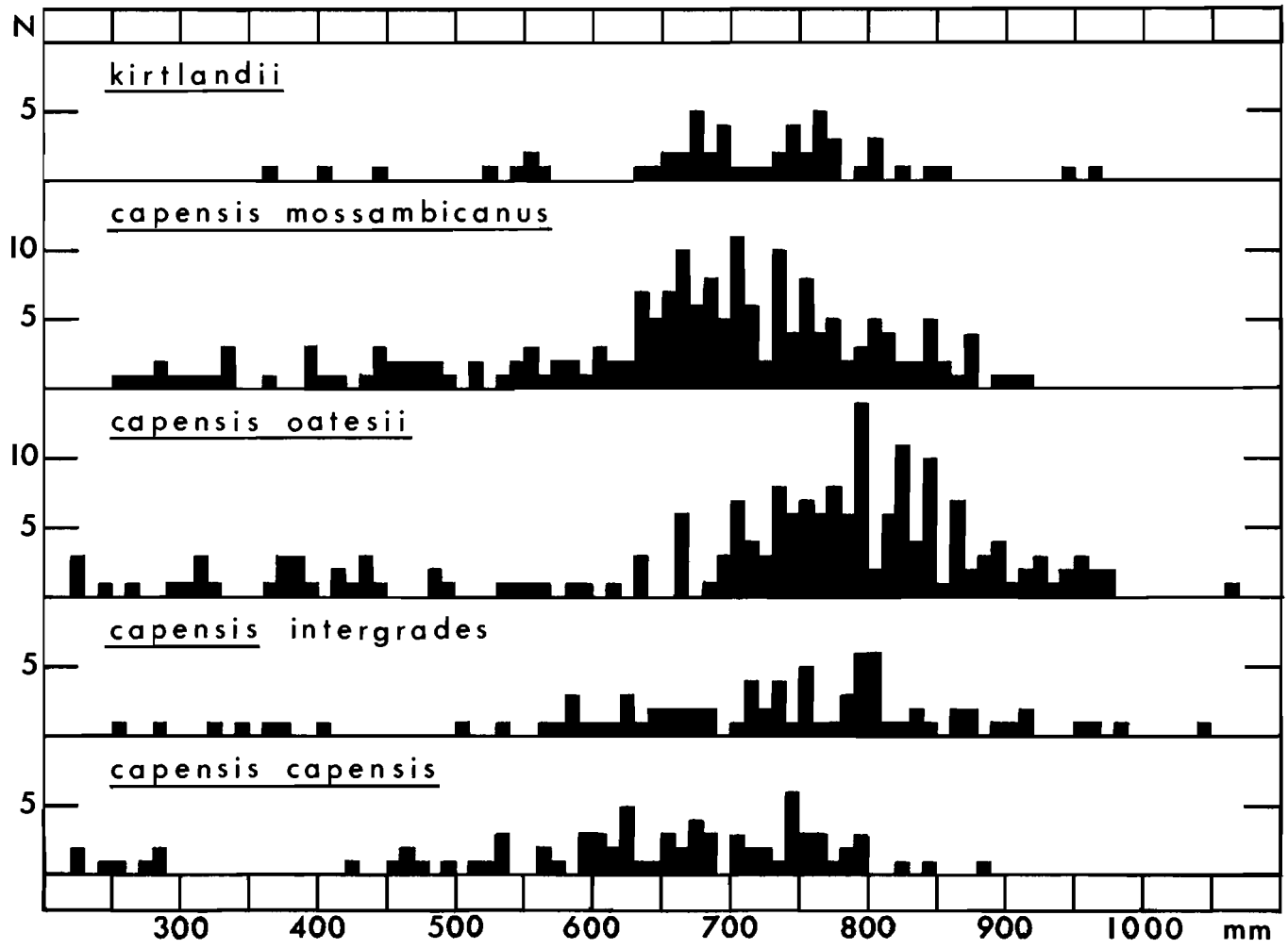

Fig. 3 *Thelotornis:* histogram to show distribution of snout-vent lengths in 10 mm units.

