

# A SECOND REMARKABLE SLUG AND A THIN-SHELLED TROCHONANINA SNAIL FROM THE UZUNGWA MOUNTAINS, TANZANIA (STYLOMMATOPHORA: HELICARIONOIDEA: UROCYCLIDAE)

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*Abstract* Two new species of Urocyclidae are described from forest in the Udzungwa Mountains, Tanzania. The first is a large slug remarkable for its prickly mantle and very long spermatophore, the longest known among African Helicarionoidea. This is assigned to the tribe Upembellini and, albeit with some uncertainty, to *Upembella* Van Goethem, otherwise known only from the Upemba National Park, southern Congo basin. The second is a snail whose anatomy is typical of the widespread East African genus *Trochonanina* Mousson, is unusual in its thin and weakly sculptured shell. Each species' affinity with other East African Helicarionoidea is briefly discussed.

*Key words* Mollusca, Urocyclidae, East Africa, taxonomy, systematics, new species, endemic

## INTRODUCTION

The Urocyclidae of East Africa (sensu Verdcourt, 2006) are an assortment of larger snails, slugs and semi-slugs forming a major component (>200 species, approx. 20%) of the terrestrial mollusc fauna. Relationships among them and the wider Helicarionoidea to which they belong remain largely unresolved (e.g. see Bouchet & Rocroi, 2005) despite two thorough African monographs (Van Mol, 1970; Van Goethem, 1977). Several new taxa, some defying categorisation, have also been discovered since these revisionary works, reflecting the scale of the problem. One such is the slug *Emphysetes udzungwensis* Verdcourt 2003, given the monotypic genus *Emphysetes* Verdcourt 2003 for its remarkable ability to inflate the keel and mantle, although its radula and genitalia are similar to those of the widespread genus *Atoxon* Simroth 1888 (Verdcourt, 2003). *Emphysetes* is apparently endemic to forest in the Udzungwa Mountains of central Tanzania, much of which lies in the Udzungwa Mountains National Park. The Udzungwa massif is celebrated for its high species diversity and endemism, even among the Eastern Arc Mountains of which it is the southernmost part (Burgess *et al.*, 2007). The fact that new taxa such as *Emphysetes* are often restricted to small, poorly-explored

areas does not lessen their importance in systematic and biogeographical studies, but does increase the likelihood that they are overlooked by them, making their description a priority. The present paper describes two further unusual urocyclids from Udzungwa, both also apparently endemic. The new species were found only at medium to high elevations (approx. 1300–1800 m asl). The species diversity of terrestrial molluscs in Udzungwa is at its greatest between these altitudes (Tattersfield *et al.*, 2006).

## MATERIALS AND METHODS

The new taxa are among other undescribed species discovered during survey work by the National Museum of Wales, Cardiff, UK (NMW; NMW.Z for accession numbers) and National Museums of Tanzania, Dar es Salaam, Tanzania (NMT) (see Tattersfield *et al.*, 2006, for further details). Material has also been deposited in the Royal Belgian Institute of Natural Sciences (RBINS). All animals were drowned in water and are preserved in 80% ethanol; lengths given for slugs are in preservation. Suprageneric classification agrees with Van Goethem (1977), Bouchet & Rocroi (2005) and Verdcourt (2006); dates of publication are from Van Goethem (1977).

## SYSTEMATICS

Family UROCYCLIDAE Simroth 1888  
 Subfamily UROCYCLINAE Simroth 1888  
 Tribe UPEMBELLINI Van Goethem 1977  
 Genus *Upembella* Van Goethem 1969

*Upembella nonae* sp. nov.

(Figs 1–2, 4–6, 8–10, 13–15, 17–22)

*Holotype* 1 ad., (total 64.50 mm, mantle 29.10 mm; NMW.Z.2003.001.00021): Tanzania, Morogoro Region, Udzungwa Mountains National Park, Mt. Mwanihana Catchment Forest Reserve (7.82° S, 36.83° E); forest at 1350 m elevation, 30.i.2003, leg. C. F. Ngereza, B. Rowson, M. B. Seddon & P. Tattersfield.

