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New species of land snails (Mollusca: Gastropoda) from two isolated karst formations in central western Madagascar: Tsingy Beanka and Antsingimavo, with additional notes on other regional endemics

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ABSTRACT

Seven new land snail species are described from the Antsingimavo and Beanka karst formations, north-east of Maintirano, central western Madagascar: *Ampelita andriamamonjyi*, *A. beanka*, *A. lindae*, *Conulinus randalanai*, *Kalidos maryannae*, *Tropidophora humbug* and *T. sericea*. Additional notes, records and illustrations are also provided for a further ten regionally endemic species.

KEY WORDS: Gastropoda, Madagascar, Tsingy Beanka, Antsingimavo, new species, karst, species inventory.

INTRODUCTION

The limestone areas east and north-east of the town of Maintirano in the central west of Madagascar (Fig. 1) were identified as areas of high land snail endemism after the first author's initial visit there in 1996. Since then a number of expeditions have been made to further investigate the diverse non-marine molluscan fauna of this area. Collections made during these expeditions have already led to the description of new land snails (Emberton 1999) and new freshwater molluscs (Köhler & Glaubrecht 2010). The principal aim of this paper is to describe a further seven new species of restricted-range land snails from the area, highlighting the importance of the spectacular but highly threatened tropical hardwood forests growing on the karstic formations (*tsingy* in Malagasy) in the region as a focus of non-marine molluscan endemism. In addition, we provide further notes and distribution data for ten other regionally endemic species for which information is currently limited, as well as an inventory of the molluscan fauna of the study areas. The geological history of the Antsingimavo and Beanka karsts is not known, but its seems probable that they are simply northern outliers of the Bemaraha formation and thus date from the Jurassic (Veress *et al*. 2008). While the limestone itself is not continuous, it is likely that all three areas were once connected by continuous forest cover.

Antsingimavo and Ansokosoko karsts (Fig. 1B)

These karsts lie approximately 90 km NNE of Maintirano, near the village of Antsingimavo, and are collectively referred to here as the Antsingimavo karsts. The limestone consists of a number of relatively small isolated karst hills, extending from 50 m to 100 m above sea level. While each separate hill covers only a small area (the largest is approx. 1 km long by a few hundred meters wide), they all consist of tall tsingy formations, with some caves. They fall into two groups: those lying to the south of the Ranobe River (Antsingimavo karst, approx. 17.443°S 44.455°E) and those lying to the north of the river (Ansokosoko karst, approx. 17.379°S 44.447°E). The Antsingimavo

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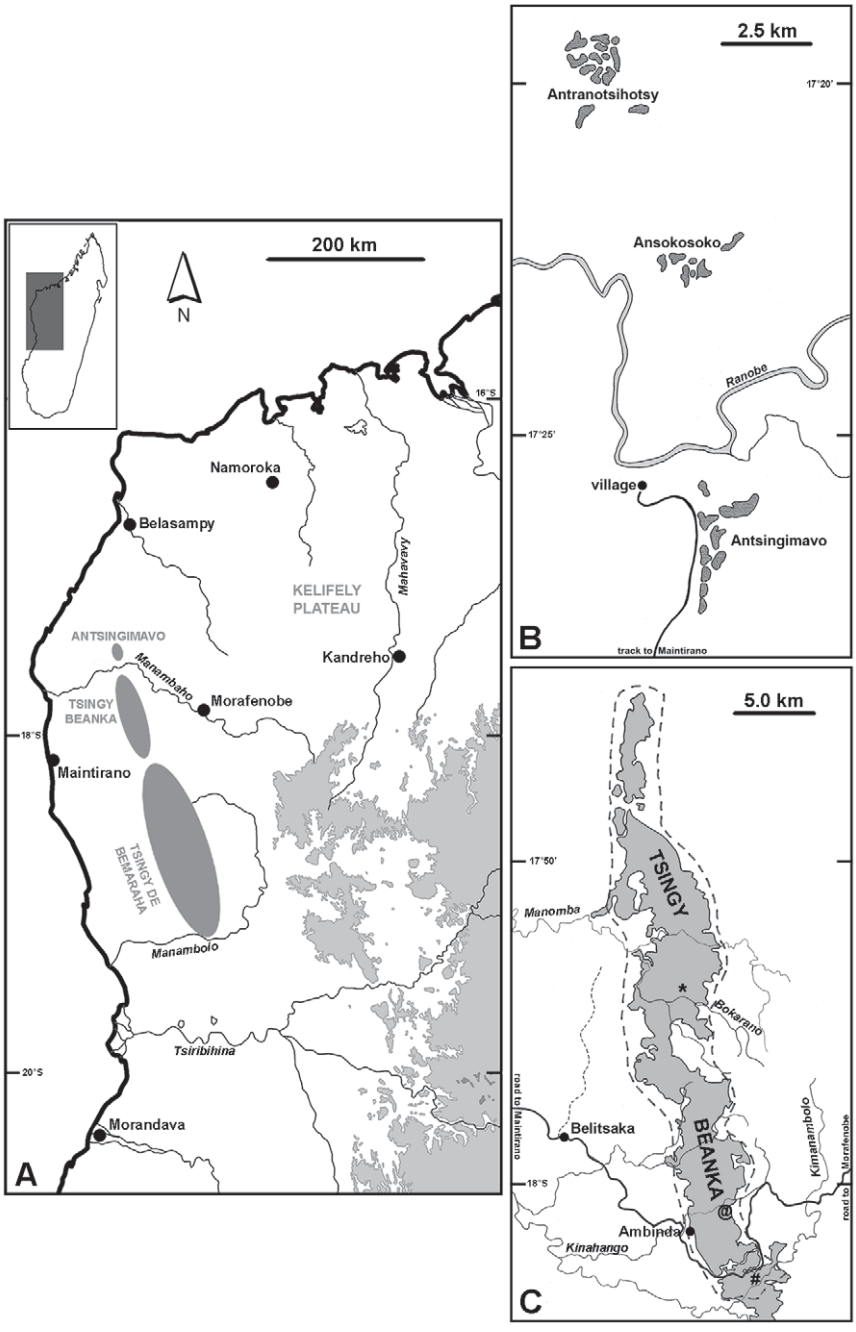

Fig. 1. Geographical location of study areas: (A) map of central western Madagascar showing the broader location of the karst (tsingy) formations studied (contour at 1000 m); (B) detail of the Antsingimavo karsts; (C) detail of Tsingy Beanka, dashed line represents approximate limits of the reserve; shaded area represents forested habitat on karst hills (redrawn from Middleton 2010). Legend: ∗ – Bokarano River Cave; # – Kimanambolo Bat Cave; @ – Kinahango Cave.

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karst itself consists of about nine karst hills extending for *ca* 3.5 km north-south, separated from one another by intervals of red soil grasslands. The Ansokosoko karst consists of about eight karst hills extending *ca* 3 km east-west. All the forest surrounding the tsingy has been destroyed, leaving only a palm and thorn-tree savannah-grassland. However, on the tsingy itself there remains moderately tall dry deciduous forest with some moist evergreen forest patches in the larger ravines and gullies within the tsingy outcrops. There is no record of these isolated karst formations ever having been explored scientifically (Middleton 2007). Further scattered karst hills at Antranotsihotsy, approx. 5 km NNW of Ansokosoko remain to be investigated.

Tsingy Beanka (Fig. 1C)

This is the name for a large area of karst *ca* 60 km ENE of Maintirano and extending to the north of the Tsingy de Bemaraha. The area consists of a narrow, continuous block of karst, cut by a number of river gorges, and runs northward from the Kimanambolo River for about 30 km, extending east-west for 3–5 km. It is covered in tall dense forest, dry deciduous in more exposed areas and evergreen in the deeper gorges. The block of forest in the south is considered to be the most pristine tall humid forest remaining in the west of Madagascar and is of very high conservation importance (S. Goodman pers. comm. 2009). Some of the first zoological collections from the region were made in the early 1900s at a site near Andrafiavelo, NE of Maintirano, and resulted in the description of two new mammal species (Grandidier 1928; Grandidier & Petit 1931). The Tsingy Beanka was briefly surveyed from a malacological perspective in 1996 as part of a DEF/Duke Stony Brook accord (Griffiths 1997), but has recently become the focus of more detailed faunistic and floristic studies resulting in the description of further new species (e.g. Goodman *et al*. 2011). Beanka means the place of many 'anka', the Madagascar Long-eared Owl, *Asio madagascariensis* (Smith, 1834).

The Antsingimavo karst has no protected status. The Tsingy Beanka is included in the list of Madagascan protected areas (Nouvelles Aires Protégées – arrêté interministériel 18633). The conservation management of Beanka is carried out by Biodiversity Conservation Madagascar (BCM), a Malagasy NGO that has been granted a 25 year conservation lease on the area. BCM is funded by Bioculture (Mauritius) Ltd as part of that company's corporate social responsibility/conservation programme.

MATERIAL AND METHODS

Sampling methodology consisted of collecting in as wide a variety of habitat types as possible within each karst area. Hand collecting was carried out on vertical limestone surfaces, on trees and under rocks and logs, under overhangs, in tsingy slots (very narrow horizontal and vertical crevices in the tsingy) and in accumulations of leaf-litter in a wide variety of sheltering microhabitats. Leaf-litter samples were also collected for subsequent sieving and sorting for micro-molluscs. Careful attention was made to look for deposits of subfossil snail shells under deep overhangs and in cave entrances.

The following abbreviations are used:

AMS – Australian Museum, Sydney, Australia;
H:D – height:maximum diameter ratio;
MNHN – Muséum National d'Histoire Naturelle, Paris, France;
NHMUK – Natural History Museum, London, UK;

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NMSA – KwaZulu-Natal Museum, Pietermaritzburg, South Africa;
OLG – O.L. Griffiths collection;
SMNH – Swedish Museum of Natural History, Stockholm, Sweden;
st'n(s) – station(s);
TMAM – Tsimbazaza Museum, Antananarivo, Madagascar.

Permits to conduct the surveys were issued by Cadre d'Appui Forestier and Conseil d'Orientation de la Recherche Environnementale, of the Direction Générale des Eaux et Forêts and later the Ministère de l'Environnement, des Eaux et Forêts et du Tourisme (permit numbers 173/06 and 205/09). In addition to the authors of this paper, the survey team included: Greg Middleton (Sydney Speleological Society), Linda Davis (NMSA), Adnan Moussalli (Museum Victoria, Melbourne), Devi Stuart-Fox (University of Melbourne), Mireille Saory (Ministère de l'Environnement, des Eaux et Forêts et du Tourisme), Hajanirina Ramino (TMAM) and Roger Randalana (Biodiversity Conservation Madagascar). Under the terms of the permit agreement, most of the material collected has been lodged in the invertebrate collection at the Tsimbazaza Museum, Antananarivo, under the curatorial care of Mrs Hajanirina Ramino. Holotypes are deposited in the AMS, with paratypes in other museums as indicated. The remaining material is in the OLG and NMSA. Full details for the sampling stations are provided in Appendix 1.

Descriptions and illustrations of radulae and distal genitalia are provided for operculate and stylommatophoran species respectively. At present it is not possible to infer much of significance from these observations due to the paucity of comparative data. They do, however, confirm that the species are referred to the appropriate genera and will provide information for future studies of comparative anatomy.

For anatomical study, living specimens were drowned overnight in sealed containers and preserved in 75 % ethanol for dissection. Prior to drowning, small fragments of the foot were excised and preserved in 99 % ethanol for future molecular work. All dissections were performed under a Wild M4 dissecting microscope with drawing tube. Photographs of shells were taken with a Nikon D70 camera and those of living specimens with a Nikon CoolPix 8800. Automontage micrographs of protoconchs were taken using a Leica MZ16 stereomicroscope and *Automontage Pro V5.0* [Syncroscopy]. Shell height and diameter measurements as well as protoconch dimensions and whorl counts were measured using the methods set out by Herbert and Moussalli (2010). Immature shells were excluded from the data used to calculate H:D ratios.

Radulae were obtained by excision of the buccal mass which was then macerated in dilute NaOH. Subsequently the radulae were rinsed thoroughly in distilled water, dehydrated in ethanol, placed on stubs with double-sided carbon tape and manipulated into position using fine entomological pins whilst air-drying. After coating with gold–palladium, the specimens were examined at low accelerating voltage (5 kv) in a Zeiss EVO 10LS scanning electron microscope.

TAXONOMY

At least 108 species of non-marine mollusc have now been recorded from the Antsingimavo and Beanka karsts and nearby non-karst areas. The full list of species collected is provided in Appendix 2. While many could not at this stage be identified with described species, it is clear that at least seven are species new to science and these are described here. The total for the Antsingimavo karst is 61 species, of which 15 (25%) are perhaps

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endemic. For the Tsingy Beanka the total number of species is 85, of which 28 (33%) may be endemic. A further 21 taxa are evidently endemic to the two areas combined. Of the total 108 taxa, only 38 (35%) have been found at both localities, suggesting a substantial difference between their respective faunas.

Family Cyclophoridae Gray, 1847
Genus *Acroptychia* Crosse & Fischer, 1877
Acroptychia bathiei Fischer-Piette & Bedoucha, 1965

Figs 2, 3, 25A

Acroptychia bathiei: Fischer-Piette & Bedoucha 1965: 61, fig. 12, pl. 1, figs 9–11; Fischer-Piette *et al*. 1993: 47, pl. 1, figs 19–21. Type loc.: 'près de la rivière Andranomavo (Ambongo)' [Perrier de la Bâthie leg.], NW Madagascar'.

Morphological notes:

External features (Fig. 25A): Head-foot mostly greyish, irregularly mottled with darker spots and blotches; eyestalks pale, but tentacles more or less uniformly dark; forehead and snout brown; tip of snout shallowly indented in mid-line; skin texture relatively smooth.

Operculum: Corneous, oligospiral with an eccentric nucleus.

Radula (Fig. 3): Formula 1+2+1+2+1; length 12 mm, with *ca* 140 tooth rows [*ca* 11.5 rows/mm]; teeth robust. Rachidian tricuspid with a rounded central cusp and two smaller

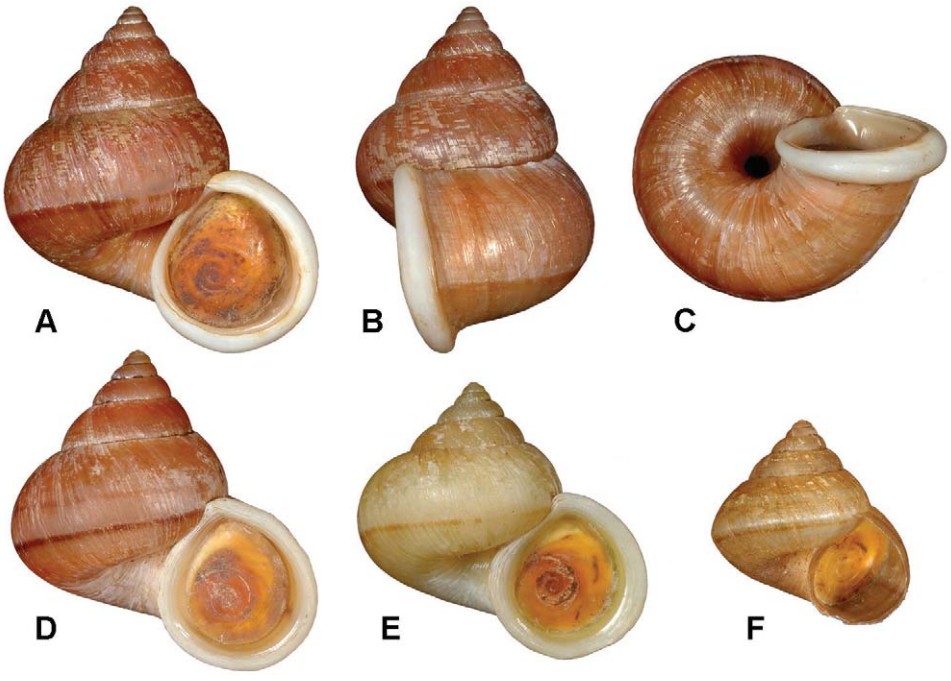

Fig. 2. *Acroptychia bathiei* Fischer-Piette & Bedoucha, 1965: (A–C) Tsingy Beanka, st'n 18/06, max. diameter 23.7 mm, NMSA L7174; (D–F) Antsingimavo, st'n 04/06, NMSA L7091: (D) typical shell, max. diameter 23.0; (E) pale yellow specimen with a less elevated spire, max. diameter 21.7 mm; (F) juvenile specimen, max. diameter 14.9 mm.

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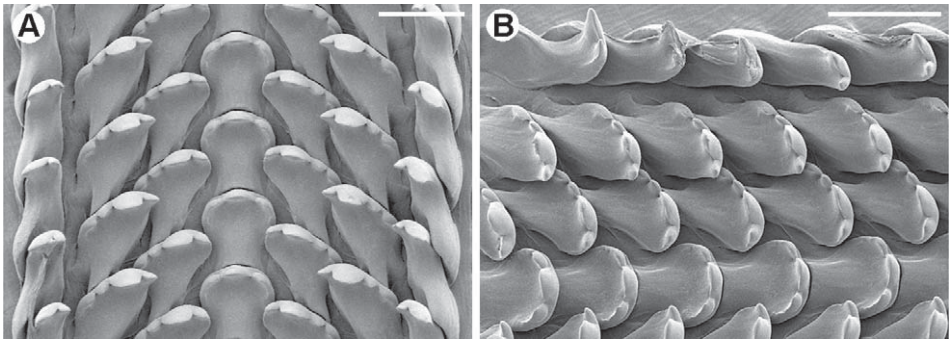

Fig. 3. *Acroptychia bathiei* Fischer-Piette & Bedoucha, 1965, radula, NMSA L7039: (A) entire width of radula; (B) oblique view of left half row. Scale bars = 100 µm.

lateral ones; inner and outer laterals similar, each with four cusps, of which the second is consistently the largest; marginals bicuspid, the outer cusp larger. Very similar to that of *A. culminans* Fischer-Piette & Bedoucha, 1965, as described and illustrated by Fisher-Piette *et al*. (1969), except that the outer lateral is mostly tricuspid in that species.

Locality data: *Namoroka*: st'ns 930/97, 932/97. *Antsingimavo*: st'ns 04/06, 06/06, 08/06. *Tsingy Beanka*: st'ns 03/06, 11/06–13/06, 16/06–18/06, 01/09, 02/09, 06/09–09/09, 11/09, 01/10, 03/10, 05/10–08/10, 10/10. *Tsingy de Bemaraha*: st'ns 07/95, 14/95, 18/95, 09/96, 10/96, 12/96, 14/96. *South bank of Tsiribihina R.*: st'n 02/99LP.

Distribution: Restricted to central W Madagascar; from the Tsiribihina R. and southern Bemaraha region through Tsingy Beanka and Antsingimavo to the Namoroka area.

Habitat: Dry mixed deciduous-evergreen forest growing on limestone; living in leaf-litter, under limestone rocks and in soil pockets on karst boulders; patchily common at both Tsingy Beanka and Antsingimavo. Also common throughout most of the Tsingy de Bemaraha reserve.

Remarks: A moderately sized, thick-shelled species with a single, well-developed, terminal, peristomal varix. Diameter rarely more than 24 mm. Shell essentially smooth save for fine axial pliculae on the early teleoconch whorls and fine, close-set growth-lines on later whorls. Umbilicus relatively narrow and deep. Juveniles have a much thinner shell that is frequently weakly angled at the periphery (Fig. 2F).

The ground colour ranges from a pale yellowish white to a deeper pinkish or orange-brown; in fresh specimens this is overlain by a fine, irregular whitish mottling, which is in turn overlain by a thin, rather glossy, corneous periostracum. However, the latter is commonly eroded in parts, after which the whitish mottling is quickly worn off and the shell becomes more uniformly coloured. A darker spiral line is frequently present just below the periphery, occasionally another just above it and sometimes a third in the middle of the base.

Family Pomatiidae Newton, 1891
Genus *Tropidophora* Troschel, 1847
Tropidophora chavani Fischer-Piette, 1949

Figs 4, 9E

Tropidophora chavani: Fischer-Piette 1949: 15, pl. 1, figs 4–6; Fischer-Piette & Bedoucha 1965: 73; Fischer-Piette *et al*. 1993: 102, pl. 5, figs 6–8. Type loc.: 'gorges de Salapanga (Bemaraka)' [= Bemaraha].

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Fig. 4. *Tropidophora chavani* Fischer-Piette, 1949: Tsingy Beanka, st'n 15/06, max. diameter 27.0 mm, NMSA L7129.

Locality data: *Tsingy Beanka*: st'ns 12/06, 14/06, 15/06, 01/09, 02/09, 06/09, 07/09, 08/09, 09/09, 01/10, 05/10, 07/10, 08/10, 09/10, 10/10. *Tsingy de Bemaraha*: st'ns 18/95, 04/96, 09/96, 10/96, 12/96.

Distribution: A narrow-range endemic; currently recorded only from the Bemaraha region and Tsingy Beanka.

Habitat: Dry forest growing on limestone; found in leaf-litter and between limestone boulders.

Remarks: A moderately common species in the central Tsingy Beanka, but usually present at rather low density. It is characterised by its low spire and uniformly fine spiral sculpture. Specimens with a similarly dense spiral sculpture have been collected at Andranavory in the Toliara [Tuléar] region, but these are more elevated and have a flaring white lip, which is broadly reflected in the columella region, half covering the umbilicus. They are closer to *T. semidecussata* (Pfeiffer, 1847) than they are to *T. chavani*.

