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A new large species of *Bitis* Gray, 1842 (Serpentes: Viperidae) from the Bale Mountains of Ethiopia

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Abstract

A new species of viperine viperid snake is described, *Bitis harenna* **sp. nov.** The new species is a member of the subgenus *Macrocerastes* based on it having three scales separating the nasal and rostral shields, and on the combination of 'divisions' of dorsal scale rows on the upper flanks and 'fusions' of rows on the lower flanks. *Bitis harenna* **sp. nov.** is distinguished from other members of the subgenus by its unique colour pattern, posterior parietal flange on the lateral wall of the braincase, and possibly by differences in scalation and head proportions. Only a single museum specimen is known, a female collected from 'Dodola' in Ethiopia probably in the late 1960s and previously identified as a possibly unusually coloured and patterned *B. parviocula*. A live, presumably male, specimen very closely resembling the holotype of *Bitis harenna* **sp. nov.** was photographed on the Harenna escarpment of the Bale Mountains National Park, Ethiopia in 2013, providing secure occurrence data and evidence that the holotype is not a uniquely aberrant specimen. A revised key to the species of *Bitis* in Ethiopia is presented. Aspects of body scalation are compared among species of the subgenus *Macrocerastes* and between species of *Macrocerastes* and *Bitis,* and several systematic characters are highlighted and clarified.

Key words: Africa, *Bitis parviocula,* Harenna, *Macrocerastes,* snake, taxonomy, viper

Introduction

Bitis Gray, 1842 is a genus of adders (used here as a common name for viperine viperids) occurring in (mostly sub-Saharan) Africa and the southwest Arabian Peninsula. The 17 nominal extant species (e.g., Wallach *et al.*, 2014) include 12 relatively small (mostly < 600 mm total length) species and five substantially larger (to > 1 m) species, indeed the genus is considered to include the world's smallest and largest viperids. The smaller species occur in southern Africa (one species in Kenya), while the larger species have distributions that extend further northwards (e.g., Geniez *et al.*, 2004; Spawls & Branch, 1995), most having larger ranges, with the notable exception of *B. parviocula* Böhme, 1977 which is restricted to deciduous forest and montane grasslands of the Ethiopian highlands. In a study based mostly on molecular data, Lenk *et al.* (1999) proposed a natural classification of *Bitis* into four subgenera. Four of the five largest species (*B. gabonica* (Duméril, Bibron & Duméril, 1854), *B. nasicornis* (Shaw & Nodder, 1792 in 1789-1813), *B. parviocula,* and *B. rhinoceros* (Schlegel, 1855)) were classified into the subgenus *Macrocerastes*, with the fifth (*B. arietans* (Merrem, 1820)) being the sole member of the subgenus *Bitis.* The phylogenetic basis of the subgeneric classification of *Bitis* proposed by Lenk *et al.* (1999) was supported by analyses of additional molecular data by Wüster *et al.* (2008), and of molecular and morphological data by Wittenberg *et al.* (2015).

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In their comprehensive catalogue of Ethiopian snakes (at that time also including Eritrea), Largen & Rasmussen (1993) reported two species of *Bitis,* the widespread (across Africa and into the Arabian Peninsula) *B. arietans* and the much more restricted (Ethiopian endemic) and poorly known *B. parviocula*. For the latter they noted three museum specimens, the holotype from the southwestern moist forest region of Ethiopia (in the highlands west of the Ethiopian Rift Valley) and two newly referred but historical specimens from the moist highlands in the vicinity of Dodola to the east of the Rift Valley. Of the two latter specimens, one was reported to agree closely with the holotype but the other differed in at least its colour pattern, though in some unspecified way. Since 1993 there have been several additional reported sightings of *B. parviocula* (all resembling the holotype in its distinctive colour pattern) from southwestern Ethiopia (e.g., Nečas *et al.* 1993a), and specimens from this region have found their way into the international pet trade (e.g., Wittenberg *et al.* 2015). The region in which the vast majority of all *B. parviocula* have been collected is one of Ethiopia's busiest for the production of coffee (the country's largest export). Through interviews with both local collectors and commercial exporters T.J.C determined that the majority of all *B. parviocula* encounters occur during either the coffee planting or harvest times as the farmers clear their fields. In contrast, no additional specimens of *B. parviocula* have been found or reported from east of the Rift Valley, and no specimens resembling the differently coloured and patterned specimen reported by Largen & Rasmussen (1993) have turned up. Böhme (1990) considered the aberrantly coloured form from Dodola to be an undescribed species of *Bitis* that he was in the process of describing with the late J.B. Rasmussen. This work was never published.

Recently, one of us (E.R.B.) observed a live viper in the Bale Mountains, approximately 70km ESE of Dodola that resembled Largen & Rasmussen's aberrant form. This sighting provides secure occurrence data for this form and evidence for the historical specimen not being uniquely aberrant in its colour markings. The sighting prompted us to reassess the historical material and we here describe this form as a new species. The new species is identified as a member of the subgenus *Macrocerastes* because the nasal and rostral shields are separated by three scales (see Lenk *et al.*, 1999), and because it has a posteriorly divergent dorsal scale row pattern with splits/duplications/divisions on upper part of flanks and fusions on lower part of flanks (see Discussion below).

Material and methods

In addition to the holotype of the new species, comparative material examined directly included the holotype of *B. parviocula* and the only two other known museum specimens of this species, and exemplars of the other three species of the subgenus *Macrocerastes* and the only species of the subgenus *Bitis*. Material examined is listed in Appendix 1.

Total length was measured with a ruler to the nearest 1 mm. Other dimensions were recorded with dial calipers, to the nearest 0.1 mm. Bilateral scale counts separated by a comma are given in left, right order. Ventrals were counted following Dowling (1951a), and the reduction formulae compiled using a modified version of the method presented by Dowling (1951b). Dorsal scale rows were counted in as short (longitudinally) a transverse zig-zag as possible. The complexity of the body scalation rendered full scale-row reduction formulae impractical. Instead, dorsal row counts were made at the anteriormost commencement of the 'neck', at the tenth ventral and every tenth ventral thereafter, and full scale formulae were generated only for a short section (60th to 80th ventral) for some specimens. A ratio of the number of dorsals per ventral was determined arbitrarily for 20 ventrals, approximately ten of which lay each anterior and posterior to the median ventral. Within that same region, a portion of the flank was drawn for specimens of each species of *Macrocerastes*, illustrating in particular the nature of divergence of the dorsal scale rows.

Skulls and mandibles of three Ethiopian *Bitis* were imaged with X-ray micro-computed tomography (μCT), a non-destructive technique enabling 3D examination of bone in situ. The heads of whole spirit-preserved specimens were scanned using the Nikon Metrology HMX ST 225 by D.S. at the Natural History Museum, London. The scan parameters for ZMUC R68254 and R68255 and ZFMK 63067, maximising the differentiation of bone tissue, were as follows: a tungsten target was used at 170 kV and 160 μA; 3,142 X-ray projections were collected over a 360° rotation; with a reconstructed voxel size of 36, 28 and 27 μm, respectively. The μCT data were reconstructed into transverse slices using a modified Feldkamp back-projection algorithm (Feldkamp *et al.*, 1984). The slices were rendered as three-dimensional volumes using Drishti (Limaye, 2012) for visualisation.

Detailed drawings were made by one of us (E.O.Z.W.). Parts of the dorsum of the head and midbody of the holotype of the new species are damaged, with many scales severely abraded. Initially, preparatory drawings were made with the aid of a camera lucida. These were reduced to a convenient size and details extrapolated, careful measurements using proportionate dividers were made, and using a fine needle each scale of the affected area was ''teased'' so that its shape and position could be accurately determined. Final drawings include these minor reconstructions and the specimen is depicted as it is interpreted to have been in life (partly informed by observations of other living *Bitis*). Midbody scalation of specimens of the other species with which the new species was compared received the same initial treatment. The drawings of midbody scalation of *B. parviocula*, *B. rhinoceros* and *B. nasicornis* were made from preserved pelts rather than complete specimens, and thus a greater degree of (somewhat subjective) reconstruction was required in order to present readily comparable views. Whatever the degree of reconstruction, all these drawings are accurate to the precision of the presence/absence of single scales.

Institutional abbreviations for specimen prefixes are as follows: BMNH (The Natural History Museum, London, UK), ZFMK (Zoological Research Museum Alexander Koenig, Bonn, Germany), ZMUC (Zoological Museum, University of Copenhagen, Denmark).

Bitis harenna **sp. nov.**
(Figs. 1–7, 12; Tables 1–2; Appendices 1–2)

Bitis parviocula Böhme, 1977: Largen & Rasmussen (1993: 383–385, in part); Spawls & Branch (1995: 120–121, in part); Largen & Spawls (2010: 615, in part); Wallach *et al.* (2014: 92, in part); Wittenberg *et al.* (2015, in part)

undescribed species of *Bitis*: Böhme (1990: 12–13, fig. 4)

Holotype. ZMUC R68255 (Figs. 1–6), Dodola (from maps: 6.98° N, 39.18° E c. 2,400 m elevation), Oromia Region, Ethiopia; deposited by Sven Joergen Birket-Smith (1920–1983); preserved in ethanol; female. The exact date of collection is unknown, but was possibly 1966 or 1967, when Birket-Smith was in charge of the Addis Ababa Natural History Museum (M.J. Largen, pers. comm.).

Diagnosis. A *Bitis* of the subgenus *Macrocerastes* (*sensu* Lenk *et al.* 1999) that differs from all other species except *B. parviocula* in lacking horns between the nostrils, in having less than four scales between the rostral and first supralabial, and in having a pale cross bar on the dorsal surface of the head behind the eyes (Figs. 1, 2). Differs from all other species of the subgenus *Macrocerastes* (including *B. parviocula*) in having a concavity on the lateral wall of the braincase for the origin of the *M. retractor pterygoidei* that is limited posteriorly by flange on the parietal, rather than extending onto the prootic (see Groombridge 1980; Fig. 3/4); in being mostly blackish dorsally with narrow pale (cream to yellowish) markings (Fig. 1); in lacking a regular, parallel-sided mid-dorsal stripe (and a series of dark, approximately semicircular markings immediately lateral to this stripe; Figs. 1, 2, 6); and in having a black middorsal marking on the head that extends anteriorly to between the nostrils (Figs. 1, 2). Among species of the subgenus *Macrocerastes,* the new species differs also from *B. rhinoceros* and *B. gabonica* in having a mostly dark rather than pale dorsal surface of the head. Unlike *B. nasicornis,* the new species lacks posteriorly notched scales. Unlike *B. parviocula,* the new species has facets on the frontals for articulation with the prefrontals that do not meet medially (Fig. 3), and it also lacks a subhorizontal ridge on the lateral surface of the prootic overhanging the foramen for the mandibular branch of the trigeminal nerve (Fig. 4). See Remarks section for additional possible differences between the new species and its most similar congener, *B. parviocula*.

