

A review of the genus *Gonionotophis* in north-eastern Africa (Squamata: Lamprophiidae)

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Abstract. The status of the material of the genus *Gonionotophis* from north-eastern Africa (north of Latitude 12°S and east of Longitude 28°E) is reconsidered. The northernmost specimens of *G. nyassae* (Günther, 1888) fall within the known range of variation for that species. The available specimens of the *G. capensis* (A. Smith, 1847) complex from this region indicate that the number of postoculars varies from none to three, so that the ‘diagnostic’ lack of postoculars in *M. fiechteri* Scortecci, 1929 is invalid. The Somali specimens should be assigned to the north-eastern form *G. chanleri* (Stejneger, 1893), of which *Simocephalus unicolor* Boulenger, 1910 is a synonym. Data for *G. chanleri* is summarised from throughout its extensive range, and compared with data for adjacent populations of *G. capensis* and *G. savorgnani* (Mocquard, 1877).

Keywords. Reptilia, Squamata, Lamprophiidae, *Gonionotophis*, north-eastern Africa, taxonomy, zoogeography.

INTRODUCTION

In the last revision of the genus *Mehelya* Csiki, 1903, Loveridge (1939) recognized three subspecies of *M. capensis* (A. Smith, 1847), the typical form from southern Africa, *M. c. fiechteri* Scortecci, 1929 (based on only two specimens from Somalia), while other records from southern Somalia (including the type of *M. somaliensis* Lönnberg and Andersson, 1913) were assigned to *M. c. savorgnani* (Mocquard, 1877). Parker (1949) accepted Loveridge’s views, although sceptical of the alleged extensive range of the latter taxon. Laurent (1956) reinstated *M. c. unicolor* (Boulenger, 1910) on the basis of two specimens from Rwanda. Hoevers and Johnson (1982) recorded *M. nyassae* (Günther, 1888) from Somalia for the first time and assigned three snakes to *M. c. savorgnani*, although noting that they had the dark venter of *M. c. unicolor*. Lanza (1983, 1990) indicated the range of *M. c. savorgnani* in Somalia. Broadley (2005) pointed out that the lost type specimen of *Heterolepis capensis* A. Smith, 1847 appears to have been a female of the taxon now called *Gonionotophis savorgnani*, which it matched in col-

our pattern (no white vertebral stripe) and a high ventral count of 241. Accordingly BMNH 91.9.15.9 from Delagoa Bay, the only specimen available to Boulenger when he prepared the species account for his *Catalogue of Snakes* in 1893, was nominated the neotype of *H. capensis* A. Smith, 1847. Kelly *et al.* (2011) published molecular data which showed that *Gonionotophis brussauxi* (Mocquard, 1889; type species) was nested within *Mehelya*, and as the former generic name had priority, the latter had to be placed in synonymy. These data also suggested that the taxa of the *G. capensis* group (represented by *capensis* and *unicolor*) constituted a distinct clade, and also that *G. unicolor* was specifically distinct from *G. capensis*. Unfortunately obtaining tissues samples of these rare snakes is very difficult, and further progress with a comprehensive molecular phylogeny for the genus will be slow.

MATERIALS AND METHODS

This study was based on the material available in Italian museums, the California Academy of Sciences, and various

museums in Africa, Europe and the United States visited by DGB. Additional data was incorporated from the publications of Laurent (1956, 1960), Vesey-Fitzgerald (1958), De Witte (1966) and Dersley (1978). Institutional acronyms follow Leviton *et al.* (1985), with the addition of KMH = Field numbers of K.M. Howell, University of Dar-es-Salaam, and MSNSSM = Museo di Storia Naturale e della Strumentazione Scientifica dell'Università di Modena.

Gender was determined by checking for the presence of hemipenes by dissection. Standard counts were taken of dorsal scale rows, ventrals, subcaudals (counted according to the method of Dowling, 1951), upper labials (and those entering orbit), lower labials (and those in contact with the anterior sublinguals), preoculars, postoculars and temporals. The anal was entire in all specimens examined. There is great intraspecific variation in proportions and number of head shields, as previously indicated by Loveridge (1939), so these characters were not analysed. Snout-vent length and tail length were measured to the nearest mm with a white-face tape, or with fishing line if set in coils. There appears to be no change in colouration between live and preserved specimens of file snakes.

RESULTS

Within the *G. capensis* complex, *G. chanleri* was readily diagnosed by its quadricarinate vertebral scale row, while *G. savognani* differed from *G. capensis* in lacking a white vertebral scale row and having higher ventral counts in both sexes (Table 1). The much smaller *G. nyassae* differs in having juxtaposed dorsal scale rows and very low ventral counts (Table 1).

