# Chapter 8. The non-marine molluscs of Tsingy Beanka, Melaky Region, western Madagascar

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## Abstract

At least 77 species of terrestrial molluscs and nine species of freshwater molluscs have been recorded from the Tsingy Beanka, with several new species having been described from there in recent years. Beanka has a high degree of endemism and high species diversity for such a (relatively) small area. This faunistic richness is attributable to Beanka's limestone (or karst) geology and to the diversity of forest types present. It is thus a very important site for land snails in Madagascar and emphasizes Beanka's conservation importance.

**Key words:** diversity, land snails, limestone, regional biogeography

## Résumé détaillé

L'étonnante faune des mollusques terrestres de Madagascar est bien représentée dans le Tsingy de Beanka. Au moins 77 espèces d'escargots terrestres et huit espèces de mollusques aquatiques y ont été recensées. Parmi, elles se trouvent de nombreuses nouvelles espèces dont sept ont été récemment décrites. Cette haute diversité peut être attribuée à la géologie des calcaires (ou karsts) de Beanka et à la diversité des habitats qui en découle, dont les forêts peuvent être réparties grossièrement en trois écozones principales, auxquelles s'additionnent trois écozones aquatiques. Les genres de mollusques représentés sont typiques des formations sur calcaires de Madagascar dans son ensemble. Ils comprennent en premier lieu des représentants des familles Acavidae, Ariophantidae, Cyclophoridae, Pomatiidae et Streptaxidae, ainsi que des Achatinidae introduites. Au niveau spécifique, la composition de la faune est en revanche caractéristique de la région. Elle comprend un pool régional d'espèces partagées avec d'autres zones calcaires dans un voisinage assez large, ainsi qu'une large proportion (26 sur 77, soit 34 %) d'endémiques locales connues jusqu'à lors uniquement de Beanka. En ce qui concerne les mollusques d'eau douce, une espèce du genre récemment décrit *Madagasikara* mérite une attention particulière comme endémique locale. L'abondance, la richesse spécifique et le haut endémisme local trouvés parmi les mollusques du Tsingy de Beanka mettent en évidence une fois de plus l'importance de ces *tsingy* isolés comme creusets de la diversité et de la diversification pour les mollusques, soulignant leur importance dans les priorités de conservation.

**Mots clés :** diversité, mollusques terrestres, substrat calcaire, biogéographie régionale

## Introduction

Madagascar has a spectacular terrestrial mollusc fauna, remarkable for its taxonomic diversity, high endemism and ancient affinities, and for the gigantic size and extensive radiations of some genera (Fischer-Piette *et al.*, 1993, 1994; Emberton, 1994; Pearce, 2003; Griffiths & Herbert, 2008). In virtually any patch of relatively intact native forest in Madagascar, one can find snails. In some areas they may occur in surprisingly large numbers, whereas in others they may be quite rare, probably limited by low pH and low-nutrient soils. In lowland urban areas, village gardens, and plantations, introduced snail species predominate. The only areas of Madagascar where indigenous snails are completely absent are the secondary grasslands of the Central Highlands. This contrasts with native grasslands on other continents that often have extensive snail faunas.

The study of Malagasy non-marine malacology can be said to have started with the description of *Helix tricarinata* (now referred to the genus *Tropidophora*) by Danish scientist O. F. Müller in 1774. In the following 200 years, considerable numbers of additional species were described from Madagascar, culminating in two monographs on Malagasy land snails by Edouard Fischer-Piette (1899-1988) and colleagues from the Muséum

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national d'Histoire naturelle in Paris (Fischer-Piette *et al.*, 1993, 1994), in which they brought together the available information and described yet more species. In total, they discussed 511 species, excluding slugs, but a few introduced snails were also included. Since 1991, fieldwork by Ken C. Emberton and colleagues, especially focusing on smaller species, resulted in much new data regarding the distribution, habitat, and ecology of Madagascar's snails, as well as the description of many new species. By the year 2000, the list of described species was up to 685 (Pearce, 2003). By 2004, the island's land snail fauna was known to consist of 993 species (Griffiths & Herbert, 2008), with many more awaiting description. Emberton (pers. com., 2005) estimated there are at least 2,500 species of Malagasy terrestrial molluscs awaiting discovery and description.

