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A SPECIES COMES OF AGE: NEW MATERIAL AND MICRO-CT SCANNING REVEAL THE ADULT OF *GULELLA BICARINATA* BLUME FROM KILIMANJARO, TANZANIA; WITH A DISCUSSION OF *MIRELLIA* THIELE FROM KENYA (PULMONATA: STREPTAXIDAE)

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Abstract Gulella (Paucidentina) bicarinata *Blume, 1965 was described from a damaged, immature shell. New topotypic material from Kilimanjaro, Tanzania includes adults which are here described with the aid of micro-CT scans of the unusual shell. The shell and anatomy of adults show similarities with the little-known central Kenyan taxon* Mirellia *Thiele, whose sole species* Ennea prodigiosa *E. A. Smith, 1903 is also scanned and dissected. Most workers have treated* Mirellia *either as a subgenus of* Gulella *L. Pfeiffer, or as a subgenus of* Ptychotrema *L. Pfeiffer. These alternatives are discussed and both species are assigned to* Mirellia*, which is here treated as a genus in its own right.*

Key words *hunter snails, East Africa, taxonomy, snails, radula, shells, genitalia, anatomy*

INTRODUCTION

Many mollusc species have been described from immature or damaged shells. The streptaxid *Gulella (Paucidentina) bicarinata* Blume, 1965 was described from a single perforated and subadult shell, with a damaged mouth (Fig. 1). This was sieved from leaf litter on Mt. Kilimanjaro, Tanzania in montane forest at 2200m, the habitat being "rainforest with tree ferns" (Blume, 1965). This paper by Werner Blume (1887–1965) reported on the molluscs obtained in 1962 by Prof. Dr. Franz from Kenya, Tanzania, the Democratic Republic of Congo, and Lake Chad, including several new species. According to Blume the collection had been lent to him by his friend, Walter Klemm (the title "Herrn Amstrat a. D." denoting a retired civil servant). Blume intended the material to go to the Zoologische Staatssammlung München, Munich, while duplicates would go to Walter Klemm and thence to Vienna. Klemm's collection was indeed later acquired by the Naturhistorische Museum, Vienna in 1978 (Boeters, 1987) and should include paratypes of some of Blume's taxa (Blume, 1965). However, Blume himself died just before the paper was published, and his holotypes remain at Munich (Zilch, 1965; 1971), including the unique specimen of *G. bicarinata* (Verdcourt, 1970).

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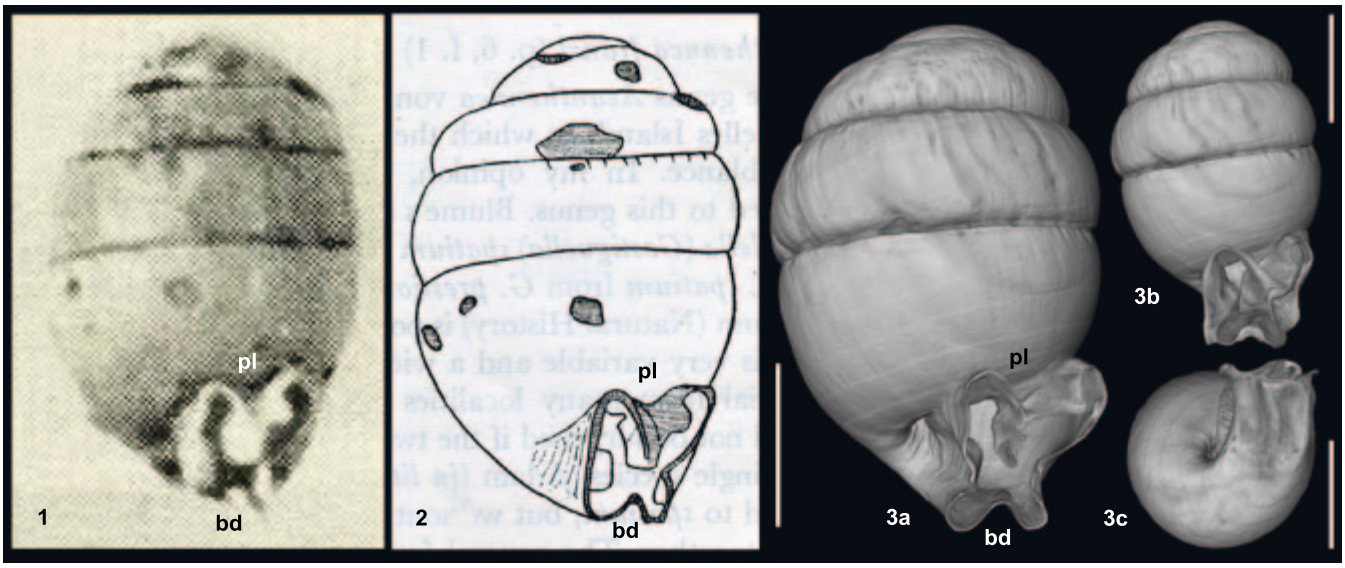
Bernard Verdcourt and William Adam examined all of Blume's (1965) holotypes in a critical reassessment of his East African species (Verdcourt, 1970). Their short note on *G. bicarinata* says that although they both agreed that Blume's shell represented a new species, they thought it should not have been described without better material. Verdcourt's unpublished notes, found inside his photocopy of Blume (1965) at the National Museum of Wales, Cardiff, add that the shell had a badly damaged (as well as immature) mouth and noted "cf. with *intrusa* etc.", in a column titled "Result of BM check" (i.e. a visit to the Natural History Museum, London). Verdcourt (1970) also provided a drawing to augment Blume's small original photograph (Fig. 2).