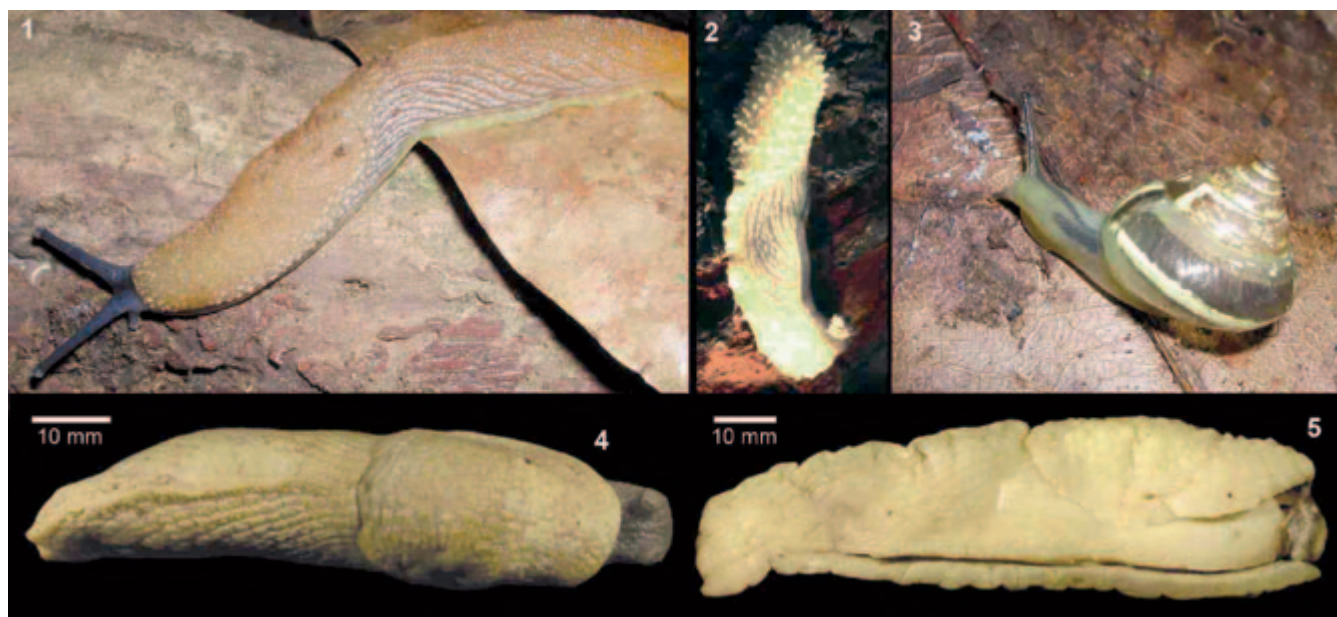
*Paratypes* Paratype 1 (1 subad., total 54.85 mm, mantle 22.40 mm; NMW.Z.2003.001.00022): data as holotype. Paratype 2 (1 ad., total 73.70, mantle 32.80 mm; NMW.Z.1997.007.00006): Tanzania, Iringa Region, south-western Udzungwa Mountains, Kigogo Forest Reserve (8.67° S, 35.25° E), forest with bamboo at 1720 m elevation, 10.ii.1997, leg. C. F. Ngereza, M. B. Seddon & P. Tattersfield. Paratype 3 (1 ad., total 71.55, mantle 31.45 mm; NMW.Z.1997.007.00007): data as paratype 2. Paratype 4 (1 total 67.60, mantle 32.50 mm; RBINS.IG.32,178; specific paratype number MT.2,615):

data as Paratype 2. Paratype 5 (1 juv., total 37.50, mantle 16.10 mm; NMT): data as Paratype 2. Paratype 6 (1 juv., total 31.05, mantle 14.30 mm; NMW.Z.1997.007.00008): data as Paratype 2.

*Type locality* Tanzania, Morogoro Region, Udzungwa Mountains National Park, Mt. Mwanihana Catchment Forest Reserve (7.82° S, 36.83° E), forest at 1350 m elevation.

*Diagnosis* Large (to 73.70 mm), heavily-built slug, plain-coloured with dark head, long, strong keel, short caudal appendage, coarsely tuberculate tail and flanks, supraperipodial grooves, and with coarsely granulate or spiky mantle without shell pore. Internally: viscera reaching the tail; genitalia with characteristically extremely long, coiled flagellum (resultant spermatophore with extremely long, barbed-wire like tail), and very short, rounded caecum; with a ligula-like structure in the atrium, a large thin-walled oviductal gland, and with only weak longitudinal pilasters inside oviduct and vagina. Jaw with weak median projection, all radula teeth tricuspid.

*External appearance* (Figs 1–2, 4–5, 6) Large (to 73.70 mm long in preservation), heavily-built slug, plain-coloured ochre or cream with dark head and tentacles (sole also dark in some specimens) lacking markings of any sort. Strong, acute



**Figures 1–5** Entire animals. 1. *Upembella nonae* sp. nov. (holotype in life, in situ; note prickly mantle and supraperipodial groove). 2. *U. nonae* (Paratype 2 in life, in situ; prickly mantle conspicuous). 3. *Trochonanina mwanihananae* sp. nov. (holotype in life, in situ, crawling with one ommatophore retracted). 4. *U. nonae* (holotype in preservation). 5. *U. nonae* (Paratype 2 in preservation after genitalia removed).

dorsal keel along whole length of tail, terminating in a very short caudal appendage. Tail and flanks coarsely tuberculate, with evident supra-peripodial groove running parallel to strong peripodial groove as far as tail. Mantle large (approx. 45% of body length) coarsely granulate, with cauliflower-like surface in preservation but acutely papillose (prickly or spiky) in life. Mantle attached at rear, with no sign of shell pore or slit. Sole unicolorous, tripartite. Juveniles (at least of 31 mm or more) similar in appearance to adults.