The Beanka karst area was identified as an area of high land snail endemism after the first author's initial visit in 1996. Subsequently, a number of expeditions have been made to investigate further the diverse non-marine molluscan fauna of this area. Collections made during these expeditions have already led to the description of new, narrowly endemic land snails (Emberton, 1999; Griffiths & Herbert, 2013) and freshwater molluscs (Köhler & Glaubrecht, 2010). Given the presently high levels of non-marine mollusc extinction (Lydeard *et al*., 2004), it is important that focal zones of land snail endemism be identified and flagged as areas of conservation concern. This is particularly so in a country such as Madagascar, where deforestation continues to be a major cause of habitat loss and environmental degradation (Harper *et al.*, 2007).

## Site description

From a malacological standpoint, the Beanka karst area, which in some zones is dominated by limestone pinnacles known as *tsingy*, falls into three broad terrestrial eco-zones and a further three broad freshwater eco-zones. The terrestrial zones are:

- tall dense dry deciduous forest,
- tall semi-deciduous forest in the deeper gorges, and
- lower dry deciduous forest in the northern parts of Beanka (not yet fully surveyed).

Each of these zones has mollusc species restricted to that particular forest type, as well as species shared with other forest types.

The freshwater eco-zones comprise:

- permanent or semi-permanent rivers that cross the limestone from east to west,
- permanent springs that rise from within the limestone, and
- seasonally flooded clay pans.

## Survey techniques

Sampling methodology consisted of collecting in as wide a variety of microhabitat types as possible. Hand collecting was carried out on vertical limestone surfaces, on trees and under rocks and logs, under overhangs, in *tsingy* slots, and in accumulations of leaf-litter within different sheltered 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. Freshwater molluscs were collected by hand and with nets. Under the terms of the permit agreement, most of the material collected has been lodged in the invertebrate collection at the museum of the Parc Botanique et Zoologique de Tsimbazaza, which is under the curatorial care of Madame Hajanirina Ramino.

## Results

The survey work at Beanka has revealed a notably diverse and species-rich molluscan fauna with at least 85 species of non-marine molluscs recorded from the Beanka karsts and nearby non-karst areas. The full list of collected species is provided in Table 8-1 (which also lists for comparison the species from the nearby Antsingimavo karst, 25 km to the north (Figure 8-1). While the suite of genera found is typical for limestone areas in Madagascar, the very high number of species, relatively high degree of snail endemism and the high snail abundance, sets this area apart.

### Main land snail groups at Beanka

Amongst the larger land snails at Beanka, six families stand out for special mention: Acavidae, Streptaxidae, Ariophantidae, Pomatiidae, and Cyclophoridae, and the introduced Achatinidae. (See Figure 8-2 for photos of live representatives of the five native families).

**Acavidae** - The most striking group is the Acavidae. These are a Gondwana relict group of medium to very large snails, confined to Madagascar, Seychelles, and Sri Lanka with affinities to closely related groups in southern Africa, Australia, South America, and India (Emberton, 1990; Stanisic, 1998). Acavids are

