



## Rhytididae (Eupulmonata) in Madagascar: reality or conjecture?

David G. Herbert<sup>1,2</sup>, Adnan Moussalli<sup>3</sup> and Owen L. Griffiths<sup>4,5</sup>

<sup>1</sup>*KwaZulu-Natal Museum, P. Bag 9070, Pietermaritzburg 3200, South Africa;*

<sup>2</sup>*School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg 3206, South Africa;*

<sup>3</sup>*Sciences Department, Museum of Victoria, Melbourne, VIC, Australia;*

<sup>4</sup>*Research Associate, Australian Museum, Sydney, Australia; and*

<sup>5</sup>*BCM Ltd, Rivière des Anguilles, Mauritius*

Correspondence: D.G. Herbert; e-mail: dherbert@nmsa.org.za

(Received 3 June 2014; accepted 13 November 2014)

### ABSTRACT

In 1990, Emberton hypothesized that the Madagascan land snail *Helix covani* Smith, 1879 was a previously unrecognized member of the Gondwanan family Rhytididae. The evidence put forward was based solely on features of the shell. The present paper sets out to explore this hypothesis in more detail, using morphological characters of the soft parts and molecular data, and so to test whether the present-day distribution of the Rhytididae includes Madagascar, a biogeographically interesting question. The results obtained from several independent suites of morphological characters are clearly inconsistent with the placement of *Helix covani* in the Rhytididae. Instead, the morphological evidence strongly supports its referral to the Acavidae, with affinity to the genus *Ampelita*, in which it has traditionally been classified. Molecular data are fully consistent with this, providing strong support for an acavid clade comprising *Acavus*, *Ampelita*, *Helicophanta* and *Helix covani*. Currently, the morphological and molecular data available are not sufficiently representative of Madagascan acavid diversity to permit further resolution of the affinities of the taxon in relation to *Ampelita* and *Helicophanta*.

### INTRODUCTION

The family Rhytididae comprises a group of small to very large carnivorous snails widely distributed in the southern hemisphere. Historically, representative taxa have been recorded from southern and eastern Africa, the Seychelles, Indonesia, Australia, New Zealand and islands in the southwestern Pacific (Solem, 1959; Richardson, 1989), a distribution pattern strongly suggesting a Gondwanan origin (Smith, 1998). However, East African species referred by Thiele (1911) to *Rhytida* Martens, 1860 are in fact helicoid streptaxids belonging to the genus *Tayloria* Bourguignat, 1889 (Pilsbry, 1919; Verdcourt, 1958). Likewise, Gerlach (1995) has shown that the genus *Priodiscus* Martens, 1898, from the Seychelles, long considered to belong to the Rhytididae (Thiele, 1931), is in fact referable to the Streptaxidae. Thus neither this island group nor East Africa belongs within the range of rhytidid taxa.

More recently, Emberton (1990) suggested that the family Rhytididae occurs in Madagascar, hypothesizing that *Helix covani* Smith, 1879 was a previously unrecognized rhytidid that had been erroneously referred to the acavid genus *Ampelita* Beck, 1837 by earlier workers (Pilsbry, 1894 in 1893–95; Fischer-Piette *et al.*, 1994). Emberton believed that the small embryonic shell possessed by *H. covani* was not consistent with a position in the Acavidae. Instead, he referred it to the Rhytididae (genus '*Rhytida*') on account of "its rounded, regularly expanding