The systematics of the pupiform Streptaxidae of Africa remains far from being resolved (e.g. Schileyko, 2000; de Winter, 2008; Rowson & Herbert, 2016). Blume had attributed *G. bicarinata* and another of his new species, *Gulella franzi* Blume, 1965 from the Aberdare Mts., Kenya, to the subgenus/section *Paucidentina* von Martens 1897 (type species *Ennea ovalis* Thiele, 1911). The subgenus attribution was not mentioned by Verdcourt (1970), although his paper showed that Blume (1965) had made several other errors in the family or genus classification of his new species.



Figures 1–3 *Mirellia bicarinata* (Blume, 1965). **1**, holotype (Blume, 1965: Abb.9). **2**, holotype (Verdcourt, 1970: Fig. 11). **3**, micro-CT scan of subadult topotype (RMNH.MOL.384757). **3a**, scan cut away to simulate the growth stage of the holotype; 3b–3c, unaltered scan of the subadult (its outer apertural margin slightly broken). pl, parietal lamella; bd, basal depression. Scalebars 1mm.

This paper deals with new material, present as both adults and subadults, found at the type locality of *G. bicarinata*. The morphology of these snails immediately suggested that the adult form of *G. bicarinata* had at last been found. The species does not appear to be widespread, since neither form was found at other sites on Kilimanjaro, Mt. Meru, or nearby areas. This identification is aided by micro-CT scanning to allow the internal structure of fresh shells to be shown and compared at different stages of accretion.

Material and Methods

Shells were figured using a Bruker Skyscanner 1172 micro-CT scanner (Naturalis Biodiversity Center, Leiden, the Netherlands). A voltage of 40 kV was used with a flux of 250 µA, at a full 360°rotation. Medium camera settings were used, with a runtime of approximately 30 minutes. Due to their small size, the shells were mounted in a Pasteur pipette tip, reinforced with some cotton wool. Projection images were trimmed and reconstructed using Bruker's NRecon software. The saved TIFF-images were fully rendered in Avizo 9.2.0 using the 3D-Volume Rendering tool and sliced to show the inside of the shells. The 3D model of the scanned shells was cut away digitally to simulate a younger growth stage.

The scanned shells are at the Naturalis Biodiversity Center, Leiden (RMNH) with the remaining material (dry and in 80% ethanol) at the National Museum of Wales, Cardiff (NMW). The collection of living animals also allows the soft anatomy and radula to be described, and for the generic placement to be reconsidered. Particular attention is paid to the somewhat similar, but currently monotypic and enigmatic (sub)genus *Mirellia* Thiele, 1933, whose anatomy has also been investigated based on material at the Natural History Museum, London (BMNH/NHMUK).

Material examined

Mirellia bicarinata (Blume, 1965): NMW.Z.1998.024.00006: TANZANIA: Kilimanjaro National Park, south-eastern slopes near Maua Route at 2700m (-3.19ºS, 37.44ºE), Afromontane forest including *Podocarpus* and *Hagenia* trees, leg. C. F. Ngereza, P. Tattersfield, and M. B. Seddon, 30 June 1998. Dark brown humic clay soil on volcanic bedrock (51 alcohol specimens). NMW.Z.1998.024.00007 (12 dry shells). RMNH.MOL.384757: data as previous (2 dry shells). RMNH.MOL.318150: data as previous (2 dry shells), data as previous.

Mirellia prodigiosa (E. A. Smith, 1903): RMNH.MOL.273000: KENYA: western Kenya ("Uganda"), ex Sowerby & Fulton, 1904 (2 dry shells). BMNH.20070673: KENYA: Ngong Hills,