*Shell* (Figs 13–14) Unguiform, to 7.5 mm long, moderately strongly mineralised, with periostracum extending over anterior and lateral margins.

*Genitalia* (Figs 8–9) No stimulator. Atrium short, walls folded, containing a single eversible, tongue-shaped ligula-like structure with thumb-print-like ridges; atrium with several moderately strong retractor muscle strands. Penial complex and vagina entering atrium near one another, vagina very short. Penial complex conspicuously long and convoluted, consisting of: short free penis (i.e. unconvoluted continuation of epiphallus 2); extremely long, semi-regularly coiled flagellum with internal axial thread; long, irregularly coiled epiphallus 1 and epiphallus 2, the latter relatively longer; epiphallic caecum very short, rounded. Penial retractor muscle with a strand continuing to caecum, arising from diaphragm. Penial papilla with a double wall, free penis also with a penial sheath. Bursa copulatrix duct robust, long, not pigmented or ornamented, internally with weak longitudinal pilasters; bursa voluminous, thin-walled. Oviduct internally with weak longitudinal pilasters. Oviductal gland large, thin-walled, separated from vagina by a free oviduct. Ototestis sited anterior to albumen gland, albumen gland extending to near tail.

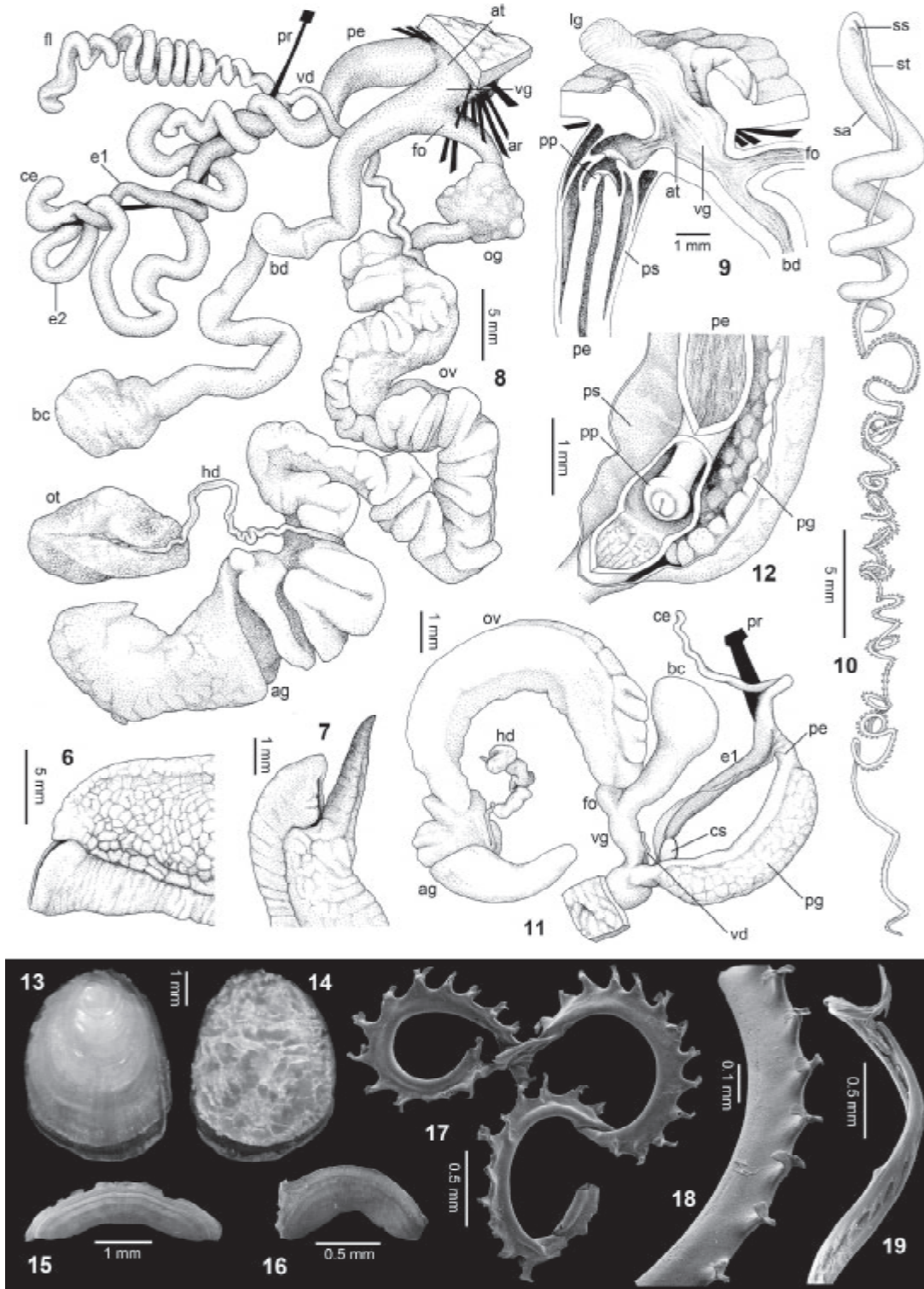
*Spermatophores* (Figs 10, 17–19) All spermatophores examined (two from bursa of holotype, four from bursa of Paratype 2) similar. Description and measurements from spermatophore from Paratype 2. Ampulla smooth, slender, with 3.5 volutions, 14.7 mm long when coiled (uncoiled, estimated [measured on digital images] 26.8 mm long). Tail thread-like, hollow, with a single keel throughout, coiled and tangled like a spool of barbed wire, extremely long (42.5 mm when coiled; uncoiled, estimated 82.4 mm). Spermatophore thus almost as long (uncoiled,