Loveridge (1937) listed as a taxon 'which sometimes occurs in rain forest, though not typical of its fauna having invaded it from the adjacent savanna'. The northern populations are very similar to *T. kirtlandii* in morphology, but occupy habitats that range from the evergreen forests of the Usambara Mountains to dry wooded *Acacia/Commiphora* steppe around Voi in Kenya. In Malawi, Mocambique and eastern Rhodesia, *T. c. mossambicanus* inhabits moist savannas and evergreen forests, while the western race *T. c. oatesii* and hybrid populations occupy drier savanna habitats.

The western populations of *T. c. oatesii* inhabit moist miombo woodlands and riparian forest as well as dry savannas with mopane (*Colophospermum*) and *Acacia*. Typical *T. capensis* inhabits a similar range of habitats.

Recognition of *T. capensis mossambicanus*

Within the species *Thelotornis capensis* there is a striking contrast between the homogeneous populations of *T. c. oatesii* and the highly variable eastern populations. It is convenient to revive *mossambicanus* (Bocage 1895), because in the southern part of its range this taxon can readily be distinguished by head markings from neighbouring populations of *oatesii, capensis* and their intergrades. Bocage's description was based on a specimen from Manica, formerly No. 1843 in the Museu Bocage, Lisbon, which I examined before it was recently destroyed by fire. It is true that many *T. c. mossambicanus* from Tanzania and Malawi resemble *T. capensis* from Botswana, Rhodesia and Transvaal in having the top of the head entirely speckled, but in *mossambicanus* the temporals are speckled with black (Fig. 1C), whereas in *capensis* they are usually black-margined as in *oatesii* (Fig. 1E).

Evolution of *Thelotornis*

Schmidt (1923) considered *Thelotornis* to be a forest snake which has secondarily invaded savanna, a view supported by Bogert (1940). Analysis of variation within the genus suggests the following sequence of events:

Two genera of back-fanged diurnal arboreal snakes evolved in Africa, *Thelotornis* inhabiting the evergreen forests extending right across Africa and *Dispholidus* (boomslang) inhabiting savannas.

At various times during the Pliocene and Pleistocene the range of *Thelotornis* was bisected by an 'arid corridor' extending from the horn of Africa to the South West Arid. The eastern forests were reduced to small relict patches and only in the north did the original forest form of *Thelotornis* persist with little modification. Elsewhere populations were forced to adapt to savanna conditions. The simple green and white (or pink) lateral head pattern was broken up by a speckled longitudinal band passing through the eye and across the temporal region, while black speckling appeared on the labials and chin. In some populations the uniform green dorsal surface of the head was broken up by pink and black speckling, initially extending along the parietal suture and then across the supraoculars to form a 'Y'.