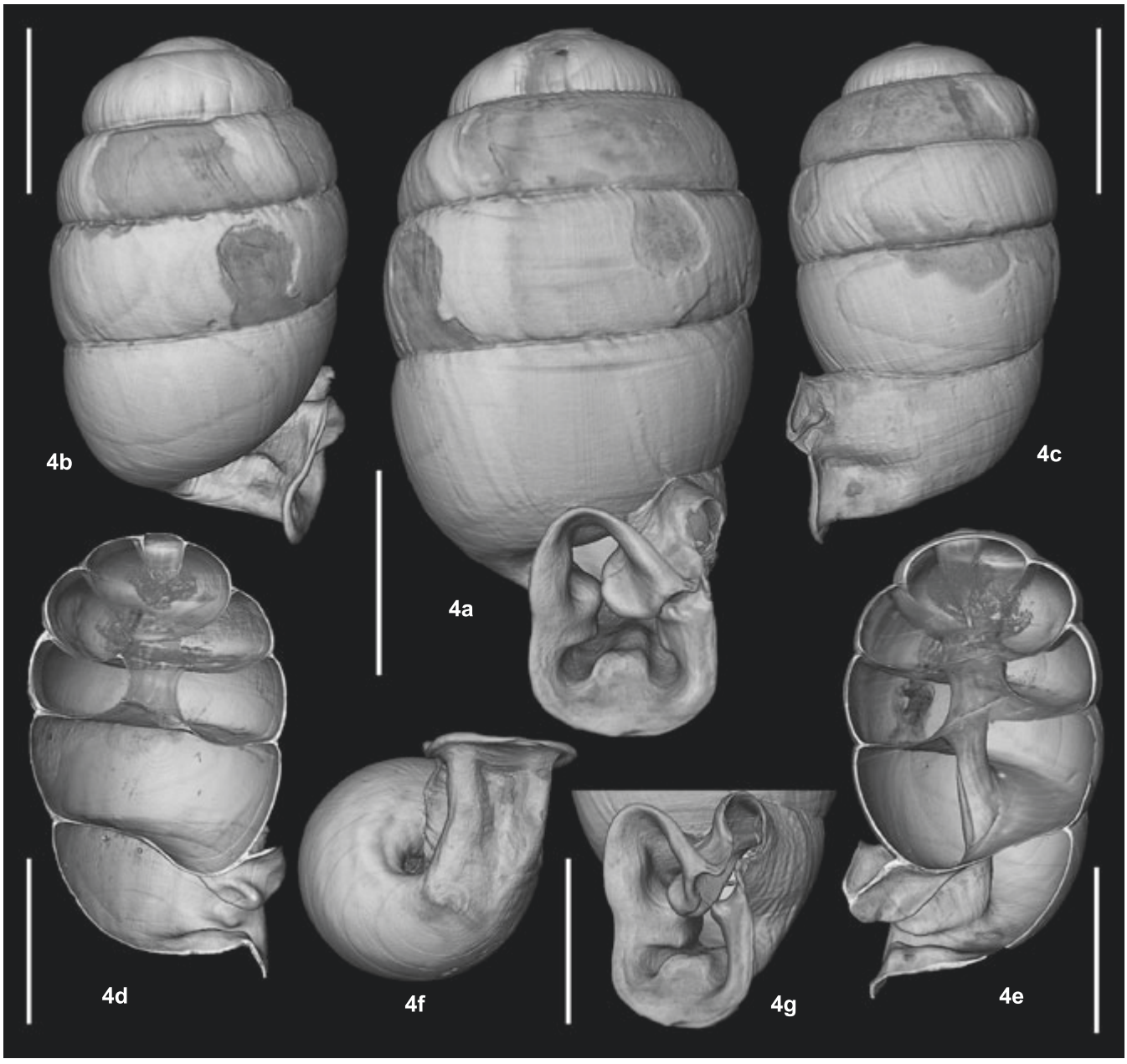


Figure 4 *Mirellia bicarinata* (Blume, 1965). Micro-CT scan of adult topotype (dried, live-collected shell; RMNH. MOL.318150), cut away to show internal structure (**4d**, **4e**). Scalebars 1mm.

Kenya, leg. & det. B. Verdcourt & R. M. Polhill, 1961 (2 alcohol specimens).

The 3D image files can be viewed online via the MorphoSource web database. *M. bicarinata* RMNH.MOL.384757: http://www.morphosource.org/Detail/MediaDetail/Show/media_id/35409; *M. bicarinata* RMNH.MOL.318150: http://www.morphosource.org/Detail/MediaDetail/Show/media_id/35410; *M. prodigiosa* RMNH.MOL.273000: http://www.morphosource.org/Detail/MediaDetail/Show/media_id/35407.

Results

Shell (Figs 1–4)

The subadult shells are an excellent match for Blume's holotype in size, shape and dentition (Fig. 3a–c). The match is even better where parts of the peristome of micro-CT scanned shells are digitally cut away to reflect an earlier growth stage (Fig. 3a). The damage to the aperture of the holotype was evidently not serious enough to make the species unrecognisable, so Blume (1965) was arguably justified in describing it as

new. Its features and affinities are much clearer in the adult, but patches of damage to the shell are evidently common even during life (Fig. 4).

Adult shells (Fig. 4) reach 3.30×1.90mm, with convex whorls and an obese-biconical body form. The protoconch and teleoconch shell are smooth when fresh, apart from weak growth wrinkles, puckering at the suture, and patches of damage. The peristome is conspicuously complete, detached, and reflexed. The large parietal lamella forms a complex V-shape, enclosing a parieto-palatal sinus shaped like an hourglass or figure-of-8 (Figs 4a, 4g). The walls of the sinus are convex, enlarging the volume of the space behind the sinus (occupied by the animal's pneumostome and nuchal lobes). The finished palatal, basal and columellar processes are subrectangular, and slightly bifid in most individuals. They extend into the aperture, corresponding to depressions on the outer surface (e.g. Fig. 4c).

In umbilical view, the basal depression is so broad that it creates the appearance of two keels (Figs 3c, 4f). Blume (1965) described his subadult as having an umbilicus and two parallel basal keels (presumably providing the etymology of "*bicarinata*"): "Das mit einem Nabelritz versehene Gehäuse hat an der Basis zwei parallel verlaufende Kiele." These features persist in the adult (Fig. 4f) although there is a little variation between individuals in the size of the umbilicus.

Young juveniles have not been found. However, interior views (Figs 4d, 4e) show that the maximum width of the shells at the penultimate whorl, as noted by Blume (1965), corresponds with a wide umbilicus in juveniles. This rapidly narrows with subsequent growth, but the displacement of the peristome away from the columella (rather than towards it as in many pupiform Streptaxidae) leaves the adult umbilicus open in most individuals (Fig. 4f). The scans reveal no deeply recessed dentition or juvenile dentition (although it is possible this could occur and be followed by resorption). The shell is thin and shows little variation in the thickness of the exterior wall, even around the peristome (Figs 4d, 4e). With the exception of the base of the penultimate whorl, the internal walls and the walls of the umbilicus are noticeably thinner.

Soft anatomy (Fig. 5)

As is typical for pupiform streptaxids, there is a single large salivary gland with two ducts (Fig. 5a). The ducts are noticeably swollen in the middle part of their length.