Description of holotype. Some morphometric and meristic data presented in Tables 1 and 2 and Appendix 2. Condition generally good, some scales rucked and/or abraded; specimen somewhat macerated in parts; 90 mm long approximately midventral incision extending back from approximately 150 mm behind snout tip, with approximately 10 mm^2 midventral section of body wall excised; outer layer of many scales lost. A large, relatively slender *Bitis*. Widest point slightly anterior to midbody; body tapers gently over anterior one-third of SVL, much more abruptly over posteriormost one-eighth of SVL. Tail short, very slender.

TABLE 1. Morphometric and meristic data for specimens of *Bitis harenna* **sp. nov.** and *B. parviocula*. Dimensions in mm; * indicates holotype; values separated by comma given in left, right order; characters in the form "X–Y" represent shortest distance between (not including) structures "X" and "Y"; distances measured in number of scales represents fewest scales between two points. Head length measured as snout tip–posterior end of retroarticular process. Mental and rostral shield dimensions are for externally exposed surfaces. Circumorbital count includes supraocular scale. Data for holotype of *B. parviocula* in parentheses from Böhme (1977). Tooth counts are recorded from µCT reconstructions. Blank cells indicate data not recorded; dash indicates data could not be recorded.

	*B. harenna** ZMUC R68255	*B. parviocula** ZFMK 16803	*B. parviocula* ZFMK 63067	*B. parviocula* ZMUC R68254
Sex	female	female	-	female
Total length	665	c.760 (752)	-	c. 890
Snout-vent length (SVL)	625	c.710 (705)	-	c.830
Tail length	39.7	47.6	-	61
Maximum width of tail	9.0	14.7	-	18.3
Maximum body circumference (C)	100	125	-	175
SVL/C	6.5	-	-	4.9
Head width (maximum)	31.5	-	43.2	60.4
Head length	44.8	45.8	52.0	55.5
Diameter of exposed part of eye	3.6	-	6.5	4.9
Eye–eye	12.3	-	16.7	19.0
Eye–lip	6.1	7.7	9.1	10.5
Eye–snout tip	11.5	13.0	14.1	17.8
Eye–naris	5.1	6.6	6.0	6.7
Naris–naris	6.5	-	9.9	10.6
Length of naris	1.8	-	2.4	2.9
Circumorbital scales	12,15	15,15 (14)	14,15	12,14
Scales circumorbitals–supralabials	2 to 3	3	3	2 to 3
Scales L–R circumorbitals	10	10 (12)	9	9
Scales L–R supranasal	2	2	3	2
Scales circumorbitals–supranasal	2,2	2,2	2,2	2,2
Scales nasal–rostral	3,3	4,4	4,4	4,4
Scales nasal–supralabial 1	2,3	3,3	4,4	3,3
Scales supranasal–rostral	3,3	3,3	3,3	3,3
Scales supranasal–supralabial 1	2,3	3,3	3,3	3,3
Width of rostral scale	5.0	5.6	7.0	7.6
Height of rostral scale	2.1	2.1	3.0	2.9
Supralabial scales	14,14	13,16 (13,14)	15 or 16,16	15,14
Infralabial scales	15,17	16,16 (15,15)	17,15	15,14
Scales first genial-first preventral	4	4	4	3 or 4
Dorsal scales last L–R supralabial	31	32	29	30
Width mental scale	5.1	5.9	6.6	7.1
Length mental scale	3.3	3.4	4.0	4.2
Preventral scales	3	3	4 or 5	3 or 4
Ventral scales	145	141 (144)	-	146
Subcaudal scales	20,19	21,21 (21,21)	-	21,21
Scale rows at base of tail	c. 17	c.21	-	c.19
Palatine teeth	2,2		2,2	2,2
Pterygoid teeth	12,12		13?, 11–13	13,13
Mandibular teeth	17,17		15,16–18	18,18

FIGURE 1. Photographs of the holotype (ZMUC R68255) of *Bitis harenna* **sp. nov.** Top panel shows whole animal in dorsal (left) and ventral (right) views. Lower panel shows head in dorsal (upper left) and ventral (upper right), and left lateral (lower left) and right lateral (lower right) views. Upper scale bar 10 cm, lower scale 2 cm. Photographs by Harry Taylor.

TABLE 2. Variation in numbers of vertebral scales aligned with 20 approximately midbody ventral scales in species of *Bitis*. Numbers separated by a comma are values reported for left, right side where that differs. Some of these specimens are illustrated in Fig. 6. All specimen numbers have BMNH prefix unless otherwise indicated.

Species and specimen	Position of 20 ventral scales	Number of vertebral scales
B. harenna **sp. nov.** ZMUC R68255	60–80	27, 25
B. parviocula ZFMK 16803	50–70	29
B. parviocula ZMUC R68254	60–80	31, 30
B. gabonica 1968.54	55–75	28
B. gabonica 96.5.14.20	55–75	35
B. gabonica 1975.1118	55–75	41
B. gabonica 1971.414	55–75	34
B. gabonica 1950.1.2.15	55–75	31
B. gabonica 1969.526	55–75	33
B. rhinoceros 1930.11.19.75	55–75	30.5
B. rhinoceros unnumbered	55–75	31
B. nasicornis '529'	50–70	37
B. nasicornis 1971.415	55–75	41
B. nasicornis 1935.10.2.1	55–75	32
B. nasicornis 1952.1.6.57 (118 ventrals)	50–70	41
B. nasicornis 1952.1.6.57 (123 ventrals)	50–70	37
B. nasicornis 1952.1.6.57 (128 ventrals)	50–70	38
B. arietans 87.11.3.32	60–80	20
B. arietans 1975.2146	60–80	21

otherwise indicated.[2]

Head posteriorly much wider than anteriormost end of body ('neck'). Distance between snout tip and posterior end of retroarticular process 43.7 mm (longitudinal distance between level of these two points 42.5 mm). Eyes surrounded by 12,15 circumorbital scales; separated from supralabials by 2 to 3 scales; pupil vertically eliptical. Left and right circumorbital series separated by at least 10 interorbital scales. Nostrils broadly oval (anteroventrally-posterodorsally oriented). Supranasal shields overhang nasals substantially, separated middorsally minimally by 2 scales, separated from circumorbitals minimally by 2 scales. Nasals and supranasals separated from rostral by 3,3 scales (> 3 mm), from first supralabial by 2,3 scales (2.5+ mm). Rostral much wider (5 mm) than high (2.1 mm at midline). Most dorsal and lateral head scales between and behind eyes keeled except supralabials and adjacent row posterior to 9th or 10th supralabial; no keels on scales of lower jaw or chin. Posteriormost left and right supralabials separated by at least 31 scales.

Supralabials 14,14. Infralabials 15,17, last of which especially small on each side; first pair contact at midline, second to fifth contact genials. Mental triangular, wider (5.1 mm) than long (3.3 mm). First pair of genials largest, contact at midline; second pair of genials much smaller and separated by one pair of smaller gulars; first pair of genials separated from first preventral by four gulars. First ventral separated from last infralabial by 8,7 scales.

Inside of mouth without pigment (except for at least tips of tongue, dark). Teeth mostly hidden in gingivae. Left fang intact, approximately 11.6 mm long.

Three preventrals (four discrete scales distributed over the length of the equivalent of three ventrals), 145 ventrals; ventrals mostly with orthoplicate posterior edges, notably convex in posteriormost ventral. Umbilical notch on posterior margin of 10th to 13th ventral scale anterior to anal scale. Anal shield single, strongly convex posterior margin; subcaudals 20,19 (excluding unpaired terminal scute), without keels; first subcaudal on left divided.

Immediately behind posterior end of lower jaw (level with sixth ventral) 43 dorsal scale rows, reducing to 36 rows ten ventrals further posteriorly. Numbers of dorsal scale rows thereafter fluctuate, most stable between approximately 50th and 110th ventral (35–40 rows, see Appendix 2). Dorsal rows reduced to 30 by 120th ventral; 28 rows at vent. Dorsal scale rows characterized by splits/duplications/divisions on upper part of flanks, fusions on lower part of flanks, beginning (anteriorly) by at least level of 15th ventral. Pattern of divisions, fusions produces posteroventrally oriented 'lines' (posteriorly diverging dorsal scale rows) accentuated visually by longitudinal keels on scales (Figs. 5, 6). Scale row formula for 60th to 80th ventral as follows:

	-4 (62/63)		-4 (65/66)		-4 (68/69) -5 (72) -4 (73)		-4 (76) -18 (76) -3 (78) -4 (79/80)	
	+9 (61)		+8 (64) +9 (65/66)		+8 (69) +3 (69) +8 (72)		+9 (75) +8 (76/77) +9 (77)	
39	----------------------	38	----------------------------	39	--	37	--	38
	+9 (63)		+8 (65)		+8 (67) +8 (68) +8 (71)		+9 (74/75) +7 (77) +9 (79)	
	-4 (61) -4 (63)		-4 (65/66)		-4 (67/68) -4 (69/70) -4 (72/73)		-4 (75) -3 (78)	

