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Review of the Dispholidini, with the description of a new genus and species from Tanzania (Serpentes, Colubridae)

D.G. BROADLEY
Research Associate, Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe
Present address: Biodiversity Foundation for Africa, P.O. Box FM 730 Famona, Bulawayo, Zimbabwe. email: broadley@telconet.co.zw

V. WALLACH
Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, U.S.A. email: vwallach@oeb.harvard.edu

SYNOPSIS. The tribe Dispholidini (Bourgeois 1968) is reviewed, paying particular attention to dentition and visceral anatomy. A new genus and species, *Xyelodontophis uluguruensis,* is described from the Uluguru Mountains in Tanzania. All five genera have enlarged rear maxillary teeth. *Thrasops* seems to be basal, *Rhamnophis* shows the development of dagger-like teeth tapering from base to tip, then the other three genera appear to radiate, with *Xyelodontophis* having more derived dagger teeth broadest in the middle, while *Dispholidus* and *Thelotornis* seem to have independently developed enlarged grooved rear fangs.

Thrasops schmidti is recognised as a relict evolutionary species. No subspecies of *Rhamnophis aethiopissa* or *Dispholidus typus* are recognised, but the population of *Dispholidus* on Pemba Island probably represents an undescribed species.

INTRODUCTION

From the time of Boulenger's catalogues (1893–96), it was customary to separate the aglyphous colubrid snakes (subfamily Colubrinae) from the opisthoglyphs (subfamily Dipsadomorphinae or Boiginae), see for example Loveridge (1957) and FitzSimons (1962).

Bourgeois (1968) erected a subfamily Dispholidinae, including the aglyphous genera *Thrasops* Hallowell 1857 and *Rhamnophis* Günther 1862, and the opisthoglyphous genera *Dispholidus* Duvernoy 1832 and *Thelotornis* A. Smith 1849. Subsequent authors have often treated *Rhamnophis* as a synonym of *Thrasops* (e.g. Hughes & Barry, 1969; Pitman, 1974; Spawls, 1978; Hughes, 1983; Trape & Roux-Estève, 1995; Chippaux, 1999) and many have considered these aglyphous snakes to be members of the tribe Philothamnini (e.g. Dowling & Duellman, 1978).

During a review of the genus *Thelotornis* in East Africa (Broadley, 2001), a snake from montane forest on the summit of the Uluguru Mountains was initially assumed to represent a new species. However, examination of its rear maxillary teeth showed that they were not the anticipated grooved fangs, but distinctive curved dagger-shaped teeth with sharp anterior and posterior ridges, which are widest midway along the tooth. To determine the relationships of this strange snake to the other taxa of the Dispholidini, its skull was prepared (after examination of the dental gland) and compared with skulls of the other genera. This prompted a review of the genera *Thrasops* and *Rhamnophis,* which appear to represent basal taxa of the Dispholidini. As the 'Dagger-tooth Vine Snake' of the Uluguru Mountains seems to be transitional between *Rhamnophis* and *Thelotornis,* but cannot be accommodated in any of the existing genera of the tribe Dispholidini, it is proposed to erect a new genus and species for it. In external appearance and scale counts it resembles *Thelotornis*, but it lacks the distinctive horizontal key-hole shaped pupil of that genus.

It is with pleasure that we dedicate this paper to Garth Underwood, in recognition of the major contributions that he has made to our understanding of African snakes.

MATERIALS AND METHODS

This study is largely based on material available in the Natural History Museum of Zimbabwe and the Museum of Comparative Zoology, Harvard, with additional data derived from the literature. Unfortunately the collections in the Natural History Museum were not accessible. Loveridge's 1944 revisions of *Thrasops, Rhamnophis* and *Thelotornis* were based largely on scalation, supplemented by maxillary tooth counts and coloration of head and neck in the case of *Thelotornis.* We have emphasised the morphology of the rear maxillary teeth and skull, and have also used data from the visceral anatomy, using the Philothamnini as the outgroup for comparative purposes. Data for good series of *Philothamnus angolensis, Hapsidophrys lineatus* and *H. smaragdina* were available [Broadley (1966) provisionally synonymised *Gastropyxis* Cope 1860 with *Hapsidophrys* Fischer 1856, and this move is supported by the visceral data]. In the species accounts we have only presented chresonymies, full synonymies are included in the review of the East African *Thelotornis* (Broadley, 2001) and investigation of the variation in the wide-ranging genus *Dispholidus* awaits future workers!

In the description of the visceral anatomy, the mean value for most characters as % snout-vent length (SVL) is presented first, followed parenthetically by the range or midpoint (MP) value. When only the name of an organ is given, the value represents its length. Ratios of two visceral characters are presented in fractional notation. When only one value is given for a character, it is identical in the two specimens or differs by less than 0.1%.

The position of the umbilicus is determined by the most anterior ventral bearing a scar (the scar usually covers three ventrals and the umbilicus exited through the medial scute). The umbilical scar-vent interval is calculated by dividing the number of ventrals from the scar to the vent by the total number of ventral scutes.

Material for which skulls or viscera were examined is listed in appendices. Institutional abbreviations follow Leviton *et al.* (1985), with the addition of:

IRSL = Instituit d'Rechereche Scientifique, Lwiro, Democratic Republic of Congo (DRC); UNAZA = Université National du Zaire, Kisangani, DRC; VW = Van Wallach dissection number (museum deposition of specimen unknown).

CHARACTER ANALYSIS

1. Rear maxillary teeth. The three rear maxillary teeth of *Thrasops flavigularis* (type species) and *T. jacksonii* are enlarged and separated from the small anterior teeth by a diastema, they taper from base to tip and have slight ridges anteriorly and posteriorly (Fig. 1A, Group B dentition of Jackson & Fritts, 1995). The posterior ridge becomes blade-like in some genera, e.g. *Heterodon* (Kardong, 1979), *Thamnophis* (Wright, *et al.*, 1979) and *Stegonotus* (Jackson & Fritts, 1995).

The same teeth in *Rhamnophis aethiopissa* (Fig. 1B) and *R. batesi* (Fig. 1C) are curved, with sharp anterior and posterior ridges, but not nearly as well developed as in the 'Dagger-tooth Vine Snake' of the Uluguru Mountains, in which the ridges are broadest midway along the tooth, which is leaf-shaped, narrowing at the base (Fig. 1F). In *Dispholidus* and *Thelotornis* the three greatly enlarged rear maxillary teeth are deeply grooved (Group D dentition of Jackson & Fritts, 1995), but these genera retain a strong ridge on the anterior face of the fangs. In *Thelotornis*, this ridge arises within the groove, so that the venom canal is divided, before petering out well before the fang tip (Fig. 1G, after Meier, 1981, fig 4). In *Dispholidus* on the other hand, the ridge runs along the anterior edge of the groove (Fig. 1H, after Meier, 1981, fig 2).

With regard to number of maxillary teeth, *Rhamnophis aethiopissa* (16 to 20 + 3) resembles *Thrasops* spp. (17 to 18 + 3), but *R. batesi* (30 to 35 + 3, Fig. 1C) is divergent in this respect. The Dagger-tooth Vine Snake has 14 + 3, thus matching *Thelotornis* (11 to 16 + III) in actual tooth number. *Dispholidus* shows a marked reduction in number of anterior teeth to 4 to 8 + III. Counts of maxillary tooth sockets are much higher in the Philothamnini: 17–48 in *Philothamnus* and 20–33 in *Hapsidophrys.*

2. Dental (Duvernoys') gland. This gland is small in *Thrasops* and *Rhamnophis* (Kochva, 1978), larger in *Thelotornis* (but smaller than the orbit), still larger in the Dagger-tooth Vine Snake (subequal to the orbit) and reaches its maximum development in *Dispholidus* (Kochva, 1978), with a large, purely serous, slightly branched, tubuloacinous Duvernoy's gland, the tubule walls highly folded, increasing the storage space within the gland (Taub, 1967), thus constituting a reservoir (Underwood, 1997). The mechanism of delivery of toxic dental gland secretions by low pressure systems has been demonstrated for *Boiga irregularis* (Kardong & Lavin-Murcio, 1993) and is effective regardless whether or not the teeth are grooved (Weinstein & Kardong, 1994).

3. Skull. The Dispholidini were first recognised (as a subfamily) by Bourgeois (1968) on the basis of their similar skull morphology (Fig. 2). She drew attention to the forked ectopterygoid, large optic fenestra and interorbital vacuity (also noted by Underwood, 1967). The ectopterygoid is shallowly forked in *Thrasops, Thelotornis* and the Dagger-tooth Vine Snake, but is very deeply forked in both species of *Rhamnophis* and in *Dispholidus.* Underwood (1967) noted the absence of a Vidian canal in the skulls of *Thrasops* and *Thelotornis*, but Vaeth (1982) found a short, but distinct, Vidian canal in the skulls of three *Thrasops jacksonii.*

4. Pupil shape. The pupil is round in *Thrasops* and *Rhamnophis* (Fig. 3) as in the Philothamnini, but in *Dispholidus* and the Dagger-tooth Vine Snake it may be more pear-shaped, due to an anterior prolongation. *Thelotornis* is distinguished by its horizontal 'key-hole' shaped pupil (Fig. 4B-D).

5. Visceral anatomy. The Dispholidini can be characterized by the following visceral characteristics (Tables 2–4): umbilical scar-vent interval 8–12% total ventrals; hyoid short with posterior tips at 7–10% SVL, heart short,1.5–3.1% (mean 2.4%); right systemic arch reduced to 0.20–0.40 left systemic arch diameter; liver narrow with midpoint at 43–46% SVL; gall bladder craniad of pancreas and spleen; testes normally unipartite but occasional specimens with bi- or tri-partite organs (the additional segments being small sections separated from the main body either posteriorly or anteriorly); kidneys compact but segmented (15–45 segments); no tracheal lung; trachea with narrow, well-separated cartilages that lack free tips, tracheal membrane expanded to 2.0–4.0 (mean = 2.9) times the circumferential width of the rings; weak development of the cardiac lung to midheart level; tracheal entry into right lung subterminal, right lung with small anterior lobe and small orifice; right lung elongate (69–70% SVL), extending to 94–97% body length, cranial vascular portion 0.15–0.25 lung length, usually with midventral avascular strip, caudal saccular portion long 0.75–0.85 lung length; faveolar parenchyma arranged in 2–3 tiers with pattern of transverse smooth muscle ribs enclosing rows of paired faveoli; semisaccular portion of lung short (0.10–0.20 vascular lung length) with abrupt termination of parenchyma along a transverse border.

The hemipenes of the genera *Thrasops, Dispholidus* and *Thelotornis* appear to be similar, being simple, capitate, with an undivided sulcus. There are large basal spines which diminish in size distally and are replaced by calyces on the distal cap (Bogert, 1940). The organs of the Dagger-tooth Vine Snake show little difference, the nude basal portion has four large hooks, the medial portion is spinose and the apical portion is calyculate. The hemipenes of *Rhamnophis* have not yet been described.

6. Dorsal head coloration. The development of complex head patterns may aid in species recognition. All four species of *Thrasops* have the head uniform olive when subadult, eventually becoming uniform black. *Rhamnophis batesii* has a uniform brown or black head, while that of *R. aethiopissa* is green, with the shields margined with black. A somewhat similar black vermiculation on a yellow or green ground is found in males of some populations of *Dispholidus typus,* but many have no colour pattern. The Dagger-tooth Vine Snake has dark margins to the head shields and yellow labials. The four species of *Thelotornis* can be distinguished by the colour pattern of the head (Broadley, 2001). The top of the head is uniform green in *T. kirtlandii* (Fig. 4B), *T. usambaricus* and some *T. mossambicanus*, but blue-green with black and pink speckling in *T. capensis* (Fig. 4D). The temporals are uniform green in *T. kirtlandii* (Fig. 4B) and *T. usambaricus*, brown with black speckling in *T. mossambicanus* (Fig. 4C), and pink margined with black in *T. capensis* (Fig. 4D). The supralabials are uniform or with faint green or grey stippling in *T. kirtlandii,* but the other taxa have black spots, usually including a speckled black triangle on the sixth labial.