The genitalia are also typical in their gross form for pupiform streptaxids (Fig. 5b). Unusual features are a conspicuous penial sheath covering the basal third of the penis, the apical entry of the vas deferens (and the lack of an epiphallic caecum) and the convoluted hermaphroditic duct diverticulum/talon. The interior of the penis (Fig. 5c) has the walls densely studded with extremely small, conical hooks, save for a narrow central longitudinal zone or channel. An elongate, orange-brown, spermatophore-like structure was present in all four dissected individuals, with its upper end attached to the penial wall.

Radula (Fig. 6)

The radula has a central tooth and a small number of laterals, with the formula (11–13)-1-(11–13). The central tooth is broad and flattened with a clear central ridge and a short central cusp; the laterals are relatively short, broad, and uniform.

Discussion and placement in *Mirellia*

The fully described *M. bicarinata* is an even more distinctive species than it was for Blume and for Verdcourt, and is clearly not synonymous with any other African species. It appears to be endemic to Kilimanjaro. The species is unusual in the hourglass-shaped sinus and the complete and detached peristome. A somewhat similar sinus occurs in *G. tracheia* Rowson, 2007 of coastal Tanzania and the Eastern Arc Mountains, and in *G. intrusa* Verdcourt, 1956 of the Eastern Arc. However these lack a detached peristome and are dissimilar to *G. bicarinata* in most respects (discussed in Rowson, 2007a); they are probably true members of *Gulella* L. Pfeiffer, 1856, sensu lato (Rowson & Herbert, 2016). A sinus and/or detached peristome occur in *Dadagulella* Rowson & Tattersfield, 2013, but the group is otherwise highly dissimilar to *M. bicarinata* and has a distinct anatomy and radula (Rowson & Tattersfield, 2013). The species *G. insolita* (Smith, 1903) and *G. aberdarensis* Preston, 1913, both from the central Kenyan highlands, have a V-shaped parietal tooth and, a complete (though not detached) peristome in some individuals. However, they lack a sinus and can look very different in overall shell form, shown by *G. franzi* Blume, 1965, from the

