NATURAL SCIENCES *Indago*, Vol. 34, No. 1, 2018, pp. 1–95

A revision of the egg-eating snakes of the genus *Dasypeltis* Wagler (Squamata: Colubridae: Colubrinae) in north-eastern Africa and south-western Arabia, with descriptions of three new species

Michael F. Bates[1] **& Donald G. Broadley**[2 †]

[1]*Department of Herpetology, National Museum, P.O. Box 266, Bloemfontein 9300, South Africa*
[2]*Department of Herpetology, Natural History Museum of Zimbabwe, P.O. Box 240, Bulawayo, Zimbabwe*
[1]*Corresponding author: E-mail: herp@nasmus.co.za*

Abstract

The genus *Dasypeltis* Wagler, 1830 in north-eastern Africa (from latitude 8ºS to the Mediterranean Sea, east of 29°E) and south-western Arabia (west of longitude 45°E) is reviewed. Ten species are recognised in this region on the basis of morphological characters, including colour pattern. *Dasypeltis fasciata* A. Smith, 1849 inhabits lowland forest in western and southern Uganda, while *Dasypeltis medici* (Bianconi, 1859) occurs in coastal forest/savannah mosaic in southern Somalia, Kenya and northern Tanzania. We show that *Dasypeltis medici lamuensis* Gans, 1957 is a junior synonym of *D. medici. Dasypeltis atra* Sternfeld, 1912—in a variety of colour phases/patterns—is widespread in the region, occurring in montane forest, moorland, forest/savannah mosaic, and savannah along the border between Tanzania and Kenya. *Dasypeltis scabra* (Linnaeus, 1758) is widely distributed in East African savannahs, except in parts of South Sudan, Uganda, western Kenya and Rwanda where *Dasypeltis confusa* Trape & Mané, 2006 infiltrates from the west, and in northern Somalia and Djibouti at 640 to 1370 m where it is replaced by *Dasypeltis taylori* Bates & Broadley **sp. nov.** *Dasypeltis bazi* Saleh & Sarhan, 2016 occurs as an isolated population in the Fayoum Depression west of Cairo, Egypt, with a possible isolate at Erkowit in the Red Sea Hills of north-eastern Sudan. We designate a lectotype for *Dasypeltis abyssina* (Duméril, Bibron & Duméril, 1854)—previously known only from the type description—and demonstrate that it is a distinct and valid species restricted to open savannah in the highlands (1800–2450 m) of north-western Ethiopia and central Eritrea; the paralectotype from Sudan is referable to *D. scabra. Dasypeltis crucifera* Bates **sp. nov.** is known only from two localities at lower elevations (600–1417 m) in northern Eritrea. *Dasypeltis arabica* Broadley & Bates **sp. nov.** inhabits the highlands of south-western Arabia (Saudi Arabia and Yemen) at elevations of 1300–2300 m. Multivariate analyses of scale characters and numbers of pattern cycles provides support for the above taxonomy. We provide a map detailing the ranges of the various species. The Horn of Africa, with at least six species (and another in Arabia), appears to be a centre of diversity for the genus *Dasypeltis*.

Keywords: *Dasypeltis*, taxonomy, morphology, zoogeography, north-eastern Africa, south-western Arabia

† Donald G. Broadley passed away on 10 March 2016.

CONTENTS

Abstract 1
INTRODUCTION 2
MATERIALS AND METHODS 3
CHARACTER ANALYSIS 6
SYSTEMATICS 8
Dasypeltis medici (Bianconi) 8
Dasypeltis confusa Trape & Mané 13
Dasypeltis scabra (Linnaeus) 15
Dasypeltis bazi Saleh & Sarhan 18
Dasypeltis taylori Bates & Broadley **sp. nov.** 27
Dasypeltis atra Sternfeld 30
Dasypeltis fasciata A. Smith 37
Dasypeltis abyssina (Duméril, Bibron & Duméril) 38
Dasypeltis crucifera Bates **sp. nov.** 42
Dasypeltis arabica Broadley & Bates **sp. nov.** 46
MULTIVARIATE ANALYSES 54
SUMMARY OF SPECIES 62
Key to the genus *Dasypeltis* in north-eastern Africa and south-western Arabia 64
DISCUSSION 65
ACKNOWLEDGEMENTS 67
REFERENCES 68
Appendix 77

Manuscript processed and edited by S. Moodley (Associate Editor).

INTRODUCTION

Carl Gans (1959) noted that the egg-eating snakes of the genus *Dasypeltis* Wagler, 1830 had attracted considerable attention because of their exclusive diet of bird eggs and the related adaptations of their skull and anterior vertebrae, but that identification of specimens was often difficult. This, he suggested, was because previous analyses had been limited to relatively small areas—and therefore geographical variation in colour pattern and scalation features was poorly understood. With this in mind he conducted a detailed taxonomical analysis on a large sample (over 1000 specimens) representing the entire range of the genus, i.e. sub-Saharan Africa, Egypt and south-western Arabia. His aim was firstly to distinguish valid species, and secondly to describe geographical and individual variation within each of these. Due to a scarcity of material from several large areas, his emphasis was on describing variation rather than attempting to validate existing subspecies or describe new taxa, and his taxonomic conclusions were therefore deliberately conservative. Gans (1959) found that colour pattern was a very useful character and used this, in combination with various other morphological features, to separate species and distinguish populations.

Gans (1959) identified nine basic dorsal colour patterns, some with sub-types. Most of these patterns, including a few of the sub-types, are now considered diagnostic of various species (see figures in this paper). For the widespread *Dasypeltis scabra* (Linnaeus, 1758) he documented a few distinct variations in dorsal colour pattern. Some of these patterns were largely or wholly restricted to particular regions. For example, Gans' (1959) 'brown' grouping included, for central and eastern Africa, three types: brown ('2B'), black ('2M') and marked ('2Bx'; typically with dark bands—often incomplete or fractured—across the back), these being referable to *Dasypeltis atra* Sternfeld, 1912 (see also Gans 1964; Broadley & Bates 2009). Specimens with the linked '5L' colour pattern, consisting of dark, more-or-less diamond-shaped saddles confluent with dark lateral bars—such that they formed bands over the body—occur in western and central Africa, and these populations are now referable to *Dasypeltis confusa* Trapé & Mané, 2006 (see also Bates 2013). Another variation was '5I' where black rectangular saddles and lateral bars form complete closure around the pale inter-saddle areas. However, most other populations of *D. scabra* throughout its extensive range had the variable non-linked '5N' dorsal pattern consisting of dark markings in the form of large 'saddles' (varying in size and shape) along the middle of the back, alternating with lateral bars.

In his taxonomic revision of *Dasypeltis*, Gans (1959) recorded only three species from north-eastern Africa: the widespread *D. scabra*, two subspecies of *Dasypeltis medici* (Bianconi, 1859)—*Dasypeltis medici medici* (pattern '8': usually dark rectangular saddles separated by narrow pale interspaces, with adjacent narrow dark lateral bars) in southern Kenya and Tanzania, and *Dasypeltis medici lamuensis* Gans, 1957 (pattern '3': usually unmarked or faintly marked) along the coast from Somalia to the Kenya-Tanzania border, and *Dasypeltis fasciata* A. Smith, 1849 (pattern '4': checker board pattern on back) which occurred marginally in western Uganda. However, in 1964 Gans recognised *Dasypeltis atra* Sternfeld, 1912 as a full species in the montane forests of the region. Broadley & Howell (1991), in a key to the Tanzanian species of *Dasypeltis*, separated '2Bx' patterned specimens of *D. atra* (see Gans 1959, 1964) from *D. scabra* on the basis of their higher numbers of pattern cycles (85–107 versus 42–79). Largen & Rasmussen (1993) recognised only a single species of egg-eater, namely *D. scabra*, in Ethiopia and Eritrea. Hughes (1997) mapped the distribution of *Dasypeltis* in Uganda, based on material in the Natural History Museum (London) and the World Museum (Liverpool), but doubted whether the '2Bx' colour phase of Gans (1959) should be assigned to *D. atra*.

In their revision of West African *Dasypeltis*, Trape & Mané (2006) revived *Dasypeltis abyssina* (Duméril, Bibron & Duméril, 1854) of Ethiopia from the synonymy of *D. scabra*, after examining the syntypes in Paris. However, they provided only scant details as to why they considered this taxon valid. Broadley & Bates (2009) documented range extensions of the patterned ('2Bx') phase of *D. atra* into savannah areas of northern Tanzania, and the dorsally uniform black and brown phases into south-western Tanzania. Largen & Spawls (2010) recorded *D. scabra* from Ethiopia and Eritrea, and *D. atra* from Ethiopia, but also illustrated a *D. abyssina* (labelled as *D. scabra*, see below) from Mulu (actually at Keriyo hamlet, S. Spawls in litt. 5 April 2011) where it is sympatric with *D. atra*. An isolated population in the Fayoum Depression in Egypt was recently described as *Dasypeltis bazi* Saleh & Sarhan, 2016.

There are currently 13 recognised species of *Dasypeltis*, namely *D. scabra*, *D. palmarum* (Leach), *D. inornata* Smith, *D. fasciata*, *D. abyssina*, *D. medici* (*D. m. medici* and *D. m. lamuensis*), *D. atra*, *D. confusa*, *D. gansi* Trape & Mané, 2006, *D. latericia* Trape & Mané, 2006, *D. sahelensis* Trape & Mané, 2006, *D. parascabra* Trape, Mediannikov & Trape, 2012, and *D. bazi* (see Gans 1959, 1964; Trape & Mané 2006; Trape *et al*. 2012; Saleh & Sarhan 2016).

Since Gans' (1959) revision, significant collections of specimens have become available for most parts of the study area, and this allowed for a more detailed evaluation of variation and patterns of geographical distribution. Several taxonomic problems for populations in north-eastern Africa and south-western Arabia require resolution. For example, there has been much uncertainty about the status and distribution of *D. atra* due to the wide variety of colour morphs and con-

fusion with patterned *D. scabra* (see Hughes 1997; Broadley & Bates 2009). Examination of most of the available *Dasypeltis* material from this region also yielded new records of *D. abyssina*—a species which until now has not been properly diagnosed from its congeners—and recognition of easily identifiable and apparently closely related populations from the Keren-Agordat area, and across the Red Sea in the highlands of the south-western Arabian Peninsula, both described here as new species. In addition, an isolated population in Somaliland and Djibouti is described as a new species.

MATERIALS AND METHODS

Study area.—The study area is defined as Egypt, other parts of Africa north of latitude 8°S and east of longitude 29°E, and the Arabian Peninsula west of longitude 45°E. It therefore includes all eastern populations of *D. atra*, and the eastern-most populations of *D. confusa* and *D. fasciata*. To the north the area extends to the Mediterranean Sea and encompasses the isolated Egyptian population of *D. bazi* (see Gans 1959; Saleh & Sarhan 2016). The countries and regions covered by this revision are therefore: south-western Saudi Arabia, western Yemen, Egypt, the eastern parts of Sudan and South Sudan, Eritrea, Ethiopia, Djibouti, Somalia, Uganda, Kenya, Rwanda (which includes a small area west of 29°E), Burundi and northern Tanzania.

Material examined and characters used.—The starting point for this study was the relevant scalation, size and colour pattern data published in Appendix 1 of Gans (1959), together with the appropriate plates. Data in Gans (1964: 293) was also used. Most of the relevant material in the Natural History Museum in London was examined by us, together with several additional important specimens in other European, North American and African museums. The institutional abbreviations used below are from Sabaj (2016), except we use 'BM' for Natural History Museum in London, 'MUZM' for Makerere University Zoology Museum in Kampala, 'AJL' for the private collection of Angelo Lambiris in Durban (to be incorporated into the Durban Natural Science Museum), and 'CG' refers to the Carl Gans collection (see Gans 1964).

AJL Angelo Lambiris private collection, Durban
AMNH American Museum of Natural History, New York
AAU Addis Ababa University, Department of Biology
BM Natural History Museum, London
CAS California Academy of Sciences, San Francisco
CG Carl Gans collection
CM Carnegie Museum of Natural History, Pittsburgh
FMNH Field Museum of Natural History, Zoology Department, Chicago
IRSNB Intitut Royal des Sciences Naturelles de Belgique, Brussels
LACM Natural History Museum of Los Angeles County, Los Angeles
LIV World Museum, Liverpool
MCZ Museum of Comparative Zoology, Harvard University, Cambridge
MHNG Muséum d'Histoire naturelle, Genève [Geneva]
MNHN Muséum national d'Histoire naturelle, Paris
MRAC Musée Royal de l'Afrique Centrale, Tervuren
MSNG Museo Civico di Storia Naturale "Giacomo Doria", Genova [Genoa]
MSNM Museo Civico di Storia Naturale di Milano [Milan]
MSNPV Museo di Storia Naturale dell'Università di Pavia [Pavia]
MUZM Makerere University Zoology Museum, Kampala
MZUF Museo di Storia Naturale di Firenze, Sezione di Zoologia "La Specola", Firenzi [Florence]
MZUT Museo di Zoologia, Università di Torino [Turin]
NMBO National Museum, Bloemfontein
NMK National Museums of Kenya, Nairobi
NMP KwaZulu-Natal Museum, Pietermaritzburg
NMW Naturhistorisches Museum, Wien [Vienna]
NMZB Natural History Museum of Zimbabwe, Bulawayo
PEM Port Elizabeth Museum, Bayworld
RMNH Naturalis Biodiversity Centre, Leiden
TMP Ditsong National Museum of Natural History, Pretoria
SMNS Staatliches Museum für Naturkunde, Stuttgart
TCWC Biodiversity Research and Teaching Collections, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station
UMMZ University of Michigan Museum of Zoology, Ann Arbor
USNM National Museum of Natural History, Smithsonian Institution, Department of Vertebrate Zoology, Washington D.C.
ZFMK Zoologisches Forschungsmuseum Alexander Koenig, Bonn
ZMB Museum für Naturkunde, Berlin
ZMUC Kobenhavns Universitet, Zoologisk Museum [Zoological Museum, University of Copenhagen], Copenhagen

Scalation and size data was also obtained from the curators of various museums (see Acknowledgements) and Barry Hughes (for Ugandan material in the World Museum, Liverpool [LIV]). In several cases we recorded or confirmed the dorsal, and in some cases also ventral, colour patterns of specimens by examining colour images of specimens from various museums (e.g. World Museum, Liverpool; Museo Civico di Storia Naturale "Giacomo Doria", Genova [Genoa]; Museo Regionale di Scienzi Naturali, Turin; National Museums of Kenya, Nairobi). Data is available for a total of 640 specimens (Appendix 1).

Material listed under 'Localities' comprises specimens examined by the authors, or specimens for which data and/or photographs were provided and allowed positive determinations. A few reliable literature references were included. All of these records were used for plotting the map (Fig. 3). In this section countries are listed from north to south, while specific localities are listed alphabetically. The mapping notation (e.g.

SE 0135B3) refers to quarter-degree units (e.g. Minter *et al*. 2004: 48; but for the last part of the code we use numbers 1 to 4 instead of letters A to D), although on the map (Fig. 3) we plot these as half-degree units.

Most of the characters used by Gans (1959) were employed and evaluated in the same way in the present study, with modifications (or explanations) as indicated below. Specimens were examined under a binocular dissecting microscope, or with the aid of magnifying lenses for some of the larger specimens. Ventrals were counted from the first scale following the posterior pair of chin shields, up to but excluding the anal plate (first ventral is always wider than long and usually similar to the next ventral; small extranumerary scales sandwiched between posterior chin shields were not included); subcaudals were counted from the first adjoining pair behind the vent up to the pair in contact with the terminal spine (spine excluded; occasional specimens had a few single subcaudals); longitudinal dorsal scale rows were counted at or near midbody (halfway between tip of snout and vent), usually by starting the count caudad and reversing in the same way at the dorsal ridge (vertebral area), but taking special care to follow the inclination of the lateral rows (usually 3–4) of serrated and reduced scales; pattern cycles refers to the number of blotches or bands ('saddles') on the back, starting after the first (often chevron) marking on the nape (which often extends onto the back of the head) up to the marking above the vent (in cases of bilateral asymmetry, fusion of dorsal markings, or when these markings were unclear, lateral bars were used as guiding criteria); texture of the frontal scale was scored as indicated under 'Character analysis'; depth of sulcus formed by the pair of prefrontal scales was scored as deep, moderate or weak (scales merely in contact) as illustrated by Gans (1959, Fig. 6). Anterior temporals are the (usually) elongated scales posterior to, and in contact with, the postoculars; the uppermost one is in contact with a parietal scale, while the lowermost one is in contact with a supralabial. Posterior temporals are in contact behind the anterior temporals; the uppermost in contact with a parietal and lowermost in contact with a supralabial. Occasional supranumerary scales between anterior and posterior temporals were excluded from counts. The temporal formula refers to the number of anterior temporals plus the number of posterior temporals (e.g. 2+3) on either side of the head. Snout-vent length (SVL) (tip of snout to vent) and tail length (vent to tip of tail) were measured with the snake aligned against a millimetre rule, but SVL of curled specimens was measured using a length of string. Measurements of truncated tails were not included in calculations.

In some cases material reported on by Gans (1959) was also examined by the authors and our scale, colour pattern and size data were used (Appendix 1). Because of known differences in numbers of ventral and subcaudal scales between males and females (e.g. Gans 1959), specimens were sexed. Sex was determined by presence[males]/absence[females] of (one or both) inverted hemipenes (slit open to reveal spines if not obvious) in the tail base, presence of everted hemipenes, and/or presence of internal reproductive structures (eggs, ovaries, oviducts, testes, sperm ducts). Only sexed specimens were used for the analysis of numbers of ventral and subcaudal scales (except MSNG 6738 from Keren in Eritrea, one of only four specimens representing a new species, taken as female based on high ventral and low subcaudal counts; see below).

For the descriptive account of *D. bazi* five specimens from Egypt were examined, comprising three of the four specimens from this region reported on by Gans (1959, but excluding ZMB 5865), as well as a specimen (ZMB 51552) discovered by Barry Hughes among undetermined material at the museum in Berlin (Frank Tillack in litt. 9 April 2014), and a specimen (NMW 26879/1) in the Naturhistorisches Museum in Vienna. A set of colour photographs of the Berlin specimens, showing dorsal, ventral and lateral aspects of the body and tail, as well as close-up views of the head (including left and right sides), of these specimens, was also later consulted. For ZMB 5865, SVL and tail measurements, and number of pattern cycles on the back, follow Gans (1959), while numbers of midbody scale rows and pairs of subcaudals were determined by F. Tillack (these corresponded with Gans' 1959 counts); other morphological data for this specimen was determined after examining the colour images. Data for specimen ZFMK 38415 (Erkowit, Sudan), which we refer to as *Dasypeltis* cf. *bazi*, was provided by Wolfgang Böhme, but colour photographs of this specimen were also examined. The ratio greatest frontal length/greatest width was determined after performing measurements on enlarged photographic images (NMW 26879–1 measured using calipers).

According to Nicola Maio (in litt. 8 September 2014) the two Egyptian specimens of *Rachiodon scaber* recorded by Panceri (1878), in the Comparative Anatomy section of Naples Museum, were transferred to the Museo Zoologico at the same university after the Second World War, but now appear to be lost. There is also no record of these specimens having been transferred to Museo Civico di Storia Naturale di Milano (S. Scali in litt. 10 September 2014). However, the old catalogue of the museum in Milan does record a few specimens from Egypt identified by Prof. F. Gasco in 1876, including one *'Rachiodon scaber'* (catalogue number 1622 – photographic image of catalogue examined), but unfortunately none of these specimens still exist at the museum, possibly having been destroyed by fire in 1943 during the Second World War (S. Scali in litt. 26 September 2014). The Cairo specimen reported on by Jan (1863) is also no longer available in the Milan collection (S. Scali in litt. 26 September 2014).

The description of the new species from Somaliland and Djibouti (see below) was based mainly on data in Gans (1959) and details available from a set of high-resolution colour photographs of all proposed type specimens showing dorsal, ventral and lateral aspects of the body and tail, as well as close-up views of the head (including left and right sides), provided by the Natural History Museum (London) and Museum National d'Histoire Naturelle (Paris), although two proposed paratypes (BM 1992.501 and MNHN 84–707) were also examined by the first author while visiting these museums in September 2011 and October 2015, respectively. While the proposed holotype of the new species from Eritrea (see below) was examined by the first author at the natural history museum in Berlin, a set of close-up photographs was also supplied subsequently; a similar set of photographs of the proposed paratypes in Italian museums—which could not be examined personally—were also supplied, together with sex, SVL and tail length measurements, and ventral, subcaudal and midbody scale counts. For the new '5I'-patterned species from Arabia (see below), similar photos were provided of the proposed holotype (and one proposed paratype, BM 1987.1018) to allow for a detailed description, although these and other proposed types were also examined by both authors at the museum in London. Greatest frontal length/greatest width for most of the above specimens was determined by performing measurements on enlarged photographic images.

In addition to the data presented in this paper, comparative data consulted for the diagnoses of species (see below) were obtained from Duméril *et al*. (1854), Mertens (1954, 1955), Gans (1959, 1964), FitzSimons (1962), Broadley (1990), Trape & Mané (2006), Trape *et al*. (2012), Bates & Ineich (2012), Bates (2013) and Saleh & Sarhan (2016). In the case of *D. atra*, to avoid inadvertently including data for mainly brown or uniform phase specimens of other species of *Dasypeltis*, the only extralimital data used was for specimens from eastern Democratic Republic of the Congo (Mount Kabobo and the 'districts' of Oriental and Kivu) with '2M', '2B' and '2Bx' dorsal colour patterns as identified by Gans (1959) in his appendix. An exceptionally low female subcaudal count of 50 for *D. gansi* (see Bates & Ineich 2012) was excluded from the ranges listed under 'Diagnosis' below, as were ventral and subcaudal counts (250 and 55 respectively) for a specimen of *D. bazi* identified as a male by Saleh & Sarhan (2016) but which is probably a female (see discussion below; these data were also excluded from the diagnostic key). Morphological data for *D. parascabra* were derived from the small type series together with a few additional specimens—for which data is available in Gans (1959)—referred to this species by Trape *et al*. (2012); ranges are as follows—males: ventrals 210–223, subcaudals 67–74; females: ventrals 224–237, subcaudals 57–64; both sexes: midbody scale rows 22–26, pattern cycles 56–70.

The following type specimens were examined for comparative purposes by the first author in September/October 2011: holotypes of *Coluber Palmarum* (= *D. palmarum*, BM 1946.1.2.35), *Dasypeltis inornatus* (= *D. inornata*, BM 1946.1.2.47), *Dasypeltis scaber* var. *breviceps* Peters, 1864 (= *D. scabra*, ZMB 3886), *Dasypeltis scaber* var. *fasciolata* Peters, 1864 (= *D. medici*, ZMB 5737), *D. lineolata* Peters, 1878 (= *D. atra*, ZMB 9224, see below), *D. confusa* (MNHN 2006.0315) and *D. sahelensis* (MNHN 2006.0315); paratypes of *D. medici lamuensis* (= *D. medici*, see below, BM 1951.1.3.72–3, BM 98.1.8.15, BM 87.11.3.31), *D. gansi* (MNHN 2006.0308) and *D. latericia* (MNHN 2006.0314); and syntypes of *Rachiodon abyssinus* (= *D. abyssina*, see below, MNHN 6567, 7227), *Dasypeltis scaber* var. *mossambicus* Peters, 1864 (= *D. scabra*) (ZMB 1856–8) and *Dasypeltis macrops* Boulenger (= *D. fasciata*, BM 1946.1.5.17–8). Photographs of the syntypes (ZMB 22516A, ZMB 22516B , ZMB 27761) of *D. scabra* var. *atra* (= *D. atra*), provided by F. Tillack, were also examined. Photographs of the holotype (SMF 46642) of *Dasypeltis scabra loveridgei* Mertens, 1954 were available online: http://www.biologie.uni-ulm.de/cgi-bin/query_all/details.pl?id=107169&stufe=7&typ=ZOO&sid=T&lang=e (accessed 26 September 2014).

Statistical and multivariate analyses.—Univariate analysis was conducted using the computer software package Statistica v. 6. Two kinds of ordination comparisons were conducted in order to determine whether samples were distinguishable using a multi-dimensional approach. For Principal Components Analysis (PCA), IBM SPSS Statistics v. 20 was used, while Statistica Six Sigma was used for Discriminant Function Analysis; PAleontological STatistics v. 3.08 was used for PERMANOVA and to produce graphs. As all population groups (= species) discussed below are considered real geographical entities, it was considered appropriate to conduct discriminant function analysis to determine if the groups are distinguishable. Because of known sexual dimorphism in numbers of ventral plates and pairs of subcaudal scales (Gans 1959; see below), males and females were analysed separately. Eleven variables (characters as defined above and by Gans 1959, and discussed below) were used in the analyses—meristic: numbers of ventrals, subcaudals, midbody scale rows, supralabials (counts for left and right sides of the head combined), preoculars (combined count), postoculars (combined count), anterior temporals (combined count), posterior temporals (combined count) and pattern cycles; and the interval variables: frontal pitting (coded as 0 if smooth, 1 if present only as one or two rows at the edges, and 2 if extensive), and depth of the inter-prefrontal sulcus (0 if weakly marked, 1 if fair/medium, and 2 if deep). Only specimens with full sets of data were included (marked by an asterisk in Appendix 1). Analyses were conducted for the entire study area, but also separately for the Horn of Africa (Ethiopia, Eritrea, Djibouti, Somalia) + Egypt (excluding *D. medici*, represented

by only a single Somalian specimen with a full set of data) to determine whether the new species were distinguishable from all other congeners in that region.

Species concept and species delimitation.—We apply a lineage-based species concept whereby a species is represented by an independently evolving metapopulation lineage (see Frost & Hillis 1990; De Queiroz 1998, 2007). Morphological characters were the operational criteria for species delimitation.

Broadley (1983, 1990) relegated *Dasypeltis scabra loveridgei* Mertens, 1954 from Namibia to the synonymy of *D. scabra*, but the former has a distinctive dorsal colour pattern (hourglass-shaped dorsal saddles alternating with more-or-less square to rectangular lateral bars; '6N' of Gans 1959) and almost always only six supralabials (2nd and 3rd in contact with the orbit) on either side of the head (Mertens 1954; Bates *et al*. 2009; Bates *et al*. unpubl. data). Apart from Mertens' (1954) types, Gans (1959) provided data for additional Namibian '6N' specimens, all but a few having the 6[2,3] supralabial formula. This combination of characters is unique to *D. s. loveridgei* which we therefore consider a good evolutionary species and formally elevate to species status as *Dasypeltis loveridgei* Mertens, 1954 **comb. nov.** It should be noted that one of Mertens' (1954) paratypes has the '5N' dorsal pattern and 7[3,4] supralabial formula and is referable to *D. scabra* (Gans 1959: 95, 219; Bates *et al*. in prep.).

CHARACTER ANALYSIS

1. **Colour phases.**—Gans (1959, e.g. Figs 9 & 10) recognised 13 colour phases (dorsal colour patterns) for the genus *Dasypeltis*, with only 'inornata' ('1'), 'loveridgei' ('6') and 'palmarum' ('7') not found in north-eastern Africa. The 'montane' form [= *D. atra*] included melanistic ('2M'), uniform brown ('2B'), and patterned ('2Bx', dorsal saddles often confluent, or in partial contact, with lateral markings) phases (Fig. 17A–M). Gans (1959, see Pl. 6, Fig. 8) recorded the 'lineolata' phase ('9', dorsum dark with narrow, interrupted, pale transverse bands) [= *D. atra*] only from central Kenya (Fig. 17D), but some specimens from other areas have similar markings (see Fig. 17E, Ethiopia). '*Dasypeltis scabra*' included true *D. scabra* ('5N', variable, but dorsal saddles not linked to lateral bars, see Gans 1959) (Figs 5A–H & 6); *D. bazi* ('5N'-like but with large, cranio-caudally elongate, brown saddles, usually bifurcated at each end with a fairly shallow but distinct notch, and spot or blotch-like lateral markings; Gans 1959, Pl. 6, Fig. 1) (Figs 7A, 9A, 11 & 12); *D. taylori* **sp. nov.** ('5N'-like but with large, closely-spaced, square to slightly rectangular saddles often separated by narrow, sharply-defined white crossbars; Gans 1959, Pl. 6, Fig. 6) (Figs 13 & 14); *D. confusa* ('5L', saddles and lateral bars linked; Gans 1959, Pl. 8, Fig. 6) (Fig. 4A–D); and *D. arabica* **sp. nov.** ('5I', rectangular saddles and lateral bars enclose pale inter-saddle areas; Gans 1959, Pl. 6, Fig. 4) (Figs 27A & 29A). *Dasypeltis fasciata* ('4') was distinguished by its 'chequerboard' pattern being expressed only on the interstitial skin and lower edges of the scales (Gans 1959, Pl. 3, Figs 1–4) (Figs 19A & C). *Dasypeltis medici*, distinguished by the darkly pigmented edges of the paired apical pits on its dorsal scales, occurred as both patterned ('8', rectangular saddles with distinct white interspaces usually in contact with elongate lateral bars) and uniform or largely uniform but feebly marked ('3' – subspecies *lamuensis*) phases (Gans 1959, Pl. 13) (Fig. 2A–E). *Dasypeltis crucifera* **sp. nov.** has a unique dorsal pattern consisting of dark brown oval saddles, and elongated lateral bars, which together almost completely enclose pale cross-markings that form the inter-saddle areas (Figs 23A & 25A). Gans (1959) did not recognise *D. abyssina*, which is now known to occur in both (dorsally) patterned ('5N'-like but with mostly oblique dark saddles, usually wider than long, and often confluent or forming zigzags on the back and tail) and uniform grey-brown phases (see below and Fig. 20A, C–G).

2. **Number of pattern cycles** (Table 1).—This is a very variable character, but patterned *D. atra*, *D. abyssina*, *D. arabica* **sp. nov.**, *D. medici* and *D. fasciata* usually have counts of 70 or above, and are usually distinguishable from *D. bazi*, *D. taylori* **sp. nov.**, *D. crucifera* **sp. nov.**, *D. confusa* and often also *D. scabra* in this regard. In the study area, high numbers of cycles (108–141) in *D. fasciata* distinguish it from all other species except *D. atra* and a couple of specimens of *D. medici*; while the lowest counts are for *D. bazi* (39–49, 38 in a specimen reported by Saleh & Sarhan 2016) and *D. taylori* **sp. nov.** (44–59).

3. **Number of ventrals** (Table 2).—*D. arabica* **sp. nov.** and *D. abyssina* have the highest counts, followed by *D. fasciata* and *D. medici*. Due to wide variation within species, and extensive overlap of ranges between species, this character on its own does not help to distinguish *D. atra*, *D. bazi*, *D. taylori* **sp. nov.**, *D. crucifera* **sp. nov.**, *D. confusa* and *D. scabra*. In *D. medici*, males and females often have similar ventral counts.

4. **Number of subcaudals** (Table 2).—The two most arboreal species, *D. fasciata* and *D. medici*, have the highest subcaudal counts, averaging over 68 in both sexes. There is considerable geographical variation in *D. scabra*, with the highest counts in the south (Tanzania). *Dasypeltis confusa*, *D. scabra*, *D. bazi* (based only on specimens examined, i.e. excluding data from Saleh & Sarhan [2016] as some of their specimens may have been incorrectly sexed), *D. taylori* **sp. nov.**, *D. atra*, *D. abyssina*, *D. crucifera* **sp. nov.** and *D. arabica* **sp. nov.** have similar mean counts (59–63 in males, 48–56 in females).

Table 1. Numbers of pattern cycles and other pattern morphs in *Dasypeltis* from north-eastern Africa and south-western Arabia. Codes in parentheses under 'Range' and 'Other morphs' are those used by Gans (1959) for the various dorsal colour patterns.

	N	Range	Mean	S.D.	Other morphs
D. medici	24	57–108 (8)	74.0	11.9	Faintly patterned to uniform (3): 37; Total patterned (8): 35
D. confusa	30	50–79 (5L)	61.7	7.1	Uniform brown: 11
D. scabra	107	46–94 (5N)	67.4	10.0	
D. bazi (Egypt)	5	39–49 (5N)	45.2	4.4	
D. cf. *bazi* (Sudan)	1	48			
D. taylori **sp. nov.**	8	44–59 (5N)	52.8	5.1	
D. atra	51	62–130 (2Bx)	91.8	14.1	Melanistic (2M): 89, Brown (2B): 91, Total 2Bx: 135
D. fasciata	5	108–141 (4)	117.8	13.3	
D. abyssina	11	65–98 (5N, 5I)	80.7	11.4	Uniform brown/tan: 7
D. crucifera **sp. nov.**	3	51-62 (5I)	55.0		
D. arabica **sp. nov.**	6	62–79 (5I)	70.0	5.7	

Table 2. Ventral and subcaudal scale counts in *Dasypeltis* from north-eastern Africa and south-western Arabia. Values for males are in bold.

	VENTRALS								SUBCAUDALS							
	Males				Females				Males				Females			
	N	Range	Mean	S.D.	*N*	Range	Mean	S.D.	*N*	Range	Mean	S.D.	*N*	Range	Mean	S.D.
D. medici	**29**	**220–252**	**235.8**	**8.1**	49	218–252	234.4	7.3	**27**	**75–109**	**88.3**	**8.1**	47	61–90	77.5	5.7
D. confusa	**14**	**199–224**	**209.9**	**7.1**	30	212–239	226.1	7.9	**12**	**51–67**	**60.2**	**5.3**	24	48–61	54.1	3.0
D. scabra	**50**	**185–226**	**209.3**	**8.9**	76	202–249	226.9	8.5	**45**	**47–73**	**62.7**	**5.6**	72	43–65	53.6	4.8
D. bazi (Egypt)	**3**	**219–229**	**225.7**	**5.8**	3	227–234	229.7	3.8	**3**	**59–60**	**59.3**	**0.6**	3	50–55	52.0	2.6
D. cf. *bazi* (Sudan)	**1**	**229**							**1**	**67**						
D. taylori **sp. nov.**	**5**	**196–216**	**202.2**	**8.0**	3	208–222	213.7	7.4	**4**	**55–68**	**60.5**	**5.4**	2	44–52	48.0	5.7
D. atra	**109**	**199–232**	**212.7**	**6.8**	167	211–256	225.7	7.9	**103**	**50–71**	**61.9**	**3.9**	151	45–64	53.5	3.3
D. fasciata	**3**	**212–230**	**223.7**	**10.1**	9	237–248	242.7	3.8	**3**	**59–76**	**68.7**	**8.7**	9	64–76	68.3	3.7
D. abyssina	**6**	**226–247**	**235.5**	**8.2**	10	241–271	256.0	9.3	**4**	**57–68**	**61.5**	**4.6**	9	49–65	56.7	5.0
D. crucifera **sp. nov.**	**1**	**226**			3	231–247	240.3	8.3	**1**	**61**			3	49–52	50.3	1.5
D. arabica **sp. nov.**	**3**	**236–244**	**239.3**	**4.2**	4	239–254	244.8	6.9	**3**	**63–65**	**63.7**	**1.2**	4	53–61	56.8	3.5

5. **Type of head pitting with reference to the frontal shield.**—Gans (1959) recognised three states: N = none, M = marginal pitting (his Fig. 2B), and A = entire surface pitted (his Fig. 2A). Pits may take the form of swollen pimple-like protrusions on the frontal, especially centrally. In the present study this scheme has been refined to show five states: 0 = smooth, no pitting; 1 = a single row of pits on the posterior and lateral margins of the frontal; 2 = more extensive marginal pitting (Fig. 2B of Gans 1959); 3 = extensive pitting, but with centre of frontal still smooth (Fig. 2A of Gans 1959); 4 = entire frontal pitted and centre of shield often rugose or corrugated. In the study area *Dasypeltis medici* and *D. taylori* **sp. nov.** almost always have extensively pitted frontals (States 3 or 4), while most other species usually have marginal pitting (States 1 or 2), but in *D. scabra* and *D. bazi* the pitting varies from absent (State 0) to extensive (State 4). The frontal shields of five specimens of *D. bazi* illustrated in Saleh & Sarhan (2016, photographs in Fig. 5) appear to be extensively pitted and sometimes also corrugated (States 3 or 4).

6. **Depth of inter-prefrontal sulcus.**—This character was classified in the same way as by Gans (1959). The sulcus was moderately to deeply sunken in *D. taylori* **sp. nov.**, *D. arabica* **sp. nov.** and some populations of *D. scabra* (but usually moderately sunken to weakly marked elsewhere), whereas it was usually weakly marked (scales merely in contact) or moderately developed in all other species.

7. **Number of supralabial shields.**—In north-eastern Africa and Arabia there are normally seven supralabials, the third and fourth entering the orbit. The 6[2,3] formula (meaning six supralabials on either side of the head, with the 2nd and 3rd in contact

with the orbital) is very rare except in *D. loveridgei* **comb. nov.** and a few other populations of the *D. scabra* species complex in southern Africa (Mertens 1954; Bates & Broadley in prep.). Occasional variations (on one or both sides of the head) in the study area were: 5[2,3], 5[3], 6[2,3], 6[3], 6[3,4], 7[2,3,4], 7[3,4,5], 8[3,4], 8[3,4,5] and 8[4,5].

8. **Number of postoculars.**—In the study area most specimens have a single preocular and two postoculars on either side of the head, but a single postocular is commonly found in western populations of *D. atra* (e.g. 93.0% of Rwanda/Burundi snakes [*N* = 43] had a single postocular on either side; by contrast 75.0% of Ethiopian snakes [*N* = 28] had two postoculars on either side). The occurrence of a single postocular is also high in extralimital populations—in a sample of 126 specimens of *D. atra* from eastern Democratic Republic of the Congo, examined by the first author at the Royal Museum for Central Africa (Tervuren, Belgium), as many as 73.8% had one postocular on either side of the head, 14.3% had one postocular on one side and two on the other, while only 11.9% had two postoculars on both sides of the head.

9. **Number of anterior and posterior temporals.**—A temporal formula of 2+3 was common for all species, with 2+2 and 2+4 occuring frequently. Two anterior temporals on either side of the head was by far the most common condition for most species in the study area; as was three posterior temporals on either side, although counts of two or four were common. Although Saleh & Sarhan (2016) also gave this formula as 2+3 for *D. bazi*, in the single Fayoum specimen examined for this study, one side of the head had three anterior temporals, while another Egyptian specimen had a formula of 3+3 on both sides of the head.

10. **Number of dorsal scale rows at midbody.**—There was considerable overlap in numbers of midbody scale rows between the different species. However, northern species (*D. arabica* **sp. nov.**, *D. abyssina*, *D. crucifera* **sp. nov.**, *D. bazi* and *D. taylori* **sp. nov.**) never had more than 25 rows (21–25 versus 22–28 rows in other species). The highest means (≥25) were for *D. scabra* and *D. confusa*, and the lowest (≤23.5) were for *D. abyssina*, *D. bazi* (based only on specimens examined, i.e. excluding data from Saleh & Sarhan [2016], see below), *D. crucifera* **sp. nov.** and *D. fasciata*.

11. **Relative tail length** (Fig. 1).—Although there was much overlap in this character between most species (see species accounts), including those for which reasonable samples were available as shown in Fig. 1, *Dasypeltis medici* males and females usually had distinctly longer tails relative to SVL compared to males and females, respectively, of other species, while *D. fasciata* tended to have a slightly longer tail than the other species. Figure 1 also illustrates sexual dimorphism in tail length, with males usually having longer tails relative to SVL; as well as sexual dimorphism in body size, with the largest females exceeding the size of the largest males.

SYSTEMATICS

Apart from the species discussed and compared below, two available names currently in the synonomy of *D. scabra* (see Gans 1959; Broadley 1990) deserve mention in light of the fact that material from three populations currently identifiable as, or referable to, *D. scabra* are here to be described as new species. *Dasypeltis scabra mossambica* (Tete and Boror in Mozambique) and *Dasypeltis scabra breviceps* ('Cafferland', i.e. Eastern Cape Province, South Africa) were described by Peters (1864). The three syntypes (ZMB 1856, juvenile male; ZMB 1857 and 1858, both adult females) of the former and holotype (ZMB 3886, adult female) of the latter were examined for this study. The types of *D. s. mossambica* have '5N'-type dorsal patterns with moderate-sized saddles generally round to oval in shape, nasal divided below the nostril, supralabial formula 7[3,4] on either side of head, postoculars two on either side, frontal smooth in juvenile but fully pitted (State 4) in adults. For other characters: ZMB 1856: inter-prefrontal sulcus weakly marked, ventrals 207, subcaudals 67, midbody scale rows 25, pattern cycles 57; ZMB 1857: sulcus deeply marked, 236, 60, 25, 50; ZMB 1858: sulcus moderately marked, 237, 59, 27, 61. The holotype of *D. scabra breviceps* has a '5N'-type dorsal pattern but the saddles and lateral bars are somewhat narrow and irregular, nasal divided below the nostril, supralabial formula 7[3,4] on either side of head, postoculars 2 on either side, frontal fully pitted (State 4), inter-prefrontal sulcus deeply marked, ventrals 203, subcaudals 61, midbody scale rows 27, pattern cycles 63. Peters (1864) noted that the ground colour of *D. scabra mossambica* was yellowish. Based on the data presented above, both of the above names are clearly synonyms of *D. scabra*.

Squamata: Colubridae: Colubrinae: *Dasypeltis* Wagler, 1830

***Dasypeltis medici* (Bianconi)**
Eastern Forest Egg-eater
Fig. 2A–F

Dipsas medici Bianconi, 1859: 277. Type locality: 'Mozambique' [= Inhambane].

Dasypeltis abyssina ? (not Duméril, Bibron & Duméril) Stejneger, 1893: 733 (Mt Kilimanjaro, Tanzania).

Dasypeltis scabra var. F Boulenger, 1894: 356 (part, Mt Kilimanjaro).

Dasypeltis scaber (not Linnaeus) Loveridge, 1929: 28 (part) & 1936: 256 (Mt Mbololo, Lamu Island); Uthmöller, 1937: 356 (part, Gomberi, Mt Kilimanjaro); Scortecci,

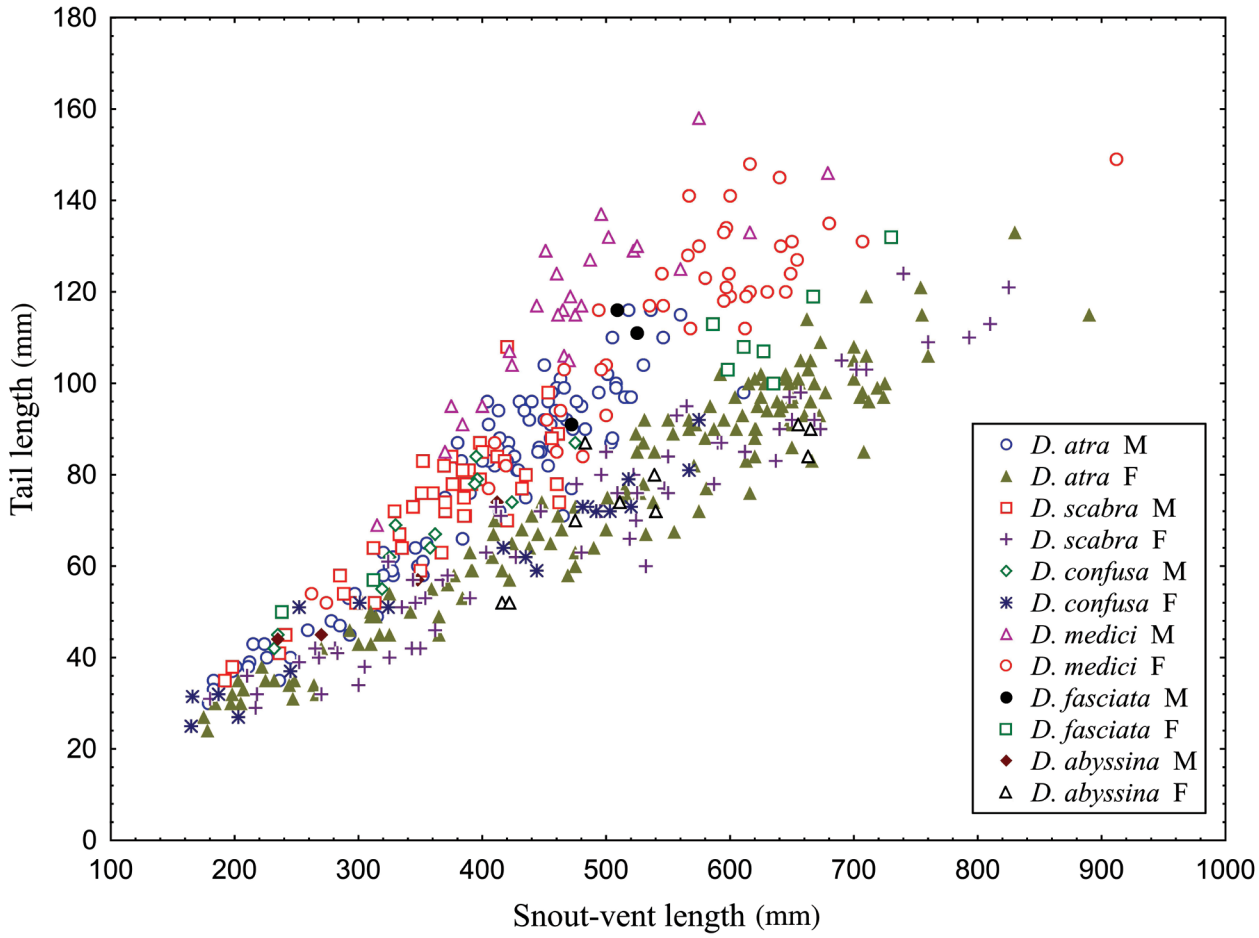


Figure 1. Tail length (mm) relative to snout-vent length (mm) in males and females of *Dasypeltis atra*, *D. scabra*, *D. confusa*, *D. medici*, *D. fasciata* and *D. abyssina* in north-eastern Africa.

1939: 276 (part, Belet Amin, Somalia).

Dasypeltis medici medici Gans, 1957: 3 & 1959: 157; Malonza *et al*., 2011: 160 (Kitobo Forest, Kenya); Göthel, 2015a: 19 & 2015h: 89.

Dasypeltis medici lamuensis Gans, 1957: 5. Type locality: Lamu Island, Kenya, holotype MCZ 40581; Loveridge, 1957: 289 (check-list); Gans, 1959: 159 & 1961: 74; Spawls, 1978: 10; Lanza, 1983: 223 (Alessandra Island near Gelib, zone of Mareri SW of Gelib, Belet Amin); Broadley & Howell, 1991: 32; Spawls *et al.*, 2002: 416; Spawls *et al.*, 2006: 129; Largen & Spawls, 2010: 490; Göthel, 2015a: 19, 2015c: 30, 2015d: 50, 2015f: 65 & 2015h: 89.

Dasypeltis medici Gans, 1971: 461; Largen & Parker, 2004: 26; Branch, 2005: 59 & 2014: 68; Vets & Safari, 2014: 43 (University of Dodoma).

Description. Dorsal colour pattern varies considerably. Patterned specimens may be similar to *D. scabra*: grey to tan with narrow, darker, rectangular saddles (longer than wide) separated by narrow cream to white interspaces, with irregular narrow dark lateral bars situated for the most part adjacent to the pale interspaces. The saddles may be much elongated and closely set and give the appearance of a broad dark vertebral stripe broken by more-or-less equally spaced pale flecks. Pattern cycles 57–108 (mean 74.0, N = 24); 1–5 chevrons (pointing forward) on nape and anterior part of body (N = 13). Some specimens are uniform pink, orange, red, grey, fawn or brown above (Spawls *et al.* 2002), but specimens with intermediate patterns also occur, e.g. reddish (Fig. 2C–D) or grey (Fig. 2E–F) with fairly vague dark dorsal markings and mere indications of whitish interspaces (e.g. CAS 135751, FMNH 251325, ZMUC 6111); NMK 1699 is reddish-brown with 3–4 vague chevrons only (anterior part of body) and a cream venter. Edges of apical pits on dorsal scales darkly pigmented. Venter usually cream, often with fine grey stippling (may be extensive as in NMW 26926); but occasionally yellowish-cream (e.g. NMK S 3956, Mount Warges; ZFMK 63582, near Mombasa [with extensive grey speckling]); or salmon-coloured with central part of each plate dark brown anteriorly in FMNH 142635 (vicinity of Nairobi).

Preoculars usually one on either side of head, but one on one side and two on the other in NMW 9964–18 and ZMB 8597, and two on either side in ZMUC 6143 (N = 61); postoculars usually two on either side of head, but one in 10.3% of specimens, and one on one side and two on the other in 4.6% of specimens (N = 87); frontal shield usually extensively pitted (States 3–4), but marginally pitted (States 1–2) in 10.5% of speci-

mens (including three snakes ≥422 mm SVL) and smooth (State 0) in one adult (MSNG 42710b) (*N* = 57); inter-prefrontal suture usually weakly marked, but moderately marked in 18.9% of specimens, and deeply marked in AMNH 143717 (*N* = 53); supralabials 12–15, usually 14 (both sides of head), usually 7[3rd and 4th entering orbit] on either side of head, but variations are: 6[2,3] on both sides in NMK 1699, 6[2,3] on right side in MSNG 427210b and USNM 16755, 6[3,4] on both sides in NMK 2535 & 3249, 7[2,3,4] on right side in ZMUC 6124, 8[3,4] on left side in SMNS 4216A, and 8[3,4,5] on left and 7[3,4,5] on right side in SMNS 4216F (*N* = 85); anterior temporals usually two on either side of head (70.5%), occasionally three (14.8%), 3 left:2 right or 2:3 (13.1%) and 4:3 in USNM 16755 (*N* = 61); posterior temporals usually three on either side of head (60.7%), occasionally 3:4 or 4:3 (14.8%), four (14.8%), 3:2 or 2:3 (4.9%), 5:4 in MCZ 40580, five in ZMB 17453 (*N* = 61), and two (left side, right damaged) in ZMB 48150; temporal formula on either side of head usually 2+3, often 2+4, occasionally 3+3 and 3+4; midbody scale rows 22–27 (mean 24.8 ± 0.97, *N* = 57); ventrals 220–252 in males (*N* = 29), 218–252 in females (*N* = 49); subcaudals 75–109 in males (*N* = 27), 61–90 in females (*N* = 47). Ratio SVL: tail length 3.5–4.7 in males (*N* = 27), 4.0–6.1 in females (*N* = 44); total length: tail length 4.5–5.7 in males (*N* = 27), 5.0–7.1 in females (*N* = 44).

Size. Largest male (NMK 2631 – Gede, Kenya) 679 mm snout-vent length [SVL] + 146 mm tail length = 825 mm total length. Largest female (FMNH 142635 – 'vicinity of Nairobi', Kenya) 912 + 149 = 1061 mm. The next largest female (MSNG 427106 – Belet Amin, Somalia) has a SVL of 845 mm (tail damaged).

Habitat. Coastal and montane forest and savannah at elevations from sea level to about 2500 m on Mount Warges (Kenya). In southern Africa it occurs in lowland evergreen forest (Broadley 1990).

Distribution. Widely distributed in the eastern parts of sub-Saharan Africa, from Mareri in southern Somalia southwards through eastern and central Kenya, eastern Tanzania, Malawi, extreme eastern Zimbabwe, Mozambique, and KwaZulu-Natal in South Africa as far south as St Lucia (see Broadley 1990; Spawls *et al*. 2002; Bates *et al*. 2014; Fig. 3). There is also an isolated Zambian record (AJL 3027) from riparian forest on the Mululangana River in the Zambezi Valley, 26 km SW of Chirundu [SE 1628B1] (Broadley *et al*. 2003).

Sympatry. Sympatric with *D. scabra* at Belet Amin (Somalia), Kilifi (Kenya), and Amani, Dodoma, Morogoro and Zanzibar (Tanzania); sympatric with *D. atra* at Nyambene Hills (Kenya) and Moshi (Tanzania); sympatric with both of these species at Mt Kilimanjaro in Tanzania (Appendix 1).

Localities. SOMALIA. Belet Amin [NE 0042B2] MSNG 42710b; near Mareri (Labadaah to Bula Yaag) [NE 0042D1] CAS 148077, MZUF 27155. KENYA. Chyulu Hills [SE 0037D2] NMK 402; Diani Beach, Ukanda [SE 0439B3] Fig. 2E–F; Gede [SE 0340A3] AMNH 88631, NMK 2597, 2619, 2631, 3200; Giriama [SE 0339D3] NMK 480; Kikambala [SE 0339D4] NMK 1050; Kilifi [SE 0339D2] BM 51.1.3.72–3; Lamu Island [SE 0240B4] MCZ 40581–2 [holotype and allotype of *D. medici lamuensis*]; Malindi [SE 0340A1] NMK 1561, 2522, 2526–7, 2529–33, 2535, 2538, 2587, 3290, 3292, ZMB 50191; Malindi, Sabaki River [SE 0340A1] photographic record (dorsum and top of head plain pale orange, edges of apical pits on dorsal scales darkly pigmented) and bottom photograph in Spawls *et al*. 2002: 417; near Mombasa [SE 0439B1] ZFMK 63582; Mombasa, 30 km south of [SE 0439B3] NMW 26926–1; Mount Mbololo [SE 0338A4] MCZ 40580; Maungu, Teita [SE 0338D2] BM 98.1.8.15; Mount Warges [NE 0037C4] NMK 3956; 'vicinity of Nairobi' [SE 0136B4] FMNH 142635; Nguni, Mwingi [SE 0137D2] NMK 2377; Nyambene Hills, Meru [NE 0037B2] NMK 1699; Taita [SE 0338A4] ZMB 9244; Takaungu [SE 0339D2] ZMB 17496; Tana River, Mchelelo Forest [SE 0140A3] NMK 4131; Taveta, Kitobo Forest [SE 0337B3] NMK 4121; Tiwi, Kwale [SE 0439B1] CAS 135751; Voi to Ndi [SE 0338D3] BM 98.1.8.14; Watamu [SE 0340A3] Fig. 2C. TANZANIA. Amani [SE 0538B1] MCZ 23274, ZMB 37598, ZMUC 6124; Bombani, East Usambara Mtns [SE 0538B1] ZMUC 6123, 6133; Dar-es-Salaam [SE 0639C4] NMW 9964–18; Dar-es-Salaam, vicinity of [SE 0639C4] Fig. 2A; Dodoma, University of Dodoma campus [SE 0635B1] photographic record in Vats & Safari (2014); East Usambara Mtns (Fig. 2B), FMNH 251325, ZMUC 6143; Gomberi, Mount Kilimanjaro [SE 0337A2] (Uthmöller 1934); Kibognoto [SE0337 A1] ZMB 37600; Kimboza Forest [SE 0737B2] ZMB 48150; Longido [SE 0236D1] ZMUC 6144; Mafia Island [SE 0739D4] MCZ 54827, NMZB 11265, SMF 19460; Makindu River [SE 0738C3] MCZ 18206; Mlinga Forest Reserve [SE 0538B1] ZMB 17318; Morogoro [SE 0637D3] AMNH 143717, USNM 62901, 62904, 62906, ZMB 27616; Moshi [SE 0337A4] SMNS 4216A–F; Mount Kilimanjaro [SE 0337A2] BM 87.11.3.31, USNM 16755; Mount Kwaraha [SE 0435B2] ZFMK 82342; Msolwa, Rubeho Mtns [SE 0736B4] ZMUC 6121; Nyange, Uluguru Mtns [SE 0637D4] MCZ 23273; Tanga [SE 0539A1] Fig. 2D, and middle photograph of reddish-brown, weakly marked specimen in Spawls *et al*. 2002: 417; Usa River near Arusha [SE 0336B3] CM 36586; Usambara Mountains, ZMB 17453, and Spawls *et al*. 2002: 417; Zanzibar Island [SE 0639A2] BM 50.1.5.40, NMK 3249, ZMB 5737, 17219, ZMUC 6111; Zanzibar Coast, ZMB 8597.