Tropidophora humbug sp. n.

Figs 5, 6, 25B

Etymology: The colour pattern of bold stripes is reminiscent of that of old-fashioned humbug sweets; used as a noun in apposition.

Diagnosis: Spire very low, shell almost planorboid, body whorl not conspicuously tumescent, umbilicus very wide; columella lip not expanded and not reflected over umbilicus; surface virtually smooth to the naked eye; boldly marked with brown spiral bands on a near white ground.

Description:

Shell: Medium sized, depressed-discoidal to planorboid; spire very low (H:D=0.46–0.62), often with only embryonic whorls projecting in apertural view; final part of last adult whorl descending prior to aperture, but not steeply so; whorls more or less evenly rounded, suture indented; umbilicus very wide, its margin evenly rounded, underside of embryonic whorls clearly visible. Protoconch of 1¼–1½ whorls, essentially smooth, but microscopically shagreened. Teleoconch of a further 2½–2¾ whorls; the first with approx. 6 weak spiral ridges crossed by numerous fine, close-set, axial threads; spirals becoming more numerous but less distinct on subsequent whorls and axials somewhat coarser; axials resembling fine, uneven, close-set growth-lines on last half-whorl of adult, these extending onto base and into umbilicus; base lacking spiral sculpture. Aperture subcircular, strongly oblique to vertical axis of shell; peristome incomplete, interrupted

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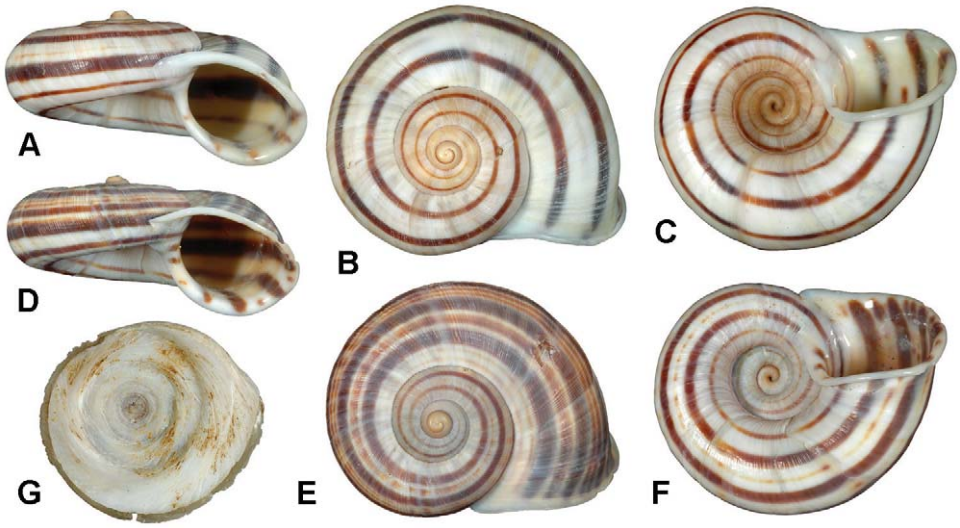

Fig. 5. *Tropidophora humbug* sp. n.: (A–C) holotype, Tsingy Beanka, max. diameter 31.5 mm, height 16.3 mm, AMS C.474165; (D–F) paratype, heavily banded specimen, Tsingy de Bemaraha, max. diameter 30.4 mm, height 14.1 mm, NMSA L8444/T2658; (G) operculum of holotype, external surface, max. diameter 11.0 mm, AMS C.474165.

briefly in parietal region; rim of peristome reflected forming a flaring lip, but this not noticeably enlarged in columella region.

Ground colour bone-white, boldly marked with dark brown spiral bands, the one at and extending just below periphery usually broadest, commonly with 2 or 3 additional bands above and a further 2 or 3 below this; an additional fine orange-brown intermediary spiral line sometimes present in intervals between bands; umbilical region with additional colour bands, often fine, such that base may have up to 7 bands in total; exceptionally, base may have only 1 or 2 colour bands; precise position of colour bands somewhat variable, but uppermost band generally not in contact with suture.

Dimensions: Holotype, max. diameter 31.5 mm, height 16.3 mm; largest specimen, max. diameter 32.0 mm.

External features (Fig. 25B): Head-foot more or less uniformly dark grey-brown, but eyestalks and tentacle bases paler; tip of snout conspicuously indented in mid-line; skin texture finely granular.

Operculum (Fig. 5G): Oligospiral; exterior portion a calcareous disc, attached to an inner and slightly larger corneous layer; external surface off-white (usually encrusted with detritus particles), lacking colour pattern, but with a broad convex spiral ridge more or less at mid-whorl; thinner toward periphery; edge of disc concave, with numerous, close-set, rather unevenly spaced transverse partitions, except along the growing (parietal) margin, which is smooth.

Radula (Fig. 6): Formula 1+2+1+2+1; length 11 mm, *ca* 35 rows/mm; dentition fine. Rachidian with seven rounded cusps, central one largest, the outermost pair small; occasionally with very small intermediary teeth between the larger ones. Inner laterals with four cusps, the second of which is bluntly rounded and consistently the largest, the

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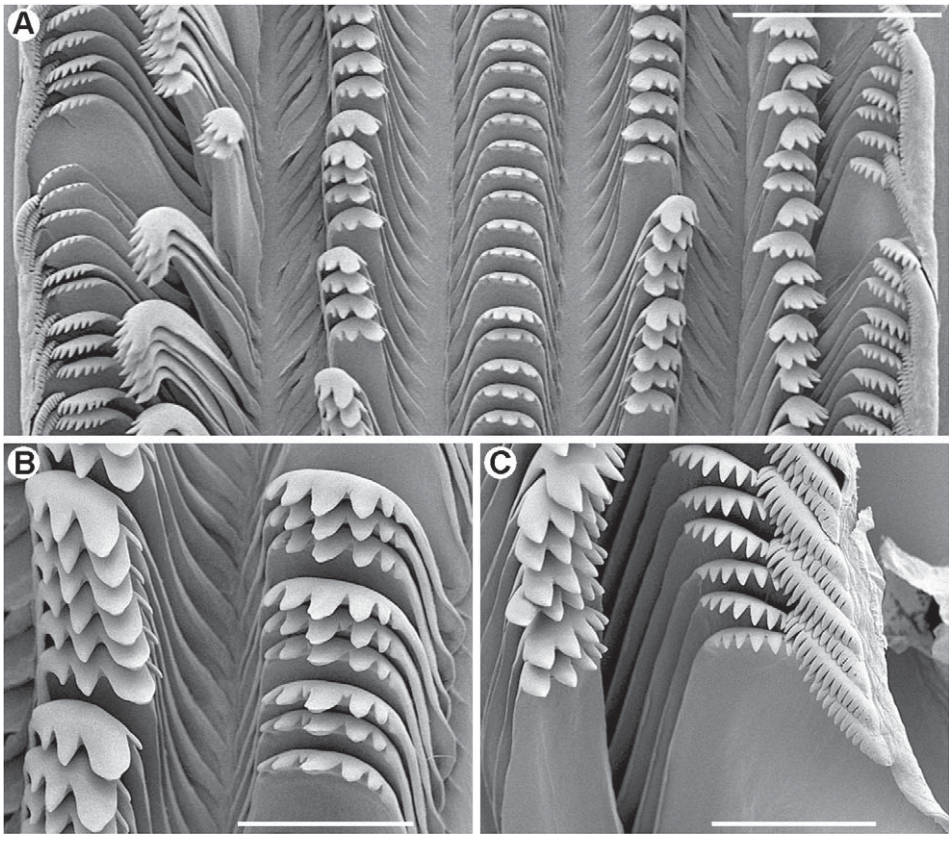

Fig. 6. *Tropidophora humbug* sp. n., radula, paratype NMSA L7042/T2961: (A) entire width of radula, scale bar = 250 µm; (B) rachidian and left inner lateral teeth, scale bar = 100 µm; (C) right outer lateral and marginal teeth, scale bar = 100 µm.

others more pointed; outer lateral with five cusps, the inner one usually slightly larger, the others progressively smaller. Marginal teeth broad, the edge comprising three regions; an inner coarsely dentate element with *ca* 9 denticles; a more finely denticulate central region, and a smooth outer portion. Such a radula conforms to the pattern seen in *Tropidophora (Ligatella)* Martens, 1880 (Fischer-Piette *et al*. 1969).

Holotype: MADAGASCAR: Central W Madagascar, *ca* 60 km E of Maintirano, tall dense dry forest growing above cliffs on E side of southern Tsingy Beanka at Andohanandranogedro, 18.05028°S 44.53786°E, 380 m, iv.2009, R. Randalana, st'n R04/09 (AMS C.474165).

Paratypes: Same data as holotype (NMSA L8547/T2962, 2 specimens); st'n 14/95 (AMS C.469588, 5 specimens); st'n 10/96 (AMS C.469587, 5 specimens); st'n 14/96 (AMS C.469589, 2 specimens); st'n 15/96 (NMSA L8444/T2658, 6 specimens); st'n 03/06 (NMSA L7042/T2961, 45 specimens, some in alcohol; MNHN IM-2010-20067, 2 specimens; NHMUK 20120013, 2 specimens); st'n 12/06 (NMSA L7204/T2984, 2 specimens); st'n R04/09 (AMS C.469590, 6 specimens; TMAM T166, 7 specimens); st'n R01/10 (TMAM T160, 5 specimens); st'n R02/10 (MNHN IM-2010-20068, 7 specimens).

Additional locality data: *Tsingy Beanka*: st'ns 05/06, 11/06, 12/06, 13/06, 16/06, 18/06, 01/09, 03/09, 11/09, 03/10, 10/10. *Tsingy de Bemaraha*: st'ns 08/96, 09/96.

Distribution: A narrow-range endemic; known only from the Tsingy Beanka and Tsingy de Bemaraha, but common at both these localities.

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Habitat: Tall semi-deciduous and deciduous western dry forest. Often found on tree trunks after rain. Aestivates in leaf-litter.

Remarks: Fischer-Piette *et al*. (1993) grouped medium-sized, low-spired Madagascan *Tropidophora* species together in their 'groupe d'espèces du *T. deshayesiana* (Petit de la Saussaye, 1844)', but with the exception of *T. vittata* (Sowerby, 1843) all members of this group have much stronger spiral sculpture than *T. humbug*, including *T. chavani* Fischer-Piette, 1949 (see above) with which it is sympatric. Besides being relatively smooth, *T. vittata*, which is recorded only from north-eastern Madagascar (Fischer-Piette *et al*. 1993), shares with *T. humbug* a similarly banded colour pattern and is undoubtedly the most similar species. However, *T. vittata* has a far more prominent spire, deeper body whorl, narrower umbilicus, and a more extensively flared aperture lip, often with a wide extension in the columella region that partially obscures the umbilicus at full maturity. Fischer-Piette *et al.* (1993) stated that the holotype of *T. vittata* was in the NHMUK, but it could not be located there (Ablett *in litt*. Nov. 2011). *T. semidecussata* (Pfeiffer, 1847), is also similar and though a very variable species, like *T. vittata*, it has a more elevated spire, tumescent body whorl, narrower umbilicus and a more well developed, strongly reflected columella lip.

Specimens of *T. humbug* from the Tsingy de Bemaraha commonly have a slightly more elevated spire than those from Tsingy Beanka, but H:D ratios for the two populations overlap considerably (H:D=0.47–0.61 compared to 0.46–0.53 respectively).

Tropidophora secunda Fischer-Piette & Bedoucha, 1965

Figs 7, 8, 25C

Cyclostoma reticulatum: Reeve 1861: pl. 9, fig. 48a, b [*non* Adams & Reeve 1850 in 1848–1850: 57, pl. 14, fig. 8].
Tropidophora reticulata: Fischer-Piette 1949: 36.
Tropidophora secunda: Fischer-Piette & Bedoucha 1965: 76. Type loc.: Madagascar.
Tropidophora (Ligatella) secunda: Fischer-Piette *et al*. 1993: 129, fig. 82.

Morphological notes:

External features (Fig. 25C): Head-foot more or less uniformly grey; tentacles and forehead slightly darker, paler toward mantle cavity; tip of snout conspicuously indented in mid-line; skin texture very finely granular.

Operculum: Oligospiral; exterior portion a calcareous disc, attached to an inner and slightly larger corneous layer; external surface very shallowly concave, lacking a distinct convex spiral ridge (cf. *T. humbug* above), but with a diffuse, dark purple-brown spiral band more or less at mid-whorl, most noticeable on last whorl; edge of disc concave, with relatively weakly developed transverse partitions (adjacent to inner surface), except along smooth growing margin.

Radula (Fig. 8): Formula 1+2+1+2+1; length 7.3 mm, *ca* 42 rows/mm; dentition fine. Rachidian with five distinct cusps, a minute additional pair sometimes discernable; central cusp largest and rounded, the outer pair small and curving inward. Inner laterals with four cusps, the inner cusp small and often obscured by the much larger second cusp; outer lateral with five or six cusps, the central three or four usually larger. Marginal teeth broad, the edge comprising three regions; an inner coarsely dentate element with *ca* 9 denticles; a more finely denticulate central region, and a smooth outer portion.

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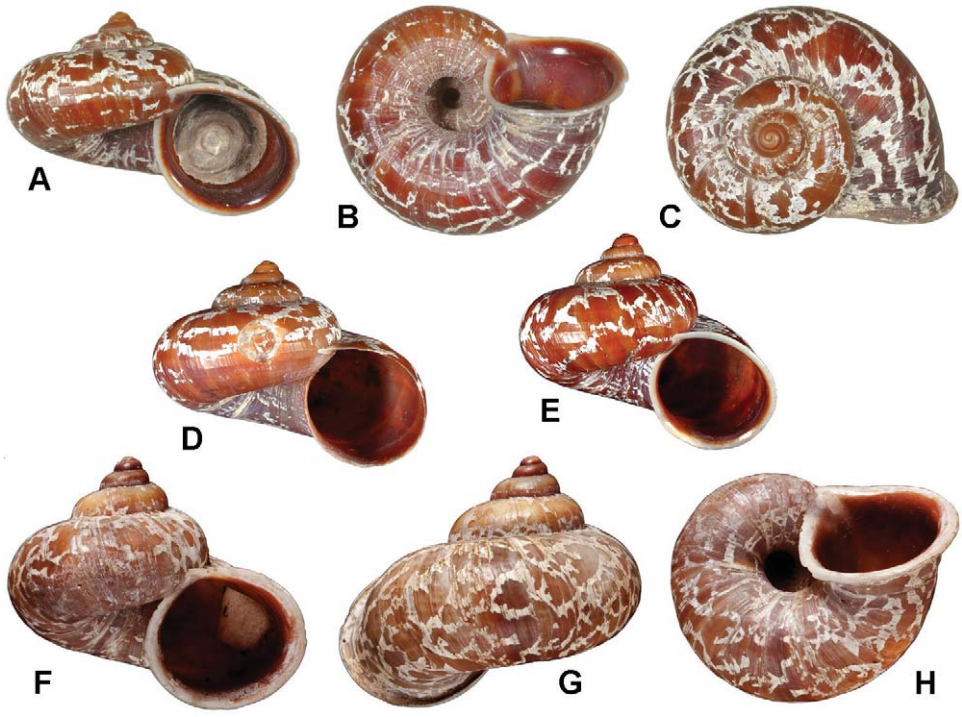

Fig. 7. *Tropidophora secunda* Fischer-Piette & Bedoucha, 1965: (A–C) Tsingy Beanka, st'n 03/06, max. diameter 21.5 mm, NMSA L7040; (D) Tsingy Beanka, st'n 03/06, subadult, max. diameter 20.0 mm, NMSA L7040; (E) Kelifely Plateau, max. diameter 18.8 mm, NMSA L6798; (F–H) holotype (faded), 'Madagascar', Cuming collection, max. diameter 22.0 mm, NHMUK 20110470.

Such a radula conforms to the pattern seen in *Tropidophora (Ligatella)* Martens, 1880 (Fischer-Piette *et al*. 1969).

Locality data: *Tsingy Beanka*: st'ns 03/06, 11/06, 12/06, 13/06, 14/06, 15/06, 17/06, 18/06, 02/09, 11/09, R01/10, 03/10, 09/10. *Kelifely Plateau*: st'ns 04/05, 10/05. *Anjajavy (Narinda north)*: st'ns 33/03, 36/03. 37/03, 38/03, 39/03, 40/03, 13/04 [abundant in this area]. *Mtn d'Ambre/Ankarana*: st'ns 12b/94, 01/01, 09/01 [uncommon].

Distribution: Central western to north-eastern Madagascar; from the southern Bemaraha region (Fischer-Piette *et al*. 1993) through Tsingy Beanka, the Kelifely Plateau and Anjajavy area, to Mtn d'Ambre and Ankarana in Antsiranana Province. Curiously, we have not found this species in our own surveys in the Tsingy de Bemaraha, nor at Antsingimavo, and whereas it is common in the southern Tsingy Beanka, it is rare in the central portion. Evidently although relatively widespread, the species has a somewhat patchy distribution within its range.

Habitat: Dry deciduous, evergreen and riverine forest in limestone areas; in leaf-litter and sheltering microhabitats amongst rocks.

Remarks: A characteristic species on account of its bold colour pattern. *T. reticulata* (Adams & Reeve, 1850), with which it was at one time confused, has a similar coloration, but is smaller (max. diameter approx. 16 mm, compared to >18.5 mm in *T. secunda*), has a more elevated shell and a narrower umbilicus (Fischer-Piette 1949)

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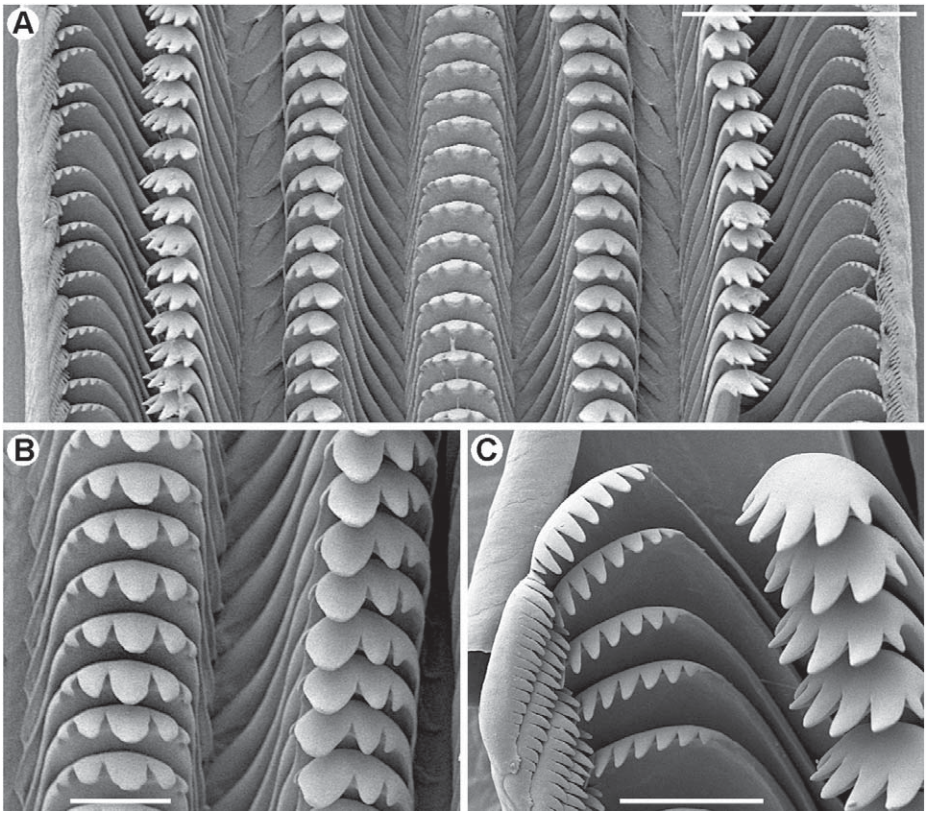

Fig. 8. *Tropidophora secunda* Fischer-Piette & Bedoucha, 1965, radula, NMSA L7040: (A) entire width of radula, scale bar = 200 µm; (B) rachidian and inner lateral teeth, scale bar = 50 µm; (C) outer lateral and marginal teeth, scale bar = 50 µm.

(Fig. 26G–I, syntype, NHMUK). The white markings of *T. secunda* are not part of the shell fabric, but are a superficial chalky deposit which can be easily scraped off. Although previously reported from few localities, the range of *T. secunda* is evidently relatively large and it is not uncommon in undisturbed dry forest habitat. In contrast, the range of *T. reticulata* has yet to be established more precisely than 'Madagascar'. Most specimens from Tsingy Beanka have a lower spire than the holotype (compare Figs 7A and 7F); however, shells of intermediate height are present both in the Tsingy Beanka and Kelifely Plateau (Fig. 5D, E).