SPECIES ACCOUNTS

Gonionotophis capensis (A. Smith, 1847) Southern File Snake

Heterolepis capensis A. Smith, 1847, Ill. Zool. S. Africa, Rept., pl. lv. Type locality: 'Eastern parts of Cape Province, South Africa'. Type lost and type locality rejected, neotype designated by Broadley (2005): BM 91.9.15.9

Delagoa Bay [= Maputo, Mozambique], donated by South African Museum.

Heterolepis Gueinzii Peters, 1874, Monatsber. Dtsch. Akad. Wiss. Berlin: 163, Pl., fig. 2. Type locality: Port Natal [= Durban], South Africa.

Heterolepis bicarinatus (not Duméril, Bibron and Duméril) Pfeffer, 1889: 9.

Simocephalus poensis (not A. Smith) Pfeffer, 1893: 86.

Simocephalus capensis Boulenger 1893: 345 (part) and 1896: 617.

Mehelya capensis Barbour and Loveridge, 1928: 114; Vesey-FitzGerald, 1958: 40; 1975: 12.

Mehelya capensis capensis Loveridge, 1939: 142; 1951: 189; Moreau and Pakenham, 1942: 62; Broadley and Pitman, 1960: 439; Pakenham, 1983: 25; Laurent, 1956: 99; Spawls *et al.*, 2002.

Diagnosis. A large species with dorsal scales in 15 rows at midbody, vertebral scale row bicarinate, dorsal scale rows widely separated by interstitial skin, dorsals with a subserrate median keel with fragmented secondary keels; ventrals 193-224 without sexual dimorphism; anal entire; paired subcaudals 39-60 without sexual dimorphism. Supralabials 7, third and fourth entering orbit. Dark brown to black above, with vertebral scale row white and other dorsals white-tipped, venter white but outer ends of ventrals black.

Description. Eye moderate, its diameter subequal to its distance from the lip; loreal little longer than deep; preocular usually single, but two in MCZ 23201 and NMK 1225; postoculars 1-2; temporals usually 1+2, but 1+3 on one side of MCZ 21011; supralabials 7, but 6 on one side of NMK 1227 and 8 on one side of NMK 1225; infralabials 8. Dorsal scales in 15-17 rows on neck, 15 at midbody, 15 before the vent, vertebral row bicarinate; ventrals 215-221 in males, 213-224 in females; anal entire; subcaudals 51-60 in males, 40-52 in females.

Dentition. Teeth firmly ankylosed, but all are replaced simultaneously, so that there may be duplicated rows of functional teeth throughout.

Table 1. Comparison of ventral and subcaudal counts for four species of *Gonionotophis* from northeastern Africa.

Species	Ventrals								Subcaudals							
	Males				Females				Males				Females			
	n	Range	Mean	SD	n	Range	Mean	SD	n	Range	Mean	SD	n	Range	Mean	SD
<i>capensis</i>	8	215-221	217.62	2.13	7	213-224	219.0	3.70	5	51-60	55.80	3.49	6	40-52	48.00	4.69
<i>savognani</i>	12	220-235	228.17	4.86	11	225-239	232.2	5.27	9	51-60	55.33	2.92	8	45-61	50.25	5.90
<i>chanleri</i>	21	215-233	223.28	4.38	20	218-243	225.4	5.67	15	44-62	56.07	4.77	15	44-57	48.73	4.53
<i>nyassae</i>	5	164-168	166.20	1.79	6	170-178	175.2	2.71	6	62-78	69.67	6.15	6	55-67	62.83	4.26

Size. Largest female from Mbala, Zambia 1245 + 155 = 1400 mm (Vesey-FitzGerald, 1958).

Diet. A specimen from Ruponda, Tanzania, contained a *Gerrhosaurus nigrolineatus* (Loveridge, 1951). A Zanzibar specimen, 1240 mm in total length, contained a *Boaedon* 889 mm long, whose tail protruded from the file snake's mouth (Pakenham, 1983).

Habitat. Savanna woodland.

Distribution. Southeastern Africa, north to eastern Angola, Zambia, south-eastern DRC (Katanga Province), Malawi and southeastern Tanzania as far north as the eastern Usambara Mountains, where parapatric with *G. chanleri*.

Localities. DEMOCRATIC REPUBLIC OF CONGO (KATANGA). Albertville [Kalemie] MRAC 4275, 9992, 16502 (Laurent, 1956). ZAMBIA. Abercorn [Mbala] IRSNB ---; Vesey-FitzGerald, 1958. TANZANIA. Amani MCZ 21011, 23201-2, 23204, NMK 1225; Dar es Salaam NMK 1226; Kwamkoro/Kwamsambia Forest Reserve NMZB 16382; Magrotto Hill NMZB 14796; Nanguru Mission, Lindi KMH 6002; Ruponda, Lindi MCZ 50070; Songea NMK 1227; Zanzibar (Pakenham, 1983).