Conservation. In terms of the regional (study area) and global distribution of this species, using IUCN



Figure 2. *Dasypeltis medici*. A: Vicinity of Dar-es-Salaam, Tanzania (Photo: W.R. Branch); B: Juvenile from East Usambara Mountains, Tanzania (Photo: W.R. Branch); C: Watamu, Kenya (Photo: S. Spawls); D: Tanga, Tanzania (Photo: S. Spawls); E & F: Diani Beach, Kenya (Photos: F. Finke). [A & B are colour pattern '8' ('medici'), C & D are pattern '3' ('lamuensis', mostly unmarked), and E & F—same individual—are intermediate (weakly marked).]

(2012, 2016) criteria, it appears to be widespread and abundant and should be regarded as Least Concern.

Remarks. The northern-most populations of *D. medici* were separated as a subspecies, *D. medici lamuensis*, by Gans (1957). This taxon was diagnosed by the lack of the typical *medici* colour pattern (saddles and lateral bars) on the body (although this may be present but poorly defined, and Gans [1964] later noted that a faint typical *medici* pattern may be present in juveniles) and lower numbers of ventrals in both sexes. However, *medici* (marked), uniform, and 'intermediate' patterns are found in many specimens from south-eastern Kenya, especially at Malindi and Gede (AMNH, NMK and ZMB material not examined by Gans; Appendix 1: Malindi: in alcohol usually uniform and mostly pale brown [e.g. NMK 1561, 2619], occasionally grey [e.g. NMK 2532], but two specimens [NMK 2526, grey; NMK 2530, pale brown] have very weakly marked darker saddles, while two young snakes [NMK 2540, 422 mm SVL; ZMB 50191, 461 mm SVL] have the typically marked [but not bold] *medici* pattern; Gede: uniform pale brown, but NMK 2631 is grey with very vague indications of darker vertebral blotches and whitish interspaces). Reddish, largely uniform specimens, with faint vertebral blotches and whitish interspaces—from Watamu (SE Kenya) and Tanga (N Tanzania)—and a greyish, largely uniform specimen, with similar markings—from Diani Beach (SE Kenya)—are illustrated in Fig.

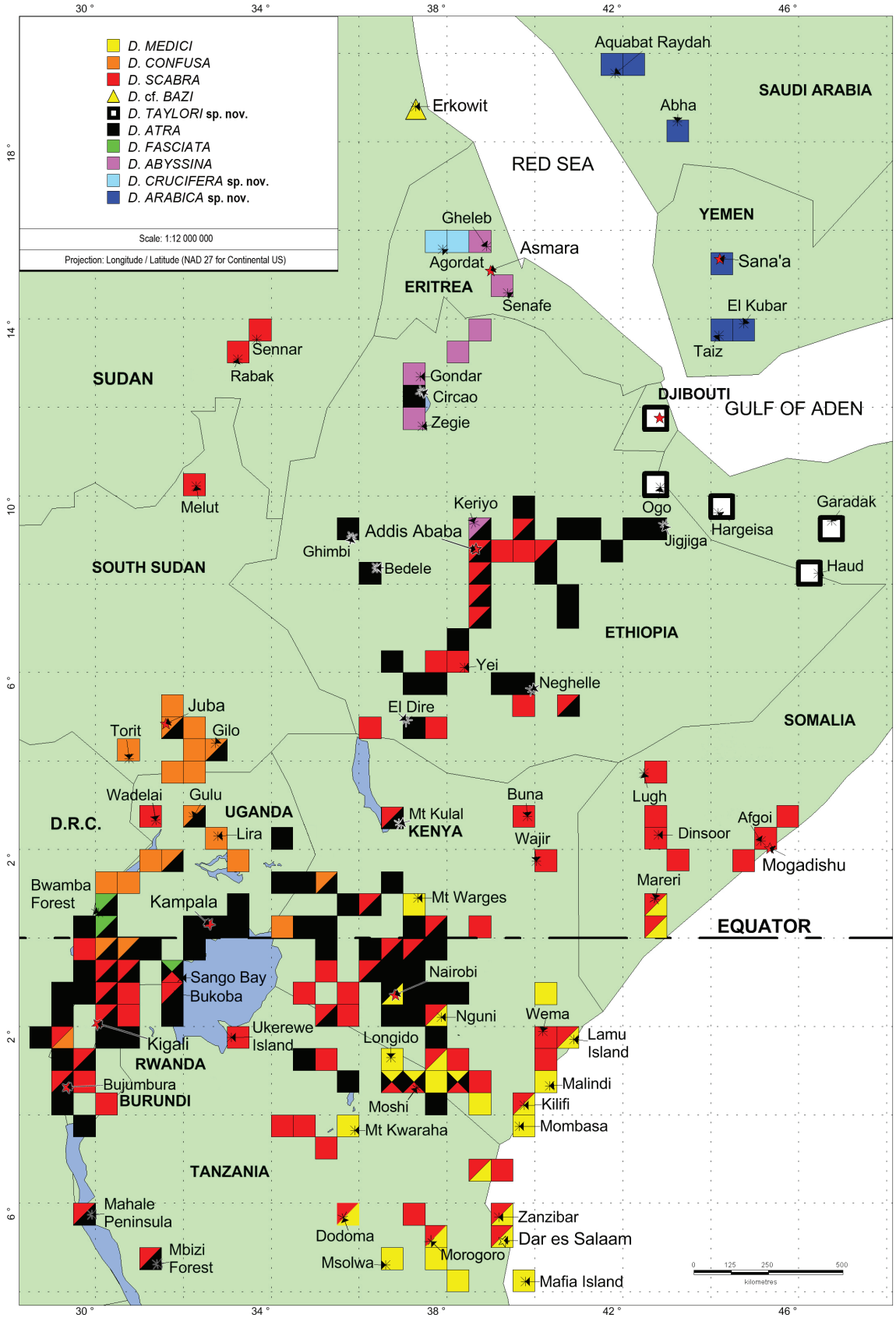


Figure 3. Geographical distribution of the genus *Dasypeltis* in north-eastern Africa and south-western Arabia.

2. Weakly marked specimens with indications of dorsal and lateral markings are also occasionally found further south, e.g. Mlola Forest on Mafia Island in Tanzania (NMZB 11265) and Bazaruto Island off the southern coast of Mozambique (NMZB 12037). The average ventral counts are indeed lower in northern populations (Somalia + Kenya), but there is considerable overlap with typical southern populations (Appendix 1), and ventral counts are actually lowest in the southern-most population in KwaZulu-Natal, South Africa: 206–215 in three males (TMP 28779, 46041, 56547), 214–223 in three females (TMP 44652, 47840, 78994) (D.G. Broadley unpubl. data). In light of this variation in colour pattern and ventral counts, we here relegate *Dasypeltis medici lamuensis* Gans, 1957 to the synonomy of *Dasypeltis medici* (Bianconi, 1859).

***Dasypeltis confusa* Trape & Mané**
Diamond-back Egg-eater
Fig. 4A–D

Dasypeltis scabra scabra (not Linnaeus) Loveridge, 1955: 46 (South Sudan).
Dasypeltis scabra (not Linnaeus) Gans, 1959: 141 (part, '5L' specimens from South Sudan and Uganda); Pitman, 1974: 116 (part, Uganda); Hughes, 1997: 68 (part, Uganda); Behangana & Goodman, 2002: 66 (part, Uganda).
Dasypeltis confusa Trape & Mané, 2006: 28. Type locality: Ibel, Senegal, holotype MNHN 2006.0303; Göthel, 2015h: 79.

Description. Dorsum grey or light brown with darker markings, usually in the form of rhombic saddles (often diamond-shaped with sharpest points aligned antero-posteriorly) which are confluent with the lateral bars (i.e. the '5L' linked pattern of Gans 1959, Pl. VIII, Fig. 6); dark markings usually have a cream to white margin around them, emphasising the pattern; pattern cycles 50–79 (mean 61.7, $N = 30$); dorsal saddles are not always joined to the lateral bars, so that the dorsal pattern may be similar to that of *D. scabra* ('5N') over small portions of the back in some specimens. A few specimens from South Sudan (six of the 14 from Torit – see Gans 1959: 203) and Uganda (MCZ 47801, 47830, UMMZ 88530) are plain light brown dorsally. Venter cream-white, often with grey stippling at the edges.

Preoculars one on either side of head ($N = 40$); postoculars usually two on either side of head, but only one on left side in FMNH 62216 ($N = 45$); frontal shield for the most part smooth, usually with 1–2 rows of shallow pits at the edges (States 1–2), but occasionally completely smooth and without pits (State 0) (ZMB 56436, UMMZ 88529) ($N = 38$); inter-prefrontal suture usually weakly marked, but moderately marked in 21.7% of specimens, and well marked (deep) in BM 1954.1.12.9 ($N = 23$); supralabials 11–14, usually 14 (both sides of head), usually 7[3rd and 4th entering orbit] on either side of head, but variations are: 6[2,3] (BM 1954.1.12.8), 6[3,4] on left side of head (FMNH 58336), and 6[3,4] on left and 5[3] on right (ZMB 77441) ($N = 42$); anterior temporals usually two on either side of head (95.3%), but 1 left: 2 right in BM 1954.1.12.8 and 2: 1 in BM 1954.1.12.9 ($N = 43$); posterior temporals usually three on either side of head (62.8%), two in NMW 9964–7, occasionally 3:4 or 4:3 (11.6%), four (11.6%), 2:3 or 3:2 (9.3%), and five in MCZ 47815 ($N = 43$); temporal formula on either side of head usually 2+3, often 2+4; midbody scale rows 23–27 (mean 25.0 ± 1.03, $N = 40$); ventrals 199–224 in males ($N = 14$), 212–239 in females ($N = 30$); subcaudals 51–67 in males ($N = 12$), 48–61 in females ($N = 24$). Ratio SVL: tail length 4.7–5.8 in males ($N = 12$), 4.9–7.5 in females ($N = 20$); total length: tail length 5.7–6.8 in males ($N = 12$), 5.9–8.5 in females ($N = 20$).

Size. Largest male (NMK 489 – Kacheliba, Kenya) 424 + 74 = 498 mm; but FMNH 62209 (Torit, South Sudan) has a SVL of 551 mm (tail damaged), and ZMB 56436 (questionable locality: Addis Ababa, Ethiopia) measures 475 + 87 = 562 mm. Largest female (FMNH 58496 – Juba, South Sudan) 575 + 92 = 667 mm; but ZMB 77441 (Lake Kivu, Rwanda) has a SVL of 620 mm (tail damaged).

Habitat. Found in savannah at elevations of 500 m to 1200 m.

Distribution. From Senegal to Nigeria in West Africa, and from Cameroon south to Angola and north-western Zambia, then eastwards through the Central African Republic, northern Democratic Republic of the Congo ('5L' patterned specimens in Gans 1959; Trape & Mané 2006; Trape *et al*. 2012; Bates 2013; Broadley & Bates unpubl. data), southern South Sudan, western and northern Uganda, to the Rift Valley at Kacheliba and Mumias in western Kenya, with an isolated record at Lake Kivu in western Rwanda (Fig. 3). It may also extend into south-western Ethiopia, based on two specimens with imprecise/questionable locality data (see below), but this requires confirmation.

Sympatry. Sympatric with *D. atra* 10 km S of Juba (South Sudan), Busingiro and Gulu (Uganda) and Kacheliba (Kenya); sympatric with *D. scabra* at Lake Kivu (Rwanda) (Appendix 1).

Mimicry. The dorsal pattern of *D. confusa* closely resembles that of the night adders *Causus rhombeatus* (Lichtenstein), *C. bilineatus* Boulenger, *C. defilippii* (Jan) and *C. maculatus* (Hallowell) which all occur in north-eastern Africa (Spawls *et al*. 2002; Rasmussen 2005; Dobiey & Vogel 2007).

Localities. SOUTH SUDAN. Juba [NE 0431D3] FMNH 58496, ZFMK 29694; Logutoic, MCZ 53401; Lokwi [NE 0432A2] FMNH 62216; Mongalla [NE 0531D1] MCZ 53402; Nimule [NE 0332C1] MCZ



Figure 4. *Dasypeltis confusa*. ['5L' colour pattern of Gans 1959] A: Bisu (Kigezi), Uganda. (BM 1951.1.3.69, Photo: M.F. Bates); B: Kacheliba, Kenya (NMK 489, Photo: P. Malonza); C: Mumias, Kenya (CAS 141784, Photo: J. Vindum); D: Lake Kivu, Rwanda (ZMB 77441, Photo: F. Tillack).

53403; 'Sudan' (probably East Equatoria state, or vicinity of Wadelai, Uganda; see Remarks under *D. scabra*) NMW 9964–7; Torit [NE 0432B1] FMNH 58361–3, 62207–14, 62217, MCZ 53404–5; Yei [NE 0430B1] FMNH 58336. ETHIOPIA. No precise locality, NMW 9964–2; 'Addis Ababa', ZMB 56436. UGANDA. Ajai Game Reserve [NE 0231C] MUZM ---; Bisu, Kigezi [NE 0131C] BM 1951.1.3.69; Bugoma Forest [NE 0130B4] LACM 39043; Busingiro, Budongo Forest [NE 0131D3] MCZ 47815; Gulu, Acholi [NE 0232C4] MCZ 47830; Kyambura Game Reserve [SE 0030A1] NMZB 14333, 15411; Lira, Lango [NE 0232B4] BM 1951.1.5.39, MCZ 47801, UMMZ 88529–30; Moyo, West Madi [NE 0331D1] BM 51.1.3.84; Nakosa [SE 0030A3] LIV 1960.51.2; Nyanshimbo [SE 0030A1] LIV 1962.106.19; Sana [SE 0030B4] LIV 1960.67.2; Semliki [NE 0130A2] BM 1954.1.12.8 ('120') & 1954.1.12.9 ('121'); Serere, Teso [NE 0133C2] BM 1976.848. KENYA. Kacheliba [NE 0135A3] NMK 485, 489; Mumias [NE 0034A4] CAS 141784. RWANDA. Lake Kivu [SE 0229A1] ZMB 77441.

Conservation. In terms of the regional (study area) and global distribution of this species, using IUCN (2012, 2016) criteria, it appears to be widespread and should be regarded as Least Concern.

Remarks. The plain phase specimens from South Sudan and Uganda reported on here (see above) are the first of their kind to be documented. Dorsally uniform, or mostly unpatterned, specimens (brown or grey) are also known for *D. scabra* (southern Africa: e.g. De Waal 1978; Broadley 1990), *D. medici* (Gans 1959; Spawls *et al*. 2002; this study), *D. gansi* (Trape & Mané 2006; Bates & Ineich 2012), *D. atra* (Gans 1959, 1964; Spawls *et al*. 2002; this study) and *D. abyssina* (see below).

***Dasypeltis scabra* (Linnaeus)**
Common Egg-eater
Figs 5A–H & 6

Coluber scaber Linnaeus, 1758: 223. Type locality: 'in Indiis' [= "via the Cape ... read as South Africa", Flower 1933: 818; restricted to "probably near Cape Town", Mertens 1954: 214].
Rachiodon abyssinus (not Duméril, Bibron & Duméril) Duméril, Bibron & Duméril, 1854: Vol. 7: 496 (part, "Nil Blanc") (MNHN 7227, paralectotype of *R. abyssinus*, see p. 39 below).
Dasypeltis scaber, var. *abyssinicus* (lapsus) (not Duméril, Bibron & Duméril) Peters, 1864: 645 (Sennar, Sudan).
Dasypeltis scabra var. B Boulenger, 1894: 356.
Dasypeltis scabra Günther, 1894: 87 (E. Kikuyu, Kenya); Boulenger, 1896: 20 (between Comia & Mategoi, Somalia), 1897: 229 (Somalia) & 1898: 720 (Lugh, Somalia); Lönnberg & Andersson, 1913: 4 (Kismayu); Loveridge, 1929: 28 (part); Corkill, 1935: 18 (Blue Nile Province, Sudan); Loveridge, 1957: 288 (check-list); Gans, 1959: 141 (part), 1961: 73, 1964: 283, 1971: 461 & 1974: 34; Gans & Laurent, 1965: 67 (Mogadiscio); Lanza, 1972: 177 (Ilala Sala, Awash National Park), 1983: 223 (part) & 1990: 436 (part); Pitman, 1974: 116 (part); Spawls, 1978: 10 (part); Emmrich, 1985: 66, 68 (Oukam, Lake Zwai); Hoevers & Johnson, 1982: 199 (Mareri); Broadley & Howell, 1991: 32; Meirte, 1992: 57; Largen & Rasmussen, 1993: 340 (part); Hughes, 1997: 68 (part); Largen, 1997: 89 (part); Behangana & Goodman, 2002: 66 (part, Uganda); Spawls *et al*., 2002: 418; Branch, 2005: 59 & 2015: 67; Spawls *et al*., 2006: 130; Ziliani *et al*., 2006: 193 (Mount Kulal, Kenya); Largen & Spawls, 2010: 490 (part); Geniez, 2015: 211 (Mount Kulal); Spawls, 2017: 31 (Maasai Mara).
Dasypeltis scaber Calabresi, 1927: 54 (Somalia); Scortecci, 1931: 208 (Giohar), 1939: 276 (part, Giohar, Belet Amin) & 1943: 285 (El Dire).
Dasypeltis scabra scabra De Witte, 1962: 139; Bourgeois, 1968: 284.
Dasypeltis scaber scaber Laurent, 1956: 258 (part).
Dasypeltis "scabra" Göthel, 2015a: 19 (part) & 2015h: 86 (part).
Dasypeltis cf. *scabra* Sindaco *et al*., 2013: 331 (part, Kenya).

Description. In the study area the dorsal pattern may vary quite considerably (see Gans 1959). Dorsum grey or light brown with darker markings ('5N' pattern of Gans 1959); saddles vary from rectangular to squarish, oval, subcircular, weakly hourglass-shaped, weakly transversely enlarged, or irregular, and often a mixture of two or more of these shapes (Figs 5 & 6). Dorsal saddles (46–94, mean 67.4, $N = 107$) are dark brown or black, and a few may be linked to the dark lateral bars. The centre of the saddle may be paler than the outer rim, as in MHNP 7227 (Sudan) where it is grey with a black edge (Fig. 6). Venter cream-white, usually with grey stipples, or dark blotches, at the edges; sometimes with large bold cones or blotches at the edges and/or mid-ventrally (see Gans 1959, e.g. Pl. 9). Top of head often with 1–2 anterior-pointing (sometimes fragmentary) chevrons and/or other dark markings.

Preoculars usually one on either side of head, but one on one side and two on the other in MCZ 30208 & USNM 62902, and two on either side in BM 01.1.3.4 & MSNG 28808 ($N = 104$); postoculars usually two on either side of head, but one on one side and two on the other in 6.0% of specimens, one on either side in 6.0% of specimens, and absent on both sides in ZMB 26832 ($N = 133$); frontal shield heavily pitted (States 3 or 4) in 57.7% of specimens (73.3% of specimens from Tanzania in the south of the study area, $N = 30$), marginally pitted (States 1 or 2) in 36.1% of specimens, and smooth (State 0) in 6.2% of specimens ($N = 97$); inter-prefrontal suture weak in 48.9% of specimens, moderately marked in 38.0% of specimens, and deeply sunken in 13.0% of specimens ($N = 92$); supralabials 11–16, usually 14 (both sides of head), usually 7 [3rd and 4th entering orbit] on either side of head, but variations are: 5[2,3] on right and 6[2,3] on left in ZMUC 6136, 6[2,3] on both sides in BM 68.2.29.101 and BM 1964.1069, 6[3,4] on both sides in ZMB 22518, 6[2,3] on one side and 7[3,4] on the other in FMNH 134939, MSNG 29239 and MZUF 2802, 6[3,4] on left and 7[3,4] on right in BM 68.2.29.100, 7[2,3] on both sides in NMK 3184, and 8[4,5] on both sides in ZMB 51835 ($N = 123$); anterior temporals usually two on either side of head (88.5%), occasionally 2 left:3 right or 3:2 (3.5%), three (3.5%), 2:1 (3.5%), and one in MRAC 18563 ($N = 113$); posterior temporals usually three on either side of head (64.6%), occasionally 3:4 or 4:3 (16.8%), 3:2 or 2:3 (7.1%), four (6.2%), two (4.4%), and five in PEM 5626 ($N = 113$); temporal formula on either side of head usually 2+3, occasionally 2+4, rarely 2+2; midbody scale rows 22–28 (mean 25.0 ± 1.38, $N = 102$); ventrals 185–226 in males ($N = 50$), 202–249 in females ($N = 76$); subcaudals 47–73 in males ($N = 45$), 43–65 in females ($N = 72$). Ratio SVL: tail length 3.9–6.2 in males ($N = 45$), 5.3–8.9 in females ($N = 65$); total length: tail length 4.9–7.2 in males ($N = 45$), 6.3–9.9 in females ($N = 65$).

Size. Largest male (LIV 1962.168.14 – Ruzinga, Ankole, Uganda) 453 + 98 = 551 mm; but MSNG 29239 (between Comia and Matagoi, Somalia) has a larger SVL: 462 + 74 = 536 mm. Largest female (NMK 3184 – Lake Naivasha, Kenya) 867 + 95 = 962 mm.

Habitat. Found in savannah and grassland from sea level to over 1500 m.

Distribution. From the south-western Cape of South Africa through Namibia, Botswana, Zambia, southern and western Democratic Republic of the Congo, much of south-eastern and eastern Africa as far north as Gojam area (too vague to map) in north-central Ethiopia, with isolated populations along the Nile Valley (see comments under 'Discussion') in south-eastern



Figure 5. *Dasypeltis scabra*. ['5N' colour pattern of Gans 1959] A: Dodoma, Tanzania (Photo: W.R. Branch); B: Masiko ya Tembo, Tanzania (Photo: W.R. Branch), C: Wajir, Kenya (Photo: S. Spawls); D: Juvenile from Loita Hills, Kenya (Photo: T. Mazuch); E: Gilgil, Kenya (Photo: S. Spawls); F: MSNM 974, Magadi, Somalia (Photo: Museo Civico di Storia Naturale, Milan); G: Awash National Park, Ethiopia (Photo: S. Spawls); H: Awash National Park, Ethiopia (Photo: S. Spawls).

Sudan and adjacent north-eastern South Sudan (see Gans 1959; Broadley 1990; Spawls *et al*. 2002; Fig. 3), as well as 50 km north of Kutum in western Sudan (see Remarks below).

Sympatry. Sympatric with *D. medici* at Belet Amin (Somalia), Kilifi (Kenya), and Amani, Dodoma, Morogoro and Zanzibar (Tanzania); sympatric with *D. confusa* at Lake Kivu (Rwanda); sympatric with *D. atra* at Aware Melca and Lake Abiata (Ethiopia), Mulema (Uganda), Lake Naivasha and Mount Kulal (Kenya), Astrida (Rwanda) and Minziro Forest Reserve (Tanzania); sympatric with both *D. medici* and *D. atra* at Mt Kilimanjaro (Appendix 1).

Localities. 'ARABIA'. No specific locality, MNHN 6565. SUDAN. Nil Blanc, MNHN 7227 (Fig. 6, paralectotype of *R. abyssinus*, see below); 40 km E of Rabak, near Kosti [NE 1333A1] RMNH 24399; Sennar State [NE 1334C], BM 09.10.15.35. SOUTH SUDAN. Melut [NE 1032A3] FMNH 134939; 'Sudan' (probably East Equatoria state, or vicinity of Wadelai, Uganda; see Remarks), NMW 9964–6. ETHIOPIA. No locality, NMW 15298; Aware Melca [NE 0939B2] BM 16.6.24.11–12; Arba Minch [NE 0637B1] AAU 494, 679, BM 1969.288; Awash National Park [NE 0839D4] (Figs 5G&H); Awash National Park, 2 km NE of entrance to [NE 0839D4] PEM 8602–3; Bulcha [NE 0638A1] ZFMK 17763; Fitu, 135 km ESE of Neghelle [NE 0540B1] '5N'/'2Bx' dorsal pattern, photographic records; Gojam, BM 1964.1069; Lake Abiata [NE 0738D1] BM 1973.3259; Lake Chamo (west shore) [NE 0537D3] AAU 489; Meki–Dukem area [NE 0838B] ZMB 51835, 77053; Neghelle, 31 km ESE of [NE 0539B2] vertebral stripe over most of back, photographic records; west of Omo River [NE 0436C], BM 00.11.29.3. SOMALIA. environs of Afgoi [NE 0245A1] MZUF 1118, 1133; Afgoi, 6 km E of [NE 0245A1] MZUF 24179; Belet Amin [NE 0042B2] MSNG 42710A; between Comia and Matagoi [NE 0143C] MSNG 29239; Ceelcillan [= El Ellan, NE 0242D1] MZUF 31459; Dinsoor [NE 0242B4] MZUF 24674; Giohar [NE 0245D3] MSNM 785; near Mareri (Labadaah to Bula Yaag) [0042D1] MZUF 27156; Lugh (= Luuq) [NE 0342D1] BM 98.1.28.14, MSNG 28808; Lugh to Ganane [NE 0342D] MZUF 21968; Maheddei Uen [NE 0245D3] MZUF 21968; Mogadishu [NE 0242A2] MZUF 2802; Uagadi [NE 0144D1] MSNM 974. UGANDA. Kaburangiri [SE 0031D3] LIV 1962.106.6; Kakoba [SE 0030C1] LIV 1960.67.6; Kayanja, LIV 1962.330.22; Mbarara, Kasheri [SE 0030D1] BM 51.1.5.79, 1961.1804, LIV 1959.83.1; Mulema [SE 0031D1] BM 03.12.2.21; Namatyobola [SE 0031D1] LIV 1962.106.5; Ruburogoto [SE 0130B1] LIV 1960.67.4, 1960.67.7, 1962.106.35; Rukoni [SE 0030C4] LIV 1962.106.20; Ruzinga, Isingiro [SE 0030D4] BM 1959.1.5.59, LIV 1962.168.14; Rwensama [SE 0029B4] LIV 1960.67.8; Wadelai [NE 0231C2] BM 07.12.1.19. KENYA. Aberdare Mtns [SE 0036B] USNM 42016; Buna, Wajir [NE 0239D3] NMK 2824; about 45 km W of Ewaro Ngiro, near Narok [SE 0135B3] PEM 5627; Gatab, Mount Kulal [NE 0236D2] MSNPV CR790–2; Gilgil [SE 0036C2] BM 01.1.3.3–4, and Fig. 5E; Hell's Gate, Naivasha [SE 0036C4] CAS 147836; Isiolo [NE 0037B3] CAS 130784–5, NMK 561; Kilifi [SE 0339D2] BM 51.1.3.70; Kithu-Uri, East Kikuyu [SE 0037A4] BM 93.11.21.72; Kora [NE 0038B1] NMK 2965; Laini, Tana River [SE 0420C2] MCZ 40584; Lake Naivasha [SE 0036C4] NMK 1415, 1472, 2083, 2343, 2853, 3184, 3319, NMP 1260; Loita Hills [SE 0135D2] Fig. 5D; Mombosasa, Witu [SE 0240B3] MCZ 40583; Moshi [0337C2] (Gans 1964); Naivasha [SE 0036C2] CAS 147837–8; Ol Ari Nyiro Ranch [NE 0036C2] NMK 3103; Solio Ranch, Laikipia [SE 0036B4] NMK 3052; Sotik, Uaso Nyiro [SE 0035C1] USNM 41974; Tsavo East National Park [SE 0338B] NMK 3021; Uaso Nyiro Plains, MCZ 11501; Voi [SE 0338B3] NMK 1022; Wajir [NE 0140C3] CAS 130661, NMK 2262, Fig. 5C, and top photograph in Spawls *et al*. 2004: 418; Wema [SE 0240A1] MCZ 40585. RWANDA. Astrida [SE 0229D1] MRAC 18559; 15 km S of Butare [SE 0229D1] PEM 5624; Gabiro [SE 0130C2] IRSNB 5499, MRAC 9209, 9214; Lake Kivu [SE 0229A1] ZMB 22518; Nyagatare [SE 0130A4] PEM 5625. BURUNDI. Kabuyenge [SE 0329A4] MRAC 18563; Kahiro District [SE 0330C3] MRAC 18565; Mugera [SE 0329B4] MRAC 18564. TANZANIA. Amani [SE 0538A4] ZMB 21062; Chai Camp [SE 0336B4] AMNH 50791; Dar es Salaam [SE 0639C4] NMW 9964–17, ZMB 26832; Dodoma [SE 0635B1] Fig. 5A; Kibwesa [SE 0629B4] ZMB 22754; Kikombo, Dodoma [0635B2] USNM 72476; Maji Malulu, Usandawi [SE 043B4] MCZ 30205; Mapenduzi, Dodoma [SE 0635B2] PEM 5626; Masiko ya Tembo, vicinity of Sanya Chini [SE 0337A3] Fig. 5B; Massailand, ZMB 11934a,b, 14097; Minziro Forest Reserve [SE 0131B1] ZMUC 6136–7; Morogoro [SE 0637D3] USNM 62902–3, 62905; Mount Kilimanjaro [SE 0337A2] BM 87.11.3.30; Mpwapwa [SE 0636B3] ZMB 13304, 19669; Ngare, Nanyuki [SE 0235C1] FMNH 27786; Serondera, Serengeti National Park [SE 0234C4] NMK 1887; Tanga [SE 0539A1] NMW 9964–9; Ukerewe Island [SE 0233A1] MCZ 30207–8; Wembere Steppe [SE 0434A] ZMB 16753; Zengeragusa, Mkalama [SE 0434B1] MCZ 18208.

Conservation. In terms of the regional (study area) and global distribution of this species, using IUCN (2012, 2016) criteria, it appears to be widespread and abundant and should be regarded as Least Concern.

Remarks. MNHN 6565 is a female from "Arabia" (without precise locality data) with a '5N' dorsal pattern consisting of 55 fairly broad saddles (some 'diabolo'-shaped), 244 ventrals and 54 subcaudals. Although its provenance is uncertain, we refer this specimen to *D. scabra*.

According to Gans (1959: 11, 205) specimen BM 07.12.1.19 was collected in 'Wadelai', north-western Uganda, by Emin Pasha (also known as Emin Bey,

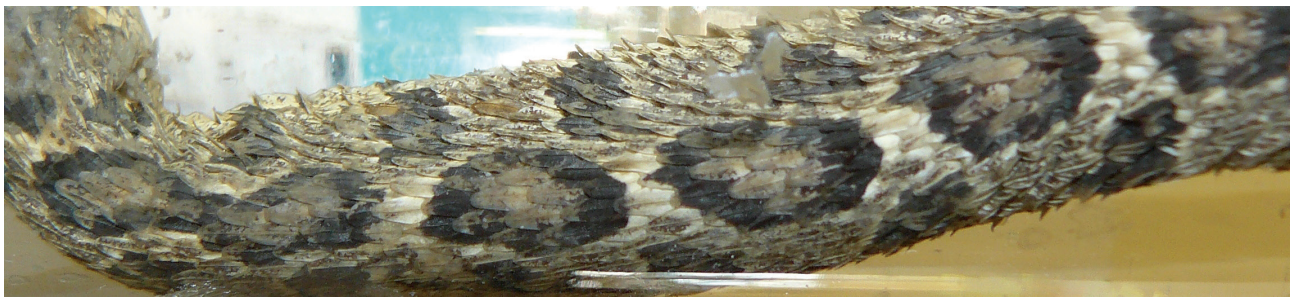


Figure 6. *Dasypeltis scabra*. Close-up dorsal view (in alcohol) of MNHN 7227 (paralectotype of *Rachiodon abyssinus*, see p. 39) from the White Nile River (possibly near Khartoum, Sudan) showing a '5N' pattern (see Gans 1959) consisting of dark oval saddles and dark dorso-ventrally elongated lateral bars, with paler centres. (Photo: M.F. Bates)

baptised E.C.O.T. Schnitzer [1840–1892]: Chisholm 1911; Anon 2017). A colour photograph of the specimen (sent by P. Campbell, Natural History Museum, London) was made available to the first author, and the '5N' dorsal pattern was confirmed. This appears to represent an isolated population of *D. scabra*. Specimens of *D. scabra* (NMW 9964–6, '5N') and *D. confusa* (NMW 9964–7, '5L') from 'Sudan', donated to the Naturhistorisches Museum Wien in 1884 by 'Emin Bey', may have been collected nearby in South Sudan's East Equatoria state, or possibly in the vicinity of Wadelai. Emin Pasha was governor of Equatoria (a region in southern South Sudan that included a portion of north-western Uganda), then a province of Anglo-Egyptian Sudan; he retreated to Wadelai in 1885 in the face of the Madhist advance (Chisholm 1911; Anon 2017).

ZFMK 32479 from 50 km north of Kutum, North Darfur State, western Sudan is a faded male specimen with a damaged head, referable to *D. scabra* on account of the following characters: '5N' dorsal pattern with dark oval saddles and whitish interspaces, pattern cycles 50, SVL 447 mm, tail length 81 mm, SVL/tail ratio 5.5, ventrals 227, subcaudals 66, midbody scale rows 23. This locality is outside the study area and is the only other known record of *D. scabra* in the north of Africa. It is not associated with the Nile River and represents an extremely isolated population, possibly a relic of a former widespread distribution (see 'Discussion' below). The nearest conspecific (RMNH 24399) is from near Kosti about 880 km ESE.

Dasypeltis bazi Saleh & Sarhan

Egyptian Egg-eater
Figs 7A–B, 8, 9A–B, 10–12

Rachiodon abyssinicus lapsus for *abyssinus* (not Duméril, Bibron & Duméril) Lichtenstein & Von Martens, 1856: 28 ("Oberaegypten" = Upper Egypt).

Rachiodon scaber (not Linnaeus) Jan, 1863: 106 (Cairo); Panceri, 1878: 22 (Egypt).

Dasypeltis scaber (not Linnaeus) Gasco, 1876: 119 (Middle Egypt).

Dasypeltis scabra (not Linnaeus) Anderson, 1896: 114, 1898: 278 (Fayum); Gans, 1959: 141 (part, Egypt, Fayum, Upper Egypt), Pl. IV, Figs 5& 6, Pl. VI, Fig. 1; Gans, 1961: 74 (part), Pl. 1, Figs A & B (Egypt); Marx, 1968: 33 (Egypt); Rehak & Osborn, 1988: 275 (Faiyum); Saleh, 1997: 146 (Faiyum); Baha El Din, 2006: 232 (Fayoum); Geniez, 2015: 210 (Fayoum).

Dasypeltis cf. *scabra* Sindaco *et al*., 2013: 93 (part, Egypt).

Dasypeltis "scabra" Göthel, 2015a: 19 (part) & 2015h: 86 (part).

Dasypeltis bazi Saleh & Sarhan, 2016: 31. Type locality: Abu-Gandir, Faiyum Governorate, Egypt, holotype AUZC-R09458.

Diagnosis. (excluding ZFMK 38415, see below) Assigned to the genus *Dasypeltis* on account of its slender form, possession of (usually 3–4) rows of reduced, oblique, keeled and serrated lateral scales (little or no serration in *D. inornata*) and head barely distinct from the neck (moderately distinct in *D. fasciata*). Distinguished from other congeners by its colour pattern consisting of: large cranio-caudally elongate dark brown saddles, usually bifurcated at each end with a fairly shallow but distinct notch, the saddles about 1.5 to 2 times as long as the pale interspaces between them (similar to *D. loveridgei* **comb. nov.**, but this species has mostly transversely enlarged and distinctly hourglass-shaped saddles which are mostly about equal in length to the pale interspaces; similar but less elongate saddles in some populations of *D. scabra*, e.g. Fig. 5G & H); low numbers of pattern cycles 38–49 (lower than all other [patterned] species/populations except *D. taylori* **sp. nov.** and a few specimens of *D. scabra*; *D. inornatus* always uniform brown; *D. gansi* uniform or weakly marked); flanks decorated with dark brown spots or blotches (similar in *D. loveridgei* **comb. nov.**, and some *D. scabra*, e.g. Fig. 5G & H) rather than vertical bars as in most other (patterned) *Dasypeltis* species/populations; and venter immaculate white to cream-white apart from a few dark markings at the edges in some specimens (extensive dark markings in *D. abyssina* and many *D. scabra*, often extensive grey stippling in *D. medici*); together with a combination of the following characters: Ventrals 213–229 in males (mostly higher than *D. taylori* **sp. nov.** 196–216, lower than *D. arabica* **sp. nov.** 236–244), 215–234 in females (lower than *D. abyssina* 241–271, *D. arabica* **sp. nov.** 239–254, *D. gansi* 235–259; mostly lower than *D. latericia* 234–262, *D. crucifera* **sp. nov.** 231–247); Subcaudals 59–61 in males (lower than *D. inornata* 81–92, *D. fasciata* 71–90, *D. medici* 69–109, *D. gansi* 68–83, *D. palmarum* 68–77, *D. parascabra* 67–74, *D. latericia* 66–86, *D.*

arabica **sp. nov.** 63–65), 50–63, 70 in females (mostly lower than *D. inornata* 69–84, *D. fasciata* 64–84, *D. palmarum* 62–77, *D. medici* 61–90); Tail of moderate length: SVL/tail length 5.0–5.9 in males, 5.1–7.2 in females (in study area, tail long in: *D. medici* 3.5–4.7 males, 4.5–5.7 females; *D. fasciata* 4.7–5.2 males, 4.8–6.4 females; see also Gans 1959); Postoculars 2 on either side of head (often one, especially in western populations, of *D. atra*); Nasal divided below the nostril (undivided in *D. sahelensis* and *D. parascabra*); Supralabials 7 (3rd and 4th enter orbit) on either side of head (usually 6[2,3] in *D. loveridgei* **comb. nov.**). Half the specimens examined had longitudinally divided anal plates; this plate is usually undivided in other species in the genus.

Description of topotype BM 97.10.28.575 from Fayoum. (At Natural History Museum, London). Adult female (stretched oviducts and three eggs observed) with a total length of 692 mm, snout-vent length 602 mm, tail length 90 mm (Gans 1959) (ratio SVL: tail length 6.7, ratio total length: tail length 7.7) from Fayoum [about 29º18'30"N, 30º51'00"E], collected by A.R. Birdwood (Gans 1959, Pl. VI, Fig. 1; Figs 7 & 8). This is the same specimen discussed and illustrated by Anderson (1898, Pl. 34; see discussion under 'Remarks' below) as *D. scabra*.

Head (somewhat dehydrated) small and barely distinct from the neck; snout rounded, rostral shield barely visible when viewed from above. The elongate nasal scale (about twice as long as high) is divided below the nostril (which is situated in the anterior half of the nasal); no loreal present. Three internasals between the rostral and paired prefrontals, but the larger, subcircular, central internasal appears to be an aberration. Each prefrontal is larger than an internasal (and the paired prefrontals together are much larger than all three internasals together), but they are of equal length (cranio-caudal orientation). Inter-prefrontal sulcus moderately marked. Frontal large, broadest anteriorly, 1.61 times as long as broad, smooth except for a single row of pits on the lateral borders, and of similar length to a supraocular. Frontal followed by a pair of large parietals, each one similar in size to the frontal. A single preocular and two postoculars present on either side of head. Temporal formula 3+3 (left), 2+3 (right). Seven supralabials on either side, the 3rd and 4th bordering the eye. First pair of infralabials in contact behind the mental, followed by a pair of large and elongate scales on the throat, and another pair of much smaller scales in contact with the first ventral plate. Eyes moderate in size, their length (front to back of eye) subequal to the distance from tip of snout to anterior part of eye socket.

Dorsal scales strongly keeled, unicarinate, in 24 rows at midbody, the third, fourth and fifth rows laterally (counted from the first row in contact with the ventral plates) are denticulate (serrated), reduced in size and obliquely positioned; vertebral scales not enlarged. There are 227 smooth ventrals, anal plate divided, with 55 pairs of smooth subcaudals. After preservation in ethanol the dorsal colouration is pale brown, with 42 large, cranio-caudally elongate, medium-brown saddles (with darker edges, especially on their anterior and posterior ends) from nape to base of tail (i.e. above vent), most of which are about 1.5 to 2 times longer than wide, and bifurcated at each end with a fairly shallow but distinct notch. Inter-saddle region cream-white, distinctly paler than the rest of the dorsal surface. Lateral markings are in the form of medium-sized, medium-brown spots or blotches, with darker edges, on either side between the saddles. Dark vertebral blotches continue along the tail, but lateral markings here are narrow and elongate. There are extensive dark (brown) markings on the top and sides of the head (including the labials), including a pair of elongated stripes on either side of the frontal, a pair of anteriorly-joined teardrop-shaped markings (blunt anteriorly) on the front of the parietals, and a pair of larger, similar markings on the posterior part of the parietals which extend onto the neck. The saddle on the nape has a spike-like anterior extension which terminates bluntly on the medial-posterior part of the parietals where it is in contact with the larger pair of (posterior) parietal markings. The latter are also narrowly fused with the smaller pair of parietal markings. Venter immaculate cream-white, apart from a few small brown spots and flecks extending from the outer edges of the ventrals to the outer scale rows.

Description of additional Egyptian material. There are six additional specimens (one is a skeleton which we assign to this species) of *D. bazi* from Egypt, mostly with inexact localities, but potentially all collected at or near Fayoum (see discussion below).

ZMB 1861 (at Museum für Naturkunde, Berlin), adult male (left side inverted hemipenis examined), from "Oberaegypten" (= Upper Egypt, a strip of land on either side of the Nile River from about Memphis just above the Nile Delta southwards to Lake Nasser in Nubia, which may include parts of northern Sudan) collected by Karl Richard Lepsius (born 1810, died 10 July 1844), a Prussian Egyptologist who was leader of an expedition to Egypt conducted between 1842 and 1846. This expedition visited places from Memphis in the north traveling along the White and Blue Nile rivers into central Sudan. The specimen, in remarkably good condition (Figs 9–11), appears to be the same snake referred to by Lichtenstein & Von Martens (1856).

ZMB 51552, adult female (left side of tail base dissected open, no hemipenis) from "Oberaegypten" (= Upper Egypt), collected by the French physician Dr Alfred Peney (1817–1861), who was together with K.R. Lepsius in Egypt and Sudan; this specimen was apparently later donated to Albert von Barnim and Robert Hartmann who visited Peney on an expedition to Egypt, Nubia and eastern Sudan between 1860 and



Figure 7. *Dasypeltis bazi*. A: Dorsal and lateral views of the largest known female (BM 97.10.28.575) from Fayoum, Egypt (Photo: M.F. Bates); B: Ventral view of the same specimen (Photo: Natural History Museum, London).



Figure 8. *Dasypeltis bazi*. Dorsal (left), lateral (middle) and ventral (right) views of the head of the largest known female (BM 97.10.28.575) from Fayoum, Egypt. (Photo: Natural History Museum, London)

1861. Barnim and Hartmann are mentioned on the jar label as donors for this specimen to the "Anatomisch-Zoologisches Museum" in Berlin, and the specimen was incorporated into the Zoologisches Museum Berlin in 1888.

ZMB 5865, adult male (inverted hemipenes present, F. Tillack in litt.) from "Aegypten" (= Egypt), purchased from Mr "Keitel"; specimen catalogued around 1867 by W.C.H. Peters as "Rachiodon abyssinicus Dum. Bib.".

NMW 26879–1, adult female (no hemipenial spines in tail, tail distinctly tapered at base) from "Omgebung v. Cairo" (= surroundings of Cairo), donated by Franz Steindachner in January 1874.

NMW 962, mounted adult skeleton with skull (few teeth present), from "Kairo" (= Cairo), donated or collected by Franz Steindachner in 1880, labelled "Dasypeltis scabra".

MNHN 1847, adult male (left side hemipenis everted) from "Egypt", collected by Baron Alphonse Marie Delort Gléon Leopard (1843–1899).

Size: ZMB 1861, male, 455 mm SVL + 79 mm tail length = 534 mm total length; ratio SVL: tail length 5.8, ratio total length: tail length 6.8; ZMB 5865, male, 427 + 78 = 505 mm, ratios 5.5 and 6.5; MNHN 1847, male, 410 + 70 = 480 mm, ratios 5.9 and 6.9; ZMB 51552, female, 503 + 70 = 573 mm, ratios 7.2 and 8.2; NMW 26879–1, female, 461 + 61 = 522 mm, ratios 7.6 and 8.6.

Scalation: All have similar scalation and general appearance to BM 97.10.28.575, except: Nostril on right side of NMW 26879–1 situated in about middle of nasal scale (not in anterior part thereof). All have a pair of internasals (not three) between rostral and paired prefrontals, and these are (individually and in combination) smaller than the prefrontals (smaller but of equal length in ZM 51552). Inter-prefrontal sulcus weakly marked in ZMB 5865 and ZMB 51552. Ratio frontal length: frontal width: 1.54 (ZMB 1861), 1.44 (ZMB 5865) and 1.40 (MNHN 1847) in males; 1.38 (ZMB 51552) and 1.43 (NMW 26879–1) in females; frontal smooth in ZMB 51552, covered by small pimple-like protrusions in MNHN 1847. Frontal slightly shorter than each supraocular in NMW 26879–1. In ZMB 1861 the pair of parietals is fused medially, with only the ends separated. Temporals 2+3 on both sides. In NMW 26879–1 and ZMB 1861 the pupils are clearly vertically elliptical. Midbody scale rows 23 or 24 (NMW 26879–1, ZMB 51552). Reduced, oblique, serrated lateral scale rows: 3 to 5 (MNHN 1847, ZMB 5865) and 3 to 6 (NMW 26879–1, ZMB 1861, ZMB 51552), but all except NMW 26879–1 and ZMB 51552 also have the scales of the second row weakly serrated although not reduced in size like the other serrated rows, nor obliquely oriented. Ventrals in males 219 (ZMB 5865), 229 (ZMB 1861, MNHN 1847); in females 228 (ZMB 51552), 234 (NMW 26879–1). Anal plate undivided in MNHN 1847, ZMB 1861 and ZMB 51552. Subcaudals in males 59 (MNHN 1847, ZMB 1861), 60 (ZMB 5865); in females 50 (NMW 26879–1), 51 (ZMB 51552).

Colour pattern: Basal colour dorsally in MNHN 1847 is grey, not pale brown. Saddles on back 39 (ZMB 5865), 48 (ZMB 1861, ZMB 51552), 49 (MNHN 1847); about 48 in NMW 26879–1 which is largely faded. Along the tail the lateral markings are in the form of small dark spots/blotches in MNHN 1847, NMW 26879–1 and ZMB 1861. Brown forward-pointing V-shaped markings on back of head and nape in MNHN 1847; distinct, backwards-curving, narrow pale band at back of head, bisected by spike-like extension of a dark and mostly blunt V-shaped marking (almost band-like) on nape in ZMB 5865; ZMB 1861 and ZMB 51552 similar to previous specimen but pale band not interrupted, and the latter with a longer and sharper anterior extension of the nape marking.

Description of ZFMK 38415 (*Dasypeltis* cf. *bazi*). Adult male (600 mm total length) from Erkowit, north-eastern Sudan [18º46'N, 37º07'E], collected dead-on-road (head damaged) in Spring 1982 by Gerhard Nikolaus (Fig. 12).

Ventrals 229, subcaudals 67, midbody scale rows 25, supralabials 7 (3rd and 4th enter orbit) on either side of head, one preocular on either side, two postoculars on either side, 3+4 temporals on either side, 48 pattern cycles. Photographs (e.g. Fig. 12) of the specimen show a dorsal pattern similar to that of BM 97.10.28.575; venter also similar, but yellowish-cream; dorsal and ventral scales, including their arrangement on the throat, similar to BM 97.10.28.575; reduced, oblique, serrated lateral scale rows 3 to 6, but second row (scales similar in size to central dorsals) weakly serrated although not reduced or oblique; frontal similar in shape to that of BM 97.10.28.575, smooth except for 1–2 rows of pits laterally, of similar length to a supraocular, but slightly larger than each of the parietals.

Size. Largest male ZMB 1861 ("Upper Egypt") 455 + 79 = 534 mm [The largest specimen identified as a male by Saleh & Sarhan 2016 measured 482 + 75 = 557 mm, but its sex requires confirmation—see below]. Largest female BM 97.10.28.575 (Fayoum, Egypt) 602 + 90 = 692 mm.



Figure 9. *Dasypeltis bazi*. Dorsal (A) and ventral (B) views of a male (ZMB 1861) from 'Upper Egypt'. (Photos: F. Tillack)

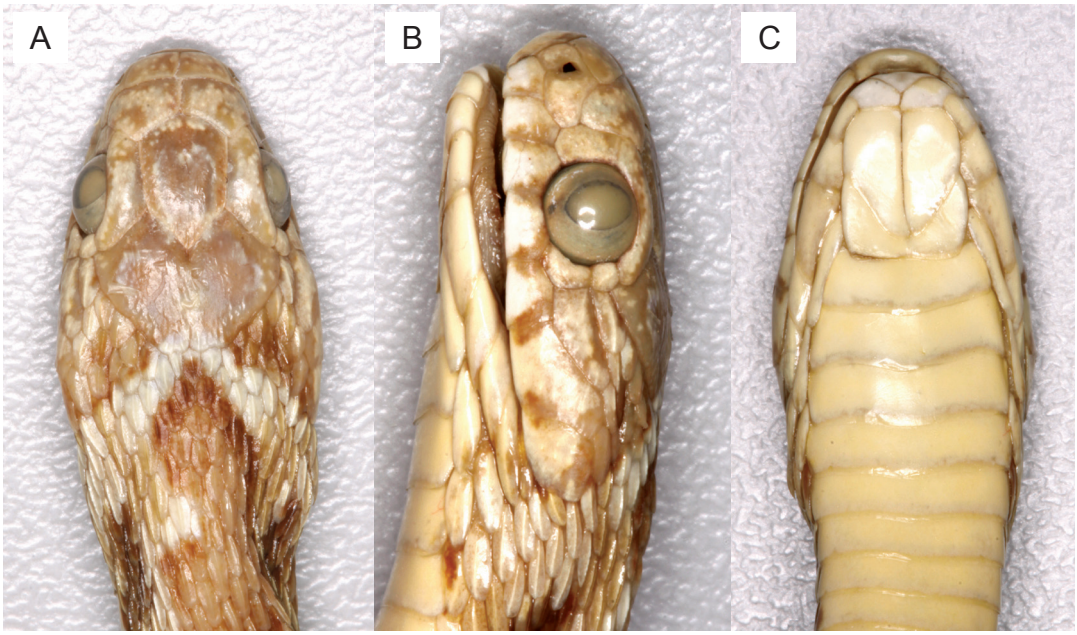


Figure 10. *Dasypeltis bazi*. Dorsal (left), lateral (middle) and ventral (right) views of the head of a male (ZMB 1861) from 'Upper Egypt'. (Photos: F. Tillack)



Figure 11. Dorsal views of *Dasypeltis loveridgei* **comb. nov.** ['6N' colour pattern of Gans 1959; specimen also has 6 supralabials on either side of head, with 2nd and 3rd in contact with orbital] (female, ZMB 33670a, top) from Otjimbingwe, Namibia, and *Dasypeltis bazi* (male, ZMB 1861, below) from 'Upper Egypt' showing the general similarity in colour pattern. (Photo: M.F. Bates)

Distribution. *Dasypeltis bazi* appears to be restricted to an area of about 300 km^2 along the El Buts channel (near the village of Ibshwai) in the Fayoum Depression, which is situated about 100 km south-west of Cairo and 40 km west of the Nile River, at elevations of 32–52 m below sea level (Saleh & Sarhan 2016). Apart from sites in the Fayoum, there are records of this species from only one other specific locality in Egypt, namely Cairo (see discussion below), but its occurrence there was not confirmed by Saleh & Sarhan (2016). Cairo is now a densely populated area, and if these records are accurate, the species may have been extirpated there. Although it has been suggested that it occurs elsewhere in Egypt along the Nile River (e.g. Anderson 1898; Baha El Din 2006), this was also not confirmed by Saleh & Sarhan (2016) who investigated potential habitats in various parts of the country.

Historical records. Based on the literature, *D. bazi* is a poorly known species. The first record of an egg-eating snake from Egypt is contained in Lichtenstein & Von Martens' (1856) list of the reptiles and amphibians in the collection of the Royal University of Berlin. They recorded a specimen of *Rachiodon abyssinicus* (lapsus for *abyssinus*) from "Oberaegypten" (= Upper Egypt). Jan (1863) later recorded *Rachiodon scaber* (=



Figure 12. *Dasypeltis* cf. *bazi*. Dorsal view of the anterior part of the body of a specimen (ZFMK 38415) from Erkowit, Sudan. (Photo: W. Böhme)

D. scabra) from Cairo with reference to a specimen in the Museo Civico di Storia Naturale di Milano. However, the latter specimen was not illustrated, nor were any morphological data provided, and it is no longer to be found at the museum in Milan (S. Scali in litt. 26 September 2014). No other mention has ever been made confirming the presence of this species in Cairo. In an account of his travels in Egypt, Gasco (1876) recorded eight specimens of *Dasypeltis scaber* (= *D. scabra*) from Middle Egypt (= Nile Valley between the Nile Delta and Asyut or Qena Bend), collected in 1873–1874. The title of Gasco's (1876) paper, the second of two reports on his travels in Egypt, actually refers to the oasis of Fayoum and excursions in the vicinity of Cairo, although it also alludes to hunting on Lake Menzala on the Nile Delta. Anderson (1896: 114) noted that "Count Peracca has been so good as to ascertain from Prof. Costa that two specimens brought back from Egypt by Prof. P. Panceri, the companion of Gasco, one a skeleton and the other in alcohol, are preserved in the Naples Museum. Panceri (1878) did in fact refer to two such specimens (number 3219, alcohol specimen; 3520, skeleton and teeth), as *Rachiodon scaber*, in his published catalogue of the collection in the Comparative Anatomy section of Università degli Studi di Napoli Federico II. It is not known whether the two specimens from Cairo in the Vienna collection, as mentioned above, were a part of the series alluded to by Gasco and Panceri, but the dates involved do coincide.

In *Zoology of Egypt*, Anderson (1898: 279) wrote: "After much correspondence with those in Egypt who have been assisting me in my researches, at last, through the efforts of Mr. A. R. Birdwood, after I had almost given up all hope of finding this species, I received the specimen herein recorded alive and am thus enabled to give a figure of it from life." According to Anderson (1898: 279) the specimen was collected in "the Fayum" (variously spelled as "Faiyum", "Fayoum", "Al Fayyum" and "El Faiyūm"), which probably refers to the oasis in general rather than the city of Fayoum itself; the area is also referred to as the Fayoum Depression. Anderson (1898, table) was of the opinion that *'D. scabra'* also occurred in the "Valley of White Nile". In fact, Anderson's (1898: 279) comment about the "wide distribution" of *'D. scabra'* and his suggestion that the species occurs "northwards along the valley of the Nile to within about 140 miles [= 225 km] of the Mediterranean [Sea]" is somewhat misleading because apart from the 'Nil Blanc' record (a syntype of *R. abyssinus*; see below) of *D. scabra* far to the south, there does not appear to have been (nor is there now) any other specific documented evidence to suggest that the Fayoum population was in fact contiguous with other *Dasypeltis* populations. For his Fayoum specimen Anderson (1898) provided scalation and size data, line drawings of the head and anterior part of the body, and an illustration (painting in colour) of the snake in the process of swallowing a pigeon's egg.