7. Throat pattern. All members of the Dispholidini (and some members of the Philothamnini) can inflate the throat in a threat display, reaching its maximum development in *Dispholidus.* Chippaux (1999, Pl. 17) illustrates this phenomenon in *Thrasops flavigularis,* where the black dorsum contrasts with the pale throat, but in *T. jacksonii* the throat often becomes entirely black. *Rhamnophis* has the dark green dorsal scales bordered with black, the throat is yellowish in *R. batesii* and green in *R. aethiopissa. Dispholidus* comes in a wide range of colour patterns, but usually

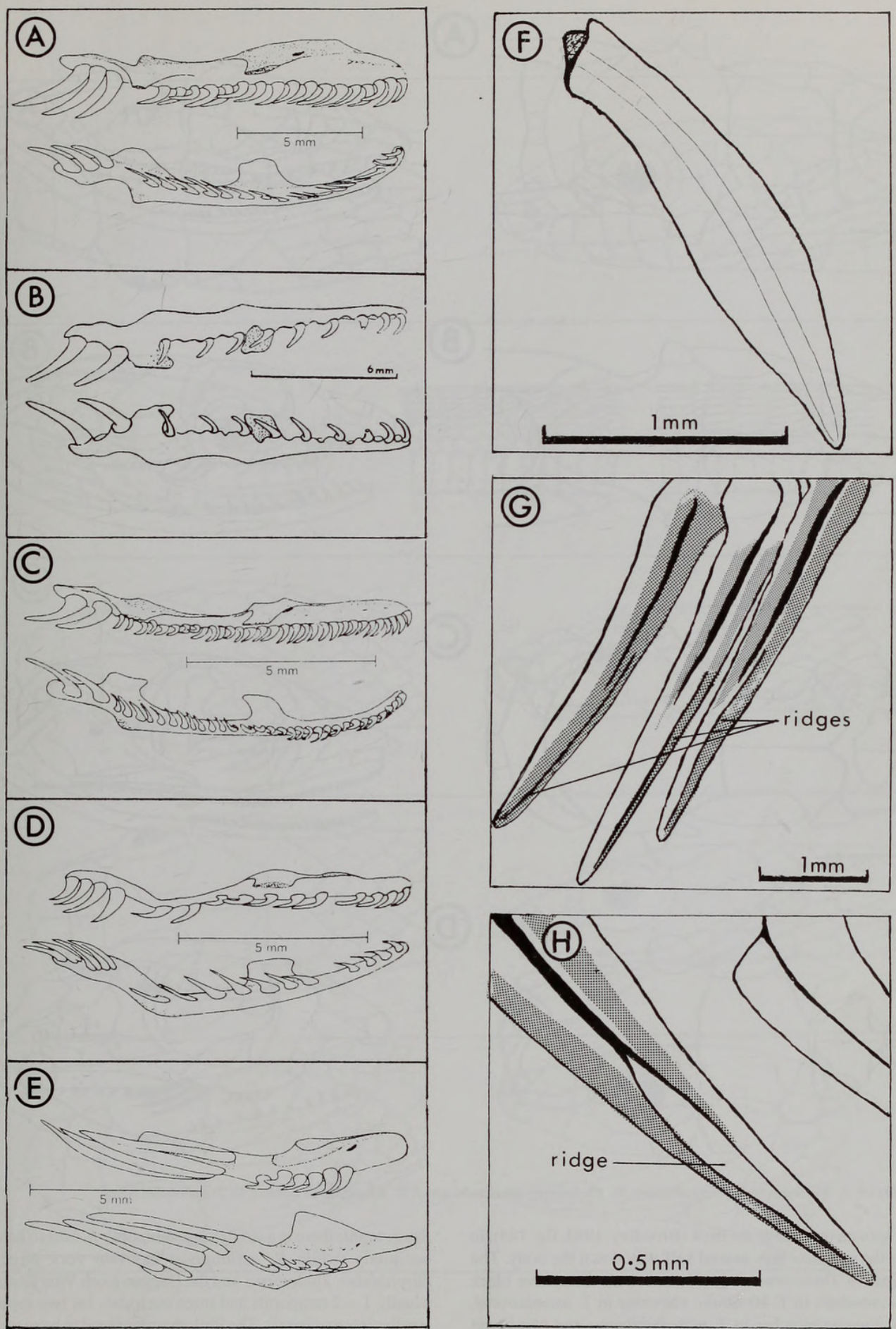


Fig. 1 Dentition: Left – maxillae of: A. *Thrasops flavigularis*; B. *Rhamnophis aethiopissa*; C. *Rhamnophis batesii*; D. *Thelotornis kirtlandii*; E. *Dispholidus typus*. Right – teeth of: F. *Xyelodontophis uluguruensis*; G. *Dispholidus typus*; H. *Thelotornis kirtlandii*. (A, C, D, E after Chippaux, 1999; B after Bourgeois, 1968; F, G, H after Meir, 1981).

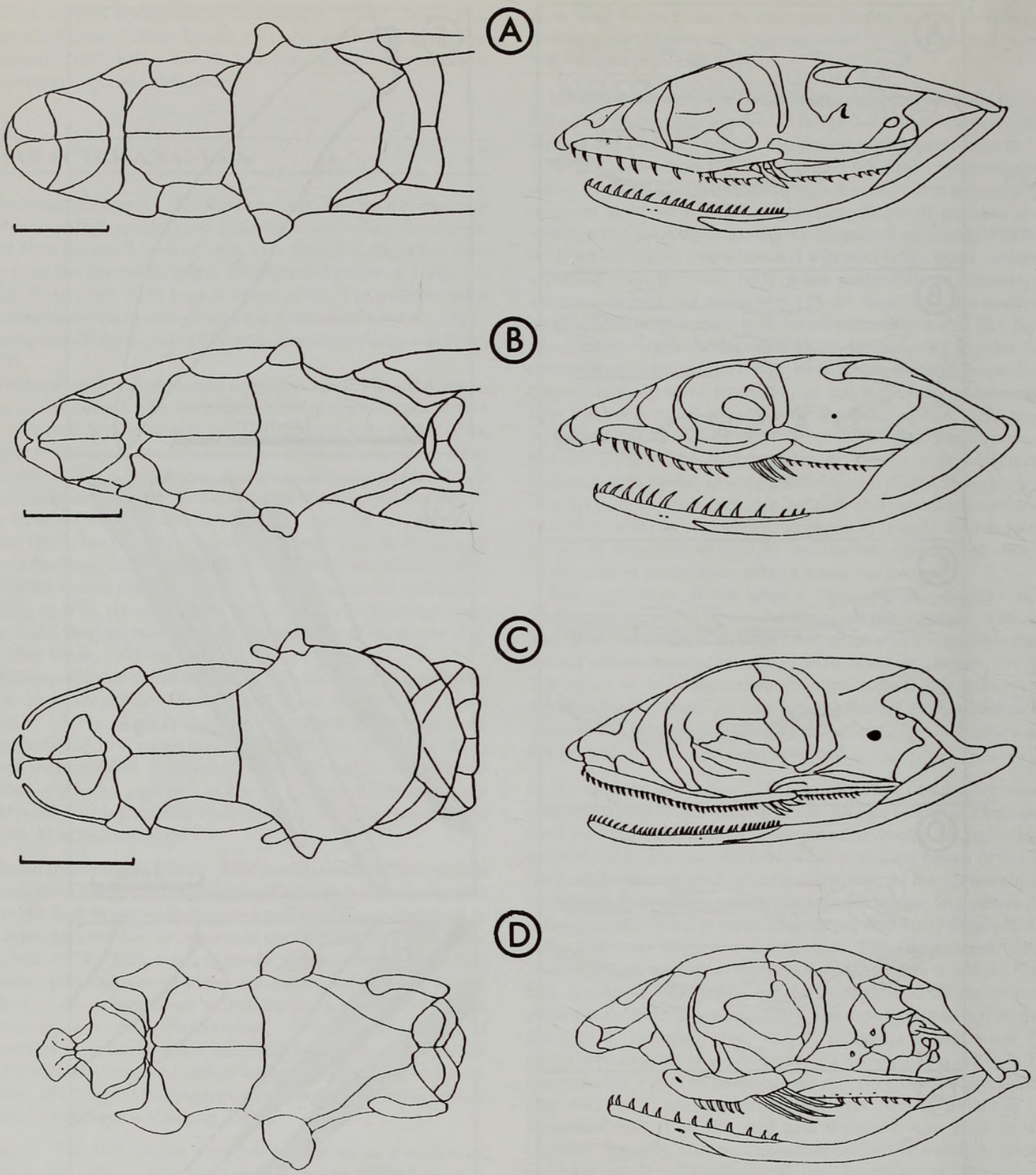


Fig. 2 Skulls of: A. *Xyelodontophis uluguruensis*; B. *Thelotornis mossambicanus*; C. *Rhamnophis batesii*; D. *Dispholidus typus.*

has a black spot on the side of the neck (Broadley, 1983, fig. 144), in this species the inflation may extend half way down the body. The inflated throat of *Thelotornis* is grey-white with distinctive black markings – crossbars in *T. kirtlandii,* chevrons in *T. usambaricus*, one or two elongate blotches in *T. mossambicanus* and two larger dorsally extensive blotches in *T. capensis*.

8. Temporals and occipitals. In *Thrasops* there are almost invariably 1 + 1 temporals and there are no enlarged occipital shields. In *Rhamnophis* there is a single large temporal: *R. batesii* has four large occipitals, while *R. aethiopissa* has two very large ones. In *Dispholidus, Thelotornis* and the Dagger-tooth Vine Snake there are usually 1 + 2 temporals and three occipitals (or two separated by a smaller interoccipital). The Philothamnini tend to have more numerous temporals (1 + 1 up to 2 + 2 + 2) and no enlarged occipitals.

9. Supralabials (Table 1). *Thrasops* usually has 8 supralabials, the fourth and fifth entering the orbit. *Rhamnophis batesii* has 7 or 8, 4

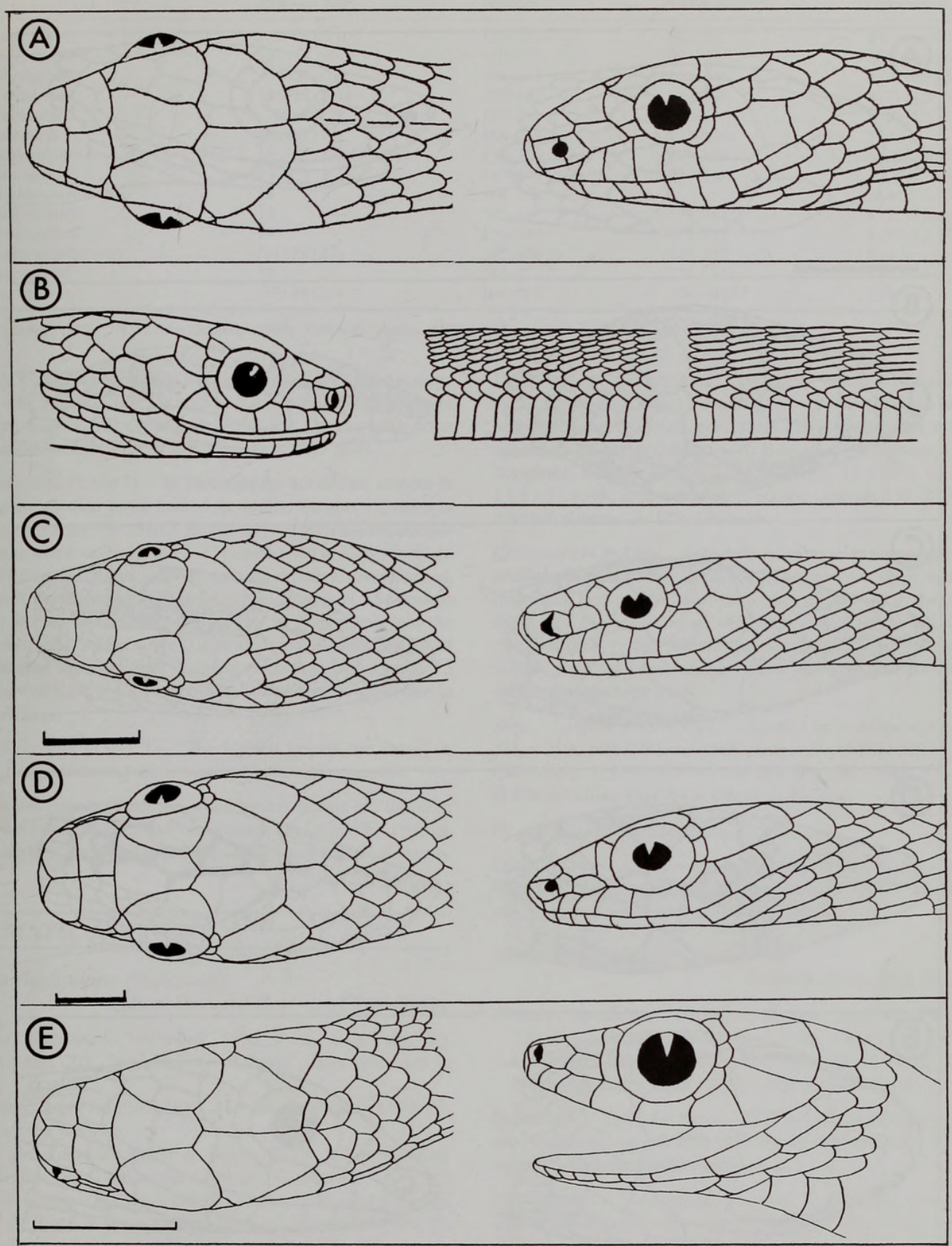


Fig. 3 Head shields of: A. *Thrasops flavigularis*; B. *Thrasops occidentalis,* with midbody scalation to the right, compared with midbody scalation of *T. flavigularis* on the far right (after Parker, 1940); C. *Thrasops jacksonii*; D. *Rhamnophis aethiopissa*; E. *Rhamnophis batesii*.