Gonionotophis savorgnani (Mocquard, 1877)
Congo File Snake

Heterolepis savorgnani Mocquard, 1887, Bull. Soc. Philom. Paris (7) 11: 27, Pl. ii, fig. 4-4b. Type locality: Ogoewe, Gabon.

Simocephalus phyllopholis Werner, 1901, Zool Anz. 24: 301, fig. 3-4. Type locality: Cameroon.

Simocephalus Butleri Boulenger, 1907, Ann. Mag. Nat. Hist. (7) 20: 489. Type locality: between Wau and ChakChak, Bahr el Ghazel Province, Sudan; Boulenger, 1911: 164 (Bussu).

Mehelya (or *Simocephalus*) *lamani* Lönnberg, 1910, Arkiv. Zool. 8 (20): 2. Type locality: Mukimbungu, Lower Congo (DRC).

Mehelya chanleri (not Stejneger) Loveridge, 1929: 21; Pitman, 1936: 271, pl. iv, fig. 5 and pl. D, fig. 1.

Mehelya capensis savorgnani Loveridge, 1939: 136 (part), Fig. 1; Laurent, 1956: 101, 372; De Witte, 1966: 64; 1975: 72; Pitman, 1974: 86, pl. iv, fig. 5 and pl. D, fig. 1; Largen and Rasmussen, 1993: 352; Spawls *et al.*, 2002; Largen and Spawls, 2010: 486 (Gambela).

Mehelya poensis (not A. Smith) De Witte, 1941: 182.

Diagnosis. A large species with dorsal scales in 15 rows at midbody, vertebral scale row bicarinate, dorsal scale rows widely separated by interstitial skin, subserrate median keel with fragmented secondary keels; ventrals 211-241 without sexual dimorphism; anal entire; paired subcaudals 45-62 without sexual dimorphism. Suprala-

bials 7, third and fourth entering orbit. Dark brown to black above, uniform, or each scale with a light apical spot, giving a speckled effect, venter white but outer ends of ventrals dark.

Description. Eye moderate, its diameter one and a half times its distance from the lip; loreal slightly deeper than long; preocular usually single, but two in MRAC 18078-9 and on one side of MRAC 18077; postoculars 1-3; temporals usually 1+2, but 2+3 on MRAC 18077 and on one side of MRAC 18078; supralabials 7, but 6 on MRAC 14272 and on one side of BM 1908.10.20.12; infralabials 8-9, but 7 in NMK 2890. Dorsal scales in 15-21 rows on neck, 15 at midbody, 15 before the vent, vertebral row bicarinate; ventrals 220-235 in males, 225-239 in females; anal entire; subcaudals 51-60 in males, 45-61 in females.

Dentition. Teeth firmly ankylosed, but all are replaced simultaneously, so that there may be duplicated rows of functional teeth throughout.

Size. Largest male (IRSNB --- Bagbele, Parc Nat. Garamba, DRC) 1122 + 180 = 1302 mm (De Witte, 1966); largest female (IRSNB --- Parc Nat. Garamba, DRC) 1405 + 200 = 1605 mm (De Witte, 1966).

Diet. In Uganda, Pitman (1974) records snakes of the genera *Causus*, *Boaedon* and *Psammophis*, lizards (*Gerrhosaurus*), and frogs and toads.

Habitat. In eastern DRC, commonly found in marshy areas (Laurent, 1956). In Uganda, recorded from larger forests and along the shores of Lake Victoria (Pitman, 1974). The only specimen from Ethiopia was found in marshy grassland near Gambela at an altitude of ca. 500 m (Largen and Spawls, 2010).

Distribution.--- Cameroon, Gabon, Congo-Brazzaville and northern Angola, east through Central African Republic and D.R.C. (sympatric with *G. chanleri* at Uvira) to southwestern Sudan, South Sudan, western Ethiopia (Gambela: Largen and Rasmussen, 1993), Uganda and western Kenya.