whorls, coarse sculpture and unreflected apertural lip" (Emberton, 1990: 106). At the same time, he noted that the discovery of a rhytidid taxon in Madagascar added "an important data point to Gondwanan biogeography". Although the malacofauna of Madagascar has much in common with that of Africa, most of the similarity relates to post-Gondwanaland elements of African or Afro-Oriental origin (Bruggen, 1981) and must thus stem from dispersal events. At a family level, Gondwanan mollusc lineages are generally not shared between southern Africa and Madagascar. Thus the southern African families Bothriembryontidae, Chlamydephoridae, Dorcasiidae, Sculptariidae and (until Emberton, 1990) also the Rhytididae were not known in Madagascar, whereas the Acavidae, highly diverse in Madagascar, are not represented in Africa. Bruggen (1980) suggested that in Madagascar the large carnivorous-mollusc niche was filled instead by large streptaxids (e.g. *Edentulina*), as it is further north in Africa. The only putatively Gondwanan family shared by both Madagascar and Africa is the Charopidae, but that this is genuinely reflective of a relict Gondwanan origin as suggested by Bruggen (1980) seems unlikely, given the ease with which small and often arboreal molluscs can be passively dispersed. Emberton's hypothesis thus represents the first suggestion that a genuinely southern-relict land snail family (Solem, 1959) occurs in both southern Africa and Madagascar, hinting at the same time at a shared precariorance malacofauna.

Emberton's conclusion has been accepted by subsequent authors, keen to see another Gondwanan fragment added to the geographic range of the Rhytididae (Bruggen, 1994; Pearce, 2003; Griffiths & Herbert, 2008). Nevertheless, Emberton (1990) based his transfer of *H. covani* from *Ampelita* to '*Rhytida*' solely on shell characters and pointed out the need for anatomical observations to establish its relationships within the Rhytididae. *Helix covani*, however, is evidently a rare taxon and anatomical data have remained lacking.

In relation to recently published studies on the Rhytididae of southern Africa (Moussalli, Herbert & Stuart-Fox, 2009; Herbert & Moussalli, 2010) and on-going research on this family as a whole, the occurrence of a putative rhytidid species in Madagascar is of considerable significance. We therefore set out to obtain living material of *H. covani* for anatomical study and molecular analysis, so as to acquire more reliable phylogenetic information regarding the relationships of this enigmatic taxon and to test the hypothesis that the family Rhytididae is present in Madagascar. We were successful in obtaining this material and here report on the results of our subsequent investigations.

## MATERIAL AND METHODS

Through prior fieldwork (O. Griffiths and A. Andriamamonjy), we were aware that *Helix covani* occurred in rainforest habitats in the Andasibe area (Perinet), east of Antananarivo. A KwaZulu-Natal Museum team therefore visited primary rainforest near Andasibe, in order to search for living specimens. We were assisted by Roger Randalana, an experienced Malagasy snail collector who had prior experience of collecting this species in the Ranomafana area. After extensive searching, a single juvenile specimen of *H. covani* was found in a decaying tree stump in rainforest near Maromizaha (18.96159°S, 48.49176°E; *c.* 1000 m a.s.l.). The specimen was photographed alive and a tissue sample taken for DNA extraction (preserved in 99% ethanol). The animal was then drowned overnight in water and subsequently preserved in 75% ethanol for anatomical examination. In addition, several specimens collected during the 1990s, including a mature individual, were loaned from the Academy of Natural Sciences of Drexel University, Philadelphia, and examined anatomically.

All dissections were performed under a Wild M4 dissecting microscope with drawing tube. Radulae were extracted by maceration of the excised buccal mass in dilute NaOH, rinsed in distilled water, dehydrated in ethanol and air-dried on stubs with double-sided carbon tape, coated with gold-palladium and examined at low accelerating voltage (5–10 kV) in a Hitachi S-570 scanning electron microscope.

### Molecular methods

For molecular analysis we sequenced *c.* 830 bp of the 5' region of the 28S ribosomal RNA using the primer pairs LSU1/LSU3 and LSU2/LSU4 (Wade & Mordan, 2000). The first primer pair encompasses the ITS2 region and *c.* 260 bp of the 5'-end of 28S. The second pair targets *c.* 570 bp of the adjacent 28S region. Only the 28S sequences were considered in this study. In addition to *H. covani*, we sequenced further representatives spanning much of the generic diversity within the Rhytididae and Acavidae. Given the evolutionary distance between these two families, and to ensure balanced taxonomic sampling for the phylogenetic analysis, we also included representatives from other families within the superfamilies Acavoidea and Rhytidoidea, namely Caryodidae, Dorcasiidae, Strophocheilidae and Chlamydephoridae, as well as the largely Gondwanan Orthalicoidea. Species belonging to the families Camaenidae, Pupillidae and Achatinidae were used as outgroups. Sequences were obtained for 40 species in total, eight of