Anderson's specimen (BM 97.10.28.575) was later examined by Gans (1959) who remarked on the uniqueness of its dorsal pattern. Gans (1959) also examined three more specimens (also listed and examined here) from Egypt and "Upper Egypt" (ZMB 1861, this is probably the snake mentioned by Lichtenstein & Von Martens 1856). One additional specimen (ZMB 51552) from "Upper Egypt" recorded here can be added to the list of old museum specimens. These non-specific localities could conceivably refer to specimens collected at other localities apart from the Fayoum Depression, perhaps along the Nile River itself or possibly in one of the country's other oases.

Rehak & Osborn (1988: 275) later recorded a specimen "collected by natives in Faiyum, September 1982" and noted that it "seems extremely rare in Egypt". Saleh (1997) subsequently provided a photograph of a specimen he collected in Fayoum, again illustrating the much-elongated saddles with spots/blotches on the flanks. Although Saleh (1997) claimed that his specimen from Fayoum was the first to be collected in almost a century, Rehak & Osborn (1988) had in fact documented a specimen collected there about 90 years after Anderson's (1898) report. Baha El Din (2006) was of the opinion that the only certain locality for '*D. scabra*' in Egypt was the Fayoum Depression, but it was also likely to occur in parts of the Nile Valley. He

added that Gasco's (1876) locality of "Middle Egypt" may be in reference to Fayoum, which is located within the northern parts of this region. Baha El Din (2006) also noted that animal collectors from Abu Rawash (30°01'55"N, 31°04'30"E; near the southern edge of the Nile Delta, about 80 km north-east of Fayoum) claimed to find specimens at pigeon breeding houses. If it does in fact occur in the vicinity of Abu Rawash, this will be the most northerly known locality for *D. bazi* and the most north-easterly extent of the range of the genus *Dasypeltis*.

The new species was therefore, prior to 2016, known to science from only 16 specimens recorded over a period of about 170 years (first specimen collected by Karl Lepsius in about 1844, see above). Saleh & Sarhan (2016) reported in detail on eight specimens collected at Fayoum in the period 1995–2015 (presumably including Saleh's [1997] specimen) and also mentioned another 17 specimens collected there since 1995 but released. There are no other records of egg-eaters from Egypt. Venchi & Sindaco's (2006) checklist of the reptiles of the Mediterranean region did not add any additional records of *Dasypeltis*. Watkins-Colwell *et al*. (2010) reported on reptiles recorded during three Yale University expeditions to Egypt in the first half of the 1960s, which included several sites along the Nile River and the Fayoum Oasis, but no *Dasypeltis* were recorded. Ibrahim (2013) recently reported on the herpetofauna of the Suez Canal Zone, surveyed between 1999 and 2012. Despite the fact that habitat changes in the area at and near the canal (which includes associated freshwater irrigation canals) have allowed 'invasive' species to expand their ranges, and that an extensive web of irrigation canals has provided passage for several species to move from the Nile River to the Suez Canal, no specimens of *Dasypeltis* were recorded. If *Dasypeltis* occurred in the Nile Delta itself, for which there is no actual evidence, this too would allow easy access to the Suez Canal.

Natural history. Saleh (1997: 146) collected a specimen from Fayoum "in an area with dense wild vegetation, not far from houses at the edge of cultivated land". Saleh & Sarhan (2016) later provided a detailed description of the habitat of the Fayoum population. All specimens were collected along the El Buts channel, a relict section of the Fayoum ancient natural drainage system. This habitat comprises a fairly deep gorge in the thick and silty Nilotic deposits in the central region of Fayoum Depression. Terraces occupy the sides where small plots of crops are grown (Saleh & Sarhan 2016). Anderson (1898: 280) noted: "On Plate XXXIX. it [his Fayoum snake—perhaps depicted while in captivity] is represented in the act of swallowing a pigeon's egg, but fowls' eggs are even within its capacity." Saleh & Sarhan (2016) later determined that several bird species that produce suitably small eggs occur in sympatry with these snakes at Fayoum. In addition, they noted that traditional pigeon towers and chicken hatcheries also provide a source of eggs. Based on the presence of three large eggs observed in the abdomen of BM 97.10.28.575, this species is, like other congeners for which data is available (e.g. Broadley 1990; Spawls *et al*. 2002), oviparous.

Mimicry. *Dasypeltis bazi* has a dorsal colour pattern similar to the saw-scaled viper *Echis pyramidum* Geoffroy Saint-Hilaire (Schleish *et al*. 1996; see photographs in Dobiey & Vogel 2007) which it appears to mimic. Like *Echis* Merrem, it has similar serrated lateral dorsals which it may engage for defensive display by coiling and rubbing together to produce a rasping sound (scale stridulation, Schleish *et al*. 1996). The type series of *Echis pyramidum lucidus* Cherlin, 1990 was collected in the Fayoum Oasis (Cherlin 1990). A specimen of the latter subspecies from Biskra in Algeria (www.megasphera.cz/african-venomoussnakes/, accessed 11 June 2014) has a dorsal pattern almost identical to *D. bazi* (e.g. Fig. 7A). *Echis pyramidum* was also collected in the Fayoum Oasis during the Yale University Expedition (Watkins-Colwell *et al*. 2010). It is one of several species of snakes that occur in the same habitat as *D. bazi* (see Saleh & Sarhan 2016). Anderson (1898) suggested that the similarity of the Fayoum snake to *Echis carinatus* (Schneider) (= ? *E. pyramidum*) might explain why this egg-eater is so seldom observed or recognised, but Saleh (1997) noted that the Fayoum *Dasypeltis* that he obtained was not particularly similar to this viper. Gans (1961, Pl. 1) illustrated the similarity between these two species using ZMB 5865 ('Egypt') and a specimen of *'E. c. carinatus'* (CAS 38722) from Cairo.

Biogeography. *Dasypeltis bazi* appears to have a relict distribution, the result of a once extensive African savannah being reduced and fragmented following dessication of the region during the Holocene (Kuper & Kröpelin 2006). This is discussed in more detail under 'Discussion'.

Conservation. The Fayoum Oasis is a depression or basin linked to the Nile River by a 24-km-long canal called the Bahr Yussef. In prehistory the oasis contained the large freshwater Lake Moeris, which received water when the Nile was in high flood, but it is now a much smaller saltwater lake referred to as Birket Qaran (= Qaroun Lake). In 2300 B.C.E. the natural waterway from the Nile to the lake was widened and deepened to control flooding, regulate water levels during the dry season, and provide the area with irrigation for crops. Unlike other oases in Egypt, which have spring water sources, cultivated land in the Fayoum is formed by fertile mud from the Nile transported there via the Bahr Yussef. The scarcity of *Dasypeltis* records from the Fayoum is perhaps not too surprising considering the high levels of human activity (e.g. crops and housing) in the region. Saleh & Sarhan (2016: 37) noted: "Through centuries of human occupation and intensive agriculture, the Faiyum natural drainage system was fundamentally modified and almost totally obliterated." Proposed tourism deve-

lopments will impose further threats to natural habitat in the area (Khalifa & El-Khateeb 2011).

Despite the benefits provided to the human population of Egypt by the building of the Aswan High Dam, which created Lake Nasser, this dam has permanently altered the ecology of the Nile River region, with some areas now under water and others changed from desert into cultivated fields or wetlands (Watkins-Colwell *et al*. 2010). Although the establishment of vegetated areas has resulted in some reptile species extending their ranges, e.g. inland from the Nile Delta (Baha El Din 2006; Watkins-Colwell *et al*. 2010), this does not appear to have benefited *Dasypeltis*. Since the construction of the dam and the resultant low flow rates, the Nile Delta no longer floods and has been converted into an intensive agricultural area (Van As *et al*. 2012). In the past specimens may have been introduced downstream—even from as far away as Sudan—during floods, on rafts of floating vegetation, but this no longer occurs. Although the delta is still an important area for a number of animal species, including large numbers of migratory birds (Mockrin & Thieme undated), no egg-eating snakes have been recorded there.

Considering the scarcity of records as indicated above, *D. bazi* may be a naturally rare species. Anderson (1898: 280) noted: "It seems remarkable that a snake of this kind, so specialized as regards its food-supply, should have been unknown to the ancient Egyptians. There is no evidence, so far as I have been able to discover, that they were acquainted with it, unless the figure, said to occur on the monuments, of a hawk-headed serpent with an egg in its mouth may have been derived from some knowledge of it." The Egyptian god Cneph is in fact occasionally represented as a serpent with an egg in its mouth (Deane 1833). Anderson (1898) also noted that he had made a special effort to obtain specimens, yet he only eventually secured a single snake, from Fayoum. Rehak & Osborn (1988) also recorded a single specimen and considered *Dasypeltis* as extremely rare in Egypt. This specimen was apparently collected by a Fayoum villager in September 1982 but was purchased from an animal dealer in Cairo (see Saleh & Sarhan 2016). Saleh (1997) and Baha El Din (2006) classified the Egyptian population of *'D. scabra'* as regionally Critically Endangered. Baha El Din (2006: 234) noted: "The impact of the large-scale ecological changes that took place in Fayoum since the beginning of last century is unknown, but probably reduced available habitat. The species is threatened by over-collection by professional animal collectors [in Egypt], who target the species." This suggestion about over-collecting appears to be based on his comment about animal collectors from Abu Rawash. Saleh & Sarhan (2016: 43) concluded that *D. bazi* was "saved from certain extinction by the development [since the mid-Holocene] of artificial breeding of pigeons and chickens in Faiyum" which provided a source of eggs. The Erkowit specimen may represent an isolated relict population of *D. bazi* in north-eastern Sudan. This population may in the past have been part of a more widespread population of *D. scabra* that became isolated following aridification of the Sahara, resulting in the evolution of a new species, *D. bazi*. The Egyptian and Erkowit populations themselves may then have become isolated, accounting for their large current-day separation. Habitat at Erkowit has been negatively affected by the impacts of a human population that has grown considerably in the last 60-odd years, with associated removal of wood, pressure from livestock grazing and browsing, and a warming climate (Vetaas *et al*. 2012). This environment has suffered continuous change from semi-evergreen woodland to open shrubland similar to that of the surrounding desert, and the area can no longer be regarded as a 'mist oasis' dominated by Afromontane and Mediterranean plant species (Vetaas *et al*. 2012). Therefore, there is some uncertainty about the conservation status of the Erkowit population.

Based on a global evaluation of its conservation status using IUCN (2012, 2016) criteria—and considering the Fayoum Oasis population as the only surviving population of this species (see above)—it is evident that *D. bazi* should be classified globally as Endangered [B1ab(i, ii, iii)] based on its small geographical range (known from an area of 300 km2 [Saleh & Sarhan 2016], extent of occurrence <5000 km2 [the entire oasis is about a third of this size]) which is severely fragmented, with an inferred continuing decline in its extent of occurrence, area of occupancy and quality of habitat (see Baha El Din 2006; Khalifa & El-Khateeb 2011; Saleh & Sarhan 2016).

Remarks. Although Anderson (1898) did not identify his Fayoum snake by a museum accession number, he did mention that reptile and amphibian specimens collected and discussed by him were lodged in the British Museum (now in the Natural History Museum, London), the Museum of Egyptian Government School of Medicine (Cairo) and a few museums on the European mainland. Baha El Din (2006: 233) actually identified Anderson's specimen as "BMNH 97.10.28.575". Based on the illustrations, measurements and scalation details provided by Anderson for his Fayoum snake, it is apparent (see below) that his specimen is indeed the same snake preserved at the Natural History Museum in London and labelled as BM 97.10.28.575, which was examined by both Gans (1959, see Pl. 6, Fig. 1) and the first author. Firstly, the body shape, and shape and proportion of dorsal markings in Anderson's (1898) Pl. 34, Fig. 3 are remarkably similar to the specimen examined (Figs 7 & 8), including the first saddle on the nape with its narrow finger-like forward projection. Secondly, measurements of SVL and tail length by Anderson (602 + 95 mm) and Gans (602 + 90) are similar. Thirdly, there are general similarities with regard to scalation. Anderson's ventral count of 230 is similar to the count of 227 determined by both

Gans and the first author. The slight difference would be accounted for if Anderson included in his count the three pairs of scales between mental and first ventral. Some of Anderson's scale counts are in exact agreement with those obtained by Gans and this author: 24 midbody scale rows, one preocular and two postoculars. Anderson's subcaudal count of 49 is slightly lower than the 54 counted by Gans and the 55 counted for the present study. However, because subcaudals in *Dasypeltis* are paired—and these paired scales are not always clearly aligned—it is possible that Anderson under-counted, thus minimising this count. Also, while Anderson recorded eight supralabials with 4th and 5th entering the orbit, both Gans and the first author recorded only seven supralabials with 3rd and 4th entering the orbit. However, an examination of Anderson's (1898) Pl. 34, Fig. 3, representing a lateral view of the right side of the head and neck, clearly shows seven supralabials with the 3rd and 4th entering the orbit. It seems that Anderson may have inadvertently or erroneously included the rostral in his count, which would have created the impression that the '4th' and '5th' supralabials entered the orbit. Anderson provided a temporal formula of 3+3, while Gans recorded 2+3, but the first author observed 3+3 on the left side of the head and 2+3 on the right.

A few inaccuracies were noted in Saleh & Sarhan's (2016) diagnosis of *D. bazi*. Firstly, these authors state that in *D. bazi* the frontal shield is longer than wide, but as long as wide in other species of *Dasypeltis*. In fact the frontal is longer than wide in most if not all congeners (e.g. Gans 1959; Broadley 1990; Trape & Mané 2006; Trape *et al*. 2012; this paper). Also, the temporal arrangement of 2+3 (two anterior and three posterior temporals on either side of the head) is common in the genus and the norm for several species (Gans 1959; Broadley 1990; this paper); while one preocular on either side of the head is the norm in all species, even though there are occasionally two or three such scales in some species (Gans 1959; this paper). Elsewhere in their paper Saleh & Sarhan (2016) recorded low numbers of longitudinal scale rows at midbody (20–21, one specimen with 22). Egyptian specimens of *D. bazi* examined for the present study had counts of 23–24. Saleh & Sarhan (2016) also counted 'anterior' and 'posterior' longitudinal scale rows, and their 'anterior' scale row counts (presumably counted halfway between tip of snout and midbody) of 21–25 were closer to the values obtained in the present study. It is possible that they did not use the same method for counting these scale rows as other authors, especially that proposed by Gans (1959) and used in this study, and therefore their comparisons with other species are untenable. Saleh & Sarhan (2016) added to the confusion when comparing 'dorsal scale rows' between species by using the total range of anterior, midbody and posterior scale row counts for *D. bazi* (i.e. '18–24'; but 18–25 in their Table III) and comparing this with what is almost certainly only midbody scale rows recorded by other authors for other species. Lastly, a specimen (AUZC-R12006) identified as a male by Saleh & Sarhan (2016) has a very high ventral count of 250 (and low subcaudal count of 55), and may be a female; the next highest ventral count for a male *D. bazi* is 229 (see above).

Dasypeltis taylori Bates & Broadley **sp. nov.**
Taylor's Egg-eater
Figs 13–14

Dasypeltis scabra var. *Medici* (not Bianconi) Mocquard, 1888: 131 ('Comalis' = Djibouti).
Dasypeltis scabra (not Linnaeus) ? Scortecci, 1930: 213 (Assab, Eritrea) (material not examined); Gans, 1959: 141 (part), Pl. VI, Fig. 6 & Pl. VII, Fig. 1; Balletto, 1968: 268 (part); Lanza, 1983: 223 (part), 1990: 436 (part); Ineich, 1999: 35 (Djibouti).
Dasypeltis scaber (not Linnaeus) Parker, 1949: 66 (Haud, Ogo and Hargeisa, Somalia).
Dasypeltis "scabra" Göthel, 2015a: 19 (part) & 2015h: 86 (part).

Holotype. BM 1949.2.2.2 (at Natural History Museum, London), a subadult male (Gans 1959) from Haud [former British Somaliland, 08°20'N, 46°00'E at 2100 ft = 640 m] in northern Somalia, collected by Colonel R.H.R. Taylor on 20 April 1932 (Fig. 13).

Paratypes. Seven specimens: SOMALIA (Somaliland). Allotype. BM 1949.2.2.3 (at Natural History Museum, London), a subadult female (Gans 1959) with the same data as the holotype, but collected on 1 May 1932 (Gans 1959, Pl. VI, Fig. 6); BM 1949.2.2.1 (subadult male) with the same data as the holotype; BM 1949.2.2.4, adult female from Hargeisa District [9°35'N, 44°05'E at 4000 ft = 1220 m a.s.l.] collected 29 May 1932; BM 1992.501, male from 2.5 km WSW of Hargeisa [09°34'N, 44°03'E at 1275 m a.s.l.] collected 29 March 1992 by M.R.K. Lambert; BM 1949.2.2.5, adult male from Ogo [10°10'N, 42°50'E at 4500 ft = 1370 m a.s.l.] collected 6 August 1933; BM 1951.1.7.69, skin of a male from Garadak [09°29'N, 46°18'E at about 1100 m a.s.l.]. DJIBOUTI. MNHN 84–707, adult female from 'Comalis' [= Djibouti] (Fig. 14).

Diagnosis. Assigned to the genus *Dasypeltis* on account of its slender form, possession of (usually 3–4) rows of reduced, oblique, keeled and serrated lateral scales (little or no serration in *D. inornata*) and head barely distinct from the neck (moderately distinct in *D. fasciata*). Distinguished from other congeners by a combination of the following characters: Colour pattern usually consists of: large, usually closely-spaced, square to slightly rectangular saddles, separated by narrow, usually sharply defined, white crossbars (a variety of '5N', Gans 1959, Pl. VI, Fig. 6); low numbers of pattern cycles 44–59 (≥62 in patterned species/populations of *D. palmarum*, *D. fasciata*, *D. abyssina*, *D. atra*, *D. arabica* **sp. nov.**; *D. inornatus* always uniform brown; *D. gansi* uniform or weakly marked);

flanks decorated with dark vertical bars (spots, blotches or squarish in *D. bazi*, *D. loveridgei* **comb. nov.** and some populations of *D. scabra*); and venter immaculate cream-white apart from a few dark markings at the edges (extensive dark markings in *D. abyssina* and many *D. scabra*); Frontal shield extensively pitted, States 3 & 4 (usually marginally pitted in most other species except *D. medici*, and some populations of *D. scabra* [especially in the south of its range] and *D. loveridgei* **comb. nov.**, which are similar); Inter-prefrontal sulcus usually moderately depressed (usually weakly marked in most other species, but moderate to well marked in *D. arabica* **sp. nov.**, weakly to moderately marked in *D. bazi*, and variable in *D. scabra* [often well marked in the south of its range]); Low numbers of ventrals: 196–216 in males (≥219 in: *D. arabica* **sp. nov.** 236–244, *D. abyssina* 226–247, *D. crucifera* 226, *D. gansi* 221–240, *D. latericia* 219–243, mostly lower than *D. medici* 215–254 and *D. bazi* 213–229), 208–222 in females (lower than *D. abyssina* 241–271, *D. arabica* **sp. nov.** 239–254, *D. gansi* 235–259, *D. latericia* 234–262, *D. crucifera* **sp. nov.** 231–247, *D. fasciata* 225–260, *D. parascabra* 224–237; mostly lower than *D. palmarum* 220–248 and *D. bazi* 215, 219, 224–234); Low numbers of subcaudals: 55–68 in males (lower than *D. inornata* 81–92, *D. fasciata* 71–90, *D. medici* 69–109; mostly lower than *D. gansi* 68–83, *D. palmarum* 68–77, *D. parascabra* 67–74, *D. latericia* 66–86), 44–52 in females (lower than *D. inornata* 69–84, *D. fasciata* 64–84, *D. parascabra* 57–64, *D. palmarum* 62–77, *D. medici* 61–90, *D. latericia* 59–72, *D. gansi* 59–73, *D. arabica* **sp. nov.** 53–61); Tail of moderate length: SVL/tail length 4.9–5.7 in males, 7.0–8.2 in females (in study area mostly greater than: *D. medici* 3.5–4.7 males, 4.5–5.7 females; *D. fasciata* 4.7–5.2 males, 4.8–6.4 females; see also Gans 1959); Nasal divided below the nostril (undivided in *D. sahelensis* and *D. parascabra*); Postoculars 2 on either side of head (often one, especially in western populations, of *D. atra*); Supralabials usually 7 (3rd and 4th enter orbit) on either side of head (usually 6[2,3] in *D. loveridgei* **comb. nov.**).

The new species is most similar to *D. scabra*, which usually has higher numbers of pattern cycles on the back—in surrounding countries/regions only two specimens, from southern Somalia (50–51 cycles) and a single snake from Sudan (54 cycles), have similarly low counts (Appendix 1).

Description of holotype. The holotype (BM 1949.2.2.2) is a subadult male with a total length of 202 mm, snout-vent length 172 mm, tail length 30 mm; ratio SVL: tail length 5.7, ratio total length: tail length 6.7.

Head small and barely distinct from the neck; snout rounded. Elongate nasal semi-divided (divided below the nostril), no loreal. Paired prefrontals much larger than paired internasals (individually and in combination). Inter-prefrontal sulcus moderately marked. Frontal large, slightly wider anteriorly, 1.51 times longer than broad, and fully pitted (State 4), slightly longer than each supraocular, and followed behind by a pair of large parietals each of which is larger than the frontal. There is a single preocular and two postoculars. Temporals 2+3. Seven supralabials, the 3rd and 4th bordering the eye. First pair of infralabials in contact behind the mental, followed by a pair of large and elongate chin shields, and another pair of much smaller scales in contact with the first ventral plate. Eyes moderate in size (with vertically elliptical pupils), their length subequal to the distance from tip of snout to anterior part of eye socket.

Dorsal scales strongly keeled, unicarinate, in 24 longitudinal rows at midbody, the third, fourth and fifth rows denticulate, reduced and (except for the 3rd row) obliquely placed. Vertebral scale row not enlarged. There are 198 smooth ventrals, the anal is entire and there are 60 pairs of smooth subcaudals. After preservation in ethanol the dorsal colouration is grey with 50 squarish dark dorsal saddles (also pattern cycles) between the nape and the base of the tail, separated by sharply defined white crossbars. Similarly dark, mostly elongate and wavy, lateral bars are linked to these crossbars on either side. Back of head with a distinct forward-pointing chevron; saddle on nape weakly forked posteriorly with a rectangular anterior prolongation. Venter immaculate cream-white apart from a few small brown spots on the outer edges of the ventrals.

Variation in paratypes (including allotype, as indicated). The seven paratypes comprise four males and three females. The largest male (BM 1949.2.2.5) measures 501 (408 + 83) mm, SVL/tail length ratio 4.9, total length/tail length ratio 5.9; one other male with measurements: BM 1949.2.2.1 (188 + 34 mm, ratios 5.5 and 6.5). Largest female (MNHN 84–707) measures 545 (477 + 68 mm, ratios 7.0 and 8.0); other females: BM 1949.2.2.4 (530 mm SVL), BM 1949.2.2.3 (189 + 23 mm, ratios 8.2 and 9.2; allotype). The paratypes have similar scalation and general appearance to the holotype, except: Snout less rounded in BM 1949.2.2.4. Inter-prefrontal sulcus weakly marked in BM 1949.2.2.1 and 1949.2.2.5. Frontal distinctly wider anteriorly in BM 1949.2.2.4, BM 1951.1.7.69, BM 1992.501 and MNHN 84–707; 1.25 to 1.53 times as long as wide; largely (not fully) pitted (State 3) in BM 1951.1.7.69 and MNHN 84–707; and about as long as (not longer than) each supraocular in BM 1949.2.2.5. Frontal about the same size as each of the parietals in BM 1992.501. One postocular (not two) on both sides of head in BM 1949.2.2.4, and one on right side in BM 1949.2.2.3 (allotype). Temporals 1+3 in BM 1949.2.2.4 and 2+2 in BM 1951.1.7.69. Six supralabials, the 2nd and 3rd bordering the eye, in BM 1949.2.2.1. In BM 1949.2.2.4 the pair of posterior chin shields is largely separated by a more-or-less quadrangular supranumerary scale which is in contact with the first ventral plate. Length of eye almost equal to distance from tip of snout to anterior part of eye socket in BM 1949.2.2.1 and BM 1951.1.7.69, distinct-



Figure 13. *Dasypeltis taylori* **sp. nov.** Body and head views of the holotype (BM 1949.2.2.2) from Haud, Somaliland. (Photos: Natural History Museum, London)

ly smaller than snout-eye distance in BM 1949.2.2.4, 1949.2.2.5 and MNHN 84–707. Midbody scale rows 23 in two specimens and 25 in two others (see Appendix 1); about 24 in BM 1992.501 (difficult to count) which has the third and fourth, and in some areas also the fifth, rows denticulate and oblique. Dorsal scales of the anal region distinctly denticulate in BM 1949.2.2.4 and MNHN 84–707, feebly denticulate in BM 1949.2.2.1, 1949.2.2.3 (allotype) and 1951.1.7.69. Ventrals 196–216 in males, 208–222 in females (see Appendix 1). Subcaudals 55–68 in males, 44–52 in females (tail truncated in BM 1992.501, male; and BM 1949.2.2.4, female) (see Appendix 1). Dorsal pattern cycles 44–59 (see Appendix 1). In a flat skin (BM 1951.1.7.69) the two halves of the vertebral saddles are not synchronised, forming an oblique pattern [Gans, 1959, Pl. VII, Fig. 1, erroneously given as 'BM 1951–1–7–59']; and several dorsal saddles are oblique in BM 1949.2.2.1. Dorsal colouration (excluding dark saddles and lateral bars) in preservative mostly rufous brown in BM 1949.2.2.3 (allotype), a mixture of rufous brown and grey in BM 1949.2.2.1 and 1949.2.2.5, and pale brown in BM 1949.2.2.4. Several lateral bars non-elongate and irregular in shape in BM 1949.2.2.5. Pale crossbars between saddles in BM 1949.2.2.4, 1949.2.2.5, 1951.1.7.69 and 1992.501 are thicker and less sharply defined than in the holotype [and allotype BM 1949.2.2.3, as illustrated in Gans 1959, Pl. VI, Fig. 6]. Saddles are mostly rectangular and somewhat elongate in BM 1949.2.2.5 and 1992.501, and in BM 1949.2.2.4 they are rectangular at midbody but vary considerably in shape elsewhere, from slightly transversely enlarged and oblique, to oval and even '5I'-like (see Gans 1959). In BM 1992.501 several lateral bars are in contact with the saddles. Back of head with anterior part of chevron somewhat fragmented in BM 1949.2.2.1 and MNHN 84–707, and bulbous in BM 1992.501; top of head somewhat faded in BM 1949.2.2.3 (allotype); saddle on nape deeply forked posteriorly in BM 1949.2.2.4 & 5, and always with a sharp anterior prolongation. Venter cream with large grey spots laterally, and smaller grey markings elsewhere, in BM 1949.2.2.5; and whitish with 1–2 longitudinal rows of brown spots at the edges of the plates in BM 1992.501 and MNHN 84–707. No live specimens or photographic images of living snakes of this species are known to the authors.

Size. Largest male (BM 1949.2.2.5 – Ogo, Somalia) 408 + 83 = 501 mm. Largest female (MNHN 84–707 – Djibouti) 477 + 68 = 545 mm.

Etymology. The name of this new species is a patronym honouring Colonel R.H.R. Taylor, who collected

about half of the type series while surveying the border between British Somaliland and Ethiopia in 1932–3.

Habitat. Grasslands to *Vachellia–Commiphora* bushland from 640 m to 1370 m (Figs 15 & 16). BM 1992.501 from 2.5 km WSW of Hargeisa was found on a limestone hillside (1275 m) with *Vachellia etbaica* Schweinfurth bushes.

Distribution. *Dasypeltis taylori* **sp. nov.** has been recorded only from the arid interior of northern Somalia (Somaliland) (Figs 15 & 16) and in adjacent Djibouti (Fig. 3).



Figure 14. *Dasypeltis taylori* **sp. nov.** Paratype (MNHN 1884.0707) from Djibouti. (Photo: I. Ineich)

Mimicry. This species appears to mimic the saw-scaled viper *Echis pyramidum* Geoffroy Saint-Hilaire (see photographs in Dobiey & Vogel 2007 and Mazuch 2013). The racer *Platyceps taylori* (Parker), in the Borama area of Somaliland, has a dorsal pattern (see photograph in Mazuch 2013) remarkably similar to that of *D. taylori* **sp. nov.**

Biogeography. *Dasypeltis taylori* **sp. nov.** is separated from *D. scabra* populations in southern Somalia by the arid Ogaden plateau of eastern Ethiopia, an area from which no *Dasypeltis* have been recorded (e.g. Mazuch 2013). The highlands of east-central Ethiopia are occupied by *D. atra*, and those of north-western Ethiopia and southern Eritrea by *D. abyssina*. *Dasypeltis taylori* **sp. nov.** may therefore represent a relictual population of a once widespread *D. scabra* ancestor. Schätti & Ineich (2004) have discussed the radiation of the snake genus *Platyceps* Blyth, which is even more speciose than *Dasypeltis* in the Horn of Africa. Similar diversification occurs in the terrapin *Pelomedusa subrufa* Bonnaterre species complex, where *P. somalica* Petzold *et al*. 2014 occurs in northern Somalia, *P. gehafie* (Rüppell) in Eritrea and eastern Sudan, and *P. barbata* Petzold *et al*. 2014 in Saudi Arabia and Yemen (Petzold *et al*. 2014). *Typhlops calabressi* Gans & Laurent has a very similar distribution to *D. taylori* **sp. nov.** (Broadley & Wallach 2009).

Conservation. Using IUCN (2012, 2016) criteria, this species appears to be widespread and should be regarded as Least Concern.

Remarks. Scortecci (1930) recorded *"D. scabra"* from Assab on the Red Sea coast of southern Eritrea. This specimen may be *D. taylori* **sp. nov.**, but as no further details are available and the specimen cannot be found, we desist from assigning it species status and exclude the record from our map.

***Dasypeltis atra* Sternfeld**
Montane Egg-eater
Figs 17A–M & 18

Dasypeltis lineolata Peters, 1878: 206. Type locality: Kitui, Kenya, holotype ZMB 9224.

Dasypeltis palmarum (not Leach) Fischer, 1884a: 12 (Arusha, Tanzania).

Dasypeltis scabra var. F, Boulenger, 1894: 356 (part, Uganda); Angel, 1925: 34 (Nairobi).

Dasypeltis palmarum ? (not Leach) Stejneger, 1894: 733 (Mount Kilimanjaro, Tanzania).

Dasypeltis scabra (not Linnaeus) Boulenger, 1896: 553 (Shoa, Ethiopia); Sternfeld, 1908: 240, 332 (Lake Haramaya, Ethiopia); Roux, 1910: 99 (Bukoba, Tanzania); Boulenger, 1909: 303 (Bugala, Sesse Islands, Uganda); Peracca, 1909: 173 (Fort Portal, Ruwenzori Mtns); Boulenger, 1911: 5 (Bussu, Uganda) & 1912: 332 (Addis Ababa); Loveridge, 1916: 79 (part, Fort Hall); Lönnberg, 1922: 7 (part, east slopes of Mount Elgon, Kenya); Loveridge, 1929: 28 (part); Parker, 1932: 220 (Lake George, Lake Naivasha); Loveridge, 1936a: 34 (part, Harar, Lake Bunyonyi) & 1936b: 256 (Uganda & Kenya); Mertens, 1938: 8 (Ngorogoro, Aberdares); Gans, 1959: 141 (part); Spawls, 1978: 10; Largen & Rasmussen, 1993: 340 (part); Flemming & Bates, 1999: 423 (Ibaya Camp, Mkomazi Game Reserve); Wagner & Böhme, 2007: 136 (USNM 49376, Kakamega Forest).

Dasypeltis scabra var. *atra* Sternfeld, 1912: 272. Type locality: 'Urwald hinter den Randbergen am Nordwestufer des Tanganyika-Sees' [= Jungle behind the border mountains on the north-west shore of Lake Tanganyika], Democratic Republic of the Congo, syntypes ZMB 22516A&B, 27761; Gans, 1961: 73.

Dasypeltis scabra var. *palmarum* (not Leach) Angel, 1925: 34 (Nairobi).

Dasypeltis scaber (not Linnaeus) Loveridge, 1929: 28 (part); Parker, 1932: 220 (Lake George, Lake Naivasha); Loveridge, 1936a: 34 (part, Harar, Lake Bunyonyi) & 1936b: 256 (Uganda & Kenya); Uthmöller, 1937: 113 (part, Moshi, Uru).

Dasypeltis scaber scaber (not Linnaeus) Bogert, 1940: 85 (part, Ganame, Ethiopia).

Dasypeltis scaber palmarum (not Leach) Loveridge, 1942: 285 (Uganda, Rwanda) & 1946: 106.

Dasypeltis scabra palmarum (not Leach) Loveridge, 1955: 11 (Gilo, South Sudan).



Figure 15. Haud, Somaliland—type locality of *Dasypeltis taylori* **sp. nov.** (Photo: T. Mazuch)

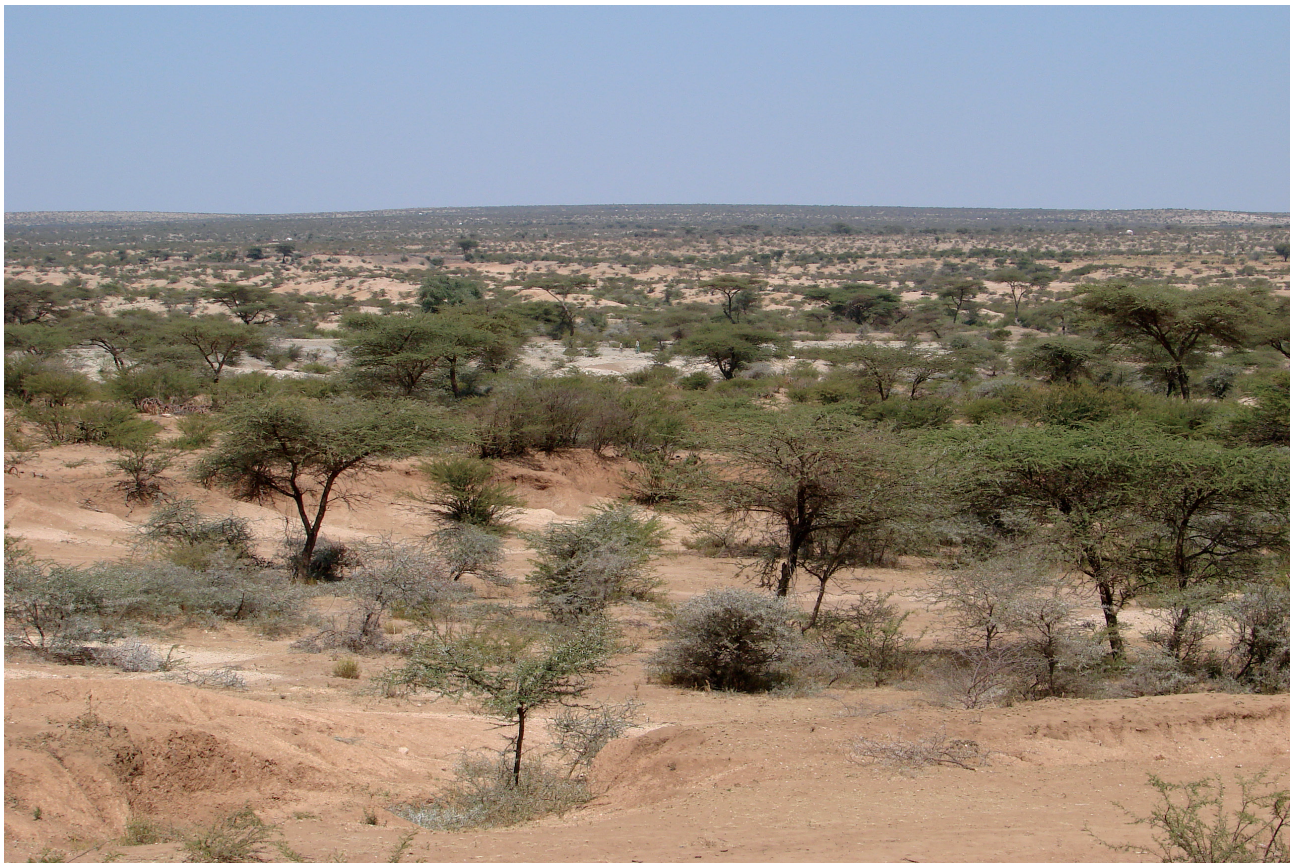


Figure 16. Vicinity of Hargeisa, Somaliland—habitat of *Dasypeltis taylori* **sp. nov.** (Photo: T. Mazuch)

Dasypeltis scaber ater Laurent, 1956: 261; Curry-Lindahl, 1956: 47 (Rwanda); Hinkel, 1986: 25 (Rwanda).

Dasypeltis scabra atra De Witte, 1962: 139; Bourgeois, 1968: 284.

Dasypeltis atra Gans, 1964: 279, 1971: 461 & 1974: 47; Laurent, 1965: 14; Pitman, 1974: 119; Hinkel & Fischer, 1988: 16 (Rwanda); Hinkel & Fischer, 1990: 137 (Nyungwe Forest, Rwanda); Broadley & Howell, 1991: 32; Fischer & Hinkel, 1992: 144 (Nyungwe and Birunga Forests, Rwanda); Hinkel, 1986: 25 (Rwanda); Meirte, 1992: 57; Largen & Rasmussen, 1993: 340; Hughes, 1997: 68; Broadley, 1998: xxxii; Gravlund *et al*., 1998: 53 (Mbizi Forest Reserve, Tanzania); Necas & Modry, 1998: 22; Gravlund, 2001: 101; Vonesh, 2001: App. A, Table 3 (Kibale National Park, Uganda); Behangana & Goodman, 2002: 66 (Uganda); Spawls *et al*., 2002: 414; ? Spawls, 2004: 17 (Keriyo; may be referable to plain phase *D. abyssina*); Spawls *et al*., 2006: 129; Largen & Parker, 2004: 25; Wagner & Böhme, 2007: 136 (Kakamega Forest); Gartner & Greene, 2008: 368; Bates & Broadley, 2008a,b (abstracts); Broadley & Bates, 2009: 50; Bates, 2009: 3; Largen & Spawls, 2010: 494 (part, 'Mulu' = Keriyo, may be plain phase *D. abyssina*); Bates *et al*., 2012: 28; Branch, 2015: 67; Göthel, 2015a: 19 & 2015h: 90; Van de Loock & Bates, 2016: 16 (Ngangao Forest, Kenya); Mannel & Kucharzewski, 2017: 43; Spawls, 2017: 31 (Maasai Mara).

Dasypeltis scaber var. *lineolata* (in error) Trape & Mané, 2006: 53.

Description. There are three basic colour morphs: dorsum black ('2M' of Gans 1959) with a grey venter (*N* = 89); dorsum brown ('2B' of Gans 1959) with a cream-white, yellowish or pale orange (e.g. Fig. 17C) venter, usually with grey stippling at the edges (*N* = 91); dorsum grey, tan brown, occasionally reddish-grey, decorated with closely-spaced, mostly narrow, transversely enlarged dark saddles, sometimes rhombic, in common or occasional contact with the equally dark lateral bars, or occasionally separated in a more-or-less '5N' pattern similar to that of *D. scabra* ('2Bx' of Gans 1959) and venter cream to white, usually with grey stippling at the edges (*N* = 135). In patterned specimens the dorsal saddles (62–130, mean 91.8, *N* = 51) are dark brown, olive or reddish; and the head may be largely grey to bluish-grey, and/or with few dark markings unlike the boldly dark-light patterned head of *D. scabra* (see images in Broadley & Bates 2009; Spawls *et al*. 2002; Göthel 2015e,h; Fig. 17F, I–K). For example, PEM R17336 (Tanzania; Fig. 17K) and BM 03.12.2.22 (Uganda) have grey bodies with reddish saddles/crossbars; but the latter specimen also has a broad red chevron on the top of the head. Saddles and lateral bars may vary in colour between specimens even at the same locality – e.g. at Kitengela in Kenya they may be olive (Fig. 17F) or brown. The 'lineolata' phase (Gans, 1959, Pl. VI, Fig. 8; Fig. 17D) shows the extreme reduction of the pattern where most of the back is dark with only narrow, often interrupted or incomplete, pale transverse bars. Some specimens with low numbers of bands are somewhat similar to *D. confusa*, but lack the large well-defined saddles.

Dorsally brown ('2B') and black ('2M') phase specimens are found together at a few localities such as Bourka in Ethiopia, Bussu, Kampala and Sipi at Mt Elgon in Uganda, and Minziro Forest Reserve in Tanzania; brown and patterned ('2Bx') phases are both found at Harar in Ethiopia, Mushongeru in Uganda, and Nairobi and Kacheliba in Kenya; black and patterned specimens both occur at Nakuru and North Nandi Forest in Kenya; and at Muko in Uganda all three colour phases occur together (Appendix 1). All specimens from South Sudan are melanistic (i.e. '2M'), except MCZ 53569 which is brown.

Preoculars usually one on either side of head (96.5% of specimens), but one on one side and two on the other in 1.8%, and two on either side in 1.8% (*N* = 227); postoculars one on either side of head (e.g. Fig. 18) in 58.3% of specimens, one on one side and two on the other in 6.8%, and two on either side in 34.9% (*N* = 307) (usually one in western populations – especially in Uganda, Rwanda and Burundi, e.g. 93.0% of Rwanda/Burundi snakes [*N* = 43] had a single postocular on either side; by contrast 77.4% of Ethiopian snakes [*N* = 31] had two postoculars on either side); frontal shield for the most part smooth, usually with 1–2 rows of shallow pits at the edges (States 1–2; 95.3% of specimens), but occasionally fully smooth (State 0; 3.3% of specimens) or extensively pitted (States 3–4; 1.4% of specimens: NMW 15299, PEM 16778, ZMUC 6122) (*N* = 213); inter-prefrontal suture usually weakly marked (87.5% of specimens), but moderately marked in 11.5%, and distinctly depressed in 1.0% (BM 1976.2265, MSNG 30412) (*N* = 200); supralabials 12–16, usually 14 (both sides of head), usually 7 [3rd and 4th entering orbit] on either side (84.7%), but variations are: 6[2,3] on either side of head (e.g. MRAC 18557) in 1.4% of specimens, 6[3,4] on either side (e.g. BM 51.1.3.74) in 5.2% (including MSNG 52410 which had left side of head damaged), 6[3,4] on left and 6[2,3] on right in ZFMK 29731, 6[2,3] on one side (e.g. CAS 122281) in 2.8%, 6[3,4] on one side (e.g. MCZ 40578) in 1.4%, 7[2,3,4] on right in ZFMK 16237, 7[2,3,4] on both sides in NMK 3182, 8[3,4] on one side (e.g. BM 1976.2265) in 1.0%, 8[3,4,5] on one side (e.g. USNM 40897) in 1.7%, and 8[3,4,5] on both sides (e.g. MRAC 15440) in 0.7% (*N* = 287); anterior temporals usually two on either side of head (93.9%), occasionally one (2.5%), 2 left:1 right or 1:2 (1.2%), 2:3 or 3:2 (1.2%), or three (1.2%) (*N* = 244); posterior temporals usually three on either side of head (52.7%), often two (18.3%) or 2:3 or 3:2 (14.1%), occasionally 3:4 or 4:3 (8.3%), four (4.1%) or five (0.8%), and exceptionally 4:5 (ZFMK 29733), 3:5 (BM 1976.2265), 5:3 (BM 34.12.15.590) or 2:4 (LIV 1960.67.1) (*N* = 241); temporal formula on either side of head usually 2+3, often 2+4, occasionally 2+2; midbody scale rows 22–28 (mean 24.1 ±1.25, *N* = 226) [28 in NMW 26879–3 only]; ventrals 199–232 in males (*N* = 109), 211–256 in females (*N* = 167); subcaudals 50–71 in males (*N* = 103), 45–64 in females (*N*

= 151). One unsexed specimen from Bujumbura, Burundi (MRAC 82–16–R4, probably a male) had 218 ventrals and as many as 75 subcaudals. The brown ('2B' of Gans 1959) female (MSNM 7202) from Circao (northern-most record for this species) has 232 ventrals, a much lower count than that of female *D. abyssina* (241–264) which also occur as brown or uniform plain phase morphs (see below); and brown *D. atra* in Ethiopia have lower ventral + subcaudal counts than plain phase *D. abyssina* (both sexes, 269–291 [*N* = 5] versus 294–323 [*N* = 7] respectively). Ratio SVL: tail length 4.2–6.7 in males (*N* = 97), 5.8–8.3 in females (*N* = 143); total length: tail length 5.2–7.7 in males (*N* = 97), 6.8–9.3 in females (*N* = 143).

Size. Largest male (MSNG 30413B – Bussu, Uganda) 611 + 98 = 709 mm; second largest male is USNM 63481 (Budongo Forest, Uganda) measuring 560 + 115 = 675 mm (also second largest SVL). Largest female (NMK 2583 – North Nandi Forest, Kenya) 890 + 115 = 1005 mm; there is only one other female >760 mm SVL, namely BM 34.12.15.592 (Mubango, Mabira Forest, Uganda) measuring 830 + 133 = 963 mm (also second largest female).

Habitat. Found mainly in high elevation savannah and forest, usually above 1500 m (e.g. Fig. 21).

Distribution. Kivu Region and vicinity of Lake Albert in eastern Democratic Republic of the Congo (Laurent 1956; Gans 1959), Rwanda, Burundi, south to Mbizi Forest in western Tanzania and east to the extreme northern parts of that country, Uganda, Kenya (excluding eastern parts), extreme southern part of South Sudan, and south-western and central Ethiopia, with the northern-most record at Circao in the northwest (Fig. 3).

Sympatry. Sympatric with *D. medici* at Nyambene Hills (Kenya) and Moshi (Tanzania); sympatric with *D. confusa* 10 km S of Juba (South Sudan), at Busingiro and Gulu (Uganda) and Kacheliba (Kenya); sympatric with *D. scabra* at Aware Melca and Lake Abiata (Ethiopia), Mulema (Uganda), Lake Naivasha and Mount Kulal (Kenya), Astrida (Rwanda) and Minziro Forest Reserve (Tanzania); sympatric with *D. abyssina* at Keriyo (Ethiopia); sympatric with both *D. medici* and *D. scabra* at Mount Kilimanjaro (Appendix 1).

Localities. ETHIOPIA. 'Abessinien', NMW 9964–2; Addis Ababa [NE 0938B2] MSNG 30412, and Fig. 17E; Aware Melca [NE 0939B2] BM 16.6.24.13; Bedele [NE 0836A4] ZFMK 57537; Bedele, 4.5 km SW of [NE 0836A4] melanistic, photographic records; Bourka [NE 0941A4] MNHN 05.208–10; Circao, Dambria [NE 1237A4] MSNM 7202; El Dire, Tertale [NE 0437C3] MSNM 2975; Fitu, 135 km ESE of Negele [NE 0540B1] '2Bx' pattern, photographic records; Ganame [NE 0841D3] AMNH 20345; Gemu, Gofa [NE 0636B] BM 1964.1068; Genale to Chamo [NE 0837D3] ZFMK 16297; Ghimbi, Wollega [NE 0935B2] BM 1973.3175; Ginir [NE 0740B1] NMW 26879–2; Gololtscha [NE 0840A1] ZFMK 5535; Gumaydo [NE 0537D1] NMW 26879–3; Harar [NE 0942A3] FMNH 4012, MCZ 34923, NMW 9964–1; Jigjiga [NE 0942B4] ZFMK 84993; Kebre Mengist to Negele [NE 0539C3] BM 1975.2144; Keriyo [NE 0938B3] Fig. 17A; near Kersa Dek, 14 km SE of Neghelle [NE 0539B1] '2Bx' pattern, photographic record; Kounni [NE0940B2] MNHN 05.211; Laga Hardine [NE 0840C4] MNHN 05.205–7; Lake Abiata [NE 0738D1] ZFMK 16236; Lake Alemeya [NE 0942A3] ZMB 27463; Lake Shala [NE 0738B3] ZFMK 16237; Let Marefia [NE 0939D2] ZMB 10286; Neghelle [0539B3] Fig. 17M; Shek Husen, 4.4 km WSW of [NE0740D1] brown dorsally with cream patches, photographic record; Shoa, MSNG 29047a; Wondo [NE 0638C2] NMW 15299. SOUTH SUDAN. Gilo, Imatong Mtns [NE 0432B2] BM 1978.379–80, FMNH 62215, MCZ 53406–8, 53569, ZFMK 29564, 29719, 34532, 59567; 10 km S of Juba [NE 0431D3] ZFMK 29567; Katire [NE 0432B2] ZFMK 26005; Talanga Forest [NE 0432B1] ZFMK 29731–3. UGANDA. Bihunga [SE 0129B4] LIV 1960.67.1, 1960.50.32; Bitereko [SE 0030B3] LIV 1960.115; Budongo Forest [NE 0131D3] USNM 63481; Bufindi, Kigezi [NE 0129B4] BM 51.1.3.68 & 79, NMZB 217; Bukakata [SE 0031A3] BM 51.1.3.80; Busingiro, Budango [NE 0131D1] BM 1951.1.5.24; Bussu [NE 0033A3] BM 11.7.8.14, MSNG 30413A&B, 52410; Butundiga, Mount Elgon [NE 0134A2] MCZ 40574; Bwamba Forest [NE 0030C3] LACM 38696, 46344; Chagwe, Mabira Forest [NE 0032D2] BM 08.10.20.14–5; Entebbe [NE 0032A2] BM 51.1.3.74; Gulu [NE 0232C4] BM 51.1.3.77; Fort Portal [NE 0030C2] CAS–SU21709–10; Kabingo, Bunyaruguru, BM 1961.1803; Kagabagara [SE 0030D3] LIV 1962.9.28; Kagando [NE 0029B2] LIV 1960.67.5; Kalinzu Forest [NE 0030A3] LACM 60705; Kampala [NE 0032A2] BM 36.7.3.32, 1984.882; Katunguru [SE 0030A1] NMZB 103; Katwe [SE 0029B2] MRAC 9997; Kayonza, Kinkizi [NE 0029D3] LACM 35090, LIV 1960.115.4, 1962.9.27, 1980.150.31, NMZB–UM 2550; Kazinga Channel [SE 0030A1] NMK 404; Kichwamba [SE 0030A1] LIV 1962.9.14; Kinani [SE 0030B4] LIV 1962.9.22; Kyamahunga, Igara [SE 0030A3] BM 51.1.3.75, 1961.1805, NMZB 2549; Kyamugorani [SE 0030B3] LIV 1962.9.4; Lake Bunyonyi [SE 0129B4] FMNH 9913–4, MCZ 34922; Lake Edward [SE 0029B] NMZB 219; Lake George [NE 0030A] BM 32.5.2.99; Lake Nabugabo [SE 0032A3] BM 51.1.3.78; Likiri [SE 0030A2] LIV 1980.150.27; Maozi-Isingiro [SE 0030D4] BM 03.12.2.23; Mihunga, Ruwenzori [NE 0030A3] MCZ 48359; Mityana [NE 0032A3] NMK 3291; Morulinga, 24 km SW of [NE 0234A4] BM 1954.1.12.37; Mubango, Mabira Forest [NE 0033A3] BM 34.12.15.592; Muko, Kigezi [SE 0129B2] BM 34.12.15.585–91, 593–4; Mulema [SE 0031D1] BM 03–12–2–22; Mushongero, Lake Mutanda [SE 0129B1] MCZ 48362–3; Nsika [SE 0030A4] LIV 1980.150.26; Nyabushozi [SE 0030B4] LIV 1962.9.23; Nyakabende [SE 0129B4] MCZ 48360–1, UMMZ 88532/1; Nyamuhumia [SE 0030C1] LIV



Figure 17. *Dasypeltis atra*. Black morph ('2M' of Gans 1959)—A: Keriyo near Mulu Cattle Farm, Ethiopia (Photo: S. Spawls); B: Limuru, Kenya (Photo: S. Spawls); Brown morph ('2B' of Gans 1959)—C: ELI 1264 (field number), Kibira Forest, Burundi (Photo: E. Greenbaum); Patterned morph ('9' of Gans 1959)—D: Holotype (ZMB 9224) of *Dasypeltis lineolata* Peters from Kitui, Kenya (Photo: M.F. Bates); Patterned morph ('2Bx' of Gans 1959)—E: Addis Ababa, Ethiopia (Photo: S. Spawls); F: Kitengela, Kenya (Photo: S. Spawls); G: Chuka Mountain, Kenya (Photo: S. Spawls); H: ELI 2760 (field number), Bwindi Impenetrable National Park, Uganda (Photo: E. Greenbaum).



Figure 17. (cont.) *Dasypeltis atra*. Patterned morph ('2Bx' of Gans 1959)—I: Addis Ababa, Ethiopia (Photo: S. Spawls); J: Masiko ya Tembo, Tanzania (Photo: W.R. Branch); K: PEM R17336, Klein's Camp, Mkomazi Game Reserve, Tanzania (Photo: W.R. Branch); L: Kakamega Forest, Kenya (Photo: T. Mazuch); M: Neghelle, Ethiopia (Photo: V. Trailin).