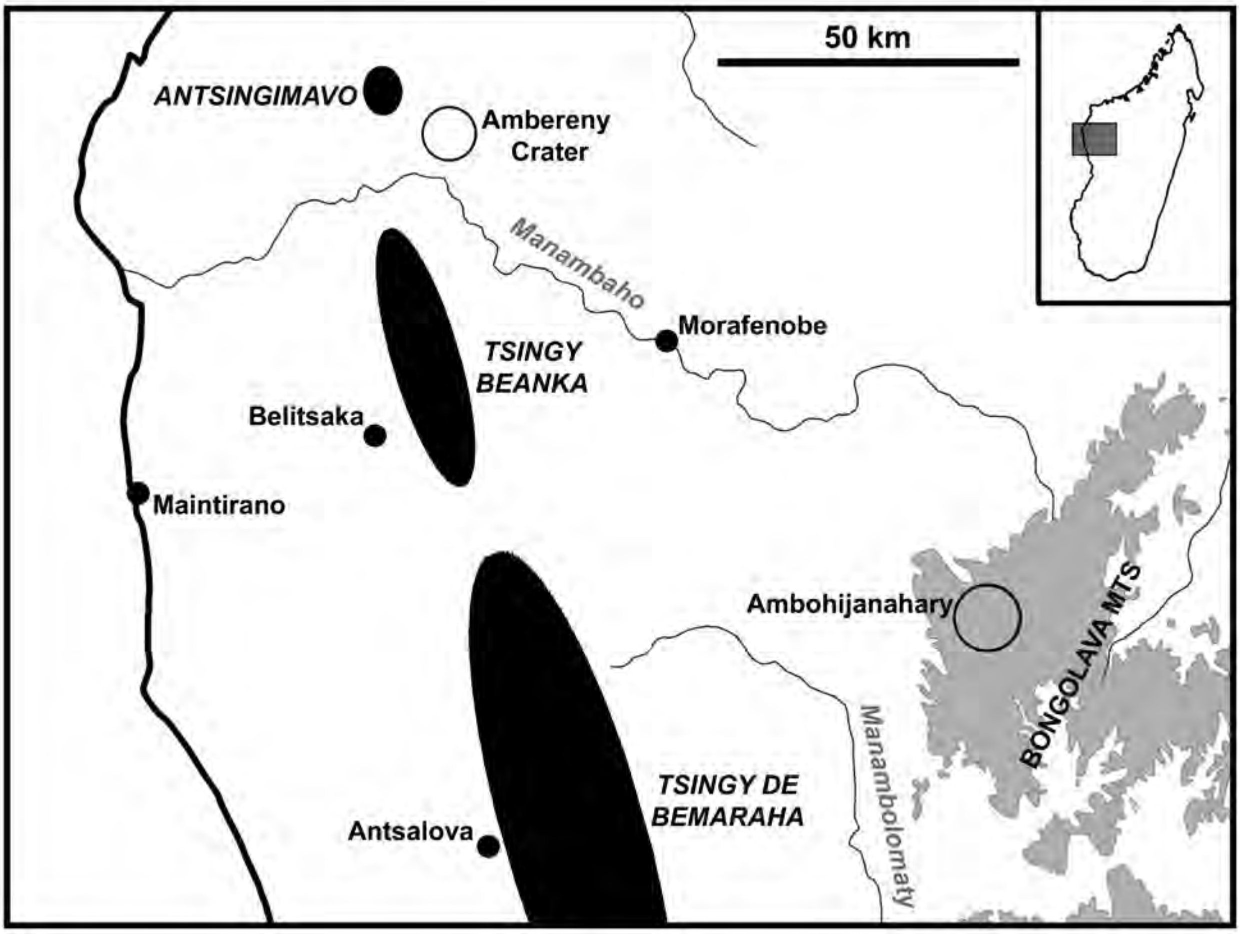


**Figure 8-1.** Map showing the geographical location of the Tsingy Beanka relative to the other areas mentioned in the text.

popularly known as “bird’s-egg snails” because of the very large eggs produced by some species (although the smaller *Ampelita* spp. have much smaller eggs). In Madagascar, especially in the eastern rainforests, they are the dominant snails, often occurring in very large numbers. Beanka has nine acavid species belonging to three genera: *Helicophanta, Clavator*, and *Ampelita.* Of these, four species are endemic to Beanka.

**Streptaxidae** - The area also has a remarkable diversity of snails of this family, which consists of small to medium-sized carnivorous species that feed mostly on other snails. The family is widely distributed in the tropics and subtropics. Madagascar has four principal genera, three of which are represented at Beanka, with at least 10 species: the larger *Edentulina*, the smaller *Gulella*, and the small, generally elongate, *Parvedentulina*.