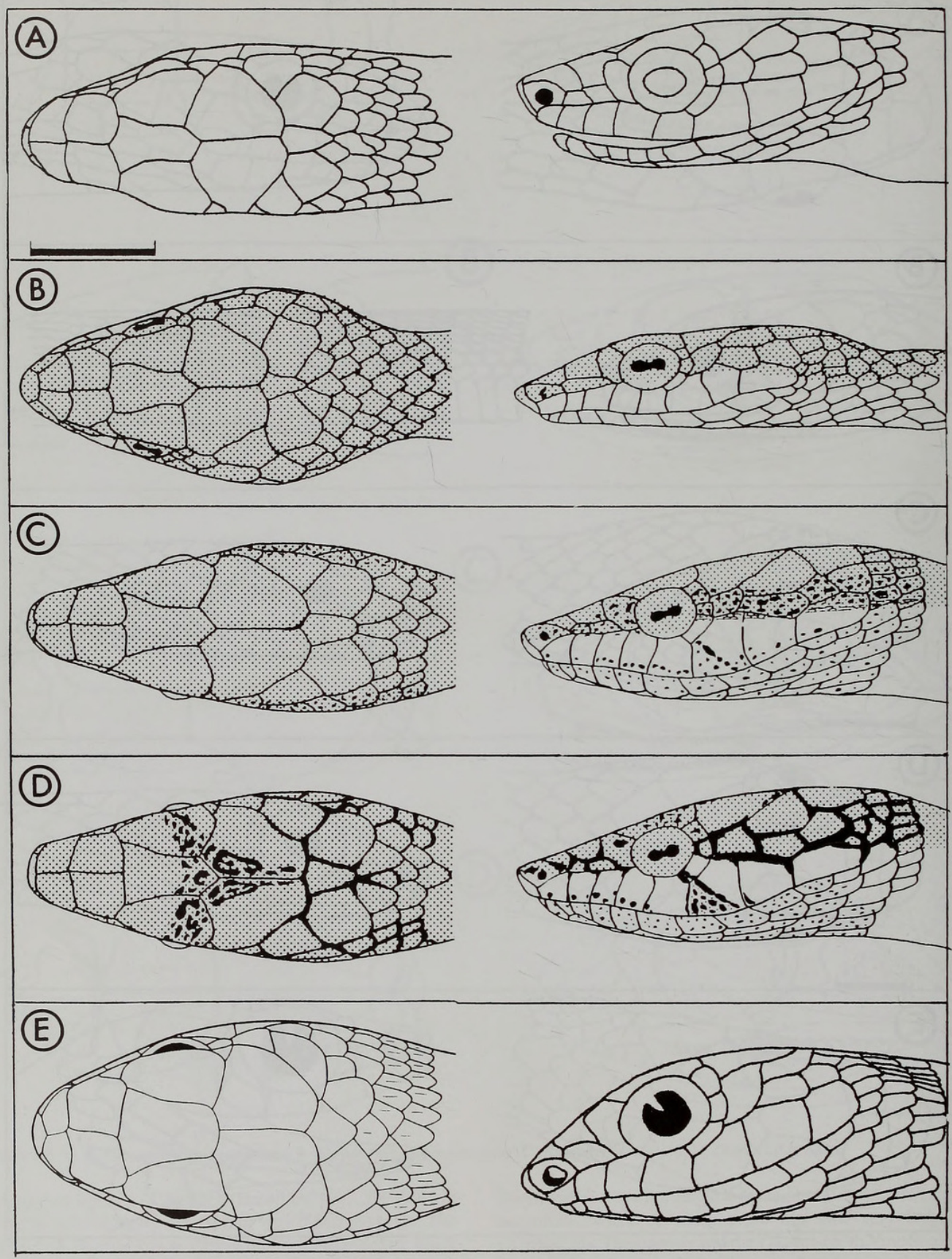


Fig. 4 Head shields of: A. *Xyelodontophis uluguruensis* (holotype); B. *Thelotornis kirtlandii*; C. *Thelotornis mossambicanus*; D. *Thelotornis capensis*; E. *Dispholidus typus*.

Table 1 Dispholidini compared with Philothamnini: variation in midbody scale rows, ventrals, subcaudals and supralabials (rare variations in parentheses).

Taxon	midbody rows	ventrals	subcaudals	supralabials [in orbit]
*Philothamnus spp.**	(13) 15	135–213	60–175	8/9 [4 to 6]
*Hapsidophrys spp.***	15	150–176	90–172	8/9 [4 to 6]
Thrasops flavigularis	13 (15)	195–215	128–146	8 (9) [4,5 (5,6)]
Thrasops occidentalis	15 – 19 (21)	175–187	119–140	8 (7) [4,5 (5,6)]
Thrasops jacksonii	(17) 19 (21)	187–211	130–155	8 (9) [4,5 (5,6)]
Thrasops schmidti	(16) 17 (19)	168–184	121–149	8 [4,5]
Rhamnophis aethiopissa	15 – 17 (19)	154–179	117–159	6 – 9 [3,4; 4,5; 5,6]
Rhamnophis batesii	13	163–179	91–114	7 – 8 [4,5; 5,6]
Xyelodontophis uluguruensis	19	168–169	?	8 [4,5]
Thelotornis kirtlandii	19	162–189	139–161	8 (7, 9) [4,5 (5,6)]
Thelotornis usambaricus	19	156–169	151–175	8 (9) [4,5 (3,4,5)]
Thelotornis mossambicanus	(17) 19 (23)	149–166	127–158	8 [4,5]
Thelotornis capensis	19	144–177	128–165	8 [4,5]
Dispholidus typus	(17) 19 (21)	164–201	104–142+ #	7 (3,4)

*Data from Hughes (1985). **Data from Chippaux (1999). #168 in D. 'pemba' (MCZ 45587).

& 5 or 5 & 6 entering orbit. The widespread *R. aethiopissa* is more variable, 6 to 9 labials, often with 3 & 4 entering orbit in southern and eastern populations. *Thelotornis* and the Dagger-tooth Vine Snake usually have 8 (4 & 5) and *Dispholidus* 7 (3 & 4).

10. Dorsal scales (Table 1). In *Thrasops* the dorsals are smooth in juveniles, the median rows keeled in adults, number of rows at midbody varies from 13–15 in *T. flavigularis* (which has the dorsals twice as long as the ventrals) to 17–21 (usually 19) in *T. jacksonii*. In *Rhamnophis* the dorsals are smooth, with the vertebral row enlarged, 13 rows in *R. batesii* and 15–19 rows in *R. aethiopissa*. The dorsals are feebly keeled and usually in 19 rows in *Thelotornis* and the Dagger-tooth Vine Snake, while *Dispholidus* usually has 19 rows of strongly keeled scales. In the Philothamnini there are usually 15 scale rows, which are usually smooth in *Philothamnus*, but keeled in *Hapsidophrys*.

11. Ventral counts (Table 1). The highest counts are found in *Thrasops flavigularis* and the lowest in *Thelotornis capensis*.

12. Subcaudal counts (Table 1). The lowest counts are found in *Rhamnophis batesii* and some populations of *Dispholidus typus*, while the highest are found in the two forest species of *Thelotornis*.

SYSTEMATIC ACCOUNT

Thrasops flavigularis (Hallowell)
Yellow-throated Bold-eyed Tree Snake

Dendrophis flavigularis Hallowell, 1852, *Proc. Acad. nat. Sci. Philadelphia*: 205. Type locality: 'Liberia', later corrected to Gabon.
Hapsidophrys niger Günther, 1872, *Ann. Mag. nat. Hist.* (4) **9**: 25. Type locality: Gaboon.
Thrasops pustulatus Buchholz & Peters, 1875, *Monatsb. Akad. Wiss. Berlin*: 199. Type locality: Mungo, Cameroon.
Thrasops flavigularis Bocage, 1895: 97; Bogert, 1940: 58; Loveridge, 1944: 132; Trape & Roux-Estève, 1995: 40; Chippaux, 1999: 95.
Thrasops flavigularis flavigularis Stucki-Stirn, 1979: 319.
Thrasops flavigularis stirnensis Stucki-Stirn, 1979: 632.

DIAGNOSIS. Dorsal scales in 13–15 rows at midbody, the dorsals much longer than the ventrals; ventrals 191–214; subcaudals 128–146; usually 2 labials in contact with the lowest postocular; no enlarged occipitals.

DESCRIPTION. Supralabials 8 (rarely 9), fourth & fifth (rarely fifth & sixth) entering orbit; infralabials 9–12, the first 3–5 in contact with anterior sublinguals; preoculars 1 or 2; postoculars 3 (rarely 2), usually 2 labials in contact with the lowest; temporals 1 + 1; no occipitals. Dorsals in 17-15-13, 17-13-11, 15-13-13, 15-13-11 or 13-13-11 rows, feebly keeled in adults; ventrals 191–214; cloacal divided; subcaudals 128–146 pairs.

COLORATION IN LIFE. Subadults olive to dark brown above, head uniform, body mottled with black and yellow, the black being on the interstitial skin and bases of the scales, the yellow in the centres of the scales, the yellow spots very pronounced on the tail. Chin and throat yellow, rest of venter chequered black and yellow. Adults usually uniform black above, venter blackish, but throat usually yellow or brownish white.

SIZE. Largest ♂ (IFAN 687 – Sibiti, Congo-Brazzaville) 1514 + 586 = 2100 mm (Villiers, 1966); largest ♀ (AMNH 50573 – Metet, Cameroon) 1235 + 505 = 1740 mm (Bogert, 1940). Stucki-Stirn (1979) gives the maximum length as 240 cm.

HABITAT. Lowland forest.

DISTRIBUTION. Southwestern Nigeria, Bioko Island, Cameroon, Gabon, Congo-Brazzaville, extreme eastern Democratic Republic of Congo and northwestern Angola (Fig. 5).

Thrasops occidentalis Parker
Western Bold-eyed Tree Snake

Thrasops occidentalis Parker, 1940, *Ann. Mag. nat. Hist.* (11) **5**: 273, fig. 1 & 2a. Type locality: Axim, Gold Coast [= Ghana]; Loveridge, 1944: 131; Cansdale, 1961: 31, Pl. vi, fig. 11 & 12; Hughes & Barry, 1969: 1018; Chippaux, 1999: 100.

DIAGNOSIS. Dorsal scales in 15–21 rows at midbody, the vertebral row widened; ventrals 175–187; subcaudals 119–140; 3 labials in contact with lowest postocular.

DESCRIPTION. Supralabials 8 (rarely 7 or 9), the fourth & fifth (rarely fifth & sixth) entering orbit; infralabials 8–10, the first 4–6 in contact with anterior sublinguals; preocular 1; postoculars 3, 3 labials in contact with the lowest; temporals 1 + 1; no occipitals. Dorsals in 15–21 rows at midbody, the median rows keeled in adults, smooth in juveniles; ventrals 175–187; cloacal divided; subcaudals 119–140 pairs.

COLORATION IN LIFE. Juveniles with head and neck olive, body

chequered in black and yellow above and below. Adults black above, chin and throat pale yellow, rest of venter dark olive.

SIZE. Largest ♂ (BMNH 66.1.28.6 – Sierra Leone, paratype) 670 + 495 = 1165 mm; largest ♀ (BMNH 1911.6.30.2 – Axim, Ghana, holotype) 682 + 403 = 1085 mm. Cansdale (1961) states that this species can exceed 210 cm.

HABITAT. Lowland forest.

DISTRIBUTION. Guinea east to southwestern Nigeria (Fig. 5).

Thrasops jacksonii Günther
Jackson's Bold-eyed Tree Snake

Thrasops Jacksonii Günther, 1895, *Ann. Mag. nat. Hist.* (6) **15**: 528. Type locality: Kavirondo, Kenya.
Rhamnophis jacksonii Boulenger, 1896: 632.
Thrasops Rothschildi Mocquard, 1905, *Bull. Mus. natn. Hist. nat.* **11**: 287. Type locality: 'Afrique orientale anglaise'.
Thrasops jacksonii jacksonii Loveridge, 1936: 249, 1944: 134 & 1957: 264; Bogert, 1940: 58; Witte, 1953: 200; Laurent, 1956: 187, 354 & 1960: 46; Roux-Estève, 1965: 66, fig. 17; Villiers, 1966: 1739; Bourgeois, 1968: 124, 278, fig. 51; Pitman, 1974: 99, Pl. G, fig. 4; Spawls, 1978: 5; Broadley, 1991: 532; Hinkel, 1992: 319, Pl. 306; Trape & Roux-Estève, 1995: 40.

DIAGNOSIS. Dorsal scales in 19 (very rarely 17 or 21) rows at midbody; ventrals 187–214; cloacal divided; subcaudals 129–155; usually two labials in contact with lowest postocular.

VARIATION. Supralabials 8 (rarely 9, very rarely 7), fourth and fifth (rarely fifth and sixth) entering orbit; infralabials 9–13, the first 4–6 in contact with anterior sublinguals; preoculars 1–2 (rarely 3); postoculars 3 (very rarely 2 or 4), usually 2 labials in contact with lowest; temporals 1 + 1 (very rarely 1 + 2); no occipitals. Dorsals keeled in 19 (very rarely 17 or 21) rows at midbody; ventrals 181–214; cloacal divided; subcaudals 129–155 pairs.

COLORATION IN LIFE. Subadults dark olive above, mottled with black and buff posteriorly, greenish yellow below, becoming chequered black and yellow posteriorly. Adults uniform black above and below, or with the throat yellow or greyish. Iris of eye black.