Figure 18. *Dasypeltis atra* from Kakamega Forest, Kenya, with a single postocular. (Photo: T. Mazuch)

1959.81.2; Nyansimbo [SE 0030B1] LIV 1962.50.33, 1980.150.33; Nyarusiza, Bufumbira [SE 0129B3] BM 1976.1849, LIV 1980.150.29–30, NMK 1496, NMZB–UM 2553; Rucho, Ankole, MCZ 54744; Ruhama [SE 0030C4] LIV 1960.67.3; Sango Bay Forest [SE 0031D3] LACM 39242; Sesse Islands, Lake Victoria [SE 0032A3] MSNG 27755a, 40764; Sipi, Mount Elgon [NE 0134A4] MCZ 40564–73. KENYA. No locality, NMK 348, 463, 1962, UMMZ 96274; Athi Plain, NMW 9964–20; Athi-Kapiti Plains, NMK 3129; Athi River [SE 0136B4] NMK 1453, 3085; Butere, Kakamega [NE 0034B1] NMK 2323 (old no. 306); Chemelil, Kisumu [SE 0035A1] CAS 148034–5; Chuka, Meru [SE 0037B3] CAS 122281, and Fig. 17G – '2Bx' pattern; Chyulu Hills [SE 0037D2] NMK 406; Elgonyi, Mount Elgon [NE 0134B1] MCZ 40575; Emakoko, Nairobi National Park [SE 0136B4] photographic record (dorsum grey with brown saddles [similar to Fig. 17F] and two postoculars on left side of head); Embakasi, Nairobi [SE 0136B4] NMK 2849; Hopcroft Ranch, Athi River [SE 0137C1] NMK 3131; Juja Farm [SE 0137A1] USNM 40897; Kabartonjo, Kamasia Mtns [NE 0035D2] CAS 111767; Kabarnet, Baringo [NE 0035D2] BM 1957.1.11.42, NMK 3329; Kabete, Kiambu [SE 0136B3] NMK 479; Kacheliba [NE 0135A3] NMK 486, 488; Kaimosi [NE 0034B2] MCZ 40576–8, 18205, UMMZ 61224, USNM 49078; Kairuni, Nyambeni Mtns [NE 0037B2] LACM 93378–9; Kakamega [NE 0034B4] BM 1959.1.5.58, CAS 142248, NMK 482, 2715, USNM 49376; Kakamega Forest [NE 0034B4] Fig. 17L, '2Bx' pattern; Karen, Nairobi [SE 0136B3] NMK 2503, 3007; Kericho [SE 0035A4] NMK 1260; Kiambu [SE 0136B2] NMK 481; Kiboko Ranch Station [SE 0237B1] NMK 2952 (4); Kijabe [SE 0036D3] NMK 2130, and top photograph of melanistic specimen in Spawls *et al*. 2002: 415; Kiganjo, Nyeri [SE 0036D4] NMK 2862; Kiserien, Baringo [SE 0136B3] NMK 3123; Kitale [NE 0135A1] NMK 3051, ZMUC 6101; Kitengela [SE 0136D2] Fig. 17F and another photograph, both '2Bx' patterned; Kitengela, Athi River [SE 0136D2] NMK 3413; Kitui [SE 0138A3] ZMB 9224 (holotype of *D. lineolata*); Lake Baringo [NE 0036C2] NMK 1791, 4174; Lake Naivasha [SE 0036C2] BM 93.11.21.72, 1932.5.2.100; Limuru [SE 0136B1] Fig. 17B, melanistic; Lorgorien, Trans-Mara, NMK 3109; Lumbwa, Pen-y-Bryn [SE 0035A4] CM 2278–9, 2281; Maralal, 13 km SSW of [NE 0036D3] LACM 66076; Mbunyi [SE 0137B4] USNM 62907 (Gans' 1959 locality of 'Morogoro' for this specimen is in error, see Loveridge 1929); Mount Elgon, NMK 657–9, 3152; Mount Kenya [SE 0037A2] USNM 40990; Mount Kulal [NE 0236D2] LACM 66395; Muranga [Fort Hall] [SE 0037C1] BM 08.9.17.4; Mweiga [SE 0036B4] LACM 50631; Mwino, Sigor [NE 0135A4] NMK 1965; Nairobi [SE 0136B4] NMK 403, 2486, 3339, 3548; Naitolia (6000 ft = 1829 m a.s.l.) [SE 0036A4] BM 01.1.3.9; Nakuru [SE 0036A3] NMK 484 and 1453, and photographs of '2Bx' patterned and melanistic specimens; Nandi [NE 0035A1] BM 06.7.6.7; Nandi Hills [NE 0035A] NMK 1158; Nanyuki, Laikipia [NE 0037A1] NMK 3490, 3512, 3557; Nbabibi, Naivasha [SE 0036C2] NMK 1960; Ngangao Forest, Taita Hills [SE 0338A4] (photograph of barred/patterned '2Bx' specimen: Van de Loock & Bates 2016, Fig. 2); Ngong [SE 0136B3] BM 1960.1.6.40; North Nandi Forest, Chemesia [NE 0034B4] NMK 2576, 2583, 2590; Nyambene Hills [NE 0037B] NMK 1487, 1489, 1699; South Nandi Forest [NE 0035A1] NMK 4176; Subukia [SE 0036A1] FMNH 58337; Timbilil, Mau Forest [SE 0035A4] NMK 3182; Uganda Railway, BM 96.3.27.18. RWANDA. Astrida [SE 0229D1] MRAC 18554–8; Bugarama [SE 0229C1] MRAC 86–01–R–10 & 11; Bugesera [SE 0230A1] ZFMK 61616; Bulimbi [SE 0130C1] MRAC 18577; Cyamudongo [SE 0228D2] ZFMK 61617; between Gikongoro and Nyungwe Forest Reserve [SE0229C2] PEM 5623; Kamohora District, MRAC 14329; Kibungo [SE 0230B1] ZFMK 55105; Kisenyi [SE 0129C1] MCZ 48364, MRAC 2723, 2725, 2757, 3821, 5871–2, 9773, ZMB 20458, 27156, 27539; Lake Gando [SE 0129C2] MRAC 14333, 14341; Mwogo River near Butare [0230A1] MRAC 74–23–R–22; Mutura, Mount Virunga [SE 0129B2] MRAC 7509; Nyanza [SE 0429B3] MRAC 15477; Ruhengeri [SE 0129D1] IRSNB 2657; Wankeri [SE 0129D1] MRAC 14331, 14340: Rwankuba [SE 0129C2] MRAC 18259; Shangugu [SE 0228B4] MRAC 4074–5; Tare, Astrida [SE 0229D1] MRAC 18560–2. BURUNDI. Bujumbura [SE 0329A4] MRAC 82–16–R3 & 4; Kamagaba Marsh, MRAC 18583; Kibira Forest [SE 0229C4] Fig. 17C; Makamba [SE 0429B2] MRAC 18584; Rumonge [SE 0329C4] MRAC 18585. TANZANIA. Bukoba [SE 0131B4] ZMB 16749–50; Ibaya Camp, Mkomazi Game Reserve [SE 0337D4] BM 1994.403, NMBO 7375; Kasoge, Mahale Peninsula [SE 0629B2] BM 1970.2177; Klein's Camp, NE Serengeti National Park [SE 0135C3] PEM 16778, 17329, 17336, 17941; Masiko ya Tembo, vicinity of Sanya Chini [SE 0337A3] Fig. 17J; Mbizi Forest Reserve [SE 0731D3] ZMUC 6122; Minziro Forest Reserve [SE 0131B1] ZMUC 6138–41; Moru area, Serengeti National Park [SE 0234D1] photograph of '2Bx' marked specimen; Moshi [SE 0337A4] ZSM 81/1936 (3); Mount Kilimanjaro [SE 0337A] ZMB 17039 (2); Oldeani [SE 0335B3] photograph of melanistic '2M' specimen; Sitete, Mahale Peninsula [SE 0629B2] BM 1970.2178.

Conservation. In terms of the regional (study area) and global distribution of this species, using IUCN (2012, 2016) criteria, it is widespread and abundant and should be regarded as Least Concern.

Remarks. *Dasypeltis scabra* var. *atra* was described by Sternfeld (1912) on the basis of three 'completely black' specimens, with single postoculars, from the forest behind the border mountains on the north-west shore of Lake Tanganyika, Democratic Republic of the Congo. Photographs of the three syntypes housed at Museum für Naturkunde, Berlin were provided by F. Tillack (pers. comm, 10 July 2017). ZMB 27761 is medium brown above and light brown below (may

have faded); ZMB 22516A and ZMB 22516B are dark brown to black above and grey below. It can be confirmed that all three specimens have a single postocular on either side of the head, and the supraocular extends over the posterior corner of the eye.

Since its description by Peters in 1878, *Dasypeltis lineolata* was used as a valid name by Fischer (1884b) in reference to a snake (247 ventrals, 69 subcaudals) from Ssibange in Gabon, probably referable to *D. fasciata* or possibly *D. palmarum*, and later by Stejneger (1894) who concluded that it was a 'colour variety' (possibly implying a subspecies) of *Dasypeltis abyssina*. The only other valid usage of the name was by Saleh & Sarhan (2016). While referring to available names, Trape & Mané (2006) erroneously used the combination *Dasypeltis scaber* var. *lineolata*. The samples of *'D.* cf. *lineolata'* from Burundi used in the 16S genetic analysis of Trape *et al*. (2012) are referable to either *D. atra* or *D. scabra*. The name *D. atra* (or *D. scaber ater* or *D. scabra atra*, as indicated), the junior synonym, has been used in the following 43 publications (25 required), by 34 authors/sets of authors (10 required), during the preceding 50 years (1968–2017), and for a period covering more than 10 years (see Article 23.9.1.2 of the ICZN 1999): Bourgeois (1968, as *D. scaber ater* and *D. scabra atra*), Gans (1971, 1974), Pitman (1974), De Witte (1975), Hinkel (1986, as *D. scaber ater*), Hinkel & Fischer (1988, 1990), Fischer & Hinkel (1992), Broadley & Howell (1991), Meirte (1992), Largen & Rasmussen (1993), Hughes (1997), Broadley (1998), Gravlund *et al*. (1998), Neças & Modry (1998a,b), Gravlund (2001), Spawls *et al*. (2002), Largen & Parker (2004), Spawls (2004), Branch (2015), Spawls *et al*. (2006), Trape & Mané (2006), Wagner & Böhme (2007), Gartner & Greene (2008), Bates (2009), Broadley & Bates (2009), Largen & Spawls (2010), Bates *et al*. (2012), Trape *et al*. (2012), Göthel (2015a–h), Van de Loock & Bates (2016), Saleh & Sarhan (2016), Mannel & Kucharzewski (2017) and Spawls (2017), thus satisfying the requirements of Article 23.9.1.2 of the ICZN (1999). However, Saleh & Sarhan's (2016) use of the name *D. lineolata* means that the provisions of Article 23.9.1.1 (i.e. senior synonym not used as a valid name after 1899; ICZN 1999) are not met. In order to maintain nomenclatural stability the ICZN has been requested (Bates 2017, submitted; Case 3750) to suppress the older name *D. lineolata* by taking action according to Article 23.9.3 by use of its plenary power (Article 81; ICZN 1999). We maintain prevailing usage of the name *D. atra* according to Article 82.1 (ICZN 1999).

***Dasypeltis fasciata* A. Smith**
Western Forest Egg-eater
Fig. 19A–C

Dasypeltis fasciatus A. Smith, 1849 (footnote to text accompanying Plate 73). Type locality: Sierra Leone.
Dasypeltis scaber fasciatus Loveridge, 1942: 284 (Bundibugyo, Uganda).
Dasypeltis fasciata Loveridge, 1957: 289 (check-list); Gans, 1959: 137 & 1961: 73; Pitman, 1974: 121; Spawls *et al*., 2002: 416; Spawls *et al*., 2006: 130; Branch, 2015: 68; Göthel, 2015a: 19 & 2015h: 81.

Description. Dorsum grey or pale brown with numerous broad dark saddle bands (108–141, *N* = 5) which are often ill-defined in preserved specimens (e.g. Fig. 19A) and usually arranged in a manner similar to the '5N' pattern, with saddles alternating with broad lateral bars; dorsal body pattern expressed as chequerboard on skin between scales and on lower edges of these (see Gans 1959, Pl. III); top of head vermiculate; venter cream to pale grey, usually with grey stippling at the edges, but sometimes extensively stippled (e.g. TCWC 23839, which also has the throat and anterior part of the belly pale yellow, Fig. 19B).

Preoculars usually one on either side of head (83.3% of specimens), but two on either side in MCZ 48357 and UMMZ 88531 (*N* = 12); postoculars usually two on either side of head, but two on left side and one on right side of MCZ 48358B, and one on both sides in LACM 46341 (*N* = 12); frontal shield for the most part smooth, usually with 1–2 rows of shallow pits at the edges (States 1–2), but more extensively pitted (State 3) in LACM 38697 (*N* = 11); inter-prefrontal suture weakly marked (*N* = 11); supralabials 13–14, usually 14 (both sides of head), usually 7 [3rd and 4th enter orbit] on either side of head, but 6 [2,3] on right side of head in LACM 46346 and MCZ 48357 (*N* = 12); anterior temporals usually two on either side of head (75.0%), occasionally 2 left: 3 right or 3:2 (16.7%), and three in LACM 46341 (*N* = 12); posterior temporals usually three on either side of head (58.3%), occasionally 3:4 or 4:3 (25.0%), two in LACM 39243, and four in LACM 46343 (*N* = 12); temporal formula on either side of head usually 2+3, occasionally 2+2, 2+4, 3+3 and 3+4; midbody scale rows 22–25 (mean 23.5 ± 0.80, *N* = 12); ventrals 212 (LACM 39243), 229–230 in males (*N* = 3), 237–248 in females (*N* = 9); subcaudals 59 (LACM 39243), 71–76 in males (*N* = 3), 64–76 in females (*N* = 9). Ratio SVL: tail length 4.7–5.2 in males (*N* = 3), 4.8–6.4 in females (*N* = 9); total length: tail length 5.7–6.2 in males (*N* = 3), 5.8–7.4 in females (*N* = 9).

Size. Largest male (LACM 38697 – Ntandi, Bwamba Forest, Uganda) 525 + 111 = 636 mm. Largest female (TCWC 23839 – Ntandi, Bwamba Forest, Uganda) 611 + 108 = 719 mm.

Habitat. Lowland forest at elevations of about 1000 m to 1147 m (Katera).

Distribution. Forested areas of West and Central Africa, from Guinea to Togo, and from south-eastern Nigeria south to north-western Angola, and east through southern Central African Republic and much of the Democratic Republic of the Congo (Gans 1959,

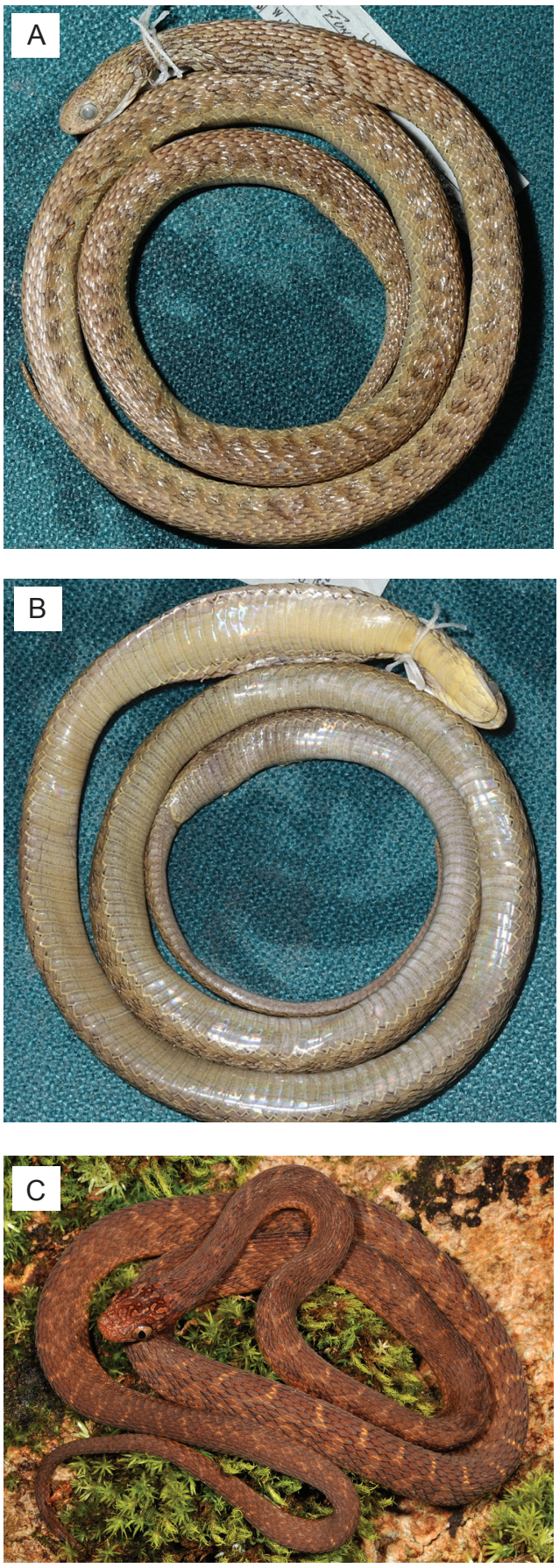


Figure 19. *Dasypeltis fasciata*. [Colour pattern '4' (checker board) of Gans 1959] A & B: Dorsal and ventral views, respectively, of TCWC 23839, Nandi, Bwamba Forest, Uganda (Photos: T. Hibbits); C: Makeni, Sierra Leone (Photo: W.R. Branch).

1964; Trape & Mané 2012), reaching its eastern limit in western and southern Uganda (Fig. 3).

Localities. UGANDA. Bundibugyo [NE 0030C] MCZ 48537, 48538a,b; UMMZ 88531; Bwamba Forest, Ntandi [NE 0030C3] LACM 38697, 46341–3, 48345–6, TCWC 23839; Katera, Sango Bay Forest [SE 0031D3] LACM 39243.

Conservation. In terms of the regional (study area) and global distribution of this species, using IUCN (2012, 2016) criteria, it appears to be widespread and abundant and should be regarded as Least Concern.

***Dasypeltis abyssina* (Duméril, Bibron & Duméril)**
Ethiopian Egg-eater
Figs 20A–G

Rachiodon abyssinus Duméril, Bibron & Duméril, 1854: Vol. 7: 496, Pl. 81, Figs 1–2. Type locality: Abyssinia, proposed lectotype MNHN 6567 (see below); Duméril, 1860: 198.

Rachiodon scaber var. *abissinicus* (lapsus) Jan, 1863: 106 (Ethiopia).

Dasypeltis abyssinicus (lapsus) Blanford, 1870: 457 (Senafe, Eritrea); Zavattari, 1930: 193.

Dasypeltis abyssina Fischer, 1884b: 48; Trape & Mané, 2006: 53; Largen & Spawls, 2010: 490; Göthel, 2015a: 19, 2015h: 92.

Dasypeltis scabra (not Linnaeus) Boulenger, 1893: 354 (var. D, Abyssinia); Calabresi, 1925: 107 (Gondar); Zavattari, 1930: 193 (Senafe); Gans, 1959: 141 (part, Eritrea, Gheleb; Pl. VI, Figs 3 &4); Largen & Rasmussen, 1993: 340 (part, 140 km NE of Gondar on road to Asmara); Spawls, 2004: 17 (Keriyo); Largen & Spawls, 2010: 488 + 490 (part, e.g. 'Mulu' = Keriyo).

Dasypeltis scaber (not Linnaeus) Loveridge, 1936: 34 (part, Gondar).

Lectotype. Dumeril *et al.* (1854) described *Rachiodon abyssinus* on the basis of two syntypes in the Muséum national d'Histoire naturelle in Paris, one from "Abyssinia" (= Ethiopia) and another collected during an expedition to the sources of the White Nile under direction of M. Arnaud (labelled "Nil Blanc" = White Nile, perhaps from above Khartoum in Sudan). Although their description is compound (e.g. ventrals are given as 222–260, clearly referring to MNHN 7227, see above and MNHN 6567, see below), the information on colour, which refers to a yellow base colour which exaggerates the darker dorsal markings, appears to be specifically in reference to the illustrated snake (MNHN 6567). Trape & Mané (2006) reinstated *D. abyssina* which has vivid '5N' dorsal colouration, heavily black-bordered ventrals and a high ventral count of 260. They were of the opinion that the two syntypes were probably referable to different species, and designated MNHN 6567 (female), illustrated in plate 81 in the description (see also Fig. 20A & B), as 'holotype' of *R. abyssinus*. Although we agree that the

two specimens do in fact represent different species, the action by these authors is not in accordance with the International Code on Zoological Nomenclature (ICZN 1999) as a syntype cannot be designated as a holotype, only as a lectotype or paralectotype.

MNHN 6567 agrees closely with the heavily-marked belly illustrated in plate 81 of Duméril *et al.* (1854), but the dorsal pattern is dissimilar (Fig. 20A). The illustration depicts a snake with a pale vertebral stripe, flanked on either side by distinct but disjointed markings. As can be seen in the photograph (Fig. 20A) of this specimen, while the centre of the back has a pale background, this is interrupted frequently by the often oblique dark markings or saddles which are continuous across the centre of the back. There is also a general separation of the saddles from the lateral bars, even though these may be in occasional contact. An indication of the cause of the poor condition of the specimen (head and neck damaged) is provided by plate 81 in which the snake is illustrated, together with a section of its skeleton comprising 13 pairs of ribs and their associated vertebrae, and a section of the vertebrae from the neck region, indicating considerable mutilation of the body. It was therefore not possible to perform a count of the ventral plates, and as an appreciable portion of the tail tip was missing, no subcaudal count was possible either. Nevertheless, there seems to be no doubt that the snake illustrated in plate 81 and described by Duméril *et al.* (1854) is the specimen represented by MNHN 6567.

We take this opportunity to designate MNHN 6567 (female, no hemipenal spines in tail) as lectotype of *Rachiodon abyssinus*. In accordance with Recommendation 74C of the 1999 Code we hereby list the following data pertaining to the lectotype, as based on a recent (September 2011) examination of the damaged specimen (Fig. 20A–B) in Paris by the first author: Type locality: "Abyssinia" (= Ethiopia). Snout-vent length about 572 mm; about 86 pattern cycles from nape to above vent. Dorsal colour pattern consists mostly of oblique dark saddles, usually wider than long, and often confluent or forming zigzags on the back and tail; lateral bars (usually extending onto the edges of the ventral plates) somewhat irregular, usually broader above than below, and often in contact with the pale interspaces between saddles, sometimes in narrow contact with the edges of the saddles, but never forming a distinct or broadly linked pattern. Ventral scales with extensive brown markings on their anterior half, consisting of a large rounded cone on either side joined to a smaller cone in the centre. Midbody scale rows 25; lateral dorsal scale rows 3 to 6 are keeled and serrated; nasal scale divided between nostril and first upper labial.

Paralectotype. Duméril *et al.*'s (1854) other syntype of *R. abyssinus*, MNHN 7227 (female, no hemipenal spines in tail) from 'Nil Blanc', now the paralectotype, is referable to *D. scabra*. It measures 673 + 90 mm and has a grey dorsum with '5N' pattern (55 pattern cycles) consisting of brown oval saddles with black borders, and lateral bars—situated adjacent to the pale inter-saddle bars—also brown with black borders (Fig. 6); venter cream-white with dark speckling and two longitudinal rows of large spots at the edges; preoculars 1 on either side of head; postoculars 2 on either side; frontal shield with marginal pitting (State 2); inter-prefrontal suture moderately developed; ventrals 226; subcaudals 52; midbody scale rows 25, rows 3–5 keeled and serrated; supralabials 7 (3rd and 4th enter orbit) on either side; nasal scale divided below the nostril; temporals 2+3.

Diagnosis. Assigned to the genus *Dasypeltis* on account of its slender form, possession of (usually 3–4) rows of reduced, oblique, keeled and serrated lateral scales (little or no serration in *D. inornata*) and head barely distinct from the neck (moderately distinct in *D. fasciata*). Occurs as both patterned and uniform (brown or grey above, immaculate cream to cream-yellow below) phases. Patterned individuals are distinguished from other species of *Dasypeltis* by their unique dorsal and ventral colour patterns, dorsally consisting mostly of oblique dark saddles, usually wider than long, and often confluent or forming zigzags on the back and tail; lateral bars much-elongated, usually broader above than below, and typically extending onto the edges of the ventral plates, irregular in shape and often in contact with the pale interspaces between saddles, sometimes in narrow contact with the edges of the saddles; pattern cycles 65–98 (≤62 in *D. crucifera* **sp. nov.**, *D. taylori* **sp. nov.** and *D. bazi*; *D. inornatus* always uniform brown above; *D. gansi* uniform or weakly marked above); and ventral scales with extensive black, grey or brown markings on their anterior half, consisting of a large rounded cone on either side joined to a smaller rounded cone in the centre (Gans 1959, Pl. 9, Fig. 7; Fig. 20B; some *D. scabra* have heavy dark markings on the venter, but never as extensive or in the same pattern as described above); in live specimens the labials and interspaces between saddles are cream-yellow (Fig. 20C–F) as illustrated for one of the two syntypes (MNHN 6567, see discussion below) which, in addition, apparently also had some yellow on the sides of the head (Duméril *et al.* 1854, Pl. 81): within the genus this combination of dark markings with extensive cream-yellow or yellow also occurs, occasionally, only in southern populations of *D. scabra* (e.g. Peters 1864; Göthel 2015h).

In addition to its colour pattern as described above, this species can also be distinguished by the following combination of characters: High ventral scale counts of 226–247 in males (higher or mostly higher than *D. scabra* 180–226, *D. taylori* **sp. nov.** 196–216, *D. confusa* 199–227, *D. sahelensis* 207–221, *D. inornata* 208–225, *D. parascabra* 210–223), 241–271 in females (higher or mostly higher than *D. scabra* 198–249, *D. taylori* **sp. nov.** 208–222, *D. sahelensis* 212–237, *D. confusa* 212–242, *D. bazi* 215–234, *D. inornata* 219–237, *D. parascabra* 224-237); Subcau-



Figure 20. *Dasypeltis abyssina*. Dorsal (A) and ventral (B) aspects of the lectotype (MNHN 6567) from Ethiopia (Photos: M.F. Bates); C: Mulu cattle farm, Ethiopia (Photo: S. Spawls); D: Mulu cattle farm, Ethiopia (Photo: C. Tilbury); E: Mulu cattle farm, Ethiopia (Photo: S. Spawls); F: Keriyo near Mulu, Ethiopia (Photo: S. Spawls); G: Eritrea (NMW 15301–3, Photo: M.F. Bates).

dals 57–68 in males (mostly higher than *D. loveridgei* **comb. nov.** 47–58; lower or mostly lower than *D. inornata* 81–92, *D. gansi* 68–83, *D. palmarum* 68–77, *D. parascabra* 67–74, *D. latericia* 66–86, *D. fasciata* 59, 71–91, *D. medici* 69–109), 49–65 in females (mostly lower than *D. inornata* 69–84, *D. fasciata* 64–84, *D. medici* 61–90); Inter-prefrontal sulcus usually weakly marked (weakly to moderately marked in *D. bazi*, usually moderately marked in *D. taylori* **sp. nov.**, moderate to well marked in *D. arabica* **sp. nov.**, and variable in *D. scabra* [often well marked in the south of its range]); Frontal marginally pitted, usually State 1 or 2 (extensively pitted, States 3 & 4, in *D. medici*, *D. taylori* **sp. nov.** and many populations of *D. scabra* especially in the south of its range); Tail of moderate length: SVL/tail length 5.3–6.1 in males, 5.5–8.1 in females (in study area mostly greater than: *D. medici* 3.5–4.7 males, 4.5–5.7 females; *D. fasciata* 4.7–5.2 males, 4.8–6.4 females; see also Gans 1959); Nasal divided below the nostril (undivided in *D. sahelensis* and *D. parascabra*); Postoculars 2 on either side of head (often one, especially in western populations, of *D. atra*); Supralabials usually 7 (3rd and 4th enter orbit) on either side of head (usually 6[2,3] in *D. loveridgei* **comb. nov.**).

Ventral counts in *D. abyssina* are mostly higher (226–247 in males; 241–271 in females) than the nearest populations of *D. scabra* in south-eastern Sudan and adjacent South Sudan (213; 222–227) and Ethiopia (212–218; 219–243), and much higher than *D. taylori* **sp. nov.** which occurs in northern Somalia and Djibouti (196–216; 208–222) (Appendix 1). Dorsally plain brown specimens are similar to the brown/grey phases of *D. atra* in north-eastern Africa and *D. scabra* in South Africa (e.g. De Waal 1978), although the venter may be yellowish-cream (MCZ 80984) rather than the usual plain cream. In addition, *D. abyssina* can often be separated from *D. atra* on account of its higher ventral counts (199–232 in *atra* males, 212–256 in females) and possession of two (rather than 1–2) postoculars on either side of the head. Plain phase *D. abyssina* are always distinguished from plain phase *D. atra* in Ethiopia (the only area where the two species are sympatric) by having higher ventral + subcaudal counts (both sexes, 294–323 [*N* =7] versus 269–291 [*N* = 5] respectively).

Description. Dorsum of patterned specimens with oblique dark saddles (65–98, *N* = 11), usually wider than long, and often confluent or forming zigzags on the back and tail. Lateral bars dark, long, mostly broader above than below, somewhat irregular and often in contact with the pale interspaces between saddles, sometimes in narrow contact with the edges of the saddles, and may extend onto the ventral plates as in the lectotype, but never forming a distinct or broadly linked pattern. Ventral scales cream-white with extensive black, grey or brown markings on the anterior half, consisting of a large rounded cone on either side joined to a smaller cone in the centre. In live specimens the labials and interspaces between saddles are cream-yellow, and there may also be some cream-yellow on the sides of the head.

Four specimens from Eritrea in the Vienna collection (NMW) were listed under *D. scabra* by Gans (1959), with the dorsal patterns of three of them recorded as '5I' (i.e. black rectangular saddles and lateral bars forming complete closure around the pale inter-saddle areas; see Gans 1959, Pl. VI, Fig. 4, and Fig. 20G). This material was examined in detail by the first author and all four specimens have at least some indication of the '5I' *D. arabica* **sp. nov.**-like dorsal pattern: NMW 15300 has almost the entire dorsum patterned '5I'; NMW 15301–3 is similar but has mostly *D. abyssina*-like markings (as described above) at midbody; NMW 15301–1 has mostly *abyssina*-like markings anteriorly and mostly '5I' markings posteriorly, although the pattern is not synchronised on either side of the midline just posterior to midbody (Gans 1959, Pl. VI, Fig. 3); while NMW 15301–2 has *abyssina*-like markings on the first quarter of the body and '5I' markings on the rest of the dorsum. Gans (1959: 125) noted that although some '5I' specimens had an immaculate venter (presumably including ZMB 7631 from Bogos = *D. crucifera* **sp. nov.** and BM 03.6.21.41 from El Kubar = *D. arabica* **sp. nov.** – see below), NMW 15301–2 (Gans, 1959, Pl. IX, Fig. 7) and NMW 15301–3 both had heavily dark-bordered ventrals like the lectotype of *D. abyssina* (Duméril, Bibron & Duméril 1854, Pl. 81, Fig. 1–2; Fig. 20B). Re-examination of this material indicated that NMW 15301–1 also has the typically well marked *abyssina*-like ventral pattern, although the markings are pale grey in colour, while the ventral pattern of NMW 15301–3 is actually somewhat different to the others in that it consists of a large bold dark spot at the edges of the ventral plates, usually with 2–3 more-or-less disconnected paler blotches towards the centre. The distinct ventral markings of NMW 15300 are brown, which is perhaps an artifact of preservation.

A plain tan brown to greyish phase with a largely unmarked cream to cream-yellow venter is also known, sometimes occurring in sympatry (at Gondar and Keriyo) with the patterned phase. In fact, one of the six males and as many as five of the 10 females are plain phase (marked by asterisks in 'Localities' below). A detailed description of two plain phase specimens follows: MCZ 80984 (Gondar to Asmara): dorsal scales are mostly pale tan, but the edges at the base and sides (anterior proximal half) of each scale is grey; NMB R10257 (Keriyo): dorsal scales pale tan with numerous tiny dark dots, and basal one-third of scale, as well as area around apical pits, grey. In both specimens the lowermost scale row on either side is without dark markings, while the scales of the adjacent row above have few dark markings on the lower edges of the scales, but the upper part of the scale base is dark; dark markings at the base of scales creates the impression of a very weak vertebral stripe and similar lateral bands, especially in NMB R10257. Dorsal scales of the latter

specimen (and the plain phased NMZB 17099, also from Keriyo) are more elongate than in patterned conspecifics, and have rounded tips (compared to dorsals less elongate, sharply triangular and acutely-tipped in NMB R10256, a patterned specimen from the same locality as NMB R10257). However, the shape and serration of dorsal scales in MCZ 80984 is similar to that of patterned specimens. Belly and subcaudal region immaculate cream. In addition, these three plain phase specimens have only two rows of weakly serrated, inclined and reduced dorsals on either side of the body.

Preoculars 1 on either side of head (N = 18), postoculars usually 2 on either side of head, but one in BM 1902.12.13.86 (N = 18); frontal shield usually for the most part smooth with marginal pitting (States 1 & 2; with a single row in most specimens examined in detail), but entirely smooth in BM 1902.12.13.85 (State 0) (N = 13); inter-prefrontal suture usually weakly marked, but moderately marked in two specimens (MZUF 783, NMW 15301–2) (N = 13); supralabials 7 (3rd and 4th enter orbit) on either side of head (N = 17), but in BM 1902.12.13.85—although the head is damaged—it is evident that only the 2nd and 3rd supralabials on either side enter the orbit; anterior temporals usually two on either side of head (94.4%), but 1 left and 2 right in NMZB 17099 (N = 18); posterior temporals three on either side of head (38.5%), 3:4 or 4:3 (23.1%), 2:3 or 3:2 (23.1%), 1:2 in BM 1902.12.13.86 and 4 on right (left side damaged) in BM 1902.12.13.85 (N = 13); temporal formula on either side of head usually 2+3, often 2+4; midbody scale rows 21–25 (mean 23.1 ± 1.27, N = 19); ventrals 226–247 in males (N = 6), 241–271 in females (N = 10); subcaudals 57–68 in males (N = 4), 49–65 in females (N = 9). Dorsally brown or grey *D. abyssina* have higher ventral + subcaudal counts than plain phase *D. atra* in Ethiopia (both sexes, 294–323 [N =7] versus 269–291 [N = 5] respectively). Ratio SVL: tail length 5.3–6.1 in males (N = 4), 5.5–8.1 in females (N = 10); total length: tail length 6.3–7.1 in males (N = 4), 6.5–9.1 in females (N = 10).

Size. Largest male (NMW 15301–3 – Eritrea) has a SVL of 504 mm (tail trunctated). Largest female (MNHN 6567 – 'Abyssina', proposed lectotype, see below) 665 + 90 = 755 mm (see Duméril *et al.* 1854).

Habitat. Open savannah in the Ethiopian Highlands at elevations of 1800–2450 m (Figs 21 & 22). A subadult male, BM 69.11.4.38, although having an 'Arabia' (e.g. Gans 1959, Appendix 1) label in its museum jar, was in fact collected at Senafe, Eritrea at 2450 m (Blanford 1870), probably in *Juniperus* coniferous forest. Keriyo, north of Addis Ababa, is the southern-most locality for this species, situated at an altitude of 2320 m (Spawls 2004).

Distribution. Restricted to central and north-western Ethiopia, and central Eritrea (Fig. 3).

Sympatry. Sympatric with *D. atra* at Keriyo (Ethiopia).

Localities. (Plain phase specimens indicated by asterisks.) ERITREA. No locality, NMW 15301–1, 15301–2, 15301–3; Gheleb [NE 1538D4] NMW 15300; Senafe [NE 1439C2] BM 69.11.4.38. ETHIOPIA. No locality, MNHN 6567 (proposed lectotype, see above); Gondar [NE 1237C2] FMNH 12728, MSNM 2699a*,b,c, MZUF 783; Gondar to Asmara [ca. NE 1338A = Ras Daschen Terera] MCZ 80984*; Keriyo [NE 0938B3] NMBO 10256–7*, NMZB 17099*; Mai Canetta [NE 1338D4] MSNM 2700A*,B*; Zegie, Lake Tsana [NE 1137C2] BM 1902.12.13.85–6*.

Biogeography. In the terrapin *Pelomedusa subrufa* Bonnaterre species complex, *P. barbata* Petzold *et al.* occurs in Saudi Arabia and Yemen, with closely-related populations of *P. gehafie* Rüppell in Eritrea and eastern Sudan, and *P. somalica* Petzold *et al.* in northern Somalia (Petzold *et al.* 2014). Similarly, *D. arabica* **sp. nov.** inhabits Saudi Arabia and Yemen, *D. crucifera* **sp. nov.** is found in northern Eritrea, *D. abyssina* is restricted to central Eritrea and the northern half of Ethiopia, while *D. taylori* **sp. nov.** occurs only in Somaliland and adjacent Djibouti.

Conservation. Using IUCN (2012, 2016) criteria, this species appears to be widespread and should be regarded as Least Concern.

Remarks. Saleh & Sarhan's (2016: 26) comment that Trape *et al.* (2012) concluded that *D. abyssina* is a valid species "based on molecular phylogenetic data" is incorrect. Trape *et al.* (2012) did not include *D. abyssina* in their genetic analysis but followed Trape & Mané (2006) who treated this species as valid on morphological grounds.

Dasypeltis crucifera Bates **sp. nov.**
Cross-marked Egg-eater
Figs 23A–B, 24A–C & 25A–B

Dasypeltis scabra (not Linnaeus) Gans, 1959: 141 (part, Bogos, Pl. V, Fig. 4; Appendix 1, p. 204); Largen & Rasmussen, 1993: 340–341 (part, Agordat, Keren).

Holotype. ZMB 7631 (at Museum für Naturkunde, Berlin), an adult female (right side ovary examined) from Bogos, Eritrea (Gans 1959, Pl. V, Fig. 4; Fig. 23A–B & 24A–C). The specimen was purchased from Edward Gerrard (a London taxidermist and dealer of natural history objects) by the Zoologisches Museum der Königlichen Friedrich-Wilhelms-Universität zu Berlin during the second half of the 19th century (F. Tillack in litt., 15 April 2016). Bogos is a name that may refer to the city of Keren (also known as Senhit or Blin: 15°46'40"N, 38°27'29"E; NE 1538C4), but it may have been used as a more general term referring to the land of the Bogo people (an indigenous ethnic group) in Anseba Region, between the highlands and lowlands of Eritrea.



Figure 21. Habitat of *Dasypeltis abyssina* and *D. atra* near Lake Tana, north of Addis Zemen, Ethiopia. (Photo: T. Mazuch)



Figure 22. Habitat of *Dasypeltis abyssina* south of Gondar, northern Ethiopia. (Photo: T. Mazuch)

Paratypes. Two specimens: ERITREA. Allotype. MZUT 3582 (at Museo Regionale di Scienze Naturali di Torino, Turin), a juvenile male from Agordat [15°33'N, 37°53'E; NE 1537D2] (the specimen tag notes 'Giachetti! cei det. 21.8.88' [Fig. 25A–B]); MSNG 6738, probably female, from Keren [15°46'40"N, 38°27'29"E; NE 1538C4].

Additional material. One specimen: ERITREA. MZUT 3469, an adult female from Agordat [as above].

Diagnosis. Where data for MZUT 3469 (see "Additional material") falls outside the ranges recorded for the type series, this is indicated below.

Assigned to the genus *Dasypeltis* on account of its slender form, possession of (usually 3–4) rows of reduced, oblique, keeled and serrated lateral scales (little or no serration in *D. inornata*) and head barely distinct from the neck (moderately distinct in *D. fasciata*). Differs from all other taxa in the genus by its unique dorsal colour pattern, in which dark brown oval saddles and lateral bars almost completely enclose pale cross-markings that form the inter-saddle areas (a variation of the '5I' pattern found in Arabian *Dasypeltis*; Figs 23A & 25A), together with a combination of the following characters: Pattern cycles 51–62 (higher than *D. bazi* 38–49; lower or mostly lower than *D. fasciata* 66-141, *D. abyssina* 65-98, *D. atra* 62-130, *D. arabica* **sp. nov.** 62-79; *D. inornatus* always uniform brown above, *D. gansi* uniform or weakly marked); flanks decorated with dark vertical bars (spots, blotches or squarish in *D. bazi*, *D. loveridgei* **comb. nov.** and some populations of *D. scabra*); and venter immaculate apart from a few dark markings at the edges (extensive dark markings in *D. abyssina* and in many *D. scabra*); Ventrals: 226 in male (higher than *D. taylori* **sp. nov.** 196–216, *D. sahelensis* 207–221, *D. inornata* 208–225, *D. parascabra* 210–223), 231–243, 247 (MZUT 3469) in females (higher than *D. taylori* **sp. nov.** 208–222); Subcaudals 61 in male (higher than *D. loveridgei* **comb. nov.** 47–58; lower than *D. inornata* 81–92, *D. fasciata* 59, 71–91, *D. medici* 69–109, *D. gansi* 68–83, *D. palmarum* 68–77, *D. parascabra* 67–74, *D. latericia* 66–86, *D. arabica* 63–65), 49–52 in females (lower than *D. inornata* 69–84, *D. fasciata* 64–84, *D. palmarum* 62–77, *D. medici* 61–90, *D. gansi* 59–73; *D. latericia* 59–72, *D. parascabra* 57–64, *D. arabica* **sp. nov.** 53–61); Inter-prefrontal sulcus weakly marked (moderately to deeply marked in *D. arabica* **sp. nov.**, weakly to moderately marked in *D. bazi*, usually moderately marked in *D. taylori* **sp. nov.**, and variable in *D. scabra* [often well marked in the south of its range]); Frontal shield marginally pitted, State 1 or 2 (extensively pitted, States 3 & 4, in *D. medici*, *D. taylori* **sp. nov.** and many populations of *D. scabra* especially in the south of its range); Nasal divided below the nostril (undivided in *D. sahelensis* and *D. parascabra*); Postoculars 2 on either side of head (often one, especially in western populations, of *D. atra*); Supralabials usually 7 (3rd and 4th enter orbit) on either side of head (usually 6[2,3] in *D. loveridgei* **comb. nov.**).

Description of holotype. The holotype (ZMB 7631) is an adult female with a total length of 506 mm, snout-vent length 442 mm, tail length 64 mm. Ratio SVL: tail length 6.9, total length: tail length 7.9.

Head small and slightly distinct from the neck; snout rounded. Elongate nasal semi-divided (divided below the nostril), nostril pierced in anterior half of nasal, no loreal. Paired prefrontals larger than the paired internasals (individually and in combination). Inter-prefrontal sulcus weakly marked. Frontal large, widest anteriorly, slightly longer than broad, and smooth except for a single row of pits on the lateral borders (State 1). There is a single preocular and two postoculars on either side of head. Temporals 2+3 on either side of head. Seven supralabials, 3rd and 4th bordering the eye, on either side of head. First pair of infralabials in contact behind the mental, followed by a pair of large and elongate chin shields in broad contact, and another pair of smaller scales in narrow contact with one another and in contact with the first ventral plate, but separated posteriorly and medially by an oval extranumerary scale in broad contact with the first ventral plate. Eyes large (with vertically elliptical pupils), their length much smaller than the distance from tip of snout to anterior part of eye socket.

Dorsal scales strongly keeled, unicarinate, in 25 rows at midbody, the third, fourth and fifth rows denticulate, reduced and obliquely placed. Dorsal scales in the anal region denticulate (see Gans 1959: 204). Vertebral scale row not enlarged. There are 231 smooth ventrals, the anal plate is entire and there are 52 pairs of smooth subcaudals. After preservation in ethanol the dorsal colouration is pale brown with 62 ocelli or pattern cycles (markings are darker brown, saddles with paler brown centres) between nape and base of tail. Pale markings on the back are in the form of crosses, largely surrounded by brown, oval or diamond-shaped (sharpest ends anteriorly and posteriorly) dorsal saddles and similarly dark lateral bars, but with the tips of the crosses often separated from the dark markings. The tail has faint dark vertebral blotches anteriorly. Head with a chevron marking, interrupted on the left, with a dark arrowhead marking present on the nape. Venter immaculate cream-white apart from a few small brown spots extending from the outer scale rows onto the outer edge of ventrals.

Variation in paratypes (including allotype, as indicated). The allotype (MZUT 3582) is a juvenile male (211 + 39 = 250 mm; ratio SVL: tail length 5.4, total length: tail length 6.4); the other paratype (MSNG 6738) is a female (368 + 45 = 413 mm, ratios 8.2 and 9.2). Both specimens have similar scalation and general appearance to the holotype, but differ as follows: frontal distinctly longer than broad in MSNG 6738; on the right side of the head of the allotype there are



Figure 23. *Dasypeltis crucifera* **sp. nov.** Dorsal (A) and ventral (B) views of the holotype (ZMB 7631) from Bogos, Eritrea (Photo: F. Tillack).

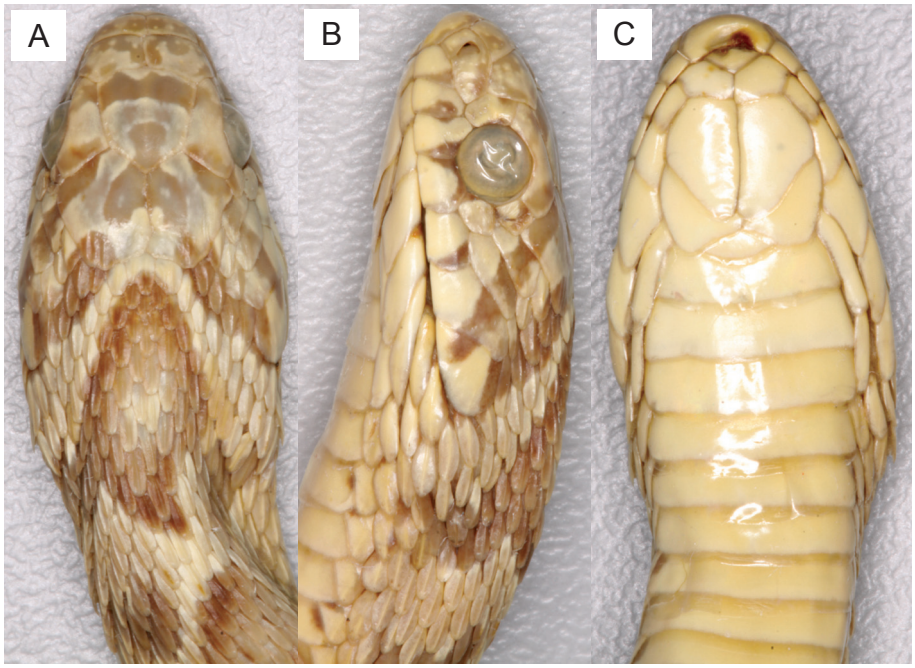


Figure 24. *Dasypeltis crucifera* **sp. nov.** Dorsal (A), lateral (B) and ventral (C) aspects of the head of the holotype (ZMB 7631) from Bogos, Eritrea (Photo: F. Tillack).

2+2 temporals; pair of small posterior sublinguals in contact with first ventral plate and not separated by an extranumerary scale (also allotype); longitudinal rows of dorsals at midbody 22 in allotype, 24 in MSNG 6738; ventrals 226 in allotype (male), 243 in MSNG 6738 (female); pairs of subcaudals 61 in allotype (male), 49 in MSNG 6738 (female); pattern cycles on the back 52 in allotype, 51 in MSNG 6738; in allotype, forward-pointing chevron marking at the back of the head is followed by a dark oval marking that extends onto the nape, where it is followed by a backwards-facing chevron; in MSNG 6738 there is a forward-pointing chevron on top of the head, followed by a forward-pointing arrowhead on the nape with a connecting stalk extending onto the neck. The dark (brown) markings (often diamond-shaped) of the allotype are less distinct than in the holotype, and only barely distinguishable from the ground colour on the posterior part of the body and on the tail; in MSNG 6738 the dark oval saddles are often more rounded at the ends such that the pale crosses are less X-like in appearance. Serration of lateral scale rows and scales above the anal region, and condition of the anal plate, not determined. No live specimens are known to the authors, nor are any photographs available.

Description of additional material: MZUT 3469 (female). This specimen is not currently available for examination and no photograph of it is available to determine its dorsal pattern (F. Andreone in litt. 3 April 2016). However, it has 247 ventrals, 50 subcaudals and 23 midbody scale rows.

Size. Largest male (allotype, MZUT 3582 – Agordat) 211 + 39 = 250 mm. Largest female (holotype, ZMB 7631 – Bogos) 442 + 64 = 506 mm.

Etymology. The name of the new species refers to the pale cross-marks between the saddles on its back.

Habitat. This species occurs in the hilly area between the lowlands associated with the drainage of the Barka River, the Sahel and the Highlands of Hamasien. Agordat is situated at low altitudes (about 600 m), while the city of Keren is at an altitude of about 1417 m (Fig. 26).

Distribution. Known from only two areas (Bogos/Keren and Agordat) in northern Eritrea (Fig. 3). Keren and Agordat are about 75 km apart.

Mimicry. *Dasypeltis crucifera* **sp. nov.** may mimic *Echis megalocephalus* Cherlin, 1990 (see photograph of *"E.* cf. *megalocephalus"* from Ginda in Dobiey & Vogel 2007; Fig. 30).

Biogeography. In the terrapin *Pelomedusa subrufa* species complex, *P. barbata* occurs in Saudi Arabia and Yemen, with closely-related populations of *P. gehafie* in Eritrea and eastern Sudan, and *P. somalica* in northern Somalia (Petzold *et al.* 2014). Similarly, *D.*



Figure 25. *Dasypeltis crucifera* **sp. nov.** Dorsal (A) and ventral (B) views of the allotype (MZUT 3582) from Agordat, Eritrea (Photo: F. Andreone).

arabica **sp. nov.** inhabits Saudi Arabia and Yemen, *D. crucifera* **sp. nov.** is found in northern Eritrea, *D. abyssina* is restricted to central Eritrea and the northern half of Ethiopia, while *D. taylori* **sp. nov.** occurs only in Somaliland and adjacent Djibouti.

Conservation. Using IUCN (2012, 2016) criteria and considering that it is known from only two areas, this species should be regarded as Data Deficient.

Remarks. The holotype (ZMB 7631) was listed under *D. scabra* ('5I' dorsal pattern) by Gans (1959) who failed to mention its distinctive cross-mark pattern, but he did indicate that while other African specimens with the '5I' dorsal pattern had heavily-marked venters (here referred to *D. abyssina*), this specimen had 'immaculate' underparts.

Dasypeltis arabica Broadley & Bates **sp. nov.**
Arabian Egg-eater
Figs 27A–C, 28A–B & 29A–B

Dasypeltis scabra (not Linnaeus) Boulenger, 1905: 180 (El Kubar, Yemen); Leviton & Aldrich, 1954, xxiii (checklist); Gans, 1959: 141 (part, El Kubar) & 1961: 73 (part, Arabia); ? Corkhill & Cochran, 1965: 485 (Little Aden oil



Figure 26. Keren, Eritrea—type locality of *Dasypeltis crucifera* **sp. nov.** (Photo: T. Mazuch)

refinery); Spanò, 1972: 132 (El Siyani, Yemen); Gasperetti, 1988: 233, 410, Fig. 39 (1) (Ajibah, Saudi Arabia); Schätti & Desvoignes, 1999: 82; Schätti & Gasperetti, 1994: 386 (Aqabat Raydah & Abha, Saudi Arabia).

Dasypeltis saeizadi Hoser, 2013: 60 ("Saudi Arabia") (*nomen dubium*); Göthel, 2015a: 19 & 2015h: 92; Saleh & Sarhan, 2016: 36.

Dasypeltis cf. *scabra* Sindaco *et al.,* 2013: 93 (part, "SW Arabia and Yemen").

Holotype. BM 1987.2192 (at Natural History Museum, London), an adult female (oviducts examined) from Sana'a, North Yemen [15º19'N, 44º14'E] collected by M. Al-Safadi (Figs 27 & 28).

Paratypes. Six specimens: YEMEN. Allotype. BM 1903.6.26.41 (at Natural History Museum, London; wrongly listed as 'xBM 03-6-21-41' by Gans 1959), an adult male (Gans 1959) from El Kubar, South Yemen [14º25'N, 45º01'E] collected by G.W. Bury; BM 1987.2193, adult female from Taiz, North Yemen [13º35'N, 44º01'E] collected by M. Al-Safadi; MSNG 52221, male from El Siyani, North Yemen, collected by G. Scortecci, 13 August 1965. SAUDI ARABIA. BM 1987.1018, female from Ajibah [19º41'N, 41º57'E] collected by J. Gasperetti (Fig. 29); MHNG 2536.41, male from Aqabat Raydah [NE 1942C]; MHNG 2536.42, female from vicinity of Abha [about 18º13'N, 42º30'S].

Diagnosis. Assigned to the genus *Dasypeltis* on account of its slender form, possession of (usually 3–4) rows of reduced, oblique, keeled and serrated lateral scales (little or no serration in *D. inornata*) and head barely distinct from the neck (moderately distinct in *D. fasciata*). Distinguished from other congeners by its unique dorsal colour pattern in which black rectangular saddles and lateral bars form complete closure around the pale inter-saddle areas (Figs 27A & 29A; this pattern also occurs on parts of the back of a few *D. abyssina* from Eritrea, see pattern'5I' of Gans 1959, Pl. VI, Fig. 4); together with a combination of the following characters: Pattern cycles 62–79 (≤62 in *D. crucifera* **sp. nov.**, *D. taylori* **sp. nov.** and *D.bazi*; *D. inornatus* always uniform brown above; *D. gansi* uniform or weakly marked); flanks decorated with dark vertical bars (spots, blotches or squarish in *D. bazi*, *D. loveridgei* **comb. nov.**, and some populations of *D. scabra*—e.g. Fig. 5G); and venter immaculate apart from a few dark markings at the edges (extensive dark markings in *D. abyssina* and many *D. scabra*); High numbers of ventrals: 236–244 in males (higher than *D. scabra* 180–226, *D. taylori* **sp. nov.** 196–216, *D. confusa* 199–227, *D. atra* 199–232, *D. sahelensis* 207–221, *D. inornata* 208–225, *D. bazi* 213–229, *D.*

parascabra 210–223 and *D. crucifera* **sp. nov.** 226), 239–254 in females (higher than *D. taylori* **sp. nov.** 208–222, *D. sahelensis* 212–237, *D. bazi* 215–234, *D. inornata* 219-237, *D. parascabra* 224–237); Subcaudals 63–65 in males (higher than *D. loveridgei* **comb. nov.** 47–58, *D. bazi* 59–61, *D. crucifera* **sp. nov.** 61; lower than *D. inornata* 81–92, *D. fasciata* 59, 71–91, *D. medici* 69–109, *D. gansi* 68–83, *D. palmarum* 68–77, *D. parascabra* 67–74, *D. latericia* 66–86), 53–61 in females (higher than *D. loveridgei* **comb. nov.** 39–50, *D. taylori* **sp. nov.** 44–52, *D. crucifera* **sp. nov.** 49–52; lower than *D. inornata* 69–84, *D. fasciata* 64–84, *D. palmarum* 62–77; mostly lower than *D. medici* 61–90); Inter-prefrontal sulcus usually moderately, occasionally deeply, marked (usually weakly marked in other species, but weakly to moderately marked in *D. bazi*, usually moderately marked in *D. taylori* **sp. nov.**, and variable in *D. scabra* [often well marked in the south of its range]); Frontal shield marginally pitted, usually State 1 (extensively pitted, States 3 & 4, in *D. medici*, *D. taylori* **sp. nov.** and many populations of *D. scabra* especially in the south of its range); Nasal divided below the nostril (undivided in *D. sahelensis* and *D. parascabra*); Postoculars 2 on either side of head (often one, especially in western populations, of *D. atra*); Supralabials 7 (3rd and 4th enter orbit) on either side of head (usually 6[2,3] in *D. loveridgei* **comb. nov.**).

Description of holotype. The holotype (BM 1987.2192) is an adult female with a total length of 714 mm, snout-vent length 625 mm, tail length 89 mm; ratio SVL: tail length 7.0, total length: tail length 8.0.

Head small and barely distinct from the neck; snout rounded. Elongate nasal semi-divided (divided below the nostril), no loreal. Paired prefrontals slightly larger than the paired internasals (individually and in combination). Inter-prefrontal sulcus moderately marked. Frontal large, widest anteriorly, 1.14 times longer than broad, and smooth except for a single row of pits on the lateral borders (State 1). There is a single preocular and two postoculars on either side of the head. Temporals 3+3 (left), 2+4 (right). Seven supralabials, 3rd and 4th bordering the eye, on either side of the head. First pair of infralabials in contact behind the mental, followed by a pair of large and elongate chin shields in broad contact which extend backwards to separate a smaller pair of posterior ones, which are followed by a pair of supranumerary shields, the right one being partially fused with the first ventral. Eyes moderate in size (with vertically elliptical pupils), their length much smaller than the distance from tip of snout to anterior part of eye socket.

Dorsal scales strongly keeled, unicarinate, in 25 rows at midbody, the third, fourth, fifth and sixth rows denticulate, reduced and (except for the 3rd row) obliquely placed. Dorsal scales in the anal region very feebly denticulate. Vertebral scale row not enlarged. There are 240 smooth ventrals, the anal plate is entire and there are 53 pairs of smooth subcaudals. After preservation in ethanol the dorsal colour pattern consists of black rectangular saddles and similarly coloured lateral bars (on a pale brown to grey background) that form complete closure around the pale (whitish) square to rectangular inter-saddle areas. There are 67 ocelli or pattern cycles (dark with pale centres) between nape and base of tail. The tail has faint dark vertebral blotches anteriorly. Head with remnants of fragmented chevrons, and a dark forward-pointing arrowhead marking is present on the nape. Venter immaculate cream to white apart from a few dark spots extending from the outer scale rows onto the outer edges of ventrals.