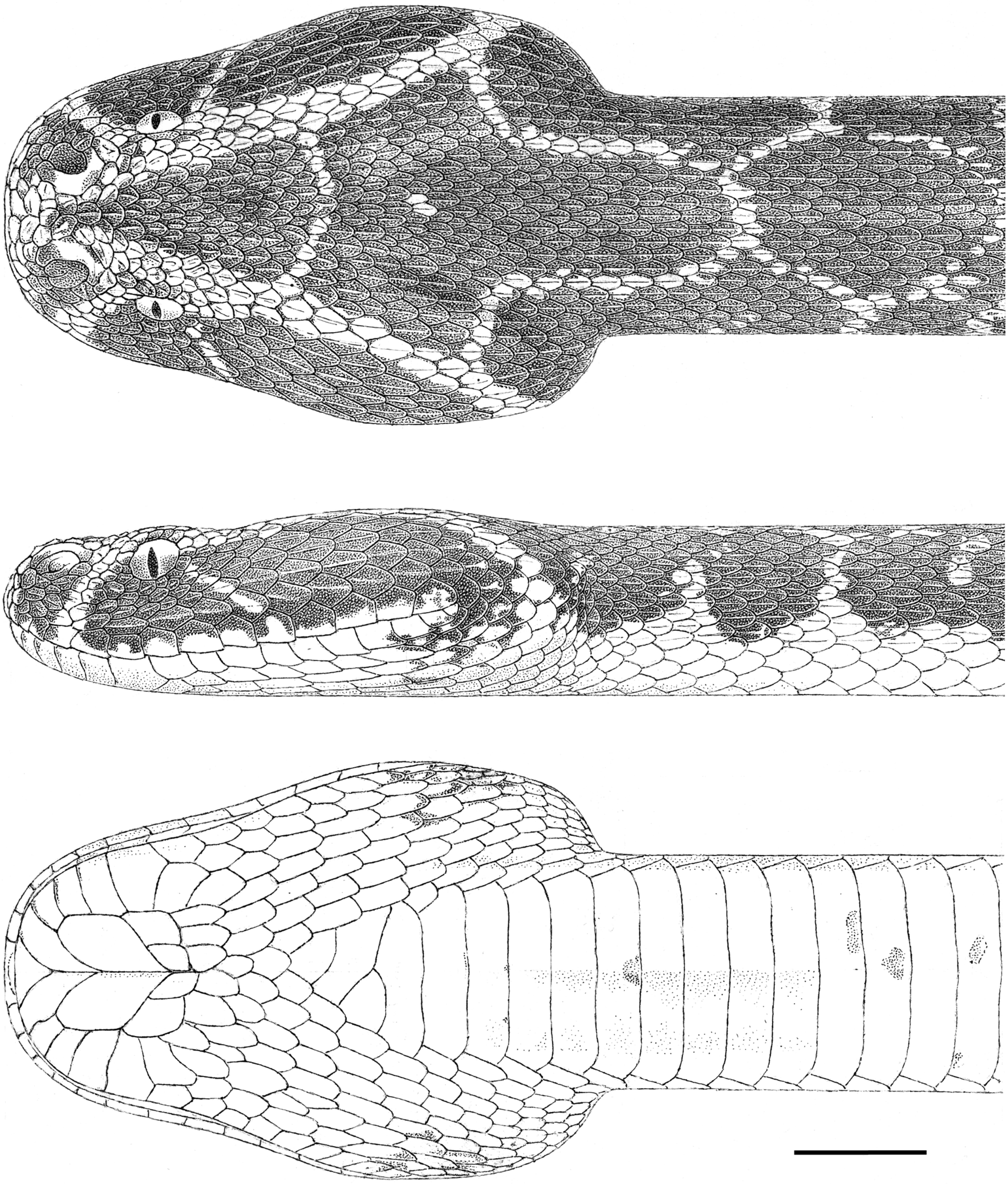

FIGURE 2. Drawings of the holotype (ZMUC R68255) of *Bitis harenna* **sp. nov.** Head and anterior of body in dorsal, left lateral and ventral views. Scale bar 10 mm. Drawings by Ed Wade.

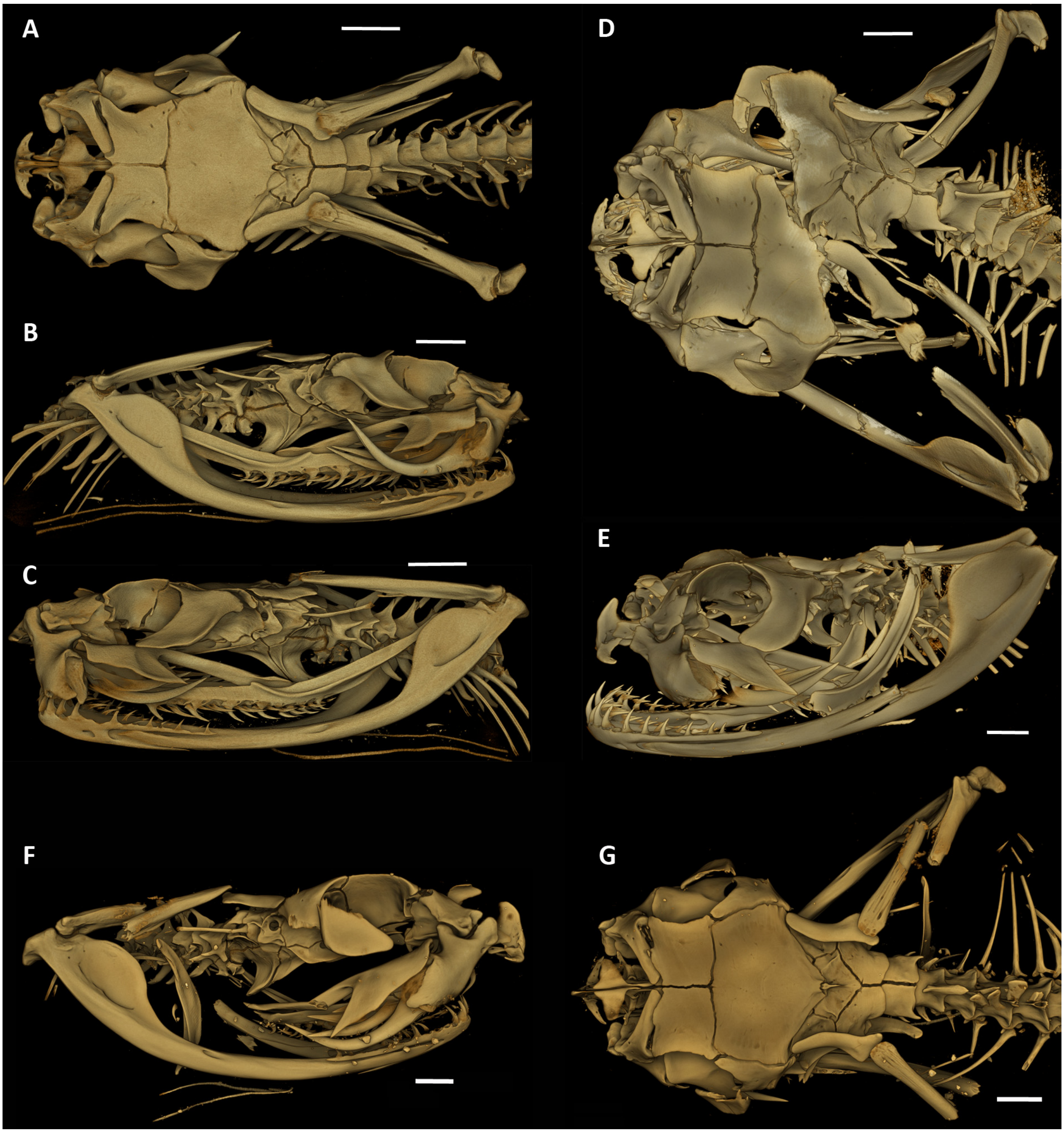

FIGURE 3. Volume reconstructions of µCT data for the skull and mandible of Ethiopian *Bitis* specimens. **A–C** holotype (ZMUC R68255) of *B. harenna* **sp. nov.** in dorsal (**A**), right lateral (**B**) and left lateral (**C**) views; **D–E** *B. parviocula* (ZMUC R68254: Dodola) in dorsal (**D**) and left lateral (**E**) views; F–G *B. parviocula* (ZFMK 63067: Bonga) in dorsal (**F**) and right lateral (**G**) views. Scale bars 5 mm.

Midvertebral scales variably single (vertebral) or double (paravertebral), for example single from level of 60th to 72nd ventral and from 74th to 80th, but double at level of 73rd ventral (Fig. 5). Twentyseven (left) and 25 (right) vertebral scales aligned with the 60th–80th ventral scales (Table 2). Approximately 17 dorsal scale rows on base of tail at level of anteriormost subcaudal.

Keels on body scales moderate, most prominent on dorsum, less prominent on lower than upper flanks, absent on first dorsal scale row; where prominent, keels extend to distal tip of scales; posterior margins of scales entire (not notched). Difficult to determine presence or absence of apical pits; seemingly present in at least some dorsal body scales, paired, close to scale tips. All scales on tail keeled except for subcaudals.