SIZE. Largest ♂ (AMNH 12288) 1320 + 580 = 1900 mm, largest ♀ (AMNH 12290) 1550 + 610 = 2160 mm, both from the Ituri Forest, Orientale Province, D.R.C. (Schmidt, 1923). Pitman (1974) puts the maximum length at about 2300 mm.

HABITAT. Rain forest and gallery forests from about 200 m in the lower Congo region to 2400 m on Mount Elgon (Pitman, 1974).

DISTRIBUTION. From the lower Congo, east through the Congo basin to southern Central African Republic, southern Sudan, Uganda, western Kenya and northwestern Zambia (Broadley, 1991) (Fig. 5).

Thrasops schmidti Loveridge
Schmidt's Bold-eyed Tree Snake

Thrasops jacksonii schmidti Loveridge, 1936, *Proc. biol. Soc. Washington* **49**: 63. Type locality: Meru Forest, Mount Kenya, Kenya; 1944: 137 & 1957: 264; Spawls, 1978: 5.

DIAGNOSIS. Dorsal scales in 17 rows; ventrals 168–184; subcaudals 121–149; two labials in contact with lowest postocular.

DESCRIPTION. Supralabials 8, the fourth and fifth entering the orbit; infralabials 10–12, the first 4 or 5 in contact with anterior sublinguals; preocular 1; postoculars 3, the lowest in contact with 2 labials; temporals 1 + 1; no occipitals. Dorsals in 17 (rarely 19) rows at midbody, faintly keeled; ventrals 172–184; cloacal divided; subcaudals 121–147 pairs.

COLORATION IN LIFE. Subadult olive brown above, greyish white below, subcaudals grey. Adults uniform black.

SIZE. Largest ♂ (MCZ 9276 – Meru Forest, Kenya, holotype) 700 + 365 = 1065 mm; largest ♀ (NMK 1222 – Embu Forest, Kenya) 1200 + 455 = 1655 mm; largest unsexed (formerly NMK – Muthaiga, Nairobi, Kenya, paratype) 1671 + 584 = 2255 mm (Loveridge, 1923, 1936).

HABITAT. Montane forest.

DISTRIBUTION. Forests of the Kenya highlands from Mount Kenya south to Nairobi (Fig. 5).

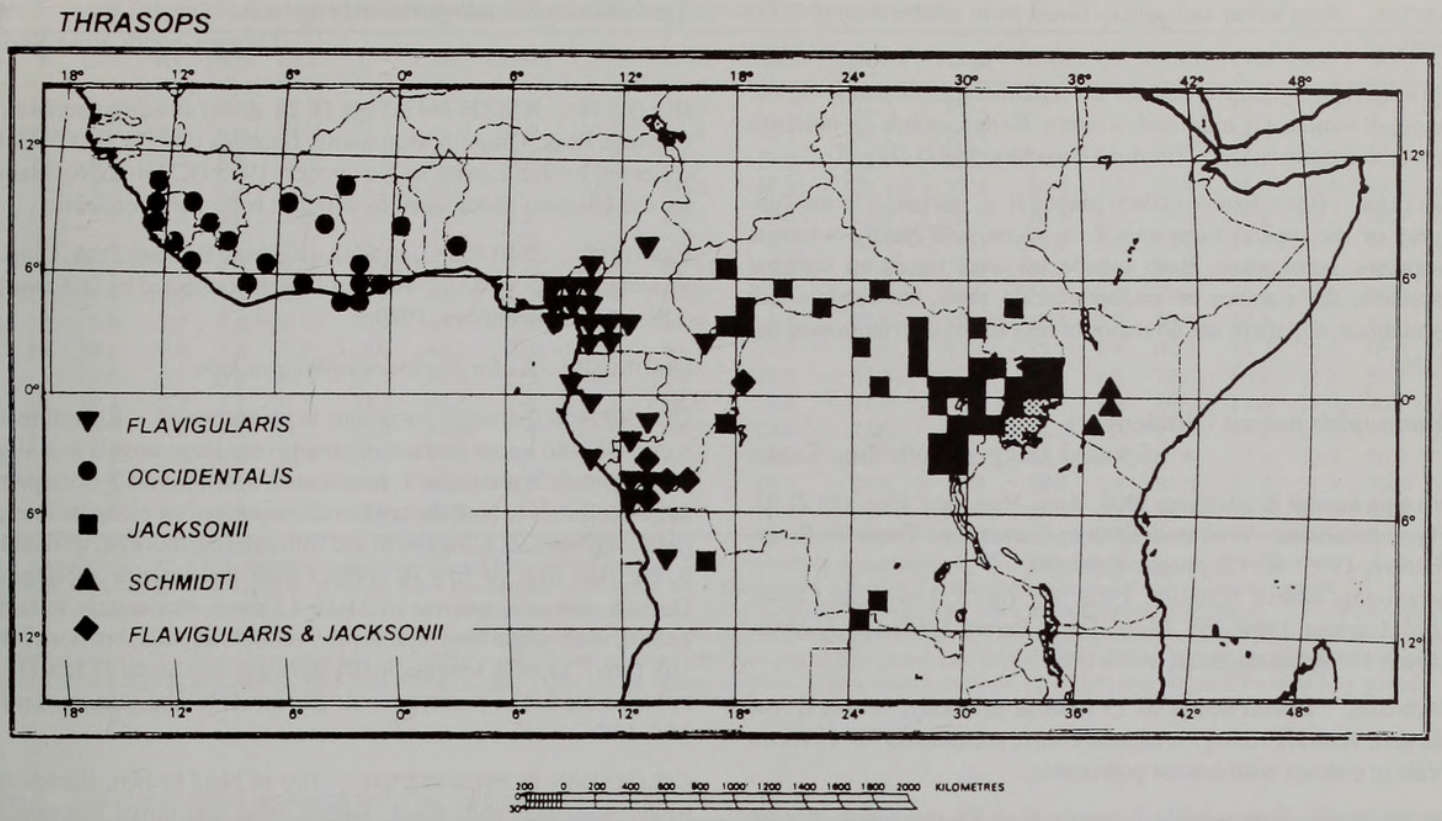
REMARKS. *T. schmidti* is readily diagnosable on ventral counts and is separated from the population of *T. jacksonii* in the Kakamega Forest by 300 km, including the dry rift valley, so it is considered to represent an independently evolving taxon.

Rhamnophis aethiopissa Günther
Splendid Dagger-tooth Tree Snake

Rhamnophis aethiopissa Günther, 1862, *Ann. Mag. nat. Hist.* (3) **9**: 129, Pl. x. Type locality: West Africa; Roux-Estève, 1965: 65, fig. 16; Chippaux, 1999: 97.
Thrasops splendens Andersson, 1901, *Bihang Till K. Svenska Vet.-Akad. Handl.* **27**(5): 11, Pl. 1, fig. 8. Type localities: Bibundi & Mapanja, Cameroon.
Rhamnophis ituriensis Schmidt, 1923, *Bull. Amer. Mus. nat. Hist.* **49**: 81, fig. 4. Type locality: Niapu, Belgian Congo [= D.R.C.]; Witte, 1941: 202.
Rhamnophis aethiopissa elgonensis Loveridge, 1929, *Bull. U. S. natn,. Mus.* **151**: 24. Type locality: Yala (= Lukosa) River at the foot of Mount Elgon, Kenya; 1944: 129.
Rhamnophis aethiopissa aethiopissa Loveridge, 1944: 126; Perret, 1961: 136; Villiers, 1966: 1739; Stucki-Stirn, 1979: 335, figs.
Rhamnophis aethiopissa ituriensis Loveridge, 1944: 128; Laurent, 1956: 189, 355; 1960: 47 & 1964: 108; Bourgeois, 1968: 109, fig. 43–46; Broadley, 1991: 532.
Thrasops aethiopissa elgonensis Loveridge, 1957: 264; Pitman, 1974: 101, Pl. T, fig. 3; Spawls, 1978: 5.
Thrasops aethiopissa aethiopissa Hughes & Barry, 1969: 1018; Trape & Roux-Estève, 1995: 40.
Thrasops (Rhamnophis) aethiopissa Hinkel, 1992: 144, Pl. 130.

DIAGNOSIS. Dorsal scales in 15–17 (rarely 19) rows at midbody, the vertebral row enlarged; ventrals 154–179; cloacal divided; subcaudals 117–159; two or three labials in contact with the lowest postocular; two large occipitals.

DESCRIPTION. Supralabials 6–9, the 3rd & 4th, 4th & 5th or 5th & 6th entering orbit; infralabials 7–11, the first 3–6 in contact with the anterior sublinguals; preocular 1 (very rarely 2); postoculars 2–3 (very rarely 4); a single temporal; two large occipitals (one longitudinally divided and the other semidivided in NMZB-UM 2548). Dorsals smooth, or vertebral and paravertebral rows keeled (Perret, 1961) in 15–17 (very rarely 13 or 19) rows at midbody (usually 17 rows in West Africa, Cameroon, Gabon and Central African Republic, 15 rows elsewhere); ventrals 154–179; cloacal divided; subcaudals 117–159 pairs, the lowest counts in Uganda and western Kenya.



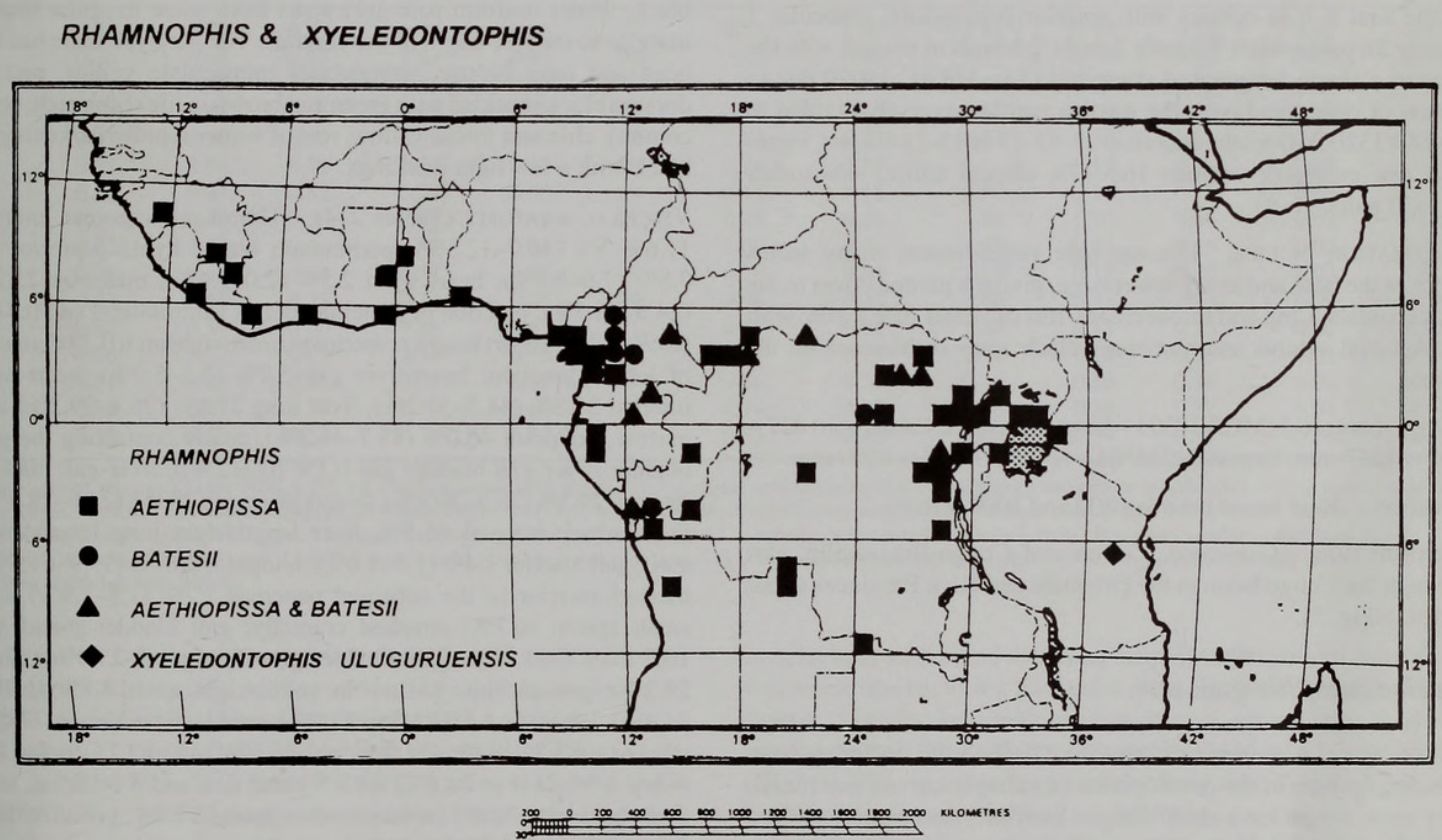


Fig. 5 Distributions of the genera *Thrasops* (upper), *Rhamnophis* and *Xyelodontophis* (lower).

COLORATION IN LIFE. Above, head olive-brown, uniform or posterior shields black-edged; body green with scales tipped or bordered with black; tail black with a green stripe on each scale row. Chin and throat yellow-green, rest of venter pale green, a dark median line on the subcaudals.