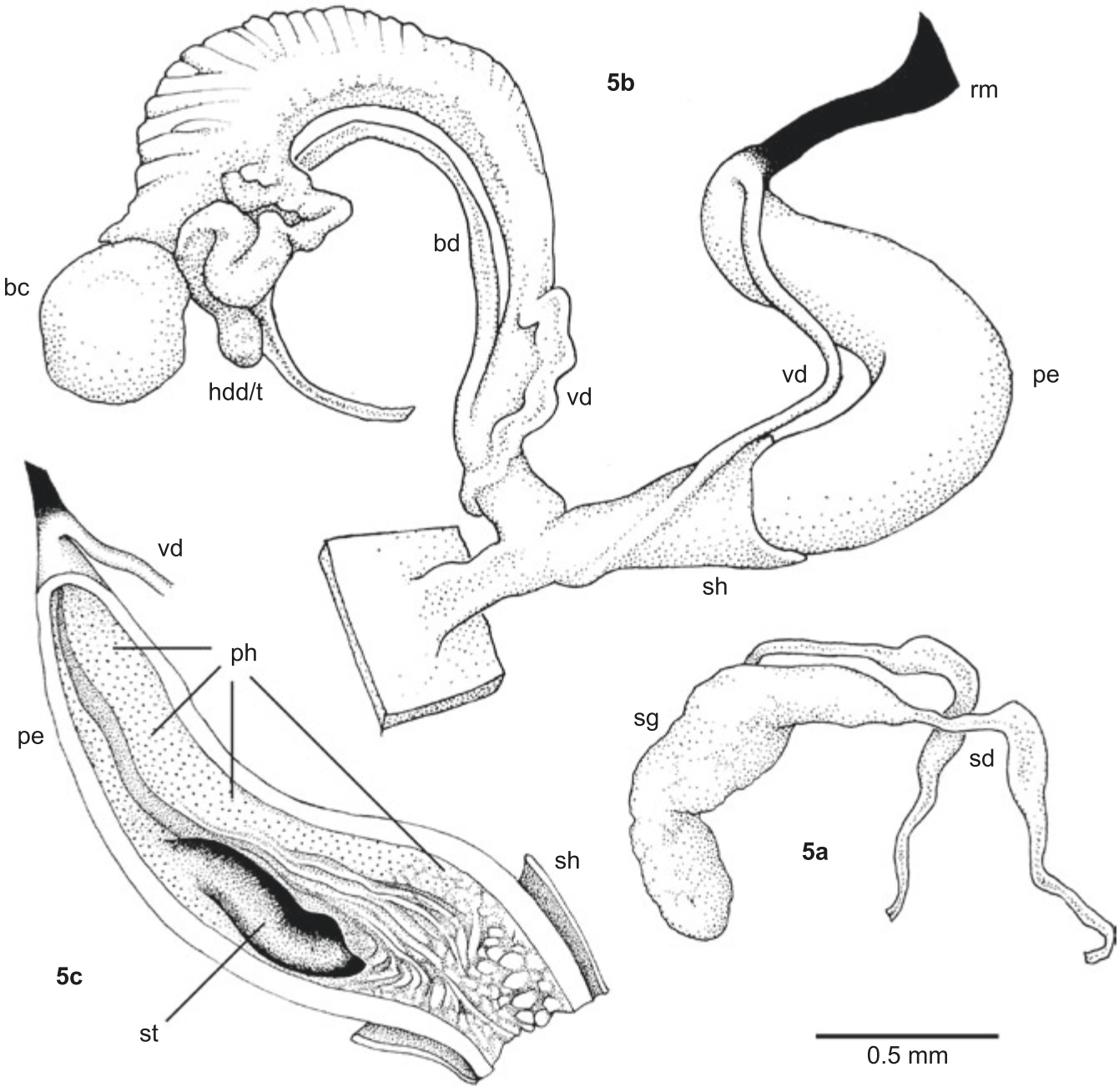


Figure 5 *Mirellia bicarinata* (Blume, 1965). Soft anatomy of adult topotype (NMW.Z.1998.024.00006). **5a**, salivary gland; **5b**, genitalia; **5c**, interior of penis. bc, bursa copulatrix; bd, bursa duct; hdd/t, hermaphroditic duct diverticulum/talon; pe, penis; ph, areas covered by penial hooks; rm, retractor muscle; sd, salivary duct; sg, salivary gland; sh, penial sheath; st, spermatophore-like structure; vd, vas deferens.

Aberdare Mts. and considered a synonym of *G. insolita* by Verdcourt (1970; 2006). These species remain anatomically unknown. A detached peristome is common in several East African genera now transferred out of *Gulella*, e.g. *Primigulella* Pilsbry, 1919 and *Juventigulella* Tattersfield, 1998; and in the edentate *Microstrophia salpinx* (Herbert, 2000) of South Africa (Rowson & Herbert, 2016). It is not, however universal in these groups.

Somewhat similar sinuses also occur in various species of *Adjua* Chaper, 1885, usually considered a subgenus of *Ptychotrema* (see Adam *et al*., 1995; de Winter, unpublished data). Well-developed but very different sinuses are present in subgenus *Excisa* d'Ailly, 1896 and genus *Sinistrexcisa* de Winter *et al*., 1998; the latter also has a detached peristome. All these West African taxa are otherwise very different in form (de

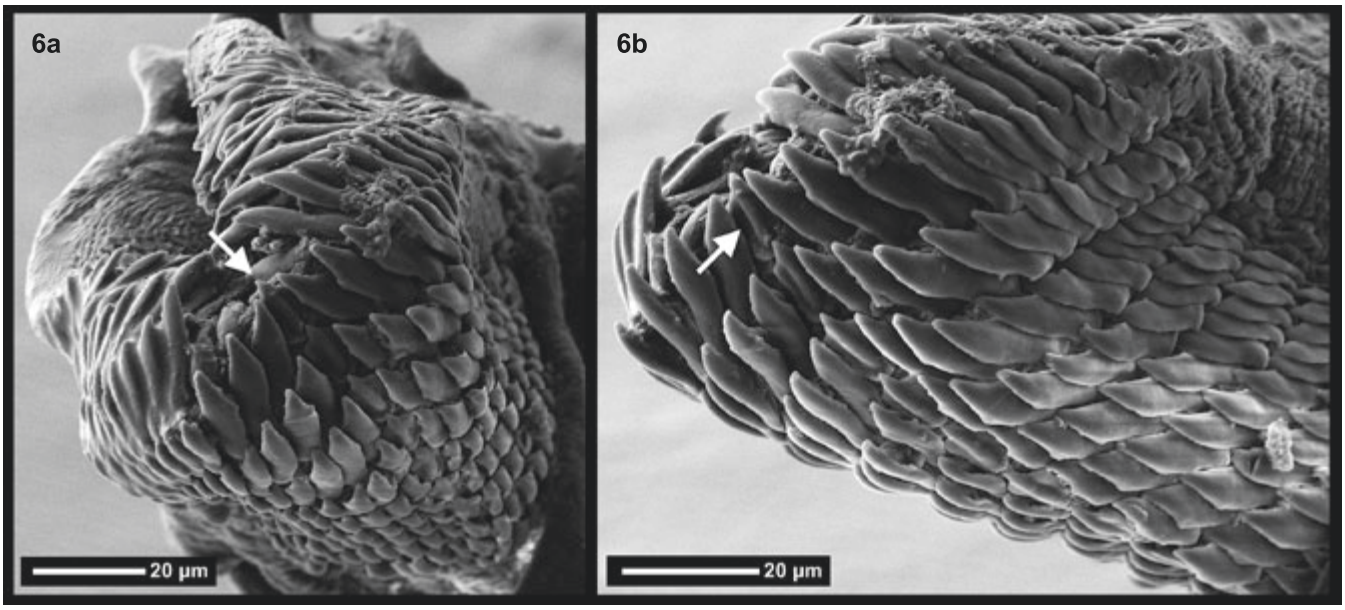


Figure 6 *Mirellia bicarinata* (Blume, 1965). Two views of radula (retained in situ on odontophore) of adult topotype (NMW.Z.1998.024.00006). Arrows indicate the position of the central tooth.

Winter *et al*., 1998, de Winter & de Gier, in prep.). That Blume's (1965) attribution of *M. bicarinata* to *Paucidentina* was unjustified is further evidenced by the adult form, which shares neither the shell nor the anatomical features of *Paucidentina* (e.g. see Schileyko, 2000).