**Ariophantidae** - The largest native snail from Beanka (with a diameter of up to 65 mm), the spectacular *Kalidos griffithshauchleri* (Figure 8-2g), belongs to this family which consists of small to very large snails, mostly thin-shelled and lacking any thickening (lip) around the shell aperture. They range throughout parts of Africa, India, and southeastern Asia. In Madagascar, the main genera are *Kalidos* and the small conical *Sitala*. While both these genera occur all over Madagascar, they are most abundant and diverse in the dry forests of the western lowlands, especially in limestone areas.

**Pomatiidae** - The other dominant group in terms of abundance and species diversity is the family Pomatiidae: shuffler snails. All of Madagascar’s pomatiids belong to either of two genera: *Tropidophora* and *Cyclotopsis*. All have flat to conical shells with a rigid, calcareous operculum. *Tropidophora* is a widespread genus, also occurring in southern and eastern Africa, Seychelles, and the Mascarene Islands. However, they reach their greatest diversity and abundance in Madagascar. While *Tropidophora* occur all over Madagascar, they are most common in the dry forests of the south, west, and north. At least 12 species occur at Beanka.

**Cyclophoridae** - This family has many large and spectacular species in the Old World tropics and several genera occur in Madagascar. Unlike the

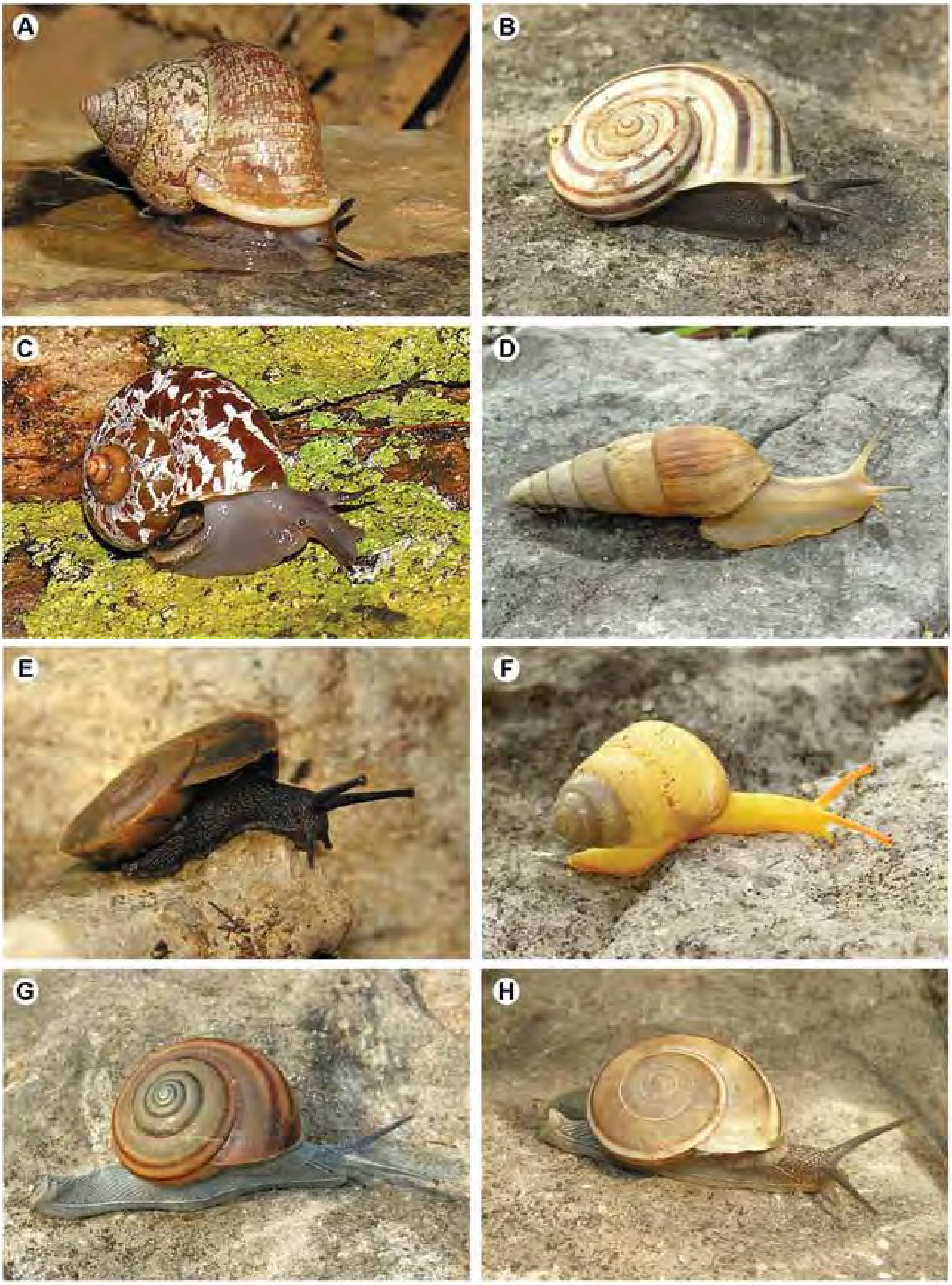


**Figure 8-2.** Tsingy Beanka land snails: A) *Acroptychia bathiei* Fischer-Piette & Bedoucha, 1965 [Cyclophoridae], shell diameter 23.2 mm (NMSA L7315); B) *Tropidophora humbug* Griffiths & Herbert, 2013 [Pomatiidae], shell diameter 28.3 mm (paratype, NMSA L7204/T2984); C) *Tropidophora secunda* Fischer-Piette & Bedoucha, 1965 [Pomatiidae], shell diameter approx. 