Localities.---SUDAN. Boma National Park NMK 2890; Wau to ChakChak BM 1946.1.14.44 (Type of *S. Butleri*). SOUTH SUDAN. Magwe FMNH 62337; Molongori FMNH 62335; Torit FMNH 62336. DEMOCRATIC REPUBLIC OF CONGO. Bagbele (De Witte, 1966); Butembo MRAC 21600; Garamba National Park NMZB 16655 (De Witte, 1966); Lubile, Pangi, Maniema MRAC 18082; Mambasa MZUF 32391; Mangureshipa, Kivu MRAC 17078-9; Mutsora, Ruwenzori MRAC 14274; Sake, Lac Kivu MRAC 14272; Teturi, Mambasa MRAC 18077; Uvira LACM 49571; Virunga National Park - Kabiro, Katara, Katuakamabi, Rugetsi, Rutshuru and Rwindi (De Witte, 1975). UGANDA. Budongo Forest BMNH 1935.10.11.7; Bussu BM 1911.7.8.5-6; Entebbe BM 1929.8.5.19; Mabira Forest BM 1908.10.20.12; Ntan-

di, Bwamba Forest LACM 46392; Rhino Camp, West Nile FMNH 13129; Saroti NMK 1418. KENYA. Chemilil, Kisumu CAS 150937; Kakamega CAS 111795, 150988; Kisumu-Nyalenda NMK 2882; Kitale NMK 3151.

Gonionotophis chanleri (Stejneger, 1839)

Unicolor File Snake

Figs. 1, 2

Simocephalus chanleri Stejneger, 1893, Proc. U.S. Natl. Mus. 16: 726. Type: USNM 20126, Wange [NOT Manda Island], Kenya; Boulenger, 1896: 617; 1915a: 621.

Simocephalus unicolor Boulenger, 1910, Ann. Mag. Nat. Hist. (8) 5: 512. Type: BMNH 1946.1.13.91, Fort Hall [= Maranga], Kenya; Boulenger, 1915a: 621.

Simocephalus poensis (not A. Smith) Leprie, 1911: 323 (Mogadiscio, Somalia).

Mehelya (Simocephalus) somaliensis Lönnberg and Andersson, 1913, Arkiv. Zool. (20) 8: 2. Type: NHRM ---- Kismayu [= Chisimaio], Somalia.

Simocephalus butleri (not Boulenger, 1907), Boulenger, 1915b: 647.

Mehelia (sic) (Simocephalus) fiechteri Scortecci, 1929, Atti. Soc. Ital. Sci. Nat. 68: 269. Type: MSNM 936, Villaggio Duca degli Abruzzi [= Giohar], Somalia.

Mehelia (sic) poensis (not A. Smith) Testi, 1935: 507 (eastern Eritrea).

Mehelya chanleri chanleri Loveridge, 1936: 24 (Rhino Camp, West Nile Province, Uganda).

Mehelya capensis savorgnani (not Mocquard) Loveridge, 1939: 137 (part), Fig. 1; Parker, 1949: 56; Hoevers and Johnson, 1982: 185; Lanza, 1983: 225 and 1990: 438; Largent and Rasmussen, 1993: 352 (part, Haud).

Mehelya capensis fiechteri Loveridge, 1939: 141; Parker, 1949: 57 (Haud, 09°N-44°E).

Mehelya capensis unicolor Laurent, 1956: 104; 1960: 24; Bourgeois, 1968: 220; Derleyn, 1978: 728-732; Broadley, 1985: 60; Broadley and Howell, 1991: 26; Hinkel, 1992: 439, pl. 338; Spawls *et al.*, 2002.

Mehelya capensis (not A. Smith) Vesey-FitzGerald, 1975: 12; Largent, 1997: 90.

Mehelya unicolor Largent and Spawls, 2010: 486 (Haud).

Description. Eye moderate to large, its diameter subequal to, or larger than its distance from the lip; loreal longer than deep, in MZUF 27065 contacting the eye below the preocular on the left side; preocular usually single, but two on both sides of MZUF 1354 and on one side of MSNM 977; postoculars 1-3, but absent on both sides of the type of *M. fiechteri* and BMNH 1949.2.1.86, and on right side of MSNM 977, postoculars may be fused with the supraocular and/or the fourth supralabial; temporals usually 1+2, but 1+1 in MZUF 1355 and