A detached peristome and sinus, together with a similar overall shell form, occur together only in the enigmatic (sub)genus *Mirellia* Thiele, 1911. For comparison, a micro-CT scan of a topotype shell of the sole species, *M. prodigiosa* (Smith, 1903) is here presented (Fig. 7) as are the first details of the anatomy (Fig. 8). The latter are based on material from Ngong Hills, Kenya, from which the shell had already been dissolved. Smith (1903) described this species as *Ennea prodigiosa,* from shells collected by Doherty on the Mau Escarpment at 6500–9000 feet. This escarpment forms the western edge of the Rift Valley that runs through central Kenya, but in Smith's time was considered part of the Eastern Province of the Uganda Protectorate. The species is unknown from modern Uganda, and has otherwise only been recorded from the Ngong Hills and Mt. Kenya, both on the other side of the Rift in central Kenya (Adam *et al*., 1995; Verdcourt, 2006).

As well as the peristome and sinus, *M. prodigiosa* resembles *M. bicarinata* in the general dentition, convex whorls, shell shape, smooth sculpture, and juvenile and adult umbilicus (as revealed by micro-CT). However it is smaller at around 2.50×1.25mm, the peristome projects further, and the whorls are still more tumid, meaning the species is unmistakeable. Importantly, the micro-CT scans reveal that the palatal and basal teeth of *M. prodigiosa* are similar in form to those of *M. bicarinata*. They can be considered short processes that correspond to short pits outside the aperture, rather than deeply-entering palatal lamellae that correspond to long spiral furrows out. The latter feature has long been considered the defining character of *Ptychotrema* L. Pfeiffer, 1853 and its subgenera (Pilsbry, 1919) (including *Ennea* H. & A. Adams, 1855).

Subsequently, two workers independently considered *E. prodigiosa* distinctive enough to be made the type of its own (sub)genus. Thiele (1933: 283) introduced the name *Mirellia* Thiele, 1933 as a new subgenus of *Ptychotrema*. Haas created *Thaumatogulella* Haas, 1951 for it as a subgenus of *Gulella*. Adam *et al*. (1995) followed Zilch (1959–1960) in keeping it as a subgenus in *Ptychotrema* while Schileyko (2000) considered it an independent genus, and Verdcourt (2006) followed Haas in treating it as a subgenus in *Gulella*. All these authors considered *Mirellia* monotypic. It is now evident that *Gulella*, *Ptychotrema* and other genera are not closely related (Rowson *et al*., 2010) but it has remained difficult to decide on the placement of *Mirellia*. If not part of *Gulella sensu lato* or *Ptychotrema sensu lato,* it could be