Variation in paratypes (including allotype, as indicated). The six paratypes comprise three males and three females. The largest male (MSNG 52221) measures 563 (486 + 77) mm, SVL/tail length 6.3, total length/tail length 7.3; BM 1903.6.21.41 (allotype) measures 325 + 56 mm, ratios 5.8 and 6.8. Measured females (BM 1987.2193: 400 + 64 mm, ratios 6.3 and 7.3; BM 1987.1018: 561 + 75 mm, ratios 7.5 and 8.5) are smaller than the holotype. The paratypes have similar scalation and general appearance to the holotype, but differ as follows: Midbody scale rows are 23 (3 specimens, including allotype), 24 (1) or 25 (2) (Appendix 1). Ventrals 236–244 in males (244 in allotype), 239–254 in females (Appendix 1). Subcaudals 63–65 in males (65 in allotype), 53–61 in females (Appendix 1). Paired prefrontals much larger than the paired internasals in MHNG 2536.41 & 42; inter-prefrontal sulcus usually moderately developed but deeply marked in MHNG 2536.41; frontal with two rows of pits (State 2) on its outer surface in MHNG 2536.41; temporals in 2+3 arrangement in MHNG 2536.41 & 42; usually third, fourth and fifth (also sixth in two specimens) lateral scale rows reduced in size, serrated and inclined; serration on scales above vent faint or absent. Pupils appear round in BM 1987.2193. In MHNG 2536.41 the dark dorsal markings are joined along only the last one-fifth of the body (from snout to vent), elsewhere being similar to the '5N' markings of *D. scabra* (see Gans 1959), while in MHNG 2536.42 most of the markings on the body are *D. scabra*-like, but with several '5I' markings posteriorly. Dorsal pattern cycles 62–79 (Appendix 1), the first neck band divided in BM 1903.6.21.41 (allotype) and MHNG 2536.42 (divided by an elongated vertebral band). A narrow, somewhat irregular, forward-pointing chevron is present on the back of the head in BM 1987.1018. No live specimens are known to the authors, nor are any photographs available. (Frontal and eye-snout measurements, and patterning on the top of the head, were not recorded for paratypes. For MSNG 52221 only size [see above], colour pattern, and numbers of supralabials, preoculars, postoculars, temporals, midbody scale rows, ventrals and subcaudals were recorded.)



Figure 27. *Dasypeltis arabica* **sp. nov.** ['5l' colour pattern of Gans 1959] Dorsal (A), ventral (B) and lateral (C) views of the holotype (BM 1987.2192) from Sana'a, northern Yemen. (Photos: M.F. Bates)



Figure 28. *Dasypeltis arabica* **sp. nov.** ['5l' colour pattern of Gans 1959] A: Dorsal (left), lateral (middle) and ventral (right) aspects of the head of the holotype (BM 1987.2192) from Sana'a, northern Yemen (Photo: Natural History Museum, London); B: Dorso-lateral aspect of the head of the holotype (in water, Photo: M.F. Bates).



Figure 29. *Dasypeltis arabica* **sp. nov.** ['5l' colour pattern of Gans 1959] A: Dorsal view of a paratype (BM 1987.1018) from Ajibah, Saudi Arabia. (Photo: M.F. Bates); B: Dorsal (left), lateral (middle) and ventral (right) aspects of the head of the paratype (Photo: Natural History Museum, London).

Size. Largest male (MSNG 52221 – El Siyani, North Yemen) 486 + 77 = 563 mm. Largest female (BM 1987.2192, holotype – Sana'a, North Yemen) 625 + 89 = 714 mm.

Etymology. The name of the new species refers to the region of origin (Arabia) of the type series.

Habitat. This species occurs in the south-western highlands of Saudi Arabia and Yemen from 1300 m to 2300 m (annual rainfall exceeds 300 mm).

Distribution. South-western part of Saudi Arabia and western Yemen (Fig. 3).

Mimicry. *Dasypeltis arabica* **sp. nov.** may mimic *Echis coloratus* Günther (see photographs from the Sinai Peninsula in Dobiey & Vogel [2007]). Gasperetti (1988) showed that *E. coloratus* also occurred from Saudia Arabia to the south coast of Yemen, and illustrated a topotype from Jabel Grayyah in Saudia Arabia (his Fig. 123) showing pale vertebral spots (described as 'pinkish' in the description of the holotype by Günther [1878]). The new species is also similar to *Echis megalocephalus* (Fig. 30).

Biogeography. *Dasypeltis arabica* **sp. nov.** has a similar distribution to *Naja arabica* Scortecci, except that the latter also occurs further east in the highlands of Dhofor, Oman (Trape *et al.* 2009). The geological history of the region is summarised by Leviton (1986): "During the entire Mesozoic and early Cenozoic, Arabia, Nubia and Somalia were assembled in one continental block at some times covered by shallow seaways (Bosellini, 1986). The onset of Neogene rifting, accompanied by the 'slight oblique drifting' of Africa and Arabia resulted in the opening of the Gulf of Aden." Boulenger (1905) described, from El Kubar in Yemen, *Atractaspis andersoni* which was considered closely related to *Atractaspis leucomelas* Boulenger of Somalia, and also *Zamenis* [= *Platyceps*] *variabilis*, closely related to *Platyceps brevis* Boulenger of Somalia. In the terrapin *Pelomedusa subrufa* species complex, *P. barbata* occurs in Saudi Arabia and Yemen, with closely-related populations of *P. gehafie* in Eritrea and eastern Sudan, and *P. somalica* in northern Somalia (Petzold *et al.* 2014). Similarly, *D. arabica* **sp. nov.** inhabits Saudi Arabia and Yemen, *D. crucifera* is limited to northern Eritrea, *D. abyssina* is restricted to central Eritrea and the northern half of Ethiopia, while *D. taylori* **sp. nov.** occurs only in Somaliland and adjacent Djibouti. Lavin & Papenpuss (2012) cite several recent molecular studies that show that the Red Sea and Gulf of Aden are barriers to various reptiles between the Arabian Peninsula and Africa.

Conservation. Using IUCN (2012, 2016) criteria, this species appears to be widespread and should be regarded as Least Concern.



Figure 30. *Echis megalocephalus* (BM 1987.3217) from Nocra Island, Dahlak Archipelago, Eritrea—a possible model species for mimicry by *Dasypeltis arabica* **sp. nov.** and *Dasypeltis crucifera* **sp. nov.** (Photo: T. Mazuch)

Remarks. Corkill & Cochran (1965) recorded a specimen (whereabouts unknown, not plotted on map) of *"D. scabra"* from Little Aden (oil terminal) on the coast in southern Yemen, but its identity remains problematic.

We concur with the opinions, recommendations and proposals of Kaiser *et al.* (2013) and Kaiser (2014) regarding best taxonomic practices, and therefore reject the unscientific and unethical taxonomy of Raymond Hoser (2013, description of *Dasypeltis saeizadi*). We note specifically that the privately published and personally edited work of Hoser (2013) is in direct violation of the spirit and intention of the Code (ICZN 1999) as indicated by, *inter alia*, Recommendation 8A which explicitly encourages publication in "appropriate scientific journals or well-known monographic series" (see also comments by Schleip [2014] regarding non-compliance with the ICZN [1999]). It can be added that in their *Snakes of the World* catalogue, Wallach *et al.* (2014: ix) state: "The *Australasian Journal of Herpetology* [in which the Hoser 2013 paper was published], of which Hoser is the editor, reviewer, publisher, and sole author, is not considered a valid publication under the spirit of the Code and therefore all proposed names are *nomina illegitima* (see Wallach *et al.*, 2009 and Kaiser *et al.*, 2013)."

Hoser (2013) named 'BMNH – 1987.1018' as holotype and sole type specimen of what he considered a new species, namely *D. saeizadi*, from 'Saudi Arabia'. His diagnosis is based entirely on a vague comparison of colour patterns between *D. scabra*, *D. abyssina* (presumably based on MNHN 6567, the Ethiopian syntype of *R. abyssinus* – the only specimen of this taxon known at the time, incorrectly referred to as the 'holotype' of *D. abyssina* by Trape & Mané 2006, see discussion above) and the proposed new species. Hoser (2013: 60) noted that the latter is "readily separated" from both *D. scabra* and *D. abyssina* "by the dorsal colouration". However, he proceeded to make the following erroneous statements in this regard: According to Hoser (2013: 60): *D. abyssina* has "indistinct markings on the head and body and a complete absence of barring on the upper labials, or if present, it [barring on supralabials] is effectively indistinct." However, the proposed lectotype (MNHN 6567) of *D. abyssina* and all other known (patterned) specimens of this species (see species account above) have very distinct dark markings dorsally and laterally on the head, body and tail, including distinct barring on the supralabials (see Duméril *et al.* 1854, Pl. 81, Fig. 1 in colour & Fig. 20 in the current paper); while even the Nil Blanc 'syntype' (paralectotype, MNHN 7227 = *D. scabra*) has distinct markings as described above. Hoser (2013: 60) then stated that his new species is "more similar to *D. scabra* in dorsal colouration, but lacks the distinctive whitish patches interspercing the dorsal midline blotches or squares. In turn these blotches or squares tend somewhat towards being pointed at the anterior end of the body". Again this is incorrect as the dorsal pattern of BM 1987.1018 differs distinctly from *D. scabra* (Gans' 1959 '5I' versus '5N' dorsal colour patterns respectively), the pale patches on its back are very distinct, and the saddles are for the most part not at all markedly pointed anteriorly (Fig. 29A). Hoser (2013: 60) added that his proposed new species "In contrast to the other two species [*D. scabra* and *D. abyssina*]" has a "darkening on the upper temples" and "Like *D. abyssina* there is a complete absence of barring on the upper labials", "or if present, it [barring on the supralabials] is effectively indistinct." Once again this is incorrect as Fig. 29A–B clearly shows that the upper temples of BM 1987.1018 are not darker than other parts of the head, nor are they noticeably darker than in *D. abyssina* (Duméril *et al.* 1854, Pl. 81, Fig. 1; Fig. 20C–G) or *D. scabra* (e.g. Gans 1959, Pl. IV-V; Broadley 1990, Fig. 152; Bates *et al.* 2014, p. 411, lower figure; Fig. 5), and the supralabials (of BM 1987.1018) are in fact distinctly barred, as are those of *D. abyssina* (Duméril *et al.* 1854, Pl. 81, Fig. 1; Fig. 20C–G). Hoser (2013) did not provide any additional features for distinguishing his proposed new species. It is therefore evident from the aforementioned that Hoser's (2013) description is a mis-representation of reality—his description is not based on the true features of the specimen he names as holotype. His description cannot therefore be considered valid and in accordance with the requirements of the Code (e.g. Article 1, which requires that an actual specimen be used for the description of an extant or extinct species of animal). More specifically, Article 1.3.1 excludes from the provisions of the Code any name proposed for a hypothetical concept, which is what Hoser's (2013) name must be considered, as it can be shown (see above) that it is not based on the features of the specimen he named as holotype (no paratypes).

According to Patrick Campbell at the Natural History Museum, London (in litt. 3 September 2015), no record exists of Raymond Hoser having ever borrowed any *Dasypeltis* from that institution, or of him having spent time at that museum examining such specimens. If Hoser had indeed examined the specimen, or even an image thereof, the characteristic '5I' dorsal pattern (see Gans 1959, and Figs 27A & 29A) of Arabian populations of *Dasypeltis* would have been obvious immediately. Hoser (2013) also disregarded Recommendation 73C of the Code (1999) by not providing full collection details for the specimen and neglecting to provide any supporting meristic or morphometric data, including ventral, subcaudal and midbody scale row counts—all considered standard fare in modern snake descriptions. The lack of any such data in his description is a further indication that he did not examine the specimen (or an illustration thereof) that he named as holotype. In consideration of the above, Hoser's (2013) name must be considered a *species inquirendum* and a *nomen dubium* and rejected as an available name for *D. arabica* **sp. nov.**

MULTIVARIATE ANALYSES

For the analysis of all populations, two-way permanova (10 000 permutations) detected that there is no interaction between gender and species (df 9, F = –16.69, p = 0.67). However, it detected significant differentiation at species level (df 9, F = 2.43, p < 0.001) and at gender level (df 1, F = 5.28, p < 0.001) respectively, justifying separate analysis of sexes. For the Horn of Africa analysis, two-way permanova (10 000 permutations) detected that there is no interaction between gender and species (df 9, F = –3.19, p = 0.53). However, it detected significant differentiation at species level (df 6, F = 1.29, p < 0.001) and at gender level (df 1, F = 2.24, p < 0.001) respectively, justifying separate analysis of sexes.

A total of 249 specimens (*D. medici*: 9 males, 20 females; *D. confusa*: 6, 13; *D. scabra*: 24, 40; *D. bazi*: 3, 2; *D. taylori*: 3, 2; *D. atra*: 40, 62; *D. fasciata*: 2, 3; *D. abyssina*: 4, 7; *D. crucifera*: 1, 2; *D. arabica*: 2, 4) had complete sets of data and were used in the analyses (separately for males and females) of the entire study area. A total of 64 specimens (*D. scabra*: 6 males, 13 females; *D. bazi*: 3, 2; *D. taylori*: 3, 2; *D. atra*: 7, 9; *D. abyssina*: 4, 7; *D. crucifera*: 1, 2; *D. arabica*: 2, 4) with complete data were used in analyses (separately for sexes) of the Horn of Africa and Egypt. In the analyses for males from the latter area, numbers of preoculars was invariable and was therefore excluded. For pattern cycles, plain coloured specimens (including 'intermediate' *D. medici* with barely distinguishable darker dorsal markings) were scored as '0'.

Principal Component Analysis for north-eastern Africa and south-western Arabia

In the analysis of males (Fig. 31) the first two principal components (PC) explained most of the variance (36.2%). Only *D. medici* formed a distinct cluster distinguishable from all other populations, mostly along PC 2 for which numbers of subcaudals (0.54) and ventrals (0.40) had the highest loadings (Table 3). For females the first two components also explained most of the variance (37.2%), and again only *D. medici* formed a distinct cluster distinguishable from all other populations (Fig. 31), with the highest loadings (on PC 2) for subcaudals (–0.49) and pattern cycles (0.49) (Table 4). However, both sexes of *D. scabra*, *D. atra* and *D. confusa* also formed clusters and were partly distinguishable along PC 2.

Discriminant Function Analysis for north-eastern Africa and south-western Arabia

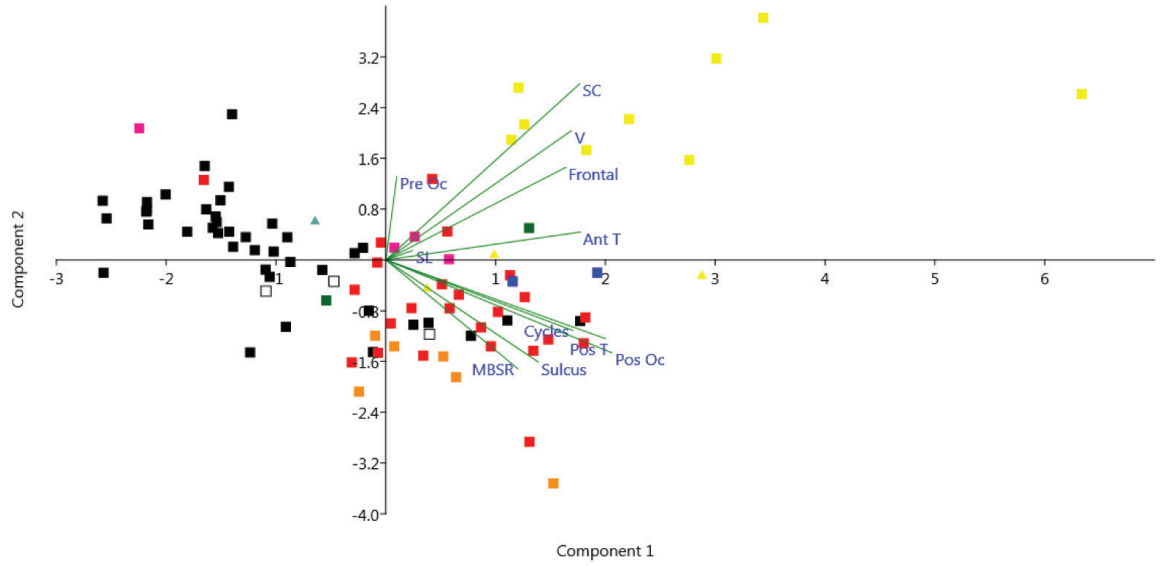
As all groups (as male or female of a species) are real geographical entities it is appropriate to conduct Discriminant Function Analysis to determine whether or not they are distinguishable. In the analysis of males of the various species (Fig. 32), 83.9% of specimens were correctly classified, but this included only 50% of *D. confusa*, while one out of three specimens of both *D. taylori* **sp. nov.** and *D. bazi* were mis-classified (Table 5). *Dasypeltis medici* was easily distinguishable from all other species along axis 1, on which numbers of subcaudals (0.81) and ventrals (0.60) load most heavily; *Dasypeltis scabra* and *D. atra* are largely separated along axis 2, on which fontal pitting (0.67) and pattern cycles (0.54) load most heavily; *D. abyssina* and *D. arabica* are also separated from *D. scabra* along axis 2, on which number of ventrals (0.41) is also an important factor (Table 6). For females (Fig. 32), 75.5% of specimens were correctly classified, but this included only 61.5% of *D. confusa*, 50% of *D. taylori* **sp. nov.**, *D. arabica* **sp. nov.** and *D. crucifera* **sp. nov.**, and neither of two specimens of *D. bazi* (Table 7). *Dasypeltis medici* is again easily distinguishable from all other species along axis 1, on which numbers of subcaudals (0.92) loads most heavily; *Dasypeltis scabra* and *D. abyssina* are well separated along axis 2, on which fontal pitting (0.67) and ventrals (0.64) load most heavily; and *D. scabra* and *D. atra* are partially separable on this axis (Table 8).

Principal Component Analysis for the Horn of Africa and Egypt

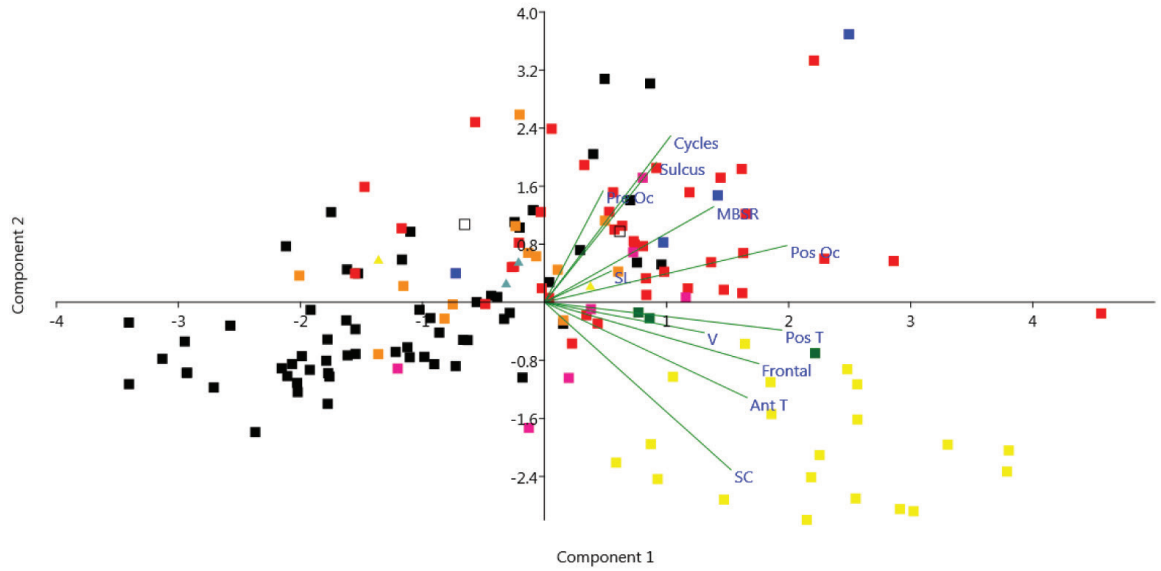
In the analysis of males the first two principal components (PC) explained most of the variance (40.1%); for females these components also explained most of the variance (38.7%). Although some species are largely distinguishable, none of the groups for males or females formed distinct clusters (Fig. 33; Tables 9 & 10).

Discriminant Function Analysis for the Horn of Africa and Egypt

In the analysis of males (Fig. 34) all specimens with the exception of one of three *D. bazi* were correctly classified, suggesting that they are 100% distinguishable in morphometric space (Table 11). All species were fully or partly (*D. abyssina* and *D. arabica* **sp. nov.**) distinguished along axis 1—on which ventrals (2.51) and midbody scale rows (2.09) load most heavily—except *D. atra* and *D. bazi* which are nevertheless largely separated along axis 2, for which pattern cycles (0.82) and frontal pitting (–0.68) load most heavily (Table 12). For females (Fig. 34), 81.6% of specimens were correctly classified; this figure was at least 75% for all species except *D. bazi* for which one of two specimens was incorrectly classified (Table 13). *Dasypeltis scabra* was distinguished from *D. arabica* **sp. nov.** and *D. abyssina* along axis 1, while the latter two species were distinguished along axis 2; *D. taylori* **sp. nov.** and *D. bazi* were distinguished from *D. arabica* **sp. nov.** and *D. abyssina* along axis 1; *D. scabra* is also distinguished from *D. crucifera* **sp. nov.** along axis 2; *D. atra* is distinguished from *D. arabica* **sp. nov.** along axis 2, and also partly from *D. scabra* on this axis (Table 14). Ventrals (1.07) load by far the most heavily on axis 1, whereas subcaudals (1.02) and pattern cycles (0.68) load most heavily on axis 2.



Males



Females

1. *D. atra*
2. *D. scabra*
3. *D. confusa*
4. *D. medici*
5. *D. fasciata*
6. *D. taylori*
7. *D. abyssina*
8. *D. arabica*
9. *D. bazi*
10. *D. crucifera*

Figure 31. Principal Component Analysis of the genus *Dasypeltis* in north-eastern Africa and south-western Arabia. (MBSR = midbody scale rows, V = ventrals, SC = subcaudals, SL = supralabials, Pre Oc = preoculars, Pos Oc = postoculars, Ant T = anterior temporals, Pos T = posterior temporals, Cycles = pattern cycles, Frontal = frontal pitting, Sulcus = Inter-prefrontal sulcus)

Table 3. Loading scores for Principal Component Analysis of *Dasypeltis* males in north-eastern Africa and south-western Arabia.

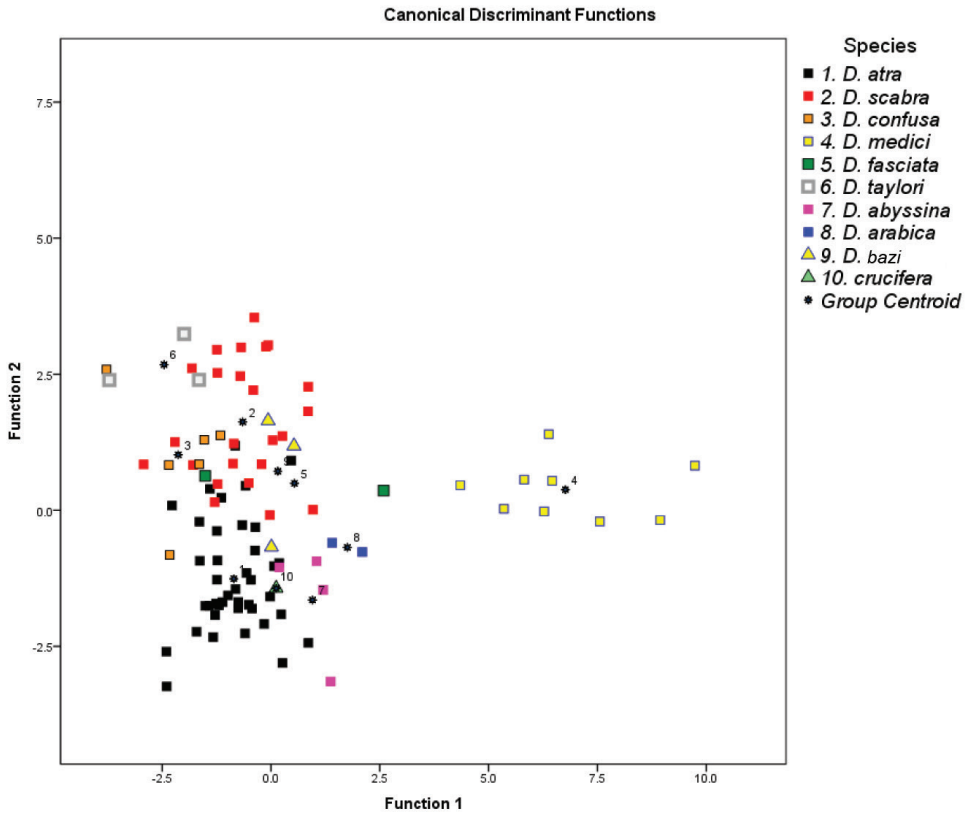
	PC 1	PC 2
Midbody scale rows	0.2344	–0.3343
Ventrals	0.3292	0.3966
Subcaudals	0.3438	0.5406
Supralabials	0.0471	0.0288
Preoculars	0.0193	0.2555
Postoculars	0.4007	–0.2850
Anterior temporals	0.3447	0.0854
Posterior temporals	0.3890	–0.2412
Pattern cycles	0.3316	–0.2163
Frontal pitting	0.3194	0.2843
Inter-prefrontal sulcus	0.2706	–0.3135

Table 4. Loading scores for Principal Component Analysis of *Dasypeltis* females in north-eastern Africa and south-western Arabia.

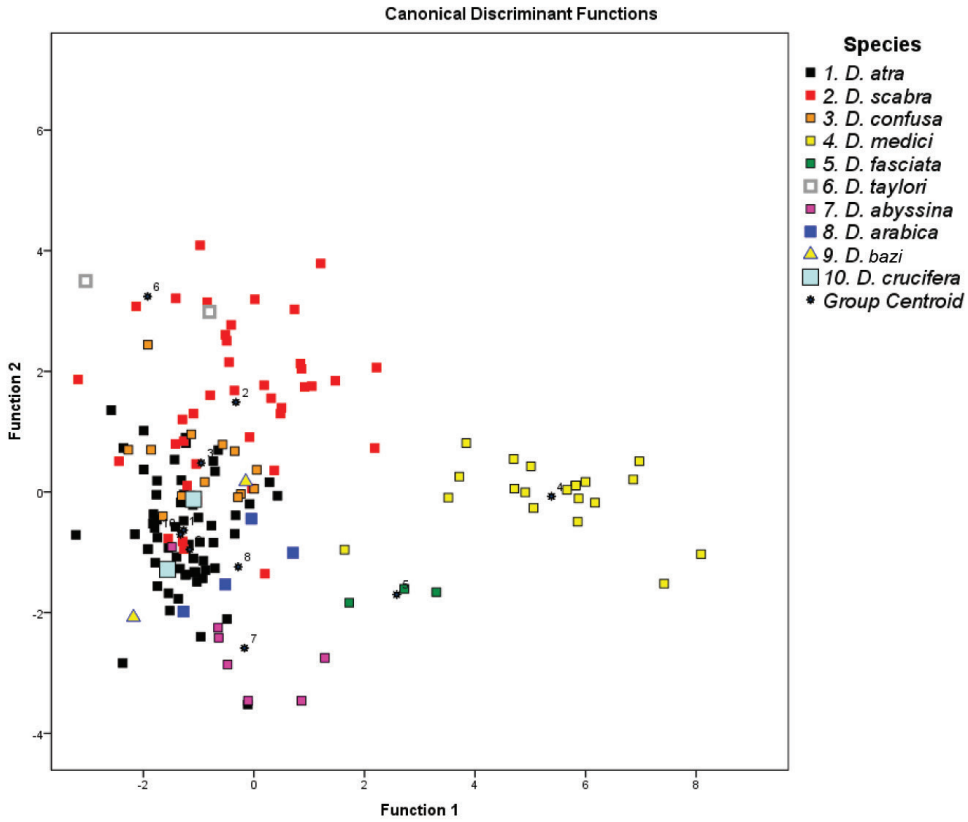
	PC 1	PC 2
Midbody scale rows	0.2960	0.2813
Ventrals	0.2792	–0.0893
Subcaudals	0.3261	–0.4928
Supralabials	0.1168	0.0920
Preoculars	0.1024	0.3277
Postoculars	0.4236	0.1670
Anterior temporals	0.3542	–0.2803
Posterior temporals	0.4146	–0.0816
Pattern cycles	0.2204	0.4892
Frontal pitting	0.3748	–0.1808
Inter-prefrontal sulcus	0.1955	0.4113

Table 5. Observed (rows) and predicted (columns) classifications of male *Dasypeltis* from north-eastern Africa and south-western Arabia according to the Discriminant Function Analysis.

	% correct	*D. atra* p = .430	*D. scabra* p = .258	*D. confusa* p = .065	*D. medici* p = .097	*D. fasciata* p = .022	*D. taylori* p = .032	*D. abyssina* p = .043	*D. arabica* p = .022	*D. bazi* p = .032
D. atra	85.0	34	5	0	0	0	0	1	0	0
D. scabra	83.3	2	20	1	0	0	0	0	0	1
D. confusa	50.0	1	2	3	0	0	0	0	0	0
D. medici	100	0	0	0	9	0	0	0	0	0
D. fasciata	100	0	0	0	0	2	0	0	0	0
D. taylori	66.7	0	1	0	0	0	2	0	0	0
D. abyssina	100	0	0	0	0	0	0	4	0	0
D. arabica	100	0	0	0	0	0	0	0	2	0
D. bazi	66.7	1	0	0	0	0	0	0	0	2
Total	83.9	38	28	4	9	2	2	5	2	3



Males



Females

Figure 32. Discriminant Function Analysis of the genus *Dasypeltis* in north-eastern Africa and south-western Arabia.

Table 6. Standardised Canonical Discriminant Function Coefficients (Sigma-restricted parameterisation) for the analysis of male *Dasypeltis* in north-eastern Africa and south-western Arabia.

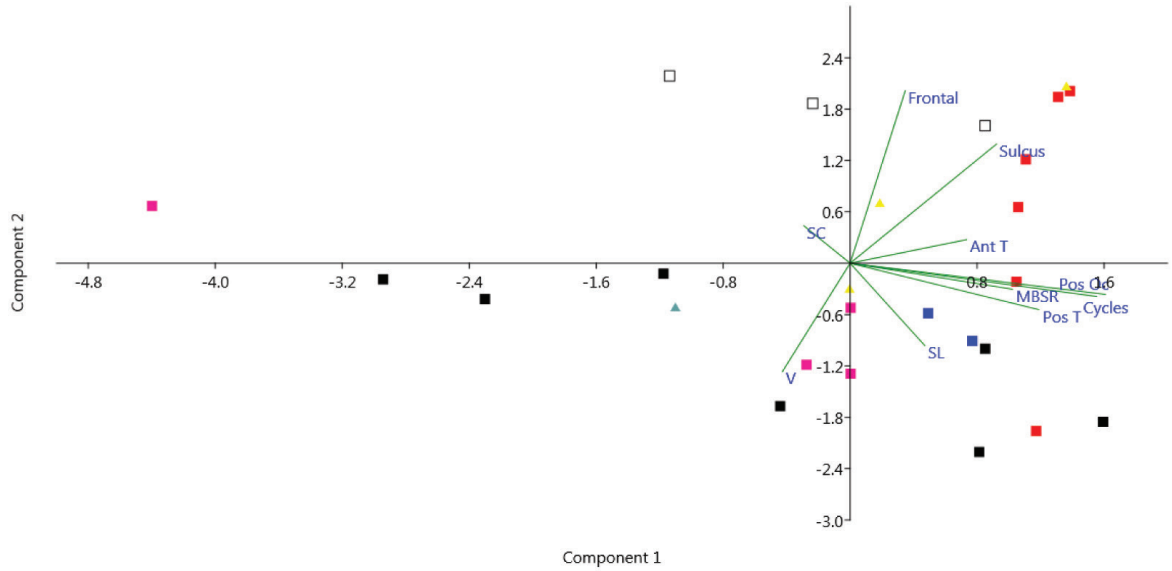
	Function 1	Function 2
Midbody scale rows	–0.001839	0.229281
Ventrals	0.604129	–0.405545
Subcaudals	0.812478	0.007712
Supralabials	0.137091	–0.034382
Preoculars	–0.006490	–0.090852
Postoculars	0.099070	0.304857
Anterior temporal	0.007210	–0.104399
Posterior temporal	–0.075543	0.170241
Pattern cycles	–0.085729	0.541770
Frontal pitting	0.190038	0.669032
Inter-prefrontal sulcus	0.020179	0.300686
Eigenvalue	**6.032452**	**2.042220**
Cumulative Proportion	0.591676	0.791982

Table 7. Observed (rows) and predicted (columns) classifications of female *Dasypeltis* from north-eastern Africa and south-western Arabia according to the Discriminant Function Analysis.

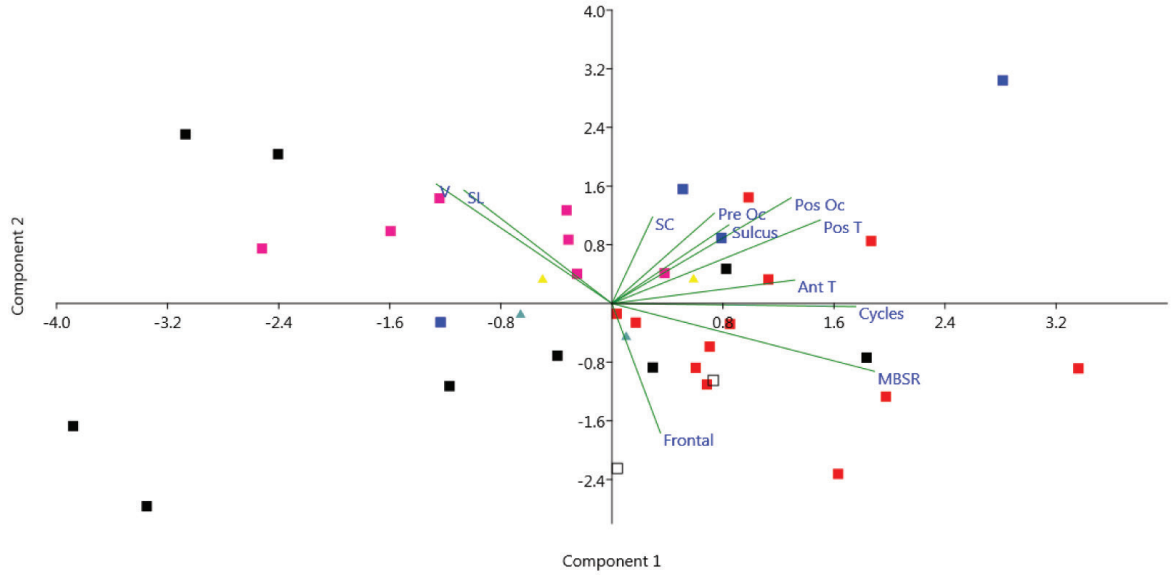
	% correct	*D. atra* p = .400	*D. scabra* p = .258	*D. confusa* p = .084	*D. medici* p = .129	*D. fasciata* p = .019	*D. taylori* p = .013	*D. abyssina* p = .045	*D. arabica* p = .026	*D. bazi* p = .013	*D. crucifera* p = .013
D. atra	74.2	46	6	6	0	0	0	3	1	0	0
D. scabra	75.0	2	30	3	0	0	2	0	2	1	0
D. confusa	61.5	3	2	8	0	0	0	0	0	0	0
D. medici	95.0	1	0	0	19	0	0	0	0	0	0
D. fasciata	100	0	0	0	0	3	0	0	0	0	0
D. taylori	50.0	0	1	0	0	0	1	0	0	0	0
D. abyssina	100	0	0	0	0	0	0	7	0	0	0
D. arabica	50.0	1	1	0	0	0	0	0	2	0	0
D. bazi	0	1	1	0	0	0	0	0	0	0	0
D. crucifera	50.0	1	0	0	0	0	0	0	0	0	1
Total	75.5	55	41	17	19	3	3	10	5	1	1

Table 8. Standardised Canonical Discriminant Function Coefficients (Sigma-restricted parameterisation) for the analysis of female *Dasypeltis* in north-eastern Africa and south-western Arabia.

	Function 1	Function 2
Midbody scale rows	0.155036	–0.307790
Ventrals	0.174019	0.644477
Subcaudals	0.919766	0.182047
Supralabials	0.000409	0.009540
Preoculars	–0.005440	0.252592
Postoculars	0.203638	–0.274530
Anterior temporal	0.420286	0.032552
Posterior temporal	–0.077620	0.051138
Pattern cycles	–0.041610	–0.269700
Frontal pitting	0.256583	–0.673860
Inter-prefrontal sulcus	–0.110640	–0.282740
Eigenvalue	**5.033508**	**1.395425**
Cumulative Proportion	0.627753	0.801783



Males



Females

- *1. D. atra*
- *2. D. scabra*
- *3. D. taylori*
- *4. D. abyssina*
- *5. D. arabica*
- *6. D. bazi*
- *7. D. crucifera*

Figure 33. Principal Component Analysis of the genus *Dasypeltis* in the Horn of Africa and Egypt. (MBSR = midbody scale rows, V = ventrals, SC = subcaudals, SL = supralabials, Pre Oc = preoculars, Pos Oc = postoculars, Ant T = anterior temporals, Pos T = posterior temporals, Cycles = pattern cycles, Frontal = frontal pitting, Sulcus = Inter-prefrontal sulcus)

Table 9. Loading scores for Principal Component Analysis of *Dasypeltis* males in the Horn of Africa and Egypt.

	PC 1	PC 2
Midbody scale rows	0.3324	–0.0988
Ventrals	0.1386	–0.4114
Subcaudals	0.0951	0.1427
Supralabials	0.1531	–0.3130
Postoculars	0.5229	–0.1184
Anterior temporal	0.2389	0.0896
Posterior temporal	0.3864	0.1763
Pattern cycles	0.5052	–0.1264
Frontal pitting	0.1129	0.6546
Inter-prefrontal sulcus	0.3001	0.4529

Table 10. Loading scores for Principal Component Analysis of *Dasypeltis* females in the Horn of Africa and Egypt.

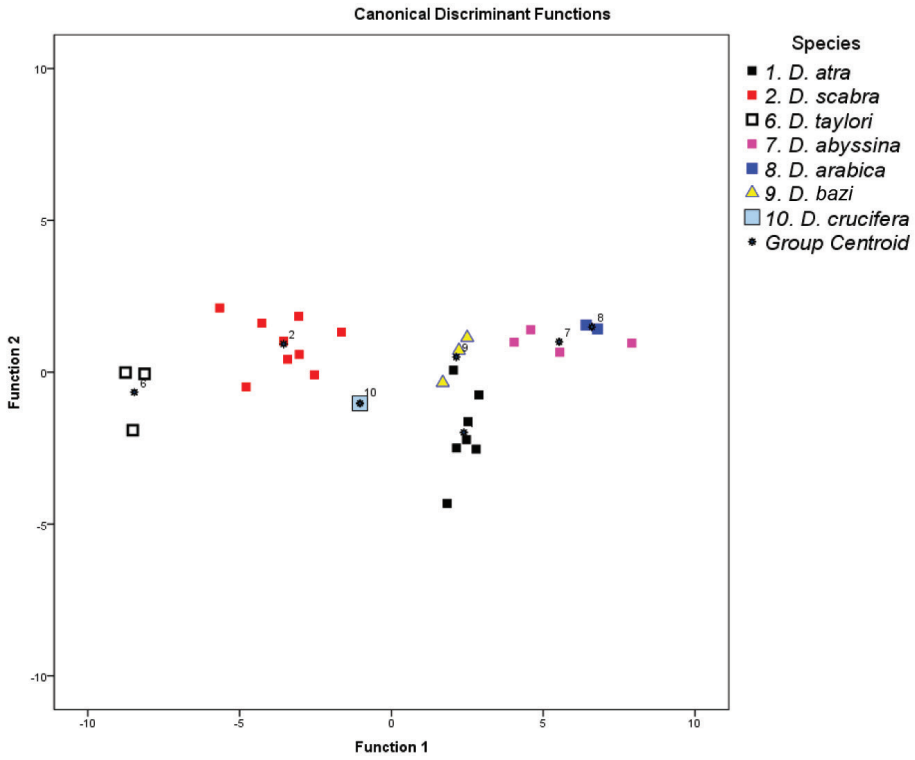
	PC 1	PC 2
Midbody scale rows	0.4654	–0.2276
Ventrals	–0.3110	0.4003
Subcaudals	0.0721	0.2901
Supralabials	–0.2623	0.3800
Preoculars	0.1817	0.3029
Postoculars	0.3175	0.3540
Anterior temporal	0.3243	0.0786
Posterior temporal	0.3693	0.2800
Pattern cycles	0.4324	–0.0104
Frontal pitting	0.0859	–0.4338
Inter-prefrontal sulcus	0.2073	0.2637

Table 11. Observed (rows) and predicted (columns) classifications of male *Dasypeltis* from the Horn of Africa and Egypt according to the Discriminant Function Analysis.

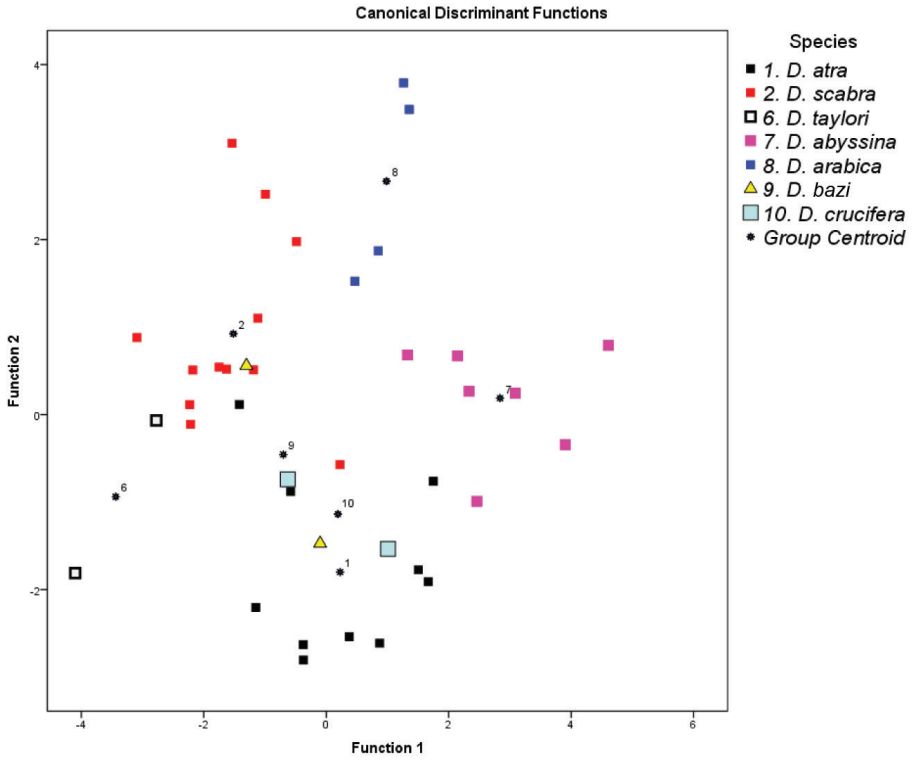
	% correct	*D. atra* p = .280	*D. scabra* p = .240	*D. taylori* p = .120	*D. abyssina* p = .160	*D. arabica* p = .080	*D. bazi* p = .120
D. atra	100	7	0	0	0	0	0
D. scabra	100	0	6	0	0	0	0
D. taylori	100	0	0	3	0	0	0
D. abyssina	100	0	0	0	4	0	0
D. arabica	100	0	0	0	0	2	0
D. bazi	66.7	1	0	0	0	0	2
Total	96.0	8	6	3	4	2	2

Table 12. Standardised Canonical Discriminant Function Coefficients (Sigma-restricted parameterisation) for the analysis of male *Dasypeltis* in the Horn of Africa and Egypt.

	Function 1	Function 2
Midbody scale rows	2.08508	–0.334990
Ventrals	2.51335	–0.269100
Subcaudals	0.08589	–0.155450
Supralabials	0.05782	–0.447450
Postoculars	–1.36866	0.590286
Anterior temporal	1.34341	0.105930
Posterior temporal	0.11259	0.006628
Pattern cycles	–0.70219	–0.824390
Frontal pitting	0.13149	–0.683300(
Inter-prefrontal sulcus	–0.36369	–0.534840
Eigenvalue	**42.25546**	**2.395576**
Cumulative Proportion	0.88362	0.933713



Males



Females

Figure 34. Discriminant Function Analysis of the genus *Dasypeltis* in the Horn of Africa and Egypt.

Table 13. Observed (rows) and predicted (columns) classifications of female *Dasypeltis* from the Horn of Africa and Egypt according to the Discriminant Function Analysis.

	% correct	*D. atra* p = .237	*D. scabra* p = .316	*D. taylori* p = .053	*D. abyssina* p = .184	*D. arabica* p = .105	*D. bazi* p = .053	*D. crucifera* p = .053
D. atra	77.8	7	1	0	1	0	0	0
D. scabra	75.0	1	9	0	0	1	1	0
D. taylori	100	0	0	2	0	0	0	0
D. abyssina	100	0	0	0	7	0	0	0
D. arabica	75.0	0	1	0	0	3	0	0
D. bazi	50.0	0	1	0	0	0	1	0
D. crucifera	100	0	0	0	0	0	0	2
Total	81.6	8	12	2	8	4	2	2

Table 14. Standardised Canonical Discriminant Function Coefficients (Sigma-restricted parameterisation) for the analysis of female *Dasypeltis* in the Horn of Africa and Egypt.

	Function 1	Function 2
Midbody scale rows	–0.187479	0.117839
Ventrals	1.074553	0.262493
Subcaudals	–0.216661	1.018205
Supralabials	–0.492329	–0.208635
Preoculars	0.097186	0.420874
Postoculars	0.178724	–0.409874
Anterior temporal	–0.063169	0.143802
Posterior temporal	0.379009	0.083376
Pattern cycles	–0.460762	0.680089
Frontal pitting	–0.298385	–0.084354
Inter-prefrontal sulcus	–0.280103	0.377127
Eigenvalue	**3.706452**	**2.549360**
Cumulative Proportion	0.462892	0.781277

SUMMARY OF SPECIES

A morphological analysis of the genus *Dasypeltis* in north-eastern Africa and south-western Arabia indicates that as many as 10 species occur there. This includes three new species (*D. taylori* **sp. nov.**, *D. crucifer* **sp. nov.** and *D. arabica* **sp. nov.**) previously subsumed under the name *D. scabra*, as well as two (*D. abyssina* and *D. bazi*) that had until recently also been considered referable to *D. scabra*. The ranges of these five species do not overlap. This taxonomy is partly supported by the multivariate analyses of scale characters and numbers of pattern cycles. Colour pattern is often diagnostic of species.

Dasypeltis medici (Bianconi)
Although it occurs as patterned, weakly patterned and unicolour morphs (dorsally), this species is easily distinguishable by the presence of paired apical pits—on the dorsal scales—which are sharply defined by dark pigment, an extensively pitted frontal shield, and high subcaudal counts (75–109 in males, 61–90 in females). Also, patterned specimens have 1–5 distinct, often narrow, chevrons on the neck (one or two similar chevrons may be present in some other species). In the study area this species is restricted to southern Somalia, south-eastern Kenya, and north-eastern Tanzania; found along the coast but also in some savannah and mountainous areas.

Dasypeltis confusa Trape & Mané
Although often similar in scalation characteristics to *D. scabra* and *D. atra*, with which it is sympatric and parapatric, this species is easily distinguished by its colour pattern of large diamond-shaped saddles (often outlined in white) confluent with the lateral bars. In the study area it occurs only in the west (southern South Sudan, Uganda, western Kenya, Rwanda).

Dasypeltis scabra (Linnaeus)
A variable species widely distributed in the study area, from Burundi and Tanzania northwards to southern Somalia and central Ethiopia, with isolated populations along the Nile River in South Sudan and Sudan. It always has the '5N' dorsal pattern, and differs from patterned *D. atra* by seldom having transversely enlarged saddles on the back, and usually also by having a more boldly marked head. There are usually two postoculars on either side of the head, while *D. atra* often has only one.

Dasypeltis bazi Saleh & Sarhan
This species has a distinctive colour pattern consisting of large cranio-caudally elongate saddles, usually bifurcated at each end with a fairly shallow but distinct notch, and the flanks are decorated with spots or blotches (not bands or vertical bars). The only locality at which this species is currently known to occur, namely the Fayoum Depression, is separated from other populations of *Dasypeltis* by over 1 300 km.

Dasypeltis taylori Bates & Broadley **sp. nov.**
This species, characterised by a combination of features including a strongly pitted frontal scale, is found in Somaliland and Djibouti, separated from populations of *D. scabra* to the south by the arid Ogaden plateau. The dorsal saddles are often large, closely-spaced, square or slightly rectangular, and separated by narrow, usually sharply defined, white crossbars; there are low numbers of pattern cycles (44–59).

Dasypeltis atra Sternfeld
Occurs as three colour phases: brown dorsally and cream to yellow or orange ventrally; black dorsally (unique in the genus) and grey ventrally; and patterned, sometimes similar to the '5N' pattern of *D. scabra* but more typically with transversely widened saddles, often in contact with the lateral bars. Typically the frontal scale is only marginally pitted and the inter-prefrontal suture weakly marked; and western populations usually have only a single postocular (rather than two), a condition rare in others of this genus. This species is widespread in the study area, from northern Tanzania to Burundi, Rwanda, Kenya, Uganda, south Sudan and Ethiopia as far north as Circao. In some areas it is sympatric and/or parapatric with *D. scabra*, *D. confusa*, *D. medici*, *D. fasciata* and *D. abyssina*.

Dasypeltis fasciata A. Smith
Dorsum patterned, with body pattern always expressed as chequerboard on skin between scales and often also on lower edges of these, rather than on most of the scales themselves as in patterned specimens of other species. Also characterised by high subcaudal counts (59, 71–76 in males, 64–76 in females). In the study area this highly arboreal species is restricted to forests in western Uganda.

Dasypeltis abyssina (Duméril, Bibron & Duméril)
Easily recognisable by the combination of its unique dorsal pattern (including oblique transversely widened saddles which may merge to form zigzags on the back) and heavily marked venter. This species also has the highest ventral counts in the genus (241–271 in females, 226–247 in males). It is restricted to the Ethiopian highlands that extend into Eritrea.

Dasypeltis crucifera Bates **sp. nov.**
Found near the northern limits of *D. abyssina*, but at lower altitudes in northern Eritrea below the Ethiopian highlands. Distinguished by its unique dorsal pattern in which dark brown oval saddles and lateral bars almost completely enclose pale cross-markings that form the inter-saddle areas; venter largely unmarked (*D. abyssina*, its nearest congener, has a markedly different dorsal pattern and a heavily marked venter).

Dasypeltis arabica Broadley & Bates **sp. nov.**
Easily distinguished by its unique dorsal pattern consisting of black rectangular saddles and lateral bars that form complete closure around the pale inter-saddle areas (pattern '5I' of Gans 1959); the venter is mostly unmarked. It has high ventral counts. This is the only species in the genus restricted to Arabia, where it occurs in the highlands of Saudi Arabia and Yemen.

Key to the genus *Dasypeltis* in north-eastern Africa and south-western Arabia

1a. Paired apical pits on dorsal scales sharply defined by dark pigment; frontal shield extensively (State 3) to entirely (State 4) pitted; patterned specimens with 1–5 distinct chevrons on neck; subcaudals 75–109 in males, 61–90 in females .... *D. medici*

1b. Paired apical pits on dorsal scales not sharply defined by dark pigment; frontal shield varies from smooth to extensively pitted (States 0–4); when present, chevrons usually restricted to nape 2

2a. Dorsum patterned, with body pattern always expressed as chequerboard on skin between scales and often also on lower edges of these; frontal usually marginally pitted (States 1–2); lateral scales always strongly serrated; subcaudals 71–76 (once 59) in males, 64–76 in females ..... *D. fasciata*

2b. Dorsum without pattern or with pattern expressed across the scales; frontal varies from smooth to extensively pitted (States 0–4); lateral serration present in varying degrees; subcaudals 47–73 in males, 43–65 in females 3

3a. Dorsum uniform black or brown; or pale brown, grey or reddish-grey with a pattern of dense, dark brown, olive or reddish, usually transversely-enlarged, saddles, often joined to the lateral bars; when present 62–130 (mean 92.6) pattern cycles from nape to base of tail; postoculars 1 or 2 on either side of head ..... *D. atra*

3b. Dorsum light brown or grey, uniform, or with a pattern of darker dorsal markings linked or alternating with lateral bars; 38–98 pattern cycles from nape to base of tail; usually 2 postoculars on either side of head 4

4a. Dark dorsal markings (saddles) usually large and diamond-shaped, linked on either side to the dark lateral bars (or dorsum uniform light brown); ventrals 199–224 in males, 212–239 in females ..... *D. confusa*

4b. Dark dorsal markings (saddles) variable in size but not diamond-shaped, usually not linked on either side to the dark lateral bars (or dorsum uniform pale brown in *D. abyssina*, but then ventrals 226 in males, 241–263 in females)..... 5

5a. Dark dorsal markings (saddles) and lateral bars completely or largely enclose a pale saddle patch; venter cream to white, unmarked except for small dark specks at the lateral edges; frontal marginally pitted (States 1 & 2). 6

5b. Dark dorsal markings (saddles) and lateral bars mostly separated, not enclosing a pale saddle patch; venter cream to white, dark markings variable; or uniform grey-brown above, immaculate (or nearly so) cream to cream-yellow below; frontal pitting variable..... 7

6a. Pale markings on the back more-or-less square and completely surrounded by dark rectangular dorsal saddles and lateral bars; pattern cycles on back 62–79; inter-prefrontal sulcus moderately to deeply marked; ventrals 236–244 in males, 239–254 in females; subcaudals 63–65 in males, 53–61 in females ..... *D. arabica* **sp. nov.**

6b. Pale markings on the back in the form of crosses, largely surrounded by dark oval dorsal saddles and lateral bars, but with the tips of the crosses often separated from the dark markings; pattern cycles on back 51–62; inter-prefrontal sulcus faintly marked; ventrals 226 in males, 231–247 in females; subcaudals 61 in males, 49–52 in females ....*D. crucifera* **sp. nov.**

7a. Dorsal markings (saddles) often oblique and wider than long, often confluent or forming zigzags, usually not linked to lateral bars; parts of the labials and interspaces between saddles are cream-yellow (in life); venter with heavy dark markings, each plate decorated by, anteriorly, a large rounded cone on either side joined to a smaller rounded cone in the centre; uniform phase pale grey-brown above, cream to cream-yellow below; inter-prefrontal sulcus usually faintly marked; frontal usually marginally pitted (States 1 or 2); ventrals 226–247 in males, 241–271 in females ..... *D. abyssina*

7b. Dorsal markings (saddles) usually not oblique, variable in shape (e.g. round, oval, square, rectangular), usually not confluent or forming zigzags; no yellowish markings; venter varies from immaculate to heavily-marked, but not as extensively as above; inter-prefrontal sulcus variable; frontal pitting variable; ventrals 185–229 in males, 202–249 in females 8

8a. Dorsal markings (saddles) variable, often oval to rectangular (antero-posteriorly); pattern cycles 46–94 (mean 67.4); markings on venter variable; ventrals 185–226 in males, 202–249 in females ..... *D. scabra*

8b. Dorsal markings (saddles) large, often broad or elongate; pattern cycles 38–59; venter usually unmarked except for a few dark spots laterally 9

9a. Dorsal markings (saddles) cranio-caudally elongate, well separated, usually bifurcated at each end with a shallow but distinct notch; flanks with spots or blotches; ventrals 213–229 in males, 215–234 in females ..... *D. bazi*

9b. Dorsal markings (saddles) broad, often squarish, usually separated by narrow sharply-defined white crossbars; flanks with elongate, wavy markings; ventrals 196–216 in males, 208–222 in females ..... *D. taylori* **sp. nov.**

For *Dasypeltis bazi*, ventral, subcaudal and pattern cycle counts in Saleh & Sarhan (2016) were incorporated into the key (excluding a high ventral count of 250 and low subcaudal count of 55 for one 'male' which require confirmation, see p. 27).