57.2 mm) or longer (uncoiled, 109.2 mm) than body of recipient. Single short spur present near apical bend at junction between ampulla and tail. Tail bears for most of its length regularly-spaced, short projections split outwards into two barbs, occasionally with a third or fourth barb, but becoming a single row of widely spaced simple barbs towards the narrow end.

*Radula and jaw* (Figs 15, 20–22) Jaw with very weak median projection. Radula with central tooth and 100 to 140 lateral teeth in a half-row, in about 130 rows. All teeth tricuspid, with mesocones largest, rather straight and without evidence of serrated outer edges to the outermost marginals.

*Etymology* After Nona, one of the three Fates in Roman mythology, who span the thread of life; with reference to the long tail of the spermatophore, that resembles a spun spool of barbed wire.

*Remarks* This species was somewhat difficult to attribute to a known genus. Its genitalia are nothing like those of the Udzungwa endemic *Emphysetes* Verdcourt 2003, which following Van Goethem's key (1977: 49) should be considered a member of the tribe Urocyclini Simroth 1888 on the basis of its short, calciferous flagellum (bursa calcifera). Using the same key, the new species is a member of one of three tribes in which the flagellum is long: the Leptichneini Van Goethem 1977, Dendrolimacini Van Goethem 1977, or Upembellini Van Goethem 1977. It keys away from Leptichneini because the viscera reach the tail, and away from Dendrolimacini because the radula teeth are much less numerous. It thus keys to Upembellini, a tribe of two currently monotypic genera. The new species is clearly not the first of these genera, *Leptichnoides* Van Goethem 1975. Its sole species *L. verdcourti* Forcart 1967 of southern Mozambique and Zimbabwe has a granulate mantle but reaches a much smaller size (31 mm) and has a comparatively far shorter flagellum. It is close only to *Upembella* whose sole species *U. adami* Van Goethem 1969 is known only from the Upemba National Park in the south-eastern Democratic Republic of Congo (in gallery forest at 1320 m elevation). Nevertheless, *U. nonae* has some peculiarities that could be considered sufficient to make it the type of a third monotypic genus in Upembellini. Here we list these in the



**Figures 6–19** Tails and internal features. 6. *Upembella nonae* sp. nov., tail (holotype). 7. *Trochonantina mwanihanae* sp. nov., tail (holotype). 8. *U. nonae*, genitalia (holotype). 9. *U. nonae*, interior of distal genitalia (Paratype 2). 10. *U. nonae*, spermatophore from bursa of Paratype 2. 11. *T. mwanihanae*, genitalia (holotype). 12. *T. mwanihanae*, interior of penis (holotype). 13–14. *U. nonae*, shell (holotype). 15. *U. nonae*, jaw (holotype). 16. *T. mwanihanae*, jaw (holotype). 17–19. *U. nonae*, fragments of a second spermatophore from bursa of Paratype 2. Abbreviations: ag albumen gland; at atrium; ar atrial retractor; bc bursa copulatrix; bd bursa duct; ce caecum; cs calc sac; e1 epiphallus 1; e2 epiphallus 2; fl flagellum; fo free oviduct; hd hermaphroditic duct; lg ligula; og oviductal gland; ot ovotestis; ov oviduct; pe penis; pg penial gland; pp penial papilla; pr penial retractor; ps penial sheath; sa spermatophore ampulla; ss spur on spermatophore; st spermatophore tail; vd vas deferens; vg vagina.

hope that further data from *U. adami* or other species will allow the matter to be resolved.

The Udzungwa species resembles *U. adami* in general respects including size and body form, supraperipodial grooves, granulose mantle, shell with periostracal fringe, short caecum, very long flagellum, and radula form (see Van Goethem, 1969, 1977). However, there are several differences between it and *U. adami*, which apparently apply to both the Mwanihana (holotype & paratype 1) and Kigogo (paratypes 2–6) populations. Externally, all specimens of the Udzungwa species have a stronger and longer keel (over more than two-thirds of the tail) lack any trace of a mantle pore or slit (even a closed one), and lack the colour markings seen in *U. adami* (including the transverse pigmentation in the bursa copulatrix duct). Van Goethem (1969, 1977) did not mention a prickly appearance to the mantle of *U. adami* in his notes on living specimens.

