

A new species of *Gulella* (Pulmonata: Streptaxidae) from montane forest in the Ndoto Mountains, Kenya

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Zool. Med. Leiden 83 (14), 9.vii.2009: 651-659, figs 1-14.— ISSN 0024-0672.

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Key words: Gastropoda, Streptaxidae, new species, Kenya, Ndoto / Ndotos.

Gulella mkuu spec. nov. is described from montane forest in the isolated Ndoto Mountains of northern Kenya. Although exceptionally large for the genus, shell, genitalia and radula features suggest it is more closely related to the "*G. sellae-ugandensis*" complex than to other very large East African species in the subgenus *Primigulella* Pilsbry. *G. mkuu* spec. nov. is apparently endemic to the Ndotos.

Introduction

The Ndoto Mountains/Ndotos (approximately 1°42'N, 37°13'E) are an isolated mountain range in Northern Kenya, reaching 2636 m ASL on the uplifted eastern edge of the Kenyan branch of the Rift Valley (fig. 1).

The Ndoto massif and the other northern ranges each attract sufficient rainfall to support a small area of evergreen montane forest, contrasting starkly with the semi-arid conditions of the intervening alluvial lowlands (Bussmann, 2002). Geological uplift of the Ndotos, Mt. Nyiro, and Mathews Range is thought to have coincided with a period of climatic cooling and aridification in the late Miocene and Pliocene, before which the forest cover would have been more continuous (Spiegel et al., 2007). Emergence of volcanoes in the Quaternary (e.g. Mt. Kulal and Mt. Marsabit) and subsequent climatic oscillations would have further isolated and reconnected the montane forest remnants (Trauth et al., 2005; Bussmann, 2002), which may have been conducive to the evolution of neoendemic land-snail species in certain areas. A number of these are known from other northern Kenyan highlands: H.B. Preston and M.W.K. Connolly each described species from Mts. Nyiro and Marsabit (see Adam, 1971), and B. Verdcourt (e.g. Verdcourt, 1960; 1962) added several from Mt. Kulal. However, there are no land-snail records definitely localised to the Ndotos (see Verdcourt, 2006 for the Kenyan list). Collections resulting from quantitative surveys of forest from 1600-2300m ASL by two of us (MBS & PT) and C.N. Lange in 1997 therefore represent the first taxa reported from these mountains. The collections (in NMW and NMK; see abbreviations below) comprise at least 34 species, including several probably new taxa and a number of long-distance range extensions, and will be published upon elsewhere. One of the species, which appears to be endemic to the Ndotos, is described and discussed here, giving details of its anatomy to facilitate future comparisons.