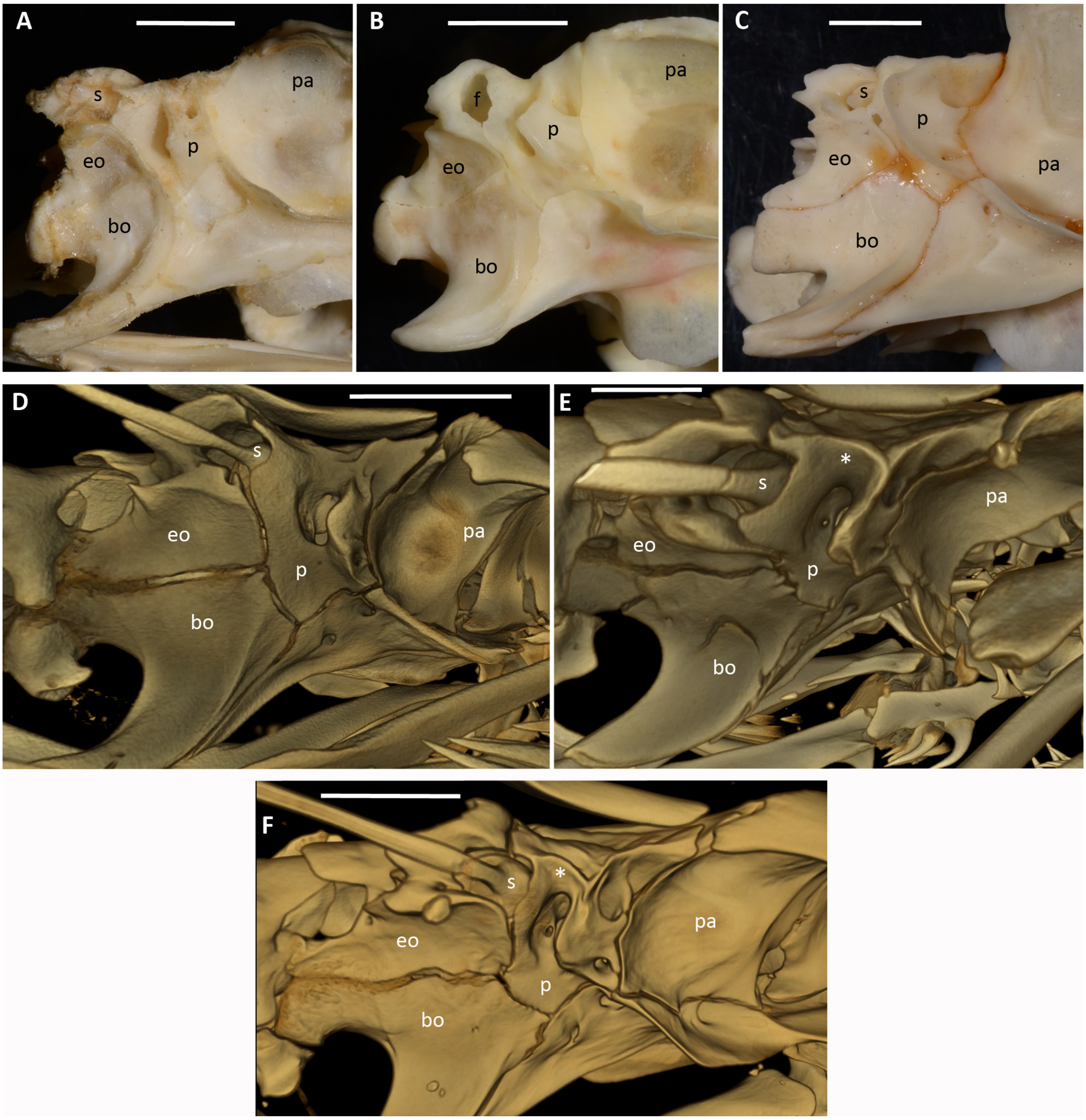

FIGURE 4. Comparison of the right lateral wall of the braincase in species of *Bitis*. Each figure part shows the braincase in approximately lateral (some more dorso- or ventro-, and some more postero or anterolateral) view. **A**) *B. arietans* (BMNH 1964.1249), **B**) *B. nasicornis* (BMNH unnumbered), **C**) *B. gabonica* (BMNH unnumbered), **D**) *B. harenna* **sp. nov.** (ZMUC R68255), **E**) *B. parviocula* (ZMUC R68254). **F**) *B. parviocula* (ZFMK 63067). Parts **A–C** are photographs of osteological preparations; parts **D, E** and **F** are µCT volume reconstructions. Scale bars 5 mm. Abbreviations: bo = basioccipital, eo = exoccipital-opisthotic, f = fenestra ovalis, p = prootic, pa = parietal, s = proximal end of stapes. * = prootic ridge present in *B. parviocula* but not in *B. harenna* **sp. nov.**

Colour in preservative essentially two tone (Fig. 1), with the dark varying from black to dark brown and the pale being ivory (off- or cream-white). Upper surface of head satin-black with two diverging ivory streaks united at the rostral, extending on to the nasal scute, contacting the upper edge of the eye, caudad to the throat and terminating at the retroarticular process. Approximately midway along length of head, the diverging ivory streaks are connected by a narrow (one scale wide), widely-open, V-shaped pale narrow band, broken at midline by 1 or 2 dark scales. Posteriorly a second pale, narrow band extends for five scales slightly obliquely posteriorly towards midline, then turns posteriorly and unites its antimere on the dorsum behind the head. The dark region on the dorsal surface of the head can be seen as a black (narrowly subtransversely bisected) arrowhead, 21 scales wide at its widest point, and reaching to within 3 scales of the rostral anteriorly. At its widest, the dark area bears a small middorsal spot across two scales. Laterally, a preorbital band, narrow but its width spread across two scales, extends from the dorsal streak, immediately anterior to the eye, to the posterior half of the 4th supralabial. A narrow postorbital bar (less than one scale wide) extends from the posterior margin of the eye to the 10th supralabial. Supralabials mostly with pale lower edges. Underside of head entirely pale except for dark anterior and posterior margins of anteriormost infralabials and few flecks posterolaterally, close to posteriormost infralabials.

Upper and lateral surfaces of body mostly dark with pale markings; ventral surface mostly pale with dark markings (Figs. 1, 2, 5). Dorsal body pattern comprises a chain of 21 black sub-lozenge-shaped saddles with approximate maxima of eight scales long by 12 (rarely 14) scales wide. Lateral margins of dark saddles demarcated by narrow (generally one scale wide), irregular pale lines, often with small breaks. The flank pattern comprises broad dark patches that approximately alternate with the dorsal saddles, separated from each other by narrow pale, more or less vertical bars, 1 scale increasing ventrally to 2–3 wide. Within these dark flank markings are small, irregular pale marks. On the mid to upper flanks these pale markings are either isolated flecks or connected to form an inverted V; approximately aligned with these on the lower flanks are larger, wider deltoid pale marks issuing from the belly. Most scales in first dorsal row are pale, such that pale deltoid marks on lower flans are often continuous (ventrally) with vertical bars. The belly has scattered series of irregular spots roughly in three ranks, the innermost two brownish on each ventral plate, the outermost more black, singly or more frequently paired longitudinally. The tail has the same general colour pattern as the body (dark dorsally, pale ventrally), though the dorsal markings are less regular.

Observation of live specimen. On 15 October, 2013, one of us (E.R.B.) observed a live specimen of *B. harenna* **sp. nov.** in the Bale Mountains National Park. The observations were made with colleagues Mark Chynoweth, James Kuria Ndung'u, Sisay Sayfu, Abdu Ibrahim and Khalifa Ali – the latter four of whom have worked in the Bale Mountains for at least three years without seeing this species before. The observation was made while driving along the road between the settlements of Rira and Delo Mena, as it passes through the Harenna Forest at approximately 2,140 m elevation (6.694525° N, 39.728576° E). This section of road is within a swath of forest that has openly spaced canopy trees (approximately 10% cover) and a very dense understory of shrubs and vines. The area is approximately 1 km from an illegal settlement ("Aboyea") within the Bale Mountains National Park. The snake was on a large roadside verge under bright but partly cloudy skies at 12.30 pm. As a result of recent road repair the verge was formed by a large amount of earth and stone (approximately 2 m wide on either side of the road) that had been moved mechanically. This section of road requires regular maintenance in the wet season thus creating fairly regular disturbance for a distance of c.3 km. Upon sighting, the driver Sisay Sayfu stopped the vehicle within 3 m of the snake, which was apparently basking on the verge and did not move for a few minutes while being observed and photographed. The animal was matt black dorsally, more glossy along the lower flanks. The pale markings were distinctly yellowish. From memory the animal was approximately 1m in total length. It moved slowly off the side of the road and into undergrowth when the observers left the vehicle for closer inspection.

The photographs (one shown in Fig. 7) show an animal clearly very similar to the holotype of *B. harenna* **sp. nov.** The colour pattern is the same with minor differences, including a more transverse (not posteromedially deflected) pale bar dorsally on the head behind the eyes. The tail is relatively longer than in the holotype, such that the live specimen is likely male. The animal has a general overall similarity (the 'jizz' of birdwatchers) to the puff adder *Bitis arietans.*

Remarks. The holotype of *Bitis harenna* **sp. nov.** was identified previously as *B. parviocula* (Largen & Rasmussen 1993, Largen & Spawls 2010) and was used by Wittenberg *et al.* (2015) to score morphological characters for that species in their phylogenetic analyses. The skulls of ZMUC R68255 (*B. harenna* **sp. nov.**) and R68254 and ZFMK63067 (*B. parviocula*), as analysed with HRXCT data, differ in several respects (Figs. 3, 4). Groombridge (1980: 140) reported a derived condition (present in the subgenus *Macrocerastes* species *B. nasicornis* and especially *B. gabonica* [including its then subjective junior synonym *B. rhinoceros*]) in which the concavity on the lateral wall of the braincase for the origin of the *M. retractor pterygoidei* is not limited posteriorly by a flange on the posterior edge of the parietal but instead extends onto the prootic. ZMUC R68255 exhibits the plesiomorphic condition, with a limiting posterior parietal flange (Fig. 4D) and R68254 (Fig. 4E) and ZFMK 63067 (Fig. 4F) a moderate manifestation of the derived condition, somewhat more like that in *B. nasicornis* (Fig. 4B) than in *B. gabonica* (Fig. 4C). The condition in *B. parviocula* was not previously reported.