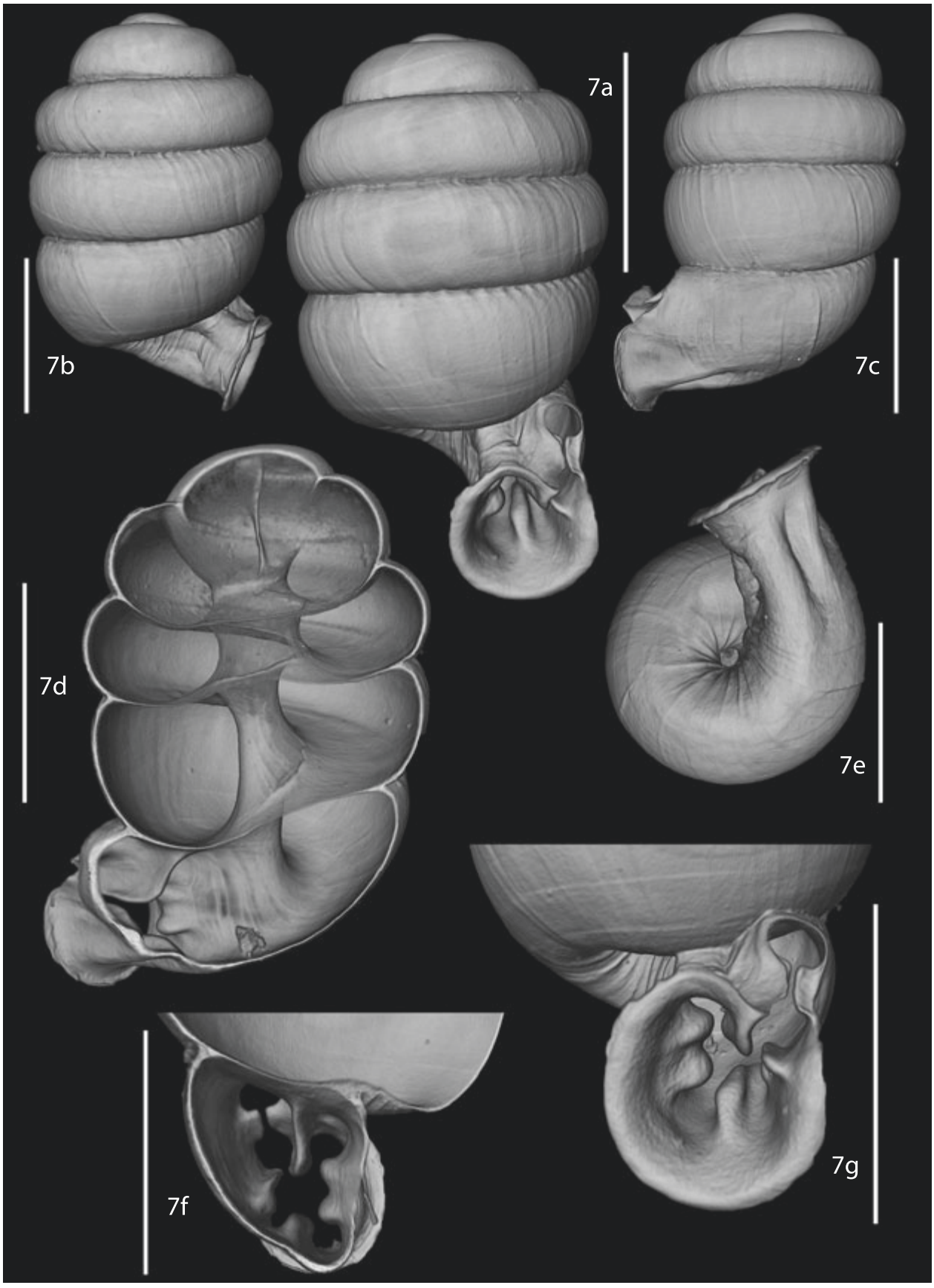


Figure 7 *Mirellia prodigiosa* (E. A. Smith, 1903). Micro-CT scan, adult topotype from "Uganda" (ex Sowerby & Fulton, 1904) (RMNH.MOL.273000 – one of two shells). Scalebars 1mm.

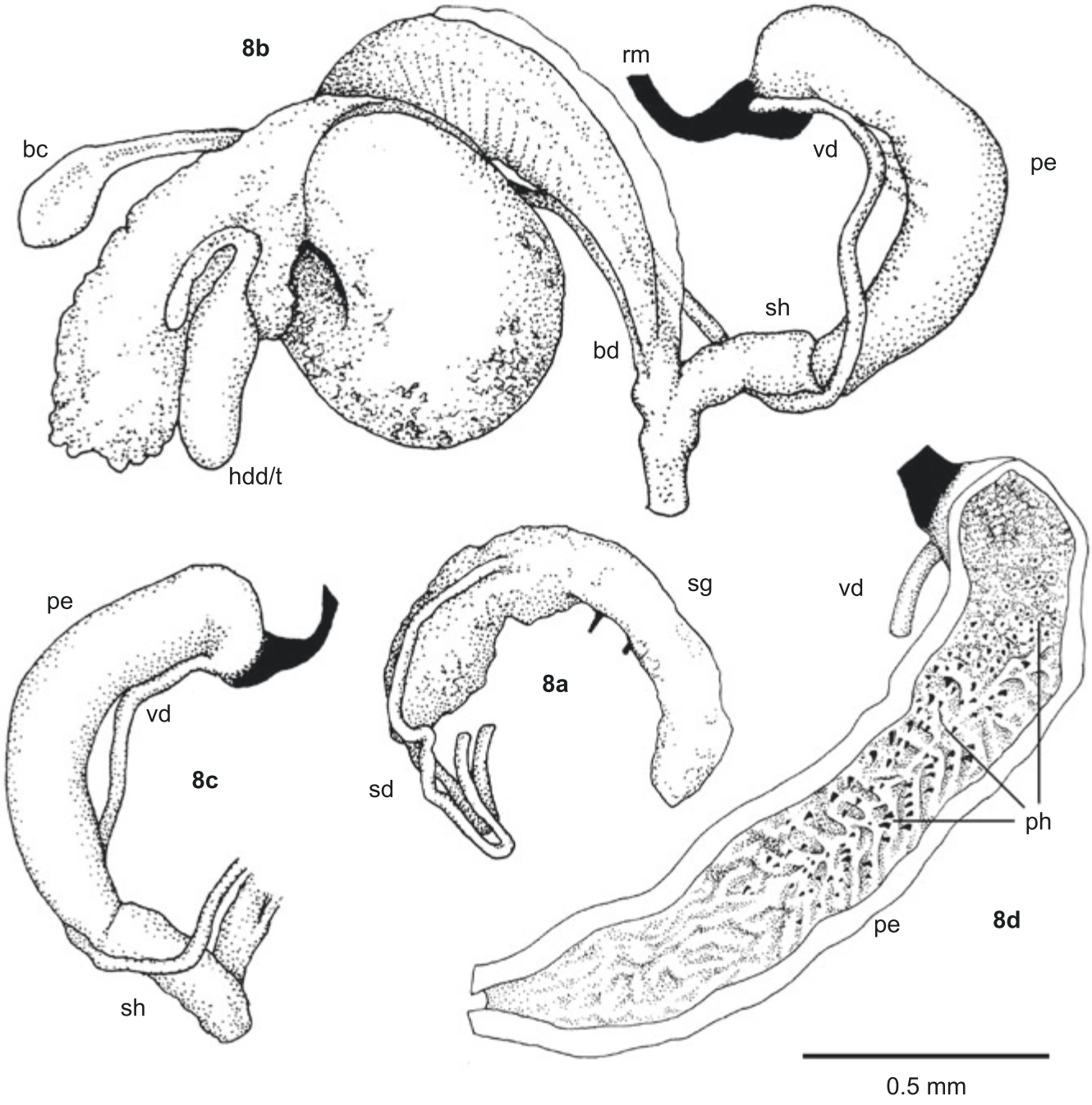


Figure 8 *Mirellia prodigiosa* (E. A. Smith, 1903), Ngong Hills, Kenya, leg. & det. B. Verdcourt & R. M. Polhill, 1961 (BMNH.20070673). Soft anatomy of adult. **8a**, salivary gland; **8b**, genitalia; **8c**, penis from other side; **8d**, interior of penis. bc, bursa copulatrix; bd, bursa duct; hdd/t, hermaphroditic duct diverticulum/talon; pe, penis; ph, areas covered by penial hooks; rm, retractor muscle; sd, salivary duct; sg, salivary gland; sh, penial sheath; vd, vas deferens.

related to other East African genera, such as *Primigulella*.