During a Pleistocene pluvial, a pioneering stock of

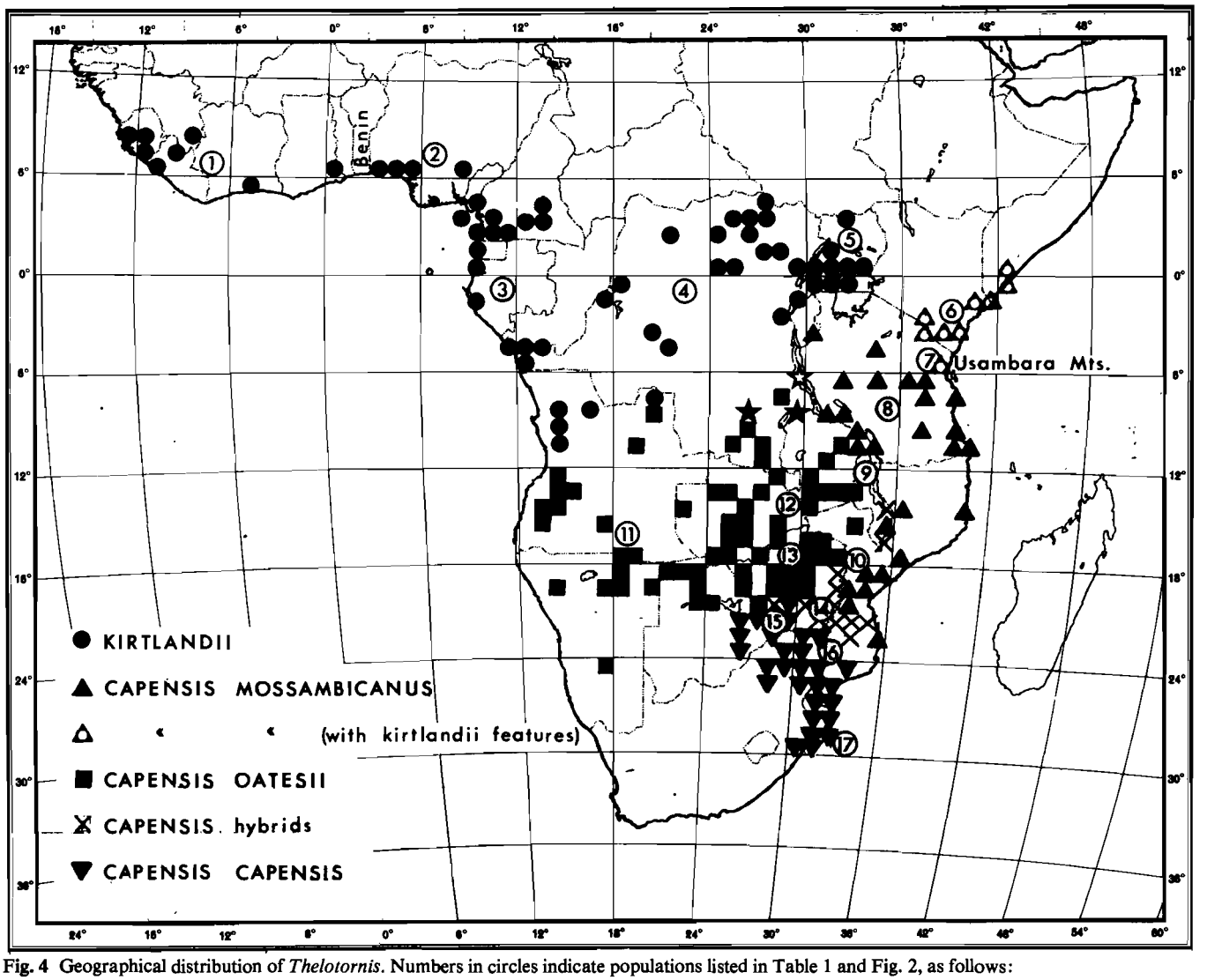

Fig. 4 Geographical distribution of *Thelotornis*. Numbers in circles indicate populations listed in Table 1 and Fig. 2, as follows:
T. kirtlandii: 1. Sierra Leone, Liberia, Ivory Coast and Ghana; 2. Nigeria; 3. Cameroun, Gabon and Congo; 4. Zaire and Angola; 5. Uganda and Sudan.
T. capensis mossambicanus: 6. Somalia and Kenya; 7. Usambara Mts; 8. Rest of Tanzania; 9. Malawi; 10. Mocambique and Rhodesia.
T. capensis oatesii: 11. Angola, South West Africa and Botswana; 12. Zaire, Zambia, Malawi and Mocambique; 13. Rhodesia.
T. capensis hybrids: 14. Rhodesia and Mocambique.
T. capensis capensis: 15. Botswana and Rhodesia; 16. Transvaal, Swaziland and Mocambique; 17. Zululand and Natal.
Stars indicate species parapatry within a degree square - solid star: *T. kirtlandii* and *T. c. oatesii;* open star: *T. kirtlandii* and *T. c. mossambicanus.*

savanna-adapted *Thelotornis* was able to cross the 'arid corridor' and establish itself in the Angola region. Subsequently isolated by the restoration of the 'arid corridor', this population continued to diverge. The top of the head became blue-green with coarse pink and black speckling restricted to a 'Y' pattern, while the temporal pattern was modified to pink with each shield bordered in black. This western form retained relatively high ventral and subcaudal counts, whereas in the southeastern populations these counts tended to be reduced.

During a subsequent pluvial, the western savanna form recrossed the 'arid corridor' and hybridized with the southeastern populations, producing a form which has the temporal pattern and sometimes the dorsal head pattern of western *oatesii,* but has the low ventral and subcaudal counts of southeastern *mossambicanus.*

Subsequent interpluvial conditions restored the 'arid corridor' and another dry zone through the Limpopo Basin, thus dividing *T. capensis* into three isolated races.

The latest amelioration of the climate allowed the savanna populations to expand, especially *T. c. oatesii.* The present distribution of the various taxa is shown in Fig. 4.