Internally, the penis and caecum of the Udzungwa species are shorter relative to the rest of the penial complex, and the caecum more rounded than in *U. adami*. Internally, the penis of *U. adami* has a penial papilla with a double wall and a penis whose sheath continues as far as the insertion of the penial retractor. In the Udzungwa species, a similar papilla is present but the sheath does not continue so far, resembling the schematics and drawings of both *U. adami* and *Dendrolimax* spp. in Van Goethem (1977) but not being an exact match for either. In the Udzungwa species, at the level of the label “ps” in Fig. 9 the penis has two walls, the inner one being thicker. In *U. adami* at a corresponding point there is a third, thinner wall. Furthermore, the Udzungwa species lacks the long atrium and the strongly dilated vagina, containing two pairs of pointed papillae, which are characteristic of *U. adami*. Instead, both atrium and vagina are short and, though muscularised, not dilated. The free oviduct between the vagina and the oviductal gland in the Udzungwa species is relatively long. The atrium (into which the vagina continues and the penis opens) contains a single ligula-like structure. Van Goethem (1977) suspected the vaginal papillae of *U. adami* played a role in copulation and it is likely that the ligula of the Udzungwa species does likewise, although the vagina of *U. adami*, at least in the subadult type material, does not appear to be eversible. It is not known whether the papillae of *U. adami* and the ligula of the Udzungwa species are homologous.

The spermatophore of the Udzungwa species is remarkably long, longer than any in Van Goethem (1977) and probably any other African Helicarionoidea. The ornamentation appears to be unique. The presence of an apical spur on the spermatophore, apparently found otherwise only in Leptichnini and Dendrolimacini, may be of systematic importance if such spurs are all homologous, perhaps uniting these two tribes with Upembellini (although crucially the spermatophore of *U. adami* has not yet been described). These are the three slug tribes that have a long flagellum in place of the bursa calcifera. Van Goethem (1977) considered the bursa calcifera homologous with the basal part of the flagellum and its presence to be an apomorphy of the Urocyclini (pp. 29, 39, 304–312). However, the absence of a bursa calcifera was not considered an apomorphy of the remaining slug genera, in part because an apparently homologous bursa calcifera occurs in many fully-shelled Urocyclidae. The flagellum-bearing genera were accordingly considered paraphyletic and were ranked in separate tribes. Unfortunately, as changes in the spermatophore are presumably not independent of changes in the flagellum, additional data will be needed to further reassess the relationships of this group of tribes.

*Distribution* This species is apparently endemic to Udzungwa (both western and eastern parts). If correctly attributed, the occurrence of *Upembella* in Udzungwa may reflect a past link to the forests of the southern Congo basin. The type locality of *U. adami* is over 1000 km away in an almost due westerly direction, in the Upemba National Park. This area itself harbours several endemic taxa including molluscs (Bruggen & Van Goethem, 2007). Another slug species formerly known only from the Udzungwa area, *Bukobia uhehensis* Verdcourt 1965 was recently reported some 600 km away in northeastern Mozambique (Muratov, 2010). The remaining genus of Upembellini, *Leptichnoides*, also has a southerly distribution.

Subfamily SHELDONIINAE Connolly 1925

Genus *Trochonanina* Mousson 1869

*Trochonanina mwanihananae* sp. nov.

(Figs 3, 7, 11–12, 16, 23–31)

*Holotype* (1 ad., width 10.50×height 8.10 mm; NMW.Z.2003.001.00023). Tanzania: Morogoro

Region, Udzungwa Mountains National Park, Mt. Mwanihana Catchment Forest Reserve (7.82° S, 36.83° E), forest at 1400 m elevation, 30.I.2003, leg. C. F. Ngereza, B. Rowson, M. B. Seddon & P. Tattersfield.

*Paratypes* Paratype 1 (1 ad., width 11.20×height 9.30 mm; NMW.Z.2003.001.00024): data as holotype but at 1350 m elevation. Paratype 2 (1 ad., width 10.35×height 9.20 mm; NMW.Z.2003.001.00025): data as holotype but at 1600 m elevation. Paratype 3 (1 ad., width 11.45×height 9.25 mm; NMW.Z.2003.001.00026): data as holotype but at 1500 m elevation. Paratype 4 (1 ad. sh., width 11.05×height 9.10 mm; NMW.Z.2003.001.00027) data as holotype but at 1695 m elevation. Paratype 5 (1 juv. sh., width 8.60×height 8.20 mm; NMT) data as holotype but at 1695 m elevation. Paratype 6 (1 ad. sh., width 10.30×height 9.20 mm; NMT) data as holotype but at 1625 m elevation. Paratype 7 (1 juv. sh., width 8.75×height 7.85 mm; NMW.Z.2003.001.00028) data as holotype but at 1625 m elevation. Paratype 8 (fragments of 1 ad. sh.; NMW.Z.2003.001.00029) data as holotype but at 1625 m elevation.

*Type locality* Tanzania: Morogoro Region, Udzungwa Mountains National Park, Mt. Mwanihana Catchment Forest Reserve (7.82° S, 36.83° E), forest at 1400 m elevation.