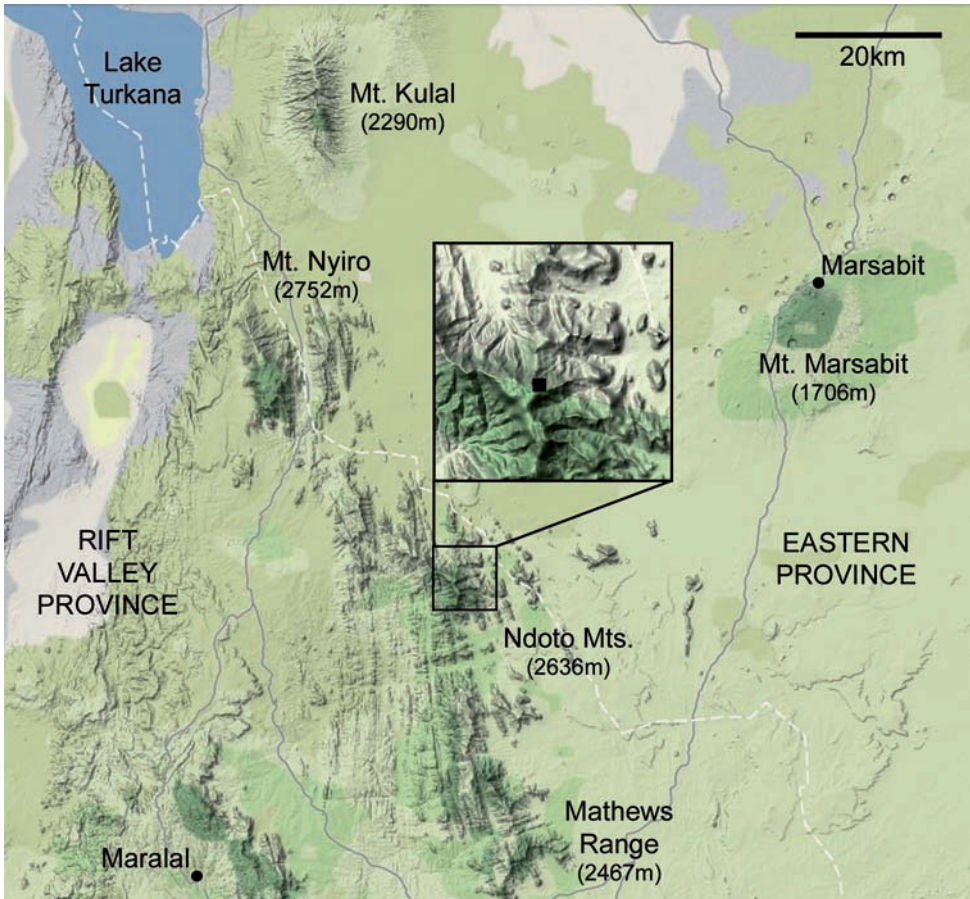


Fig. 1. The highlands of northern Kenya. The inset shows the relief around the type locality, indicated by a black square.

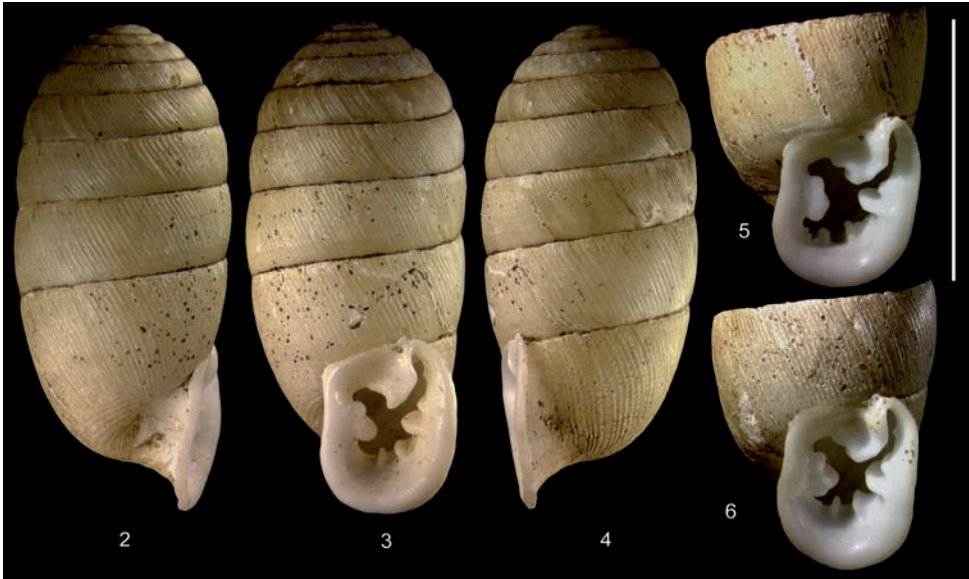
Abbreviations

NMK, National Museums of Kenya, Nairobi, Kenya; NMW.Z, National Museum of Wales, Cardiff, UK; RMNH, National Museum of Natural History, Leiden, The Netherlands; RNIBS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

Description

Gulella mkuu spec. nov.
(figs 2-13)