Although clear-cut evidence of sympatry between *T. kirtlandii* and *T. capensis oatesii* in Angola and Zaire is scanty (Witte 1953 recorded both taxa from Musosa, Shaba, Zaire; Laurent 1954, 1964 recorded both taxa from the vicinity of Dundo, Angola), there is certainly no evidence of intergradation in this region. Further east, there is parapatry between *T. kirtlandii* and *T. c. mossambicanus* on the Mahali Peninsula on the eastern side of Lake Tanganyika, unfortunately there is only one specimen of each taxon available in the British Museum (Nat. Hist.) and the forest species was taken 600 m higher than the savanna form.

Superficially, the vine snakes from savannas of southern Somalia and eastern Kenya and the forested Usambara Mountains look like intergrades, for many have the top of the head and temporal region uniform green and in some specimens the rostral and nasals are recurved to the upper surface of the head as is usual in *T. kirtlandii* (Bogert 1940, Fig. 10). Their ventral counts are intermediate between those of *T. kirtlandii* (which probably has more ventrals

than the ancestral form) and *T. c. mossambicanus* and there is considerable variation in number of loreals, but they have the high infralabial count of *capensis* (Table 1). These northeastern *Thelotornis* populations are well separated from the nearest *T. kirtlandii* populations in Uganda by the highlands of Kenya and northern Tanzania and it seems likely that the characters of the ancestral forest form have been preserved in the relict forests on the Usambara Range rather than recently acquired through contact with *T. kirtlandii*.

In Malawi *T. c. mossambicanus* occurs in the forested highlands and *T. c. oatesii* in the hot dry country along the shores of Lake Malawi and in the Shire Valley. No intermediates have been recorded from this area, but Stevens (1974) reports that the two forms are sympatric on the Chileka Plain north of Blantyre. In Rhodesia *T. c. oatesii* hybridizes extensively with *T. c. mossambicanus* in the east and *T. c. capensis* in the south, these mixed populations extend well across the Mocambique Plain and virtually divide pure populations of *mossambicanus* from those of typical *capensis*. Generally the head markings of *oatesii* are dominant in the hybrids and the mean ventral counts are intermediate between those of *oatesii* and *capensis/mossambicanus* (Fig. 2).

A key to the genus *Thelotornis* A. Smith

1a. Temporal region uniform green like the top of the head, labials without black speckling; distinct black cross-bands on neck; rostral and nasals recurved onto top of snout; infralabials usually 7—10; loreals usually two in West Africa, one in Central Africa ..... *kirtlandii*

1b. Temporal region usually with dark speckling or each temporal margined with black; black lateral blotches on neck; rostral and nasals usually not recurved onto top of snout; infralabials usually 10—13; loreals usually two 2

2a. Top of head uniform green or with black speckling; temporals usually with dark stippling mossambicanus ..... *capensis*

2b. Top of head blue-green with black and pink speckling, often restricted to a 'Y' shaped marking; temporals pink margined with black 3

3a. Ventrals usually more than 162; top of head always blue-green with black and pink speckling restricted to a 'Y' shaped marking with its shaft along the parietal suture and the arms extending to the supraoculars ..... *capensis oatesii*

3b. Ventrals usually less than 162; top of head with dark speckling extensive or restricted to a 'Y' shaped marking ..... *capensis capensis*

Acknowledgements

I am grateful to the following colleagues for facilities granted while I examined *Thelotornis* material in their care: Ms A.G.C. Grandison (British Museum, Nat. Hist.); W.D. Haacke (Transvaal Museum) and G. Sacarrão (Museu Bocage, Lisbon). I also thank the following for sending material on loan: C.J. McCoy, Jr. (Carnegie Museum); H. Marx (Field Museum of Natural History); M.J. Penrith (State Museum, Windhoek); J.L. Perret (Geneva Natural History Museum); U. de V. Pienaar (Kruger National Park); J.A. Pringle (Natal Museum); R. Rau (South African Museum); N. Schaefer (Port Elizabeth Museum); P.H. Skelton (Albany Museum); E.E. Williams (Museum of Comparative Zoology, Harvard); G.R. Zug (U.S. National Museum of Natural History); and R.G. Zweifel (American Museum of Natural History). B. Lanza (Museo Zoologico de 'La Specola', Firenze) kindly provided data for six Somali specimens of *T. capensis mossambicanus*.

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