Fischer-Piette and Bedoucha (1965) selected as the 'type' for this species the specimen illustrated as *Cyclostoma reticulatum* by Reeve (1861: pl. 9, fig. 48a, b, 'Mus. Cuming'), which they stated was present in the 'British Museum' [NHMUK]. Fischer-Piette (1949) had earlier examined this specimen, citing its diameter as 22 mm. No specimen identified as the holotype of *Tropidophora secunda* was present in the NHMUK, but a specimen labelled *Cyclostoma reticulatum* is present in the Cuming collection (Ablett pers. comm. Nov. 2011). This is 22 mm in diameter and closely resembles the figure given by Reeve (1861), though the colour pattern is not a perfect match. It seems very probable that this is the specimen referred to by Fischer-Piette and Bedoucha (1965), and

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we consider it to be the holotype of *Tropidophora secunda* (NHMUK 20110470, Fig. 7F–H). It is not clear why Fischer-Piette, after having examined the Cuming specimen illustrated by Reeve (1861) and designated it to be the type, subsequently stated for *T. secunda* 'localisation du type: ?' (Fischer-Piette *et al*. 1993).

Tropidophora sericea sp. n.

Fig. 9

Etymology: From Latin *sericeus* (silky); in reference to the silky texture of the shell.

Diagnosis: Spire very low, shell almost planorboid, body whorl not conspicuously tumescent, umbilicus very wide; columella lip weakly reflected, but not broadly expanded over umbilicus; sculpture finely decussate, comprising low, close-set spiral ridges crossed by similar axial pliculae; yellowish white with traces of fine orange-brown spiral lines.

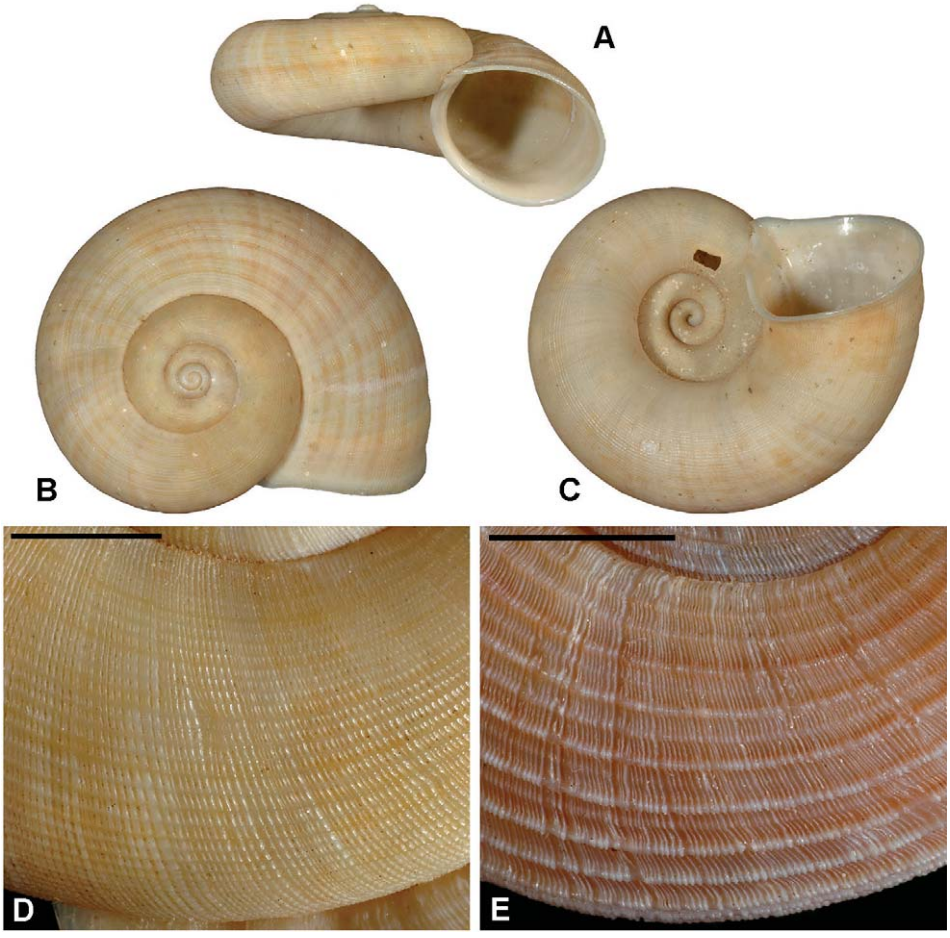

Fig. 9. *Tropidophora sericea* sp. n. and *T. chavani*: (A–C) *T. sericea*, holotype, Tsingy Beanka, max. diameter 37.3 mm, height 18.9 mm, AMS C.474166; (D, E) adult teleoconch sculpture of *T. sericea* (holotype) and *T. chavani* (NMSA L8447) respectively, scale bars = 2.5 mm.

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Description:

Shell: Medium to large, depressed-discoidal to planorboid, spire very low with little other than embryonic whorls projecting in apertural view; final part of last adult whorl descending gently prior to aperture; whorls more or less evenly rounded, suture indented; umbilicus very wide, its margin evenly rounded; underside of embryonic whorls clearly visible. Protoconch of 1¼–1½ whorls, essentially smooth, but microscopically shagreened. Teleoconch of a further 2¾–3 whorls; first whorl initially with 6 or 7 low spiral ridges increasing to double this by end of whorl; ridges crossed by numerous, close-set axial pliculae producing a finely decussate sculpture; intervals between ridges 2–3 times wider than those between pliculae; subsequent whorls with additional spiral ridges arising by intercalation, but sculpture remaining finely decussate more or less throughout, including base; spiral ridges more close-set on later whorls and sculptural interstices less axially elongate; ridges with minute granules where crossed by axial pliculae. Aperture subcircular, strongly oblique to vertical axis of shell; peristome virtually complete, somewhat angled in parietal region; aperture expanding slightly prior to lip and lip also weakly reflected.

Ground colour dirty white to yellowish buff; the freshest specimens retaining evidence of a pattern of fine orange-brown spiral lines above the periphery, that at periphery strongest; similar lines just below periphery but umbilicus and most of base lacking colour pattern.

Dimensions: Holotype, max. diameter 37.3 mm, height 18.9 mm; largest specimen, max. diameter 41.4 mm.

Holotype: MADAGASCAR: Central W Madagascar, *ca* 60 km E of Maintirano, NE of Belitsaka, central part of Tsingy Beanka, in slots and small caves above Bokarano R. gorge, next to low dry deciduous forest, 17.90517°S 44.48240°E, *ca* 215 m, 22.ix.2010, O. Griffiths & R. Randalana, st'n 09/10 (AMS C.474166).

Paratypes: Same data as holotype (NMSA L8524/T2979, 3 specimens); st'n 06/09 (AMS C.469585, 3 adult specimens); st'n 07/09 (TMAM T161, 1 adult specimen); st'n 08/09 (AMS C.469586, 9 adult specimens); st'n 08/10 (MHNP IM-2010-20083, 4 adult specimens).

Additional locality data: *Tsingy Beanka*: st'ns 06/10, 07/10, 09/12.

Distribution: A narrow-range endemic; currently known only from the central region of the Tsingy Beanka.

Habitat: Found only in subfossil form in deep slots and crevices within the tsingy, in dry deciduous forest.

Remarks: Like *T. humbug*, this species is referable to the 'groupe d'espèces du *T. deshayesiana* (Petit de la Saussaye, 1844)' of Fischer-Piette *et al*. (1993). Within this group, it is closest to *T. chavani* Fischer-Piette, 1949 (see above) in having a very low spire, relatively fine spiral sculpture and a colour pattern of narrow, brownish, spiral bands. It is, however, considerably larger than *T. chavani*, attaining as much as 41.4 mm in max. diameter (compared to 32 mm for *T. chavani*). Furthermore, its sculpture is considerably finer than that of *T. chavani*, with subequal spiral and axial elements. In *T. chavani* the axial pliculae are crisp, and much finer and more close-set than the spiral cords (compare Figs 9D and 9E). At some localities, *T. chavani* occurs in subfossil form together with *T. sericea*, but the two remain clearly distinct.

T. moulinsii (Grateloup, 1840) (Fig. 26A–C, holotype, NHMUK) and *T. thesauri* Fischer-Piette, 1949 (Fig. 26D–F), both from the north-eastern tip of Madagascar, are of a more similar size (attaining 38 mm or more in max. diameter), but *T. thesauri* has

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much deeper whorls, a higher spire, narrower umbilicus, irregular scale-like subsutural pliculae and lacks the finely decussate microsculpture of *T. sericea*. *T. moulinsii* has stronger, cord-like, spiral sculpture, more tumescent whorls and a higher spire.

Family Cerastidae Wenz, 1923
Genus *Conulinus* Martens, 1895
Conulinus randalanai sp. n.
Fig. 10

Etymology: Named for Roger Randalana, on-site manager of the Tsingy Beanka reserve and participant in many malacological expeditions throughout Madagascar.

Diagnosis: Shell bulimiform, whorls relatively elongate, body whorl comprising approx. 66% of total shell height; spire profile cyrtoconoid; columella reflected, umbilicus narrow; sculptured by microscopic axial riblets and even finer spiral threads; lustreless, mauve-brown, paler apically.

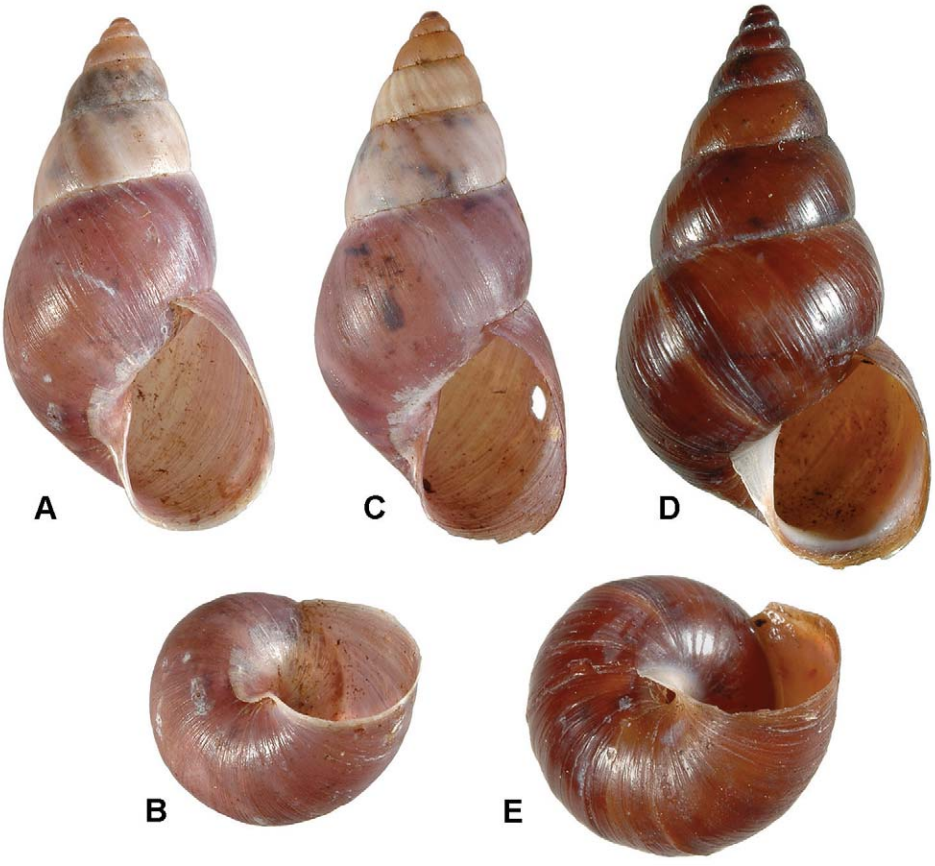

Fig. 10. *Conulinus randalanai* sp. n. and *C. rufoniger* (Reeve, 1849): (A, B) *C. randalanai*, holotype, height 16.9 mm, AMS C.469591; (C) *C. randalanai*, paratype, height 17.5 mm, NMSA L8469/T2897; (D–E) *C. rufoniger*, Diego Suarez [Antsiranana] district, 8 km south of Orangea, height 18.6 mm, NMSA L8443.

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Description:

Shell: Elongate-bulimiform, thin; body whorl comprising approx. 66% of total shell height; spire profile cyrtoconoid, suture not strongly indented; whorls weakly convex, base a little more strongly so, periphery rounded; umbilicus reduced to a narrow tube-like channel by reflected upper portion of columella lip. Protoconch of approx. 1¼ whorls, smooth. Teleoconch of a further 4¾–5 whorls; appearing smooth, but microsculptured by numerous, very fine, close-set axial riblets, and even finer microscopic spiral threads; axial riblets becoming less regular with growth and resembling fine, uneven growth-lines on last adult whorl, spiral sculpture persisting throughout and extending on to base. Aperture elongate-ovate; somewhat oblique to vertical axis of shell; peristome incomplete, simple and thin; no subterminal thickening evident inside outer lip; upper part of columella reflected and compressed against preceding whorl such that its edge is narrow (pleat-like in some specimens) and the umbilicus restricted to a very narrow, tube-like channel.

Shell somewhat lustreless rather than glossy; predominantly mauve-brown in the freshest specimens, with some axial variations in intensity particularly on middle spire whorls; paler pinkish brown to fawn apically.

Dimensions: Holotype, height 16.9 mm, max. diameter 8.5 mm; largest specimen, height 17.5 mm.

Holotype: MADAGASCAR: Central W Madagascar, *ca* 60 km E of Maintirano, E of Belitsaka, E part of Tsingy Beanka, 18.06145°S 44.52595°E, *ca* 450 m, in leaf-litter and tsingy slots in comparatively lush tall dry deciduous/evergreen forest on south-facing hill, 2.x.2006, O. Griffiths, R. Randalana, D. Herbert & L. Davis, st'n 12/06 (AMS C.469591).

Paratypes: St'n R02/10 (NMSA L8469/T2897, 1 specimen; AMS C.469584, 4 specimens; MNHN IM-2010-20069, 1 specimen).

Additional locality data: *Tsingy Beanka*: st'ns 03/10, 11/10.

Distribution: Evidently a narrow-range endemic; known only from the Tsingy Beanka.

Habitat: Fresh dead shells have been found in tall, relatively lush dry deciduous and evergreen forest. No living specimens known.

Remarks: The only comparable species known from Madagascar is *C. rufoniger* (Reeve, 1849), but that species differs in having more rounded whorls, a less elongate shape and a darker, chestnut brown colour (Fig. 7D, E). It also lacks spiral sculpture, and has a wider umbilicus and a thickened white varix inside the outer lip at maturity. *C. rufoniger* has been mostly recorded from north-eastern Madagascar (Fischer-Piette *et al*. 1994), but we can also confirm its presence at Antsingimavo (st'ns 04/06, 06/06), Tsingy Beanka (st'ns 01/09, 02/09, 09/09) and in the Tsingy de Bemaraha (Manombolo River).

In the absence of anatomical data, our referral of this species to *Conulinus* is tentative. In its shape and spiral microsculpture, *C. randalanai* also resembles some species of *Rachis* Albers, 1850, but it lacks the colour pattern of dark spots and/or spiral bands commonly seen in species of that genus. Indeed, the referral of *C. rufoniger* to *Conulinus* also requires confirmation.

Family Acavidae Pilsbry, 1895
Genus *Clavator* Martens in Albers, 1860
Clavator griffithsjonesi Emberton, 1999
Figs 11, 25D

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Clavator griffithsjonesi: Emberton 1999: 93, figs 13, 14. Type loc.: Madagascar: N Bemaraha Reserve (18°1'S 44°31'E) [= the area now known as Tsingy Beanka].

Morphological notes:

External features (Fig. 25D): Head-foot mostly greyish cream with pedal margin tinged orange-brown; dorso-lateral areas of neck yellowish, mid-dorsal region greyish; distal half of optic tentacles grey.

Distal genitalia (Fig. 11): Penis slender and cylindrical, with relatively muscular wall; apical ⅔ comprising a blind ending caecum, above insertion of epiphallus; retractor muscle inserted at apex of caecum; interior of penis with approx. 6 well-developed, longitudinal pilasters; epiphallus somewhat recurved at its insertion, opening into a deep cleft in one pilaster, near to base of penis; pilasters dividing and anastomosing somewhat in caecum. Epiphallus extremely long and convoluted, its convolutions and those of vas deferens enveloped in membranous covering of connective tissue and attached to lower spermoviduct and free oviduct; a short flagellum present at junction of vas deferens and epiphallus; interior wall of epiphallus with one large longitudinal pilaster and 6 or 7 smaller longitudinal ridges, these continue into flagellum, evanescing near its tip; vas deferens discharges into epiphallus via a pore situated on large pilaster; vas deferens passing over and down lower sperm-oviduct to its origin at base of prostate; lumen of vas deferens for the most part simple, but broadening just prior to junction with epiphallus, and inner wall with 3 longitudinal folds each with side branches. Genital atrium short and simple; bursa copulatrix duct arising after a short vagina; duct very long, of more or less even width, its wall relatively sturdy; bursa copulatrix situated just below level of albumen gland, bean-shaped with a slightly pointed apex; bursa and its duct brownish in colour. Free oviduct short.

Locality data: *Tsingy Beanka*: st'ns 11/06, 12/06, 15/06 (subfossil), 16/06, 18/06, 06/09, 07/09, 08/09 (subfossil and fresh), 09/09.

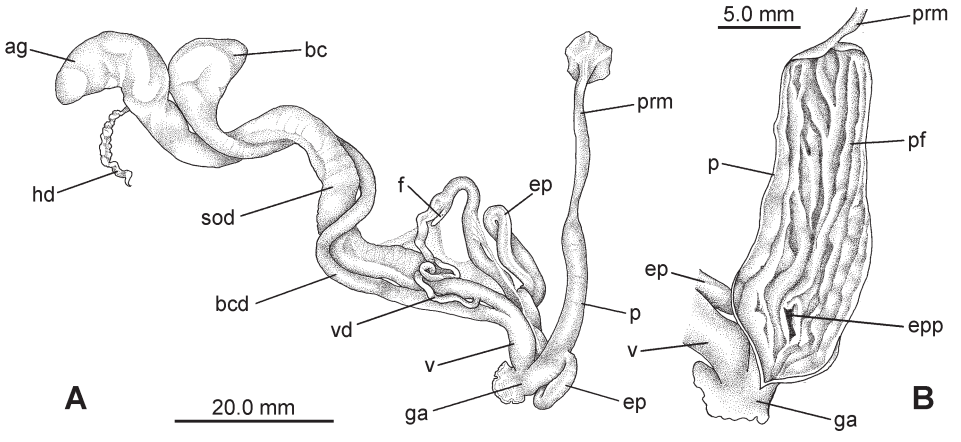

Fig. 11. *Clavator griffithsjonesi* Emberton, 1999, genitalia, NMSA L7236: (A) entire reproductive tract (minus ovotestis); (B) penis opened longitudinally to show internal folds and pore at insertion of epiphallus. Abbreviations: ag – albumen gland, bc – bursa copulatrix, bcd – bursa copulatrix duct, ep – epiphallus, epp – epiphallus pore, f – flagellum, ga – genital atrium, hd – hermaphrodite duct, p – penis, pf – folds lining penis lumen, prm – penial retractor muscle, sod – spermoviduct, v – vagina, vd – vas deferens.

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Distribution: Evidently a narrow-range endemic; not found in either the Tsingy de Bemaraha or at Antsingimavo, and currently known to occur only in the Tsingy Beanka.

Habitat: Mostly found in tall deciduous forest growing on limestone in the southern areas of Tsingy Beanka; less common as one moves north. Buries shallowly in leaf-litter during the dry season.

Remarks: A characteristic element of the Tsingy Beanka malacofauna and the only species of *Clavator* recorded from central western Madagascar.

The distal genitalia closely resemble those figured by Schileyko (1999) for *C. eximius* (Shuttleworth, 1852). Fischer-Piette *et al*. (1975) illustrated the genitalia of two further *Clavator* species, of these *C. clavator* (Petit de la Saussaye, 1844) is similar to *C. griffithsjonesi*, but it has a more slender bursa copulatrix duct. These authors did not differentiate between an epiphallus and vas deferens in *C. clavator*, neither did they report a flagellum at the junction of the epiphallus and vas deferens, but this may have been overlooked. *C. moreleti* (Deshayes, 1851) differs considerably in having a much shorter epiphallus/vas deferens that inserts just below the apex of the penis. It also has a shorter, very slender bursa copulatrix duct.

Genus *Ampelita* Beck, 1837

Ampelita andriamamonjyi sp. n.

Fig. 12

Etymology: Named for Aldus Andriamamonjy, Executive Director of Biodiversity Conservation Madagascar that manages and protects the forests of the Tsingy Beanka.

Diagnosis: Shell lenticular, periphery rounded; aperture strongly descendant; umbilical width moderate; whitish to fawn, characteristically patterned with 3 or 4 dark brown spiral bands, 1 or 2 above periphery, 2 below; sculpture of close-set, incised spiral striae; apertural rim reflected.

Description:

Shell: Medium sized, lenticular (H:D=0.489–0.586); whorls slightly flattened, periphery rounded; suture weakly indented, final part of last adult whorl descending conspicuously prior to aperture; umbilicus of moderate width, steep-sided and distinctly narrower internally. Protoconch of *ca* 1½–2¾ whorls, superficially etched in most specimens but some individuals with evidence of fine, close-set spiral threads on last whorl; junction with teleoconch usually ill-defined. Teleoconch of a further 2¼ whorls; sculptured by numerous, close-set, incised spiral striae; striae crossed by frequent fine, irregular growth-lines rendering the former wavy; basal sculpture similar, but weakening at umbilical rim and evanescing within. Aperture elongate-ovate, strongly oblique to vertical axis of shell; peristome incomplete, interrupted in parietal region, elsewhere its rim reflected, forming a flaring lip.