This uncertainty about the genus can now be informed, if not fully resolved, by the anatomical data, which seem to present a mixture of characters. As noted by Thiele (1933) the radula of *M. prodigiosa* has a central tooth and 11 uniform lateral teeth on each side, in both of which it resembles *M. bicarinata* (Fig. 6, Fig. 9). Although streptaxids of most genera possess a central tooth (even if much reduced, as in *Gulella* s. str.), a broad, flat central tooth with a central cusp, like that of *M. bicarinata* and *M. prodigiosa*, occurs in *Juventigulella* (Rowson, 2007b) and *Primigulella*

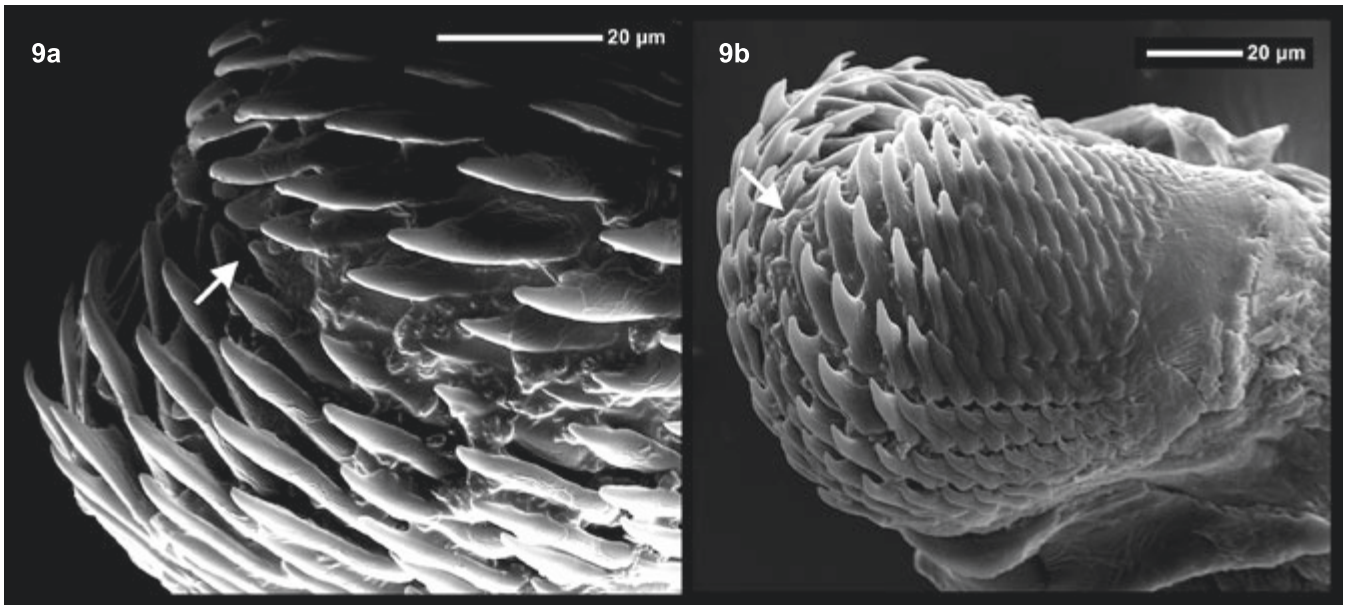


Figure 9 *Mirellia prodigiosa* (E. A. Smith, 190, Ngong Hills (BMNH.20070673). Two views of radula (retained in situ on odontophore) of adult. Arrows indicate the position of the central tooth.

(Rowson, unpubl.). Swollen salivary gland ducts are a feature so far unknown in *Gulella* s. l., and have been found only in *Primigulella* and some other East African species (Rowson & Herbert, 2016; Rowson, unpubl.). Those of *M. bicarinata* are swollen but those of *M. prodigiosa* are not. The penis of *M. prodigiosa* is entered apically by the vas deferens, i.e. lacks an epiphallic caecum, and has a short, basal penial sheath. It shares both of these features with *M. bicarinata*. Neither is seen in *Gulella* s. l. (Rowson & Herbert, 2016), and both occur in *Primigulella* and other species with a detached peristome (Rowson, unpubl.). Spermatophore-like structures such as that found *in M. bicarinata* have been reported in some species of *Gulella* s. l. and *Dadagulella* (Rowson & Tattersfield, 2013; Rowson & Herbert, 2016). However they also occur in *Primigulella* and other East African genera (Rowson, unpubl.), and the West African *Sinistrexcisa* (de Winter *et al*., 1998).

The distribution of these characters makes the potential dilemma of monotypic (sub)genera difficult to resolve. Neither species is remotely like the type species of the speciose genera *Gulella* or *Ptychotrema*, and both appear more similar to one another. Given the shell, radula, and some anatomical similarities, *M. bicarinata* could be assigned to *Mirellia* as easily as to *Primigulella* or related genera. It seems equally likely that both species, *M. bicarinata* and *M. prodigiosa*, are related to *Primigulella* and its East African relatives than to the mainly West African *Ptychotrema* (represented by relatively few species on East African mountains) or *Sinistrexcisa* (which is strictly West African). Therefore we here suggest that *M. bicarinata* be transferred to *Mirellia*, and that this be treated as a genus outside of both *Gulella* and *Ptychotrema*. This accords with Schileyko, and avoids the conflict between Thiele/Adam/Zilch on the one hand (*Mirellia* in *Ptychotrema*) and Haas/Verdcourt on the other (*Thaumatogulella* in *Gulella*). We also acknowledge, however, that molecular study (ideally of both species) is required to better determine their position.

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