SIZE. Largest ♂ (MRAC 12257 – Kiroziret Forest, Kivu, D.R.C.) 948 + 509 = 1457 mm (Laurent, 1956); largest ♀ (NHRM 1979 – Bibindi, Cameroon, syntype of *T. splendens*) 950 + 520 = 1470 mm (Andersson, 1901).

HABITAT. Rain forest and gallery forest from sea level up to 2000 metres.

DISTRIBUTION. Guinea east to the Democratic Republic of the Congo, Rwanda, Uganda and western Kenya, south to northern Angola and northwestern Zambia (Broadley, 1991) (Fig. 5)..

REMARKS. Roux-Estève (1965) placed *R. a. ituriensis* in the synonymy of the typical form and *R. a. elgonensis* hardly warrants subspecific recognition. Both subspecies were based on variable characters: the number of midbody scale rows, subcaudals and supralabials, and there are no major breaks in the distribution of the species.

Rhamnophis batesii (Boulenger)
Spotted Dagger-tooth Tree Snake

Thrasops batesii Boulenger, 1908, *Ann. Mag. nat. Hist.* (8) **2**: 93. Type localities: Akok and Efulen, Cameroon; Trape & Roux-Estève, 1995: 40; Chippaux, 1999: 99.

Rhamnophis batesii Schmidt, 1923: 83, fig. 5; Loveridge, 1944: 125; Laurent, 1956: 355, Pl. xx, fig. 1; Perret, 1961: 136; Villiers, 1966: 1739; Stucki-Stirn, 1979: 339.

DIAGNOSIS. Dorsal scales in 13 rows at midbody, vertebral row enlarged; ventrals 163–179; cloacal entire; subcaudals 92–119; two labials in contact with lowest postocular.

DESCRIPTION. Supralabials 7 (rarely 6 or 8), the fourth & fifth (rarely third & fourth or fifth & sixth) entering orbit; infralabials 8 or 9, the first 4–6 in contact with anterior sublinguals; preocular 1 (rarely 2); postoculars 3 (rarely 2 or 4), 2 labials in contact with the lowest; a single temporal; 4 occipitals (3 in MRAC 19070 due to fusion of right hand pair; the median pair transversely divided in NMZB 13206). Dorsals smooth in 13-13-11 or 13-13-9 rows, vertebral row enlarged; ventrals 163–179; cloacal entire; subcaudals 92–123 pairs.

COLORATION IN LIFE. Dorsum pale violet-brown, many scales black at the base and along lower edge, giving a plaited effect to the supracaudals. Chin and throat cream, rest of venter pale green, with black labial sutures and numerous black spots or blotches on the venter.

SIZE. Largest ♂ (MCZ 38393 – Batouri District, Cameroon) 827 + 390 = 1217 mm; largest ♀ (BMNH —) 1450 + 350 = 1800 mm.

HABITAT. Rain forest between 400 and 1000 metres.

DISTRIBUTION. Cameroon, Gabon and Congo-Brazzaville, east through the Congo basin to the Orientale and Kivu Provinces of the D.R.C. (Fig. 5).

Xyelodontophis gen. nov.

DIAGNOSIS. A member of the tribe Dispholidini, differing from the other genera in the development of strongly curved rear maxillary teeth, which have sharp flanges anteriorly and posteriorly and narrow at the base, hence the name *Xyelodontophis* = Dagger-tooth Snake. Both species of *Rhamnophis* also have 'dagger-shaped' rear maxillary teeth, but they are less well developed and the teeth taper from base to tip, while *Thelotornis* and *Dispholidus* have large deeply grooved rear fangs. The new genus agrees with *Thrasops* and *Thelotornis* in having a shallowly forked ectopterygoid bone, whereas *Rhamnophis* and *Dispholidus* have a deeply forked ectopterygoid. In general form and scalation the new snake agrees with *Thelotornis*, but it lacks the distinctive horizontal pupil of that genus.

Xyelodontophis uluguruensis sp. nov.
Dagger-tooth Vine Snake

HOLOTYPE. NMZB 7443 (Figs 1f, 2a, & 4a) an adult female from Lupanga Peak, Uluguru Mountains, Tanzania (06° 52' S: 37° 43' E), collected by Jon Lovett in November, 1983 (KMH 2636). Named for the Uluguru Mountains, to which it is probably endemic.

PARATYPE. ZMB 48153, an adult male from Bondwa Peak, Uluguru Mountains (06° 54' S: 37° 40' E) at 1650 m, collected by D. Emmrich (DE 413) in November, 1989.

DIAGNOSIS. As for *Xyelodontophis* gen. nov.

DESCRIPTION (paratype variations in parentheses). Rostral feebly recurved onto upper surface of snout; very large nostril in a single nasal; loreals 2; preocular 1; postoculars 3; temporals 1 + 3; a pair of large occipitals behind the temporals, separated by elongate interparietal; supralabials 8, the fourth and fifth entering the orbit; infralabials 9, the first four or five in contact with the anterior sublinguals. Dorsals elongate, narrow, in 21-19-13 rows, moderately to feebly keeled, with single large apical pits; ventrals angular, but not keeled, 168 (169); cloacal longitudinally divided; subcaudals 132+ (18+), tail truncated. The paratype male has an umbilical scar on ventrals 147–149.

COLORATION IN PRESERVATIVE. Top of head brown, shields narrowly margined with black, labials, chin and throat immaculate. Body grey-brown, bases of scales (and interstitial skin anteriorly) black; venter uniform pale grey apart from some irregular brown margins to the free edges of the ventrals. The paratype male has the head and nape bronze, supralabials immaculate yellow, rest of dorsum black speckled with green and brown in life (Emmrich, pers. comm.); chin and throat yellow, rest of venter rapidly darkening to black with a few light markings.

VISCERAL ANATOMY (Tables 2–4). Umbilical scar-vent interval 11.6% VS (10.7–12.5%); peritoneum black; hyoid posterior tip 7.8% (7.6–8.1%); heart short 2.3% (2.0–2.6%), midpoint 25.2% (24.9–25.5%), junction of systemic arches ventrolateral and 0.71% (0.69–0.74%) heart length posterior to heart, right arch 0.33 diameter of left at junction; heart-liver gap 5.7% (5.5–5.9%), heart-liver interval 35.8% (34.3–37.2%); liver long 27.8% (26.4–29.2%) and narrow, midpoint 46.0% (45.7–46.2%), nearly contacting the gall bladder (liver-gall bladder gap 0.1% [0–0.2%]); liver-gall bladder interval 29.3% (28.3–30.4%), liver-kidney gap 28.0% (27.6–28.4%), liver-kidney interval 65.5%, liver length/right lung length ratio 0.40; gall bladder 1.4% (1.2–1.6%), midpoint 60.7% (59.9–61.5%), located anterior to the subequal pancreas 1.7% (1.5–1.9%) with small spleen (0.7%) attached cranially; gall bladder-gonad gap 10.7% (9.7–11.8%), gall bladder-gonad interval 23.0% (22.8–23.2%); gonads light yellow in color, right testis 4.8% (MP = 74.4%), left testis 4.1% (MP = 79.9%), total testis midpoint 77.4%; right ovary 5.3% (MP = 74.9%) with 6 small ova and 7 follicles, left ovary 4.9% (MP = 81.6%) with 5 small ova and 8 follicles, total ovary midpoint 78.0%, total gonad midpoint 77.7%; gonad-kidney gap 4.8% (4.4–5.3%); adrenal glands orange, very narrow and elongate, adjacent to posterior end of gonads, right adrenal 2.3% (2.2–2.5%), midpoint 75.4% (74.8–76.1%), left adrenal 2.6% (2.5–2.7%), midpoint 81.6% (81.2–82.1%), total adrenal midpoint 78.5% (78.4–78.6%); gall bladder-kidney gap 26.4% (26.3–26.5%), gall bladder-kidney interval 37.5% (36.3–38.8%); kidneys dark brown, segmented but compact with deep creases, right kidney 9.2% (8.0–10.4%) with 20 segments, midpoint 92.4%, right kidney length/liver length ratio 0.34; left kidney 7.0% (6.1–7.9%) with 21 segments,

Table 2 Adult Dispholidini compared with Philothamnini: visceral characters as % snout-vent length

GS	*n*	U-V	Hy	HLG	HLI	L	LMP	LGBG	LGBI	GBMP	GBGG	GBKG	TGMP	GKI	TA	TAMP	TMP	RL	PT	LL
PA	55	8.6	8.1	7.3	29.0	18.8	42.8	3.5	24.2	56.6	11.7	23.9	79.7	23.7			13.7	76.9	95.5	1.4
HL	24	7.9	14.6	9.0	29.0	17.3	45.6	10.3	29.3	65.3	10.1	20.2	79.8	22.1			14.6	76.1	98.1	1.4
HS	30	6.8	11.4	8.8	29.3	17.7	46.6	5.6	29.5	66.2	17.0	22.1	83.2	20.0	1.2	84.7	15.1	78.4	97.9	0.8
TF	5	8.2	7.7	8.8	25.2	14.2	45.6	6.2	22.6	60.0	11.3	23.3	77.4	24.4	3.2	77.9	15.5	68.4	97.5	2.6
TJ	15	8.9	7.2	8.7	26.6	15.5	44.5	7.7	20.0	52.6	9.8	23.4	76.1	26.3	5.3	74.0	14.6	69.5	96.4	2.9
TO	2	7.8	6.7	9.9	26.0	14.0	43.9	7.5	23.0	59.2	8.8	25.1	76.1	28.2	2.6	75.8	14.1	71.9	97.6	5.3
TS	2	9.2	10.7	9.3	26.9	14.8	44.8	9.0	25.0	61.7	7.3	20.8	76.0	27.2	4.6	77.0	14.8	68.6	96.4	3.9
RA	12	7.4	10.2	7.4	27.1	17.4	44.0	5.3	24.4	58.8	12.5	27.3	79.0	25.3	3.9	79.6	14.5	69.3	96.3	1.2
RB	2	9.0	9.9	7.6	30.0	20.1	45.1	7.1	28.4	62.8	13.4	23.6	79.6	20.4	2.9	80.4	14.3	71.4	97.7	1.4
DT	12	10.1	9.0	7.3	29.0	19.0	44.1	7.2	27.5	61.7	7.7	18.8	77.0	35.1	2.9	69.7	14.2	70.5	96.3	2.3
DP	1	9.6	6.4	6.0	30.2	21.7	42.9	5.5	28.5	59.9	12.1	27.5	79.5	27.6	4.9	77.5	13.6	71.8	96.6	1.3
TC	4	11.4	8.2	7.1	31.9	22.3	44.2	7.8	31.8	64.0	8.2	18.6	78.6	23.4	3.0	79.9	13.6	71.0	96.1	1.3
TK	13	9.9	7.1	7.2	32.2	22.8	47.8	6.4	31.0	66.5	10.5	21.6	82.7	20.2	2.2	83.8	15.2	67.2	95.7	1.1
TM	5	9.4	7.2	6.9	36.3	26.9	45.7	4.5	33.3	64.6	9.3	19.3	80.5	21.9	2.5	81.6	13.4	72.5	96.9	1.5
TU	3	12.5	7.2	6.5	34.0	25.5	44.9	6.0	33.2	64.5	10.5	20.8	80.5	20.8	1.8	81.8	13.4	71.1	96.0	1.0
XU	2	11.6	7.8	5.7	35.8	27.8	46.0	0.1	29.3	60.7	10.7	26.4	77.7	25.4	4.9	78.5	13.8	68.6	93.4	1.4

(GS = genus/species: PA = *Philothamnus angolensis*, HL = *Hapsidophrys lineatus*, HS = *Hapsidophrys smaragdinus*, TF = *Thrasops flavigularis*, TJ = *Thrasops jacksonii*, TO = *Thrasops occidentalis*, TS = *Thrasops schmidti*, RA = *Rhamnophis aethiopissa*, RB = *Rhamnophis batesii*; DT = *Dispholidus typus*, DP = *Dispholidus* 'pemba', TC = *Thelotornis capensis*, TK = *Thelotornis kirtlandii*, TM = *Thelotornis mossambicanus*, TU = *Thelotornis usambaricus*, XU = *Xyelodontophis uluguruensis*; *n* = sample size, UV = umbilical scar to vent as % total ventrals, Hy = hyoid posterior tip, HLG = heart-liver gap, HLI = heart-liver interval, L = liver length, LMP = liver midpoint, LGBG = liver-gall bladder gap, LGBI = liver-gall bladder interval, GBMP = gall bladder midpoint, GBGG = gall bladder-gonad gap, GBKG = gall bladder-kidney gap, TGMP = total gonad midpint, GKI = gonad-kidney interval, TA = total adrenal length, TAMP = total adrenal midpoint, TMP = trachea midpoint, RL = right lung length, PT = right lung posterior tip, LL = left lung length).