*Diagnosis* Medium-sized (shell width to 11.45 mm) snail with long caudal appendage and lacking mantle shell-lobes. Shell conical-turbinate, weakly keeled, with tiny umbilicus, pale corneous, transparent, extremely thin, glossy when fresh. Sculpture weak and visible only under high magnification: apically with fine spiral striae, later with fine close-set spiral lines with no radial element, then almost smooth; weak spiral striae below. Shell reminiscent of *Afroconulus* (Euconulidae: see below) but much larger. Internally: flagellum in the form of a bursa calcifera; penis with large penial gland and conspicuous internal papilla.

*External appearance* (Figs 3, 7) Snail with cephalopodium olive-yellow, tentacle retractors and long, tapering, caudal appendage blue-grey. Mantle shell-lobes absent. Mantle with bright cream margin and bright cream spiral band between two dark coffee-coloured bands, bands

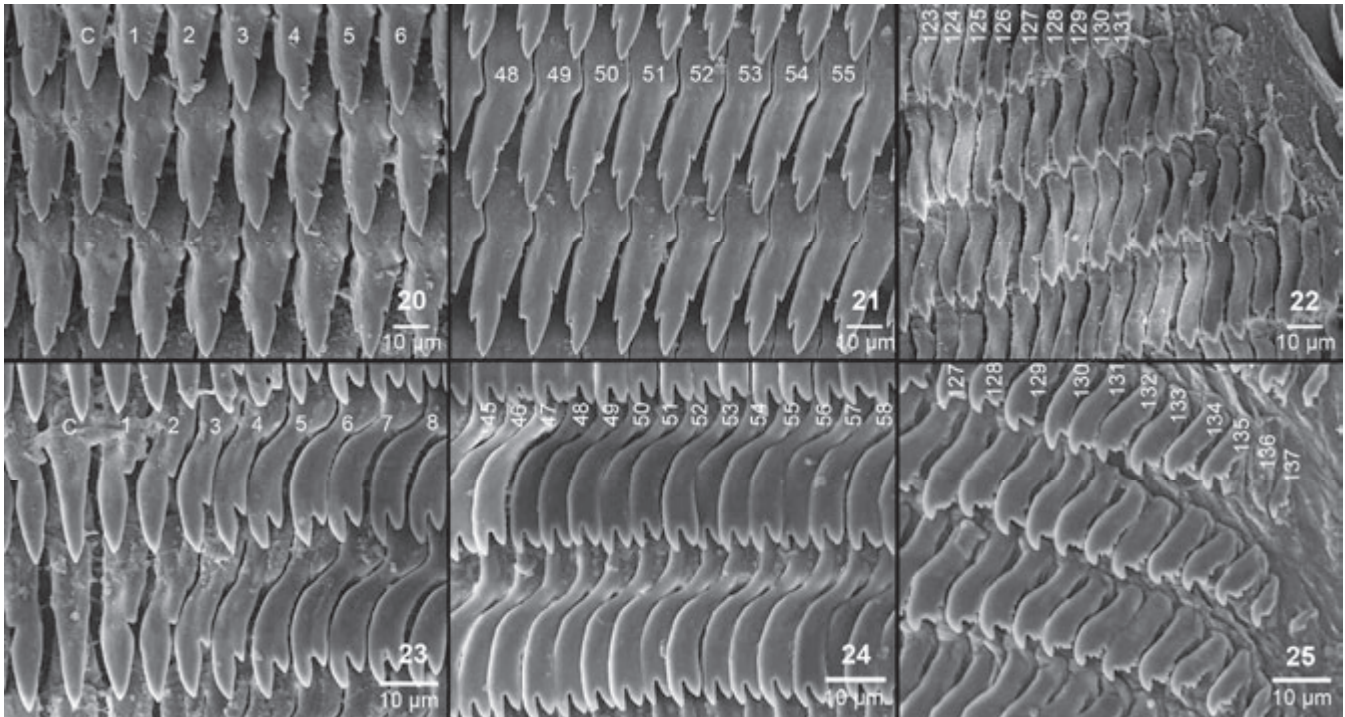
breaking up into spots after the first half-whorl, all visible through shell.

*Shell* (Figs 26–31) Medium-sized (adult shell height to 9.30 mm, width to 11.45 mm), conical-turbinate, of about up to 4.5–5 rather rapidly expanding whorls, weakly keeled at periphery, rounded at base, with tiny umbilicus, virtually covered by thin lip. Sides of spire slightly concave, whorls very slightly tumid. Shell pale corneous, transparent, extremely thin and fragile, glossy when fresh. Sculpture weak and visible only under high magnification, scarcely detectable where periostracum worn. Apical sculpture of very fine spiral striae, later sculpture of very fine close-set incised spiral lines with no radial element save for smoothed growth ridges, striae becoming invisible on later whorls which are almost smooth. Weak, more widely-spaced spiral striae below.