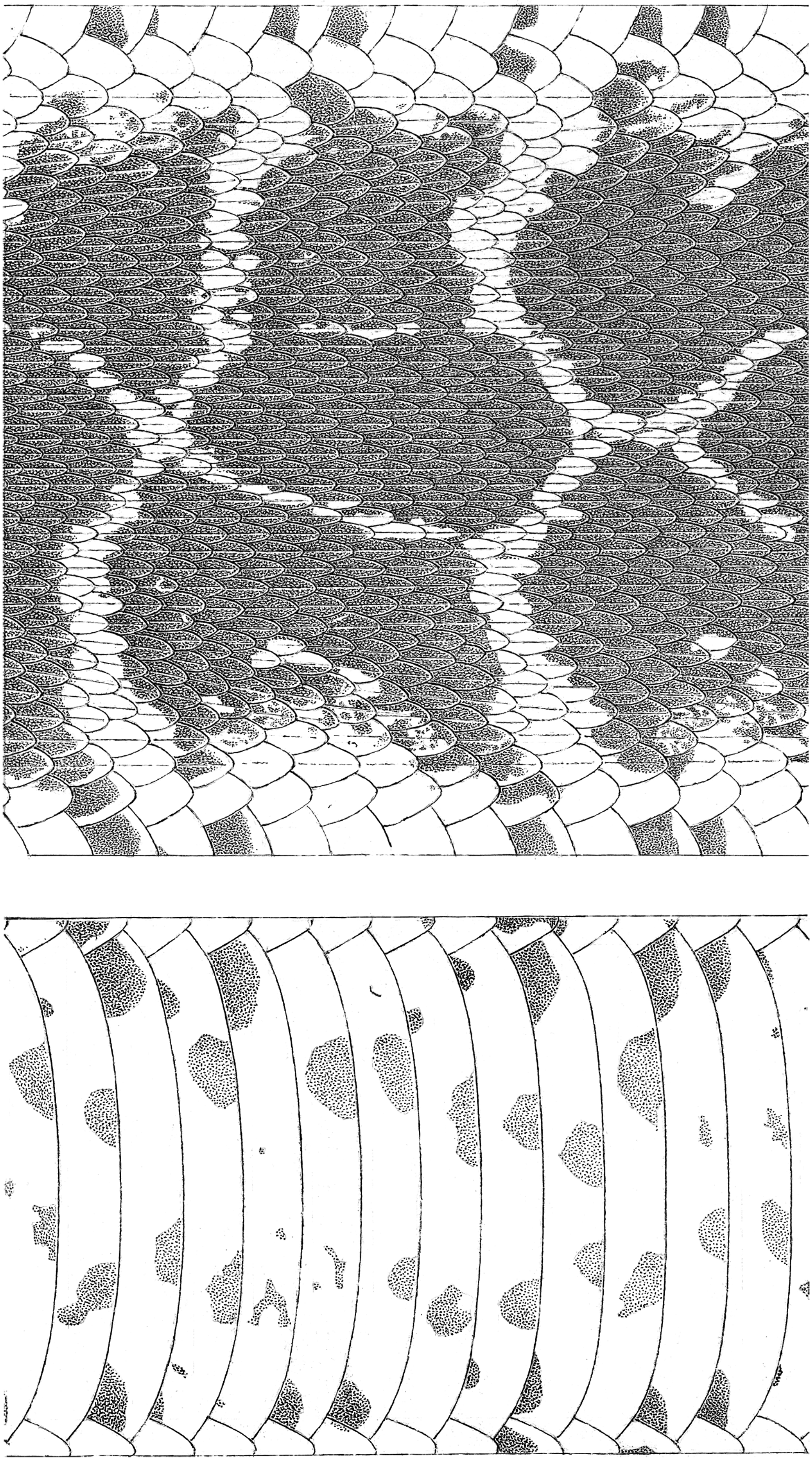

FIGURE 5. Drawing of the holotype (ZMUC R68255) of *Bitis harenna* **sp. nov.** showing the dorsal (upper) and ventral (lower) body scalation (between the levels of the 64th and 77th ventral scale) Drawing by Ed Wade.

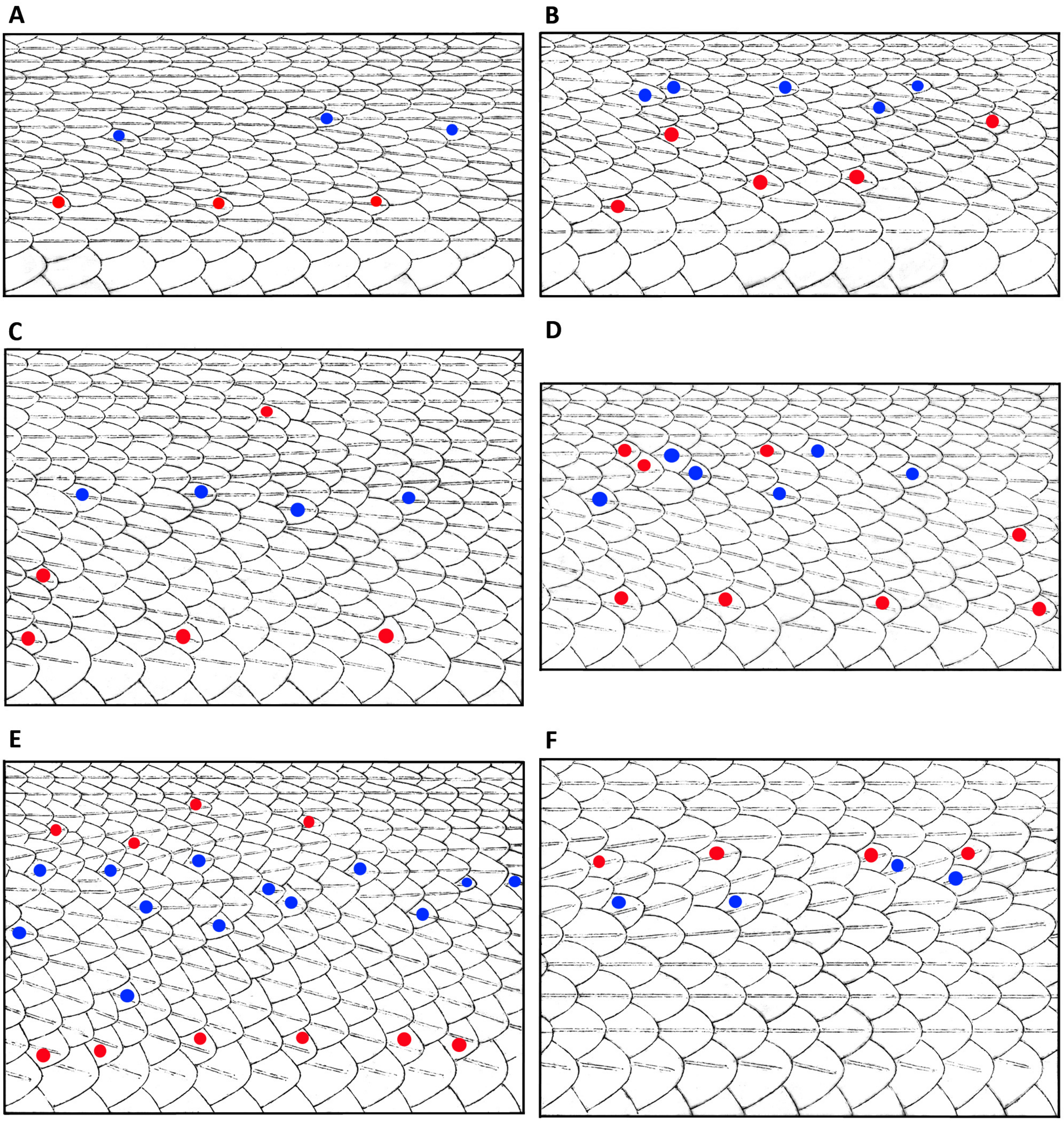

FIGURE 6. Comparison of dorsal scale row patterns in species of *Bitis*. Each figure part shows an approximately midbody section of the flank in left lateral view. **A**) *B. harenna* **sp. nov.** (ZMUC R68255), **B**) *B. parviocula* (ZMUC 68254), **C**) *B. gabonica* (BMNH 1968.54), **D**) *B. rhinoceros* (BMNH 1930.11.19.75), **E**) *B. nasicornis* (BMNH '529'), **F**) *B. arietans* (BMNH 87.11.3.32). Red dots mark scale row losses, blue dots mark scale row gains. Drawings by Ed Wade.

In the *B. parviocula* specimens ZFMK 63067 (Fig. 4F) and ZMUC R68254 (*B. parviocula*: Fig. 4E) the prootic forms a strong ridge overhanging the foramina for the mandibular branch of the trigeminal nerve, whereas this ridge is absent in R68255 (*B. harenna* **sp. nov.**: Fig. 4D). A strong ridge here is present also in the dried skulls of *B. gabonica* and *B. arietans* examined in this study, but much smaller or absent in *B. nasicornis.* The facets on the anterodorsal edges of the frontals for the medial process of the prefrontals are clearly separated at the midline in the holotype of the new species (ZMUC R69255: Fig. 3A) but continuous in the *B. parviocula* specimens ZMUC R68254 (Fig. 3D) and ZFMK 63067 (Fig. 3G). The *B. harenna* **sp. nov.** condition for this character is also present in the skeletal material of *B. arietans, B. gabonica,* and *B. nasicornis* examined here. Böhme (1990) suggested that the fangs of *B. harenna* **sp. nov.** are relatively longer than those of *B. parviocula*, but we do not find that to be the case. Although there are very small differences in numbers of teeth between ZMUC R68255 and 68254, making accurate and precise tooth counts from HRXCT data is not easy, and counts for ZFMK63067 suggest there are not clear interspecific differences (Table 1).

FIGURE 7. Live (uncollected) specimen of *Bitis harenna* **sp. nov.** photographed in the Harenna Forest of the Bale Mountains National Park in October 2013. The snake was approximately 1 m in total length.

The holotype (ZFMK 16803) and the only other known museum specimens (ZFMK 60367, ZMUC R68254) of *Bitis parviocula* are shown in Figs. 8–10. Although the skull of ZMUC R68254 is partly smashed (Fig. 3), the proportions of the head of this *B. parviocula* specimen are nonetheless interpreted as being genuinely different to (more slender than) those of ZMUC R68255. The distance between the snout tip and eye in the holotype of the new species (ZMUC R68255) is 25.7% of the head length but this value in the ZMUC *B. parviocula* specimen is 32.1% - both specimens were measured on the left side of the head, the left mandible being largely intact in both. This proportion in the less damaged head of ZFMK 63067 is 28.2%, and is approximately 28.4 in the smashed (Fig. 8) head of the holotype ZFMK 16803. Although a small individual of *B. parviocula* (from S.S.'s memory approximately 25 cm long) has the appearance of being relatively slim (Fig. 11 top left panel; Dobiey & Vogel 2007: 116; Nečas *et al.* 1993a: fig. 1; Nečas 1997: 59), all photographs of recently wild-caught, larger and presumably adult individuals (examples shown in Fig. 11) show heavily bodied, stout animals approximately similar to *B. nasicornis, B. rhinoceros* and *B. gabonica*, whereas the holotype of *B. harenna* **sp. nov.** and conspecific animal observed live in the Harenna Forest appear somewhat more slender, contributing (along with an apparently more slender, posteriorly elongate head) to its more puff-adder-like form. *Bitis parviocula* is clearly quite variable in colour and colour pattern (Fig. 11; Dobiey & Vogel 2007) but no specimens approach the distinctive appearance of *B. harenna*.