Shell somewhat glossy; embryonic whorls buffish brown, slightly darker below suture; first teleoconch whorl with two dark brown spiral bands, lower one broad, situated just above abapical suture, the other narrower, lying a short distance below adapical suture; interval between upper brown band and suture almost white; upper brown band usually fading and disappearing with growth (sometimes within first half whorl), but persisting throughout in some individuals; ground colour becoming paler with growth, a rather

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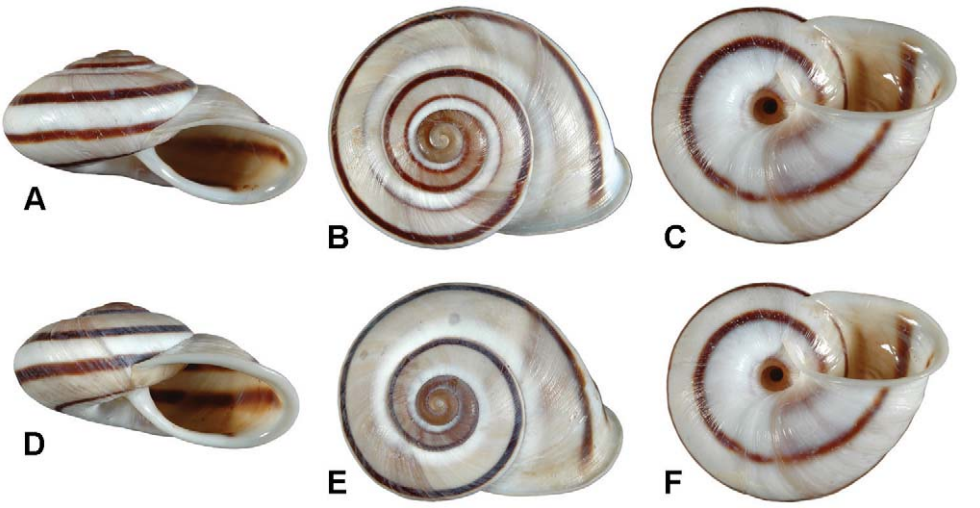

Fig. 12. *Ampelita andriamamonjyi* sp. n.: (A–C) holotype, max. diameter 29.3 mm, height 15.1 mm, AMS C.474164; (D–F) paratype, max. diameter 27.7 mm, height 14.5 mm, NMSA L8441/T2657.

uneven dirty white on last adult whorl; base with two further dark brown spiral bands, one just below periphery (emerging close to insertion of outer lip), the other midway between this and umbilical rim; ground colour between supra- and sub-peripheral brown lines paler, almost white; pale subsutural zone persisting throughout. Aperture lip white, colour bands clearly visible internally.

Dimensions: Holotype (largest specimen), max. diameter 29.3 mm, height 15.1 mm.

Holotype: MADAGASCAR: Central W Madagascar, *ca* 60 km E of Maintirano, southern part of Tsingy Beanka, S side of Tana–Maintirano road, in tall moist forest growing on limestone on south-facing slopes, above N bank of Kimanambolo River, 18.06178°S 44.52494°E, *ca* 330 m, iv.2010, R. Randalana, st'n R02/10 (AMS C.474164).

Paratypes: Same data as holotype (TMAM T162, 1 adult specimen); st'n R03/98 (NMSA L8441/T2657, 2 adult specimens); st'n 04/06 (AMS C.469582, 1 adult specimen); st'n 16/06 (NMSA L7128/T2656, 1 sub-adult specimen); st'n R04/09 (MNHN IM-2010-20070, 1 adult specimen); st'n R01/10 (AMS C.469581, 3 adult specimens).

Additional locality data: *Tsingy Beanka*: st'ns 13/06, 16/06, 02/09, 08/09 (subfossil), R04/09, R01/10.

Distribution: Fresh material has been found only in the Tsingy Beanka. A single subfossil shell is known from Antsingimavo, but the species is now perhaps extinct there. Not recorded from the Tsingy de Bemaraha.

Habitat: Fresh dead shells found most commonly in and amongst limestone rocks, predominantly in the taller moister forests of the southern part of Tsingy Beanka. Not yet found alive.

Remarks: Compared to other spirally banded *Ampelita* species, the banding pattern of *A. andriamamonjyi* is distinctive. *A. akoratsara* Emberton, 1999 (from Marojejy in far north-eastern Madagascar) has a somewhat similar pattern of dark brown spiral lines with whitish subsutural and peripheral bands, but it has a sharply keeled body whorl and lacks the mid-basal brown spiral band of *A. andriamamonjyi*. Unlikely to be confused with any other known *Ampelita* species.

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Ampelita decaryi Fischer-Piette, 1952

Fig. 13

Ampelita decaryi: Fischer-Piette 1952: 13, pl. 1, figs 7–9; Emberton 1990: fig. 4d, 1994: 176; Fischer-Piette *et al*. 1994: 97, pl. 7, figs 4–16. Type loc.: Madagascar.

Locality data: *Antsingimavo*: st'n 04/06. *Kelifely Plateau*: st'ns 08/05, 10/05. *Tsingy de Bemaraha*: st'n 15/96.

Distribution: Restricted to central western Madagascar; currently recorded only from Tsingy de Bemaraha and Antsingimavo. Not yet recorded from Tsingy Beanka, but known in subfossil form from the Kelifely Plateau. A record from the Ambositra area (Emberton 1994) almost certainly represents *A. caderyi* (see below).

Habitat: Dry mixed deciduous-evergreen forest on karst outcrops. No living specimens found, but considerable numbers of empty shells were collected from slots within the tsingy and under overhangs.

Remarks: The holotype of this species had no provenance beyond 'Madagascar', but Fischer-Piette (1952) mentioned a young individual from 'Antsingy (Madagascar Ouest)'. Emberton (1990) and Fischer-Piette *et al*. (1994) placed this locality in the region of Tsingy de Bemaraha and additional material has since been found there (Griffiths, st'n 15/96). Emberton (1994) also identified under this name specimens from non-calcareous, rain forest habitats in the Ambositra area (Fianarantsoa Province). However, in reality this latter material is more probably referable to *A. caderyi* Fischer-Piette *et al*., 1994, the type locality for which lies in the same vicinity. Although they are undoubtedly similar, the differences between the two taxa were clearly stated by Fischer-Piette *et al.* (1994).

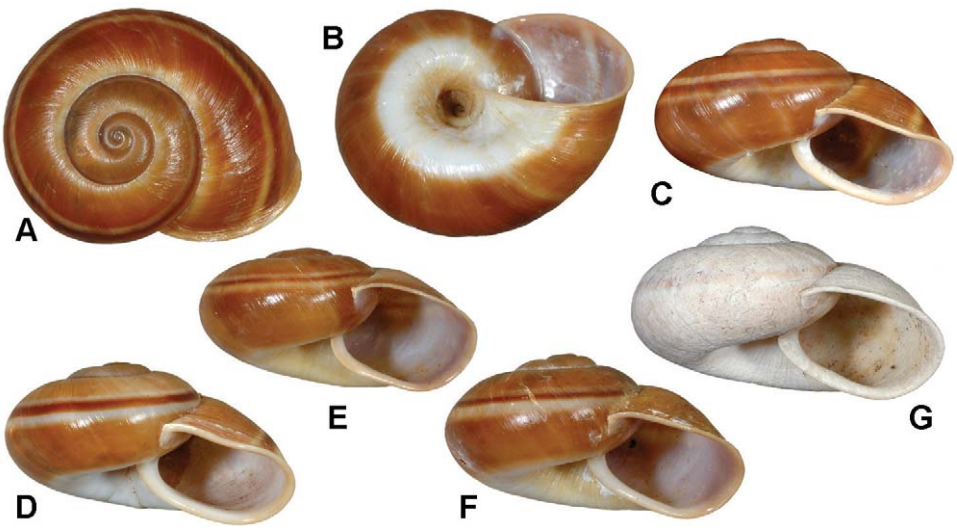

Fig. 13. *Ampelita decaryi* Fischer-Piette, 1952: (A–C) typical specimen, max. diameter 40.7 mm; (D–F) specimens showing variation in shell proportions and in relative width of supra-peripheral spiral bands [max. diameter: D, 39.4 mm; E, 38.0 mm; F, 40.9 mm]; (G) subfossil, max. diameter 43.0 mm. (A–F) Antsingimavo, st'n 04/06, NMSA L7090; (G) Kasijy Forest, Kelifely Plateau, st'n 08/05, NMSA L7010.

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In terms of shape and coloration, the Antsingimavo material closely resembles the holotype of *A. decaryi* figured by Fischer-Piette (1952). However, whilst some adult shells in the Antsingimavo population match the holotype in size (max. diameter 35 mm), most are somewhat larger (max. diameter reaching 42 mm). The abundance of empty shells indicates that the species was once not uncommon at this locality. Though much of this material is clearly old, some specimens were of fresh appearance and retained the periostracum, indicating that the species is probably still extant at the site, even though we found no live specimens during our survey. Subfossil shells from the Kelifely Plateau (Fig. 13G) are indistinguishable from the Antsingimavo material, except that the colour pattern is much faded.

Ampelita (Eurystyla) griffithsi Emberton, 1999

Ampelita (Eurystyla) griffithsi: Emberton 1999: 91, figs 11, 12.

Locality data: *Tsingy Beanka*: st'n R01/11.

Distribution: Previously known from Kirindy (near Morondava) and the southern and central areas of the Tsingy de Bemaraha. Now known also from the southern Tsingy Beanka.

Habitat: Deciduous scrub, semi-deciduous forest and riverine gallery forest (Emberton 1999).

Remarks: The occurrence of *A. griffithsi* in riverine forest along the Namela River on the southern boundary of Tsingy Beanka Reserve represents a considerable northern range extension for the species.

Ampelita lindae sp. n.

Fig. 14

Etymology: Named for Linda Davis, manager of the Mollusca collection at the KwaZulu-Natal Museum and one of the members of the team that discovered this species.

Diagnosis: Shell discoidal, spire flat or nearly so, periphery rounded; aperture strongly descendant with reflected rim; umbilicus wide; surface rough, sculptured by raised collabral vermiform granules; lustreless, mid-brown with whitish, flake-like markings and a pale peri-umbilical band.

Description:

Shell: Medium sized, relatively thin, discoidal with very low spire (H:D=0.357–0.485); periphery at or just above mid-whorl, rounded or weakly angled; a very weak supra-peripheral gutter evident in occasional individuals, particularly near start of last whorl; suture indented, final part of last adult whorl descending steeply prior to aperture; umbilicus wide, funnel-shaped. Protoconch of *ca* 1¼–1½ whorls, the first smooth, thereafter with numerous, irregular, axially elongate granules; junction with teleoconch ill-defined. Teleoconch of a further 2½ whorls; with irregular growth-lines and an uneven sculpture of raised vermiform granules, in a primarily collabral alignment (Fig. 14D); surface thus rendered rough to the touch; granules not simply periostracal, but present on underlying shell; this sculpture continues onto base and into umbilicus. Aperture elongate-ovate, strongly oblique to vertical axis of shell; peristome incomplete, interrupted in parietal region; rim of peristome reflected forming a flaring lip.

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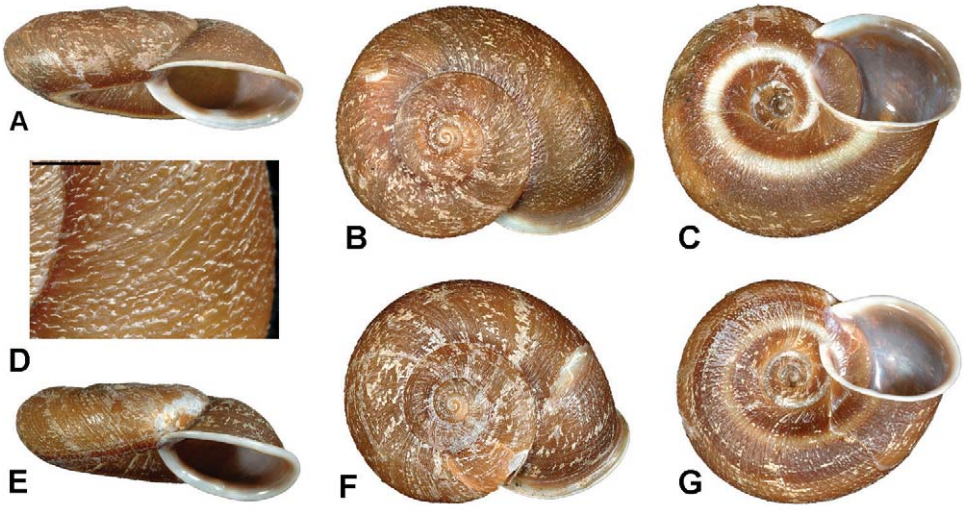

Fig. 14. *Ampelita lindae* sp. n.: (A–C) holotype, max. diameter 30.5 mm, height 12.6 mm, AMS C.474167; (D) holotype, microsculpture one quarter whorl prior to outer lip, scale bar = 2.5 mm; (E–G) paratype, max. diameter 29.0 mm, height 12.0 mm, NMSA L8468/T2903.

Shell lustreless, covered with a predominantly mid-brown periostracum when fresh, with irregular, pale, flake-like markings; underlying shell mostly pale with darker brownish spiral bands either side of a pale, peri-umbilical band; sometimes also darker behind flared aperture lip. Aperture lip white, interior greyish brown in fresh material.

Dimensions: Holotype, max. diameter 30.5 mm, height 12.6 mm; largest specimen, max. diameter 31.4 mm, height 12.7 mm.

Holotype: MADAGASCAR: Central W Madagascar, *ca* 10 km NE of Belitsaka and *ca* 60 km E of Maintirano, E side of Tsingy Beanka, in leaf-litter and amongst limestone boulders in tall moist east-facing forest growing on limestone, above Bokarano River Cave, 17.90568°S 44.48822°E, *ca* 230 m, 29.x.2009, O. Griffiths, D. Herbert, L. Davis & R. Randalana, st'n 07/09 (AMS C.474167).

Paratypes: Same data as holotype (NMSA L8468/T2903, 1 adult specimen); st'n 07/10 (AMS C.469580, 3 adult specimens); st'n 09/10 (AMS C.469579, 1 adult specimen); st'n 07/10 (TMAM T163, 1 adult specimen).

Distribution: Evidently a narrow-range endemic, currently known only from Tsingy Beanka; not yet known from either Tsingy de Bemaraha or Antsingimavo.

Habitat: Known only from fresh dead shells collected in leaf-litter in tall, east-facing, evergreen forest in the central part of Tsingy Beanka.

Remarks: With its relatively small, very depressed shell and rough, vermiform microsculpture, *A. lindae* is a distinctive species. *A. granulosa* (Deshayes, 1840) (from the north-eastern tip of Madagascar), another species with coarse microsculpture, is much larger and has distinct periostracal bristles arising from the granules, a feature not evident in the present species.

Additional material resembling *A. lindae* has been found as subfossils in the Kasijy Forest (Kelifely Plateau). These are larger (max. diameter 32.9–35.0 mm, height 15.3–17.9 mm) than the present material but are clearly morphologically close to it. The material available, however, is inadequate to permit thorough study and meaningful comparison.

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Ampelita beanka sp. n.

Figs 15, 16, 17A, 17B

Etymology: Named after the type locality, Tsingy Beanka.

Diagnosis: Profile distinctive due to low spire, strongly shouldered whorls and descendant suture; umbilicus wide; protoconch with close-set axial riblets; teleoconch with close-set lamellate axial pliculae; lustreless, more or less uniformly mid to dark brown.

Description:

Shell: Relatively small with sharply angled periphery situated well above mid-whorl; spire very low, frequently almost flat; apical surface of whorls weakly convex, becoming slightly concave toward periphery; suture shallowly indented, but progressively descending below peripheral keel on last adult whorl giving shell a stepped profile; umbilicus wide, its rim roundly angular. Protoconch of 1¼–1½ whorls, max. diameter variable 3.7–4.1 mm; initially smooth, rather flat and somewhat sunken, thereafter more convex, bearing numerous, close-set, curved, axial riblets; riblets occasionally bifurcating or anastomosing (Fig. 17A). Teleoconch of a further 2–2¼ whorls; sculptured by close-set, axial pliculae, each with a thin periostracal crest in living specimens, rendering the pliculae somewhat lamellate (Fig. 17B); growth irregularities frequent; basal sculpture the same, continuing into umbilicus. Aperture rounded basally, somewhat angled at periphery and flattened above this; strongly oblique to vertical axis of shell; peristome incomplete, interrupted in parietal region; rim of peristome slightly thickened and flaring in adult, more strongly so basally.

Shell lustreless with a well-developed, predominantly mid to dark brown periostracum when fresh; slight radial unevenness in intensity; apical whorls often slightly paler; umbilicus commonly darker internally, its margin sometimes delineated by a paler band, but this rarely evident in fresh material.

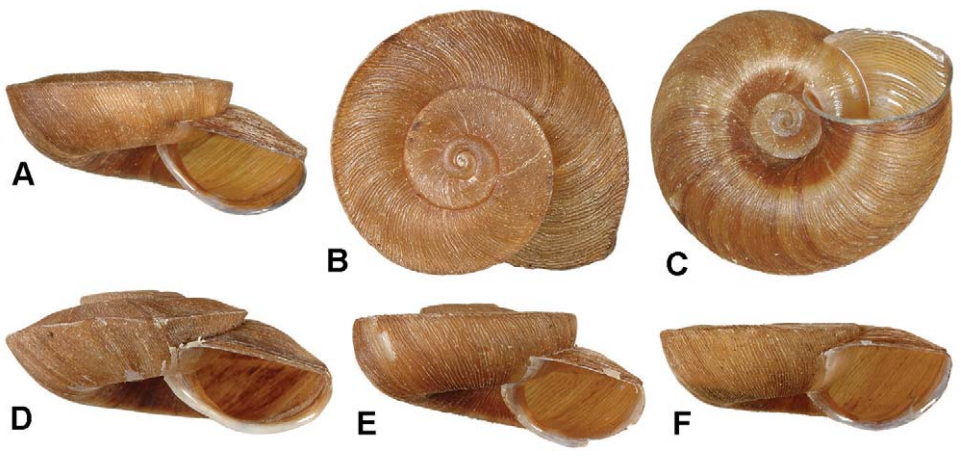

Fig. 15. *Ampelita beanka* sp. n.: (A–C) holotype, max. diameter 17.7 mm, height 8.0 mm, AMS C.474166; (D) specimen with less strongly shouldered whorls, max. diameter 19.1 mm, st'n 07/09, paratype, NMSA L8501/T2981; (E–F) specimens of the same size and collected from the same station R01/09, showing the differing extent to which the suture descends below the shoulder, max. diameter 17.1 mm, paratypes, NMSA L8507/T2982.

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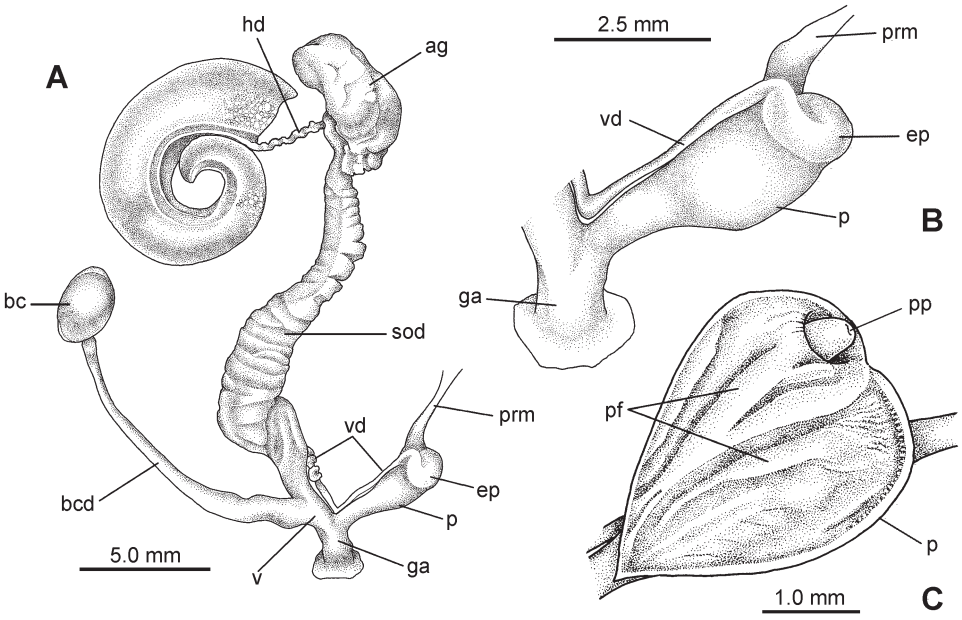

Fig. 16. *Ampelita beanka* sp. n., genitalia, paratype, NMSA L8504/T2983: (A) entire reproductive tract; (B) external view of penial complex; (C) penis opened longitudinally to show internal folds and raised papilla at insertion of epiphallus. Abbreviations: ag – albumen gland, bc – bursa copulatrix, bcd – bursa copulatrix duct, ep – epiphallus, ga – genital atrium, hd – hermaphrodite duct, p – penis, pf – folds lining penis lumen, pp – penis papilla, prm – penial retractor muscle, sod – spermoviduct, v – vagina, vd – vas deferens.