*Genitalia* (Figs 11–12) No stimulator. Penial complex robust, consisting of: free penis attended along its length by brown penial gland of large acini, both enclosed in thin sheath; long epiphallic caecum; epiphallus tubular, darkly pigmented; flagellum, at junction of vas deferens and epiphallus, very short, conspicuous, white (i.e. taking the form of a bursa calcifera sensu Van Goethem, 1977). Epiphallus and flagellum attended by a thin membrane or sheath (possibly a blood vessel or nerve). Penial retractor muscle attached at junction of epiphallus and caecum, arising from diaphragm. Penis internally with a conspicuous papilla of characteristic shape with slit-like pore. Penial gland not an opening through an obvious duct, although more closely adhering to penis and possibly opening to it around the level of the penial papilla. Bursa copulatrix and duct robust, clavate. Vagina longer than free oviduct.

*Radula and jaw* (Figs 16, 23–25) Jaw with very weak median projection. Radula with central tooth, two to three laterals, and 135 to 145 marginal teeth in a half-row, in about 105 rows. Central tooth unicuspid, others bicuspid, marginals strongly curved. Outer marginals with serrated outer edges, but serrated outer edges also present on at least some inner marginals as well.

*Etymology* After Mwanihana, the mountain, as if she were a female person.

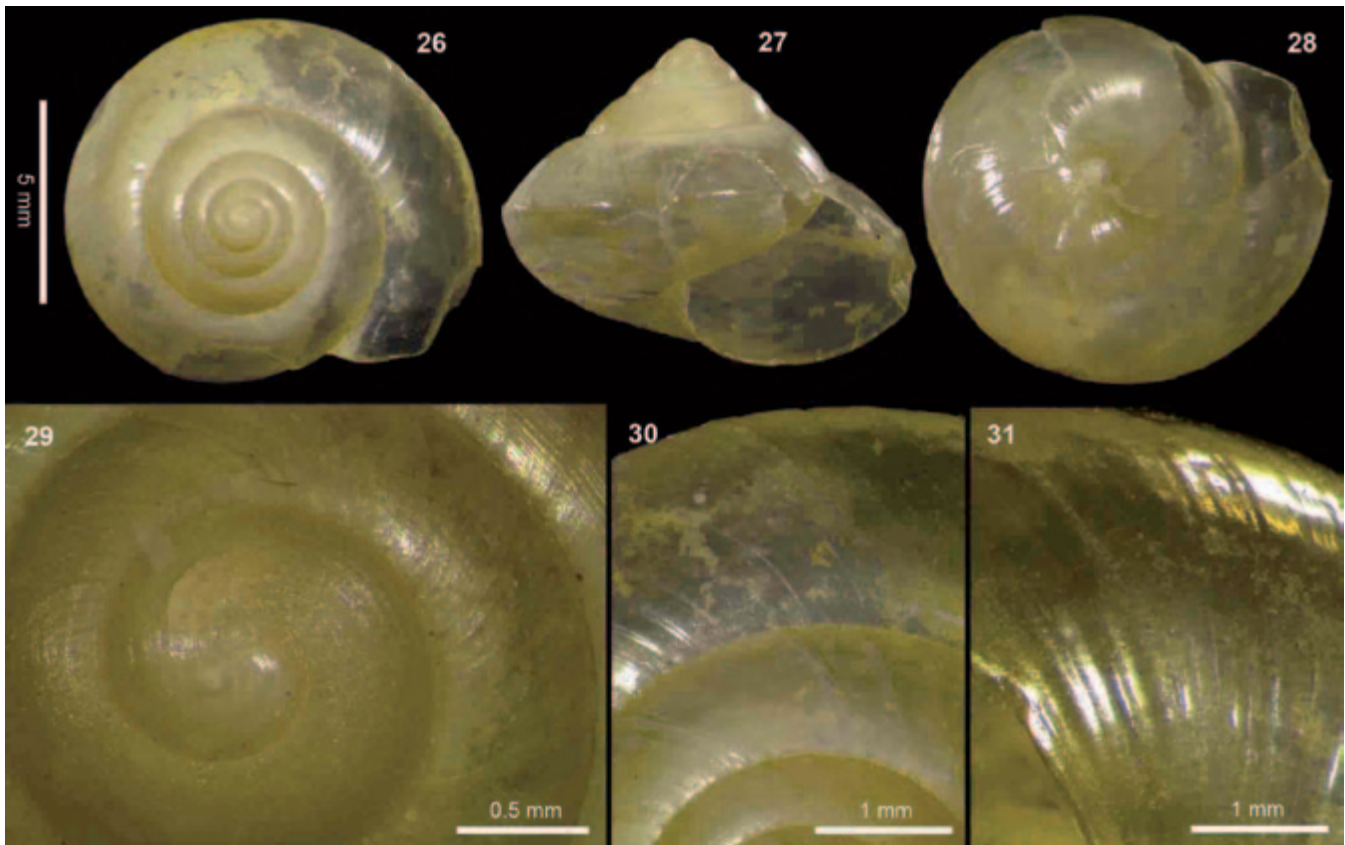


**Figures 20–25** Representative teeth from radulae (numbers indicate tooth positions in a single row; C is the central tooth). 20–22. *Upembella nonae* sp. nov. (holotype). 23–25. *Trochonanina mwanihanae* sp. nov. (holotype).