The scales of ZMUC R68255 (*B. harenna* **sp. nov.**) are slightly different in texture to those of R68254 (*B. parviocula*), being less horny, but this might be attributable to differences in preservation. The dorsal scalation pattern of ZMUC R68254 (*B. parviocula*) is generally similar to the holotype of *B. harenna* **sp. nov.**, though the fluctuations in the formula for the 60th to 80th ventral are even more pronounced:

-4 (61) -4 (62/63)	-3 (64) -8 (64)	-4 (66/67)	-6 (69/70) -3 (69/70) -9 (70) -3 (71)		-4 (73/74) -4 (75)	-3 (77/78) -5 (79)
+7 (61) +6 (63)	+8 (65) +8 (65/66)		+8 (69) +9 (70) +9 (70/71)	+8 (72)	+7 (74) +7 (75)	+9(77) +14 (79) +8(79/80)
39 ---- 40	---- 41	---- 40	---- 38	---- 39	---- 40	---- 41
+9 (61/62) +8 (63)	+8 (66)	+8 (67)	+7 (70)	+8 (71/72) +9 (72/73)	+8 (74/75) +7 (76/77)	+9 (77) +9 (80)
-4 (62)	-4 (65)	-4 (66/67)	-5 (69/70) -3 (71)	-6 (72)	-4 (74) -4 (75/76)	-7 (78 -3 (78/79)

The midvertebral scales in R68254 are also more variable: single from the level of 60th to 73rd ventral and from 74th to 77th, but double at level of 73rd and of 78th to 80th ventral. Compared with the holotype of *B. harenna* **sp. nov.**, R68254 has more (30–31 versus 25–27: Table 2) vertebral scales aligned with the 60th–80th ventrals, and the posteroventral 'lines' of dorsal scales on the lower flanks are more steeply inclined (Fig. 5). The range of variation in all characters noted in this paper for *B. harenna* **sp. nov.** and *B. parviocula* can be expected to expand (with unknown magnitude) as more specimens are examined, such that characterization of these two species will need revision in future. A map of the known distribution of the three species of Ethiopian *Bitis* is presented in Fig. 12).

Böhme (1977) named *B. parviocula* for its seemingly small eyes, and this morphological feature was interpreted as an indication that the species was somewhat fossorial. The eyes of the type (and at that time only known) specimen of *B. parviocula* are small by artefact—this specimen was found dead and squashed on the road, and live specimens of the species do not have notably small eyes (Spawls 1994).

Etymology. Named for the Harenna forest and escarpment, in the Bale Mountains National Park, where a live specimen of the new species was recently sighted. For nomenclatural purposes the specific epithet is considered a noun in apposition.

Suggested common name. Bale Mountains adder (English).

Conservation status. We obviously know very little about *Bitis harenna* **sp. nov.** and thus its conservation status is likely to be Data Deficient based on IUCN Red List criteria. However, any large snake, especially a probably venomous one, is likely to face persecution in Ethiopia. We are unable to support Nečas *et al.*'s (1993b) comments about *B. parviocula* being revered and protected by local folklore, and all three specimens of this species in museum collections have been damaged and were likely killed (or at least smashed post mortem) by local people. The region as a whole is under great pressure from agriculture and increasing urbanization, exacerbated by very high human population growth. The only known precise locality for *B. harenna* sp. nov, the Harenna escarpment of the Bale Mountains, is within a National Park but is also under great environmental pressure by human modification of habitats (see Gower *et al.*, 2013). Thus, we suggest there should be urgent concern about the well being of this species in the absence of evidence to the contrary.

Revised key to the *Bitis* of Ethiopia. Largen and Rasmussen (1993: 383) provided a key to the then two known species of *Bitis* from Ethiopia. Their key will not work with the addition of the new species, and here we offer the following, modified key to the three nominal Ethiopian species of *Bitis*:

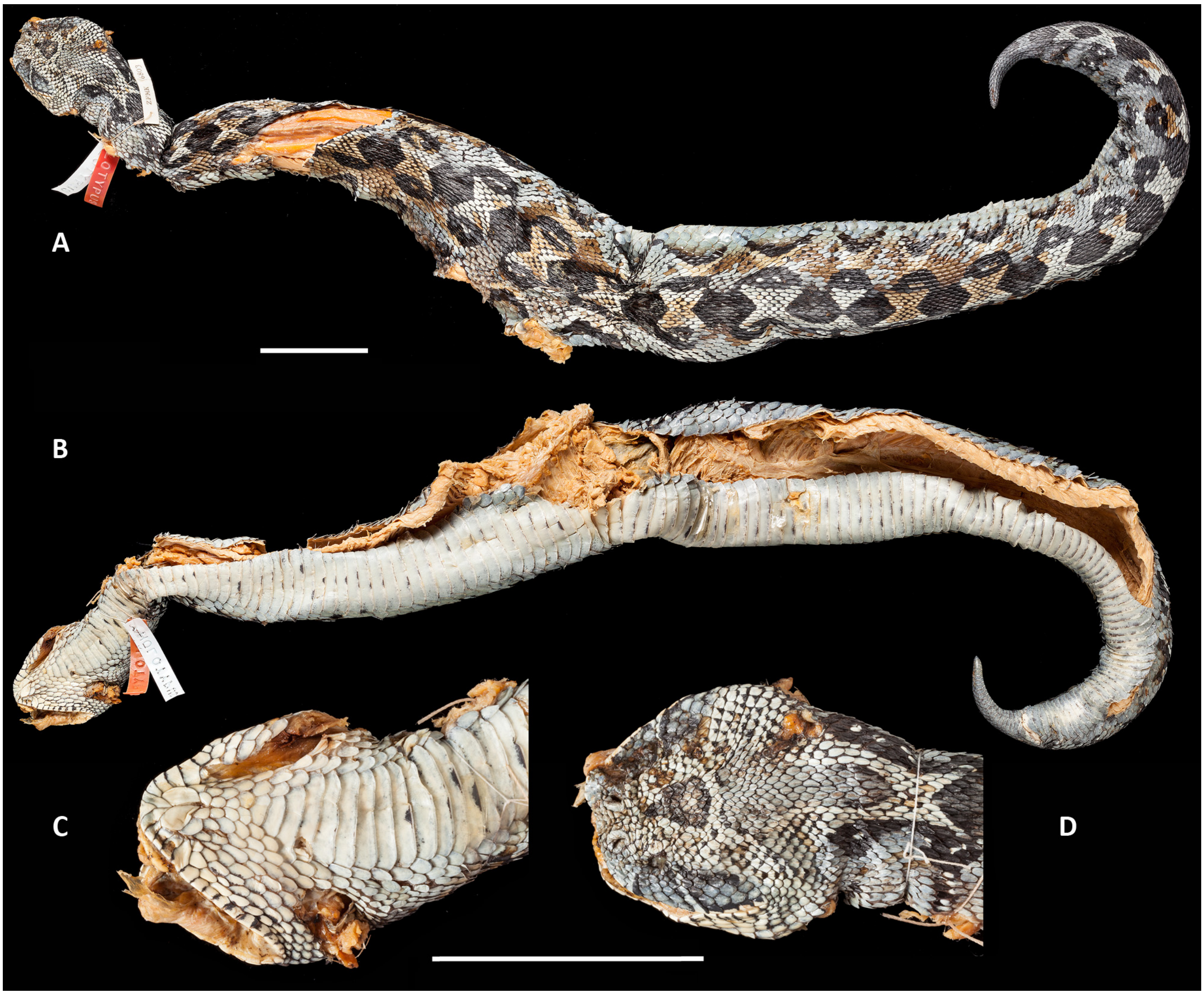

FIGURE 8. Photographs of holotype (ZFMK 16803) of *Bitis parviocula*. Whole animal in **A**) dorsal and **B**) ventral views, and head in **C**) ventral and **D**) dorsal views. Scale bars 5 cm. Photographs by Harry Taylor.

1	Dorsal pattern consists of V-shapes pointing tailwards; pale interocular stripe running between posterior edge of eyes	*Bitis arietans*
-	Dorsal pattern not comprising V-shapes; pale transverse stripe on dorsum of head substantially behind level of eyes (as far behind eyes as eyes are from snout tip).	2
2	Ground colour yellow, tan or brown, dorsal pattern consists of alternate blackish hexagons and yellowish butterfly shapes.	*Bitis parviocula*
-	Ground colour black, dorsal pattern consists of fine to broad yellowish reticulations	*Bitis harenna* **sp. nov.**

Discussion

Although the new species is very similar in scalation to *Bitis parviocula*, we are convinced that it is distinct, while recognizing that we currently have little to no understanding of variation in the diagnostic features we report. We are confident that the holotype and live specimen observed in 2013 of *B. harenna* **sp. nov.** are not hybrids of *B. parviocula* x *B. arietans*. Probable hybrids of large species of *Bitis* have been reported (Hughes 1968, 2012; Broadley & Parker 1976; Branch 1978; Dobiey & Vogel 2007) and, where documented, these very clearly present intermediate as well as a mix of parental phenotypic features, the like of which we do not observe in *B. harenna*. For similar reasons, Böhme (1977) had discounted the possibility that the then single known specimen of *B. parviocula* was a hybrid (a possibility raised by Groombridge 1980: 39). We are also confident that the new species is not simply based on melanistic individuals of *B. parviocula* because the colour pattern of the former is not only generally darker but, for example, lacks a regular, parallel-sided dorsal stripe, and because there are other differences between the two species beyond colour pattern. As far as we know, melanism in other *Bitis* (e.g., *B. arietans*: Branch, 1988: plate 12) is associated with only generally darker colouration rather than modifications of colour pattern. New fieldwork is urgently required to locate surviving populations of *B. harenna* **sp. nov.** Only three museum specimens are known for *B. parviocula* and all of these are damaged. This remains a poorly known snake (see also e.g., Wittenberg *et al.*, 2015) and we suggest that further studies and collections are made in future. It would help to advance knowledge of the biology of *B. parviocula* if (especially wild caught) specimens currently in captivity in Europe and North America could eventually find their way into publicly accessible museum collections. We hope that our description of *B. harenna* prompts further study of especially the Ethiopian *Macrocerastes*.

FIGURE 9. Photographs of a referred specimen (ZFMK 63067) of *Bitis parviocula*. Head shown in **A**) dorsal, **B**) ventral, **C**) left lateral, and **D**) right lateral views. Scale bar 5 cm. Photographs by Harry Taylor.

The locality records for the ZMUC *B. parviocula* and *B. harenna* **sp. nov.** specimens are both for the town of Dodola, which is on the main route between the Rift Valley and the chief settlements of the Bale Mountains region, Dinsho, Robe and Goba. Dodola lies on a heavily farmed plateau, and there is very little tree cover in the immediate vicinity of the town. We suspect that both specimens might have been brought to J. Birkett-Smith (probably by local people) from further afield, especially given that ZMUC R68254 is preserved as a head, tail and skin and that the head has been smashed. In the latter part of the 20th Century (and still today), many Ethiopians commonly walked large distances, and it is probably very difficult to constrain the collection localities of these specimens beyond 'within reach of Dodola'. Two of us (T.J.C., S.S.) have independently had colubrid snake specimens brought to them from at least a 10 km radius in Ethiopia after telling local people of their interest in snakes. We are confident at least that the two ZMUC specimens are very likely to be from East of the Rift Valley.