Dimensions: Holotype, max. diameter 17.7 mm, height 8.0 mm; largest specimen, max. diameter 19.1 mm.

External features: Data on coloration of living animals not available; in preserved specimens head-foot mostly dark brown to blackish, but with evidence of a paler longitudinal band extending down neck from each optic tentacle; skin texture uniformly granular; lining of mantle cavity heavily pigmented with black and patterned with pale circular blotches, mostly on the right (upper) side.

Distal genitalia (Fig. 16): Relatively simple and largely typical of the genus. Penis short to moderate in length (4.0–5.0 mm) and rather stout; vas deferens running beside and loosely attached to its basal portion, but becoming more closely attached near penis apex; at apex of penis vas deferens turns sharply back on itself and broadens noticeably before inserting some distance below penis apex; this latter portion, perhaps constituting an epiphallus, has a thicker, pale flesh-coloured wall and is fused to outer wall of penis. Penis retractor muscle attaches apically, enveloping recurved portion of vas deferens and penis apex. Interior of penis with a Y-shaped longitudinal fold in the centre of which is a distinct, rounded papilla at insertion of epiphallus; this primary fold bordered on each side by a further longitudinal fold; remainder of lumen largely smooth, but with evidence of microscopic papillation in apical region. Genital atrium and vagina, simple and short; bursa copulatrix duct long, basal portion somewhat broader; bursa itself of moderate size, ovate to subcircular.

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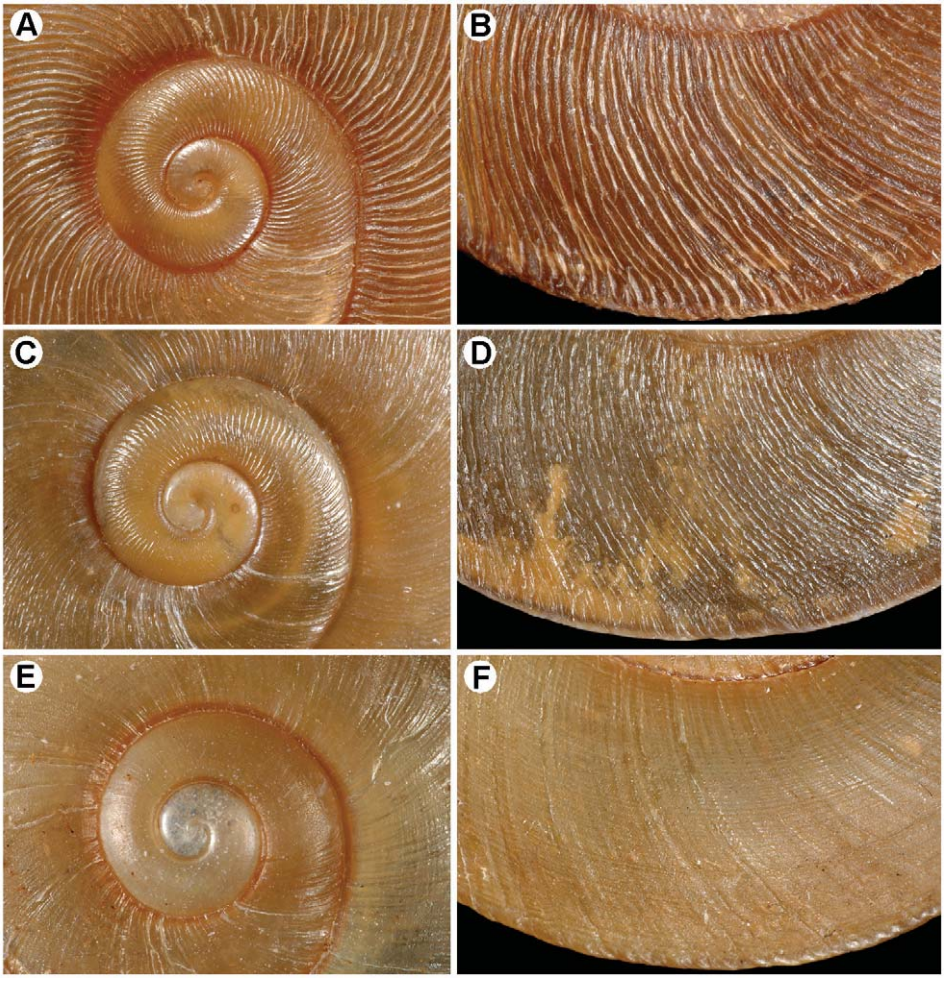

Fig. 17. *Ampelita beanka* sp. n., *A. milloti* Fischer-Piette, 1952 and *A. namerokoensis* Fischer-Piette, 1952, protoconch morphology and teleoconch microsculpture: (A, B) *A. beanka*, protoconch diameter 4.1 mm, st'n R04/09, respectively paratype, NMSA L8504/T2983, and holotype, AMS C.474166; (C, D) *A. milloti*, protoconch diameter 4.4 mm, both st'n 07/09, NMSA L8502; (E, F) *A. namerokoensis*, protoconch diameter 3.5 mm, respectively st'n 18/06, NMSA L8439, and st'n 03/06, NMSA L7038.

Holotype: MADAGASCAR: Central W Madagascar, *ca* 60 km E of Maintirano, in tall dense dry forest growing above cliffs on E side of Tsingy Beanka at Andohanandranogedro, 18.05028°S 44.53786°E, 380 m, iv.2009, R. Randalana, st'n R04/09 (AMS C.474166, body in alcohol).

Paratypes: Same data as holotype (NMSA L8504/T2983, 9 specimens, bodies in alcohol; NHMUK 20120014, 1 specimen); st'n 07/10 (NMSA L8525/T2980, 6 specimens); st'n 07/09 (NMSA L8501/T2981, 4 specimens, one in alcohol); st'n R01/09 (NMSA L8507/T2982, 2 specimens); st'n 01/10 (AMS C.469583, 4 specimens; TMAM T165, 1 specimen); st'n 09/09 (MNHN IM-2010-20071, 1 specimen).

Additional locality data: *Tsingy Beanka*: st'ns 11/06, 09/09, 01/10.

Distribution: A narrow-range endemic currently recorded only from Tsingy Beanka.

Habitat. Fresh dead shells found most commonly in and amongst limestone rocks predominantly in the taller moister forests. Living individuals usually found in leaf-litter.

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Remarks: In terms of its shape and coloration, *A. beanka* resembles *A. milloti* and *A. namerokoensis* (below), both of which occur in the Bemaraha-Beanka region. *A. namerokoensis* differs in lacking significant axial sculpture on the protoconch and in having distinct spiral microsculpture on the teleoconch (Fig. 17E, F). It also attains a larger size, has the peripheral keel closer to mid-whorl, has a somewhat narrower umbilicus, and the suture, if descendant at all, is at most weakly so and then only near the end of the last adult whorl.

Ampelita milloti is perhaps more similar in having axial riblets on the protoconch and lacking spiral microsculpture, but its teleoconch sculpture is finer, the axial elements more irregular and fragmented, appearing granular rather than lamellate (particularly evident on the base). Furthermore, as in *A. namerokoensis*, the suture of *A. milloti* is never strongly descendant. The smaller size, shouldered profile, strongly descendant suture and lamellate axial sculpture of *A. beanka* render it distinctive. The descent of the suture below the peripheral keel, though characteristic of the species and well developed in the holotype, is somewhat variable in its extent, but usually commences at least one half whorl prior to the aperture. The position of the peripheral keel is also somewhat variable, lying closer to mid-whorl in some specimens (Fig. 15D).

We have considered the possibility that these differences may reflect ecological factors and that the stepped profile may result from damage to the mantle edge at the suture, as is evident in some specimens of both *A. milloti* and *A. namerokoensis*. However, the stepped profile of *A. beanka* is present in specimens showing no growth scars indicative of earlier damage to the outer lip, and we can consistently discriminate between *A. beanka* and the other two species in terms of the microsculptural differences detailed above. There are also significant differences evident in the morphology of the penis (see below). All three species occur in the Tsingy Beanka and have been found to co-occur at a number of sampling sites. Emberton (1999) described a similar lamellar axial microsculpture in *A. analamerae* Emberton, 1999, from far north-eastern Madagascar, but that species is larger, is keeled at mid-whorl and has a much more prominent spire and narrower umbilicus.

Ampelita milloti Fischer-Piette, 1952

Figs 17C, 17D, 18, 25E

Ampelita milloti: Fischer-Piette 1952: 34, pl. 3, figs 31–34; Fischer-Piette *et al*. 1994: 123, pl. 15, figs 1–4. Type loc.: 'Gorge de Salapango [= Salapanga], Bemaraha', Madagascar.

Morphological notes:

External features (Fig. 25E): Head-foot uniformly dark, charcoal-grey to black; skin texture uniformly granular throughout; lining of mantle cavity heavily pigmented with black and patterned with pale circular blotches (observations based on a single live-collected individual).

Distal genitalia: The single preserved specimen available (shell diameter 19.2 mm) possessed an immature reproductive tract. The distal genitalia were thus poorly developed and inadequate for comparative study. From what could be seen of the penis, it appeared similar to that of *A. namerokoensis*.

Locality data: *Antsingimavo*: st'ns 4/06, 8/06 (all subfossil). *Tsingy Beanka*: st'ns 12/06, 14/06, 16/06, 18/06, 02/09, 06/09, 07/09, 08/09, 01/10, 06/10, 07/10, 08/10, 09/10. *Tsingy de Bemaraha*: st'ns 07/95, 10/95, 14/95, 18/95, 19/95, 9/96, 10/96, 12/96. *South bank of Tsiribihina River*: st'ns 01/99LP, 02/99LP.

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Fig. 18. *Ampelita milloti* Fischer-Piette, 1952, Tsingy Beanka, st'n 16/06, max. diameter 24.8 mm, NMSA L7127.

Distribution: Evidently a narrowly endemic species, currently known only from the south bank of Tsiribihina River, Tsingy de Bemaraha and Tsingy Beanka. Subfossil at Antsingimavo where it now appears to be locally extinct.

Habitat: Living specimens are most commonly found amongst limestone rocks and in leaf-litter. In Tsingy Beanka, it occurs predominantly in the taller, moister forests of the southern part.

Remarks: Shell lenticular, of moderate size (max. diameter <33 mm), with a very low spire and sharply angled periphery; last whorl descending at most slightly just prior to aperture; uniformly tan-brown with a yellow to white band around umbilicus. Specimens from Tsingy Beanka are noticeably smaller than those from Bemaraha and Antsingimavo (maximum adult diameter 20–25 *vs* 28–32 mm).

Resembles *A. namerokoensis* (below) in size and shape, but easily separated from that species due to the almost complete absence of microscopic spiral striae (some traces may be visible on the base). Instead the microsculpture of *A. milloti* comprises irregular, elongate granules aligned in a roughly radial (collabral) pattern (Fig. 17D). Furthermore, *A. milloti* attains a somewhat larger size and has a wider umbilicus than *A. namerokoensis*, and its protoconch is larger (diameter approx. 4.4 *vs* approx. 3.5 mm) and bears distinct close-set axial riblets (Fig. 17C), whereas that of *A. namerokoensis* is more or less smooth (Fig. 17E). Features separating *A. milloti* from *A. beanka* are discussed above.

Ampelita namerokoensis Fischer-Piette, 1952

Figs 17E, 17F, 19, 20, 25F

Ampelita namerokoensis: Fischer-Piette 1952: 35, pl. 3, figs 35–39; Fischer-Piette *et al*. 1994: 123, pl. 15, figs 5–8. Type loc.: 'Gorges de Salapango [= Salapanga], Bemaraha', Madagascar.

Morphological notes:

External features (Fig. 25F): Head-foot mostly dark grey-brown with uniformly granular skin texture; optic tentacles slightly paler, running into similarly pale bands along neck; skin granules with microscopic ochre-brown pigment granules; lining of mantle cavity with some black pigmentation (not dense) and a pattern of pale circular blotches.

Distal genitalia (Fig. 20): Resembling those of *A. beanka*, but differing considerably in penis morphology, particularly its internal structure. Penis shorter (*ca* 3.2 mm) and

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Fig. 19. *Ampelita namerokoensis* Fischer-Piette, 1952: (A–C) typical specimen, Tsingy Beanka, st'n 07/09, max. diameter 22.1 mm, NMSA L8445; (D) depressed specimen, Tsingy Beanka, st'n 12/06, max. diameter 23.1 mm, NMSA L8440.

more slender than in *A. beanka*, and the apical region less swollen; vas deferens follows a similar path alongside penis, running to its apex and then recurving before inserting subterminally via a short, somewhat broader, pale flesh-coloured epiphallus; details of recurved vas deferens and epiphallus mostly concealed by attachment of retractor muscle. Interior of penis with a small conical papilla at insertion of epiphallus, from which a single mid-line fold runs to penis base; additional concentric folds surround papilla on both sides, these converging and evanescing toward penis base; the resultant pattern of folds differing considerably from that of *A. beanka*.

Locality data: *Tsingy Beanka*: st'ns 03/06, 11/06, 12/06, 14/06, 16/06, 18/06, 02/09, 06/09, 07/09, 08/09, 09/09, 11/09, 01/10, 02/10, 05/10, 07/10, 08/10, 09/10, 10/10. *Bemaraha*: st'ns 14/95, 09/96, 12/96.

Distribution: Restricted to central western Madagascar, with reliable records only from the Tsingy de Bemaraha and Tsingy Beanka; not found at Antsingimavo and, despite its name, evidently does not occur in Nameroko [Namoroka] (see Remarks below).

Habitat: Living specimens are found most commonly amongst limestone rocks and in leaf-litter. In Tsingy Beanka, it occurs mostly in the southern region, in taller, moister forests.

Remarks: Shell lenticular, of moderate size (max. diameter <26 mm, but rarely more than 23 mm), carinate at periphery; uniformly light brown when fresh, with a pale yellowish band around the umbilicus. Protoconch essentially smooth (Fig. 17E), but sometimes with microscopic traces of oblique, close-set striae on last embryonic whorl, forming an extremely fine criss-cross pattern. Teleoconch with fine spiral sculpture (Fig. 17F).

The choice of name for this species is puzzling since the type locality [Salapanga] is in the Tsingy de Bemaraha. Fischer-Piette (1952) mentioned material from Ambongo (collected by G. Petit and H. Perrier de la Bâthie), which he equated with the 'Tsingy de Nameroko'. Elsewhere, however, Fischer-Piette and Bedoucha (1965: 62) stated that Salapanga [known to be in the Bemaraha] was also in the Ambongo region, suggesting in this case that Ambongo equates with Bemaraha. In line with this, S. Goodman (pers. comm. 2010), confirmed that Ambongo has been used for both Bemaraha and Namoroka. There is therefore some doubt regarding the occurrence of this species in Namoroka and despite survey work (Griffiths in 1997 and Emberton in 2007), no specimens have been found there.

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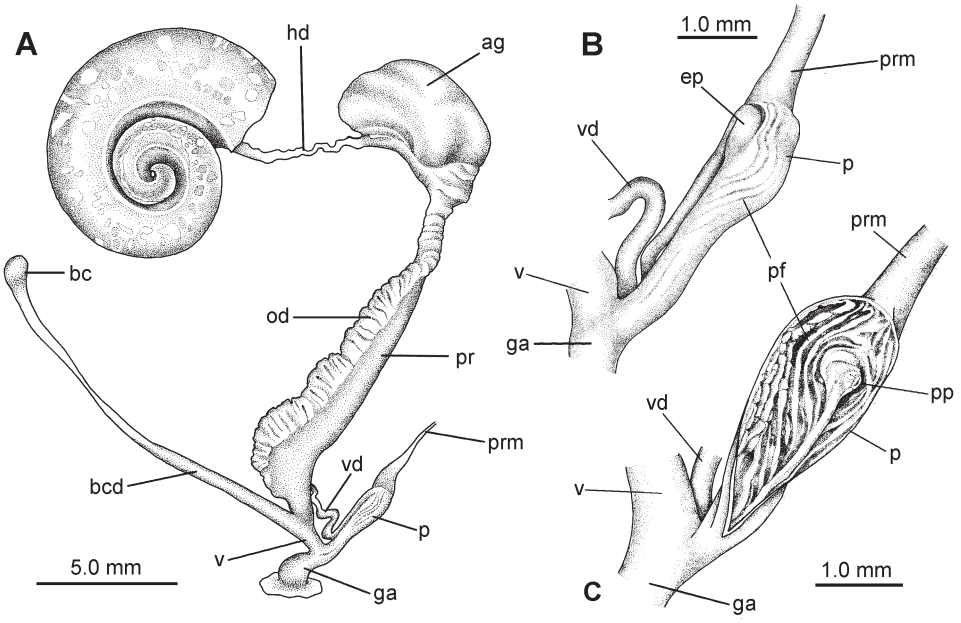

Fig. 20. *Ampelita namerokoensis* Fischer-Piette, 1952, genitalia, NMSA L8442: (A) entire reproductive tract; (B) external view of penial complex; (C) penis opened longitudinally to show internal folds and raised papilla at insertion of epiphallus. Abbreviations: ag – albumen gland, bc – bursa copulatrix, bcd – bursa copulatrix duct, ep – epiphallus, ga – genital atrium, hd – hermaphrodite duct, od – oviduct, p – penis, pf – folds lining penis lumen, pp – penis papilla, pr – prostate, prm – penial retractor muscle, v – vagina, vd – vas deferens.

Additional material from the Kelifely Plateau (st'ns 06/05, 10/05) resembles this species in having spiral sculpture, but the protoconch is sculptured with distinct axial riblets like that of *A. milloti*. At this stage its identity remains puzzling. Further subfossil or very old dead specimens from limestone caves in the Anjajavy–Narinda area, north-east of Mahajanga (Griffiths pers. observ.) may also be referable here.

Family Helicarionidae Bourguignat, 1877
Genus *Bathia* Robson, 1914
Bathia madagascariensis Robson, 1914

Fig. 21

Bathia madagascariensis: Robson 1914: 383, pl. 35, figs 11–13; Fischer-Piette *et al*. 1966: 11; 1994: 203, text-fig. 94, pl. 31, figs 10–12; Schileyko 2002: 1242, fig. 1633. Type loc.: 'Namoroku (Ambongo)' [= Namoroka].

Locality data: *Namoroka*: st'n 930/97. *Tsingy Beanka*: st'ns 03/12, 06/12.

Distribution: Recorded only from the Tsingy de Namoroka Strict Nature Reserve and Tsingy Beanka in north-western Madagascar.

Habitat: Dry deciduous forest on limestone; dead shells have been found reasonably commonly at two sites in the southern part of Tsingy Beanka, in a cave and under overhangs. The snail occurs in similar conditions at Namoroka.

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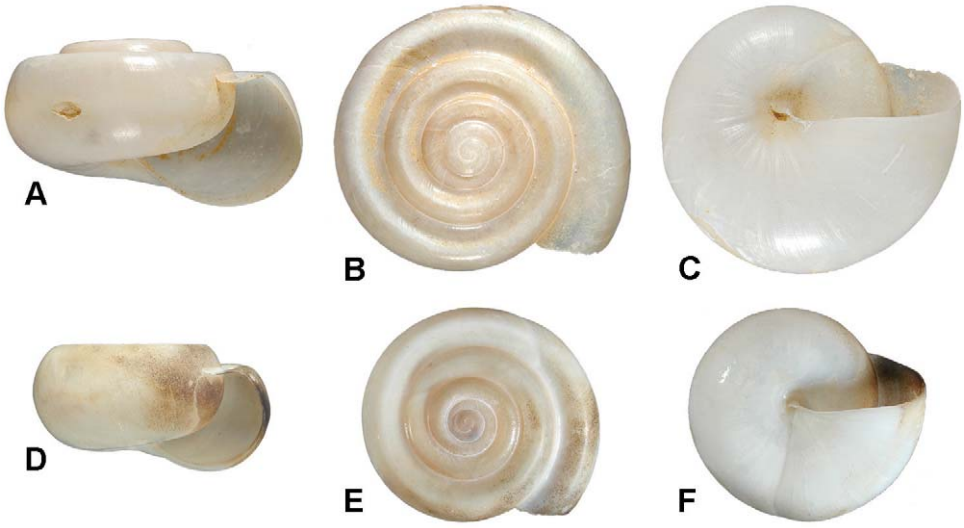

Fig. 21. *Bathia madagascariensis* Robson, 1914: (A–C) Tsingy Beanka, st'n 03/12, max. diameter 24.4 mm, NMSA L8829; (D) Tsingy de Namoroka, st'n 930/97, max. diameter 19.5 mm, NMSA L8828.

Remarks: *Bathia madagascariensis* was previously known only from the Namoroka Reserve, which lies approx. 180 km to the north-east of Tsingy Beanka. The present record of its occurrence in Tsingy Beanka represents a considerable southward range extension. Although only dead shells were found at this locality, some of these are fresh, indicating that the species is almost certainly still extant there.

Specimens from Tsingy Beanka attain a larger size than those at Namoroka (max. height 12.9 mm, max. diameter 25.5 *vs* 10.5 mm and 19.5 mm respectively at Namoroka). Furthermore, in Tsingy Beanka material the spire whorls are raised above the final whorl, but are level with it in Namoroka specimens (compare Figs 21A and 21D). In the absence of evidence to suggest otherwise, we consider these differences to reflect geographical variation. As noted by Fischer-Piette *et al*. (1966) and Schileyko (2002), determination of the true affinities of this species must await morphological examination of the soft parts. Its placement in the Helicarionidae follows Fischer-Piette *et al*. (1994), but must be considered provisional.