Material.— Holotype (NMK), Kenya, Rift Valley Province, Samburu District, Ndoto Mountains (1°43'17" N, 37°14'10" E), plot IE, 27.vi.1997, leg. M.B. Seddon, P. Tattersfield, C.N. Lange and local hired collectors; Paratype 1 (NMW.Z.1997.037.00001); same data but plot IA; Paratype 2 (NMW.Z.1997.037.00002),



Figs 2-6. Shells of *G. mkuu*, spec. nov. 2-4, three views of holotype; 5, aperture of Paratype 3; 6, aperture of Paratype 5. Scalebar: 10 mm.

same data, plot IC; Paratype 3 (NMW.Z.1997.037.00003), same data, plot IC; Paratype 4 (RMNH.114168), same data, plot IA; Paratype 5 (RNIBS.MT2170), same data, plot IA; Paratype 6 (worn) (NMW.Z.1997.037.00004), same data, plot IC. All types are adult empty shells except Paratypes 1 and 2, which are adult live-collected animals preserved in 80% ethanol and the source of the anatomical observations below.

Additional, non-type material: 2 adults and 7 juveniles, plot ID (lodged at NMK in 1997); 3 juveniles, plot IA (NMW); 7 juveniles, plot IC (NMW); 3 juveniles, plot IE (NMW).

Habitat at type locality.— Leaf litter in mixed evergreen indigenous forest including *Podocarpus*, on an east-facing steep slope near the summit of a ridge at 2300 m ASL, with much moss on ground and surfaces, abundant dead wood in litter layer, a sparse herb layer of *Impatiens*, *Dracaena* and regenerating trees, and *Usnea*-type lichens in the canopy (30-35 m).

Etymology.— From Swahili noun or adjective *mkuu*, meaning great, principal, elder, chief, etc. As a noun in apposition, with reference to the size of the shell, but also to Dr A.C. van Bruggen, a distinguished and esteemed contributor to African malacology.