Table 3 Adult Dispholidini compared with Philothamnini: visceral characters as ratios

GS	R/LSA	K/L	RK/L	LK/RK	KOL	NTR	AL/LL	RB/LL	LB	SS/DV	V/S	LL/RL	LW/LL
PA	0.39	0.39	0.37	0.83	0.76	72	0.54	1.00	2.83	0.19	0.18	0.02	0.42
HL	0.36	0.68	0.67	0.83	0.80	75	–	0.41	0.53	0.14	0.17	0.02	0.30
HS	0.39	0.49	0.47	0.85	0.77	101	–	0.23	0.56	0.13	0.16	0.01	0.42
TF	0.33	0.88	0.66	0.83	0.38	90	0.31	0.13	0.60	0.09	0.25	0.04	0.21
TJ	0.41	0.70	0.57	0.75	0.40	92	0.36	0.21	0.67	0.10	0.23	0.04	0.22
TO	0.37	0.86	0.71	0.75	0.45	120	0.24	0.10	0	0.11	0.24	0.08	0.13
TS	0.20	0.93	0.82	0.78	0.50	89	0.13	0.11	0.50	0.10	0.26	0.06	0.29
RA	0.29	0.48	0.50	0.69	0.48	76	0.87	0.24	1.45	0.10	0.16	0.02	0.26
RB	0.22	0.48	0.46	0.81	0.76	79	1.00	0.19	1.67	0.13	0.15	0.02	0.35
DT	0.24	0.65	0.54	0.78	0.36	79	0.76	0.80	1.29	0.17	0.20	0.03	0.29
DP	0.25	0.41	0.33	0.74	0.40	99	0.90	0.21	4.00	0.21	0.15	0.02	0.30
TC	0.32	0.59	0.50	0.68	0.52	71	0.57	0.21	1.00	0.13	0.15	0.02	0.28
TK	0.26	0.37	0.37	0.74	0.55	75	0.54	0.19	2.7	0.14	0.15	0.01	0.25
TM	0.31	0.45	0.41	0.72	0.57	76	0.68	0.20	2.75	0.16	0.14	0.02	0.24
TU	0.38	0.43	0.39	0.79	0.63	71	0.79	0.17	3.00	0.14	0.12	0.01	0.39
XU	0.33	0.35	0.34	0.76	0.67	59	0.83	0.42	1.00	0.39	0.13	0.02	0.20

(genus/species acronyms as for Table 2, R/LSA = right systemic arch diameter/left systemic arch diameter, K/L = total kidney length/liver length, RK/L = right kidney length/liver length, RA/RK = right adrenal length/right kidney length, LK/RK = left kidney length/right kidney length, KOL = kidney overlap/total kidney length, NTR = estimated number of tracheal rings/10% SVL, AL/LL = anterior lobe length/left lung length, RB/LL = right bronchus length/left lung length, LB = mean number of cartilages in left bronchus (including bronchial ring), SS/DV = semisaccular lung/dense vascular lung, V/S = vascular lung/saccular lung, LL/RL = left lung length/right lung length, LW/LL = left lung width/left lung length).

midpoint 94.0%, left kidney length/liver length ratio 0.26; left kidney/right kidney 0.76, kidney overlap 0.67; kidney-vent interval 12.2% (11.6–12.8%), kidney-vent gap 2.5% (2.1–2.9%).

Trachea 25.1% (25.0–25.2%) with an estimated 149 rings (144–154) or 58.9 (58.6–59.2) per 10% SVL, trachea midpoint 13.8% (13.7–13.9%), tracheal rings narrow and well-separated from their neighbours, lacking free tips, tracheal membrane expanded to 3.5 times the tracheal ring circumference; tracheal lung lacking, only slight development of a cardiac lung (0.7%) anterior to the right lung; tracheal entry into right lung subterminal; right bronchus 0.3% with 3 cartilages; anterior lobe of right lung very short 1.0% (0.9–1.2%), its connecting orifice of moderate diameter; right lung 68.6% (66.0–71.2%), right lung midpoint 60.1% (59.1–61.2%), vascular portion of right lung 8.0% (7.2–8.7%) with three tiers of faveoli distributed dorsoventrally around inner lung circumference; vascular lung lacking midventral avascular strip; faveolar pattern consists of transverse ribs enclosing transverse rows of paired diamond-shaped faveoli; vascular lung with semisaccular or sparse/dense vascular portion ratio 0.39 (0.35–0.42); saccular (avascular) lung 59.6% (58.0–61.3%), vascular lung/saccular lung ratio 0.13 (0.12–0.14), posterior tip of lung 93.9% (91.7–96.2%).

Left lung complex consists of an orifice at 26.3% (26.2–26.5%), a bronchus 0.1% with two rings in female (bronchus absent in male), and a vestigial lung 1.4% (1.1–1.6%). The left lung, with a left lung/right lung ratio of 0.02, supports a reticulated network of trabeculae and has a width/length ratio of 0.20 (0.15–0.25).

Xyelodontophis, while resembling *Thelotornis* in external morphology, is distinct from the latter genus in a number of internal characters: heart-liver gap, heart-liver interval, liver length, gall bladder midpoint, gall bladder-kidney gap, total gonad midpoint,

Table 4 Comparison of generic means for visceral characters

G	no.	Hy	HLG	HLI	L	LMP	LGBI	GBKG	KVI	TG	TGMP	GKG	TA	TMP	RL	PT	LL	RK/L	TK/L	A/K	L/RL	NTR	TTR	SS/DV	U-V
Ph	12	13	7.2	30	20	44.6	30.2	22.8	12.4	8.5	79.7	1.5		15	77	94.8	1.0	0.52	0.56		0.28	70	180	0.19	7.7
Hy	2	13	8.9	29	18	46.1	29.4	21.2	11.9	6.2	80.9	1.8	1.2	15	77	98.0	1.1	0.57	0.58	0.08	0.23	80	219	0.17	7.2
Tr	4	8	8.7	25	14	43.3	23.4	22.1	20.5	3.7	76.7	2.8	3.8	14	70	96.5	3.0	0.68	0.85	0.23	0.22	93	252	0.10	7.8
Rh	2	11	7.5	28	18	44.4	24.9	26.2	13.0	3.7	77.3	4.3	3.8	15	69	96.3	1.2	0.53	0.60	0.22	0.36	77	212	0.12	9.0
Di	2	9	7.0	29	19	44.7	27.6	20.6	16.3	5.6	77.2	0.3	4.7	15	70	96.5	2.2	0.52	0.67	0.36	0.21	77	206	0.16	10
Th	4	8	6.9	31	23	44.4	32.0	20.3	13.6	6.0	81.0	4.6	2.5	14	69	96.0	1.2	0.41	0.46	0.21	0.39	74	191	0.14	10
Xy	1	8	5.7	36	28	46.0	29.3	26.4	12.2	9.6	77.7	4.8	4.9	14	69	93.9	1.4	0.34	0.35	0.39	0.81	59	149	0.39	12

(Ph = *Philothamnus*, Ha = *Hapsidophrys*, Tr = *Thrasops*, Rh = *Rhamnophis*, Di = *Dispholidus*, Th = *Thelotornis*, Xy = *Xyelodontophis* ; G = genus, no. = number of species, measurements as % SVL : Hy = hyoid posterior tip, HLG = heart-liver gap, HLI = heart-liver interval, L = liver length, LMP = liver midpoint, LGBI = liver-gall bladder interval, GBKG = gall bladder-kidney gap, KVI = kidney-vent interval, TG = total gonad length (adults), TGMP = total gonad midpoint, GKG = gonad-kidney gap, TA = total adrenal length, TMP = trachea midpoint, RL = right lung length, PT = right lung posterior tip, LL = left lung length; and as ratios: RK/L = right kidney length/liver length, TK/L = total kidney length/liver length, A/K = total adrenal length/total kidney length, L/RL = liver length/right lung length, NTR = estimated number of tracheal rings/10% SVL, TTR = estimated total number of tracheal rings, SS/DV = semisaccular lung/dense vascular lung, UV = umbilical scar/vent interval as % total ventrals.

gonad-kidney interval, total adrenal length and midpoint, adrenal/kidney length ratio, total kidney/liver length ratio, number of tracheal rings, right bronchus/left lung ratio, semisaccular/dense vascular lung ratio, right lung posterior tip, left bronchus cartilages, and left lung width/length ratio. *Xyelodontophis* is also unique in differing from the rest of the Dispholidini in the means of the following characters: heart-liver interval, liver length, liver midpoint, liver-gall bladder gap, total gonad length, liver-kidney interval, gall bladder-kidney gap, total gonad length, right kidney and total kidney/liver length ratios, number of tracheal rings, semisaccular/dense vascular lung ratio, lack of ventral avascular strip in vascular lung, liver/right lung length ratio, and posterior tip of right lung.

In contrast to other Dispholidini, *Xyelodontophis* is most similar to *Thelotornis* in hyoid length, liver-gall bladder interval, and trachea midpoint; it is most similar to *Rhamnophis* and *Thelotornis* in total kidney midpoint, kidney-vent interval, and left lung length; it is most similar to *Dispholidus*, *Rhamnophis* and *Thelotornis* in total gonad midpoint; and it is most similar to *Dispholidus* in total adrenal length and adrenal/kidney length ratios.

HEMIPENIS. In the paratype male the single organs extend to the seventh subcaudal, the sulcus spermaticus is simple (on the left organ the sulcus lies on the medial side, on the right organ it lies on the lateral surface). In situ, the basal portion (2 subcaudals) is nude with four large hooks, the medial portion (2 sc) is spinose and the apical portion (2 sc) is calyculate. The sulcus is bordered by two basal hooks 5 mm long and the two largest hooks (7 mm) are on the asulcate side. The calyces on the apex are smooth and form a network (with 1–2 mm cavities) very similar to the faveoli of the snake lung. The proximal 2–4 calyces are spinose with several tiny spinules on each calyx. The spines completely surround the organ and are arranged in 7–8 rows, increasing in size from distal (4 rows, 1 mm long) through medial (3 rows, 2 mm) to proximal (1 row, 3 mm); there are 7 large spines on the right organ and 8 on the left. The everted organ would probably show some resemblance to that of *Thelotornis kirtlandii* (Doucet, 1963: Fig. 40).

SIZE. Length 740 + 407+ mm (snout-vent 830 mm, tail truncated near base).

DIET. The holotype contained a recently swallowed leaf chameleon, *Rhampholeon uluguruensis,* an endemic species recently described from Bondwa Peak (Tilbury & Emmrich, 1996).

HABITAT. Montane evergreen forest. The habitat is described by Tilbury & Emmrich (1996).

DISTRIBUTION. Probably endemic to the Uluguru Mountains (Fig. 5).

Thelotornis kirtlandii (Hallowell) Forest Vine Snake

Leptophis Kirtlandii Hallowell, 1844, *Proc. Acad. nat. Sci. Philadelphia*: 62. Type locality: Liberia, type ANSP 5271.
Oxybelis Lecomtei Duméril & Bibron, 1854, *Erpét. Gen.*, **7**: 821. Type locality: Gabon.
Tragophis rufulus Duméril & Bibron, 1854, *Erpét. Gen.*, **7**: 827. Type locality: Senegal.
Oxybelis violacea Fischer, 1856, *Abhand. Nat. Ver. Hamburg,* **3**: 91, Pl. ii, fig. 7. Type locality: Edina, Grand Bassa County, Liberia.
Dryiophis Kirtlandii Bocage, 1895: 119 (part).
Thelotornis kirtlandii Schmidt, 1923: 112, Pl. xiv; Bogert, 1940: 69; Witte, 1953: 247, fig. 82; Laurent, 1964: 116.
Thelotornis kirtlandii kirtlandii Loveridge, 1944: 149 (part).

DIAGNOSIS. Top of head, including temporal region, uniform green; neck with black crossbands; supralabials immaculate or with fine green or grey stipple; rostral and nasals strongly recurved onto top of snout; infralabials 7–11 (mode 9); ventrals 162–189; subcaudals 132–172.

DESCRIPTION. Rostral and anterior nasals recurved onto top of snout; a single loreal (in eastern populations); preocular 1; postoculars 3 (2 in two specimens from Digba through fusions with supraocular or fifth labial) ; temporals 1+2 (very rarely 1+1 or 2+2); supralabials 8 (rarely 9 or 10), the fourth and fifth (rarely fifth and sixth) entering the orbit: infralabials 7 to 11, the first 4 or 5 (very rarely 3) in contact with the anterior sublinguals. Dorsal scales feebly keeled in 19-19-13 rows (17 rows at midbody in four specimens from Kivu: Laurent, 1956, 1960); ventrals 164–179 in ♂♂, 164–189 in ♀♀; cloacal divided; subcaudals 135–157 in ♂♂, 138–165 in ♀♀.

COLORATION. Top of head uniform green, supralabials white, often with fine green or grey stipple; body mottled grey, green and brown, with black crossbars anteriorly (ZMUC R631282 lacks black markings on the neck), lighter below. The specimen illustrated by Hinkel (1992: fig. 129) appears to be uniform dark brown on top of the head, with heavy brown infuscation on the labials. This could be a captive specimen that has been exposed to strong sunlight, such a change has been observed in a captive *Thelotornis* at Watamu on the Kenya coast (S. Spawls, pers comm.).

SIZE. Largest ♂ (AMNH 12279 – Niangara, D.R.C.) 850 + 480 = 1330 mm, largest ♀(ZMUC R631282 – Massisiswi, Udzungwa Mts, Tanzania) 1050 + 660 = 1710 mm.

HABITAT. Lowland forest in west and central Africa, relict populations in montane forests in Tanzania.