19.0 mm; D) *Clavator griffithsjonesi* Emberton, 1999 [Acavidae], shell height 94.8 mm (NMSA L7192); E) *Ampelita milloti* Fischer-Piette, 1952 [Acavidae], shell diameter 19.2 mm (NMSA L8502); F) *Edentulina battistinii* Fischer-Piette, Blanc & Salvat, 1975 [Streptaxidae], juvenile, shell length 15.2 mm (NMSA L7202); (G) *Kalidos griffithshauchleri* Emberton, 2002 [Ariophantidae], shell diameter approx. 60 mm; (H) *Kalidos maryannae* Griffiths & Herbert, 2013 [Ariophantidae], shell diameter 22.5 mm (paratype, NMSA L7193/T2944). NMSA = KwaZulu-Natal Museum, South Africa.

**Table 8-1.** Molluscs recorded from the Antsingimavo and Tsingy Beanka karst areas. Notes: † – in subfossil form only; ‡ – in neighboring 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* Griffiths & Herbert, 2013 | - | 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 one broken shell. | x | - | x |
| 19 | *Tropidophora secunda* Fischer-Piette & Bedoucha, 1965 | - | x | x |
| 20 | *Tropidophora semidecussata* (Pfeiffer, 1847) | x | - | x |
| 21 | *Tropidophora sericea* Griffiths & Herbert, 2013 | - | 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 | - | - |
| 25 | *Tropidophora* sp. 2: Solid, chunky, glossy with two 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 sp. 6 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 one fresh dead specimen | - | x | - |
| **Cerastidae** | | | | |
| 38 | *Conulinus randalanai* Griffiths & Herbert, 2013 | - | x | - |
| 39 | *Conulinus rufoniger* (Reeve, 1849) | x | x | x |
| 40 | *Rachis ambongoensis* Fischer-Piette, 1964 | x | x | x |