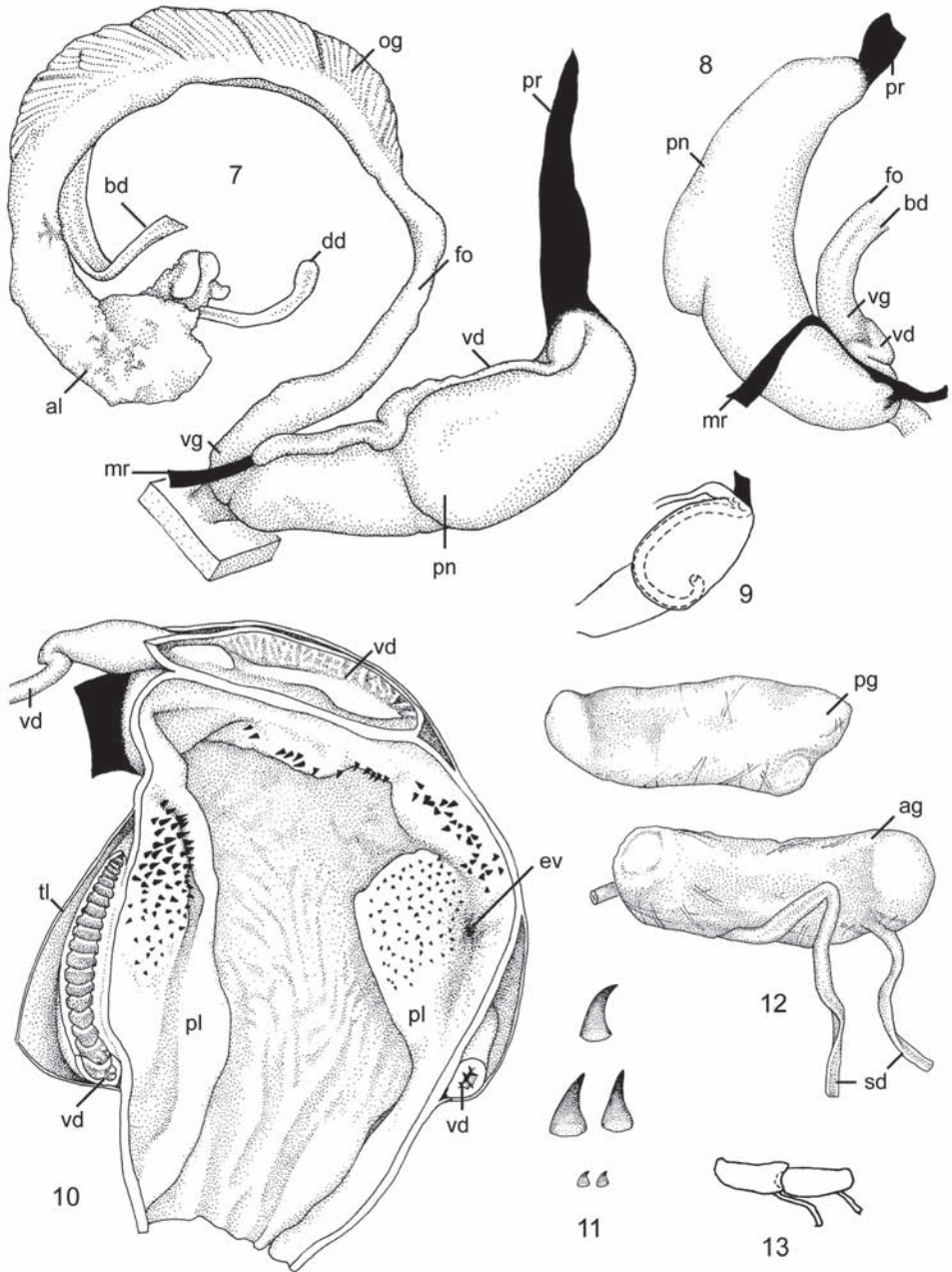
Diagnosis.— Shell exceptionally large for the genus, cylindrical-barrel-shaped, with coarse oblique axial striae; peristome complete, apertural dentition seven- to ten-fold: an excavated parietal tooth, three to five palatal teeth, two basal teeth, and one or two columellar teeth, the larger bifid or trifid; embryonic shell virtually smooth.

Description.— Shell (figs 2-6) exceptionally large (height 18.70-20.75 mm, width 8.10-8.80 mm) for the genus, cylindrical-barrel-shaped, consistently of 8-9 nearly straight-sided whorls (counted using the method of Kerney & Cameron, 1979). Intraspecific variation in shell shape moderate. Penultimate whorl and body whorl together comprise about 54% of total shell height. Aperture (including peristome) comprises about

37% of total shell height. Peristome complete, thickened and reflected, and strongly flaring, concave in columellar part. Body whorl little constricted adjacent to aperture. Umbilicus closed along a lunulate suture, columella straight. Apertural dentition strongly developed, with seven to ten processes as follows: (1) a large, thick parietal tooth, entering only shallowly as a lamella, adpressed to parietal surface and clearly excavated in front, slightly bifid on columellar edge; (2) usually three palatal teeth, one being a sinular denticle, the lower two much larger and shallowly entering, palatal slab little raised (Paratype 3 has two extra palatal denticles); (3) two basal teeth, shallowly entering (one a little bifid in Paratype 3); (4) a strong, very shallow columellar process, bifid or trifid, with none, one or two columellar denticles below it. Parieto-palatal sinus wide, simple. Parietal callus thick and clearly distinct from body whorl. Outer apertural wall with a weak indentation corresponding to palatal slab, and no indentation corresponding to basal teeth. Shell straw-coloured to weak brown, matt (a thin but persistent periostracum); peristome dirty white. Shell surface as follows: embryonic whorls (2.5) virtually smooth, with very faint and irregular spiral scratches visible in some specimens under a light microscope (60 × magnification). Later whorls with major sculpture of coarse, oblique, nearly straight, regular axial ribs which are smoothed where contacting the shell surface, 2-3 per mm on body whorl of holotype, rising to 7 per mm on earliest whorls. On the later whorls of some specimens, including the holotype, ribs are interrupted by a coarse and irregular spiral element, especially around the umbilicus. Juvenile shells are expressly excluded from the type series, but show no sign of juvenile dentition (not seen in dissected adults). Young juveniles have an open umbilicus (less than 20% of shell width, decreasing to less than 10% by 5-whorl stage) and a weak keel or shoulder to the shell.