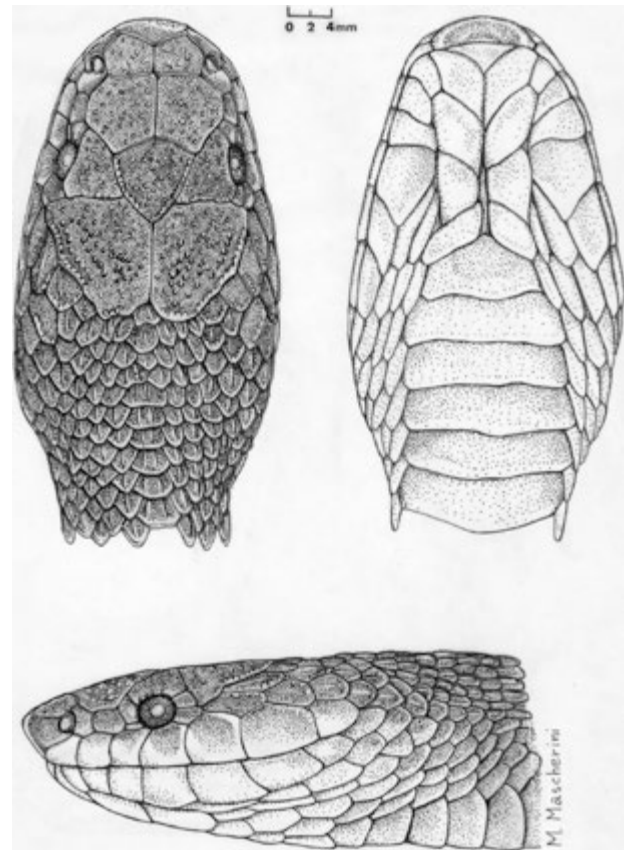


Fig. 1. *Gonionotophis chanleri*: dorsal, lateral and ventral views of the head of MZUF 1354 from Afgoi, Somalia.

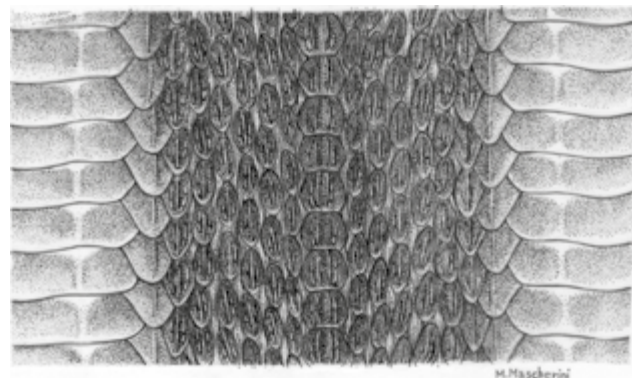


Fig. 2. *Gonionotophis chanleri*: scalation at midbody of MZUF 1354 from Afgoi, Somalia.

2+3 in five specimens recorded by Laurent (1956, 1960) from Rwanda and Kivu, and on one side of CAS 122368 from Voi; supralabials 7, but 6 on one side of MCZ 55495 and MRAC 20786, 8 in NMK 1341; infralabials 8, but 7

in NMK 2749 and 2996, and on one side of MSNM 936, MZUF 1355 and MCZ 55495. Dorsal scales in 17-19 rows on neck, 15 at midbody, 15-17 before the vent, vertebral row often quadricarinate [unique in the genus]; ventrals 215-233 in males, 218-243 in females; anal entire; subcaudals 44-62 in males, 44-57 in females, paired, but the proximal ones sometimes, more or less irregularly, single, as follows:

Mogadiscio ? female, 6 single + 3 paired + 7 single + all paired (Lepri, 1911)

MZUF 1354 female, 2 paired + 1 single + all paired

MZUF 2061 female, 3 single + all paired

MZUF 27064 female, 9 single + 1 paired + 3 single + all paired (Hoevers and Johnson, 1982)

MZUF 27065 male, 2 paired + 1 single + all paired

MZUF 27643 female, 2 single + all paired

Dark brown above, lighter brown below, chin and throat and distal edges of ventrals white. However the type of *S. savorgnani* had a yellow venter, while NMK 1417 from Voi is white and brown laterally with a brown stipple mesially, and CAS 122368 from near Voi has light patches mesially.

Dentition. In NMZB 3186 from Arusha, Tanzania, two rows of teeth are present on all dentigerous bones, the maxillary and dentary teeth are being replaced medial to the bones, while the palatine and pterygoid teeth are being replaced lateral to the bones. Simultaneous replacement of teeth does not seem to have been recorded in any other genus.

Size. Largest male (MRAC 20786 Kabuye, Astrida, Rwanda) 1311 + 174+ mm (tail truncated). Largest female (Kidwange, Astrida, Rwanda: Laurent, 1960) 1249 + 166 = 1415 mm.

Diet. At Fort Hall, Kenya, a specimen was killed while swallowing a 53 cm *Causus rhombeatus* (Loveridge, 1939). In Burundi, captive specimens consumed all snakes offered to them, including the genera *Lycophidion*, *Gonionotophis* (accidental), *Boaedon*, *Philothamnus*, and juveniles of *Bitis arietans* and *B. gabonica*, together with chameleons of the genera *Chamaeleo* and *Trioceros* (Derleyn, 1978).

Habitat. In Burundi, collected on the Ruzizi plain and along the shores of Lake Tanganyika (Derleyn, 1978). In Kenya, usually in savanna woodland (Spawls *et al.*, 2002). In Tanzania, montane forest in the Arusha National Park (NMZB 3186).