DISTRIBUTION. Islands of the Bijagós Archipelago, Guinea Bissau, east through forested areas of west Africa and the Congo basin to Uganda and southern Sudan, south to northern Angola, northwestern Zambia (Broadley, 1991) and south-central Tanzania (Rasmussen, 1997) (Fig. 6).

Thelotornis usambaricus Broadley Usambara Vine Snake

Thelotornis kirtlandii (not Hallowell) Stejneger, 1893: 733.
Thelotornis kirtlandii kirtlandii (not Hallowell) Loveridge, 1944: 149 (part).
Thelotornis capensis mossambicanus (not Bocage) Broadley, 1979: 126 (part); Rasmussen, 1997: 138 (part).
Thelotornis usambaricus Broadley, 2001, *Afr. J. Herpetol.* **50** (2): 58. Type locality: Amani Nature Reserve, (Kwamkoro/Kwemsambia Forest Reserve), East Usambara Mountains, Tanzania. Holotype: NMZB 16182

DIAGNOSIS. Top of head, including temporal region, uniform green; neck with black chevrons; supralabials with scattered black spots, usually including a triangle on the sixth labial; rostral and nasals not, or only feebly, recurved onto top of snout; infralabials 9–13 (mode 11); ventrals 145–169; subcaudals 143–175.

DESCRIPTION. Rostral just visible from above; nasal entire; loreals 1 or 2; preocular 1; postoculars 3; temporals 1 + 2 (very rarely 1 + 3); occipitals 2, separated by a small interoccipital; supralabials 8 (very rarely 9), the fourth and fifth or third, fourth and fifth entering the orbit; infralabials 9 to 13, the first 4 or 5 in contact with the anterior sublinguals. Dorsal scales very feebly keeled, in 19-19-13 or 19-19-11 rows; ventrals 156–166 in ♂♂, 145–169 in ♀♀; cloacal divided; paired subcaudals 146–175 in ♂♂, 143–169 in ♀♀.

COLORATION. Top of head, including temporals, uniform green in

life, supralabials, chin and throat white or pale orange, with a few black spots and usually a speckled black triangle extending back from the eye through the lower postocular and sixth labial to the lip, a few black spots on posterior sublinguals and gulars; dorsum mottled brown, green and pale grey, three or four vague black chevrons on neck (more distinct in subadults); venter mottled pale brown and green.

SIZE. Largest ♂ (BMNH 1974.547) 640 + 454 = 1094 mm; largest ♀(ZMUC R631310) 790 + 490 = 1280 mm, both from Amani.

HABITAT. Coastal forest.

DISTRIBUTION. The Usambara Mountains, with apparently relict populations on the lower slopes of other isolated mountains in the Eastern Arc chain and on the Kenya coast (Fig. 6).

Thelotornis mossambicanus (Bocage) Eastern Vine Snake

Oxybelis Lecomtei (not Duméril & Bibron) Peters, 1854: 623 (part).
Thelotornis Kirtlandii (not Hallowell) Peters, 1882: 131 (part), Pl. xix, fig. 2
Dryiophis Kirtlandii var. *mossambicana* Bocage, 1895, *Herp. Angola & Congo*: 119. Type locality: Manica, Mozambique. Lectotype MBL 1843 (destroyed).
Thelotornis kirtlandii capensis (not A. Smith) Mertens, 1937: 14.
Thelotornis capensis (not A. Smith) Bogert, 1940: 70 (part), fig. 11.
Thelotornis capensis capensis (not A. Smith) Laurent, 1956: 230 & 378.
Thelotornis capensis mossambicanus Broadley, 1979: 129.
Thelotornis mossambicanus Broadley, 2001: 60.

DIAGNOSIS. Top of head green to pale brown, uniform or speckled with black; temporals brown speckled with black; neck with black lateral blotch; supralabials with scattered black spots, including a triangle on the sixth labial; rostral and nasals not, or only feebly, recurved onto top of snout; infralabials 9–13 (mode 11); ventrals 144–172; subcaudals 123–167.

DESCRIPTION. Rostral and nasals barely visible from above; loreals usually 2 (rarely 1, very rarely 0 or 3); preocular 1; postoculars 3 (rarely 2 or 4); temporals 1 + 2 (very rarely 1 + 1, 1 + 3 or 2 + 2); supralabials 8 (rarely 9, very rarely 6 or 7), the fourth and fifth (rarely fifth and sixth, very rarely third and fourth, or third, or fifth only) entering orbit; infralabials 9–13, mode 11, the first 4 or 5 in contact with the anterior sublinguals; dorsal scales usually in 19-19-11 or 19-19-13 rows, very rarely 17, 21 or 23 rows at midbody (23 recorded by Rasmussen, 1997); ventrals 144–168 in ♂♂, 145–172 in ♀♀; cloacal divided; subcaudals 131–167 in ♂♂, 123–153 in ♀♀.

COLORATION. Crown of head uniform green or with a black speckled Y-shaped marking, or brownish, entirely speckled with black (the two extremes may occur within a population, as on Mafia Island); temporal region always brown, speckled with black; supralabials white spotted with black, including a triangle on sixth labial, chin and throat speckled with black; dorsum ash grey with diagonal rows of whitish blotches and flecks of brown and pink or orange, neck with one or two elongate black blotches; venter greyish, streaked with brown.

SIZE. Largest ♂ (MHNG 1376.34 – Newala, Tanzania) 910 + 525+ (tail truncated); largest ♀ (NMZB-UM 4157 – Mutare, Zimbabwe) 895 + 510 = 1405 mm, but MCZ 18476 from Zengeragusu, Tanzania, has a snout-vent length of 920 mm (tail truncated).

HABITAT. Savanna and coastal forest.

DISTRIBUTION. Southern Somalia south to central Mozambique at about 22°30' S, west to the shores of Lake Tanganyika, Malawi and eastern Zimbabwe (Fig. 6).

Thelotornis capensis capensis A. Smith Southeastern Savanna Vine Snake

Thelotornis capensis A. Smith, 1849, *Ill. Zool. S. Africa, Rept.* App.: 19. Type locality: 'Kaffirland and the country towards Port Natal', i.e. Durban (type lost).
Thelotornis kirtlandii capensis Loveridge, 1944: 154 (part).
Thelotornis capensis capensis Broadley, 1979: 126.

DIAGNOSIS. Top of head blue-green with pink and black speckling forming a 'Y' or 'T' marking, or speckling covering entire top of head; temporals pink margined with black; neck with black lateral blotches; supralabials with scattered black spots, including a triangle on the sixth labial; rostral and nasals not, or only feebly, recurved onto top of snout; infralabials 9–13 (mode 11); ventrals 144–164; subcaudals 127–155.

DESCRIPTION. Rostral and nasals barely visible from above; loreals usually 2 (rarely 1, very rarely 0 or 3); preocular 1; postoculars 3 (rarely 2 or 4); temporals 1 + 2 (very rarely 1 + 1 or 1 + 3); supralabials 8 (very rarely 7 or 9), the fourth and fifth (very rarely third & fourth, fifth & sixth or third, fourth and fifth) entering orbit; infralabials 9–13, mode 11, the first 4 or 5 (very rarely 3 or 6) in contact with anterior sublinguals; dorsal scales usually in 19-19-13 rows , rarely in 17 rows at midbody (15 rows only in TMP 45554); ventrals 144–160 in ♂♂, 148–162 in ♀♀; cloacal divided; subcaudals 133–155 in ♂♂, 127–147 in ♀♀.

SIZE. Largest ♂ (NMZB 6389 – Gwanda, Zimbabwe) 830 + 506 = 1336 mm; largest ♀ (TMP 5615 – Hectorspruit, Mpumalanga, South Africa) 911 + 455 = 1366 mm.

HABITAT. Savanna.

DISTRIBUTION. Southwestern Zimbabwe and southeastern Botswana, south through the northern provinces of South Africa and Swaziland to southern Mozambique and KwaZulu-Natal (Fig. 6).

Thelotornis capensis oatesii (Günther) Oates' Savanna Vine Snake

Oxybelis Lecomtei (not Duméril & Bibron) Peters, 1854: 623 (part, Tete).
Dryiophis oatesii Günther, 1881, In *Oates' Matabeleland and the Victoria Falls,* App. : 330, Col. Pl. D. Type locality: Matabeleland (= western Zimbabwe), type BMNH 1946.1.9.76.
Thelotornis Kirtlandii (not Hallowell) Peters, 1882: 131 (part).
Thelotornis kirtlandii capensis Loveridge, 1944: 154 (part).
Thelotornis capensis (not A. Smith) Witte, 1953: 249, fig. 82.
Thelotornis kirtlandii oatesii Loveridge, 1953: 277.
Thelotornis capensis oatesii Laurent, 1956: 231, fig. 35

DIAGNOSIS. Top of head blue-green with pink and black speckling forming a 'Y' or 'T' marking; temporals pink margined with black; neck with black lateral blotches; supralabials with scattered black spots, including a triangle on the sixth labial; rostral and nasals not, or only feebly, recurved onto top of snout; infralabials 9–13 (mode 11); ventrals 150–177; subcaudals 126–168.

DESCRIPTION. Rostral and nasals barely visible from above; loreals usually 2 (rarely 1, very rarely 0); preocular 1; postoculars 3 (rarely 2, very rarely 1 or 4); temporals 1 + 2 (very rarely 1 + 3 or 1 + 1); supralabials 8 (rarely 7, very rarely 9), the fourth and fifth (very rarely third & fourth, fifth & sixth, third, fourth & fifth, or third, or

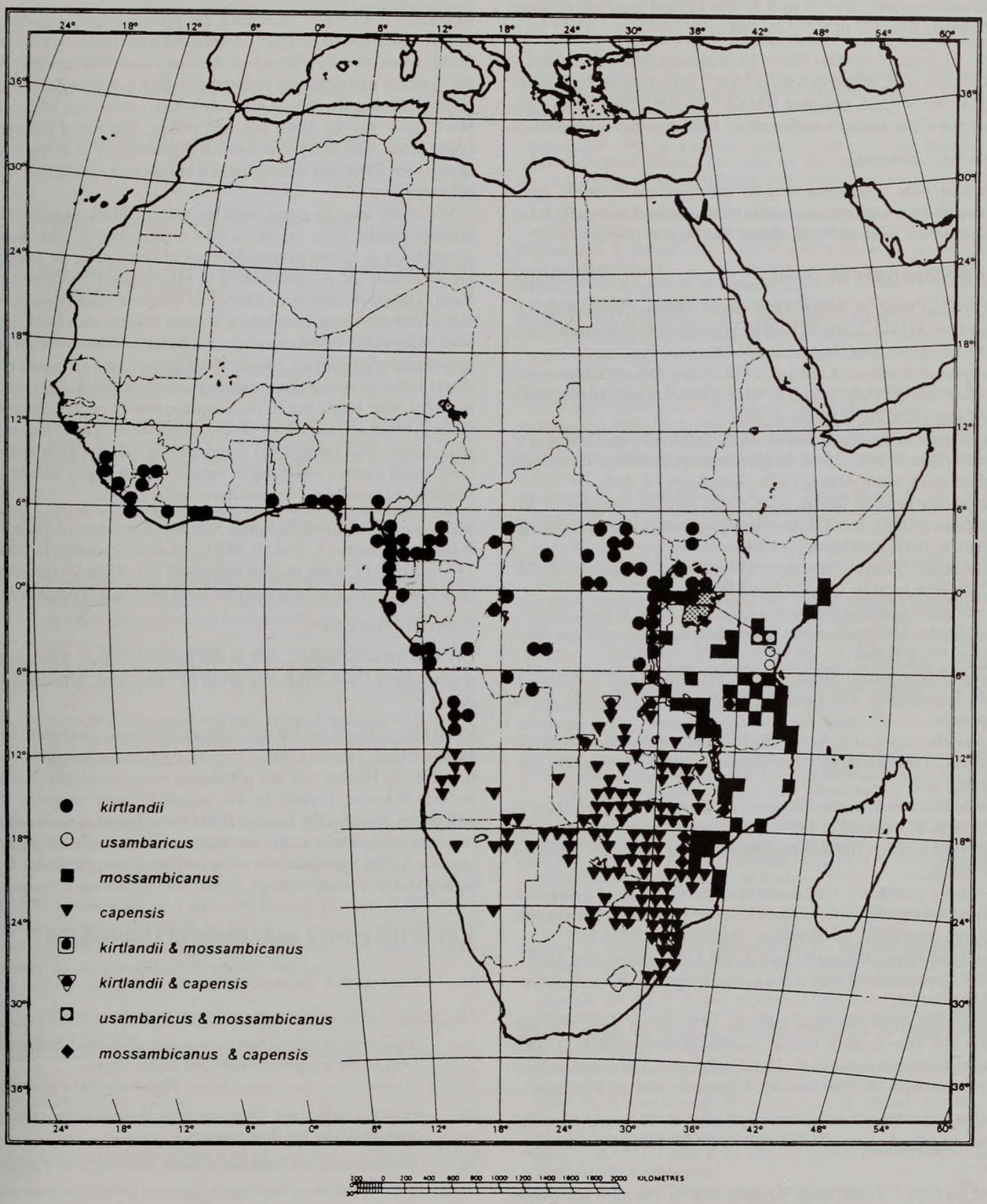


Fig. 6 Distribution of the genus *Thelotornis*.

fourth only) entering orbit; infralabials 9–13, mode 11, the first 4 or 5 (rarely 3) in contact with anterior sublinguals; dorsal scales usually in 19-19-11 or 19-19-13 rows, very rarely 17 rows at midbody; ventrals 150–177 in ♂♂, 153–177 in ♀♀; cloacal divided; subcaudals 132–173 in ♂♂, 126–168 in ♀♀.