**Table 8-1.** (cont.)

| | **Terrestrial Gastropoda** (cont.) | **Antsingi-mavo** | **Tsingy Beanka** | **Other areas** |
|---|---|---|---|---|
| **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 |
| 44 | *Ischnoglessula* sp. 'Be 1': Early whorls like *P. 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*: Moderately common, fresh dead. | x | - | x |
| 54 | *Gulella* sp. cf. *nakamaroa*: 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* 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* Griffiths & Herbert, 2013 | x† | x | - |
| 62 | *Ampelita beanka* Griffiths & Herbert, 2013 | - | x | - |
| 63 | *Ampelita decaryi* Fischer-Piette, 1952 | x | - | x |
| 64 | *Ampelita griffithsi* Emberton, 1999 | - | x | x |
| 65 | *Ampelita lindae* Griffiths & Herbert 2013 | - | 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 |
| 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* Griffiths & Herbert, 2013 | 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 colored with 2 peripheral brown bands. First two whorls almost smooth, rest of whorls with very fine spiral sculpture. Medium-sized: max diam. 25.5 mm. Common; fresh dead. | x | - | - |

**Table 8-1.** (cont.)

| | **Terrestrial Gastropoda** (cont.) | **Antsingi-mavo** | **Tsingy Beanka** | **Other areas** |
|---|---|---|---|---|
| 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 three 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 | - | - |
| **Euconulidae** | | | | |
| 95 | *Microcystis* sp.: Horn colored, 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 colored; fine spiral sculpture over all of shell, five 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* Kohler & 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. *T. granifera* (Lamarck, 1816) or *T. lineata* (Wood, 1828): Namela River. Det. Frank Köhler. (alien) | - | x | x |
| **Planorbidae** | | | | |
| 106 | *Biomphalaria* sp.: In seasonal pans and side pools. | x | x | x |
| 107 | *Bulinus* sp.: In seasonal pans. | - | x | x |
| **Freshwater Bivalvia** (det. Christian Albrecht) | | | | |
| **Sphaeriidae** | | | | |
| 108 | *Eupera ferruginea* (Krauss, 1848): Under limestone rocks in small river. | - | x | x |
| 109 | *Pisidium reticulatum* Kuiper, 1966: Under limestone rocks in small river. | - | x | x |

pomatiids, cyclophorids generally have a flexible, horny operculum, although it may be calcareous in some genera (e.g. *Cyathopoma* and *Cyclotus*). Most species in Madagascar are very small, and often have strangely shaped shell apertures (Emberton, 2002, 2003). The principal small-sized genera at Beanka are *Cyclotus, Cyathopoma*, and *Boucardicus*. The largest species belongs to *Acroptychia*, a medium-sized conical snail that is especially abundant at Beanka.

**Achatinidae** - This originally African family includes two very large and widespread species: *Achatina immaculata* (Lamarck, 1822) and *A. fulica* (Bowdich,1822) that were introduced to Madagascar in early colonial times (or before). Férussac, in 1827 reported that specimens of *A. fulica* were brought to La Réunion (Bourbon) "for medicinal purposes from Ile St Marie", i.e. prior to 1827 (Germain, 1921). These two species occur throughout the coastal and lowland areas of Madagascar. However, *A. immaculata* is the dominant species in drier areas and is relatively common at Beanka where it attains a large size (average maximal adult shell length 145 mm), while *A. fulica* is the more common species along the east coast and is relatively rare at Beanka.

### The freshwater molluscs of Beanka

The Beanka area has seven species of freshwater gastropod and two species of freshwater bivalve. The freshwater species separate out according to their preferred eco-zone: *Bulinus* sp. and *Biomphalaria* sp. (schistosomiasis vectors), *Pila cecillei*, and *Cleopatra madagascariensis* live in seasonally dry ponds and pans; *Madagasikara vivipara* at Beanka is restricted to springs arising from the limestone and the two freshwater bivalves *Eupera ferruginea* and *Pisidium reticulatum*, the widespread *Melanoides turberculata*, and the introduced *Tarebia* sp. occur in the river systems only.