Distribution. Eastern Democratic Republic of the Congo (Kivu Province), Rwanda, Burundi, northern and western Tanzania, Kenya, Somalia and Eritrea (Fig. 4).

Localities. ERITREA. 'Eastern slope' (Anonymous, 1933; Testi, 1935) MSNSSM ----. SOMALIA. Afgoi MZUF 1354; Alessandra Island MZUF 2061; Balad MZUF 1355; Eggi MZUF 2298; Gelib MZUF 27643; Gio-

har [Villaggio Duca degli Abruzzi] MSNM 936 [Type of *S. fiechteri*], 977; Haud at 9°N, 44°E BMNH 1949.2.1.86; Kismayu NMRM 2419 [Type of *M. somaliensis*]; Mareri CAS 153341, MZUF 27064-5. KENYA. Kiboko Range Research Station NMK 2996, 3029; Kirwa, Meru NMK 3155; Makuweni, Machakos NMK 1341; Malindi NMK 2654, 2749; Fort Hall [Muranga] BMNH 1946.1.13.91 [Type of *S. unicolor*], NMK 1345; Nyambeni Mts NMK 1719; Sotik NMK 1343; Voi CAS 122368, NMK 1417; Wange USNM 20126 [Type of *S. chanleri*]; Watamu CAS 184312. TANZANIA. Iku, Rukwa Valley MCZ 55495; Kibondo NMZB 227; Samaria NMZB 17104; Tengeru, Arusha NMZB 3186. RWANDA. No precise locality MNHN 1996.7544; Buhanga-Ndara MRAC 20785; Kabuye MRAC 20786-7; Kidwange (Laurent, 1960); Nyakatare MRAC 8305, 10988. BURUNDI. No precise locality MNHN 1990.4626; Bujumbura (Derleyn A2-6), RNHM 26257; IMBO Sud [= Rumonge] (Derleyn A1); Ntita (Derleyn A7). DEMOCRATIC REPUBLIC OF CONGO (KIVU). Remera (Laurent, 1960); Uvira MRAC 21412.

Gonionotophis nyassae (Günther, 1888)

Dwarf File Snake

Fig. 3

Simocephalus nyassae Günther, 1888, Ann. Mag. nat. Hist. (6) 1: 328. Type: BMNH 1946.1.14.52, Lake Nyassa [= Malawi]; Boulenger, 1915a: 622.

Gonionotophis degrijsi Werner, 1906, Zoöl. Anz. 30: 53. Type locality: Usambara Mountains, Tanzania.

Mehelya nyassae Loveridge, 1936: 243; 1939: 148; 1955: 183; 1956: 11; 1959: 38; Parker *et al.*, 1940; Moreau and Pakenham, 1941: 108; Hoevers and Johnson, 1982: 186; Pakenham, 1983: 25; Spawls *et al.*, 2002; Spawls *et al.*, 2006: 102.

Diagnosis. A small species with 15 scale rows throughout the length of the body; dorsal scales imbricate, with a strong median keel and short apical keels laterally; ventrals 164-177 in males, 170-193 in females; subcaudals 62-78 in males, 54-74 in females; eye small to moderate in size; supralabials usually seven, the third and fourth entering the orbit. Uniform dark brown to black above, venter brown, white or mottled.

Description. Eye small, its diameter less than its distance from the lip; loreal nearly twice as long as deep; preocular 1; postocular 1 (rarely 2); temporals 1+2; supralabials 7, the third and fourth entering the orbit; infralabials 8, the first 5 (rarely 4) in contact with the anterior sublinguals. Scales in 15 rows, dorsals with a simple median keel and two short lateral ones apically (but fully tricarinate in NMZB 11805, a 218 mm juvenile from Zanzibar), vertebral scale row bicarinate; ventrals