Body colour: Alcohol-preserved specimens nearly unicolourous tan-cream, including digestive gland, without differently coloured tentacles, patterning on the mantle, etc. Eyes black.

Genitalia (figs 7-11): Penis subcylindrical to club-shaped, not elongate (8.70 mm when straightened, or 0.5 whorls when bent). Penial appendix absent. Vas deferens thick, rounded, lightly bound to penis where in contact, with clear whitish swelling at apex of penis. Vas deferens here narrows and ultimately enters penis in central part, after running back down and around outer surface of penis. This last region of vas deferens tightly bound to penis and covered by a thin layer of tissue, which is contiguous with walls of penis (i.e. dissimilar to the penial sheath of many other Streptaxidae); internally, this region of vas deferens with delicate longitudinal and then transverse pilasters (fig. 10). Thick penial retractor muscle attaching to penis apically, obtaining from the free muscle system and not from the body wall. Minor retractors attached to lower part of penis and vas deferens. Interior surface of penis (fig. 10) consisting of two major, bulky, muscular, longitudinal pilasters running full length of penis, one with a free, muscular subrectangular lobe near ultimate entry of vas deferens. Penial wall between major pilasters thin and with delicate, irregular, low, raised longitudinal anastomosing pilasters. Chitinous spines or hooks present in apical two-thirds of penis, scattered over surfaces of major pilasters, only occasionally raised on low, irregular, subrhombic pads. Hooks not large (<0.05 mm long), simple, little recurved, yellow-brown, decreasing markedly in size away from apex of penis and stopping abruptly. Total number of hooks in penis: approximately 160. Albumen gland moderately sized and with a uniform



Figs 7-13. Anatomy of *G. mkuu*, spec. nov. (Paratype 1): 7, genitalia; 8, penis and vagina from below; 9, course of vas deferens; 10, interior of penis; 11, penial hooks; 12, salivary gland halves; 13, undisturbed position of glands. Abbreviations: ag, anterior half of salivary gland; al, albumen gland; bd, bursa duct; dd, diverticulum of hermaphroditic duct; ev, entry of vas deferens; fo, free oviduct; mr, minor retractor; pg, posterior half of salivary gland; pl, penial pilaster; pn, penis; pr, penial retractor; tl, tissue layer; og, oviductal gland; sd, salivary ducts; vd, vas deferens; vg, vagina.

structure of small and indistinct vesicles or acini. Hermaphroditic duct diverticulum ("talon" of some authors) enlarged, with a single long, stiff vermiform extension curved around columella, not hidden within albumen gland. Bursa copulatrix (located in one specimen only) not large, subrectangular, attending albumen gland; duct arising near bottom of oviduct. Acini of oviductal gland elongate, narrow, distinct, relatively numerous. Acini of prostate small and indistinct. Free oviduct long, with thin walls, without eggs or embryos present. Vagina very short, little muscularised. Atrium short in one specimen, stretched long in the other, little muscularised.

Salivary gland (figs 12-13): Large, 13.0 mm long, swollen and tumid, free of oesophagus, with numerous criss-crossing muscle fibres in coating. Unusually, gland easily separated into anterior and posterior halves with little agitation. Anterior duct exiting gland subapically; posterior duct exiting apex of end of posterior half of gland. Neither salivary duct substantially thickened prior to point of entry to buccal mass.