DISCUSSION

Dasypeltis scabra is by far the most widespread species in the genus, and the most widely distributed of the 10 species found in north-eastern Africa and south-western Arabia. It ranges from the Cape of Good Hope through large parts of southern, central (excluding forests) and eastern Africa (most '5N' specimens in Gans 1959; Broadley 1990; this study), with apparently isolated populations along the Nile River (Sudan and South Sudan) and near Kutum (western Sudan). The isolated Egyptian population in the Fayoum Depression is now considered a separate species (*D. bazi*), as are populations in Somaliland/Djibouti (*D. taylori* **sp. nov.**), northern Eritrea (*D. crucifera* **sp. nov.**), the northern Ethiopian highlands (*D. abyssina*) and western Arabia (*D. arabica* **sp. nov.**). *Dasypeltis confusa* has a large range in western and central Africa ('5L' of Gans 1959), extending as far east as South Sudan, Uganda, western Kenya and Rwanda. *Dasypeltis fasciata* is arboreal and restricted to forests, but it has a large range in western and central Africa, extending as far east as Uganda. *Dasypeltis medici*, now considered a monotypic species, occurs in coastal and inland forests from southern Somalia to northern KwaZulu-Natal in South Africa; it also occurs in savannah where it may be sympatric with *D. scabra*. *Dasypeltis atra*, at one time considered a montane forest subspecies of *D. scabra*, is clearly a separate species (e.g. Gans 1964; Broadley & Bates 2009) with an extensive range from eastern Democratic Republic of the Congo to Rwanda, Burundi, Uganda, South Sudan, Kenya, northern Tanzania and the Ethiopian highlands. The range of *D. atra* is overlapped almost entirely by that of *D. scabra*, and although the two species appear to be mostly parapatric, the former also occurs in some savannah areas (e.g. Broadley & Bates 2009) where it is sympatric with the latter.

Gans (1959) considered that evolutionary relationships might be indicated by how dorsal colour patterns were derived. For example, he demonstrated how a generalised '5N' *D. scabra* pattern could have given rise to the '5L' *D. confusa* pattern, leading to the *D. palmarum* pattern (saddles and lateral bars confluent and much narrowed with increased inter-saddle areas), and how the marked *D. medici* pattern could have been derived from '5N'. His diagrammatic scheme of evolutionary history, in which the more derived species are smaller (body length), have better developed lateral body serration, and increased pitting on the head, places *D. inornata* as the basal species, followed by *D. fasciata*, "montane" (= *D. atra*), *D. palmarum*, and *'D. scabra'* (including '5N' = *D. scabra*, '5L' = *D. confusa* and '5I' = *D. arabica* **sp. nov.**), with *D. medici* as the most derived species. Gans (1959: 172) noted that *D. scabra* may have been derived "separately from the montane population [= *D. atra*], representing an invasion of the savannah habitat from the forest, and *D. palmarum* would be derived from *scabra* as a form adapted to the coastal dry belt of central West Africa." However, Gans (1959: 173) warned that in *Dasypeltis* "...the use of different characters permitted the erection of sharply differing phylogenies."

It is now generally accepted that the genus *Dasypeltis*, along with the mainly African genera *Crotaphopeltis*, *Telescopus*, *Dipsadoboa*, *Toxycodryas* and *Boiga*, is part of the Boigini clade of the colubrid subfamily Colubrinae (Gravlund 2001; Kelly *et al.* 2003; Lawson *et al.* 2005; Figueroa *et al.* 2016). Relationships within the genus, however, are not well understood, with only three published molecular phylogenies, one (16S only) dealing mainly with West African species (Trape *et al.* 2012), another using the same data but with two samples of *D. bazi* from Egypt added (Saleh & Sarhan 2016), and a multigene study that used the same species as Trape *et al.* (2012) but added additional samples, including three '*D. atra*' (Figueroa *et al.* 2016). The phylogeny of Trape *et al.* (2012) indicated that *D. confusa* (samples from Togo) was the sister group to all other West African species (including *D. fasciata*) as well as *D. scabra* from 'South Africa" and *'D.* cf. *lineolata'* (possibly *D. atra*) from Burundi. Trape *et al.*'s (2012) study supported species status for all West African taxa (including *D. latericia*, previously considered a subspecies of *D. gansi*). It also suggested a close relationship between *D. fasciata*, *D. gansi* and *D. latericia*, and between *D. sahelensis* and *D. parascabra*. With the inclusion of one additional species, *D. bazi*, Saleh & Sarhan's (2016) phylogeny suggested different relationships, but most of these were not well supported (e.g. *D. scabra* was paired with *D. latericia*, and *D. confusa* paired with *D.* cf. *lineolata* [? *D. atra*]). The phylogeny of Figuero *et al.* (2016) identified two main clades, one with *D. confusa* + *D. fasciata* versus the rest, but *D. fasciata* was also included in the larger clade. This latter clade was divided into two well supported subclades, one consisting of *D. atra*, *D. scabra* and *D. latericia*, and the other containing *D. atra*, *D. gansi*, *D. fasciata* and *D. sahelensis*. The confounding positions of both *D. fasciata* and *D. atra* in different clades may suggest the presence of cryptic species, but alternatively it may reflect incorrect identification of specimens. The relationships indicated by these studies may change or be resolved further with greater taxon sampling, particularly of north-eastern, eastern and southern African lineages (A. Barlow *et al.* in prep.).

Geniez & Guillod (2003) considered the populations of *Dasypeltis* in Morocco, Egypt and south-western Arabia as being Afrotropical relicts. *Dasypeltis bazi* appears to have a relict distribution indicative of a former widespread range in northern Africa that was reduced and fragmented following dessication of the region during the Holocene (Kuper & Kröpelin 2006). Oases such as the Fayoum appear to be vestiges of what was once an expansive savannah, probably with riparian-fringed links like the Nile River, and may act as climatic refuges. The geographical ranges of some snakes in Egypt, such as *Telescopus dhara obtusus*

(Reuss), are closely associated with the Nile Valley, and this species also occurs in apparent isolation on the Red Sea coast in the south-east of the country. Its distribution range may be similar to the past distribution of *D. bazi*, a species that is perhaps also represented by an apparently isolated population near the Red Sea coast at Erkowit.

During the Last Glacial Maximum and terminal Pleistocene (21000–8500 B.C.E.) the Sahara desert extended about 400 km further south than it does now, probably incorporating, *inter alia*, all of modern-day Sudan (Kuper & Kröpelin 2006). Monsoon rains that started 8500 B.C.E. resulted in hyperarid conditions being replaced by savannah-like environments, similar to the current-day Sahel, with formation of lakes and temporary rivers (Baha El Din 2006), perhaps allowing *Dasypeltis* (and many other animal species) from areas in central Africa to disperse and establish populations as far north as Morocco and Egypt. However, retreating monsoonal rains from 5300 B.C.E. resulted in dessication of the Eastern Sahara, with a return to full desert conditions throughout Egypt by 3500 B.C.E. (Kuper & Kröpelin 2006). Most Afrotropical animal species (or at least most populations) would then have retreated southwards as the only favourable (non-desert) habitat remaining in the region would have been in the Nile Valley and at scattered oases (Baha El Din 2006) such as Fayoum, Siwa, Qara, Bahariya, Farafra, Dakhla and Kharga. Although populations of *Dasypeltis* in Egypt (Fayoum and possibly in the Nile Valley itself) could be relics of a former widespread species that became established there during favourable conditions, they may alternatively be the descendants of populations that dispersed north along the Nile Valley in later times, using the valley as a 'green corridor' (see also Escoriza 2010). According to Baha El Din (2006), the Nile River (and its associated valley) varied considerably in size and impact during the Quaternary, before achieving its current form; and its function as a conduit for African fauna and flora was established as recently as 800 000 BP. Saleh & Sarhan's (2016) study indicated that divergence times between *D. bazi* and other African *Dasypeltis* species predate the formation of the Nile River by about a million years, and this together with the absence of *Dasypeltis* records in the Nile Valley [in Egypt], suggests that the occurrence of these snakes in Fayoum is the result of vicariant events related to the formation of the Sahara rather than dispersion across this arid desert.

Geniez & Guillod (2003) were of the opinion that while the Nile Valley represented a northward corridor of the Ethiopian region for some species of sub-Saharan reptiles, the Moroccan population (now known as *D. sahelensis*, with most of its range in the Sahel; Trape & Mané 2006) is isolated. According to Escoriza (2010), the occurrence of '*D. scabra*' and '*Boaedon fuliginosus*' (Boie) in northern Africa may be the result of range expansions during humid paleoclimatic conditions in the late Pleistocene or recent Holocene. Escoriza (2014) suggested that populations of *D. sahelensis* crossed the Western Sahara desert from the Sahel (or associated savannahs) to north-western Africa (Western Sahara and Morocco) in humid conditions 6000–9000 years ago during the Holocene. This species, together with populations of the widespread snakes *'B. fuliginosus'* and *Bitis arietans* (Merrem), was subsequently isolated in the relatively moist Atlantic coastal region of north-western Africa during the next period of aridification (Schleich *et al.* 1996; Geniez & Guillod 2003).

The nearest record to *D. bazi* from the Fayoum Oasis in Egypt is Erkowit in eastern Sudan near the Red Sea coast, but the latter town is situated about 1330 km away to the south-east. The specimen from Erkowit (*D.* cf. *bazi*) may represent an isolated relict population of *D. bazi*. This specimen is similar to Egyptian specimens of *D. bazi*, both in terms of colour pattern and scalation. This Egyptian/Erkowit population may in the past have been part of a more widespread population of *D. scabra* that became isolated following aridification of the Sahara during the Holocene, resulting in the evolution of a new species, *D. bazi*. The two populations may then have become isolated as climatic and environmental conditions changed, with the Fayoum Oasis (*D. bazi*) and Red Sea Hills (*D.* cf. *bazi* = Erkowit population) functioning as refuges, and accounting for their large current-day separation. Erkowit is a small town situated on a minor plateau (mostly 1000–1200 m a.s.l.) in the Red Sea Hills—a northern extension of the Ethiopian Plateau—at the eastern edge of the arid Sahel. Sea mist is blown in by north-easterly winds during winter to provide a moisture-temperature gradient at Erkowit, which has evergreen Afromontane vegetation only 10 km from the surrounding desert shrub (Vetaas *et al.* 2012). The Erkowit area was once regarded as a mist oasis in the desert, representing a potential refugium for *Dasypeltis*. Baha El Din (2006) suggested that some species of Afrotropical reptiles extended their ranges into Saharan Africa using the Nile River (and its associated valley) and Red Sea coast and mountains as conduits, although some populations in these areas are merely relicts. The cobra *Naja nubiae* Wüster & Broadley, 2003, for example, has a patchy distribution in eastern Chad, Sudan, Eritrea and at sites along the Nile River in Egypt.

Corkhill (1935) noted that in Sudan, *D. scabra* occurred only in 'Blue Nile Province'—a region which his map indicates as being situated slightly east and south of Khartoum—but he did not list any specific localities. There are in fact four known *Dasypeltis* records for Sudan and one for South Sudan (none appear to be referrable to *D. bazi*), all but one located at or near the banks of the White Nile River. The exception is the newly-reported specimen (ZFMK 32479) from 50 km north of Kutum in Sudan, situated 1750 km from Fayoum and 1395 km WSW of Erkowit, identifiable as *D. scabra* (see above). One of the two syntypes

of *Rachiodon abyssinus* (= *Dasypeltis abyssina*), collected in the mid-19th century during an expedition to the sources of the White Nile under the direction of M. d'Arnaud, and labelled "Nil Blanc" (= White Nile, possibly above Khartoum in Sudan), was examined by the first author and is in fact a *D. scabra* (MNHN 7227, female, '5N' dorsal pattern – dark-bordered brown saddles with vertically-elongate dark lateral bars between them, 54 pattern cycles, 226 ventrals, 53 pairs of subcaudals; Fig. 6). Khartoum, where the White and Blue Niles converge, is about 600 km south-west of Erkowit. A specimen (BM 09.10.15.35) of *D. scabra* from 'Sennar State' (which straddles the White Nile; Fig. 3) in south-eastern Sudan has some '5N' markings dorsally, but also the peculiar '5I' dorsal pattern over parts of its back (photograph examined) as described by Gans (1959) for some populations of Eritrean and Arabian '*D. scabra*', where the dark saddles and lateral bars are joined, enclosing a pale inter-saddle region. This female specimen was in fact examined by Gans (1959) who recorded 65 pattern cycles, 227 ventrals and 52 pairs of subcaudals. The fourth Sudanese specimen (RMNH 24399, female) was collected 40 km north of Rabak, near Kosti (Fig. 3), on the banks of the White Nile and has the typical '5N' *D. scabra* dorsal pattern, 50 pattern cycles, 222 ventrals and 55 pairs of subcaudals. There is one additional *D. scabra* record (FMNH 134939: male, '5N' pattern, 64 pattern cycles, 213 ventrals, 62 pairs of subcaudals) on the White Nile (east bank) at Melut in the north-eastern part of South Sudan. Other records of *Dasypeltis* in adjacent parts of Eritrea and north-western Ethiopia are referable to *D. taylori* **sp. nov.**, *D. abyssina*, and *D. atra* . The four above-mentioned '5N' *D. scabra* records on the White Nile, possibly representing a single population, appear to be considerably isolated from other populations of this species. The northern-most *D. scabra* record in the Nile Valley is Sennar State, about 700 km south-west of Erkowit. Apart from Erkowit, the nearest other *D. scabra* locality is the Addis Abeba area (Largen & Spawls 2010; Fig. 3) about 740 km ESE of Melut. There is one additional (apparently isolated) record of *D. scabra* from Wadelai, much further upstream, on the Albert Nile in north-western Uganda (Fig. 3).

As discussed in the species account, some Eritrean specimens of *D. abyssina* have the '5I' dorsal pattern typical of *D. arabica* **sp. nov.** over parts of their backs. This, together with other morphological similarities (e.g. high numbers of ventrals and subcaudals) between *D. abyssina* and *D. arabica*, together with their geographical proximity, suggests a close evolutionary relationship. A continuous population may have been separated by the opening of the Gulf of Aden (see Leviton 1986), with subsequent divergence of the resultant sub-populations. The dorsal colour pattern of *D. crucifera* **sp. nov.** is similar to this '5I' pattern and their close geographical proximity suggests that it may be closely related to the high-elevation *D. abyssina*. *Dasypeltis taylori* **sp. nov.** is separated from the nearest populations of *D. scabra*—a species it most resembles—by the arid Ogaden plateau, and may represent a relictual population of a once widespread *D. scabra*.

A molecular phylogeny of the genus, including samples of all species and with reasonable coverage of their ranges, will go a long way towards elucidating evolutionary relationships. Considering the vast areas covered by the ranges of most species, the possibility of additional (possibly cryptic) species cannot be discounted. Sampling of all species may be difficult at this time as some parts of Africa are still relatively inaccessible, not only physically, but in some cases also as a result of armed conflicts (e.g. parts of Somalia, Sudan, South Sudan, Eritrea-Djibouti border). Relationships and levels of divergence for the various isolated populations of *D. scabra* (e.g. 50 km N of Kutum, Sudan; populations along the Nile River in Sudan/South Sudan; Wadelei, Uganda) and *D.* cf. *bazi* (Erkowit, eastern Sudan) should also be investigated.

ACKNOWLEDGEMENTS

We thank the following museums and their curators and collection managers for providing access to specimens: Natural History Museum, London (C.J. McCarthy, P. Campbell); Museum National d'Histoire Naturelle, Paris (I. Ineich, N. Vidal); Museum für Naturkunde, Berlin (R. Günther, F. Tillack); Naturhistorisches Museum, Vienna (Silke Schweiger); Musée Royal de l'Afrique Centrale, Tervuren (D. Meirte); Museum of Comparative Zoology, Harvard (J.P. Rosado); Field Museum of Natural History, Chicago (A. Resetar); American Museum of Natural History, New York (C.W. Myers, D. Kizirian, D.A. Dickey); United States National Museum, Washington (G.R. Zug); University of Michigan Museum of Zoology, Ann Arbor (A.G. Kluge); California Academy of Sciences, San Francisco (R.C. Drewes, J.V. Vindum); Addis Ababa University Museum (G. Redda); Makerere University Zoological Museum, Kampala (R. Kityo); National Museums of Kenya, Nairobi (P.K. Malonza); Port Elizabeth Museum/Bayworld (W.R. Branch, W. Conradie); and KwaZulu-Natal Museum, Pietermaritzburg (C. Stoffels).

We thank the curators of the following museums for sending us material on loan: Los Angeles County Museum (R. Bezy); Museum Alexander Koenig, Bonn (W. Böhme); Muséum d'Histoire Naturelle, Geneva (A. Schmitz); National Museum of Kenya, Nairobi (P.K. Malonza); Naturhistorisches Museum, Vienna (H. Grillitsch); and Statens Naturhistoriske Museum, Københavns Universitet, Copenhagen (J.B. Rasmussen); and the curators and other individuals associated with the following museums for providing us with meristic data and/or images of specimens in their care: Museo Civico di Storia Naturale, Genova (G. Doria, M. Petri); Museo Civico di Storia Naturale, Milan (S. Scali); Museo di Storia Naturale, Università di Pavia, Pavia (E. Razzetti); Museo Zoologico "La Specola",

Università di Firenze (A. Nistri); Museo Regionale di Scienze Naturali di Torino, Turin (F. Andreone); Museum Alexander Koenig, Bonn (W. Böhme, M. Flecks, U. Bott); Statens Naturhistoriske Museum, Københavns Universitet, Copenhagen (J.B. Rasmussen); Institut Royal des Sciences Naturelles de Belgique, Brussels (G. Lenglet); National Museums of Kenya, Nairobi (P.K. Malonza); Port Elizabeth Museum/Bayworld (W.R. Branch, W. Conradie); Natural History Museum, London (P. Campbell); Museum National d'Histoire Naturelle, Paris (I. Ineich); Zoologisches Museum der Universität, Berlin (F. Tillack); California Academy of Sciences, San Francisco (J. Vindum); and Texas A&M University, Texas (T. Hibbits).

We also thank B. Hughes for providing scalation data for Ugandan specimens in the collection of the World Museum, Liverpool; the following individuals for photographs of *Dasypeltis* (see figures for credits): W.R. Branch, F. Finke, E. Greenbaum, T. Mazuch, S. Spawls, C. Tilbury and V. Trailin; V. Trailin for additional photographic records of *D. scabra* and *D. atra* in Ethiopia; S. Spawls for additional photographic records of *D. atra* and *D. scabra* in Kenya, and *D. atra* in Tanzania; T. Mazuch for additional photographic records of *D. scabra* and *D. atra* in Ethiopia; J. Marais for photographic records of Kenyan *D. medici* (Malindi) and *D. atra* (Emakoko); T. Dudu for photographic records of *D. atra* from Serengeti in Tanzania; C. Doria for a photographic record of a melanistic *D. atra* from Oldeani in Tanzania; A. Bauer, T. Mazuch, F. Tillack, D. Meirte, C. Kucharzewski, M.-O. Rodel, I. Ineich and R. Charles for access to old literature; S. Spawls for helping to trace various localities; and U. Ziliani for helping to trace records of *D. scabra* from Turkana County in Kenya. Frank Tillack provided collection details for Egyptian specimens in the collection in Berlin.

The first author's trip to the natural history museums in London, Paris and Berlin in September and October 2011 was funded by the Reptile Speciation Project (a South African National Research Foundation [NRF] grant to K.A. Tolley, South African National Biodiversity Institute, Cape Town), his visit to the Royal Museum for Central Africa in Tervuren in October 2012 was made possible by an African Biodiversity Information Centre scholarship, and a later trip (September/October 2015) to the museum in Paris was funded by the National Museum (Bloemfontein).

We are indebted to J. Kersten (Bulawayo) and M. van Rensburg (National Museum, Bloemfontein) for preparing the distribution map; Zhongning Zhao (University of the Free State, Bloemfontein) for assistance with multivariate analyses; and W.R. Branch (Port Elizabeth Museum) for commenting on parts of the manuscript. The reviewers, Prof. A.M. Bauer (Villanova University, Philadelphia, U.S.A.) and S. Spawls (Norwich, England) are thanked for their valuable comments and suggestions for improving the manuscript.

REFERENCES

ANDERSON, J. 1896. *A contribution to the herpetology of Arabia, with a preliminary list of the reptiles and batrachians of Egypt.* London, 122 pp.

ANDERSON, J. 1898. *Zoology of Egypt: Volume First. Reptilia and Batrachia*. Bernard Quaritch, London, pp. i–lxv, 1–371.

ANGEL, F. 1925. *Voyage de Ch. Allaud et R. Jeannel en Afrique Orientale (1911–12) Résultats scientifiques. Reptiles et batraciens*. P. Lechevalier, Paris, 63 pp.

ANON. 2017. "Emin Pasha". Wikipedia. (http://en.wikipedia.org/wiki/Emin_Pasha , accessed: 31 October 2017).

BAHA EL DIN, S.M. 2006. A *Guide to the Reptiles and Amphibians of Egypt*. The American University in Cairo Press, Cairo, 359 pp.

BALLETTO, E. 1965. Contributo alla biogeographia della Somalia. *Bollettino dei Musei e degli Istituti Biologici dell'Universita di Genova* **36** (248): 191–280.

BATES, M.F. 2009. The egg-eating snakes of Africa. *Culna* **64**: 2–4.

BATES, M.F. 2013. First records of the egg-eating snake *Dasypeltis confusa* Trape & Mané, 2006 in Nigeria and Chad, with range extensions for Ghana. *Navorsinge van die Nasionale Museum, Bloemfontein* **29** (2): 17–27.

BATES, M.F. 2017. *Dasypeltis atra* Sternfeld, 1912 (Reptilia: Serpentes): proposed precedence over *Dasypeltis lineolata* W. Peters, 1878. *Bulletin of Zoological Nomenclature* (submitted, Case 3750).

BATES, M.F. & BROADLEY, D.G. 2008a. Geographical Variation in Egg-eating Snakes of the Genus *Dasypeltis* in Africa south of Latitude 12° S. Sixth World Congress of Herpetology, Manaus, Brazil (17–22 August 2008). Available on CD with conference abstracts.

BATES, M.F. & BROADLEY, D.G. 2008b. Geographical variation in scalation and colour pattern in the egg-eating snakes of the genus *Dasypeltis* in Africa south of Latitude 12° S. Ninth Conference of the Herpetological

Association of Africa, Sterkfontein Dam, Harrismith, South Africa (26–30 November 2008). Published in Abstract booklet.

BATES, M.F. & INEICH, I. 2012. A new size record for the West African egg-eating snake *Dasypeltis gansi* Trape & Mané, 2006, with new distribution records. *Navorsinge van die Nasionale Museum, Bloemfontein* **28** (3): 41–48.

BATES, M.F., BRANCH, W.R., BAUER, A.M., BURGER, M., MARAIS, J., ALEXANDER, G.J. & DE VILLIERS, M.S. (Eds). 2014. *Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland. Suricata* **1**. South African National Biodiversity Institute, Pretoria, pp. i–xvii + 1–485.

BATES, M.F., BROADLEY, D.G., BARLOW, A., WÜSTER, W. & TOLLEY, K.A. 2009. Egg-eating snakes of the genus *Dasypeltis* in Southern Africa: how many species are there? Abstracts: 50th Anniversary Conference of the Zoological Society of Southern Africa, Illovo Beach, South Africa, 21-25 July 2009. Pp. 69–70.

BATES, M.[F.], BROADLEY, D.[G.], BARLOW, A., WÜSTER, W. & TOLLEY, K.[A.] 2012. Taxonomy and distribution of the African egg-eating snakes of the genus *Dasypeltis*. Abstracts: Seventh World Congress of Herpetology, Vancouver, Canada, 8–14 August 2012. *African Herp* News **58**: 27–28.

BEHANGANA, M. & GOODMAN, J.D. 2002. Key to genera of snakes of Uganda (with a checklist and vernacular names). *The Uganda Journal* **48**: 33–70.

BIANCONI, J.J. 1850–1862. Specimina Zoologica Mosambicana. *Bononiae Fascimile* 1–16, 406 pp. [Fascimile 14 (1859), pp. 277–278, table 14]

BLANFORD, W.T. 1870. *Observations on the geology and zoology of Abyssinia made during the progress of the British expedition to that country in 1867–1868*. London, xii + 487 pp.

BOGERT, C.M. 1940. Herpetological results of the Vernay Angola Expedition with notes on African reptiles in other collections. Part I – Snakes, including an arrangement of African Colubridae. *Bulletin of the American Museum of Natural History (New York)* **77** (1): 1–107.

BOSELLINI, A. 1986. East Africa continental margins. *Geology* **14**: 76–78.

BOULENGER, G.A. 1894. *Catalogue of the snakes in the British Museum (Natural History), 2, containing the conclusion of the Colubridae Aglyphae*. London, xi + 382 pp.

BOULENGER, G.A. 1896a. A list of the reptiles and batrachians collected by Dr. Ragazzi in Shoa and Eritrea. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)*, (Ser. 2) **16**: 545–554.

BOULENGER, G.A. 1896b. Report on Capt. Bottego's second collection of reptiles and batrachians from Somaliland. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)*, (Ser. 2) **17**: 15–23.

BOULENGER, G.A. 1896c. *Catalogue of the snakes in the British Museum (Natural History), 3, containing the Colubridae (Opisthoglyphae and Proteroglyphae), Amblycephalidae and Viperidae*. London, xi + 382 pp.

BOULENGER, G.A. 1897. A list of the reptiles and batrachians of Somaliland and Gallaland. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)*, (Ser. 2) **17**: 275–280.

BOULENGER, G.A. 1898. Concluding report on the late Capt. Bottego's collection of reptiles and batrachians from Somaliland and British East Africa. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)*, [1897–1898] (Ser. 2) **18**: 715–723, Pls 9–10.

BOULENGER, G.A. 1905. Descriptions of three new snakes discovered in South Arabia by Mr. G.W. Bury. *Annals and Magazine of Natural History (London)*, (Ser. 7) **16** (93): 178–180.

BOULENGER, G.A. 1909. Collezioni zoologische fatte nell' Uganda dal Dott. E. Bayon. III. On a second collection of reptiles, batrachians and fishes made by Dr. E. Bayon in Uganda. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)*, (Ser. 3) **4**: 302–307.

BOULENGER, G.A. 1911. Collezioni zoologische fatte nell' Uganda dal Dott. E. Bayon. XIV. On a third collection of reptiles, batrachians and fishes made by Dr. E. Bayon in Uganda. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)*, (Ser. 3) **5**: 161–169.

BOULENGER, G.A. 1912. Missione per la frontiera Italo-Etiopica sotto il Comando del Capitano Carlo Citerni. Risultati Zoologici. List of the reptiles and batrachians. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)*, (Ser. 3) **5**: 329–332.

BOURGEOIS, M. 1968. Contribution à la morphologie comparée du crâne des ophidiens del'Afrique centrale. Publications de l'Université Officielle du Congo à Lubumbashi **18**: 1–293.

BRANCH, B. [W.R.] 2005. *A Photoguide to Snakes other reptiles and amphibians of East Africa*. Struik Publishers, Cape Town, 144 pp.

BRANCH, B. [W.R.] 2015. *A Photoguide to Snakes other reptiles and amphibians of East Africa*. Revised edition. Struik Nature (Random House Publishers), Cape Town, 160 pp.

BROADLEY, D.G. 1983. *FitzSimons' Snakes of Southern Africa*. Delta Books, Johannesburg, 376 pp.

BROADLEY, D.G. 1990. *FitzSimons' Snakes of Southern Africa*. Revised edition with addendum. Delta Books, Johannesburg, 376 pp. + Addendum.

BROADLEY, D.G. 1998. Introduction to the Reptilia, pp. ix–xxxiii. **In:** *Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909–1915. Part I. Turtles, crocodiles, lizards and chameleons. Part II. Snakes. By Karl Patterson Schmidt*. Reprint: Society for the Study of Reptiles and Amphibians, Ithaca.

BROADLEY, D.G. & BATES, M.F. 2009. New range extensions for *Dasypeltis atra* Sternfeld in Tanzania (Serpentes: Colubridae), with a review of the distribution of colour phases. *African Journal of Herpetology* **58** (1): 50–55.

BROADLEY, D.G., DORIA, C.T. & WIGGE, J. 2003. *Snakes of Zambia*. Chimaira, Frankfurt am Main, 280 pp.

BROADLEY, D.G. & HOWELL, K.M. 1991. A checklist of the reptiles of Tanzania, with synoptic keys. *Syntarsus* (Bulawayo) **1**: 1–70.

BROADLEY, D.G. & WALLACH, V. 2009. A review of the eastern and southern African blind-snakes (Serpentes: Typhlophidae), excluding *Letheobia* Cope, with the description of two new genera and a new species. *Zootaxa* **2255**: 1–100.

CALABRESI, E. 1925. Anfibi e rettili raccolti dal Signor Ugo Ignesti nell'Abissinia settentrionale. *Atti della Sociatà Italiana di Scienze Naturali e dei Museo Civico di Storia Naturale in Milano* **62** (2): 100–118.

CALABRESI, E. 1927. Anfibi e rettili raccolti nella Somalia dal Proff. G. Stefanini e N. Puccioni (Gennaio-Luglio 1924). *Atti della Sociatà Italiana di Scienze Naturali e dei Museo Civico di Storia Naturale in Milano* **66** (1–2): 14–60.

CHERLIN, V.A. 1990. Taxonomic revision of the snake genus Echis (Viperidae). II. An analysis of taxonomy and description of new forms. *Proceedings of the Zoological Institute, Leningrad* **207**: 193–223.

CHISHOLM, H. (Ed.). 1911. "Emin Pasha". Encyclopaedia Britannica 9. Eleventh Edition, Cambridge University Press, Cambridge (https://en.wikisource.org/wiki/1911_Encyclop%C3%A6dia_Britannica/Emin_Pasha , accessed: 31 October 2017).

CORKILL, N.L. 1935. *Notes on Sudan snakes: a guide to the species represented in the collection in the Natural History Museum, Khartoum*. Sudan Government Natural History Museum, Khartoum, 40 pp.

CORKILL, N.L. & COCHRAN, J.A. 1965. The snakes of the Arabian peninsula and Socotra. *Journal of the Bombay Natural History Society* **62** (3): 474–506.

CURRY-LINDAHL, K. 1956. Ecological studies on mammals, birds, reptiles and amphibians in the eastern Belgian Congo. Part I (Report no. 1 of the Lund University Congo Expedition 1951–1952). *Annales du Musée Royal du Congo Belge (Tervuren), (8vo, Sciences Zoologiques)* **42**: 1–78.

DEANE, J.B. 1833. *The worship of the serpent traced throughout the world; attesting the Tempation and Fall of Man by the instrumentality of a Serpent Tempter*. Second edition. Gilbert and Rivington, London, pp. i–xiv, 1–475.

DE QUIEROZ, K. 1998. The General Lineage Concept of Species, Species Criteria, and the Process of Speciation. A Conceptual Unification and Terminological Recommendations. Pp. 55-75. **In:** Howard, D.J. & Berlocher, S.H. (eds), *Endless forms: species and speciation*. Oxford University Press, U.S.A.

DE QUIEROZ, K. 2007. Species Concepts and Species Delimitation. *Systematic Biology* **56** (6): 879–886.

DE WAAL, S.W.P. 1978. The Squamata (Reptilia) of the Orange Free State, South Africa. *Memoires van die Nasionale Museum, Bloemfontein* **11**: i–iii + 1–160.

DE WITTE, G.-F. 1962. Genera des Serpents du Congo et du Ruanda-Urundi. *Annales de Musée Royal de l'Afrique Centrale (Tervuren), (8vo, Sciences Zoologiques)* **104**: 1–203 + 215 pls.

DE WITTE, G.-F. 1975. Boidae, Colubridae, Elapidae et Viperidae. **In:** Serpents. *Exploration du Parc National des Virunga* (2) **24**: 62–121.

DOBIEY, M. & VOGEL, G. 2007. *Venomous Snakes of Africa*. Terralog 15, Chimaira, *Frankfurt am Main*., pp. 1–148 + foldout.

DUMÉRIL, A.M.C., BIBRON, G. & DUMÉRIL, A.H.A. 1854. *Erpétologie générale ou histoire naturelle compléte des Reptiles*, Imprimerie Roret, Paris, vol. 7, part 1, xvi + 780 pp.

EMMRICH, D. 1985. Bemerkungen und daten zur verbreitung eineger schlangenarten jn Athiopien. *Aquarien Terrarien* **32** (85): 65–68, 100–104, 136–140.

EMMRICH, D. 1986. Die Afrikanische Eierschlange – *Dasypeltis scabra*. *Aquarien Terrarien* **33** (86): 208–211, 241–244, 277–281, 317–319, 350–354, 356.

EMMRICH, D. 1992. Remarks on the distribution of some snake species of Ethiopia. *Walia* **14**: 16–22.

ESCORIZA, D. 2010. Ecological niche modeling of two Afrotropical snakes: is the Sahara desert a true barrier for these species? *Revista Española Herpetología* **24**: 93-100.

ESCORIZA, D. 2014. *Dasypeltis sahelensis* Trape & Mané, 2006 in Morocco and Western Sahara. Available from: http://www.moroccoherps.com/en/ficha/Dasypeltis_sahelensis/ (Date of access: 3 September 2014).

FIGUEROA, A., McKELVY, A.D, GRISMER, L.L., BELL, C.D. & LAILVAUX, S.P. 2016. A Species-Level Phylogeny of Extant Snakes with Description of a New Colubrid Subfamily and Genus. *PLoS ONE* **11** (9): e0161070.doi:10.1371/journal.pone.0161070.

FISCHER, E. & HINKEL, H. 1992. *Natur Ruandas/La Nature du Rwanda*. Université Johannes Gutenberg (Institut de Botanique spéciale & Institut de Zoologie) et l'Institut de Recherche Scientifique et Technologique, Butare, 452 pp.

FISCHER, J.G. 1884a. Über einige africanische Reptilien, Amphibien und Fische des Naturhistorischen Museums. I. Über die von Herrn Dr. G.A. Fischer im Massai-Gebiete (Ost-Afrika) auf seiner in Veranlassung der Geographischen Gesellschaft in Hamburg unternommenen Expedition gesammelten Reptilien, Amphibien und Fische. *Jahrbuch Hamburgen Wissenschaftliche Anstalten* **1**: 1–32.

FISCHER, J.G. 1884b. Herpetologische Bemerkungen. *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg* **8** (2): 43–51 (alternative page numbering: 3–11).

FITZSIMONS, V.F. 1962. *Snakes of Southern Africa*. Purnell & Sons, Cape Town, 423 pp.

FLEMMING, A.F. & BATES, M.F. 1999. Reptiles of Mkomazi. Pp. 411–428. **In:** Coe, M., McWilliam, N., Stone, G. & Packer, M. (Eds), *Mkomazi: The ecology, biodiversity and conservation of a Tanzanian savanna*. Royal Geographical Society, London, pp. i–viii + 1–608 + map.

FLOWER, S.S. 1933. Notes on the Recent Reptiles and Amphibians of Egypt, with a List of the Species recorded from that Kingdom. *Proceedings of the Zoological Society of London*. Pp. 735–851.

FROST, D.R. & HILLIS, D.M. 1990. Species in concept and practice: Herpetological applications. *Herpetologica* **46** (1): 87–104.

GANS, C. 1957. *Dasypeltis medici lamuensis*, a new race of egg-eating snake (Ophidia, Reptilia) from coastal East Africa. *Breviora* **79**: 1–13.

GANS, C. 1959. A taxonomic revision of the African snake genus *Dasypeltis* (Reptilia : Serpentes). *Annales du Musée Royal du Congo Belge (Tervuren)*, (8vo, Sciences zoologiques) **74**: 1–237.

GANS, C. 1961. Mimicry in procryptically colored snakes of the genus *Dasypeltis*. *Evolution* **15** (1): 72–91.

GANS, C. 1964. Further comments on the forms of the African snake genus Dasypeltis (Reptilia : Serpentes). *Revue de Zoologie et de Botanique Africaines* **69** (3–4): 279–295.

GANS, C. 1971. Beobachtungen an afrikanischen Eierschlangen. *Natur und Museum* [1970] **100** (10): 460–471.

GANS, C. 1974. *Biomechanics: An Approach to Vertebrate Biology*. Lippincott, Philadelphia, i–x, 261 pp.

GANS, C. & LAURENT, R.F. 1965. IV. Snakes. **In:** Gans, C., Laurent, R.F. & Pandit, H. Notes on a herpetological collection from the Somali Republic. *Annales du Musée Royal de L'Afrique central (Tervuren)*, (8vo, Sciences zoologiques) **134**: 47–70.

GARTNER, G.E.A. & GREENE, H.W. 2008. Adaptation in the African egg-eating snake: a comparative approach to a classic study in evolutionary functional morphology. *Journal of Zoology, London* **275**: 368–374.

GASCO, F. 1876. Viaggio in Egitto dei socii P. Panceri e F. Gasco nell'anno 1873–1874. Parte seconda. Ritorno da Assuan. L'oasi del Fayum. Escursioni nei dintorni del Cairo. Caccia sul Lago Menzaleh. *Annuario dell'Associazione dei Naturalisti e Medici per la mutua Istruzione*, Napoli, **1876**: 1–146.

GASPERETTI, J. 1988. Snakes of Arabia. *Fauna of Saudi Arabia* **9**: 169–450.

GENIEZ, P. 2015. *Serpents d'Europe, d'Afrique du Nord et du Moyen-Orient*. Delachaux et Niestle, Paris, 380 pp.

GENIEZ, P. & GUILLOD, M. 2003. Status and new records of *Dasypeltis scabra* (Linnaeus, 1758), in Morocco. *Herpetozoa* **16** (1/2): 88–91.

GÖTHEL, H. 2015a. Die Pazifisten unter den Schlangen – Afrikanische Eierschlangen der Gattung *Dasypeltis*. *Draco* **16** (61): 6–21.

GÖTHEL, H. 2015b. Abgepacktes Futter – Vogeleier als Nahrungsquelle. *Draco* **16** (61): 22–27.

GÖTHEL, H. 2015c. Das Fressverhalten Afrikanische Eierschlangen. *Draco* **16** (61): 28–37.

GÖTHEL, H. 2015d. Mimikry und Abwehrverhalten bei Eierschlangen. *Draco* **16** (61): 46–52.

GÖTHEL, H. 2015e. Afrikanische Eierschlangen in Terrarium. *Draco* **16** (61): 54–61.

GÖTHEL, H. 2015f. Nachzucht von Afrikanischen Eierschlangen. *Draco* **16** (61): 62–69.

GÖTHEL, H. 2015g. Erkrankungen und Parasiten bei Eierschlangen. *Draco* **16** (61): 70–76.

GÖTHEL, H. 2015h. Die Eierschlangenarten Afrikas. *Draco* **16** (61): 78–92.

GRAVLUND, P. 2001. Radiation within the advanced snales (Caenophidia) with special emphasis on African opistoglyph colubrids, based on mitochondrial sequence data. *Biological Journal of the Linnaean Society* **72**: 99–114.

GRAVLUND, P., BERGGREEN, A. & ANDERSEN, M. 1998. Geographical distribution: *Dasypeltis atra. Herpetological Review* **29** (1): 53.

GÜNTHER, A. 1878. On reptiles from Midian collected by Major Burton. *Proceedings of the Zoological Society of London*, pp. 977–978.

GÜNTHER, A.L.G. 1894. Report on the collection of reptiles and fishes made by Dr. W. Gregory during his expedition to Mount Kenia. *Proceedings of the Zoological Society of London*, pp. 84–91.

HINKEL, H. 1986. *Reptilien Ruandas*. Mainz, 28 pp.

HINKEL, H. & FISCHER, E. 1988. *Reptiles et Amphibiens du Rwanda et leurs Environnement*. Edition Bureau de Coordination, Kigali, Rwanda, 48 pp + 20 pls.

HINKEL, H. & FISCHER, E. 1990. Checklist of amphibians and reptiles of Nyungwe Forest, Rwanda. Pp. 135–138. **In:** Dowsett, R.J. (Ed.), Enquête faunistique et floristique dans la Forêt de Nyungwe, Rwanda [Survey of the fauna and flora of Nyungwe Forest, Rwanda]. Tauraco Research Report 3.

HOEVERS, L.G. & JOHNSON, P.M. 1982. Notes on a collection of snakes from the middle Juba region, Somalia. *Monitore zoologico italiano*, N.S. Supplement xvi (8): 173–203.

HOSER, R. 2013. A new egg-eating snake from the southern Arabian Peninsula (Squamata: Serpentes: Colubridae: Colubrinae: Boigini). *Australasian Journal of Herpetology* **21**: 59–63.

HUGHES, B. 1997. *Dasypeltis scabra and Lamprophis fuliginosus* – two pan-African snakes in the Horn of Africa: a tribute to Don Broadley. *African Journal of Herpetology* **46** (2): 68–77.

IBRAHIM, A.A. 2013. The Herpetology of the Suez Canal Zone, Egypt. *Vertebrate Zoology* **63** (1): 87–110.

ACOCKS, J.P.H. 1953. The veld types of South Africa. *Memoirs of the Botanical Survey of South Africa*. **28**: 1–128.

INEICH, I. I. 1999. Reptiles & Amphibiens de la République de Djibouti. Bilan des connaissances à l'aube du Troisième millénaire. Bureau National de la Diversitè Biologique (BNDB), Union International Pour la Conservation de la Nature (UICN), Programme des Nations-Unies pour le Développement (PNUD), Djibouti & Muséum National d'Histoire Naturelle (MNHN), Paris, pp. 1–60.

ICZN [International Commission on Zoological Nomenclature]. 1999. *International Code of Zoological Nomenclature*. Fourth Edition. International Trust for Zoological Nomenclature, London, XXIX + 306 pp.

IUCN [International Union for Conservation of Nature]. 2012. *IUCN Red List Categories and Criteria: Version 3.1*. Second edition. IUCN, Gland, Switzerland and Cambridge, UK.

IUCN [International Union for Conservation of Nature] [Standards and Petitions Subcommittee]. 2016. Guidelines for Using the IUCN Red List Categories and Criteria. Version 12. Prepared by the Standards and Petitions Subcommittee.
Downloadable from: http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

JAN, G. 1863. Elenco Sistematico degli ofidi descritti e disegnati per l'Iconographia generale. Tipografia di A. Lombardi, Milano, viii + 143 pp.

KAISER, H. 2014. Best Practices in Herpetological Taxonomy: Errata and Addenda. *Herpetological Review* **45** (2): 257–268.

KAISER, H., CROTHER, B.I., KELLY, C.M.R., LUISELLI, L., O'SHEA, M., OTA, H., PASSOS, P., SCHLEIP, W.D. & WÜSTER, W. 2013. Best Practices: In the 21st Century, Taxonomic Decisions in Herpetology are Acceptable Only When Supported by a Body of Evidence and Published via Peer-Review. *Herpetological Review* **44** (1): 8–23.

KELLY, C.M.R., BARKER, N.P. & VILLET, M.H. 2003. Phylogenetics of Advanced Snakes (Caenophidia) Based on Four Mitochondrial Genes. *Systematic Biology* **52** (4): 439–459.

KHALIFA, M.A. & EL-KHATEEB, S.M. 2011. Fayoum Oasis between problems and potentials: Towards enhancing ecotourism in Egypt. Urbenviron Cairo 2011: 4th International Congress on Environmental Planning and Management. Green Cities: A Path to Sustainability. December 10 – 13, 2011. Cairo and El-Gouna, Egypt, pp. 1–16.

KUPER, R. & KRÖPELIN, S. 2006. Climate-Controlled Holocene Occupation in the Sahara: Motor of Africa's Evolution. *Science* **313**: 803–807.

LANZA, B. 1972. The reptiles of the Awash National Park (Shoa, Ethiopia). *Monitore Zoologico Italiano*. Supplement **4** (7): 159–184.

LANZA, B. 1983. A list of the Somali amphibians and reptiles. *Monitore Zoologico Italiano (Firenze)*, (Ser. 2), Supplement **18** (8): 193–247.

LANZA, B. 1990. Amphibians and reptiles of the Somali Democratic Republic: checklist and biogeography. *Biogeographia (Bologna)*, (1988) **14**: 407–465.

LARGEN, M.J. 1997. An annotated checklist of the amphibians and reptiles of Eritrea, with keys for their identification. *Tropical Zoology (Firenze)* **10**: 63–115.

LARGEN, M.J. & RASMUSSEN, J.B. 1993. Catalogue of the snakes of Ethiopia (Reptilia Serpentes), including identification keys. *Tropical Zoology (Firenze)* **6** (2): 313–434.

LARGEN, M.J. & PARKER, A.R. 2004. *Catalogue of the spirit-preserved herpetological collections in the Liverpool Museum*. National Museums, Liverpool, 47 pp.

LARGEN, M. & SPAWLS, S. 2010. *The Amphibians and Reptiles of Ethiopia and Eritrea*. Chimaira, Frankfurt am Main, 693 pp.

LAURENT, R.F. 1956. Contribution à l'Herpetologie de la région des Grands Lacs de l'Afrique centrale. I: Généralitiés—II. Chéloniens – III. Ophidiens. *Annales du Musée Royal du Congo Belge (Tervuren), (8vo, Sciences Zoologiques)* **48**: 1–390, pls. 1–31.

LAURENT, R.F. 1960. Notes complémentaires sur les Chélonians et les Ophidiens du Congo oriental. *Annales du Musée Royal du Congo Belge (Tervuren), (8vo, Sciences Zoologiques)* **84**: 1–86.

LAURENT, R.F. 1965. Contribution à l'histoire de l'herpetologie congolaise et bibliographie generale. *Academie Royal des Sciences d'Outre Mer. Classe des Sciences naturelles et médicales* (N.S.) **16**: 1–55.

LAVIN, B.R. & PAPENFUSS, T.J. 2012. The phylogenetic position of *Chalcides ocellatus* (Squamata: Scincidae) from Yemen and Somalia. *Zootaxa* **3221**: 26–36.

LAWSON, R., SLOWINSKI, J.B., CROWTHER, B.I. & BURBRINK, F.T. 2005. Phylogeny of the Colubroidea (Serpentes): New evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* **37**: 581–601.

LEVITON, A.E. 1986. Description of a new species of *Coluber* (Reptilia: Serpentes: Colubridae) from the southern Tihama of Saudi Arabia, with comments on the biogeography of southwestern Arabia. *Fauna of Saudi Arabia* **8**: 436–446.

LEVITON, A.E. & ALDRICH, M.L. 1984. John Anderson: a zoologist in the Victorian period, pp. v–xxxv. **In:** K. Adler (Ed.), *Herpetology of Arabia*, by John Anderson. Reprint edition, Society for the Study of Amphibians and Reptiles, Athens, Ohio.

LICHTENSTEIN, M.H.C. & VON MARTENS, C.E. 1856. Nomenclator reptilium et amphibiorum Musei Zoologici Berolinensis. Namenverzeichniss der in der zoologischen Sammlung der Königlichen Universität zu Berlin aufgestellten Arten von Reptilien und Amphibien nach ihren Ordungen, Familien und Gattungen. *Buchdrukerei der Königlichen Akademie der Wissenschaften*, Berlin, 48 pp.

LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, diferentiis, synonymis, locis*. Holmia [Stockholm], Laurentii Salvii. Tenth edition. Vol. 1, 825 pp.

LÖNNBERG, E. 1922. Sammlungen der Schwedischen Elgon-Expedition im Jahre 1920. 6. Reptiles. *Arkiv för Zoologi (Uppsala)* **14** (12): 1–8.

LÖNNBERG, E. & ANDERSSON, L.G. 1913. On a collection of reptiles from Kismayu. *Arkiv för Zoologi (Uppsala)* **8** (20): 1–6.

LOVERIDGE, A. 1916. Report on the collection of Ophidia in the Society's Museum. *Journal of the East Africa and Uganda Natural History Society (Nairobi)* **5** (10): 76–87.

LOVERIDGE, A. 1929. East African reptiles and amphibians in the United States National Museum. *Bulletin of the United States National Museum (Washington)* (151): 1–135.

LOVERIDGE, A. 1936a. African reptiles and amphibians in Field Museum of Natural History. *Field Museum of Natural History Zoological Series (Chicago)* **22** (1): 5–111.

LOVERIDGE, A. 1936b. Scientific results of an expedition to rain forest regions in eastern Africa. V. Reptiles. *Bulletin of the Museum of Comparative Zoology (Harvard)* **79** (5): 209–337, Pls 1–9.

LOVERIDGE, A. 1942. Scientific results of a fourth expedition to forested areas in East and Central Africa. *Bulletin of the Museum of Comparative Zoology (Harvard)* **91** (4): 237–373, Pls 1–6.

LOVERIDGE, A. 1946. A guide to the snakes of the Nairobi district. *Journal of the East Africa Natural History Society (Nairobi)* **18** (3&4): 97–115.

LOVERIDGE, A. 1956. On snakes collected in the Anglo-Egyptian Sudan by J.S. Owen, Esq. *Sudan Notes and Records (Khartoum)* (1955) **36**: 37–56.

LOVERIDGE, A. 1957. Check list of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). *Bulletin of the Museum of Comparative Zoology (Harvard)* **117** (2): 151–362 + i–xxxvi.

MALONZA, P.K., BWONG, B.A. & MUCHAI, V. 2011. Kitobo Forest of Kenya, a unique hotspot of herpetofaunal diversity. *Acta Herpetologica* **6** (2): 149–160.

MÄNNEL, E. & KUCHARZEWSKI, C. 2017. Von exotischen Kaltblütern zum deutschen vollblut – Leben und Werk des Herpetologen und Hippologen RICHARD STERNFELD (1884 – 1943). *Sekretär* **17** (1): 3–50.

MARX, H. 1968. Checklist of the Reptiles and Amphibians of Egypt. Special Publication, United States Naval Medical Research Unit Number Three, Cairo, pp. i-iii, 1–91.

MAZUCH, T. 2013. *Amphibians and Reptiles of Somaliland and Eastern Ethiopia, based on two field trips in 2010 / 2011*. Tomáš Mazuch, Dříteč, Czech Republic.

MEIRTE, D. 1992. Clés de determination des serpents d'Afrique. *Annalen Zoologische Wetenschappen* **267**: 1–152.

MERTENS, R. 1938. Über eine herpetologische Sammlung aus dem Gebiete des Njarasa-Grabens Ost-Afrika. *Veröffentlichungen aus dem Deutschen Kolonial-und Übersee-Museum in Bremen* **2** (1): 1–16.

MERTENS, R. 1954. Neue Schlangenrassen aus Südwest- und Südafrika. *Zoologischer Anzeiger*, Leipzig **152** (9/10): 213–219.

MERTENS, R. 1955. Die Amphibien und Reptilien Südwestafrikas. Aus den Ergebnissen einer im Jahre 1952 ausgeführten Reise. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **490**: 1–172.

MINTER, L.R., BURGER, M., HARRISON, J.A., BRAACK, H.H., BISHOP, P.J. & KLOEPFER, D. 2004. *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland*. SI/MAB Series no. 9. Smithsonian Institution, Washington D.C.

MOCKRIN, M. & THIEME, M. (Undated). Nile Delta flooded savanna. Available from: http://www.worldwildlife.org/ecoregions/pa0904 (Date of access: 11 June 2014).

MOCQUARD, F. 1888. Sur une collection de reptiles et batraciens rapports des Pays Çomalis et de Zanzibar par M.C. Révoil. *Mémoires Publies par la Société Philomathique a l'Occasion du Centenaire de sa Fondation*, pp. 109–134.

NEÇAS, P. & MODRY, D. 1998a. Commentarios sobre la biologia, matenimento y reproduccion de *Dasypeltis atra. Reptilia* **4**: 22–27.

NEÇAS, P. & MODRY, D. 1998b. Remarks on the biology, keeping and breeding of the African egg-eating snake *Dasypeltis atra*. *Reptilia, The European Herp Magazine* **4**: 22-27.

PANCERI, P. 1878. Catalogo Sistematico del Gabinetto di Anatomia Comparata nella Regia Universita degli Studi di Napoli. Supplemento II. Tipografia dell' Accademia Reale delle Scienze, Napoli, 55 pp.

PARKER, H.W. 1932. Scientific results of the Cambridge expedition to the East African lakes 1930–1. 5. Reptiles and amphibians. *Journal of the Linnean Society, London, Zoology* **38** (258): 213–229.

PARKER, H.W. 1949. The snakes of Somaliland and the Sokotra Islands. *Zoologische Verhandelingen (Leiden)*, (6), 1–115.

PERACCA, M.G. 1909. Rettili ed amfibii. Pp. 165–180. **In:** De Filippi, F. & Amedeo di Savoia, L. (Eds), *Il Ruwenzori. Relazioni scientifiche. Resultati scientific della Spedizione Condotta da S.A.R. il Duca degli Abruzzi al Ruwenzori. Vol. I. Zoologia, botanica*. Ulrico Hoepli Libraio della Real Casa, Milano.

PETERS, W.C.H. 1864. Eine neue Art der Baumvipern, *Atheris polylepis*, aus Liberia. *Monatsberichte der königliche Preussischen Akademie der Wissenschaften zu Berlin*, pp. 642–645 (footnotes pp. 644–645).

PETERS, W.C.H. 1878. Über die von Hrn. J.M. Hildebrandt während seiner letzen ostafrikanischen Reise gesammelten Säugethiere und Amphibien. *Monatsberichte der königliche Preussischen Akademie der Wissenschaften zu Berlin* **1878**: 194–209.

PETZOLD, A., VARGAS-RAMÍREZ, M., KEHLMAIER, C., VAMBERGER, M., BRANCH, W.R., DU PREEZ, L., HOFMEYR, M.D., MEYER, L., SCHLEICHER, A., ŠIROKÝ, P. & FRITZ, U. 2014. A revision of African helmeted terrapins (Testudines: Pelomedusidae: *Pelomedusa*), with descriptions of six new species. *Zootaxa* **3795** (5): 523–548.

PITMAN, C.R.S. 1974. *A Guide to the Snakes of Uganda*. Revised edition. Wheldon & Wesley, Codicote, 289 pp.

RASMUSSEN, J.B. 2005. On the identification and distribution of the Two-Striped Night Adder (*Causus bilineatus*) and related forms. *African Journal of Herpetology* **54** (1): 1–15.