The new species is very clearly not abundant and/or frequently encountered. Biologists, including several of the authors of this paper, have spent many hours in the Bale Mountains National Park, especially the Harenna Forest, without seeing any specimens. T.J.C. and D.J.G. have independently shown pictures of *B. parviocula* to local people in the Bale Mountains (both North and South of the Sanetti Plateau) and none made a positive identification of a large viper. S.S. showed locals photographs of live *B. arietans* and *B. parviocula* and of the preserved holotype of *B. harenna* **sp. nov.** to local people in Wondo Genet (c. 1,700 m elevation) on the eastern escarpment of the Rift Valley and at Dodola and in the Harenna Forest. At Wondo Genet, people claimed to recognize both *B. parviocula* (described as living on a forested hill) and *B. harenna* **sp. nov.** (in forest along a river); in Dodola people claimed to recognize all three species; in Harenna, honey collectors recognized *B. parviocula* only. Clearly the distribution of *B. harenna* **sp. nov.** and of *B. parviocula* (especially to the east of the Rift Valley) is extremely poorly known and in need of additional research. Without this it is not possible to know if *B. parviocula* and *B. harenna* are sympatric or syntopic anywhere across their ranges. Böhme (1977), Largen & Rasmussen (1993) and Largen & Spawls (2010) pointed out that *B. parviocula* occurs in dense forest habitats and *B. arietans* does not. This ecological separation could be interpreted as additional evidence that specimens of *B. harenna* **sp. nov.** are not hybrids of the former two species. The only precise locality for *B. harenna* **sp. nov.** is within a generally forested area (though successional and increasingly with more open patches of woodland as well as grassland: Gower *et al.*, 2013), suggesting that it might be ecologically more similar to *B. parviocula* than to *B. arietans*. A caveat to these interpretations is the report of a *B. arietans* exuvium from montane (c. 2,200 m elevation) forest only c. 60 km from the type locality of *B. parviocula* (Nečas *et al.*, 1993b). Species of *Bitis,* including *B. parviocula*, are predominantly nocturnal (e.g., Largen & Spawls, 2010). Although most previous fieldwork in the Bale Mountains that we are aware of has taken place in the daytime, night work has been carried out (e.g., Gower *et al.*, 2013), and more of this might be required to better understand the biology of Ethiopian *Bitis.*

Upon receipt of E.R.B.'s photographs of live *B. harenna* **sp. nov.** in late October of 2013, one of us (T.J.C.) traveled to the precise locality and installed drift fence trap arrays along both sides of the road. This method has successfully trapped fossorial and secretive snakes elsewhere, including *Bitis* species. These traps remained open for 10 days (November 6–16, 2013) with T.J.C. checking them and performing both daytime and nighttime searches of both the immediate area and suitable habitat within a 4 km radius of the sighting. These traps remained open for approximately one more month with local volunteers checking them daily. It is possible that the sole sighting of this rare and/or secretive snake was associated causally with the road repair that took place immediately before it was photographed. However, this same section of road has been heavily traveled, before and after recent repair, by E.R.B., T.J.C, D.J.G. and others in both the day and at night without another sighting of *B. harenna* **sp. nov.**

FIGURE 10. Photographs of a referred specimen (ZMUC R68254) of *Bitis parviocula*. Top panel shows whole animal in ventral (above) and dorsal (below) views. Lower panel shows head in (from left to right) dorsal, right and left lateral, and ventral views. Upper scale bar 10 cm, lower scale 2 cm. Photographs by Harry Taylor.

FIGURE 11. Photographs of nine wild-caught individuals of *Bitis parviocula* from southwestern Ethiopia. The animal in the top left panel is the small individual reported by Nečas *et al.* (1993a, b), the animal in the lower right panel is a roadkill specimen (ZFMK 63067) from 20km west of Bonga photographed before preservation, both photographs by Stephen Spawls. The other seven specimens (photographs courtesy of John Tashjian) were in the pet trade in Europe and are not in museum collections.

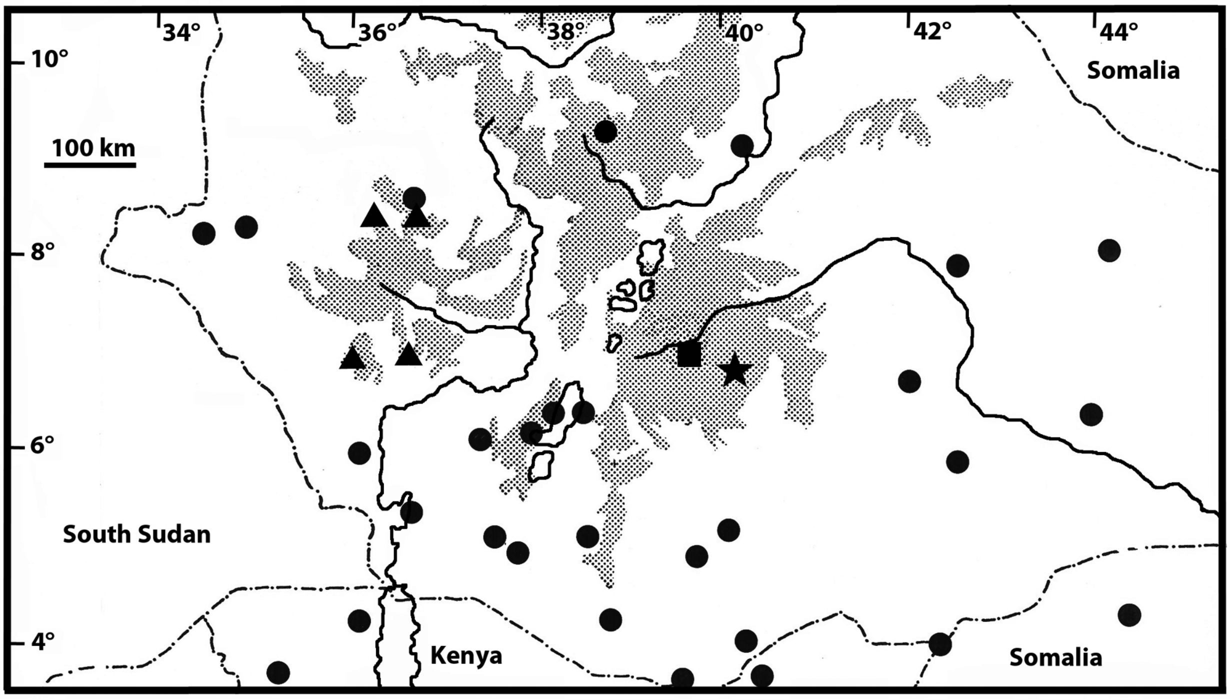

FIGURE 12. Map of southern and western Ethiopia showing the distribution of the three native species of *Bitis*. Incomplete lines depict country borders; solid lines depict major rivers and lakes; stippled area indicates land above 2,000 m elevation. Circles = *B. arietans* localities from Largen & Spawls (2010); triangles = *B. parviocula* localities in southwest Ethiopia from Largen & Spawls (2010); square = town of Dodola (reported locality of holotype of *B. harenna* **sp. nov.** and single specimen of *B. parviocula*); five-pointed star = locality of recent sighting of live specimen of *B. harenna* **sp. nov.**

Encounters of *B. parviocula* in a natural setting are also very rare. Local farmers reported (to S.S.) sightings of *B. parviocula* in southwest Ethiopia adjacent to buttress-rooted trees. In an interview with T.J.C. the Ethiopian commercial collector attributed to seeding the pet trade with nearly 100 specimens admitted that he had never actually found a single snake in the forest. Rather, all specimens were encountered as coffee fields were burned and cleared, or brought to him by farmers who had recently cleared or planted their coffee fields. In southwestern Ethiopia the coffee fields are harvested and planted in tune with the bi-annual wet season in April–May and September–October. This is also the period of highest snake activity and movement, such that it is no surprise that this is when most encounters occur. The collector of the holotype of *B. parviocula* told W.B. that he was told by local people that this snake was responsible for several fatalities each year at the type locality.

Lenk *et al.* (1999: 36) characterized the dorsal body scalation of members of the subgenus *Macrocerastes* as "Lateralmost body scales in oblique rows. Dorsal scale rows often duplicated." We agree in finding dorsal scalation features to diagnose *Macrocerastes* (including the two Ethiopian species) but prefer instead to describe this as 'a posteriorly divergent dorsal scale row pattern with splits/duplications/divisions on upper part of flanks and fusions on lower part of flanks'. This is illustrated in Fig. 6. The details differ among the figured specimens and more work is required to understand the degree to which this represents genuine interspecifc variation. However, features that we interpret as likely to be systematically informative include the number of vertebral scales relative to number of ventral scales (1:1 in *B. arietans*; 1.8+:1 in *B. nasicornis*; < 1.4 in *B. harenna* **sp. nov.**; 1.4–1.75:1 in the other species: see Table 2), and the presence of posterodorsally inclined 'lines' of dorsal scales on upper flanks in addition to posteroventrally inclined 'lines' on lower flanks (strongly developed in *B. nasicornis*; moderately developed in *B. gabonica* and possibly *B. rhinoceros*; absent in *B. parviocula* and *B. harenna* **sp. nov.**). Notwithstanding the superficial resemblance of *B. harenna* **sp. nov.** to *B. arietans,* the flank scalation of the latter is radically different in a number of features; there is no loss of scale rows on the lower flanks, nor posteroventrally orientated oblique rows. Instead, there are scale additions, the rows are upwardly orientated, and the middorsal:ventral ratio is almost equal. We note that the arrangement of flank scales in *Macrocerastes* resembles (at least superficially) that seen in *Atheris* more than in, for example, *Echis* and *Cerastes* (E.O.Z.W., pers. obs.).

There are currently few data to make an assessment of the likely phylogenetic position of *B. harenna* **sp. nov.** However, evidence from dorsal scale patterns and the number of scales between the nasal and rostral scales suggests that the new species can be included in the subgenus *Macrocerastes* on the basis of morphological synapomorphies. An additional probable synapomorphy of *Macrocerastes* is a scale microstructure that comprises a finely reticulate surface texture on the cristae, contrasting with the smooth cristae of, for example, *B. arietans* (Beyerlein, 1994). Within the subgenus *Macrocerastes*, the non-Ethiopian members (*B. gabonica, B. nasicornis, B. rhinoceros*) perhaps form a clade based on the derived conditions of four or more scales between the nasal and the first supralabial scale, and some dorsal scale row fusions/losses occurring dorsal to scale row scale row divisions/ duplications. The seemingly plesiomorphic condition of the site of origin of the *M. retractor pterygoidei* on the parietal in *B. harenna* **sp. nov.** and perhaps this species' more puff-adder- (*B. arietans*) like overall appearance and lack of a regular, parallel-sided mid-dorsal stripe indicates that the new species might lie outside a clade comprising all other species of the subgenus *Macrocerastes*, but further analysis is clearly required to test this.