Family Ariophantidae Godwin-Austen, 1888
Genus *Kalidos* Gude, 1911
Kalidos griffithshauchleri Emberton, 2002

Figs 22, 25G

Kalidos griffithshauchleri: Emberton 2002: 259, fig. 1. Type loc.: 15 km E Antsalova, nr Tsingy de Bemaraha.

Morphological notes:

External features (Fig. 25G): Head-foot grey, with pale grey tubercles clearly delineated by dark grey skin grooves; lateral pedal grooves and peripodial groove distinct; caudal pit well developed but caudal horn not prominent; mantle lobes pale grey, minutely specked with darker spots.

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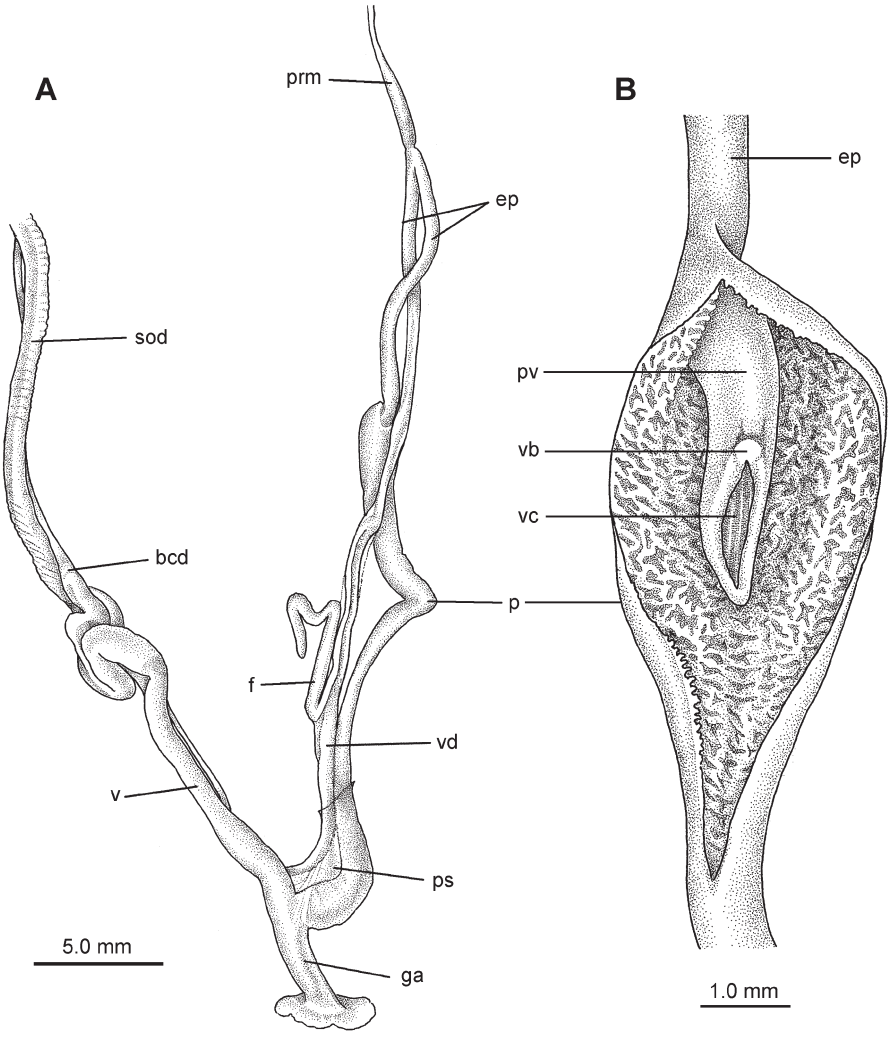

Fig. 22. *Kalidos griffithshauchleri* Emberton, 2002, genitalia, NMSA L7191: (A) lower portion of reproductive tract – gonad, albumen gland and bursa copulatrix missing; (B) upper part of penis, opened longitudinally to show well-developed penial verge extending from epiphallus. Abbreviations: bcd – bursa copulatrix duct, ep – epiphallus, f – flagellum, ga – genital atrium, p – penis, ps – penis sheath, pv – penial verge, prm – penial retractor muscle, sod – sperm-oviduct, v – vagina, vb – boss on penial verge, vc – cleft in penial verge, vd – vas deferens.

Distal genitalia (Fig. 22): The largest preserved specimen available (shell diameter 54 mm) proved to have a subadult or inactive reproductive tract. The organs of the distal tract were clearly differentiated, but the sperm-oviduct was immature or inactive. We illustrate the features observed, but caution that this may not truly reflect the mature condition.

Penis long (*ca* 21 mm) and slender, surrounded basally by a thin sheath; proximal end slightly swollen prior to junction with very long, slender epiphallus; internally

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this swollen region with a well-developed penial verge extending from insertion of epiphallus; verge digitiform, the distal third with a longitudinal cleft through which epiphallus discharges; hind end of cleft preceded by a raised boss; inner lining of penis comprising a mosaic of irregularly shaped pits; epiphallus with a sharp bend at insertion of penial retractor muscle and thus divided into proximal and distal limbs; proximal limb somewhat longer than distal one; a long narrow flagellum arises at junction of vas deferens and epiphallus; basal part of flagellum running close to vas deferens and both embedded in membranous sheath; apical half of flagellum free and sinuous; vas deferens continues beside penis and inside its basal sheath before recurving and running beside vagina; vagina long, its proximal end convoluted before insertion of bursa copulatrix duct; bursa duct, somewhat broader basally, but narrowing alongside sperm-oviduct. Sperm-oviduct poorly developed. Bursa copulatrix and proximal portions of reproductive tract missing.

Locality data: *Tsingy Beanka*: st'ns 03/06, 12/06, 14/06, 16/06, 17/06, 18/06, 02/09, 05/09, 06/09, 07/09, 08/09, 09/09, 01/10, 07/10. *Tsingy de Bemaraha*: st'ns 07/95, 18/95, 10/96, 12/06.

Distribution: A regional endemic; known only from Tsingy de Bemaraha and Tsingy Beanka.

Habitat: Dry deciduous and evergreen forest on limestone; dead shells are common in caves and under overhangs. During dry periods living specimens aestivate in caves and deep within slots in the tsingy, attached to the rock well above ground level. They emerge after rains and can be locally common.

Remarks: This, the largest species of *Kalidos*, is a conspicuous element of the Bemaraha–Beanka karst formations. Specimens from the southern part of Bemaraha, near Bekopaka, are noticeably smaller than those occurring further north with a max. diameter of 41–46 mm (*vs* 64 mm in the Tsingy Beanka). The genital anatomy is broadly consistent with that of other species of *Kalidos*, although the penis and vagina are particularly long.

Kalidos maryannae sp. n.

Figs 23, 24, 25H

Etymology: Named for Mary-Ann Stanley, wife of Owen Griffiths.

Diagnosis: Shell globose-lenticular, periphery rounded, aperture weakly descendant, umbilicus narrow; sculpture of fine, uneven spiral lines crossed by growth-lines; lustreless, pale coffee-brown, with a bold white spiral band just above periphery, bordered above and below by thinner, dark brown spiral lines.

Description:

Shell: Medium sized, globose-lenticular with a relatively elevated spire (H:D=0.57–0.67); periphery at mid-whorl, rounded in adults, somewhat angled in juveniles; suture indented but not strongly so, situated at whorl periphery, occasionally slightly descendant prior to aperture; umbilicus narrow. Protoconch of approx 1¼ whorls, smooth except for numerous, close-set, microscopic, spiral threads; junction with teleoconch often indistinct. Teleoconch of a further 3½–4 whorls; initially lustreless and smooth, save for weak growth-lines, but with fine, irregular spiral sculpture developing with growth; last adult whorl with surface cut by somewhat stronger, rather uneven spiral lines, crossed by irregular growth-lines, creating low, weakly and unevenly pustular spiral

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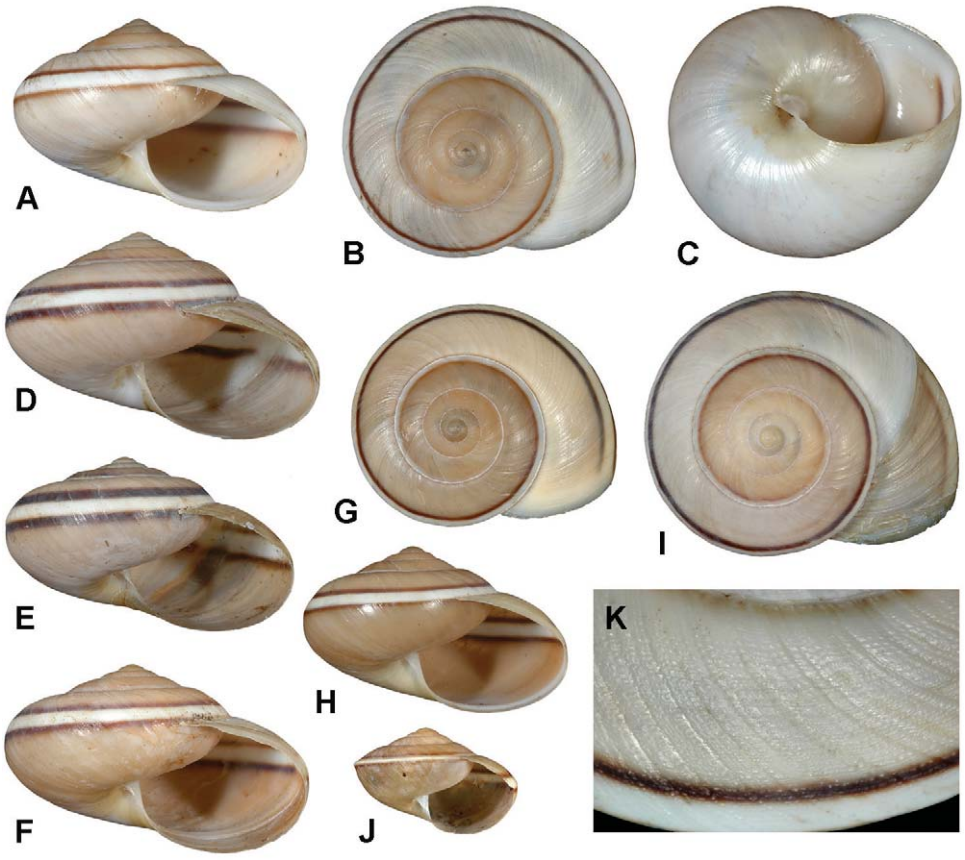

Fig. 23. *Kalidos maryannae* sp. n.: (A–C) holotype, max. diameter 27.3 mm, height 17.7 mm, AMS C.474168; (D–J) paratypes, NMSA L8470/T2904: (D) specimen with bands of intermediate strength, max. diameter 29.3 mm; (E) specimen with broad brown bands and low spire, max. diameter 27.0 mm; (F) specimen spire of intermediate height, max. diameter 28.3 mm; (G, H) fresh subadult with unfaded colour pattern, max. diameter 24.8 mm; (I) large specimen with additional ⅛ whorl of growth, max. diameter 29.3 mm; (J) juvenile showing angular periphery, max. diameter 15.2 mm; (K) holotype, portion of last adult whorl showing sculpture of growth-lines and spiral threads.

ridges (Fig. 23K), these more distinct toward periphery, but evanescing on base which is more glossy and sculptured only with close-set, microscopic, incised spiral threads, rendered irregularly undulant by growth-lines. Aperture ovate-reniform, peristome strongly oblique to vertical axis of shell, interrupted by base of penultimate whorl; outer lip simple and thin; upper part of columella lip reflected and partially covering umbilicus.

Shell strikingly coloured, with a bold white spiral band (1.0–2.0 mm wide) just above periphery, bordered above and below by thinner, dark brown spiral lines; white band and upper brown line visible on penultimate whorl, but generally absent on spire whorls; remainder of shell rather unevenly washed with buff to pale coffee-brown in fresh specimens, fading to dirty white with time and loss of periostracum. Colour bands often ceasing a short distance before lip edge, and clearly visible inside aperture. In the

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largest specimens, an additional ⅛ whorl is added to the mature lip (Fig. 23I). These may represent individuals that survive through the dry season after maturity has been reached and begin another phase of growth when the rains return the following year.

Dimensions: Holotype, max. diameter 27.3 mm, height 17.7 mm; largest specimen, max. diameter 29.4 mm, height 18.8 mm.

External features (Fig. 25H): Head-foot mostly pale, but somewhat darker anteriorly, with yellowish white tubercles contrasting with darker, brownish skin grooves; lateral pedal grooves and peripodial groove distinct; caudal pit and surmounting horn well developed; optic tentacles darker greyish brown; mantle lobes pale with numerous yellowish white pigment granules.

Distal genitalia (Fig. 24): Penis of moderate length (approx. 12.5 mm), apical portion swollen and with a deep indentation; basal ¾ encased in a thin sheath; apical bulb of penis containing a well-developed verge; verge much contracted but possessing a deep longitudinal groove confluent with opening of epiphallus; lower portion of penis with 5 or 6 broad, low folds with a microscopically velvety texture; epiphallus cylindrical, with a sharp bend at insertion of penial retractor muscle and thus divided into proximal and distal limbs; proximal limb slightly shorter than distal one (distal limb might also be considered part of penis rather than epiphallus); a short flagellum, comprising just over one tight loop, arises at junction of vas deferens and epiphallus; flagellum and vas

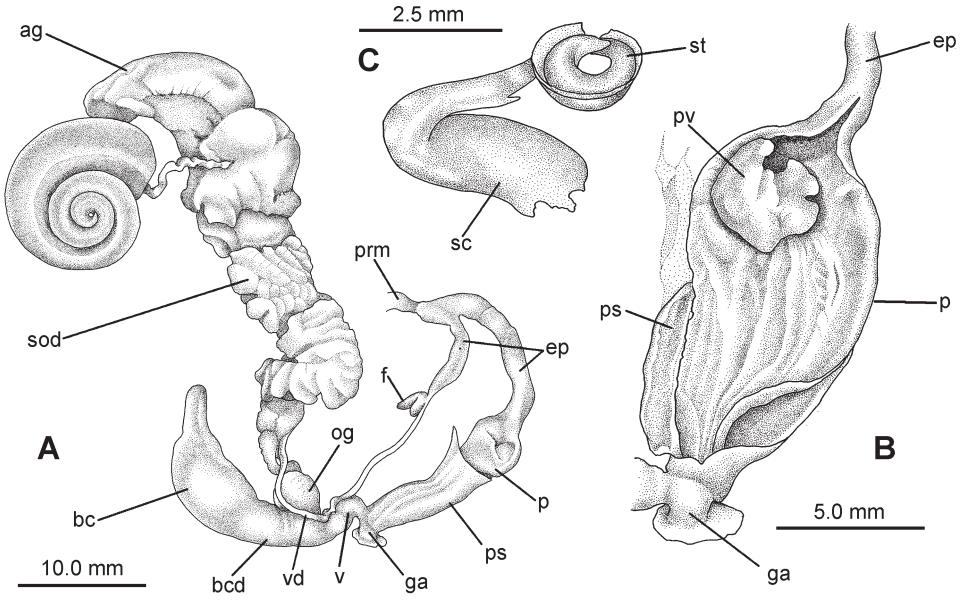

Fig. 24. *Kalidos maryannae* sp. n., genitalia, paratype, NMSA L8470/T2904: (A) entire reproductive tract; (B) penis opened longitudinally to show well-developed penial verge extending from epiphallus; (C) allospermatophore from bursa copulatrix, head end missing. Abbreviations: ag – albumen gland, bc – bursa copulatrix, bcd – bursa copulatrix duct, ep – epiphallus, f – flagellum, ga – genital atrium, og – oviducal gland, p – penis, ps – penis sheath, pv – penial verge, prm – penial retractor muscle, sc – spermatophore capsule, sod – sperm-oviduct, st – spermatophore tail, v – vagina, vd – vas deferens.

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deferens wrapped in connective tissue, but flagellum not connected to penis by muscle bands; lumen of flagellum with a rod-like process extending from its blind end; vas deferens passes along vagina and free oviduct to its origin at base of sperm-oviduct; retractor muscle of right optic tentacle passes to right of penis, i.e. between penis and vagina; bursa copulatrix large, narrowing apically and with a short broad duct; wall of duct thick and muscular, lined internally with longitudinal folds, wall of bursa much thinner; bursa with one moderately fresh allospermatophore and the remains of at least one more; free oviduct swollen prior to its junction with vagina (peri-vaginal or oviducal gland); sperm-oviduct well developed, twisted and with numerous superficial folds. Spermatophore with well-developed capsule (head and body) and a looped tail piece corresponding with shape of flagellum; tail piece with prominent flange-like spiral ridge; a small 'filling nipple' present at level of vas deferens.

Holotype: MADAGASCAR: Central W Madagascar, *ca* 60 km E of Maintirano, S part of Tsingy Beanka, S side of Tana–Maintirano road, above N bank of Kimanambolo R., tall moist forest growing on limestone on south-facing slopes, 18.06325°S 44.52861°E, *ca* 345 m, ii.2010, R. Randalana, st'n R01/10 (AMS C.474168).

Paratypes: Same data as holotype (NMSA L8470/T2904, 10 specimens, body of one in alcohol); 12/06 (NMSA L7193/T2944, 3 specimens, body of one in alcohol); st'n 8/10 (NMSA L8471/T2943, 1 specimen); st'n R01/09 (NMSA L8475/T2912, 1 specimen, body in alcohol); st'n 08/09 (AMS C.469578, 12 specimens); st'n 03/10 (MNHN IM-2010-20072, 3 specimens; NHMUK 20120015, 3 specimens); st'n 07/09 (TMAM T166, 6 specimens).

Additional locality data: *Antsingimavo*: st'n 04/06 (subfossil). *Tsingy Beanka*: st'ns 12/06, 14/06, 15/06, 18/06, 02/09, 06/09, 07/09, 08/09, 09/09, 11/09, 01/10, 04/10, 06/10, 07/10, 08/10, 09/10.

Distribution: Evidently now confined to the Tsingy Beanka, where it is moderately common; not recorded from the Tsingy de Bemaraha, but a single subfossil specimen was found at Antsingimavo.

Habitat: Fresh dead shells are found most commonly amongst limestone rocks, predominantly in the taller moister forests of the southern part of Tsingy Beanka. Living specimens are usually found in leaf-litter. Appears to aestivate sealed to limestone rocks or deep in tsingy slots.

Remarks: In its moderate size and pattern of peripheral banding (two dark brown spiral lines separated by a broader whitish band) this species resembles *K. bathensis* (Robson, 1914), *K. bournei* Robson, 1914, *K. ekongensis* (Angas, 1877), *K. hova* (Odhner, 1919), and *K. namorokae* Emberton, 2007. In *K. bournei* and *K. namorokae*, however, the shell is smaller and the upper brown spiral line is situated further from the whorl periphery. In contrast, *K. bathensis* is larger than the present species, paler in colour and the median spiral band between the brown spiral lines is not distinctly paler than the remaining shell. In addition, it has a third brown spiral line below the suture and the supra-peripheral spiral line is clearly present on the spire whorls.

Undoubtedly, the most similar species in terms of size and colour pattern are *K. ekongensis* and *K. hova*, both of which, as presently conceived, are poorly delineated species. In his description of *K. hova* Odhner (1919) noted a fawn peripheral band on an otherwise brownish shell, but he made no mention of this band being bordered above and below by dark brown spiral lines, neither are these clearly evident in his figure nor in the type material (Fig. 26J–L, syntype, SMNH). He also stated that the shell was smooth and glossy and that the spiral microsculpture was more distinct on the base. This is not the case in *K. maryannae* in which the shell is lustreless and the spiral sculpture strongest above the periphery of the last whorl.