*Remarks* As throughout the Helicarionoidea, shells provide insufficient and sometimes misleading (i.e. conflicting) data on classification, yet cannot be ignored. The Mwanihana species even shows a resemblance to the non-helicarionoid genus *Afroconulus* Van Mol & Bruggen 1971, although its genitalia and radula are very different and *Afroconulus* is much smaller (shell width to 6.2 mm). The shell of *T. mwanihanae* rules out the semi-slug helicarionoid genera (e.g. Van Mol, 1970) and no East African species treated by Verdcourt (2006) in the helicarionoid snail genera *Sitala* H. Adams 1865, *Trochozonites* Pfeffer 1883 or *Thapsia* Albers 1860 has a shell matching it, despite the occurrence of spiral sculpture in several of them. As has frequently been noted, none of these have an East African type species. Membership of *Zingis* von Martens 1878, an East African genus with several subgenera (sensu Verdcourt, 2006), and the Malawian *Carinazingis* Bruggen & Winter 1990, despite some shell similarity, can be ruled out by the radula form and the presence of a penial gland in the Mwanihana species (Verdcourt, 1998b; Schileyko, 2002). The manuscript notes of J.-J. Van Mol at NMW, drawn upon by Verdcourt (1998), do not further help identify the Mwanihana species among these genera,

leaving *Trochonanina* and its various subgenera (sensu Verdcourt, 2006) as the most likely group. Furthermore this genus has an East African type species, *T. mozambicensis* (Pfeiffer 1855).

Although the shell of *T. mwanihanae* does not match any Eastern Arc species of *Trochonanina* (sensu Verdcourt, 2006), it has no shell feature not shown by at least one species of this group. The shells of *T. mozambicensis* and similar species (*Trochonanina* s.s.) differ from that of *T. mwanihanae* in being thicker, having coarse radial sculpture and a sharp keel, usually being less conical, and having a larger umbilicus. However, *T. mwanihanae* keys to *Trochonanina* s.s. in Verdcourt's (1961) anatomical key due to the presence and form of the flagellum and penial gland, and the position of the penial retractor. Verdcourt's (1961, 1998a) anatomical details of several East African species in the group (*T. mozambicensis*, *T. elatior* [Martens 1866], and *T. lessensis* Pilsbry 1919), show their genitalia and radula to be structurally similar to the Mwanihana species. It also resembles *T. mozambicensis* (and presumably the others) in lacking shell-lobes to the mantle. Another species of neighbouring Eastern Arc mountain ranges, *T. episcopalis* (Smith 1890) is thin and similarly-shaped, and has spiral apical striae, but bears very closely spaced and



Figures 26–31 Shell of *Trochonanina mwanihanae* sp. nov. (holotype, soft body removed).

clear fine radial striae (plus a brown peripheral band). Verdcourt (1986), again drawing on notes by Van Mol, discussed *T. episcopalis* and species with similar shells, indicating a variety of genitalia and a radula that were not dissimilar from *T. mozambicensis*. Another species of neighbouring Eastern Arc ranges and the coast, *T. gwendolinae* (Preston 1910) (= *Ledoulxia pseudojenynsi* Thiele 1931) shows fine spiral shell striae like the Mwanihana species, but is much more strongly keeled and a brown peripheral band (Verdcourt, 1992). Internally it has a much longer caecum (called the “lime gland” by Verdcourt [1992]), and a smaller penial gland. The form of the radula is similar to the Mwanihana species except that there are more (up to 10) laterals before the change to more evenly bicuspid marginals and no serrated outer edges of the marginal teeth. The latter feature was among those used by Verdcourt (1963) to unite the coastal *Sitala jenynsi* (Pfeiffer 1845) and the Eastern Arc *S. leroyi* (Bourguignat 1889) in the genus *Sitala*, which Verdcourt (2006) treats in a separate family (Ariophantidae). However these two species, despite the radular

similarity, were said by Verdcourt (1963) to have a dart sac and a large stimulator (*S. leroyi*) or no stimulator and the vestige of a dart sac (*S. jenynsi*), so are very different to one another in genitalia, and both unlike the Mwanihana species. Furthermore, the serrated edges of the marginal teeth also occur in the thin-shelled, globose *T. membranacea* d’Ailly 1910 of Kilimanjaro, made the sole species of *Trochonanina* subgenus *Sjostedtina* Verdcourt 1961 on the basis of a genital anatomy that was *Trochonanina*-like (although different to the Mwanihana species) (Verdcourt, 1961). Convergence in the Helicarionoidea does not rule out more distant affinities, but given the current state of knowledge, the closest relative of *T. mwanihanae* seems at least to be among East African species already assigned to *Trochonanina* s.l., if not to *Trochonanina* s.s.

*Distribution* As far as is known this species is endemic to the type locality, elevation and habitat, where rainfall and humidity are high year-round. Such conditions might favour a reduction in shell thickness and sculpture.



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