REHAK, I. & OSBORN, D.J. 1988. Notes on the distribution of reptiles and amphibians in Egypt. *Véstník Ceskoslovenské Společnosti Zoologické* **52**: 271–277.

ROUX, J. 1910. Reptilien und Amphibien. *Revue Suisse de Zoologie (Geneve)* **18**: 95–103.

SABAJ, M.H. 2016. Standard symbolic codes for institutional resource collections in herpetologyand ichthyology: an Online Reference. Version 6.5 (16 August 2016). American Society of Ichthyologists and Herpetologists, Washington, D.C. (http://www.asih.org/ , accessed 25 October 2017).

SALEH, M.A. 1997. Amphibians and Reptiles of Egypt. *Publication of the Biodiversity Unit* **6**: 1–234.

SALEH, M. & SARHAN, M. 2016. The egg-eating snake (Colubridae: *Dasypeltis*) of Faiyum, Egypt, with the description of a new species. *Bulletin de la Société Herpétologique de France* **160**: 25–48.

SCHÄTTI, B. & DESVOIGNES, A. 1999. *The herpetofauna of southern Yemen and the Sokotra Archipelago*. Museum d'Histoire naturelle Geneve, 178 pp., 40 pls.

SCHÄTTI, B. & GASPERETTI, J. 1994. A contribution to the herpetofauna of southwest Arabia. *Fauna of Saudi Arabia* **14**: 348–423.

SCHÄTTI, B. & INEICH, I. 2004. A new racer of the genus *Platyceps* Blyth from Djibouti (Reptilia: Squamata: Colubrinae). *Revue suisse de Zoologie* **111** (4): 685–690.

SCHLEICH, H.H., KÄSTLE,W. & KABISCH, K. 1996. *Amphibians and Reptiles of North Africa*. Koeltz, Koenigstein, 627 pp.

SCHLEIP, W.D. 2014. Two New Species of *Leiopython* Hubecht, 1879 (Pythonidae: Serpentes): Non-compliance with the International Code of Zoological Nomenclature Leads to Unavailable Names in Zoological Nomenclature. *Journal of Herpetology* **48** (2): 272–275.

SCORTECCI, G. 1930. Rettili ed anfibi raccolti dal prof. E. Zavattari in Eritrea. *Atti della Società Italiana si Scienze Naturali e del Museo Civico di Storia Naturale in Milano* **9** (3–4): 193–217.

SCORTECCI, G. 1931. Terzo contributo alla conoscenza dei rettili della Somalie Italiana (Ofidi). *Atti della Società Italiana si Scienze Naturali e del Museo Civico di Storia Naturale in Milano* **70** (1): 203–215.

SCORTECCI, G. 1932. Rettili del Yemen. *Atti della societa italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano* **69** (3–4): 319–321.

SCORTECCI, G. 1939. Spedizione zoological del Marchese Saverio Patrizi nel Basso Guiba e nell'Oltregiuba. Giugno-Agosto 1934 XII. Rettili. Ofidi. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)* **58**: 263–291.

SCORTECCI, G. 1943. Reptilia. **In:** *Missione Biologica Sagan-Omo*, 7. *Zoologia* **1**: 267-305.

SINDACO, R., VENCHI, A. & GRIECO, C. 2013. R*eptiles of the Western Palearctic. 2. Annotated checklist and distributional atlas of the snakes of Europe, North Africa, Middle East and Central Asia, with update to the Vol. 1*. Edizioni Belvedere, Latina (Italy), 543 pp.

SMITH, A. 1838–1849. *Illustrations of the zoology of South Africa, consisting chiefly of figures and descriptions of the objects of natural history collected during an expedition into the interior of South Africa, in the years 1834, 1835 and 1836, fitted out by 'The Cape of Good Hope Association for Exploring Central Africa.'* Vol. III. Reptilia. Smith, Elder & Co., London, 191 pp., Pls. 1–78 + app.

SPANO, S. 1972. Missioni Scortecci nell'Arabia Meridionale (1962–1965): Leptotyphlopidae e Colubridae (Ophidia). *Bolletino di Museo di Istituto di Zoologia dell'Università di Genova* **40**: 131–135.

SPAWLS, S. 1978. A checklist of the snakes of Kenya. *Journal of the East Africa Natural History Society and National Museum (Nairobi)* **31** (167): 1–18.

SPAWLS, S. 2004. A New Species of *Pseudoboodon* (Reptilia: Serpentes) from the Central Highlands of Ethiopia; with notes on some other members of the genus. *African Journal of Herpetology* **53** (1): 13–19.

SPAWLS, S. 2017. *A Guide to Amphibians and Reptiles of the Maasai Mara*. Privately published: Stephen Spawls, 40 pp.

SPAWLS, S., HOWELL, K.M. & DREWES, R.C. 2006. *Pocket guide to the reptiles and amphibians of East Africa*. A.C. Black, London, 240 pp.

SPAWLS, S., HOWELL, K., DREWES, R. & ASHE, J. 2002. *A field guide to the reptiles of East Africa (Kenya, Tanzania, Uganda, Rwanda and Burundi)*. Academic Press, San Diego, 543 pp.

STEJNEGER, L. 1894. On some collections of reptiles and batrachians from East Africa and the adjacent islands, recently received from Dr. W.L. Abbott and Mr. William Astor Chanler, with descriptions of new species. *Proceedings of the United States National Museum (Washington)* [1893] **16** (970): 711–741.

STERNFELD, R. 1908a. Zur Schlangenfauna Ostafrikas. I. Schlange aus Süd-Abessinien. *Mittheilungen aus dem Zoologischen Museum in Berlin* **4** (1): 239–241.

STERNFELD, R. 1908b. Zur Schlangenfauna Ostafrikas. II. Schlange aus Britisch-Ostafrika. *Mittheilungen aus dem Zoologischen Museum in Berlin* **4** (1): 242–245.

STERNFELD, R. 1912. Reptilia. Pp. 197–280, Pls VI–IX. **In:** Schubotz, H. (Ed.), *Wissenschaftliche Ergebnisse der deutschen Zentral-Afrika-Expedition, 1907–1908*. **4**, Zoologie II, Klinkhardt & Biermann, Leipzig. [Entire volume published in 1913].

TRAPE, J.-F. & MANÉ, Y. 2006. Le genre *Dasypeltis* Wagler (Serpentes: Colubridae) en Afrique de l'Ouest: description de trois espèces et d'une sous-espèce nouvelles. *Bulletin de Société Herpétologique de France* **119**: 27–56.

TRAPE, J.-F., CHIRIO, L., BROADLEY, D.G. & WÜSTER, W. 2009. Phylogeography and systematic revision of the Egyptian cobra (Serpentes: Elapidae: *Naja haje*) species complex, with the description of a new species from West Africa. *Zootaxa* **2236**: 1–25.

TRAPE, S., MEDIANNIKOV, O. & TRAPE, J.-F. 2012. When colour patterns reflect phylogeography: new species of *Dasypeltis* (Serpentes: Colubridae: Boigini) from West Africa. *Comptes Rendus Biologies* **335**: 488–501.

UTHMÖLLER, W. 1937. Beitrag zur Kenntnis der Schlangenfauna des Kilimandscharo (Tanganyika-Territory, ehemaliges Deutsch-Ostafrika). *Temminckia (Leiden)* **2**: 97–134.

VAN AS, J., DU PREEZ, J., BROWN, L. & SMIT, N. 2012. *The story of life and the environment: an African perspective*. Struik Nature, Cape Town, 456 pp.

VAN DE LOOCK, D. & BATES, M.F. 2016. *Dasypeltis atra*, Montane Egg-eater: Diet and distribution: *African Herp News* **63**: 16–18.

VATS, R. & SAFARI, I. 2014. Diversity of Snakes at the University of Dodoma Campus, Tanzania. *American Journal of Zoological Research* **2** (3): 41–45.

VENCHI, A. & SINDACO, R. 2006. Annotated checklist of the reptiles of the Mediterranean countries, with keys to species identification. Part 2 – Snakes (Reptilia, Serpentes). *Annali del Museo di Storia Naturale "G. Doria", Genova* **98**: 259–364.

VETAAS, O.R., SALIH, E.A. & JURASINSKI, G. 2012. Vegetation changes in the Red Sea Hills: from mist oasis to arid shrub. *Plant Ecology & Diversity* **5** (4): 527–539.

VONESH, J. 2001. Natural history and biogeography of the amphibians and reptiles of Kibale National Park, Uganda. *Contemporary Herpetology* **2001** (4): 1–14.

WAGLER, J. 1830. Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vögel. Ein Beitrag zur vergleichenden Zoologie. Munchen. Pp. iii–vi, 1–354.

WAGNER, P. & BÖHME, W. 2007. Herpetofauna Kakamegensis – The amphibians and reptiles of Kakamega Forest, western Kenya. *Bonner zoologische Beitrage* **55** (2): 123–150.

WALLACH, V., WILLIAMS, K.L. & BOUNDY, J. 2014. Snakes of the World: *A Catalogue of Living and Extinct Species*. CRC Press, Boca Raton.

WALLACH, V., WÜSTER, W. & BROADLEY, D.G. 2009. 2009. In praise of subgenera: taxonomic status of cobras of the genus *Naja* Laurenti (Serpentes: Elapidae). *Zootaxa* **2236**: 26-36.

WATKINS-COLWELL, G.J., DORNBURG, A., HAWLENA, D. & MOORE, J.A. 2010. The Amphibians and Reptiles of the 1962–1965 Yale University Prehistoric Expedition to Nubia. *Bulletin of the Peabody Museum of Natural History* **51** (2): 179–197.

WÜSTER, W. & BROADLEY, D.G. 2003. A new species of spitting cobra (*Naja*) from north-eastern Africa (Serpentes: Elapidae). *Journal of Zoology, London* **259**: 345–359.

ZAVATTARI, E. 1930. Gli animali velenosi della Colonia Eritrea. **In:** *Bono, S.E.E. – Ministro delle Colonie – della Missione Scientifica per l'Eritrea (Parma)* **8**: 171–205.

ZILIANI, U., SINDACO, R., RAZETTI, E., WASONGA, V., MODRÝ, D., NECAS, P., CARUGATI, C & FASOLA, M. 2006. The herpetofauna of the Eastern side of the Lake Turkana (Northern Kenya). Pp. 192–193. **In:** Bologna, M.A., Capula, M., Carpaneto, G.M., Luiselli, L., Marangoni, C. & Venchi, A. Abstracts: 6° Congresso Nazionale della Societas Herpetologica Italica (Roma, 27 September – 1 October 2006), Stilografica, Roma.

Appendix 1. Morphological data for specimens of *Dasypeltis* used in this study. Museum catalogue numbers with asterisks (*) denote specimens with full sets of data used in the multivariate analyses; a few specimens with full data, obtained subsequent to these analyses, are marked by +. Under 'Sex': M = male, F = female, U = undetermined. Counts for supralabials, preoculars, postoculars, anterior temporals and posterior temporals include both sides of the head. Under 'Cycles': B denotes plain brown or greyish specimens with no discernible dorsal pattern; for *D. medici*, patterned specimens for which cycle counts are not available are indicated as P, while dorsally uniform or weakly marked specimens are coded as L. For *D. atra*, patterned specimens for which cycle counts are not available are indicated as '2Bx', while specimens of the 'lineolata' morph (a variety of '2Bx') are indicated as 'lin' (see Gans 1959). Frontal pitting: 0 = smooth, 1 = marginally pitted (States 1 & 2), 2 = extensively pitted (States 3 & 4); Inter-prefrontal sulcus: 0 = weakly marked, 1 = moderately marked, 2 = deeply sunken. Notes: In some cases BM catalogue numbers (as often used by Gans 1959) may be listed without the first two numbers (e.g. BM 02.12.13.85 instead of BM 1902.12.13.85). NMW catalogue numbers (e.g. NMW 15301–2) refer to individual snakes.

Species	Catalogue No.	Country	Locality	Sex	SVL	Tail	SVL/Tail	Midbody scale rows	Ventrals	Subcaudals	Supralabials	Preoculars	Postoculars	Anter-Temps	Poster-Temps	Pattern cycles	Frontal pitting	Inter-prefrontal sulcus
D. abyssina	NMW 15301–2*	ERITREA	?	M	412	74	5.568	23	239	60	14	2	4	4	5	77	1	1
D. abyssina	NMW 15301–3	ERITREA	?	M	504			24	247		14	2	4	4	6	93	1	0
D. abyssina	BM 69.11.4.38*	ERITREA	Senafe	M	270	45	6	24	239	61	14	2	4	4	5	67	1	0
D. abyssina	FMNH 12728*	ETHIOPIA	Gondar	M	348	57	6.105	23	236	57	14	2	4	4	5	95	1	0
D. abyssina	BM 1902.12.13.85	ETHIOPIA	Zegie, Lake Tsana	M				23	226			2	4	4	8	65	0	0
D. abyssina	BM 1902.12.13.86*	ETHIOPIA	Zegie, Lake Tsana	M	235	44	5.341	23	226	68	14	2	2	4	3	B	1	0
D. abyssina	NMW 15301–1*	ERITREA	?	F	539	80	6.738	23	251	54	14	2	4	4	7	73	1	0
D. abyssina	NMW 15300*	ERITREA	Gheleb	F	540	72	7.5	24	271	54	14	2	4	4	7	81	1	0
D. abyssina	MNHN 6567	ETHIOPIA	?	F	665	90	7.389	25	260									
D. abyssina	MSNM 2699A	ETHIOPIA	Gondar	F	655	91	7.198	22	248	59	14	2	4	4		B		
D. abyssina	MZUF 783*	ETHIOPIA	Gondar	F	416	52	8	25	254	49	14	2	4	4	6	98	1	1
D. abyssina	NMBO 10256*	ETHIOPIA	Keriyo	F	422	52	8.115	25	264	51	14	2	4	4	6	89	1	0
D. abyssina	NMBO 10257*	ETHIOPIA	Keriyo	F	483	87	5.552	22	241	65	14	2	4	4	7	B	1	0
D. abyssina	NMZB 17099*	ETHIOPIA	Keriyo	F	475	70	6.786	22	247	59	14	2	4	3	6	B	1	0
D. abyssina	MSNM 2700A	ETHIOPIA	Mai Canetta	F	663	84	7.893	21	263	60	14	2	4	4		B		
D. abyssina	MCZ 80984*	ETHIOPIA	Ras Dashen Terara	F	511	74	6.905	24	261	59	14	2	4	4	6	B	1	0
D. abyssina	MSNM 2699B	ETHIOPIA	Gondar	U	364	59	6.169	22	222	61	14	2	4	4		73		
D. abyssina	MSNM 2699C	ETHIOPIA	Gondar	U	240			22	228		14	2	4	4		77		
D. abyssina	MSNM 2700B	ETHIOPIA	Mai Canetta	U	220	28	7.857	21	257	58	14	2	4	4		B		
D. arabica	MHNG 2536.42*	SAUDI ARABIA	vicinity of Abha	M				24	238	63	14	2	4	4	6	69	1	1
D. arabica	BM 1903.6.26.41*	YEMEN	El Kubar	M	325	56	5.804	23	244	65	14	2	4	4	8	72	1	1
D. arabica	MSNG 52221	YEMEN	El Siyani	M	486	77	6.312	23	236	63	14	2	4	4	6			
D. arabica	BM 1987.1018*	SAUDI ARABIA	Ajibah	F	561	75	7.5	23	246	55	14	2	2	4	6	79	1	1
D. arabica	MHNG 2536.41*	SAUDI ARABIA	Aqabat Raydah	F		43		25	254	61	14	2	4	4	6	71	1	2
D. arabica	BM 1987.2192*	YEMEN	Sana'a	F	625	89	7.022	25	240	53	14	4	4	5	7	67	1	2

D. arabica	BM 1987.2193*	YEMEN	Taiz	F	400	64	6.25	25	239	58	14	2	4	4	7	62	1	1
D. atra	MRAC 18583	BURUNDI	Kamagaba Marsh	M	457	86	5.314	24	208	57	14	2	2	4	5	2Bx	1	0
D. atra	MRAC 18585	BURUNDI	Rumonge	M	457			24	215		12	2	2	4	6	2Bx	1	0
D. atra	NMW 9964– 2^{+}	ETHIOPIA	'Abessinien'	M	350	65	5.385	24	209	57	14	2	4	4	7	76	1	0
D. atra	MSNG 30412	ETHIOPIA	Addis Ababa	M					227	50	14	2	4	2	4		0	2
D. atra	ZFMK 57537*	ETHIOPIA	Bedele, Ullubabor	M	505	88	5.739	22	220	57	14	2	2	4	7	M	1	0
D. atra	MNHN 05-209	ETHIOPIA	Bourka	M	478			23	230		14	2	4	4	6	B	1	0
D. atra	MNHN 05-210*	ETHIOPIA	Bourka	M	293	45	6.511	22	231	58	14	2	4	4	4	M	1	0
D. atra	BM 1964.1068*	ETHIOPIA	Gemu Gofa District	M	435	75	5.8	25	224	58	14	2	4	4	6	85	0	0
D. atra	ZFMK 16297*	ETHIOPIA	Genale to Chamo	M	504	87	5.793	25	214	55	14	2	4	4	6	B	0	0
D. atra	BM 1973.3175	ETHIOPIA	Ghimbi, Wollega	M	390	76	5.132			61	14	2	4	4	6	M	1	0
D. atra	MCZ 34923	ETHIOPIA	Harar	M	259	46	5.63	23	225	60	14	2	4	4	6	2Bx	1	1
D. atra	NMW 9964-1*	ETHIOPIA	Harar	M	352	58	6.069	22	232	58	14	2	4	4	6	B	1	1
D. atra	MNHN 05-205	ETHIOPIA	Laga Hardine	M	328	58	5.656	25	211	61	14					2Bx	1	0
D. atra	MNHN 05-206*	ETHIOPIA	Laga Hardine	M	325	60	5.417	25	219	58	14	2	4	4	6	74	1	0
D. atra	ZMB 27463	ETHIOPIA	Lake Alemaya	M	245	40	6.125	23	231	60	14	2	4	4	5	2Bx	1	1
D. atra	ZFMK 16237*	ETHIOPIA	Lake Shala	M	414	72	5.75	23	220	58	14	2	4	6	8	79	0	0
D. atra	MSNG 29047A	ETHIOPIA	Shoa	M				22	216	54	14	2	2	4			1	1
D. atra	BM 96.5.19.57	ETHIOPIA	Shoa (Ragazzi)	M	315	49	6.429	22	221	59	14	2	4	4	7	M		0
D. atra	NMK 483	KENYA	?	M	453	96	4.719		216	67	14		2			B		
D. atra	CAS 148035*	KENYA	Chemelil, Kisumu	M	420	83	5.06	23	209	62	14	2	3	4	6	M	1	0
D. atra	CAS 122281*	KENYA	Chuka, Meru	M	505	110	4.591	23	201	67	13	2	4	4	6	B	1	0
D. atra	BM 04.12.23.10*	KENYA	Fort Hall (= Murang'a)	M	183	33	5.545	26	221	67	14	2	4	4	6	106	1	0
D. atra	NMK 3329	KENYA	Kabarnet, Baringo	M	454				199		14		2			B		
D. atra	NMK 479	KENYA	Kabete, Kiambu	M	520	97	5.361		215	57	14		2			B		
D. atra	MCZ 40577*	KENYA	Kaimosi	M	346	64	5.406	24	211	65	14	2	3	4	6	M	1	0
D. atra	CAS 142248*	KENYA	Kakamega Forest Stn.	M	515	97	5.309	23	209	59	14	2	4	4	6	M	1	0
D. atra	NMK 3007	KENYA	Karen, Nairobi	M	464	93	4.989		206	61	14		4			B		
D. atra	NMK 2952/1	KENYA	Kiboko Ranch Station	M	198	37	5.351		206	67	14		2			2Bx		
D. atra	NMK 2862	KENYA	Kiganjo, Nyeri	M	428	81	5.284		200	55	14		2			M		
D. atra	CG 2278	KENYA	Lumbwa, Pen-y-Bryn	M	508	99	5.131	23	213	62		2	3	4	6	106	1	0
D. atra	CG 2279	KENYA	Lumbwa, Pen-y-Bryn	M	285	47	6.064	24	213	58		2	4	6	7	62	1	0
D. atra	NMK 659	KENYA	Mount Elgon	M	434	94	4.617		211	60						B		
D. atra	LACM 50631*	KENYA	Mweiga	M	476	96	4.958	23	210	59	15	2	2	4	6	B	1	0
D. atra	NMK 3339	KENYA	Nairobi	M	483	90	5.367		222	61	14		2			76		

D. atra	NMK 3548	KENYA	Nairobi	M	421	85	4.953		212	62	14		2			95		
D. atra	NMK 403	KENYA	Nairobi	M	384	66	5.818		207	59	14		2			B		
D. atra	BM 1960.1.6.40*	KENYA	Ngong	M	420	83	5.06	23	209	65	14	2	4	4	6	88	1	1
D. atra	NMK 2576	KENYA	North Nandi Forest, Chemisia	M	456	98	4.653		208	59	14		2			M		
D. atra	NMK 2590	KENYA	North Nandi Forest, Chemisia	M	466	99	4.707		208	60	14		2					
D. atra	NMK 1497	KENYA	Nyambene Hills, Meru	M	421	87	4.839		207	61	12		2			B		
D. atra	NMK 4506	KENYA	Ol Ari Nyiro Ranch	M	365			26	210		14	2	4	4	6	74	1	0
D. atra	NMK 4176	KENYA	South Nandi Forest	M	465	71	6.549		208	50	14		2			M		
D. atra	FMNH 58337	KENYA	Subukia	M	546	110	4.964	23	212	60	14	2	2	4	4	2Bx	1	
D. atra	MRAC 18554	RWANDA	Astrida	M	297	54	5.5	23	210	61	14	2	2	4	6	2Bx	1	0
D. atra	PEM R5623	RWANDA	Btwn Gikongoro & Nyungwe For. R.	M	429	81	5.296	23	211	59	14	3	3	4	6	2Bx	1	0
D. atra	ZFMK 61616*	RWANDA	Bugesera	M	426	84	5.071	24	216	62	14	2	2	4	6	M	1	0
D. atra	MRAC 2723	RWANDA	Kisenyi	M		70		22	207	66	14	3	2	4	5	2Bx	1	0
D. atra	MRAC 2725	RWANDA	Kisenyi	M	404	96	4.208	22	207	66	14	2	2	2	4	2Bx	1	0
D. atra	MRAC 2727*	RWANDA	Kisenyi	M	414	88	4.705	23	218	63	13	2	2	4	5	B	1	0
D. atra	MRAC 3821*	RWANDA	Kisenyi	M	383	83	4.614	24	210	66	14	2	2	4	4	B	1	0
D. atra	MRAC 5871	RWANDA	Kisenyi	M	413	94	4.394	24	208	66	14	2	2	4	7	2Bx	1	0
D. atra	MRAC 15477	RWANDA	Nyanza	M	226	40	5.65	24	212	63	14	2	3	5	6	2Bx	1	0
D. atra	MRAC 14331	RWANDA	Rwankeri District	M	352	61	5.77	23	212	60	14	2	2	4	6	2Bx	1	0
D. atra	MRAC 18562	RWANDA	Tare, Astrida	M				24					2	4	5	B		0
D. atra	BM 1978.380	SOUTH SUDAN	Gilo, Imatong Mtns	M	530	104	5.1	23			14	2	2	4	4	M	1	0
D. atra	FMNH 62215	SOUTH SUDAN	Gilo, Imatong Mtns	M	501	102	4.912	23	219	63	14	2	3	4	6	M	1	
D. atra	MCZ 53406*	SOUTH SUDAN	Gilo, Imatong Mtns	M	536	116	4.621	24	210	66	14	2	4	4	6	M	1	0
D. atra	MCZ 53407	SOUTH SUDAN	Gilo, Imatong Mtns	M	459	94	4.883	23	212	60	14					M	1	0
D. atra	MCZ 53408*	SOUTH SUDAN	Gilo, Imatong Mtns	M	518	116	4.466	23	217	65	14	2	2	4	6	M	1	0
D. atra	ZFMK 29564	SOUTH SUDAN	Gilo, Imatong Mtns	M				24	221	56	15	2	2	4	8	M		
D. atra	ZFMK 29719	SOUTH SUDAN	Gilo, Imatong Mtns	M				24	218	63	14	2	2	4	6	M		
D. atra	ZMUC 6116	SOUTH SUDAN	Gilo, Imatong Mtns	M	493			23	210		14	2	2	4	4	M	1	0
D. atra	ZFMK 26005	SOUTH SUDAN	Katire	M				22	219	65	14	2	2	4	6	M	1	
D. atra	ZFMK 29731	SOUTH SUDAN	Talanga Forest	M				23	214	66	12	2	2	4	4	M		
D. atra	ZMB 16749*	TANZANIA	Bukoba	M	398	79	5.038	23	213	67	14	2	2	4	5	100	1	0
D. atra	ZMB 16750	TANZANIA	Bukoba	M	278	48	5.792	23	214	59	14	4	2	4	6	2Bx	1	1
D. atra	BM 1994.403*	TANZANIA	Ibaya Camp, Mkomazi G.R.	M	453	82	5.524	26	224	59	14	2	4	4	6	90	1	0
D. atra	NMBO 7375	TANZANIA	Ibaya Camp, Mkomazi G.R.	M	211	38	5.553	26	220	65			4	4	6	92	1	1
D. atra	BM 1970.2177	TANZANIA	Kasoge, Mahale Peninsula	M	405	91	4.451	25			14	2	2	2	7	109	1	0

D. atra	ZMUC 6122	TANZANIA	Mbizi Forest Reserve	M	398			23	200	67	14	2	3	4	6	B	2	1
D. atra	ZMUC 6139*	TANZANIA	Minziro Forest Reserve	M	455	91	5	23	211	66	14	2	2	4	6	M	1	0
D. atra	ZSM 81/1936a	TANZANIA	Moshi	M	355			23	208		14					2Bx		
D. atra	ZSM 81/1936b	TANZANIA	Moshi	M	370	75	4.933	23	206	58	14					2Bx		
D. atra	LIV 1980.150.30	UGANDA	?	M	445	85	5.235		205	58			2	4	4	B		
D. atra	LIV 1960.67.1	UGANDA	Bihunga, Bukwezi	M	440	96	4.583		215	69			2	6	6	M		
D. atra	USNM 63481	UGANDA	Budongo Forest	M	560	115	4.87	23	221	63	14	2	3	4	5	M	1	
D. atra	LIV 1962.50.32	UGANDA	Buhunga, Buweju	M	494	98	5.041			62						2Bx		
D. atra	BM 11.7.8.14*	UGANDA	Bussu, Jinja	M	480	95	5.053	24	212	63	14	2	4	4	6	M	1	1
D. atra	MSNG 30413B*	UGANDA	Bussu, Jinja	M	611	98	6.235	23	209	65	14	2	4	4	4	B	1	0
D. atra	BM 51.1.3.74*	UGANDA	Entebbe	M	183	35	5.229	25	202	62	12	2	4	4	6	B	1	0
D. atra	CAS-SU 21710*	UGANDA	Fort Portal, Kingami	M	438	92	4.761	23	212	63	14	2	3	4	6	B	1	0
D. atra	LIV 1962.9.28	UGANDA	Kagabagara, Isingiro	M	508	100	5.08		210	62			2	4	5	B		
D. atra	BM 36.7.3.32	UGANDA	Kampala	M	463	101	4.584	23	208	64	14	2	2	4	6	2Bx	1	0
D. atra	LIV 1980.150.31	UGANDA	Kayonza, Kinkizi, Kigezi	M	292	53	5.509		208	61			2	4	6	B		
D. atra	NMZB-UM 2550*	UGANDA	Kayonza, Kinkizi, Kigezi	M	450	92	4.891	22	210	63	14	2	3	4	6	M	1	0
D. atra	NMK 404	UGANDA	Kazinga Channel	M	380	87	4.368		221	66	14		2			B		
D. atra	LIV 1962.9.14	UGANDA	Kichwamba, Bunyaruguru	M	348	60	5.8		210	57			4	4	6	2Bx		
D. atra	ZMB 27539	UGANDA	Kisenyi	M	224	43	5.209	23	217	67	14	2	2	4	6	2Bx	1	0
D. atra	BM 1961.1805*	UGANDA	Kyamuhunga, Igara, Ankole	M	405	83	4.88	23	208	63	14	2	2	4	5	M	1	0
D. atra	FMNH 9914	UGANDA	Lake Bunyonyi	M	446	86	5.186	24	211	61	14	2	2	4	8	2Bx	1	
D. atra	BM 32.5.2.99*	UGANDA	Lake George	M	450	104	4.327	24	208	71	14	2	3	4	6	B	1	0
D. atra	BM 51.1.3.78*	UGANDA	Lake Nabugabo	M	468	92	5.087	23	220	69	14	2	2	4	5	B	1	0
D. atra	LIV 1980.150.27	UGANDA	Lukiri, Mitoma	M	447	85	5.259		215	61			2	4	6	M		
D. atra	BM 08.10.20.14*	UGANDA	Mabira Forest, Chagwe	M	179	30	5.967	25	218	61	14	2	2	4	6	B	1	0
D. atra	BM 03.12.2.23*	UGANDA	Msozi - Isingiro	M	455	98	4.643	24	214	67	14	2	2	3	5	M	1	0
D. atra	BM 34.12.15.585*	UGANDA	Muko, Kigezi	M	355	65	5.462	23	205	61	14	2	2	4	6	M	0	0
D. atra	BM 34.12.15.586*	UGANDA	Muko, Kigezi	M	410	82	5	24	208	64	14	4	2	4	4	85	1	0
D. atra	BM 34.12.15.587*	UGANDA	Muko, Kigezi	M	201	38	5.289	23	206	65	14	2	2	4	6	107	1	0
D. atra	BM 34.12.15.589	UGANDA	Muko, Kigezi	M	215	43	5	24	204	68	14	2	2	4	5	2Bx	1	0
D. atra	BM 34.12.15.590	UGANDA	Muko, Kigezi	M	420			23	211		14	2	3	4	8	M	1	0
D. atra	BM 34.12.15.591*	UGANDA	Muko, Kigezi	M	455	88	5.17	23	207	64	14	2	2	4	5	B	1	0
D. atra	BM 34.12.15.593	UGANDA	Muko, Kigezi	M	327	59	5.542	23	218	63	14	2	2	4	7	2Bx		0
D. atra	MCZ 48363	UGANDA	Mushongero, Lake Mutanda	M	320	63	5.079	24	206	63	14	2	2	4	6	2Bx	1	0
D. atra	LIV 1980.150.26	UGANDA	Nsika, Buhwezi	M	320				212				3	4	6	M		

D. atra	LIV 1962.9.23	UGANDA	Nyabushozi	M	400	83	4.819		213	65			2	4	6	M		
D. atra	UMMZ 88532/1	UGANDA	Nyakabende	M	236	35	6.743	24	205	63	14	2	2	4	4	2Bx	1	
D. atra	LIV 1962.50.33	UGANDA	Nyansimbo, Mitoma	M	328	62	5.29		206	62			4	4	5	B		
D. atra	NMZB-UM 2549	UGANDA	Nyanuhunga, Igara, Ankole	M	430	96	4.479	24	204	63	14	2	2	4	6	2Bx	1	0
D. atra	LIV 1980.150.29	UGANDA	Nyarusiza, Bufumbira, Kigezi	M	460	99	4.646		220	65			2	4	4	2Bx		
D. atra	NMZB-UM 2553*	UGANDA	Nyarusiza, Bufumbira, Kigezi	M	320	58	5.517	22	208	62	14	2	2	4	5	103	1	0
D. atra	MSNG 40764*	UGANDA	Sesse Islands, Lake Victoria	M	472	77	6.13	23	214	67	14	2	4	4	7	B	1	0
D. atra	MCZ 40567*	UGANDA	Sipi, Mount Elgon	M	212	39	5.436	23	208	62	14	2	2	4	4	B	1	0
D. atra	MCZ 40568	UGANDA	Sipi, Mount Elgon	M	473	90	5.256	23	219	64	14	2	2	4	6	2Bx		0
D. atra	MCZ 40570*	UGANDA	Sipi, Mount Elgon	M	518	97	5.34	23	211	59	14	2	3	4	4	B	1	0
D. atra	MRAC 82-16-R-3*	BURUNDI	Bujumbura	F	615	100	6.15	25	215	57	14	2	2	4	6	130	0	0
D. atra	MRAC 18584*	BURUNDI	Makamba	F	184	30	6.133	24	219	56	14	2	2	4	6	B	1	0
D. atra	BM 16.6.24.13*	ETHIOPIA	Aware Melca	F	247	31	7.968	26	239	52	14	2	2	4	7	B	1	0
D. atra	MNHN 05-208	ETHIOPIA	Bourka	F	712	96	7.417	22	243	52	13	2	3	3	4	2Bx	1	0
D. atra	MSNM 2702	ETHIOPIA	Circao, Dambria	F	530			22	232		14	2	4	4	10	B		
D. atra	AMNH 20345*	ETHIOPIA	Ganame	F	660	93	7.097	22	256	56	15	2	4	4	6	M	1	0
D. atra	NMW 26879–2^{+}	ETHIOPIA	Ginir	F	346	46	7.522	26	231	50	13	2	4	4	7	82	1	1
D. atra	ZFMK 5535*	ETHIOPIA	Gololtscha	F	666	83	8.024	23	250	50	15	2	4	4	6	M	1	1
D. atra	NMW 26879–3	ETHIOPIA	Gumaydo	F	609			28	234		14	2	4	4	4	81	1	0
D. atra	FMNH 4012*	ETHIOPIA	Harar	F	248	35	7.086	26	231	53	14	2	4	4	5	85	1	0
D. atra	ZFMK 84993*	ETHIOPIA	Jigjiga	F	490	64	7.656	27	222	45	14	2	4	4	8	72	1	0
D. atra	MNHN 05-211	ETHIOPIA	Kounni	F	178	24	7.417	27	219	48	14	2	4	4	4	2Bx	1	0
D. atra	MNHN 05-207*	ETHIOPIA	Laga Hardine	F	264	34	7.765	26	228	51	14	2	4	4	6	B	1	0
D. atra	ZFMK 16236*	ETHIOPIA	Lake Abiata	F	532	67	7.94	25	244	50	14	2	4	4	8	72	1	0
D. atra	ZMB 10286*	ETHIOPIA	Let Marefia	F	266	32	8.313	22	243	48	14	2	2	4	4	M	1	0
D. atra	NMW 15299*	ETHIOPIA	Wondo	F	708	85	8.329	23	239	47	14	2	2	4	4	M	2	0
D. atra	UMMZ 96274	KENYA	?	F	610	93	6.559	24	221	55	12	2	4	2	7	M	1	
D. atra	LACM 66076*	KENYA	13 km SSW of Maralal	F	244	34	7.176	25	225	53	14	4	4	4	6	81	1	0
D. atra	NMW 9964–20^{+}	KENYA	Athi Plain	F	478	64	7.469	27	223	47	14	2	2	4	6	B	1	0
D. atra	NMK 3085	KENYA	Athi River	F	416	59	7.051		245	54	14		4			B		
D. atra	NMK 3129	KENYA	Athi-Kapiti Plains	F	461	71	6.493		228	58	14		4			B		
D. atra	NMK 4174	KENYA	Baringo	F	198	32	6.188		231	49	14		4			B		
D. atra	NMK 2323	KENYA	Butere, Kakamega	F	314	49	6.408		234	53	14		4			79		
D. atra	CAS 148034	KENYA	Chemelil, Kisumu	F	605	90	6.722	25	225		14	2	4	2	4	M	1	1
D. atra	NMK 406	KENYA	Chyulu Hills, Makueni	F	571	82	6.963		228	51	14		2			B		

D. atra	MCZ 40575	KENYA	Elgonyi	F	310	43	7.209	24	223	51	14	2	4	4	6	2Bx	1	0
D. atra	NMK 2849	KENYA	Embakasi, Nairobi	F					232	58	14		4			B		
D. atra	BM 08.9.17.4	KENYA	Fort Hall (= Murang'a)	F	500			27	230		14	2	4	4	6	lin	1	0
D. atra	NMK 3131	KENYA	Hopcroft Ranch, Athi River	F	512	75	6.827		244	57	12		2			B		
D. atra	USNM 40897	KENYA	Juja Farm	F	575	72	7.986	26	241	55	15	2	4	4	6	lin	1	
D. atra	BM 1957.1.11.42*	KENYA	Kabarnet, Baringo	F	595	92	6.467	23	236	56	12	2	2	4	6	M	1	0
D. atra	CAS 111767	KENYA	Kabartonjo, Kamasia Mtns	F	645	102	6.324	25	229	55	13	2	2	4	6	B	1	
D. atra	NMK 486	KENYA	Kacheliba	F	440	71	6.197		228	58	14		4			2Bx		
D. atra	MCZ 40576*	KENYA	Kaimosi	F	700	101	6.931	24	220	51	12	2	2	4	6	M	1	0
D. atra	MCZ 40578*	KENYA	Kaimosi	F	707	98	7.214	24	225	55	13	2	4	4	7	M	1	0
D. atra	USNM 49078	KENYA	Kaimosi	F	724	97	7.464	24	217	50	14	2	2	4	4	M	1	
D. atra	MCZ 18205	KENYA	Kaimosi (Yala River)	F	610			24	221		14	2	3	4	4	2Bx	1	0
D. atra	UMMZ 61224	KENYA	Kaimosi (Yala River)	F	620	88	7.045	23	223	50	12	2	2	4	6	M	1	
D. atra	LACM 93378*	KENYA	Kairuni, Nyambeni Mts	F	662	114	5.807	26	222	56	14	3	4	4	6	102	1	1
D. atra	LACM 93379*	KENYA	Kairuni, Nyambeni Mts	F	203	35	5.8	26	226	57	14	2	4	4	7	B	1	0
D. atra	BM 1959.1.5.58	KENYA	Kakamega	F	665	105	6.333		221	51	14	2	4	4	8	M	0	
D. atra	USNM 49376	KENYA	Kakamega	F	448	74	6.054	22	213	55	13	2	4	2	4	M	1	
D. atra	NMK 2503	KENYA	Karen, Nairobi	F	550	92	5.978		223	56	12		2			B		
D. atra	NMK 2952/3	KENYA	Kiboko Ranch Station	F	175	27	6.481		216	51	14		2			2Bx		
D. atra	NMK 2952/4	KENYA	Kiboko Ranch Station	F	230				247		14		2			2Bx		
D. atra	NMK 2130	KENYA	Kijabe	F	584	95	6.147		219	51	12		2			B		
D. atra	ZMUC 6101*	KENYA	Kitale	F	647	91	7.11	25	225	51	14	2	2	4	4	M	1	0
D. atra	NMK 3413	KENYA	Kitengela, Athi River	F	581	77	7.545		232	58	14		2			B		
D. atra	ZMB 9224	KENYA	Kitui	F	555	67.5	8.162	27	233	49	14	2	4	4	6	lin	1	0
D. atra	BM 1932.5.2.100*	KENYA	Lake Naivasha	F	640	94	6.809		230	50	14	2	4	4	5	M	1	0
D. atra	BM 93.11.21.72*	KENYA	Lake Naivasha	F	672	93	7.226	25	223	52	14	2	4	4	7	M	1	0
D. atra	NMK 3109	KENYA	Lorgorien, Trans-Mara	F	655	101	6.485		225	52	14		4			B		
D. atra	USNM 62907	KENYA	Mbunyi	F	765			23	227		13	2	2	4		M	1	0
D. atra	NMK 657	KENYA	Mount Elgon	F	539	85	6.341		217	53	14		2			M		
D. atra	USNM 40990	KENYA	Mount Kenya	F	622	95	6.547	26	231	54	14	2	4	4	6	M	1	
D. atra	LACM 66395*	KENYA	Mount Kulal	F	464	68	6.824	24	233	54	14	2	4	4	8	102	1	0
D. atra	NMK 1965	KENYA	Mwino, Sigor	F	359	55	6.527		235	52	14		2			B		
D. atra	PEM 873*	KENYA	Nairobi	F	650	96	6.771	23	219	54	13	2	2	4	4	B	1	0
D. atra	MCZ 54108	KENYA	Nairobi (?)	F	650	86	7.558		233	53	14	2	4	4	8	lin	1	0
D. atra	NMK 2486	KENYA	Nairobi (Westlands)	F	524	89	5.888		236	54	14		2			105		

D. atra	BM 01-1-3-9	KENYA	Naitolia (6000 feet)	F	495			27	238		14	2	4	4	7	81	1	0
D. atra	NMK 1453	KENYA	Nakuru	F	604	97	6.227		218	53	14		2			B		
D. atra	NMK 484	KENYA	Nakuru	F	554	89	6.225		220	55	14		4			B		
D. atra	BM 06.7.6.7*	KENYA	Nandi	F	384	53	7.245	23	218	50	14	2	2	3	5	M	1	0
D. atra	NMK 1158	KENYA	Nandi Hills	F	700	105	6.667		224	50	14		4			M		
D. atra	NMK 3490	KENYA	Nanyuki River, Laikipia	F	531	92	5.772		224	53	14		2			M		
D. atra	NMK 3512	KENYA	Nanyuki River, Laikipia	F	611				223		14		4			M		
D. atra	NMK 1960	KENYA	Nbabibi, Naivasha	F	469	58	8.086		231	48	14		4			B		
D. atra	NMK 2583	KENYA	North Nandi Forest, Chemisia	F	890	115	7.739		218	53	14		4			M		
D. atra	CG 2281	KENYA	Pen-y-Bryn Farm , Lumbwa	F	705	97	7.268	26	231	49		2	4	4	6	M	1	
D. atra	BM 96.3.27.18*	KENYA	Uganda Railway	F	232	35	6.629	24	212	51	14	2	2	4	5	104	1	0
D. atra	MRAC 18555	RWANDA	Astrida	F	613	83	7.386	24	224	58	14	2	2	4	4	2Bx	1	0
D. atra	MRAC 18556	RWANDA	Astrida	F		40		25		50	14	2	2	4	6	2Bx	1	0
D. atra	MRAC 18557	RWANDA	Astrida	F	372	56	6.643	24	214	51	12	2	2	4	4	2Bx	1	1
D. atra	MRAC 18558	RWANDA	Astrida	F	207	33	6.273	24	222	54	14	2	2	4	5	2Bx	1	0
D. atra	MRAC 86-01-R-10	RWANDA	Bugarama	F	567	90	6.3	25	219	54	14	3	2	4	7	2Bx	1	0
D. atra	MRAC 86-01-R-11	RWANDA	Bugarama	F	642	95	6.758	24	218	55	14	2	2	4	6	2Bx	1	0
D. atra	MRAC 18577	RWANDA	Bulimbi	F				24	221		14	2	2	4	6	2Bx	1	0
D. atra	ZFMK 61617	RWANDA	Cyamudongo	F	656	100	6.56	24	230	58	12	2	2	4	5	2Bx	1	0
D. atra	MRAC 14329	RWANDA	Kamohorora District	F	293	46	6.37	24	234	58	14	2	3	4	6	2Bx	1	0
D. atra	ZFMK 55105*	RWANDA	Kibungo, Rusumo	F	432	68	6.353	24	224	55	14	2	2	4	5	B	1	1
D. atra	MCZ 48364*	RWANDA	Kisenyi	F	572	91	6.286	25	227	59	14	2	2	4	5	115	1	0
D. atra	MRAC 5872	RWANDA	Kisenyi	F	424	65	6.523	24	222	50	14	2	2	4	6	2Bx	1	0
D. atra	MRAC 9773	RWANDA	Kisenyi	F	755	115	6.565	24	236	53	14	2	2	4	6	2Bx	1	0
D. atra	ZMB 20458	RWANDA	Kisenyi	F	517	75	6.893	24	222	51	14	2	2	4	5	2Bx	1	0
D. atra	ZMB 27156	RWANDA	Kisenyi	F	409	67	6.104	25	221	54	14	2	2	4	6	2Bx	1	0
D. atra	MRAC 14333	RWANDA	Lake Gando	F	663	103	6.437	24	226	54	14	2	2	4	5	2Bx	1	0
D. atra	MRAC 14341	RWANDA	Lake Gando	F		65		25	218	54	14	2	2	4	4	2Bx	1	0
D. atra	MRAC 7509	RWANDA	Mutura, Mount Virunga	F	587	90	6.522	24	229	59	14	2	2	4	4	2Bx	1	0
D. atra	MRAC 74-23-R-22	RWANDA	Mwogo near Butare	F				24	217		14	2	2	4	4	2Bx	1	0
D. atra	MRAC 14340	RWANDA	Rwankeri District	F	377	58	6.5	24	219	52	14	2	2	4	5	2Bx	1	0
D. atra	MRAC 15440	RWANDA	Rwankeri District	F	673	109	6.174	24	225	60	16	2	2	4	7	113	1	
D. atra	MRAC 18259*	RWANDA	Rwankuba	F	632	100	6.32	25	228	54	14	2	2	4	7	B	1	0
D. atra	MRAC 4074*	RWANDA	Shangugu	F	525	85	6.176	24	225	59	14	2	2	4	8	93	1	0
D. atra	MRAC 4075*	RWANDA	Shangugu	F	373	58	6.431	26	229	54	14	2	2	4	5	108	1	0

D. atra	MRAC 18560	RWANDA	Tare, Astrida	F	719	99	7.263	25	225	51	13	2	2	4	6	B		0
D. atra	MRAC 18561	RWANDA	Tare, Astrida	F	542			24	224		14	2	2	4	6	B	1	0
D. atra	ZFMK 29567	SOUTH SUDAN	10 km S of Juba	F	760			24	236	57	13	2	2	4	5	M		
D. atra	ZFMK 29565	SOUTH SUDAN	Aweil	F	760			23	225	51	14	2	2	4	4	M		
D. atra	BM 1978.379	SOUTH SUDAN	Gilo, Imatong Mts	F	625	97	6.443	24	229		13	2	4	4	6	M	1	0
D. atra	MCZ 53569	SOUTH SUDAN	Gilo, Imatong Mts	F	372			26	228		14	2	4	4	6	B	1	1
D. atra	ZFMK 34532	SOUTH SUDAN	Gilo, Imatong Mts	F				24	228	63		2	2	4	6	M		
D. atra	ZFMK 29732	SOUTH SUDAN	Talanga Forest	F	500			24	227	54	14	2	2	4	6	M		
D. atra	ZFMK 29733	SOUTH SUDAN	Talanga Forest	F	430			24		59	14	2	2	4	9	M		
D. atra	PEM 17329	TANZANIA	Klein's Gate, N.E Serengeti	F	317	45	7.044	27	240	56	14	2	4			92	1	0
D. atra	PEM 17336	TANZANIA	Klein's Gate, N.E Serengeti	F	434			25	227		14	2	4			100	1	0
D. atra	PEM 17941	TANZANIA	Klein's Gate, N.E Serengeti	F	345			25	225		14	2	4	4	6	80	1	1
D. atra	ZMUC 6140*	TANZANIA	Minziro Forest Reserve	F				23	227	54	14	2	2	4	6	M	1	0
D. atra	ZSM 81/1936c	TANZANIA	Moshi (Uru)	F	475	60	7.917	23	235	47	14					2Bx		
D. atra	ZMB 17039A*	TANZANIA	Mount Kilimanjaro	F	197	30	6.567	25	240	55	14	2	4	4	6	93	1	0
D. atra	ZMB 17039B	TANZANIA	Mount Kilimanjaro	F	408	62	6.581	26	233	56	14	2	4	4	6	2Bx	1	0
D. atra	LIV 1960.115.3	UGANDA	Bitereko, Igara	F	638	96	6.646		223	54			2	4	5	M		
D. atra	BM 51.1.3.68	UGANDA	Bufundi, Kigezi	F	501	75	6.68	24	222	55	14	2	2			108	1	0
D. atra	BM 51.1.3.79	UGANDA	Bufundi, Kigezi	F	665	96	6.927	24	216	50	14	2	2	4	6	2Bx	1	0
D. atra	NMZB 217 = SRM 3.2*	UGANDA	Bufundi, Lake Bunyonyi	F	580	88	6.591	25	221	52	14	2	2	4	6	B	1	0
D. atra	BM 51.1.3.80*	UGANDA	Bukakata	F	645	101	6.386	24	227	56	14	2	2	4	5	B	1	0
D. atra	BM 1951.1.5.24*	UGANDA	Busingiro, Budango	F	760	106	7.17	23	230	54	14	2	4	4	6	M	1	0
D. atra	MCZ 40574	UGANDA	Butandiga, Mount Elgon	F	650	97	6.701	24	224	52	14	2	4	4	6	2Bx	1	0
D. atra	LACM 38696*	UGANDA	Bwamba Forest (Ntandi)	F	567	92	6.163	25	226	55	14	2	2	4	6	B	1	0
D. atra	LACM 46344*	UGANDA	Bwamba Forest (Ntandi)	F				24	217	64	14	2	3	4	6	B	1	1
D. atra	CAS-SU 21709	UGANDA	Fort Portal, Kingami	F	410	70	5.857	25	228	60	14	2	2	4	6	2Bx	1	1
D. atra	MCZ 54738*	UGANDA	Fort Portal, Kingami	F	700	108	6.481	27	216	54	14	2	2	4	7	M	1	0
D. atra	BM 51-1-3-77*	UGANDA	Gulu	F	475	63	7.54	26	232	48	14	2	4	4	6	88	1	1
D. atra	BM 1976.2265	UGANDA	Ibanda	F	390	63	6.19	22		52	15	2	2	5	8	M	1	2
D. atra	BM 12.10.12.2*	UGANDA	Jinja	F	422	57	7.404	26	230	51	14	2	4	4	6	B	1	0
D. atra	BM 1961.1803*	UGANDA	Kabingo, Bunyaruguru	F	445	67	6.642	25	211	53	14	2	4	4	6	B	1	0
D. atra	LIV 1960.67.5	UGANDA	Kagando, Kigagati	F	205	30	6.833		219	49			4	4	6	2Bx		
D. atra	LACM 60705*	UGANDA	Kalinzu Forest	F	392	59	6.644	25	213	53	15	2	2	4	6	M	1	0
D. atra	BM 1984.882*	UGANDA	Kampala	F	710	119	5.966	23	223	57	14	2	2	4	6	B	1	0
D. atra	MUZM	UGANDA	Kampala	F	475	73	6.507	25	224	56	14		3			B		

D. atra	MUZM	UGANDA	Kampala	F	310	49	6.327	25	220	54	14	2	2	4	6	M		
D. atra	LACM 39242*	UGANDA	Katera, Sango Bay Forest	F	668	100	6.68	25	222	56	14	2	2	4	6	B	1	0
D. atra	NMZB 103 = SRM 3.1*	UGANDA	Katunguru	F	325	54	6.019	25	216	56	14	2	2	4	8	M	1	0
D. atra	MRAC 9997*	UGANDA	Katwe	F				25	217	60	14	2	4	4	6	M	1	0
D. atra	LACM 35090*	UGANDA	Kayonza, Impenetrable F.	F	530	87	6.092	24	224	57	14	2	2	4	6	B	1	0
D. atra	LIV 1962.9.27	UGANDA	Kayonza, Kinkizi	F	657	105	6.257		216	53			2	4	6	M		
D. atra	LIV 1962.9.22	UGANDA	Kinani, Nyabushozi	F					222				2	4	4	M		
D. atra	BM 51.1.3.75	UGANDA	Kyamahunga	F	630	94	6.702	24	225	55	14	2	2	4	6	2Bx	1	0
D. atra	LIV 1962.9.4	UGANDA	Kyamogorani, Kashari	F	648	100	6.48		226	55			2	4	6	B		
D. atra	FMNH 9913	UGANDA	Lake Bunyonyi	F	527	76	6.934	24	224	52	14	2	2	4	4	2Bx	1	
D. atra	MCZ 34922	UGANDA	Lake Bunyonyi	F	628	100	6.28	24	223	51	15	2	2	4	4	2Bx	1	0
D. atra	NMZB 219 = SRM 3.4*	UGANDA	Lake Edward	F	620	101	6.139	26	218	54	14	2	2	4	6	B	1	0
D. atra	BM 08.10.20.15*	UGANDA	Mabira Forest, Chagwe	F	391	59	6.627	26	219	54	14	2	4	4	6	B	1	0
D. atra	BM 51.1.3.76*	UGANDA	Masese, Jinja	F	754	121	6.231	24	225	56	14	2	2	4	6	B	1	0
D. atra	MCZ 48359	UGANDA	Mihunga, Ruwenzori	F	230			24	222		14	2	2	4	6	M	1	0
D. atra	NMK 3291	UGANDA	Mityana	F	530	78	6.795		232		14		4			M		
D. atra	BM 1954.1.12.37*	UGANDA	Morulinga, 24 km S of Moroto	F	300	43	6.977	24	224	54	14	2	4	4	6	82	1	1
D. atra	CAS 85300*	UGANDA	Mount Elgon	F	620	90	6.889	23	220	52	14	2	2	4	4	M	1	0
D. atra	BM 34.12.15.592*	UGANDA	Mubango, Mabira Forest	F	830	133	6.241	23	230	59	14	2	2	4	6	M	1	0
D. atra	BM 34.12.15.588	UGANDA	Muko, Kigezi	F	625	102	6.127	24	214	55	14	2	2	4	6	2Bx	1	0
D. atra	BM 34.12.15.594*	UGANDA	Muko, Kigezi	F	365	45	8.111	24	222	52	14	2	2	4	6	M	1	0
D. atra	BM 03–12–2–22*	UGANDA	Mulema	F	500	68	7.353	25	226	51	14	2	4	4	6	92	1	0
D. atra	MCZ 48362*	UGANDA	Mushongero, Lake Mutanda	F	438	64	6.844	24	230	52	14	2	2	4	6	B	1	0
D. atra	MCZ 48360	UGANDA	Nyakabande	F	677	98	6.908	25	226	53	14	2	2	5	10	2Bx	1	0
D. atra	MCZ 48361	UGANDA	Nyakabande	F	538	74	7.27	24	223	51	14	2	2	4	6	2Bx	1	0
D. atra	UMMZ 88532/2	UGANDA	Nyakabende	F	325	45	7.222	25	216	51	14	4	2	4	6	2Bx	1	
D. atra	LIV 1959.83.2	UGANDA	Nyamuhumia, Igara	F	365	49	7.449		218	47			4	4	4	2Bx		
D. atra	LIV 1980.150.33	UGANDA	Nyansimbo, Mitoma	F	222	38	5.842		223	55			2	4	5	B		
D. atra	BM 1976.1849*	UGANDA	Nyarusiza, Bufumbira, Kigezi	F	270	42	6.429	24	214	53	14	2	2	4	6	95	1	0
D. atra	NMZB-UM 2552*	UGANDA	Nyarusiza, Bufumbira, Kigezi	F	310	50	6.2	24	216	54	14	2	2	4	6	96	1	0
D. atra	MCZ 54744	UGANDA	Rucho, Ankole	F	592	102	5.804	25	225	59	14	2	2	4	6	2Bx	1	0
D. atra	LIV 1960.67.3	UGANDA	Ruhama, Rwampara	F	455	65	7		220	52			4	4	6	2Bx		
D. atra	MSNG 27755A*	UGANDA	Sesse Islands, Lake Victoria	F	616	76	8.105	22	229	55	14	2	4	4	4	B	1	0
D. atra	MCZ 40564*	UGANDA	Sipi, Mount Elgon	F	725	100	7.25	23	224	55	14	2	2	4	4	M	1	0
D. atra	MCZ 40565*	UGANDA	Sipi, Mount Elgon	F	621	90	6.9	24	218	52	14	2	2	4	4	M	1	0