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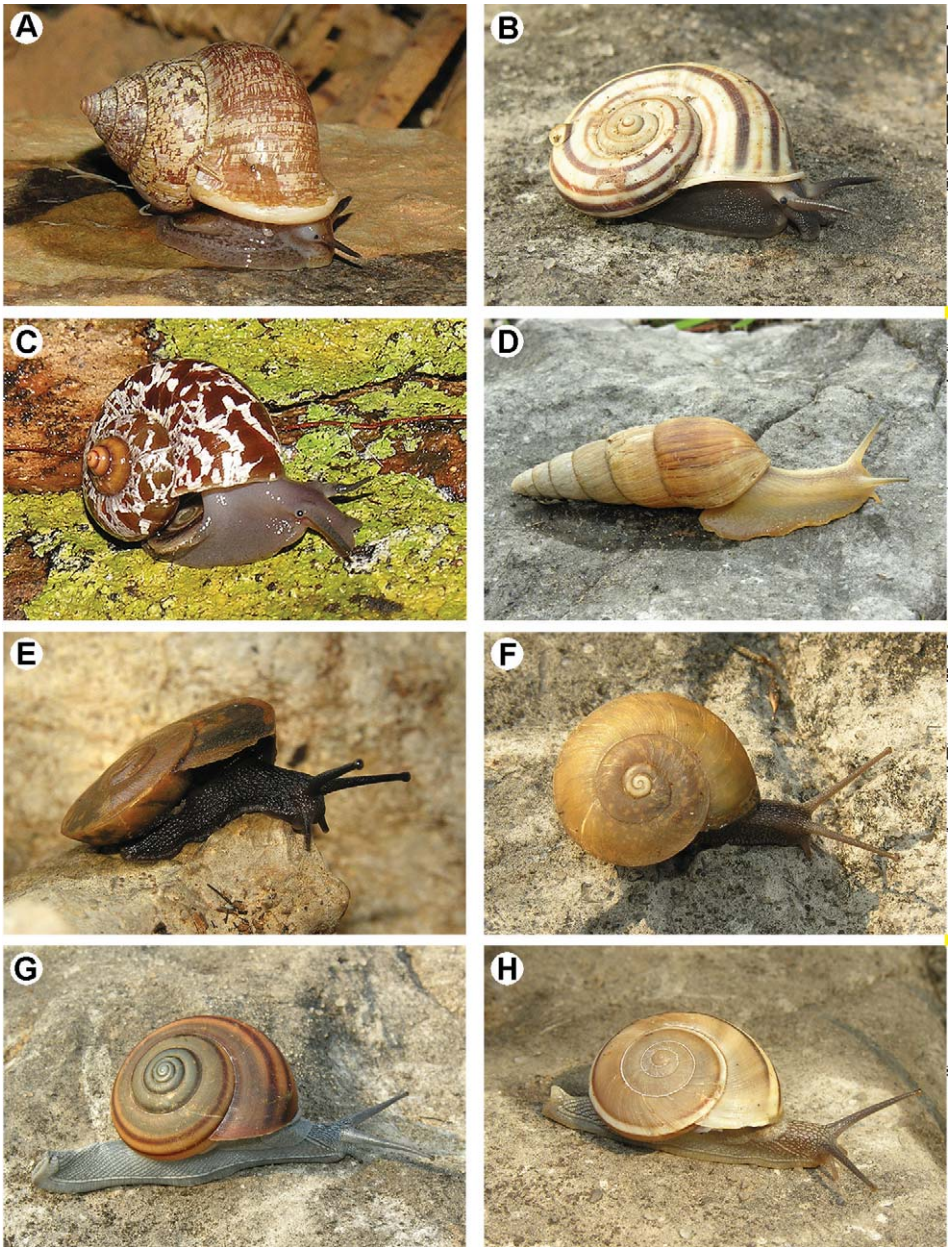

Fig. 25. Living animals from Tsingy Beanka: (A) *Acroptychia bathiei* Fischer-Piette & Bedoucha, 1965, st'n 13/06, shell diameter 23.2 mm, NMSA L7315; (B) *Tropidophora humbug* sp. n., st'n 12/06, shell diameter 28.3 mm, paratype, NMSA L7204/T2984; (C) *Tropidophora secunda* Fischer-Piette & Bedoucha, 1965, st'n 03/06, shell diameter approx. 19.0 mm; (D) *Clavator griffithsjonesi* Emberton, 1999, st'n 12/06, shell height 94.8 mm, NMSA L7192; (E) *Ampelita milloti* Fischer-Piette, 1952, st'n 07/09, shell diameter 19.2 mm, NMSA L8502; (F) *Ampelita namerokoensis* Fischer-Piette, 1952, st'n 12/06, shell diameter 20.3 mm, NMSA L8442; (G) *Kalidos griffithshauchleri* Emberton, 2002, st'n 12/06, shell diameter approx. 60 mm; (H) *Kalidos maryannae* sp. n., st'n 12/06, shell diameter 22.5 mm, paratype, NMSA L7193/T2944.

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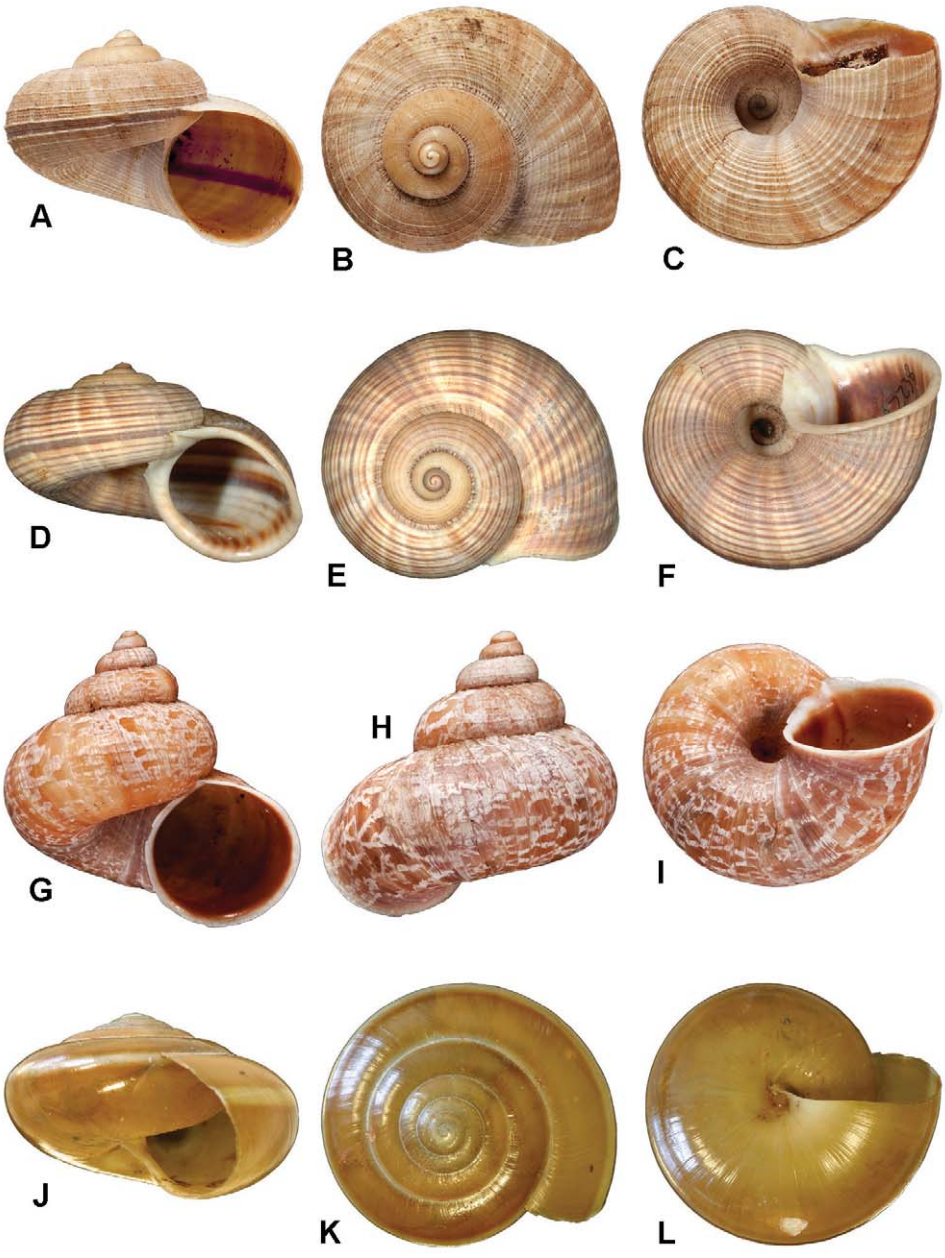

Fig. 26. Species illustrated for comparative purposes: (A–C) *Tropidophora moulinsii,* holotype of *Cyclostoma moulinsii* Grateloup, 1840, 'Madagascar', max. diameter 33.1 mm, NHMUK 1907.11.22.12; (D–F) *Tropidophora thesauri* Fischer-Piette, 1949, Orangea, Diego Suarez [= Antsiranana] district, max. diameter 38.0 mm, NMSA L8438; (G–I) *Tropidophora reticulata*, one of three syntypes of *Cyclostoma reticulatum* (Adams & Reeve, 1850), 'Madagascar', max. diameter 15.1 mm, NHMUK 1874.12.11.231; (J–L) *Kalidos hova*, syntype of *Nanina hova* Odhner, 1919, Catsèpe, Madagascar, max. diameter 24.4 mm (SMNH).

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K. ekongensis is more difficult to assess since the type material is now missing. A paratype reportedly in the NHMUK (Fischer-Piette *et al*. 1966) is not in fact present there (Ablett pers. comm. Nov. 2011). The original description is not detailed, but the figure shows a shell closely resembling the present material. However, Fischer-Piette *et al*. (1966) noted, after examination of the NHMUK paratype, that the shell was thin and very glossy. Again this is not a description that would apply to the present material. Fischer-Piette *et al*. (1966, 1994) interpreted *K. ekongensis* very loosely, including in it a variety of different forms from widely disjunct localities with widely differing habitats. Almost certainly these are not conspecific and their true identity requires further investigation.

In addition to having relatively coarse spiral sculpture on the last adult whorl, rendering it lustreless, *K. maryannae* also differs from *K. ekongensis* and *K. hova* in having more rapidly expanding whorls. Another distinctive feature of *K. maryannae* is that the colour bands are evident only on the penultimate and final whorls, the spire whorls being of a uniform colour.

The genital anatomy of *K. maryannae* conforms to the common pattern evinced by *Kalidos* species (Fischer-Piette *et al*. 1975; Schileyko 2002) and is fully consistent with referral of the species to this genus. In this regard it is perhaps most similar to *Kalidos oleatus* (Ancey, 1902) as figured by Schileyko (2002), but in the present species the flagellum is shorter and more tightly coiled and it is not connected to the penis by muscle bands, and the bursa copulatrix duct is shorter and much broader.

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APPENDIX 1

Field numbers of sampling stations. Stations are listed in order, starting with the second component of the number, which reflects the year of collection. Collectors: DH – Dai Herbert; HR – Hajanirina Ramino; LD – Linda Davis; OLG – Owen Griffiths; RR – Roger Randalana; VF – Vincent Florens.

12b/94 In leaf-litter in bamboo dominated forest next to Besaboba River, on E side of Ankarana massif, *ca* 6 km N of Matsabory Mahamasina, Ankarana, N Madagascar, coll. OLG, 11.x.1994. 12.950°S 49.167°E.

07/95 In leaf-litter in dry forest growing on limestone, in low slots on tsingy, S bank of Manombolo River at start of western side of gorge, 2 km E of Bekopaka, Tsingy de Bemaraha, central W Madagascar, coll. OLG, VF & RR, 14.vi.1995. 19.1433°S 44.8150°E.

10/95 In leaf-litter in tall riverine gallery forest growing on limestone, S bank of Manombolo River at Andimaka, *ca* 6 km E of start of gorge, E of Bekopaka, Tsingy de Bemaraha, central W Madagascar, coll. OLG, VF & RR, 15.vi.1995. 19.1350°S 44.8817°E.

14/95 In leaf-litter in dry forest growing in tsingy slots, at Vazimba Relic Cave, N bank of Manombolo River at start of gorge, 2 km E of Bekopaka, Tsingy de Bemaraha, central W Madagascar, coll. OLG, VF & RR, 17.vi.1995. 19.1267°S 44.8100°E.

18/95 In leaf-litter in dry forest growing along western face of tsingy wall *ca* 2 km E of Kinajao, 11 km NE of Bekopaka, Tsingy de Bemaraha, central W Madagascar, coll. OLG, VF & RR, 18.vi.1995. 19.04°S 44.80°E.

19/95 In leaf-litter in tall forest growing in tsingy slots, in the 'Grand Tsingy', *ca* 5 km NE of Kinajao, 16 km NE of Bekopaka, Tsingy de Bemaraha, central W Madagascar, coll. OLG, VF & RR, 19.vi.1995. 19.0083°S 44.7817°E.

04/96 In tall dry semi-deciduous forest with almost closed canopy and low scrubby understorey with some pachypodiums, growing on flat tsingy in the middle of the pass, *ca* 20 km E by road from Belitsaka, 77 km E of Maintirano, central W Madagascar, coll. OLG & C. Jones, 23.vi.1996. 18.0583°S 44.5283°E, alt. 460 m.

08/96 In tall scrubby south-facing riverine forest growing on a tsingy slope along the N bank of Beboka River, *ca* 5 km SE of Andranonidahy Spring, 11 km E of Berano in central part of Tsingy de Bemaraha Reserve, E of Antsalova, central W Madagascar, 27.vi.1996. 18.7883°S 44.7900°E, alt. 250 m.

09/96 In tall semi-deciduous forest with almost closed canopy growing on and between tsingy near the entrance to the Grotte d'Anjahimbazimba, *ca* 8 km N of Berano village, in Tsingy de Bemaraha Reserve, E of Antsalova, central W Madagascar, 27.vi.1996. 18.6933°S 44.7183°E, alt. 150 m.

10/96 In tall semi-deciduous forest with closed canopy and some palms and *Pandanus*, growing on a low south-facing hillside, 500 m N of Andranonidahy Spring, 6 km E of Berano in central part of Tsingy de Bemaraha Reserve, E of Antsalova, central W Madagascar, 27.vi.1996. 18.7567°S 44.7567°E, alt. 280 m.

12/96 In tall semi-deciduous forest with almost closed canopy, with some palms and *Pandanus*, growing on flat ground in tsingy slots next to the track, midway between Berano and Andranonidahy Spring, in central part of Tsingy de Bemaraha Reserve, E of Antsalova, central W Madagascar, 28.vi.1996. 18.7617°S 44.7333°E, alt. 140 m.

14/96 In tall semi-deciduous forest with NW aspect growing on steep tsingy hill 250 m S of Beboka River on S bank, opposite Andranonidahy Spring, 6 km E of Berano, central part of Tsingy de Bemaraha Reserve, E of Antsalova, central W Madagascar, 29.vi.1996. 18.765°S 44.780°E, alt. 280 m.

15/96 In scrubby low deciduous forest with thin tall trees and vine thickets growing amongst tsingy, on top of hill above tall dense riverine forest, on the S bank of Beboka River, *ca* 5 km SE of Andranonidahy Spring, 11 km E of Berano in central part of Tsingy de Bemaraha Reserve, E of Antsalova, central W Madagascar, 30.vi.1996. 18.7933°S 44.7833°E, alt. 300 m.

930/97 In limestone scree at entrance to Anjohiambovonomby Cave, SE part of Namoroka Reserve, NW of Vilanandro, Soalala Dist., W Madagascar, coll. OLG, x.1997. 16.470°S 45.347°E.

932/97 In limestone scree next to tsingy bluff, W of Anjohiambovonomby Cave, SE part of Namoroka Reserve, NW of Vilanandro, Soalala Dist., W Madagascar, coll. G. Middleton, x.1997. 16.4663°S 45.3290°E.

R03/98 In dry forest growing on limestone along western side of escarpment, *ca* 7.5 km E of Belitsaka, southern part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. RR, v.1998. No co-ordinates available.

01/99LP In Tsiribihina gorge on S side of river, cascade tsingy, Tsiribihina River, central W Madagascar, coll. H. Steiner, 1.vii.1999. 19.7585°S 45.1958°E.

02/99LP On S side of river, at entrance to Lakata Zafera Cave, Tsiribihina River, central W Madagascar, coll. L. Price, 2.vii.1999. 19.7521°S 45.1954°E.

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04/01 In dry deciduous forest growing on old lava flows, next to road, *ca* 6 km WSW of Bobakilandy on road to Andranomiditra Cave, W slopes of Mtn D'Ambre, N Madagascar, coll. OLG, 20.x.2001. 12.64217°S 48.99483°E.

09/01 In dry deciduous forest growing on old lava flows, next to road, *ca* 1 km WNW of Bobakilandy, W slopes of Mtn D'Ambre, N Madagascar, coll. OLG, 22.x.2001. 12.6260°S 49.0463°E.

33/03 In limestone scree in dry deciduous forest growing on E side of low limestone hill, just SW of Amboaboaka village, on S side of Ankorotsakoa River, 15 km W of Antonibe, Narinda North, N of Mahajanga, NW Madagascar, coll. OLG, 25.ix.2003. 15.09882°S 47.24057°E, alt. *ca* 50 m.

36/03 In tall dry forest growing in narrow valley between low limestone bluffs at Grotte des Sakalavas, *ca* 1 km E of Anjajavy Hotel, Pointe Anjajavy, *ca* 22 km NW of Antonibe, Narinda North, N of Mahajanga, NW Madagascar, coll. OLG, 26.ix.2003. 15.0077°S 47.2389°E.

37/03 At cave entrance and inside cave, on low limestone hill with remnant patch of dry deciduous forest, Lavaka Ampesekina Cave, *ca* 1 km S of Amboaboaka village, *ca* 15 km W of Antonibe, Narinda North, N of Mahajanga, NW Madagascar, coll. OLG, 27.ix.2003. 15.1080°S 47.2444°E.

38/03 In and around Lavaka Ambohimenamaso Cave, in dry deciduous forest growing on S and W side of low limestone hill, *ca* 2 km N of Amboaboaka village, *ca* 15 km W of Antonibe, Narinda North, N of Mahajanga, NW Madagascar, coll. OLG, 28.ix.2003. 15.0807°S 47.2732°E.

39/03 In degraded dry deciduous forest on tall limestone bluff, beside road to Anjajavy, *ca* 4 km NW of Amboaboaka village, *ca* 19 km W of Antonibe, Narinda North, N of Mahajanga, NW Madagascar, coll. OLG, 29.ix.2003. 15.0643°S 47.2309°E.

40/03 In tall dry deciduous forest growing on very rugged low limestone, *ca* 500 m from the sea at 'Anjajavy Lemur Skull Cave', *ca* 500 m E of Anjajavy Hotel, Pointe Anjajavy, *ca* 22 km NW of Antonibe, Narinda North, N of Mahajanga, NW Madagascar, coll. OLG, 29.ix.2003. 14.99083°S 47.22917°E (at Hotel).

13/04 In low scrubby dry deciduous forest growing on limestone, *ca* 3 km E of Ambalatsingy, *ca* 22 km N of Antonibe, Narinda North, NW of Port Berge, NW Madagascar, coll. RR, 27.xi.2004. 14.95°S 47.40°E.

04/05 In tall dry deciduous forest growing on shale and limestone soils, south-facing slope on E bank of Mahavavy River, downstream from Kandreho, *ca* 260 km NW of Tananarive, Madagascar, coll. OLG, DH, LD, RR & HR, 6.vi.2005. 17.112067°S 46.035333°E.

06/05 In tall dry deciduous/evergreen forest growing on limestone, on south-facing slope of hill in northern part of Kasijy Forest, on W bank of Mahavavy River, downstream from Kandreho, *ca* 260 km NW of Tananarive, Madagascar, coll. OLG, DH, LD, RR & HR, 7.vi.2005. 17.06283°S 45.99310°E.

08/05 Under limestone rock piles in tall dry deciduous/evergreen forest with palms and *Dracaena*, on south-facing scree slope of low limestone hill, 1.5 km W of river in northern part of Kasijy Forest, on W bank of the Mahavavy River, downstream from Kandreho, *ca* 260 km NW of Tananarive, Madagascar, coll. OLG, RR & J. Hauchler, 8.vi.2005. 17.0382°S 45.9828°E.

10/05 In dry deciduous forest growing on limestone, west-facing rocky scree-covered slope, E bank of the Mahavavy River, N of Kasijy Forest, downstream from Kandreho, *ca* 260 km NW of Tananarive, Madagascar, coll. OLG, DH, LD, RR & HR, 9.vi.2005. 16.97783°S 46.02630°E.

03/06 In tall deciduous/evergreen forest on broken limestone, under rocks and in litter, S part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. DH, LD, A. Moussalli & D. Stuart-Fox, 23.ix.2006. 18.06298°S 44.51388°E, alt. *ca* 300 m.

04/06 In slots in tall tsingy, with tall dry deciduous/evergreen forest, northern most tsingy block, *ca* 3 km E of Antsingimavo, *ca* 85 km NNE of Maintirano, central W Madagascar, coll. OLG, DH, LD & RR, 25.ix.2006. 17.4414°S 44.4522°E, alt. *ca* 100 m.

05/06 Live and dead under limestone rocks, in savanna-grassland amongst tsingy outcrops, *ca* 3 km N of Ranobe River, N of Antsingimavo, *ca* 89 km NNE of Maintirano, central W Madagascar, coll. OLG, DH, LD & RR, 26.ix.2006. 17.39467°S 44.44649°E, alt. *ca* 100 m.

06/06 At Ansokosoko in tall dry deciduous/evergreen forest, in tall tsingy blocks, S & W facing, 6 km N of Ranobe River, N of Antsingimavo, *ca* 91 km NNE of Maintirano, central W Madagascar, coll. OLG, DH, LD & RR, 27.ix.2006. 17.38228°S 44.44660°E, alt. *ca* 120 m.

08/06 In leaf-litter and tsingy slots, with low dry deciduous forest growing on flat-topped tsingy hill bedded with mudstone, *ca* 4 km E of Antsingimavo, *ca* 85 km NNE of Maintirano, central W Madagascar, coll. DH & LD, 30.ix.2006. 17.42732°S 44.43627°E.

11/06 In good dry deciduous forest growing on flat-topped tsingy hill, amongst tsingy rocks in leaf-litter, E side of Tsingy Beanka, E of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG & RR, 2.x.2006. 18.04468°S 44.53357°E, alt. *ca* 490 m.

12/06 In leaf-litter and tsingy slots in comparatively lush tall dry deciduous/evergreen forest on south-facing hill, E part of Tsingy Beanka, E of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, RR, DH & LD, 2.x.2006. 18.06145°S 44.52595°E, alt. *ca* 450 m.

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13/06 In leaf-litter in tall dry deciduous forest with baobabs, growing on broken tsingy platform, SE part of Tsingy Beanka, E of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, RR, DH & LD, 2.x.2006. 18.05795°S 44.54197°E, alt. *ca* 400 m.