SIZE. Largest ♂ (NMZB 3828 – Mtorashanga, Zimbabwe) 1062 + 620 = 1682 mm; largest ♀ (NMZB 3600 – Lake Kariba, Zimbabwe) 975 + 560 = 1535 mm, but NMZB-UM 1061 from Shurugwe, Zimbabwe, has a snout-vent length of 1050 mm (tail truncated).

HABITAT. Savanna.

DISTRIBUTION. Southern Angola and northern Namibia, west through northern Botswana, Zambia and southeast Katanga (D.R.C.) to Zimbabwe, western Mozambique and Malawi (Fig. 6).

Dispholidus typus (A. Smith) Boomslang

Bucephalus typus A. Smith, 1828, *South African Commercial Advertiser* **3** (144): 2, col. 4. Type locality: Eastern districts of South Africa; 1829, *Zool. Journ.*, **4**: 441 (*B. typicus*).

Bucephalus Jardineii A. Smith, 1828, *South African Commercial Advertiser* **3** (144): 2, col. 4. Type locality: Cape Town, South Africa; 1829, *Zool. Journ.*, **4**: 422.

Bucephalus gutturalis A. Smith, 1828, *South African Commercial Advertiser* **3** (144): 2, col. 4. Type locality: Forests of the eastern districts of South Africa; 1829, *Zool. Journ.*, **4**: 442.

Bucephalus Bellii A. Smith, 1828, *South African Commercial Advertiser* **3** (144): 2, col. 4. Type locality: Eastern districts of South Africa; 1829, *Zool. Journ.*, **4**: 442.

Dispholidus Lalandii Duvernoy, 1832, *Ann. Sci. Nat.* (Paris) **26**: 150. Type locality: Cape of Good Hope.

Dendrophis colubrina Schlegel, 1837, *Essai Phys. Serp.* **2**: 238, Pl. ix, fig. 14–16. Type locality: Rondesbosch, [Western] Cape Province, South Africa.

Bucephalus viridis A. Smith, 1838, *Illus. Zool. S. Africa, Rept.*: Pl. iii. Type locality: Old Latakoo [Northern Cape Province], South Africa.

Bucephalus capensis A. Smith, 1841, *Illus. Zool. S. Africa, Rept.*: Pl. x–xiii. Type locality: Cape Province, South Africa; Bocage, 1895: 121.

Dendrophis pseudodipsas Bianconi, 1848, *Nuovi Ann. Sci.Nat.* (2) **10**: 108, Pl. iv, fig. 2 & 1850. *Spec. Zool. Mosamb.* **40**, Pl. iv, fig. 2. Type locality: [Inhambane] Mozambique. Holotype: Bologna 100296.

Thrasops jacksonii mossambicus Mertens, 1937, *Abhand. senckenberg. naturf. Ges.*, No. 435: 13. Type locality: Cheringoma Farm, Inhaminga, Mozambique. Holotype SMF 22246.

Dispholidus typus kivuensis Laurent, 1955, *Revue Zool. Bot. Afr.* **51**: 127. Type locality: Uvira, Kivu. Congo Belge [= D.R.C.]. Holotype MRAC 17505.

Dispholidus typus punctatus Laurent, 1955, *Revue Zool. Bot. Afr.* **51**: 129. Type locality: Dundo, Angola. Holotype MRAC 17395.

Dispholidus typus occidentalis Perret, 1961, *Bull. Soc. neuchateloise Sci. nat.* **84**: 138. Type locality: Cameroon, no type designated.

DIAGNOSIS. Dorsal scales strongly keeled in 19 (rarely 17 or 21) rows at midbody; ventrals 164–201; anal divided; subcaudals 94–142.

DESCRIPTION. Supralabials 7 (rarely 8 or 6), the third and fourth (rarely 5th & 6th) entering orbit; lower labials 8–13, the first 3–6 in contact with anterior sublinguals; preocular 1; postoculars 3 (very rarely 2 or 4), the lower in contact with two labials; temporals 1 + 2 (very rarely 1 +1, 1 + 3, 2 + 1, 2 + 2 or 2 +3); three enlarged occipitals, the middle one subtriangular. Dorsals strongly keeled in 19 (rarely 17 or 21) rows; ventrals 164–201; cloacal divided; subcaudals 94–142 pairs.

COLORATION IN LIFE. Juveniles are speckled dark grey-brown above, with paired blue spots on some adjacent scales that become visible when the skin is stretched, the lower scale rows are grey and the venter is white, heavily stippled with dark red-brown. The head is brown above, the labials and chin white, sometimes with some black spots, and the throat is bright yellow. The iris of the eye is bright green. The juvenile coloration is gradually lost as the snake approaches one metre in length and there is great variation in adult colour pattern.

Males are usually green, with or without black-edged scales, females usually olive or brown above, paler below. This sexual dimorphism in colour pattern does not always apply, for example green females are not uncommon in Mozambique and KwaZulu-Natal, while in southwestern Zimbabwe some males are olive-brown above and duck-egg blue below. In East Africa a uniform black phase may occur in either sex. In the Eastern Cape Province (the 'type locality') males are usually black above, each scale and head shield with a green or yellow spot, venter yellow-green, each ventral bordered with black, but in the southwestern Cape the dorsum is uniform black and the venter yellow. In the western form described as *D. t. punctatus* Laurent, the males are black above, each scale or head shield with an orange spot, ventrals violet edged with black. Females are usually red-brown above, paler below.

SIZE. Largest ♂ (NMZB 3947 – Mutoko, Zimbabwe) 1290 + 530 = 1820 mm; largest ♀ (NMZB 3820 – Makote, Newala, Tanzania) 1447 + 475 = 1922 mm (tail tip truncated). C.J.P. Ionides recorded a brown male from Tanzania that measured 2134 mm (Pitman, 1974).

HABITAT. Savanna.

DISTRIBUTION. Senegal east to the Horn of Africa, south to the southwestern Cape, excluding areas of rain forest, grassland and desert.

REMARKS. The data for the solitary specimen examined from Pemba Island, Tanzania (MCZ 45587), confirm the long held opinion of Barry Hughes that this population is taxonomically distinct: he will describe it when he has access to more material. The subspecies described by Laurent (1955) were based on male coloration and subcaudal counts, but there is clinal variation in both characters. The species needs to be reviewed, using material from throughout its extensive range.

Key to the genera and species of Dispholidini

1a. Nasal divided; rear maxillary teeth not grooved 2

1b. Nasal entire; enlarged grooved fangs on posterior maxilla 8

2a. Head elongate with two loreals in tandem; temporals 1+2; maxillary teeth 17, the last three enlarged and dagger-shaped ..... *Xyelodontophis uluguruensis*

2b. Head short with single loreal; temporals 1+1 or one only; maxillary teeth 20–38, the last three enlarged 3

3a. Vertebral scale row enlarged; a single temporal; 2 or 4 enlarged occipitals 4

3b. Vertebral scale row not enlarged; 1+1 temporals; no enlarged occipitals 5

4a. Cloacal shield entire; midbody scale rows 13; occipitals 4 ..... *Rhamnophis batesii*

4b. Cloacal shield divided; midbody scale rows 15–19; occipitals 2 ..... *Rhamnophis aethiopissa*

5a. Dorsal scales twice as long as lower row of laterals and ventrals; midbody scale rows 13 (rarely 15) ..... *Thrasops flavigularis*

5b. Dorsal scales subequal in length to the ventrals; midbody scale rows 15–19 (rarely 21) 6

6a. Three supralabials in contact with lower postocular .... *Thrasops occidentalis*

6b. Two supralabials in contact with lower postocular 7

7a. Midbody scale rows usually 19; ventrals 187–214 .... *Thrasops jacksonii*

7b. Midbody scale rows usually 17; ventrals 168–184 .... *Thrasops schmidti*

8a. Head elongate; pupil horizontal, keyhole shaped; eight supralabials, fourth and fifth entering orbit 9

8b. Head short; pupil round or pear-shaped; seven supralabials, third and fourth entering orbit ..... *Dispholidus typus*

9a. Top of head, including temporal region, uniform green; black crossbands or chevrons on neck; habitat forest 10

9b. Top of head uniform green or black speckled, temporal region always brown, speckled with black, or pink, shields margined with black; neck with black lateral blotches; habitat usually savanna 11

10a. Rostral and nasals strongly recurved onto top of snout; infralabials 7–11, mode 9; supralabials immaculate or with fine green or grey stipple ..... *T. kirtlandii*

10b. Rostral and nasals not, or only slightly, recurved onto top of snout; infralabials, 9–13, mode 11; supralabials with scattered black spots, usually including a triangle on the sixth labial ..... *T. usambaricus*

11a. Top of head bright green to pale brown, uniform or speckled with black; temporals brown speckled with black .... *T. mossambicanus*

11b. Top of head blue-green with pink and black speckling forming a 'Y' or 'T' marking, or speckling covering entire top of head; temporals pink margined with black ..... *T. capensis*

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Appendix 1. Material for which skulls were prepared:

Dispholidus typus (NMZB-UM 3058; NMZB 922, 1350, 1658, 3322, 10870, 13378); *Rhamnophis aethiopissa* (NMZB 10793, 16726); *Rhamnophis batesii* (NMZB 13206); *Xyelodontophis uluguruensis* (NMZB 7443 – holotype); *Thelotornis capensis* (NMZB-UM 88, 16199, 17922); *Thelotornis kirtlandii* (NMZB 32185); *Thelotornis mossambicanus* (NMZB-UM 3058; NMZB 11390); *Thelotornis usambaricus* (NMZB 15629); *Thrasops flavigularis* (NMZB 16725); *Thrasops jacksonii* (NMZB 10717).

Appendix 2. Material examined internally:

Dispholidus typus (BMNH 1979.205; FMNH 58379; IRSL 2 unnumbered; IRSNB 13281a–b, MCZ 18223, 32475, 32478, 53458, 53730–31, 55250, 55255, 67927), *Dispholidus* 'pemba' (MCZ 45587), *Hapsidophrys lineatus* (BMNH 1979.165–67; IRSL 15 unnumbered; SDSU unnumbered; UNAZA 4 unnumbered; VW 1010), *Hapsidophrys smaragdinus* (BMNH 1979.157–59; FMNH 179036; IRSL 14 unnumbered; MZUSP 8159; PEM 3363, 3403; UNAZA 4 unnumbered; VW 907, 1012, 1026, 1068, 1099), *Philothamnus angolensis* (IRSL 23 unnumbered; MZUSP 8174–75, 8177; NMV D55548; PEM 3382–83; SDSNH 63865–66; UF 52485, 80395–99, 80671; UNAZA 4 unnumbered; VW 1086, 1197, 1211, 1254, 1429–30, 1451, 1745, 1986–87, 1990, 2226; ZRC 2.3427), *Philothamnus bequaerti* (MCZ 47846), *Philothamnus carinatus* (UNAZA 2 unnumbered), *Philothamnus dorsalis* (UNAZA 2 unnumbered), *Philothamnus heterodermus* (UNAZA 1 unnumbered), *Philothamnus heterolepidotus* (LSUMZ 40781), *Philothamnus hoplogaster* (BYU 30895), *Philothamnus macrops* (MCZ 23244), *Philothamnus nitidus* (UNAZA 1 unnumbered), *Philothamnus occidentalis* (VW 6360), *Philothamnus punctatus* (MCZ 52666), *Xyelodontophis uluguruensis* (NMZB 7443; ZMB 48153), *Rhamnophis aethiopissa* (IRSL 6 unnumbered; MCZ 13607, 258900, 38392, 48343, 178494; SDSNH 63873; SDSU unnumbered), *Rhamnophis batesii* (IRSNB 2813; MCZ 13604, 38393), *Thelotornis capensis* (FMNH 191163; MCZ 41963, 44581, 69036; ZMB 23526), *Thelotornis kirtlandii* (FMNH 205972, 214828; IRSL 1 unnumbered; IRSNB 5370, 5371a–b, 6451, 6454; MCZ 22523, 49687, 49734, 51835; SDSU unnumbered; ZMB 21627), *Thelotornis mossambicanus* (FMNH 248040; MCZ 51628, 56922; ZMB 16783, 28001), *Thelotornis usambaricus* (MCZ 23349; ZMB 16786, 21130), *Thrasops flavigularis* (MCZ 8776–77; MHNG 967.20, 1520.68, 1520.75, 1520.78), *Thrasops jacksonii* (BMNH 1979.190–91; UF 52476; MCZ 25954; MZUSP 8178–79; UNAZA 5 unnumbered; VW 1077, 1083, 1230, 1232, 1965, 2350), *Thrasops occidentalis* (MCZ 55232; UG C34P12), *Thrasops schmidti* (MNHN 1940.197, 1974.1; NRM 2297b).