Radula: Beloglossan, of aculeate lateral teeth. 21 teeth in each half row at tip of odontophore, becoming fewer towards ends of ribbon. Total number of rows not determined but probably approximately 95. Central tooth absent. Lateral teeth decrease regularly in size towards margins from a maximum in centre; basal area of attachment up to half of tooth length. Basal anchors (Aiken, 1981) present.

Comparison and remarks.— The genus *Gulella* L. Pfeiffer, 1856 is now notoriously in need of revision and includes many species, subgenera and sections that do not together constitute a monophyletic group. This is, in part, confirmed by molecular and morphological study on the Streptaxidae (Rowson, PhD thesis in prep., Rowson et al., in prep.) which is the source of some of the observations below. On morphological grounds, we contend that *G. mkuu* is related to, but not part of, the "*Gulella sellae-ugandensis* group" revised by Verdcourt (1970): *G. sellae* (Pollonera, 1906) and *G. ugandensis* (E.A. Smith, 1901), assigned *inter alia* to *Gulella s.l.* or the artificial subgenus *Molarella* Connolly, 1922. Verdcourt also described two subspecies, *G. u. cheranganiensis* Verdcourt, 1970 (since renamed *G. u. brathayi* Verdcourt, 1983; homonymy) and *G. u. elgonensis* Verdcourt, 1970. Together this group are the largest *Gulella* widespread in the Kenyan and Ugandan highlands (mean shell size 11.51 mm × 5.96 mm).

G. mkuu is strikingly larger (fig. 14), being the largest known Kenyan *Gulella*

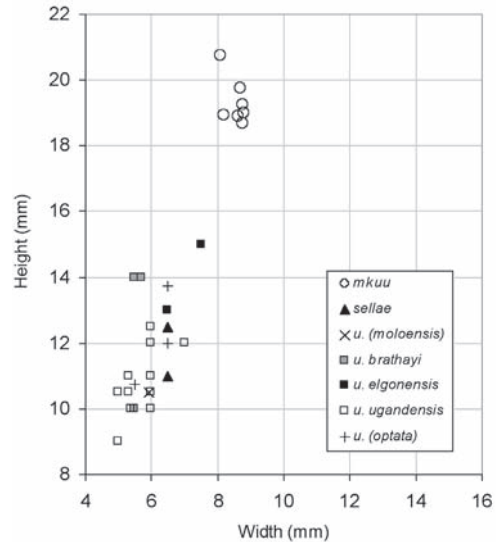


Fig. 14. Shell size of *G. mkuu* and Kenyan/Ugandan specimens of the "*G. sellae-ugandensis* group"; data from Verdcourt (1970), Pollonera (1906) and Preston (1911, 1913). Only the maximum dimensions are plotted from Verdcourt (1970), who gave a range for each population; holotypes are plotted separately where measurements were given. Verdcourt (1970) also synonymised *G. moloensis* Adam, 1965 with *G. u. ugandensis*, while *G. optata* (Preston, 1911) and its varieties *obesa* and *majuscula* (Preston, 1911) were later synonymised with *G. u. ugandensis* (Verdcourt, 2006).