## Discussion

### Comparison with the molluscan fauna elsewhere in Madagascar

The terrestrial snails of Beanka mostly comprise obligate limestone dwellers that do not occur in forests growing on other substrate types. Only eight snail species have also been found in the adjacent forest growing on red soil. Similarly, because of the overwhelming preponderance of calciphile species at Beanka, it shares virtually no species with the Central Highland forests at Ambohijanahary resting on red soils and some 90 km to the southeast. However, Beanka has many land snail species in common with the limestone habitats to the south (Bemaraha) and the limestone area of Antsingimavo, 25 km to the north (Figure 8-1). There is evidently a regional pool of calciphile species common to such habitats in the broader vicinity. Thus, of the Beanka terrestrial snail fauna (77 species), 44 species (57%) also occur in Bemaraha and 33 (42%) at Antsingimavo. Similarly, of the 55 species occurring at Antsingimavo, 34 (62%) also occur in Bemaraha.

This notwithstanding, the snail fauna at each of these localities has characteristic elements due to the presence of a significant number of snails endemic to that locality. In the case of Beanka, 26 of the 77 species (34%) have been found only at this locality, for Antsingimavo the figure is 14 of 55 species (25%). This local endemicity is linked to the fact that these three limestone areas are not contiguous, and thus, for taxa of very limited vagility, such as snails, they effectively represent limestone 'islands' between which there is little or no dispersal. The populations have thus diverged over time, leading to speciation and narrow-range endemism in some lineages. Snail endemism is now recognized to be a distinctive feature associated with isolated limestone formations and highlights their significance not only as areas of high molluscan species diversity and abundance, but also as cradles of snail diversification. Therefore, such areas are priorities for conservation (Stanisic, 1997; Herbert, 2002; Schilthuizen, 2004; Clements *et al*., 2006, 2008; Willan *et al*., 2009; Siriboon *et al*., 2013).

### Snail ecology – coping with the dry season

The life cycles of the snails of Beanka, as well as those of other components of the local biota, are strongly linked to the regional rainfall regime. In the dry season (April to October), although dead snails are everywhere, live snails are not active and, thus, they are relatively difficult to locate. Depending on the species, they will have different aestivation strategies to cope with the many months without rain. Some species, like *Kalidos griffithshauchleri*, aestivate deep inside limestone slots and caves were they 'cement' themselves to a near vertical rock face with dried mucous secretions, well out of reach of vertebrate predators. Smaller species of *Kalidos* cement themselves to dead leaves, *Conulinus* adheres to tree branches, and *Rachis* to shaded *tsingy* walls. Most of the other species including *Tropidophora*, *Acroptychia*, and *Helicophanta* bury themselves deeply in sheltering accumulations of leaf-litter between and beneath limestone slabs and boulders. Whatever their strategy, as soon as rains fall, the *tsingy* comes alive with snails, seemingly in a hurry to make up for time lost during the dry season!

### Relationship with other taxa in *tsingy* habitat

Given their abundance and yearlong availability, land snails represent a significant food resource for many species of animals living in the *tsingy*. Broken (depredated) snail shells can be found under virtually every rock overhang. In such cases, the likely predator is either a rodent or bird, although bush pigs (*Potamochoerus*) and tenrecs (*Tenrec*) also feed on snails. Members of the genera *Tropidophora* and *Kalidos* are common victims of rodents. Fresh empty snail shells, particularly subulinids or juvenile *Achatina* spp., can often be found amongst the discarded "rubbish-piles" found around the large nests of the ant *Aphaenogaster* sp. suggesting that they also feed on snails or at least collect the empty shells. One species of large fly (perhaps Sciomyzidae) lays its eggs on live snails with the larva eating the snail and then using the snail shell as a shelter for the pupal stage (pers. obs. of first author).

## Conclusion

Although it is clear that land snail diversity and abundance is high in the Tsingy Beanka, our malacological exploration of the area is still at an early and largely descriptive stage. Much remains to be discovered, particularly in the less sampled northern portions of the formation. Undoubtedly, the number of new, restricted range endemics will grow as more areas and habitats are sampled, and as the currently unidentified species are studied in more detail. This will serve not only to further emphasize the conservation significance of the region from a malacological perspective, but also to allow more meaningful comparison of levels of diversity, abundance, and endemism with other areas.

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