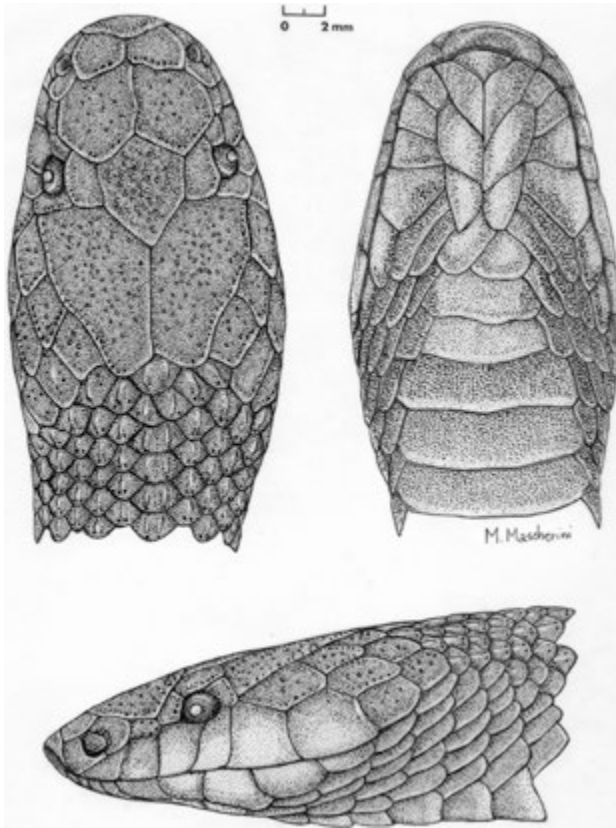


Fig. 3. *Gonionotophis nyassae*: dorsal, ventral and lateral views of the head of MZUF 27066 from Mareri, Somalia.

164-168 in males, 170-178 in females; anal entire; subcaudals 62-78 in males, 55-67 in females. Uniform dark brown to black above, lighter brown below, the ventrals with the distal margin bordered with whitish.

Dentition. Teeth hinged (Savitsky, 1981), which is presumably an advantage as the diet consists largely of well-armoured fossorial skinks (*Mochlus* and *Afroablepharus*), in addition, this does not appear to be a powerful constrictor.

Size. Largest male (Pakenham, 1983, from Zanzibar) 485+118 mm, largest female (MZUF 27066 - Mareri, Somalia) 455+115 mm.

Diet. The stomach of a female from Kilwa contained two skinks of the genera *Mochlus* and *Afroablepharus* (Loveridge, 1956). Two males from Liwale each held an *Afroablepharus wahlbergii* (Loveridge, 1959).

Breeding. A gravid female from Wema contained three eggs measuring 10 x 4 mm on June 13 (Loveridge, 1936).

Habitat. In Kenya, one taken in grass on the banks of the Tana River (Loveridge, 1939). At Liwale, two males were taken among rotting vegetation bordering gardens following a night of fairly heavy rain (Loveridge, 1959).

Low savanna, coastal thicket and woodland, from sea level to ca. 1 200 m altitude (Spawls *et al.*, 2006).

Distribution. From southern Somalia south to Kwa-Zulu-Natal, South Africa, extending inland to Rwanda, Burundi, eastern Democratic Republic of Congo, Zambia, Botswana and northern Namibia.

Localities. SOMALIA. Mareri CAS 153342; MZUF 27066. KENYA. Wema, Ngatana MCZ 40482. TANZANIA. No precise locality ZMB 17412; Kilwa MCZ 54519-20, NMK 973; Liwale I 8311, 8320; MCZ 52643; Makonde Scarp 2 KMH 26741; Tamota MCZ 54820; Tunduru MCZ 52644; Usambara Mts NMW --- [Type of *G. degrijsi* Werner]; Zanzibar (Pakenham, 1983) NMZB 11805. RWANDA. ZMH --- between Lakes Tanganyika and Kivu.

Key to the north-east African species of Gonionotophis based on external characters.

- 1a. Dorsal scale rows widely separated by interstitial skin; secondary keels on body scales all strongly developed; ventrals 215-243; subcaudals 40-62; maximum total length over 1600 mm 2
 1b. Dorsal scale rows juxtaposed; secondary keels on dorsal scales reduced to two short ones apically; ventrals 164-178; subcaudals 55-78; maximum total length 645 mm *nyassae*
 2a. Vertebral scale row bicarinate; venter white, ends of each ventral dark 3
 2b. Vertebral scale row often quadricarinate; venter usually dark brown to black *chanleri*
 3a. Vertebral scale row white; ventrals 215-221 in males, 213-224 in females *capensis*
 3b. Vertebral scale row dark; ventrals 220-235 in males, 225-239 in females *savorgnani*

DISCUSSION

The three taxa previously considered subspecies of *Gonionotophis capensis* are readily distinguished by their colour patterns. *G. capensis* has a well defined white stripe on the bicarinate vertebral scale row and a white venter. *G. savorgnani* has the dorsum uniformly dark, or with the scales white-tipped, the venter is white. The north-eastern form *G. chanleri* is uniformly dark above and below, or with the dorsal scales white-tipped, or the chin and throat white and white median patches on some ventrals (only uniformly pale in the type of *S. chanleri*). Table 1 shows ventral and subcaudal counts for *G. chanleri* from throughout its range, compared with populations of *G. capensis*, *G. savorgnani* and *G. nyassae* (Fig. 3) from north of Latitude 12°S and east of Longitude 28°E.