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manuscript. The authors dedicate this paper to the late Jens Rasmussen in memory of his work on African snakes, including those of Ethiopia.

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APPENDIX 1

Material examined. Institutional abbreviations for specimen prefixes are as follows: BMNH (The Natural History Museum, London, UK), EOZW (E.O.Z. Wade collection, London, UK), ZFMK (Zoological Research Museum Alexander Koenig, Bonn, Germany), ZMUC (Zoological Museum, University of Copenhagen, Denmark). † indicates specimen illustrated in this paper. § indicates scalation data for specimen presented in this paper. * indicates type specimen(s). Specimens preserved in alcohol unless stated.

Bitis (Macrocerastes) harenna **sp. nov.**
†§ZMUC R68255* (Dodola, Ethiopia)

Bitis (Macrocerastes) parviocula
†§ZFMK 16803* (between Metu and Bedelle, Ethiopia)
†§ZFMK 63067 (20 km west of Bonga, Ethiopia)
†§ZMUC R68254 (Dodola, Ethiopia)

Bitis (Macrocerastes) gabonica
†§BMNH 1968.54 (Bota, Cameroon)
BMNH 79.11.12.1 (Ushambola, Zanzibar, Tanzania) [= Usambara mountains, close to what used to be referred to as the 'Zanzibar coast']
§BMNH 95.5.14.20 (Africa)
§BMNH 1975.1118 (Mabia Forest, Uganda)
§BMNH 1971.414 (southeast Nigeria)
§BMNH 1906.11.13.3 (Walikale, Democratic Republic of the Congo)
§BMNH 1950.1.2.15 (Kumba, Cameroon)
§BMNH 1969.526 (Bota, Cameroon)
§BMNH 96.5.14.20 (Lake Tanganyika)
BMNH 1964.1029 (no data) [dry osteological specimen only – potentially *B. rhinoceros*]
†BMNH unnumbered (no data) [dry osteological specimen only – potentially *B. rhinoceros*]

Bitis (Macrocerastes) nasicornis
§BMNH 1952.1.6.57 (Hakitengya, Bwamba, Uganda) [3 specimens]
§BMNH 1971 415 (Bachuontai, Mamfe, Cameroon)
§BMNH 1935.10.2.1 (Uganda)
†§BMNH unnumbered (specimen tag '529'; Congo)
BMNH 1964.1133 (Bibianaha, Ghana) [dry osteological specimen only]
BMNH unnumbered (specimen tag '316'; West Africa) [dry osteological specimen only]
†BMNH unnumbered (no data) [dry osteological specimen only]

Bitis (Macrocerastes) rhinoceros
§BMNH unnumbered (Africa)
§BMNH unnumbered (no data)
BMNH 65.5.4.155 (Guinea)
†§BMNH 1930.11.19.75 (Sierra Leone)

Bitis (Bitis) arietans
†BMNH 1964.1249 (no data) [dry osteological specimen only]

Bitis (Bitis) arietans arietans
§BMNH 1906.10.31.14 (Souss, Marocco)
§BMNH 1975.690–696 (Zaria, Nigeria)
†§BMNH 87.11.3.32 (Kilimanjaro, Tanzania)
§BMNH 1930.6.11.63 (Semliki Valley, Uganda)
§BMNH 97.6.9.143 (Nyika Plateau, Malawi)
BMNH 1930.5.8.945 (South Africa) [dry osteological specimen only]
§EOZW (captive born) (Saudi Arabia)

Bitis (Bitis) arietans somalica
§BMNH 1975.2146 (Negelle, Ethiopia)
§BMNH 1971.785 (Shoa, Ethiopia)
§BMNH 1931.7.20.409 (Bihen, Somaliland)
§BMNH 1905.10.30.133-134 (Derbera, Somaliland)
§BMNH 1931.7.20.408* (Somaliland)
§BMNH 1949.2.3.1–3* (Bohole, Somaliland)
§BMNH 1905.11.7.58 (Berbera, Somaliland)
§BMNH 1931.10.2.2 (Sheikh, Somaliland)
BMNH 1973.3279 (Tendaho, Ethiopia)

APPENDIX 2. Variation in dorsal scale rows level with every tenth ventral scale in various taxa of *Bitis*. Numbers in parentheses represent first (immediately behind posterior end of mandible) and last (posteriormost) ventral for which dorsal scale rows were counted. All specimen numbers have BMNH prefix unless otherwise indicated. See Appendix 1 for specimen localities.

	Number of dorsal rows level with particular ventral scale														
Species and specimen	first	10	20	30	40	50	60	70	80	90	100	110	120	130	140	last
B. parviocula ZFMK 16803	45	38	36	?	40	42	42	41	42	41	39	35	33	28	27	29 (141)
B. parviocula ZMUC R68254	42 (4)	34	36	36	37	41	39	40	41	40	38	34	34	28	28	29 (146)
B. harenna sp. nov. ZMUC R68255	43 (6)	36	32	34	36	37	39	39	38	39	35	38	30	28	25	28 (145)
B. gabonica 1968.54	55 (5)	42	36	34	35	35	37	36	35	34	31	27	24			26 (126)
B. gabonica 1975.1118	53 (4)	40	35	35	38	39	41	37	40	36	33	31	27			24 (127)
B. gabonica 1971.414	53 (4)	42	36	35	39	35	37	37	36	34	31	28	26			25 (125)
B. gabonica 1906.11.13.3	57 (4)	43	39	36	37	39	37	38	38	35	32	28	25			25 (127)
B. gabonica 1950.1.2.15	54 (4)	40	35	37	35	36	37	37	35	34	33	31	25			24 (129)
B. gabonica 1969.526	53 (4)	39	39	38	38	37	37	37	34	31	30	28	25			24 (127)
B. gabonica 96.5.14.20	55 (4)	45	40	40	39	38	40	39	39	36	35	33	30			26 (129)
B. rhinoceros 1930.11.19.75	52 (5)	38	32	33	32	33	33	33	32	32	28	26	24			23 (125)
B. rhinoceros 65.5.4.155	50 (4)	41	37	34	35	35	36	35	36	34	29	28	25			24 (129)
B. rhinoceros no data	56 (4)	39	34	34	34	33	34	36	34	24	29	?	?			?
B. nasicornis '529'	36 (5)	30	27	30	30	35	34	33	32	29	26	22	22			22 (122)
B. nasicornis 1971.415	39 (4)	40	34	34	38	39	40	41	40	36	33	29	26	24		26 (134)
B. nasicornis 1952.1.6.57	38 (3)	30	30	30	33	34	34	36	36	30	27	23	23			23 (123)
B. nasicornis 1952.1.6.57	38 (4)	33	34	33	36	40	40	41	40	37	30	29	26			24 (128)
B. nasicornis 1952.1.6.57	39 (4)	34	31	34	38	40	38	38	35	32	28	26				25 (119)
B. nasicornis 1935.10.2.1	31 (5)	28	27	27	30	31	32	30	32	29	24	21	19			22 (124)
B. arietans arietans 1906.10.31.14	35	33	30	29	29	31	33	33	34	31	29	27	24	22	22	23 (143)
B. arietans arietans 1930.6.11.63	34	31	28	29	29	31	33	31	32	31	29	26	24	22		23 (137)

……*continued on the next page*

APPENDIX 2. (Continued)

Species and specimen	Number of dorsal rows level with particular ventral scale															
	first	10	20	30	40	50	60	70	80	90	100	110	120	130	140	last
B. arietans arietans EOZW unno.	35	31	29	29	31	32	33	34	31	31	29	26	23			25 (126)
B. arietans arietans 97.6.9.143	37 (5)	27	29	29	29	29	33	33	31	31	30	28	25	23		21 (136)
B. arietans ?arietans 87.11.3.32	38 (6)	31	29	28	29	30	31	32	31	29	29	27	23	23	21	22 (141)
B. arietans arietans 1975.690	39 (5)	29	27	27	30	29	31	31	32	30	29	24	22	21		23 (133)
B. arietans arietans 1975.691	36 (3)	29	29	29	30	31	34	35	34	34	30	29	26	24		24 (138)
B. arietans arietans 1975.692	35 (2)	30	27	28	29	30	32	34	33	30	28	27	24	24		24 (136)
B. arietans arietans 1975.693	35 (4)	29	28	28	28	29	31	33	35	32	28	28	25	24		23 (138)
B. arietans arietans 1975.694	36 (5)	30	30	29	30	30	34	36	35	29	27	27	24			22 (126)
B. arietans arietans 1975.695	38 (6)	32	27	28	28	31	31	31	31	29	28	26	25	23		24 (139)
B. arietans arietans 1975.696	33 (5)	31	30	31	29	29	31	32	35	31	30	26	22	21		20 (137)
B. arietans somalica 1905.11.7.58	35 (6)	29	29	28	29	30	31	31	30	29	29	25	23	23		24 (137)
B. arietans somalica 1931.10.2.2	35 (5)	30	28	32	29	31	31	32	32	31	29	27	25	22		23 (135)
B. arietans somalica 1975.2146	43 (5)	35	31	31	32	35	35	36	37	35	31	29	29	25	24	25 (144)
B. arietans somalica 1971.785	36 (6)	33	30	29	30	32	34	33	33	34	31	29	26	23		26 (140)
B. arietans somalica 1931.7.20.409	38 (5)	33	31	29	31	31	32	33	34	34	31	31	27	24	22	24 (142)
B. arietans somalica 1905.10.30.13-4	40 (5)	32	29	29	31	30	31	32	32	31	28	28	28	23		25 (140)
B. arietans somalica 1931.7.20.408	37 (6)	35	29	29	29	31	33	33	32	32	32	28	26	24		22 (138)
B. arietans somalica 1949.2.3.1	33 (5)	29	25	25	26	27	27	29	29	29	28	26	24	23		20 (139)
B. arietans somalica 1949.2.3.2	38 (3)	29	27	27	29	29	31	29	29	29	30	28	25	22		22 (132)
B. arietans somalica 1949.2.3.3	37 (2)	30	29	31	31	31	35	34	33	32	29	28	25	23	22	24 (141)