D. atra	MCZ 40566	UGANDA	Sipi, Mount Elgon	F	515	77	6.688	24	218	52	14	2	2	4	4	2Bx	1	0
D. atra	MCZ 40569*	UGANDA	Sipi, Mount Elgon	F	710	106	6.698	24	232	53	14	2	3	4	6	M	1	0
D. atra	MCZ 40571*	UGANDA	Sipi, Mount Elgon	F	620	84	7.381	24	220	52	14	2	3	4	7	M	1	0
D. atra	MCZ 40572	UGANDA	Sipi, Mount Elgon	F	342	50	6.84		218	50	14	2	4	4	4	B		
D. atra	MCZ 40573	UGANDA	Sipi, Mount Elgon	F	225	35	6.429		223	54	14	2	4	4	4	B		
D. atra	MRAC 82-16-R4	BURUNDI	Bujumbura	U				23	218	75	14	2	2	4	5	B	1	0
D. atra	MSNM 2975	ETHIOPIA	El Dire, Tertale	U	277	42	6.595	24	219	49	14	2	4	4	6	69		
D. atra	BM 1973.3175	ETHIOPIA	Ghimbi	U												M		
D. atra	BM 1975.2144	ETHIOPIA	Kebre Mengist to Negele	U	170						14	2	2	4	6	2Bx	1	1
D. atra	NMK 1962	KENYA	?	U	377	72	5.236		203	59	14		4			2Bx		
D. atra	NMK 348	KENYA	?	U	192	27	7.111		212	53	12		4			B		
D. atra	NMK 1348	KENYA	Athi River	U	636	93	6.839		221	50	14		4			B		
D. atra	NMK 488	KENYA	Kacheliba	U	536	87	6.161		229	54	14		2			98		
D. atra	NMK 482	KENYA	Kakamega	U	257	39	6.59		216	48	14		2			B		
D. atra	NMK 2715	KENYA	Kakamega	U	411	65	6.323		221	54	14		2			2Bx		
D. atra	NMK 1260	KENYA	Kericho	U	712	101	7.05		216	51	16		4			B		
D. atra	NMK 481	KENYA	Kiambu	U	199	32	6.219		226	69	12		4			B		
D. atra	NMK 2952/2	KENYA	Kiboko Ranch Station	U	182	29	6.276		251	64	14		4			2Bx		
D. atra	NMK 3123	KENYA	Kiserian, Baringo	U	235	33	7.121		227	51	14		4			B		
D. atra	NMK 3051	KENYA	Kitale	U	317	69	4.594		214	52	14		2			2Bx		
D. atra	NMK 1791	KENYA	Lake Baringo	U	619	107	5.785		228	57	14		2			104		
D. atra	NMK 3152	KENYA	Mount Elgon	U	208	40	5.2		214	59	12		4			2Bx		
D. atra	NMK 658	KENYA	Mount Elgon	U	565	90	6.278		221	52	12		2			B		
D. atra	NMK 3557	KENYA	Nanyuki River, Laikipia	U	539	91	5.923		221	54	14		4			M		
D. atra	NMK 1489	KENYA	Nyambene Hills, Meru	U	594	97	6.124		225	52	14		2			92	1	1
D. atra	NMK 3182	KENYA	Timbilil, SW Mau Forest	U	195				232		14		4			B		
D. atra	IRSNB 2657	RWANDA	Ruhengeri	U	245	46	5.326	23	209	69	14	2	2	4	5	106	1	0
D. atra	PEM 16778	TANZANIA	Klein's Camp, N.E. Serengeti	U	251			27	244		14	2	4			75	2	0
D. atra	ZMUC 6138	TANZANIA	Minziro Forest Reserve	U	212	38	5.579	22	216	61	14	2	2	4	6	M	1	0
D. atra	ZMUC 6141	TANZANIA	Minziro Forest Reserve	U				23	214	68	12	2	2	4	6	B	1	0
D. atra	BM 1970.2178	TANZANIA	Sitete, Mahale Peninsula	U	435	43				64	14	2	2	4	4	B	1	0
D. atra	MSNG 30413A	UGANDA	Bussu, Jinja	U	786	102	7.706	25	230	60	14	2	4	4	6	M	1	0
D. atra	MSNG 52410	UGANDA	Bussu, Jinja	U	586	71	8.254	23	226	54	12	2	4	4		B		
D. atra	LIV 1960.115.4	UGANDA	Kayonza, Kinkizi	U									2	4	5	B		
D. atra	NMK 1495	UGANDA	Nyarusiza	U	664	93	7.14		226	50	14		2					

D. atra	NMK 1496	UGANDA	Nyarusiza	U	591	94	6.287		221	59	14		2			B		
D. bazi	NMW 26879–1	EGYPT	Cairo, surroundings of	F	461	61	7.557	24	234	50	14	2	4	4	6		1	1
D. bazi	ZMB 1861*	EGYPT	Oberaegypten	M	455	79	5.759	23	229	59	14	2	4	4	6	48	1	1
D. bazi	MNHN 1847*	EGYPT		M	410	70	5.857	23	229	59	14	2	4	4	6	49	2	1
D. bazi	ZMB 5865*	EGYPT		M	427	78	5.474	23	219	60	14	2	4	6	6	39	2	2
D. bazi	BM 97.10.28.575*	EGYPT	Fayoum	F	602	90	6.689	24	227	55	14	2	4	5	6	42	1	1
D. bazi	ZMB 51552*	EGYPT	Uberegypte	F	503	70	7.186	24	228	51	14	2	4	4	6	48	0	0
D. cf. *bazi*	ZFMK 38415	SUDAN	Erkowit	M				25	229	67	14	2	4	6	8	48	1	
D. confusa	NMW 9964–2*	ETHIOPIA	?	M	362	67	5.403	24	208	57	14	2	4	4	7	75	1	0
D. confusa	ZMB 56436*	ETHIOPIA	'Addis Ababa'	M	475	87	5.46	24	213	57	14	2	4	4	6	79	0	1
D. confusa	NMK 485	KENYA	Kacheliba	M	319	55	5.8		212	51	14		4			67		
D. confusa	NMK 489	KENYA	Kacheliba	M	424	74	5.73		216	54	14		4			65		
D. confusa	MCZ 53403*	SOUTH SUDAN	Nimule	M	232	42	5.524	26	208	63	14	2	4	4	6	55	1	1
D. confusa	FMNH 58361	SOUTH SUDAN	Torit	M	396	79	5.013	25	224	67	14	2	4	4	6	B	1	
D. confusa	FMNH 58362	SOUTH SUDAN	Torit	M	330	69	4.783	23	210	63						B	1	
D. confusa	FMNH 62209	SOUTH SUDAN	Torit	M	551			25	203		14	2	4	4	6	B	1	
D. confusa	FMNH 62214	SOUTH SUDAN	Torit	M	394	78	5.051	24	220	64	14	2	4	4	5	54	1	
D. confusa	FMNH 62217	SOUTH SUDAN	Torit	M	235	45	5.222	25	212	64	14	2	4	4	6	B	1	
D. confusa	MUZM 10/R1*	UGANDA	Ajai Game Reserve	M	395	84	4.702	25	200	66	14	2	4	4	8	50	1	0
D. confusa	MCZ 47815*	UGANDA	Busingiro, Budongo Forest	M	358	64	5.594	26	199	54	14	2	4	4	10	54	1	1
D. confusa	BM 1951-1-5-39*	UGANDA	Lira, Lango	M	325	62	5.242	25	205	62	14	2	4	4	6	62	1	0
D. confusa	UMMZ 88529	UGANDA	Lira, Lango	M		45		25			14	2	4	4	7	61	0	
D. confusa	LIV 1960.51.2	UGANDA	Nakosa, Bunyaruguru	M	390				208				4	4	6			
D. confusa	CAS 141784*	KENYA	Mumias	F	203	27	7.519	26	226	48	14	2	4	4	6	63	1	0
D. confusa	ZMB 77441	RWANDA	Lac Kivu	F	620			24	224		11	2	4	4	6	71	1	0
D. confusa	ZFMK 29694	SOUTH SUDAN	10km S of Juba	F		25				55	14	2	4	4	6	50		
D. confusa	FMNH 58496	SOUTH SUDAN	Juba	F	575	92	6.25	26	228	54	14	2	4	4	8	54	1	
D. confusa	MCZ 53401*	SOUTH SUDAN	Logutoic	F		77		26	221	55	14	2	4	4	6	60	1	0
D. confusa	FMNH 62216	SOUTH SUDAN	Lokwi	F	165	25	6.6	25	229	49	14	2	3	4	6	69	1	
D. confusa	MCZ 53402	SOUTH SUDAN	Mongalla	F	524			23	225		14	2	4	4	6	58	1	0
D. confusa	NMW 9964–7[+]	SOUTH SUDAN	'Sudan' (taken as East Equatoria)	F	465	67	6.940	25	231	55	14	2	4	4	4	62	1	0
D. confusa	FMNH 58363	SOUTH SUDAN	Torit	F	492	72	6.833	25	223	54	14	2	4	4	6			
D. confusa	FMNH 62207	SOUTH SUDAN	Torit	F	369			25	239		14	2	4	4	6	61	1	
D. confusa	FMNH 62208	SOUTH SUDAN	Torit	F	428			25	236		14	2	4	4	6	B	1	
D. confusa	FMNH 62210	SOUTH SUDAN	Torit	F	417	64	6.516	24	230	55	14	2	4	4	6		1	

D. confusa	FMNH 62211	SOUTH SUDAN	Torit	F	187	32	5.844	25	233	56	14	2	4	4	6	B	1	
D. confusa	FMNH 62212	SOUTH SUDAN	Torit	F	435	62	7.016	25	238	53	14	2	4	4	6	68	1	
D. confusa	FMNH 62213	SOUTH SUDAN	Torit	F	378			25	237		14	2	4	4	5	64	1	
D. confusa	MCZ 53405*	SOUTH SUDAN	Torit	F	324	51	6.353	25	236	57	14	2	4	4	6	73	1	1
D. confusa	MCZ 53404	SOUTH SUDAN	Torit	F	546			24	236		14	2	4	4	6	64	1	1
D. confusa	FMNH 58336	SOUTH SUDAN	Yei	F	252	51	4.941	27	226	58	13	2	4	4	7	58		
D. confusa	BM 1951.1.3.69*	UGANDA	Bisu, Kigezi	F	518	79	6.557	26	222	56	14	2	4	4	6	61	1	0
D. confusa	LACM 39043*	UGANDA	Bugoma Forest	F	166	31.5	5.188	23	213	61	14	2	4	4	6	61	1	0
D. confusa	MCZ 47830*	UGANDA	Gulu, Acholi	F	301	52	5.788	23	212	56	14	2	4	4	6	B	1	0
D. confusa	NMZB 14333*	UGANDA	Kyambura Game Reserve	F	520	73	7.123	25	229	52	14	2	4	4	8	63	1	0
D. confusa	NMZB 15411*	UGANDA	Kyambura Game Reserve	F	485	73	6.644	26	215	52	14	2	4	4	5	B	1	0
D. confusa	MCZ 47801*	UGANDA	Lira, Lango	F	444	59	7.525	25	228	50	14	2	4	4	8	B	1	0
D. confusa	UMMZ 88530	UGANDA	Lira, Lango	F		56		27	218	50	14	2	4	4	8	B	1	
D. confusa	BM 1951.1.3.84*	UGANDA	Moyo, West Madi	F	245	37	6.622	26	229	57	14	2	4	4	6	55	1	0
D. confusa	LIV 1962.106.19	UGANDA	Nyanshimbo, Ibanda	F	501				226				4	4	7			
D. confusa	LIV 1960.67.2	UGANDA	Sanga, Nyabushozi	F	481	73	6.589		213	53			4	4	7			
D. confusa	BM 1954 1.12.8*	UGANDA	Semliki	F	503	72	6.986	24	218	52	12	2	4	3	6	59	1	0
D. confusa	BM 1954 1.12.9*	UGANDA	Semliki	F		77		26	215	55	14	2	4	3	6	55	1	2
D. confusa	BM 1976.848*	UGANDA	Serere, Teso	F	567	81	7	26	227	55	14	2	4	4	5	B	1	0
D. crucifera	MZUT 3582*	ERITREA	Agordat	M	211	39	5.41	22	226	61	14	2	4	4	5	52	1	0
D. crucifera	ZMB 7631*	ERITREA	Bogos	F	442	64	6.906	25	231	52	14	2	4	4	6	62	1	0
D. crucifera	MZUT 3469	ERITREA	Agordat	F				23	247	50								
D. crucifera	MSNG 6738*	ERITREA	Keren	F	368	45	8.178	24	243	49	14	2	4	4	6	51	1	0
D. fasciata	LACM 38697	UGANDA	Ntandi, Bwamba Forest	M	525	111	4.73	23	230	71	14	2	4	4	7		2	0
D. fasciata	LACM 46342*	UGANDA	Ntandi, Bwamba Forest	M	509	116	4.388	23	229	76	14	2	4	4	6	141	1	0
D. fasciata	LACM 39243*	UGANDA	Sango Bay Forest, Katera	M	472	91	5.187	24	212	59	14	2	4	4	4	108	1	0
D. fasciata	MCZ 48357	UGANDA	Bundibugyo, Bwamba	F	667	119	5.605	24	241	68	13	4	4	4	6		1	0
D. fasciata	MCZ 48358A	UGANDA	Bundibugyo, Bwamba	F	730	132	5.53	23	239	67	14	2	4	4	6		1	0
D. fasciata	MCZ 48358B	UGANDA	Bundibugyo, Bwamba	F	635	100	6.35	25	248	66	14	2	3	4	6			0
D. fasciata	UMMZ 88531	UGANDA	Bundibugyo, Bwamba	F	627	107	5.86	23	248	64	14	4	4	4	6		1	
D. fasciata	LACM 46341	UGANDA	Ntandi, Bwamba Forest	F	238	50	4.76	22	237	76	14	2	2	6	7		1	0
D. fasciata	LACM 46343*	UGANDA	Ntandi, Bwamba Forest	F	586	113	5.186	24	241	71	14	2	4	5	8	116	1	0
D. fasciata	LACM 46345*	UGANDA	Ntandi, Bwamba Forest	F	312	57	5.474	24	242	71	14	2	4	4	6	111	1	0
D. fasciata	LACM 46346	UGANDA	Ntandi, Bwamba Forest	F	598	103	5.806	24	245	65	13	2	4	5	6		1	0
D. fasciata	TCWC 23839*	UGANDA	Ntandi, Bwamba Forest	F	611	108	5.657	23	243	67	14	2	4	4	7	113	1	0

D. medici	NMK 2631	KENYA	Gede	M	679	146	4.651		220	78	14		4			L		
D. medici	NMK 3200	KENYA	Gede	M	384	91	4.22		235	80	14		2			L		
D. medici	BM 1951.1.3.73*	KENYA	Kilifi	M	465	116	4.009	24	229	87	14	2	4	4	6	L	2	0
D. medici	MCZ 40581*	KENYA	Lamu Island	M	502	132	3.803	23	226	94	14	2	4	4	6	L	2	0
D. medici	NMK 1561	KENYA	Malindi	M	487	127	3.835		230	84	14		4			L		
D. medici	NMK 2535	KENYA	Malindi	M	560	125	4.48		220	75	12		4			L		
D. medici	NMK 2558	KENYA	Malindi	M					241	79	14		2			L		
D. medici	NMK 3292	KENYA	Malindi	M	616	133	4.632		241	80	14		4			L		
D. medici	ZMB 50191	KENYA	Malindi	M	461	115	4.009	24	239	91	14	2	4	4	5	P	1	0
D. medici	NMK 3956	KENYA	Mount Warges, Wamba	M	466	106	4.396	24	239	83	14	2	4	4	6	P	2	0
D. medici	NMK 1699	KENYA	Nyambene Hills, Meru	M	424	104	4.077		233		14	2	4	4	6	P	2	0
D. medici	CAS 135751	KENYA	Tiwi, Kwale District	M	370	85	4.353	24	224	84	14	2	4	4	6	P	2	1
D. medici	MZUF 2028	SOMALIA	Alessandra Island, Gelib	M	422	107	3.944	24	233	93	12	2	4	4	6		1	1
D. medici	CAS 148077*	SOMALIA	Mareri, Lower Juba River	M	375	95	3.947	24	230	89	14	2	4	4	6	L	2	1
D. medici	MZUF 27155	SOMALIA	Mareri, Lower Juba River	M	496	137	3.62	24	231	98	13	2	4	4	6		2	
D. medici	NMW 9964–18^{+}	TANZANIA	Dar-es-Salaam	M	430	104	4.135	24	246	94	14	3	4	4	6	66	2	0
D. medici	FMNH 251325	TANZANIA	East Usambara Mts	M	400	95	4.211	24	249	89	14	2	3	4	5	P	2	0
D. medici	ZMUC 6144*	TANZANIA	Longido	M	522	129	4.047	24	239	89	14	2	4	4	6	79	2	1
D. medici	SMF 19460*	TANZANIA	Mafia Island	M	471	119	3.958	23	252	98	14	2	4	4	7	68	2	0
D. medici	MCZ 18206*	TANZANIA	Makindu River	M	525	130	4.038	24	240	89	14	2	4	4	6	67	2	0
D. medici	NMZB 17318	TANZANIA	Mlinga Forest Res.	M	460	124	3.71	23	240	103	14	2	4	4	6	P	2	0
D. medici	USNM 62904	TANZANIA	Morogoro	M	475	115	4.13	24	237	83	14	2	4	5	7	67	2	
D. medici	USNM 62906	TANZANIA	Morogoro	M	470	105	4.476	24	248	86	14	2	4	4	6	P	2	
D. medici	SMNS 4216E	TANZANIA	Moshi	M				26	230		14	2	4	4	6	72	2	0
D. medici	SMNS 4216F	TANZANIA	Moshi	M	315	69	4.565	26	232	80	15	2	4	4	7	92		1
D. medici	ZMUC 6121*	TANZANIA	Msolwa, Ruhebo Mtns	M	444	117	3.795	25	234	81	14	2	2	4	6	70	2	0
D. medici	ZMB 17453*	TANZANIA	Usambara	M	575	158	3.639	25	242	109	14	2	4	6	10	64	2	0
D. medici	ZMB 8597*	TANZANIA	Zanzibar Coast	M	480	117	4.103	24	243	94	14	3	4	5	6	69	2	0
D. medici	NMK 3249	TANZANIA	Zanzibar Island	M	451	129	3.496		235	93	12		2					
D. medici	NMK 402	KENYA	Chyulu Hills	F	616	120	5.133		239	66	14		4					
D. medici	AMNH 88631	KENYA	Gede	F	641	130	4.931	25	235	80	14	2	3	4	6		2	0
D. medici	NMK 2597	KENYA	Gede	F	600	141	4.255		229	82	14		2			L		
D. medici	NMK 2619*	KENYA	Gede	F	580	123	4.715	26	227	81	14	2	4	6	7	L	2	0
D. medici	NMK 480	KENYA	Giriama, Kilifi	F	466	103	4.524		226	72	14		4					
D. medici	ZMB 37600	KENYA	Kibognoto – Kilimanjaro	F	496	103	4.816	27	218	74	14	2	4	6	8		1	0

D. medici	NMK 1050	KENYA	Kikambala, Kilifi	F	612	112	5.464		231	79	14		4					
D. medici	BM 1951.1.3.72*	KENYA	Kilifi	F	600	119	5.042	25	228	80	14	2	3	4	6	L	2	0
D. medici	MCZ 40582*	KENYA	Lamu Island	F	575	130	4.423	24	226	84	14	2	4	4	6	L	2	0
D. medici	NMK 2522	KENYA	Malindi	F	567	141	4.021		229	80	14		2			L		
D. medici	NMK 2526	KENYA	Malindi	F	707	131	5.397		235	77	14		4			L		
D. medici	NMK 2527	KENYA	Malindi	F	545	124	4.395		247	85	14		4			L		
D. medici	NMK 2529	KENYA	Malindi	F	654	127	5.15		232	76	14		4			L		
D. medici	NMK 2530	KENYA	Malindi	F	616	148	4.162		234	79	14		4			L		
D. medici	NMK 2531	KENYA	Malindi	F	597	134	4.455		225	82	14		4			L		
D. medici	NMK 2532	KENYA	Malindi	F	494	116	4.259		227	79	14		4			L		
D. medici	NMK 2533	KENYA	Malindi	F	535	117	4.573		220	76	14		2			L		
D. medici	NMK 2587	KENYA	Malindi	F	566	128	4.422		239	75	14		4			L		
D. medici	NMK 3290	KENYA	Malindi	F	597	121	4.934		234	79	14		2			L		
D. medici	BM 98.1.8.15*	KENYA	Maungu	F	452	92	4.913	25	228	81	14	2	4	5	8	L	2	0
D. medici	NMW 26926[+]	KENYA	Mombasa, 30 km S of	F	289	66	4.379	26	233	81	14	2	4	4	6	86	2	0
D. medici	BM 87.11.3.31*	KENYA	Mount Kilimanjaro	F	500	104	4.808	24	230	80	14	2	4	5	6	L	2	0
D. medici	USNM 16755*	KENYA	Mount Kilimanjaro	F	702			25	232	67	13	2	4	7	6	L	2	0
D. medici	MCZ 40580	KENYA	Mount Mbololo	F	645	120	5.375	26	231	72	14	2	4	6	9	L		
D. medici	ZFMK 63582	KENYA	near Mombasa	F	613	119	5.151	25	231	74	14	2	4	4	6		2	0
D. medici	NMK 2377	KENYA	Nguni, Mwingi	F	481	84	5.726		223	82	14		4					
D. medici	ZMB 9244*	KENYA	Taita	F		105		25	232	73	14	2	3	4	7	L	2	0
D. medici	ZMB 17496	KENYA	Takaungu	F	405	77	5.26	25	238	74	14	2	4	6	8		2	1
D. medici	FMNH 142635*	KENYA	'Vicinity of Nairobi'	F	912	149	6.121	25	235	71	14	2	4	6	8	L	2	1
D. medici	BM 98.1.8.14	KENYA	Voi to Ndi	F	274	52	5.269	24	241	75	14	2	4	4	6	P	2	0
D. medici	MSNG 42710B	SOMALIA	Belet Amin	F	845			22	232		13	2	4	4	6	L	0	0
D. medici	MCZ 23274*	TANZANIA	Amani, Usambara Mts	F	640	145	4.414	26	241	87	14	2	4	4	6	108	2	0
D. medici	ZMB 37598*	TANZANIA	Amani, Usambara Mts	F	546	117	4.667	26	241	82	14	2	4	4	7	77	2	0
D. medici	ZMUC 6123	TANZANIA	Bombani, E. Usambara Mts	F	649	124	5.234	25	239	73	14	2	4	4	6	P	2	0
D. medici	ZMUC 6133*	TANZANIA	Bombani, E. Usambara Mts	F	599	124	4.831	25	245	78	14	2	4	4	6	76	2	0
D. medici	NMZB 11265*	TANZANIA	Mafia Island	F	410	87	4.713	26	252	88	14	2	4	4	6	L	2	0
D. medici	AMNH 143717	TANZANIA	Morogoro	F	262	54	4.852	24	243	83	14	2	4	4	6	64	2	2
D. medici	USNM 62901	TANZANIA	Morogoro	F	595	118	5.042	25	240	81	14	2	4	4	6	59	2	
D. medici	ZMB 27616*	TANZANIA	Morogoro	F	630	120	5.25	26	237	72	14	2	4	4	6	70	2	0
D. medici	SMNS 4216A*	TANZANIA	Moshi	F	680	135	5.037	24	237	75	15	2	4	5	7	L	2	1
D. medici	SMNS 4216B*	TANZANIA	Moshi	F		117		25	233	69	14	2	4	5	8	L	2	0

D. medici	SMNS 4216C*	TANZANIA	Moshi	F	500	93	5.376	26	233	61	14	2	4	5	7	L	1	0
D. medici	SMNS 4216D*	TANZANIA	Moshi	F	419	82	5.11	25	232	75	14	2	4	6	8	L	2	0
D. medici	ZFMK 82342	TANZANIA	Mount Kwaraha	F	287			25	235		14	2	4	4	6	78	1	0
D. medici	MCZ 23273*	TANZANIA	Nyange, Uluguru Mts	F	463	94	4.926	25	244	82	14	2	4	4	6	57	2	0
D. medici	CM 36586	TANZANIA	Usa River, Arusha	F	460	85	5.412	26	232	75	14	2	4	4	6	L		
D. medici	BM 50.1.5.40	TANZANIA	Zanzibar	F	650	131	4.962	25	247	77	14	2	4	4	6	P	2	0
D. medici	ZMB 17219*	TANZANIA	Zanzibar	F	568	112	5.071	25	242	77	14	2	4	6	8	82	2	0
D. medici	ZMB 5737*	TANZANIA	Zanzibar	F	595	133	4.474	25	247	90	14	2	4	5	8	80	2	0
D. medici	NMK 4121	KENYA	Kitobo Forest, Taveta	U	672	106	6.34		233	66	14		4					
D. medici	NMK 2538	KENYA	Malindi	U	597	134	4.455		231	70			2			L		
D. medici	NMK 2540	KENYA	Malindi	U	422	123	3.431		229	79			4			P		
D. medici	NMK 4131	KENYA	River Tana, Mchelelo Forest	U	484	83	5.831		232	84	12		4					
D. medici	ZMUC 6124	TANZANIA	Amani, E. Usambara Mts	U	330	73	4.521	26	246	84	14	2	4	4	8	91	2	
D. medici	ZMUC 6143	TANZANIA	East Usambara Mts	U	182	46	3.957		230	92	14	4	4	4	5	59	1	1
D. medici	ZMB 48150	TANZANIA	Kimboza Forest	U					241		14	2	4	4	4	75		
D. medici	MCZ 54827	TANZANIA	Mafia Island	U							14	2	4	6	7	P	2	1
D. medici	ZMUC 6111	TANZANIA	Zanzibar Island	U	382	78	4.897	25	251	83	14	2	4	4	6	P	2	0
D. scabra	PEM 8602*	ETHIOPIA	Entrance to Awash Nat. Park	M	385	71	5.423	23	212	57	14	2	4	5	6	51	2	2
D. scabra	BM 1973.3259*	ETHIOPIA	Lake Abiata	M	435	80	5.438	24	215	56	14	2	4	4	6	75	1	1
D. scabra	ZMB 51835*	ETHIOPIA	Meki	M	420	70	6	23	214	57	16	2	4	4	7	77	1	0
D. scabra	BM 00.11.29.3	ETHIOPIA	west of Omo River	M	445			24	212		14	2	4	4	6	60	2	0
D. scabra	AAU 489	ETHIOPIA	west shore of Lake Chamo	M	313	52	6.019	25	218	62	14	2	4	4	4			
D. scabra	MSNPV CR790*	KENYA	Gatab, Mount Kulal	M	384	81	4.741	24	220	63	14	2	4	4	6	92	1	1
D. scabra	MSNPV CR792*	KENYA	Gatab, Mount Kulal	M	312	64	4.875	24	219	66	14	2	4	4	6	84	1	2
D. scabra	BM 01.1.3.3*	KENYA	Gilgil	M	398	79	5.038	26	208	65	14	2	2	4	7	76	2	0
D. scabra	CAS 130785*	KENYA	Isiolo	M	385	75	5.133	25	203	60	14	2	4	4	6	79	1	0
D. scabra	NMK 561	KENYA	Isiolo	M	386	71	5.437		220	59	14		4			81		
D. scabra	BM 93.11.21.72*	KENYA	Kithu-Uri, E. Kikuyu	M	350	59	5.932	25	206	54	14	2	4	4	6	66	1	0
D. scabra	NMK 2965	KENYA	Kora	M	456	88	5.182		221	62	14		4			65		
D. scabra	NMK 1472	KENYA	Lake Naivasha	M	367	63	5.825		213	61	14		4			80		
D. scabra	NMK 2343	KENYA	Lake Naivasha	M	412	84	4.905		206	57	14		4			69		
D. scabra	NMK 3052	KENYA	Solio Ranch, Laikipia	M	288	54	5.333		204	50	14		4			66		
D. scabra	NMK 3021	KENYA	Tsavo East N.P.	M	236	41	5.756		208	47	14		4			57		
D. scabra	NMK 1022	KENYA	Voi	M	298	52	5.731		208	52	14		4			73		
D. scabra	PEM 5624	RWANDA	15 km S of Butare	M	351	76	4.618	25	197	67	14	2	4	4	7		1	1

D. scabra	MRAC 18559	RWANDA	Astrida	M	136			25	192		14	2	4	4	5	61		1
D. scabra	MRAC 9209*	RWANDA	Gabiro	M	192	35	5.486	26	201	63	14	2	4	4	7	58	1	2
D. scabra	ZMB 22518*	RWANDA	Lake Kivu	M	420	108	3.889	24	201	73	12	2	3	4	7	64	1	0
D. scabra	MZUF 24179	SOMALIA	6 km E of Afgoi	M	376	78	4.821	23	208	63	14	2	4	4	8		2	
D. scabra	MSNG 29239	SOMALIA	Btwn Comia and Matagoi	M	462	74	6.243	25	214	62	13	2	4	4	6		2	1
D. scabra	MZUF 31459*	SOMALIA	Ceelcillan = El Ellan	M	389	81	4.802	25	204	62	14	2	4	4	6	74	2	0
D. scabra	MZUF 24674*	SOMALIA	Dinsoor	M	285	58	4.914	24	209	64	14	2	4	4	6	70	2	2
D. scabra	MSNM 2071	SOMALIA	Giohar	M	397			22	203		14	2	4	4	4	50		
D. scabra	MZUF 21968*	SOMALIA	Lugh - Ganame	M	391	78	5.013	24	210	62	14	2	4	4	6	76	2	1
D. scabra	MZUF 1134	SOMALIA	Maheddei Uen	M	461	89	5.18	22	209	63	14	2	4	4	6		2	2
D. scabra	FMNH 134939*	SOUTH SUDAN	Melut	M	370	72	5.139	25	213	62	13	2	4	4	6	64	1	0
D. scabra	NMW 9964–6[+]	SOUTH SUDAN	'Sudan' (taken as East Equatoria)	M	449	88	5.102	23	215	67	14	2	4	4	4	59	1	0
D. scabra	AMNH 50791	TANZANIA	Chai Camp	M	241	45	5.356	27	208	69	14	2	4	4	8		2	
D. scabra	NMW 9964/17	TANZANIA	Dar es Salaam	M				23	205		14	2	4	4	6	60		1
D. scabra	ZMB 26832*	TANZANIA	Dar es Salaam	M	369	82	4.5	24	201	68	14	2	0	4	5	69	2	0
D. scabra	BM 1954.1.2.154*	TANZANIA	Kange Estate	M	400	85	4.706	23	206	67	14	2	2	4	6	71	2	1
D. scabra	ZMB 22754	TANZANIA	Kibwesa	M	432	77	5.61	25	221	61	14	2	4	4	7		1	0
D. scabra	MCZ 30205	TANZANIA	Maji Malulu, Usandawi	M	181			27	225		14	2	4	4	6	54	2	1
D. scabra	ZMB 14097*	TANZANIA	Massailand	M	387	78	4.962	27	223	69	14	2	3	4	6	67	1	0
D. scabra	USNM 62902*	TANZANIA	Morogoro	M	335	64	5.234	24	218	62	14	3	4	4	5	69	2	0
D. scabra	ZMB 19669*	TANZANIA	Mpwapwa	M	398	87	4.575	26	214	69	14	2	4	4	6	54	2	0
D. scabra	NMK 1887	TANZANIA	Seronera, Serengeti N.P.	M	344	73	4.712		211	72	14		4					
D. scabra	ZMB 16753*	TANZANIA	Wembere Steppe	M	418	83	5.036	26	215	63	14	2	4	4	7	56	2	1
D. scabra	BM 68.2.29.101*	TANZANIA	Zanzibar	M	370	74	5	24	214	72	12	2	4	4	6	47	2	0
D. scabra	MCZ 18208*	TANZANIA	Zengeragusa, Mkalama	M	460	78	5.897	25	226	58	14	2	4	4	6	79	1	1
D. scabra	LIV 1962.330.22	UGANDA	Kayanja, Nyabusonji	M	360	76	4.737		200	66								
D. scabra	BM 51.1.5.79*	UGANDA	Mbarara, Ankole	M	375	84	4.464	25	207	68	14	2	4	4	7	78	2	0
D. scabra	LIV 1960.67.4	UGANDA	Ruborogoto, Ishingiro	M	198	38	5.211		188	63			4	4	6			
D. scabra	LIV 1960.67.7	UGANDA	Ruborogoto, Ishingiro	M	329	72	4.569		200	65			4	4	8			
D. scabra	LIV 1962.168.14	UGANDA	Ruzinga, Ankole	M	453	98	4.622		199	63			4	4	5			
D. scabra	LIV 1960.67.8	UGANDA	Rwensama, Kashali	M	352	83	4.241		185	64			4	4	6			
D. scabra	BM 07.12.1.19*	UGANDA	Wadelai	M	333	67	4.97	23	214	67	14	2	4	4	6	65	1	0
D. scabra	MNHN 6565*	'ARABIA'	?	F	252	39	6.462	24	244	54	14	2	4	4	6	55	2	1
D. scabra	MRAC 18563*	BURUNDI	Kabuyenge	F	702	103	6.816	26	234	60	14	2	2	2	4	75	2	1
D. scabra	MRAC 18565*	BURUNDI	Kahiro Dist.	F	547	77	7.104	25	227	53	14	2	4	4	6	52	2	1

D. scabra	MRAC 18564*	BURUNDI	Mugera	F	495	72	6.875	25	220	52	14	2	4	4	6	60	2	1
D. scabra	NMW 15298*	ETHIOPIA	?	F	590	87	6.782	28	219	53	14	2	4	6	7	56	2	1
D. scabra	AAU 494	ETHIOPIA	Arba Minch	F					229	48	14	2	4	4	6			
D. scabra	AAU 679	ETHIOPIA	Arba Minch	F	668	92	7.261	22	243	54	14	2	4	4	5			
D. scabra	BM 16.6.24.12*	ETHIOPIA	Aware Melca	F	415	71	5.845	24	221	59	14	2	4	4	6	56	1	0
D. scabra	ZFMK 17763*	ETHIOPIA	Bulcha	F	522	80	6.525	27	241	50	14	2	4	4	6	79	1	0
D. scabra	PEM 8603*	ETHIOPIA	Entrance to Awash Nat. Park	F	217	29	7.483	24	234	57	14	2	4	4	6	54	2	1
D. scabra	BM 1964.1069	ETHIOPIA	Gojam District	F	525	76	6.908	23	219	47	12	2	4	4	7		0	0
D. scabra	ZMB 77053*	ETHIOPIA	Meki	F	825	121	6.818	25	231	57	14	2	4	4	6	85	0	2
D. scabra	BM 00.11.29.2*	ETHIOPIA	W of Omo River	F	593	87	6.816	25	226	53	14	2	4	4	6	55	2	1
D. scabra	PEM 5627	KENYA	45 km W of Ewaro Ngiro (Narok)	F				26	236	49	14	2	4	4	7		1	0
D. scabra	USNM 42016	KENYA	Aberdare Mtns	F	305	38	8.026	26	220	47	14	2	4	4	6	69		
D. scabra	NMK 2824	KENYA	Buna, Wajir Dist.	F	411	73	5.63		222	55	14		4			67		
D. scabra	MSNPV CR791*	KENYA	Gatab, Mount Kulal	F	324	61	5.311	22	219	64	14	2	4	4	6	94	1	1
D. scabra	BM 01.1.3.4*	KENYA	Gilgil	F	532	60	8.867	28	229	43	14	4	4	5	6	73	2	0
D. scabra	CAS 147836	KENYA	Hell's Gate, Naivasha	F	350	42	8.333	26	233	46	14	2	4	4	6		2	1
D. scabra	CAS 130784*	KENYA	Isiolo	F	550	76	7.237	26	234	51	14	2	4	4	7	88	1	0
D. scabra	BM 51-1-3-70	KENYA	Kilifi	F	480			25	227		14	2	2	4	6	70	2	0
D. scabra	MCZ 40584*	KENYA	Laini, Tana River	F	427	62	6.887	25	225	53	14	2	4	4	6	83	1	0
D. scabra	NMK 1415	KENYA	Lake Naivasha	F					230	50	14		4			72	2	1
D. scabra	NMK 2083	KENYA	Lake Naivasha	F					229	52	14		4			72	1	2
D. scabra	NMK 2855	KENYA	Lake Naivasha	F	247				240		14		4			74		
D. scabra	NMK 3184	KENYA	Lake Naivasha	F	867				230		14		4					
D. scabra	NMK 3319	KENYA	Lake Naivasha	F	657	98	6.704		215	50	14		4			72		
D. scabra	NMP 1260*	KENYA	Lake Naivasha	F	509	76	6.697	27	228	52	14	2	4	4	8	72	1	1
D. scabra	NMK 2819	KENYA	Lolgorien, Trans-Mara	F	372	58	6.414		232	55	14		6			69		
D. scabra	NMK 3005	KENYA	Lolgorien, Trans-Mara	F	281	42	6.69		233	53	14		4			73		
D. scabra	NMK 930	KENYA	Manyani, Tsavo West N.P.	F	368	57	6.456		231	52	14		4			60		
D. scabra	MCZ 40583	KENYA	Mombosasa, near Witu	F	648	97	6.68	25	228	55	14	2	4	4	6	76		
D. scabra	CAS 147837*	KENYA	Naivasha	F	300	34	8.824	26	238	45	14	2	4	4	6	67	1	1
D. scabra	CAS 147838*	KENYA	Naivasha	F	325	40	8.125	25	226	45	14	2	4	4	6	75	2	1
D. scabra	NMK 3103	KENYA	Ol Ari Nyiro Ranch	F	390	53	7.358		228	49	14		4			75		
D. scabra	USNM 41974	KENYA	Sotik, Uaso Nyiro	F	343	42	8.167	26	230	45	14	2	4	4	6	71	2	
D. scabra	MCZ 11501*	KENYA	Uaso Nyiro Plains	F	362	46	7.87	26	221	47	14	2	4	3	6	75	1	1
D. scabra	CAS 130661	KENYA	Wajir	F	565	95	5.947	26		65	14	2	4	4	6	56	2	2

D. scabra	NMK 2262	KENYA	Wajir	F					232	50	14		2			63	2	0
D. scabra	MCZ 40585*	KENYA	Wema (Ngatana)	F	268	40	6.7	25	215	55	14	2	4	4	6	73	0	0
D. scabra	MRAC 9214*	RWANDA	Gabiro	F	637	83	7.675	25	235	48	14	2	4	5	6	83	2	0
D. scabra	MZUF 1118*	SOMALIA	Afgoi	F	180	31	5.806	25	218	56	14	2	4	6	7	55	0	0
D. scabra	MZUF 1133*	SOMALIA	Afgoi	F	344	57	6.035	24	228	64	14	2	4	4	7	74	2	1
D. scabra	MSNG 42710A	SOMALIA	Belet Amin	F	587	78	7.526	23	216	51	14	2	4	4	6		1	0
D. scabra	MZUF 24996*	SOMALIA	Dinsoor	F	557	93	5.989	28	222	57	14	2	4	4	7	68	2	0
D. scabra	MSNG 28808	SOMALIA	Lugh	F	519	66	7.864	24	222	54	14	4	4	6	4		2	1
D. scabra	BM 98.1.28.14*	SOMALIA	Lugh	F	218	32	6.813	26	227	58	14	2	4	4	6	58	2	0
D. scabra	MSNM 2148	SOMALIA	Magadi (= Uagadi)	F	496	80	6.2	22	202	57	14	2	4	4	6	51		
D. scabra	MZUF 2802*	SOMALIA	Mogadishu	F	210	36	5.833	25	224	59	13	2	4	4	6	76	2	0
D. scabra	MZUF 27156*	SOMALIA	near Mareri	F	367	57	6.439	24	215	54	14	2	4	4	7	79	1	0
D. scabra	RMNH 24399	SUDAN	40 km E of Rabak	F					222	55						50		
D. scabra	MNHN 7227*	SUDAN	Nil Blanc	F	673	90	7.478	25	226	52	14	2	4	4	6	55	1	1
D. scabra	BM 09.10.15.35	SUDAN	Sennar Province	F	240			23	227		14	2	4	4	6	65	1	1
D. scabra	ZMB 21062*	TANZANIA	Amani, Usambara Mtns	F	740	124	5.968	27	234	65	14	2	4	4	7	63	2	1
D. scabra	PEM 5626*	TANZANIA	Mapenduzi, Dodoma	F	265	42	6.31	26	249	60	14	2	3	6	10	60	2	2
D. scabra	ZMB 11934A*	TANZANIA	Massailand	F	283	41	6.902	26	231	61	14	2	3	3	6	59	2	0
D. scabra	ZMB 11934B*	TANZANIA	Massailand	F	793	110	7.209	27	242	54	14	2	4	4	6	69	2	0
D. scabra	USNM 62903	TANZANIA	Morogoro	F	500	85	5.882	26	232	57	14	2	4	5	8	67	0	
D. scabra	USNM 62905	TANZANIA	Morogoro	F	447	72	6.208	26	223	59	14	2	4	4	6	79	2	
D. scabra	BM 87.11.3.30*	TANZANIA	Mount Kilimanjaro	F	346	52	6.654	25	230	58	14	2	2	3	6	67	1	0
D. scabra	ZMB 13304*	TANZANIA	Mpwapwa	F	403	63	6.397	27	225	57	14	2	2	4	6	62	2	0
D. scabra	FMNH 27786	TANZANIA	Ngare, Nanyuki	F	539			26	229	55	14	2	4	4	8	69	2	
D. scabra	NMZB 1681*	TANZANIA	Tumba, Rukwa Valley	F	710	103	6.893	26	238	54	14	2	3	4	6	60	2	2
D. scabra	NMZB 659*	TANZANIA	Tumba, Rukwa Valley	F	760	109	6.972	26	236	53	14	2	4	4	6	65	2	2
D. scabra	MCZ 30207*	TANZANIA	Ukerewe Island	F	524	70	7.486	26	223	49	14	2	4	4	8	62	2	1
D. scabra	MCZ 30208	TANZANIA	Ukerewe Island	F	708			25	231		14	3	4	4	6	64	2	1
D. scabra	BM 68.2.29.100*	TANZANIA	Zanzibar	F	476	78	6.103	25	226	59	13	2	4	4	6	46	2	0
D. scabra	BM 68.2.29.102*	TANZANIA	Zanzibar	F	335	51	6.569	27	233	58	14	2	4	4	7	53	2	0
D. scabra	LIV 1962.106.6	UGANDA	Kaburangiri, Kashali	F	270	32	8.438		216	52			4	4	5			
D. scabra	LIV 1960.67.6	UGANDA	Kakoba, Kashari	F	612	85	7.2		216	49			3	4	6			
D. scabra	LIV 1959.83.1	UGANDA	Mbarara, Ankole	F	640	90	7.111		217	51			2					
D. scabra	BM 1961.1804*	UGANDA	Mbarara, Kashari	F	690	105	6.571	25	216	53	14	2	4	4	6	71	2	2
D. scabra	BM 03.12.2.21*	UGANDA	Mulema	F	550	84	6.548	27	219	54	14	2	4	4	6	72	2	0

D. scabra	LIV 1962.106.5	UGANDA	Namatyobola, Kashali	F	354	53	6.679		206	51			3	4	6			
D. scabra	LIV 1962.106.35	UGANDA	Ruborogoto, Ishingiro	F	810	113	7.168		222	53			4	4	6			
D. scabra	LIV 1962.106.20	UGANDA	Rukoni, Kwampala	F	480	63	7.619		220	50			4	4	6			
D. scabra	BM 1959.1.5.59	UGANDA	Ruzinga, Isingiro	F	650	92	7.065		230	57	14	2	4	4	6	78	1	1
D. scabra	BM 1969.288	ETHIOPIA	Arba Minch	U	155	27	5.741	26	213	59	14	2	4	4	7	82	0	0
D. scabra	BM 16.6.24.11	ETHIOPIA	Aware Melca	U	210	28	7.5	25	235	55	14	2	4	4	6	66	1	1
D. scabra	IRSNB 5499	RWANDA	Gabiro	U	443	66	6.712	26	226	54	14	2	4	4	5	70		
D. scabra	PEM 5625	RWANDA	Nyagatare	U	163	31.5	5.094	25	194	59	14	2	4	4	6	55	2	0
D. scabra	USNM 72476	TANZANIA	Kikombo, Dodoma	U	200	28	7.143	26	253	67	14	2	4	4	6	68	1	
D. scabra	ZMUC 6136	TANZANIA	Minziro Forest Reserve	U	176	27	6.519	25	216	52	11	2	4	3	5	63	2	1
D. scabra	ZMUC 6137	TANZANIA	Minziro Forest Reserve	U	188	31	6.065	26	226	56	14	2	4	4	6		1	0
D. scabra	NMW 9964–9[+]	TANZANIA	Tanga	U	195	37	5.270	25	204	63	14	2	3	4	6	65	1	0
D. taylori	BM 1992.501	SOMALIA	2.5 km SW of Hargeisa	M	305				199		14	2	4	4	6	44	2	1
D. taylori	BM 1951.1.7.69*	SOMALIA	Garadak	M				23	202	59	14	2	4	4	4	49	2	1
D. taylori	BM 1949.2.2.1*	SOMALIA	Haud	M	188	34	5.529	23	196	55	12	2	3	4	6	55	2	0
D. taylori	BM 1949.2.2.2*	SOMALIA	Haud	M	172	30	5.733	24	198	60	14	2	4	4	6	50	2	1
D. taylori	BM 1949.2.2.5	SOMALIA	Ogo	M	408	83	4.916	25	216	68	14	2	4	4	6	53		0
D. taylori	MNHN 84-707*	DJIBOUTI	?	F	477	68	7	25	222	52	14	2	4	4	6	59	2	1
D. taylori	BM 1949.2.2.4	SOMALIA	Hargeisa Dist.	F	530			24	208		14	2	2	2	6	53	2	1
D. taylori	BM 1949.2.2.3*	SOMALIA	Haud	F	189	23	8.217	24	211	44	14	2	3	4	6	59	2	1

INSTRUCTIONS TO AUTHORS

POLICY

Manuscripts, i.e. full-length papers and short communications (maximum 2 000 words), in English or Afrikaans, containing original research results on African topics related to the approved research disciplines of the National Museum, Bloemfontein, and/or those based on study collections of the Museum, and/or studies undertaken in the Free State will be considered. Submission of a manuscript will be taken to imply that the material is original and that no similar paper is being or will be submitted for publication elsewhere. Authors will bear full responsibility for the factual content of their publications. All contributions will be critically reviewed by at least two appropriate external referees, but the editorial committee's decision whether or not to accept a manuscript is final. Contributions should be e-mailed (herp@nasmus.co.za) to: **The Editor, *Indago, National Museum, P.O. Box 266, Bloemfontein, 9300, South Africa.***

MANUSCRIPTS

Manuscripts should be of uniform style, 1.5-spaced and typewritten in A4 format with 25 mm margins all around, and submitted electronically by email (herp@nasmus.co.za). Submitted manuscripts should not exceed 200 pages (including illustrations). Use MSWord or a compatible programme. All pages should be numbered serially starting with the title page. Tables and legends should be typed on separate pages. Position of tables and illustrations must be indicated in capitals in the text. English spelling should follow the Oxford English Dictionary and Afrikaans spelling should follow HAT. Consult a recent issue of the Journal for typographic conventions. The final accepted and updated manuscript should also be submitted electronically.

Layout should be arranged as follows:

(a) Title: Must be concise and specific and followed by the name(s) of author(s), address(es) of author(s) and number of figures in the text in parentheses. The email address of the senior author should also be provided.

(b) Abstract: An abstract of 300 words or less must be included. For all Afrikaans manuscripts, an English abstract is required. For Human Sciences manuscripts only, an Afrikaans summary is also required. A maximum of six key words may be included at the end.

(c) The main text: This should be divided into principal sections with major headings. Sub-headings should be used sparingly. The headings of a section or chapter must be typed in upper case bold and all headings of sub-sections in lower case bold type.

(d) Acknowledgements.

(e) References (see below).

(f) Gazetteer, appendices, *etc*. (if applicable).

ILLUSTRATIONS

(a) Figures must be submitted as a PDF binder.

(b) High resolution images or graphics (minimum 300 dpi) should be provided electronically only once the manuscript has been accepted for publication.

(c) Halftone photographs: Submit high quality images of a size capable of reduction rather than enlargement. Tables and figures submitted should not be larger than A4 format and each figure and table should have a title. In the text these should be abbreviated as Fig. 1, Figs 3 & 4.

REFERENCES

(a) Author's name and year of publication cited in the text must not be separated by a comma, *e.g*. (Smith 1969).

(b) Use suffixes *e.g*. a, b after the year for more than one paper by the same author in that year.

(c) Where multiple authorship is cited use an ampersand (&) instead of *and* in the text and reference list.

(d) For books, give title (in italics), edition (ed.) and volume number (if any).

(e) The title of a journal should be given in full and italicised.

(f) Series should appear in parentheses *e.g*. Ser. (II), volume number in bold, and part of volume should be given in parentheses only if each part starts at page 1.

(g) Only capitalise the initials of proper names in the titles of articles and books.

Examples (note capitalisation and punctuation):

DIRCH, V.M. 1965. *The African genera of Acridoidea*. Cambridge: University Press.

ENDRöDY-YOUNGA, S. 1978. Coleoptera, pp. 797-821. **In:** Werger, M.J. (Ed.). *Biogeography and ecology of Southern Africa*. The Hague: W. Junk.

DEAN, W.R. & SKEAD, D.M. 1979. Whiskered terns breeding in western Transvaal. *Ostrich* **50**: 118-119.

PARKINGTON, J.E. 1976. *Follow the San*. Ph.D. dissertation. University of Cambridge, Cambridge.

For listing historical references, see: Van der Merwe, P.J. 1972. *The source list and footnotes* (translated from Afrikaans by A.M. Davey). Cape Town: Tafelberg; Van Schoor, M.C.E. & Eales, M. 1985. *Handleiding by die saamstel van werkstukke* (Hersiene uitgawe). Bloemfontein: Universiteit van die Oranje-Vrystaat.

NOTES

If essential, notes must be indicated by serial superscripts in the text and in order of citation at the foot of the relevant page. Footnotes must also be separated from the text by a horizontal line.

ZOOLOGICAL NOMENCLATURE

This is governed by the rulings of the latest International Code of Zoological Nomenclature issued by the International Trust for Zoological Nomenclature (particularly articles 22 & 51). The Harvard System of reference should be used in synonymy lists and full references should be incorporated under REFERENCES and not given in contracted form in the synonymy list.

GENERAL

Italicise foreign words such as *e.g*., *etc*. and scientific names (genus and species).

Specific epithets should be preceded by the generic name or its initial, *e.g. R. norvegicus* or *Rattus norvegicus* and not just *norvegicus*.

Vernacular names should be accompanied by the appropriate scientific names the first time each is mentioned. Each word in the vernacular name of a species should start with a capital letter in the text, *e.g*. House Sparrow, Fork-marked Sand Snake, but must be lower case where no species in particular is being referred to, *e.g*. sparrow, sand snake.

Numbers one to nine inclusive should be spelled out and number 10 onwards given in numerals. In a series, use numerals throughout.

Dates should be written as 4 August 1974 and times of the days as 08:00.

When four or more authors are cited in the text, quote the surname of the first followed by *et al*. and the date. Note that in the list of references the names of all authors should be given.

PAGE CHARGES

Page charges and/or costs of colour plates may be levied on manuscripts submitted by contributors who are not employed at the National Museum.

PROOFS AND REPRINTS

Proofs will be sent to the senior author, who should consult with co-authors. The senior author accepts final responsibility for corrections. Proofs should be returned within two weeks. A pdf copy of the manuscript will be e-mailed to the senior author after hard copies have been distributed. In addition, 15 reprints are supplied free of charge to the senior author if requested.

Navorsinge van die Nasionale Museum, Bloemfontein

VOLUME 30 2014

Part 1: **Bullock, K.L., Viljoen, F. & Kotze, J.J.** Habitat associations and impact of habitat degradation on small mammals in the Heritage Park, North West Province, South Africa 1

Part 2: **Olbricht, G. & Sliwa, A.** Elephant shrews (sengis) – neither rodent nor shrew: A historical perspective 18

Part 3: **Kneidinger, C.M., Van Heerden, H., MacFadyen, D., Van der Merwe, M., Avenant, N.L. & Van der Bank, H.** Species identification, habitat preferences and population genetics of *Mastomys natalensis* (A. Smith, 1834) and *M. coucha* (A. Smith, 1836) in an enclosed area, Kruger National Park, South Africa 31

Deel 4: **Haasbroek, H.** Die ontstaan van die unieke ondergrondse Reservoir-galery (2002) by Oliewenhuis-kunsmuseum in Bloemfontein 47

Part 5: **Coetzee, L.** Rare new species of the genus *Afroleius* Mahunka, 1984 (Acari, Oribatida, Mycobatidae) from South Africa 71

Part 6: **Hugo-Coetzee, E.A.** A new species of *Adrodamaeus* (Acari, Oribatida, Gymnodamaeidae) from South Africa 87

VOLUME 31 2015

Part 1: **Bezuidenhout, H., Bradshaw, P.L., Bradshaw, M. & Zietsman, P.C.** Landscape units of Mokala National Park, Northern Cape Province, South Africa 1

Deel 2: **Haasbroek, H.** Die 1922-debat rondom die strewe na en besluit oor 'n nuwe Bloemfonteinse markterrein 29

Part 3: B**adenhorst, S. & Boshoff, W.S.** Animal remains from an early Twentieth Century Rural Farming Community at Orange River Railway Station, South Africa 49

Indago

VOLUME 32 2016

Neethling J.A. & Haddad C.R. A systematic revision of the South African pseudoscorpions of the family Geogarypidae (Arachnida: Pseudoscorpiones) 1

Conradie, W., Reeves, B., Brown, N. & Venter, J.A. Herpetofauna of the Oviston, Commando Drift and Tsolwana nature reserves in the arid interior of the Eastern Cape Province,South Africa 81

Du Bruyn, D. A Baker garden with a touch of Jekyll: Early history (1903–1905) of the garden at Westminster Estate near Tweespruit, Free State, with special reference to the role played by the Duke of Westminster, Sir Herbert Baker and Gertrude Jekyll 99

Haasbroek, H. Henry Selby Msimang en die loonagitasie van 1919 in Bloemfontein 119

VOLUME 33 2017

Erasmus, P.A. & De Graaf, B.J.H. 'They say a Dog wears a Ticket' – Legal Classification instead of Self-Identification 1

Moodley, S. Soldiers of the *Koma* 13

Botes, M. & Wessels, A. "Blazen en snorken en "Woest ridjen": Verkeersweë en vervoer in Bloemfontein teen die laat-negentiende eeu 23

De Klerk, J.J. & Avenant, N.L. Further evidence in support of small mammals as ecological indicators in areas cleared of alien vegetation in South Africa 49

INDAGO

MARCH 2018 **VOLUME 34, NUMBER 1** **ISSN 0067-9208**

RESEARCH ARTICLE
NATURAL SCIENCES

A revision of the egg-eating snakes of the genus *Dasypeltis* Wagler (Squamata: Colubridae: Colubrinae) in north-eastern Africa and south-western Arabia, with descriptions of three new species
M.F. Bates & D.G. Broadley 1–95



NATIONAL MUSEUM
NASIONALE MUSEUM • MUSIAMO WA SETJHABA
BLOEMFONTEIN

an agency of the
Department of Arts and Culture