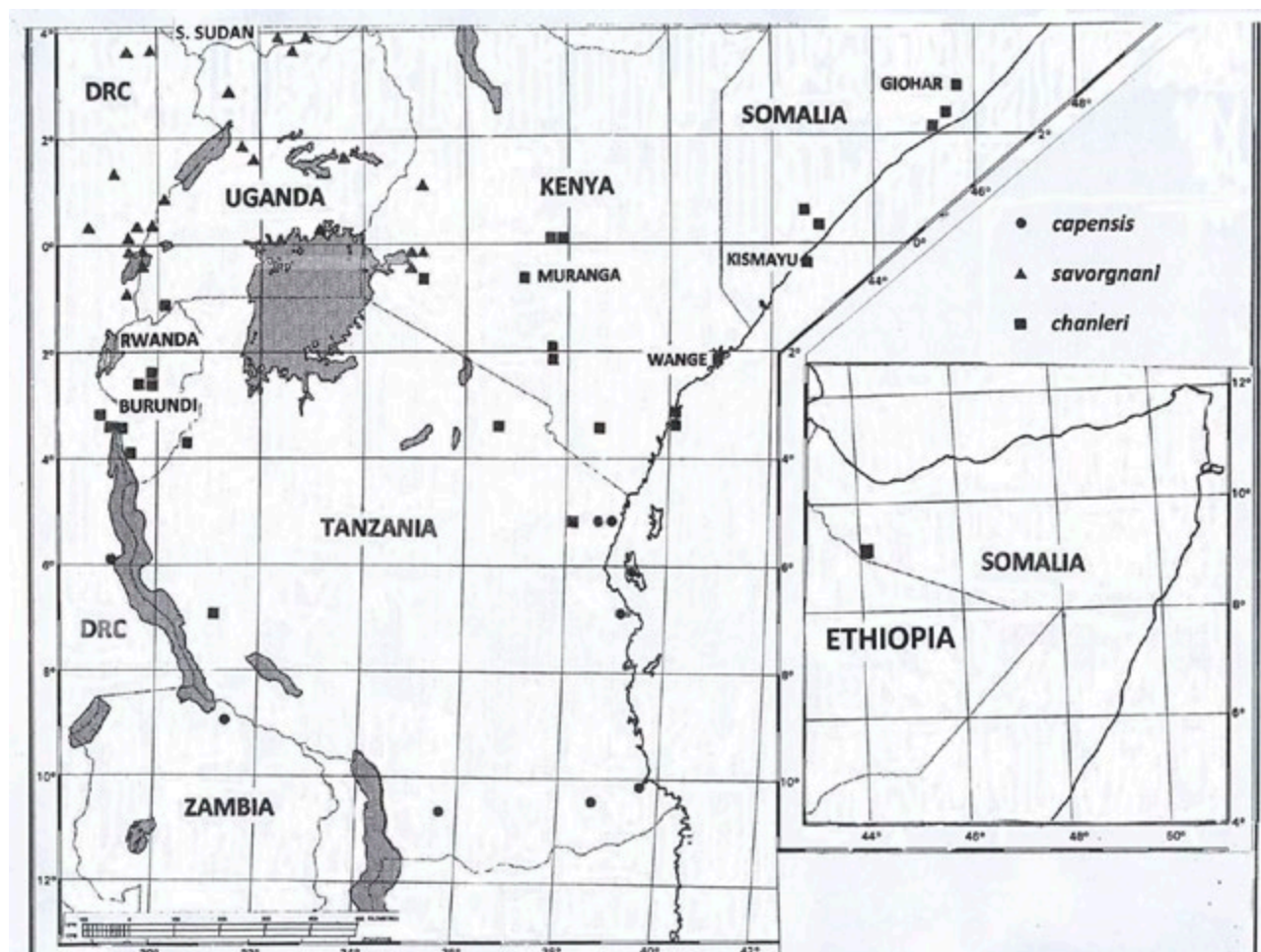


Fig. 4. The distribution by quarter degree cells of the taxa belonging to the *Gonionotophis capensis* complex in Africa north of Latitude 12'S and east of Longitude 28'E. The inset map at bottom right fits above the main map in the top right corner.

While the former two taxa are clearly separated on the basis of ventral counts, those for *G. chanleri* completely overlap them both. When he reinstated *M. unicolor* as a subspecies of *M. capensis*, Laurent (1956) also presented data showing that in the eastern Democratic Republic of Congo there was little overlap in ventral counts between *M. c. capensis* (215-222) and *M. c. savognnani* (221-236). *L. chanleri* differs from all other species in the genus in the strong development of secondary keels on the vertebral scale row, this is particularly well marked in the holotype, Somali material, and the specimen from Eritrea, where the vertebrae are distinctly quadricarinate.

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