and one of the largest in the genus so far (the South African *G. planti* [L. Pfeiffer, 1856] reaching 21.5 mm; Herbert & Kilburn, 2004). *G. mkuu* shares with the *sellae-ugandensis* group the basic pattern and variability in apertural dentition, yet the excavated parietal tooth appears to be unique, and the new species always has at least two basal teeth. The *sellae-ugandensis* group usually have one, the exception being some specimens of *G. u. elgonensis* which have two (Verdcourt, 1970). The latter is relatively large and strongly striate, and resembles *G. mkuu* most closely, but the striae are much finer (4-5 per mm) and have fine decussate sculpture in the interstices (Verdcourt, 1970) which are lacking in *G. mkuu*. Anatomically, *G. mkuu* shows general features common to several large *Gulella*. Verdcourt (1990) indicated that *G. u. brathayi* had a broadly similar genital anatomy, albeit with "several hundred spinules" (markedly more than in *G. mkuu*). Dissection of several other specimens of *G. ugandensis* (s.l.) from Kenya and Uganda confirms these differences. In addition, *G. mkuu* is unique in the path taken by the vas deferens and its median entry to the penis, its covering by a layer of tissue, and the near-separate salivary glands. Secondarily separate salivary glands are seen in the very large (to 40 mm) East African species of *Edentulina* L. Pfeiffer, 1855 but are otherwise rare in Streptaxidae. The radula of *G. mkuu* shows many of the features outlined by Aiken (1981) for South African *Gulella*. However it includes a mix of features characteristic of Aiken's "Group A" (number of teeth, presence of basal anchors, absence of central tooth) and "Group B" (smaller area of attachment, regular decrease in size from centre). These groupings may thus not be applicable to tropical East African species: while Verdcourt (1990) attributed the radula of the large Kenyan *G. taitensis* Verdcourt, 1963 to "Group B", he could not attribute that of *G. u. brathayi* to either. It resembles that of *G. mkuu* in lacking a central tooth and having 20 teeth in each half-row. Anatomical features, including the radula, do not allow a close relationship with the very large-bodied (to 22 mm × 12 mm; Von Martens, 1897) subgenus *Primigulella* Pilsbry, 1919. Although the size, dentition and complete peristome of *G. mkuu* are superficially similar to this group, the species all have a penial appendix, a central tooth on the radula (see Verdcourt, 1990) and swollen salivary gland ducts. The Tanzanian *G. (Molarella) usambarica* (Craven, 1880) shares these anatomical features except for a very unusual multicuspid radula and appears to be closely related to *Primigulella*. Its assignment to *Molarella* (e.g. by Verdcourt, 2006) shows the extent to which shell characters alone are not sufficient for streptaxid classification.

Discussion

Verdcourt's (1970) conclusions after reviewing many populations of *G. sellae* and *G. ugandensis* from across Kenya and Uganda led him not to synonymise the species but discuss them as separate lineages dispersing repeatedly between highland areas during climatic optima. The western subspecies *G. u. brathayi* and *G. u. elgonensis* further formed part of this view: that populations in marginal areas evolved differences when isolated and became new taxa. It was therefore not surprising to discover the more distinct *G. mkuu* in the Ndotos which is both isolated and near the northern edge of the group's range (*G. sellae* has been recorded from Mt. Marsabit [Verdcourt, 1960]). *G. mkuu*'s ancestor probably arrived on one of several Pliocene or Quaternary forest expansions, and has been isolated ever since, a scenario that would explain the other apparent endemics

present in the Ndotos collection. As the fossil record (Pickford, 1995) shows, the *Primigulella* group is distantly related to true *Gulella* and the two have evolved separately in Kenya for at least 20 million years. Now, the *G. sellae-ugandensis* group is virtually absent from Tanzania (Verdcourt, 1970), and only one species of *Primigulella* is known from Kenya despite being speciose in Tanzania (Verdcourt, 2006). This leads us to speculate that *G. mkuu*'s resemblances to the *Primigulella* group are convergences that may result from the latter's long-term absence from the area. Conversely, *G. usambarica*'s resemblances to the *G. sellae-ugandensis* group may reflect the absence of this group in Tanzania's Usambara mountains, or even character displacement in the presence of the other species of *Primigulella*. It remains to be seen, however, how useful streptaxid shells are as a predictor of their ecology, a question well posed by van Bruggen (1992).

Acknowledgements

This paper is dedicated to Dr A.C. van Bruggen on the occasion of his 80th birthday.

The field survey was in part funded by the UK government's Darwin Initiative and the National Museum of Wales. Charles Lange, Mussombi Kibberenge and Richard Bagine of the National Museums of Kenya provided invaluable support during the set-up of this expedition. The Kenyan Wildlife Service provided contacts and approved the research plan for the Northern Kenyan region.

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Received: 31.iii.2009

Accepted: 12.v.2009

Edited: A.J. de Winter