14/06 In leaf-litter in tall dry deciduous/evergreen forest on south-facing slope, with tsingy bedded with mudstones, SE part of Tsingy Beanka, E of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, RR, DH & LD, 2.x.2006. 18.06020°S 44.53167°E.

15/06 In dry deciduous forest growing on west-facing tsingy slope, W side of Tsingy Beanka, just E of village of Ambinda, E of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. RR & G. Middleton, 2.x.2006. 18.04465°S 44.50112°E, alt. *ca* 300 m.

16/06 In leaf-litter and tsingy slots, in tall relatively lush dry deciduous/evergreen forest, growing on steep southeast-facing tsingy hill, E side of Tsingy Beanka, E of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG & RR, 3.x.2006. 18.04082°S 44.52760°E, alt. *ca* 400 m.

17/06 In dry deciduous forest growing on broken tsingy blocks with many giant bulbous vines, west-facing slope, SE part of Tsingy Beanka, E of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. DH & LD, 3.x.2006. 18.05417°S 44.53333°E, alt. *ca* 350 m.

18/06 In tall relatively lush, dry deciduous/evergreen forest, growing on steep south-facing limestone scree slope in gorge on N bank of Kimanambolo River, S part of Tsingy Beanka, E of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, DH, LD & RR, 4.x.2006. 18.06097°S 44.54170°E, alt. *ca* 250 m.

01/09 At Burial Coffin Cave, W side of escarpment in dry deciduous forest growing on limestone, S part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, 26.x.2009. 18.03820°S 44.49247°E.

02/09 Near Kimanambolo Bat Cave, on N side of Kimanambolo River, in tall humid south-facing forest growing on limestone, S part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. DH, LD & RR, 26.x.2009. 18.05882°S 44.58185°E, alt. *ca* 300 m.

03/09 Adhering to underside of limestone rocks in pools of Kinahango River and in moist forest nearby, S part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, 26.x.2009. 18.02405°S 44.507117°E, alt. *ca* 275 m.

05/09 Under limestone overhangs in dry forest growing on limestone, along tributary of Manomba River, central part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, DH, LD, RR, 28.x.2009. 17.882483°S 44.473417°E, alt. *ca* 145 m.

06/09 Subfossil and fresh, in deep horizontal shelves under limestone overhangs in dry forest growing on limestone, in centre of tsingy, Tsingy Beanka, *ca* 14 km NE of Belitsaka and *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, DH, LD & RR, 29.x.2009. 17.88750°S 44.48085°E, alt. *ca* 190 m.

07/09 In leaf-litter and amongst limestone boulders in tall moist east-facing forest growing on limestone, above Bokarano River Cave, E side of Tsingy Beanka, *ca* 10 km NE of Belitsaka and *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, DH, LD & RR, 29.x.2009. 17.90568°S 44.48822°E, alt. *ca* 230 m.

08/09 Subfossil and fresh, in shelves under limestone overhangs in tall dry forest growing on limestone, in centre of tsingy, and in dry clay pans nearby, Tsingy Beanka, *ca* 14 km NE of Belitsaka and *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, DH, LD & RR, 30.x.2009. 17.88022°S 44.48281°E, alt. *ca* 200 m.

09/09 In shelves under limestone overhangs in low dry forest on limestone, above entrance to W side of gorge of Manomba R., Tsingy Beanka, *ca* 14 km NE of Belitsaka and *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, DH, LD & RR, 31.x.2009. 17.87039°S 44.48842°E, alt. *ca* 190 m.

11/09 In tall moist forest along road, S part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, DH, LD & RR, 1.xi.2009. 18.06165°S 44.52545°E.

R01/09 In leaf-litter in forest on limestone, Belitsaka area, southern Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. RR, x.2009. 18.06325°S 44.52861°E, alt. 345 m.

R04/09 In tall dense dry forest growing above cliffs on E side of southern Tsingy Beanka at Andohanandranogedro, *ca* 60 km E of Maintirano, central W Madagascar, coll. RR, iv.2009. 18.05028°S 44.53786°E, alt. 380 m.

01/10 Inside Kinahango River Cave, next to tall moist forest growing on limestone, S part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG & RR, 18.ix.2010. 18.02062°S 44.51733°E.

03/10 In tall evergreen forest growing on limestone on S side of road, S part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, 19.ix.2010. 18.0633°S 44.5283°E.

05/10 In tall dry deciduous forest growing on limestone pavement along upper Bokarano River, NE of Belitsaka, central part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG & RR, 20.ix.2010. 17.88702°S 44.47722°E.

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06/10 At base of tall limestone cliff, above small deep cave, in small patch of tall evergreen forest growing on limestone, at Ambilany, *ca* 2 km from Bokarano River Cave, central part of Tsingy Beanka, NE of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG & RR, 21.ix.2010. 17.88827°S 44.48125°E.

07/10 In tall southwest-facing evergreen forest growing on limestone, just above the entrance to Bokarano River Cave, central part of Tsingy Beanka, NE of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG & RR, 22.ix.2010. 17.90575°S 44.48995°E, alt. *ca* 230 m.

08/10 In tall southwest-facing evergreen forest growing at base of limestone cliffs, N of Bokarano River Cave, at Ankoandava, central part of Tsingy Beanka, NE of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. RR, 22.ix.2010. 17.89852°S 44.48767°E, alt. *ca* 240 m.

09/10 In tsingy slots and small caves above Bokarano River gorge, next to low dry deciduous forest, central part of Tsingy Beanka, NE of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG & RR, 22.ix.2010. 17.90517°S 44.48240°E, alt. *ca* 215 m.

10/10 In tall dry deciduous forest growing on west-facing tsingy slope, just above village of Ambinda, Tsingy Beanka, E of Belitsaka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, 24.ix.2010. 18.03085°S 44.50038°E.

11/10 In tall dry forest growing on limestone, next to the Kinahango R., S part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG & RR, 24.ix.2010. 18.02405°S 44.50752°E.

R01/10 In tall moist forest growing on limestone on south-facing slopes, above N bank of Kimanambolo River, S side of Tana–Maintirano road, S part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. RR, ii.2010. 18.06325°S 44.52861°E, alt. 345 m.

R02/10 In tall moist forest growing on limestone on south-facing slopes, above N bank of Kimanambolo River, S side of Tana–Maintirano road, southern part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. RR, iv.2010. 18.06178°S 44.52494°E, alt. 330 m.

R01/11 In riverine forest growing along southern bank of Namela River, S of Ambinda on southern boundary of Tsingy Beanka Reserve, *ca* 60 km E of Maintirano, central W Madagascar, coll. RR, ix.2011. 18.107°S E44.550°E, alt. *ca* 225 m.

03/12 Under rocky limestone scree inside northern main entrance to Kinahango River Cave, next to tall moist forest growing on limestone, southern part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, ix.2012. 18.020617°S 44.517333°E, alt. *ca* 300 m.

06/12 Under limestone scree inside tsingy slots in tall dry forest growing on limestone hill, 2.2 km SE of Ambinda, southern part of Tsingy Beanka, *ca* 60 km E of Maintirano, central west Madagascar, coll. OLG & RR, 24.ix.2012. 18.04040°S 44.51113°E, alt. 418 m.

07/12 In tall south west facing evergreen forest growing on limestone, just above the entrance to Bokorano River cave, central part of Tsingy Beanka, N.E of Belitsaka, *ca* 60 km E of Maintirano, central west Madagascar, coll. OLG, ix.2012. 17.90575°S 44.48995°E, alt. *ca* 230 m.

09/12 In caves and scree, in dry deciduous forest growing on limestone, along western side of the escarpment, and in clear limestone springs at base of tsingy, next to Anahitrano Village, northern part of Tsingy Beanka, *ca* 60 km E of Maintirano, central W Madagascar, coll. OLG, ix.2012. 17.77683°S 44.45588°E, alt. *ca* 160 m.

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APPENDIX 2

Molluscs recorded from the Antsingimavo and Tsingy Beanka karst areas. Species in bold font are discussed further in the present paper.
Notes: † – in subfossil form only; ‡ – in neighbouring Ambereny Crater, east of Ambahivahy.

Terrestrial Gastropoda		Antsingi-mavo	Tsingy Beanka	Other areas
	Hydrocenidae			
1	*Georissa aurata* (Odhner, 1919)	x	-	x
2	*Georissa verreti* Fischer-Piette, Blanc, Blanc & Salvat, 1993	x	x	x
	Cyclophoridae			
3	***Acroptychia bathiei* Fischer-Piette & Bedoucha, 1965**	x	x	x
4	*Boucardicus bemarahae* Emberton, 2002	x	x	x
5	*Boucardicus petiti* Fischer-Piette & Bedoucha, 1965	x	-	x
6	*Boucardicus pupillidentatus* Emberton, 2002	-	x	x
7	*Boucardicus* sp.: Conoid-fusiform, 2.25 mm. Uncommon, old dead.	-	x	-
8	*Cyathopoma bemarahae* Emberton, 2003	x	x	x
9	*Cyclotus bemarahae* Emberton, 2004	x	x	x
10	*Cyclotus griffithsi* Emberton, 2004	x	x	x
11	*Cyclotus mamillaris* Odhner, 1919	-	x	x
12	*Cyclotus* sp. 'Be 1': No spiral cords, periostracum with dense radial riblets, no hairs; shell smooth beneath periostracum. Common, fresh dead.	x	x	-
	Pomatiidae			
13	***Tropidophora chavani* Fischer-Piette, 1949**	-	x	x
14	***Tropidophora humbug* sp. n.**	-	x	x
15	*Tropidophora morondavensis* Fischer-Piette, 1949	x	x	x
16	*Tropidophora* sp. cf. *morondavensis*: As above, but last whorl detached from penultimate whorl. Uncommon.	x	-	-
17	*Tropidophora pyrostoma* (Sowerby, 1843): Rim of Ambereny crater, east of Ambahivahy.	x‡	-	-
18	*Tropidophora salvati* Fischer-Piette & Bedoucha, 1965: Identification tentative, from 1 broken shell.	x	-	x
19	***Tropidophora secunda* Fischer-Piette & Bedoucha, 1965**	-	x	x
20	*Tropidophora semidecussata* (Pfeiffer, 1847)	x	-	x
21	***Tropidophora sericea* sp. n.**	-	x†	-
22	*Tropidophora vignali* Fischer-Piette, 1949	x	x	x
23	*Tropidophora* sp. cf. *vignali*: As above, but spiral sculpture much weaker. Height 11 mm.	x	x	-
24	*Tropidophora* sp. 1: Uniform orange-brown; smooth to eye but with faint spiral cords; small, conical, lip not reflected. Height 12 mm, max. diam. 11 mm. Uncommon.	x	-	-

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APPENDIX 2 (*continued*)
Molluscs recorded from the Antsingimavo and Tsingy Beanka karst areas.

25	*Tropidophora* sp. 2: Solid, chunky, glossy with 2 prominent spiral bands and up to 10 thinner brown spiral bands. Smooth except for dense spiral sculpture in umbilicus. Max. diam. 12 mm. Common.	-	x	x
26	*Tropidophora* sp. cf. *lineata* Pfeiffer, 1854: Common.	x	x	-
27	*Tropidophora* sp. 3: As above but with higher spire; umbilical area with weak spiral sculpture. Common.	x	x	-
28	*Tropidophora* sp. 4: Solid, white, with one brown band below periphery, spire low, wide umbilicus; apical surface with strong spiral sculpture, weak spiral sculpture on base. Max. diam. 13.5 mm. Common.	-	x	-
29	*Tropidophora* sp. 5, *liratoides* group: Shell thin with brown band below periphery, uniform weak spiral cords on upper and lower sides of shell. Max. diam. 15 mm.	-	x	x
30	*Tropidophora* sp. 6, *liratoides* group: Shell thin, uniform light brown, weak spiral cords on apical surface, base smooth. Height 12 mm, max. diam. 15 mm.	x	-	-
31	*Tropidophora* sp. 7, *liratoides* group: As species 5 but smaller and markedly more conical. Height 10 mm, max. diam. 10 mm.	x	-	-
	Assimineidae			
32	*Omphalotropis griffithsi* Emberton, 2004	-	x	x
	Veronicellidae (det. Suzete Gomes)			
33	*Rhopalocaulis grandidieri* (Crosse & Fischer, 1871)	x	x	x
	Vertiginidae			
34	*Nesopupa minutalis* (Morelet, 1881)	x	x	x
35	*Nesopupa* sp. cf. *rodriguezensis* Connolly, 1925	x	-	x
36	*Pupisoma* sp.	x	x	x
	Orculidae			
37	*Fauxulus* sp.: Known from 1 fresh dead specimen.	-	x	-
	Cerastidae			
38	***Conulinus randalanai* sp. n.**	-	x	-
39	*Conulinus rufoniger* (Reeve, 1849)	x	x	x
40	*Rachis ambongoensis* Fischer-Piette, 1964	x	x	x
	Achatinidae			
41	*Achatina fulica* Bowdich, 1822 (alien)	x	x	x
42	*Achatina immaculata* Lamarck, 1822 (alien)	x	x	x
	Subulinidae			
43	*Subulina mamillata* (Craven, 1880)	x	x	x

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APPENDIX 2 (*continued*)

Molluscs recorded from the Antsingimavo and Tsingy Beanka karst areas.

44	*Ischnoglessula* sp. 'Be 1': Early whorls like *Pseudopeas valentini,* but strong radial ribs continue over all of shell; suture deep. Height 10 mm. Uncommon, fresh dead.	-	x	-
45	*Opeas* sp.	-	x	x
46	*Pseudopeas valentini* Fischer-Piette, Blanc, Blanc & Salvat, 1994	x	x	x
	Streptaxidae			
47	*Edentulina battistinii* Fischer-Piette, Blanc & Salvat, 1975	-	x	x
48	*Edentulina bemarahae* Emberton, 1999	x	x	x
49	*Edentulina minor* (Morelet, 1851)	x	-	x
50	*Gulella andreana* Fischer-Piette, Blanc & Vukadinovic, 1974	-	x	x
51	*Gulella bebokae* Emberton, 2001	-	x	x
52	*Gulella vakinifia* Emberton, 2001	x	x	x
53	*Gulella* sp. cf. *josephinae* Emberton, 2001: Moderately common, fresh dead.	x	-	x
54	*Gulella* sp. cf. *nakamaroa* Emberton, 2001: Lacks deep columella baffle. Uncommon, fresh dead.	x	x	x
55	*Gulella* sp. 'Be 1': Like *G. andreana* but with mid-basal tooth. Common, fresh dead.	x	-	-
56	*Gulella* sp.: Like *G. namorokae* Emberton, 2001 but smaller and with mid-basal tooth. Uncommon.	-	x	-
57	*Parvedentulina bemarahae* Emberton, 2002	x	x	x
58	*Parvedentulina unescoae* Emberton, 2002	-	x	x
59	*Parvedentulina* sp. cf. *tsisubulinas* Emberton, 2002	x	-	-
60	*Parvedentulina* sp.: Height 2.25 mm. Uncommon.	-	x	-
	Acavidae			
61	***Ampelita andriamamonjyi* sp. n.**	x†	x	-
62	***Ampelita beanka* sp. n.**	-	x	-
63	***Ampelita decaryi* Fischer-Piette, 1952**	x	-	x
64	***Ampelita griffithsi* Emberton, 1999**	-	x	x
65	***Ampelita lindae* sp. n.**	-	x	-
66	***Ampelita milloti* Fischer-Piette, 1952**	x	x	x
67	***Ampelita namerokoensis* Fischer-Piette, 1952**	x	x	x
68	***Clavator griffithsjonesi* Emberton, 1999**	-	x	-
69	*Helicophanta goudotiana* (Férussac, 1839)	x	x	x
	Helicarionidae			
70	***Bathia madagascariensis* Robson, 1914**	-	x	x

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APPENDIX 2 (*continued*)

Molluscs recorded from the Antsingimavo and Tsingy Beanka karst areas.

71	*Ctenophila* sp. cf. *vorticella* (Adams, 1868): Strong radial sculpture over all of shell; wide umbilicus. Max. diam. 2 mm. Identical to *C. vorticella* from Mauritius.	-	x	-
72	*Ctenophila* sp. 'A': Strong radial sculpture on upper side, weak spiral sculpture on base. Max. diam. 5.5 mm.	x	-	-
73	*Ctenophila* sp. 'B': As above but with strong spiral sculpture on base of shell.	x	-	-
74	*Ctenophila* sp. 'C': Strong radial sculpture, weak spiral sculpture on base.	-	x	-
75	*Kaliella* sp. cf. *barrakporensis* (Pfeiffer, 1853)	x	x	x
76	*Kaliella* sp. 1: No basal spiral sculpture; peristome partially reflected over umbilicus and forming flat plate. Height 4.0 mm.	-	x	-
77	*Kaliella* sp. 2: Strong radial ribs on upper and lower part of shell, keel raised and serrated. Height 4.5 mm.	-	x	-
78	*Kaliella* sp. 3: Strong spiral sculpture over all of shell. Height 2.0 mm.	x	x	-
79	*Louisia* (?) sp. 1: Apical surface with decussate sculpture, base with fine spiral sculpture; periphery rounded with thin raised cord; peristome reflected over umbilicus.	-	x	-
80	*Louisia* (?) sp. 2: Small, brown, low-spired, with angled periphery. Max. diam. 1.5 mm.	-	x	-
81	*Louisia* (?) sp. 3: Brown; angled periphery. Max. diam. 5 mm.	-	x	-
	Ariophantidae			
82	*Kalidos ekongensis* (Angas, 1877)	-	x	x
83	***Kalidos griffithshauchleri* Emberton, 2002**	-	x	x
84	***Kalidos maryannae* sp. n.**	x†	x	-
85	*Kalidos* sp. 'A': Glossy, white to horn, fine granulose/spiral sculpture, some with thin sub-sutural brown band. Large, max. diam. 36 mm. Uncommon; old dead shells.	x	-	-
86	*Kalidos* sp. 'B': Glossy, horn coloured with 2 peripheral brown bands. First 2 whorls almost smooth, rest of whorls with very fine spiral sculpture. Medium-sized: max diam. 25.5 mm. Common; fresh dead.	x	-	-
87	*Kalidos* sp. 'C': Moderately thin, white to horn-brown with two darker brown bands; strong keel. Max diam. 15 mm. Common; live and fresh dead. Some with more inflated last whorl may be a different species.	x	x	x
88	*Kalidos/Macrochlamys* sp.: Flat, thin, uniform horn-brown; spiral sculpture. Max. diam. 15 mm.	-	x	-
89	*Malagarion* sp. '1.06': Small, fine spiral sculpture.	x	-	-
90	*Malagarion* sp. '2.06': Larger, strong fine spiral sculpture on first 3 whorls.	-	x	-
91	*Malagarion* sp. '3.06': Medium-sized, fine spiral sculpture.	-	x	-
92	*Sitala antsingiana* Fischer-Piette, Blanc & Salvat, 1975	-	x	x
93	*Sitala* sp. 'A': Similar to above but more conical, stronger radial ribs; less prominent keel.	-	x	-
94	*Sitala* sp. 'B': Spiral cords present, strong radial ribs, underside smooth. Height 8 mm.	x	-	-

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APPENDIX 2 (*continued*)

Molluscs recorded from the Antsingimavo and Tsingy Beanka karst areas.

	Euconulidae			
95	*Microcystis* sp.: Horn coloured, fine spiral sculpture over all of shell. Max. diam. 11 mm.	-	x	-
96	*Microcystis* sp. '1.06': Shell flat, white; deep excavated umbilicus; strong spiral sculpture over all of shell. Max. diam. 3 mm.	-	x	-
97	*Microcystis* sp. '2.06': Horn coloured; fine spiral sculpture over all of shell, 5 whorls; well margined suture. Max. diam. 6 mm.	-	x	-
98	*Microcystis* sp. '3.06': Shell slightly conical, brown, smooth and glossy, no spiral sculpture. Max. diam. 7 mm.	x‡	-	-
99	*Microcystis* sp. '4.06': Shell white, flat, smooth, no spiral sculpture. Max. diam. 6.5 mm.	-	x	-
100	*Microcystis* sp. '5.06': Shell white, flat, smooth. Max. diam. 8 mm.	x	-	-
Freshwater Gastropoda				
	Ampullariidae			
101	*Pila cecillei* (Philippi, 1848): Abundant in seasonal pans.	x	x	x
	Pachychilidae			
102	*Madagasikara vivipara* Köhler & Glaubrecht, 2010: Local rivers and streams.	x	x	-
	Paludomidae			
103	*Cleopatra madagascariensis* (Crosse & Fischer, 1872): In seasonal pans and side pools.	x	x	x
	Thiaridae			
104	*Melanoides tuberculata* (Müller, 1774): Local rivers.	x	x	x
105	*Tarebia* sp. cf. *granifera* (Lamarck, 1816) or *lineata* (Wood, 1828): Namela River (alien). Det. Frank Köhler.	-	x	x
	Planorbidae			
106	*Biomphalaria* sp.: In seasonal pans and side pools.	x	x	x
Freshwater Bivalvia (det. Christian Albrecht)				
	Sphaeriidae			
107	*Eupera ferruginea* (Krauss, 1848): Under limestone rocks in small river.	-	x	x
108	*Pisidium reticulatum* Kuiper, 1966: Under limestone rocks in small river.	-	x	x

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