which originated from Wade, Mordan & Naggs (2006) and were downloaded from GenBank (see Table 1 for accession numbers). Molecular laboratory protocol, including DNA extraction and amplification, followed that described by Moussalli *et al.* (2009). PCR products were purified by ethanol precipitation, with sequence reactions and capillary separation done by Macrogen (Seoul, Korea). Nucleotide sequences were first aligned using CLUSTALW (Thompson, Higgins & Gibson, 1994) followed by manual appraisal. New sequences are lodged with GenBank, accession numbers: KP23053-KP230534 (Table 1).

In addition to a maximum likelihood analysis, implemented using the program RAXML v. 7.4.2 (Stamatakis, 2006), we also used Bayesian inference to reconstruct phylogenetic hypotheses, implemented in BEAST v. 1.7.5 (Drummond *et al.*, 2012) and MrBayes v. 3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). The best-fitting model, GTR+G, was determined using Mega v. 5.2 (Tamura *et al.*, 2011). In all analyses representatives of the families Camaenidae, Pupillidae and Achatinidae were collectively constrained as the outgroup. One hundred thorough bootstraps were conducted in RAXML. For the BEAST analysis we used the uncorrelated (lognormal) relaxed-clock model with a Yule speciation prior and ran two independent runs of 50 million generations sampled every 1,000 generations. A relaxed model was deemed appropriate as variation in rates among branches (uclsd.stdev) was moderately high (95% highest posterior density HPD intervals: lower = 0.205, upper = 0.6019), indicating departure from a molecular clock assumption. We assessed convergence across all parameters and ensured adequate estimated sample size (ESS) in Tracer (Rambaut & Drummond, 2007). For the MrBayes analysis we performed two simultaneous runs (each with four chains) of 5 million generations sampled every 100 generations, and determined convergence by assessing the average standard deviation of split frequencies (<0.01).

### Institutional abbreviations

ANSP, Academy of Natural Sciences of Drexel University, Philadelphia  
NHMUK, Natural History Museum, London, UK  
NMSA, KwaZulu-Natal Museum, Pietermaritzburg, South Africa

## RESULTS

### Systematic description

#### **'*Helix*' covani Smith, 1879**

(Figs 1–6)

*Helix* (*Macrocyclus*) *covani* Smith, 1879: 338.

*Helix* (*Macrocyclus*?) *covani*—Smith, 1882: 381, pl. 21, figs 10–12.

*Helix corani* [*sic*]—Crosse & Fischer, 1889: pl. 14, fig. 2. Chevallier, 1964: 31.

*Helix* (*Ampelita*) *covani*—Pilsbry, 1890 in 1890–91: 44, pl. 7, figs 89–91.

*Ampelita covani*—Pilsbry, 1894 in 1893–95: 157. Kobelt, 1909: 89. Fischer-Piette, 1952: 17. Fischer-Piette & Garreau de Loubresse, 1965: 141. Fischer-Piette *et al.*, 1994: 104, pl. 9, figs 7–9, map 9.

'*Rhytida*' *covani*—Emberton, 1990: 106, fig. 5. Pearce, 2003: 558. Griffiths & Herbert, 2008: 239.

*Identification* (Fig. 1): Identification of specimens was made with reference to the type material (see below). The shape of the shell is similar to that of a number of low spired, subglobose, broadly umbilicate *Ampelita* species. However, it is rendered distinctive by features of the peristome, microsculpture and embryonic shell. In *H. covani* the peristome is thickened and reflected only in the columella region and then only weakly so. The outer lip

## RHYTIDIDAE IN MADAGASCAR?

**Table 1.** Provenance of specimens sequenced for 28S rRNA analyses.

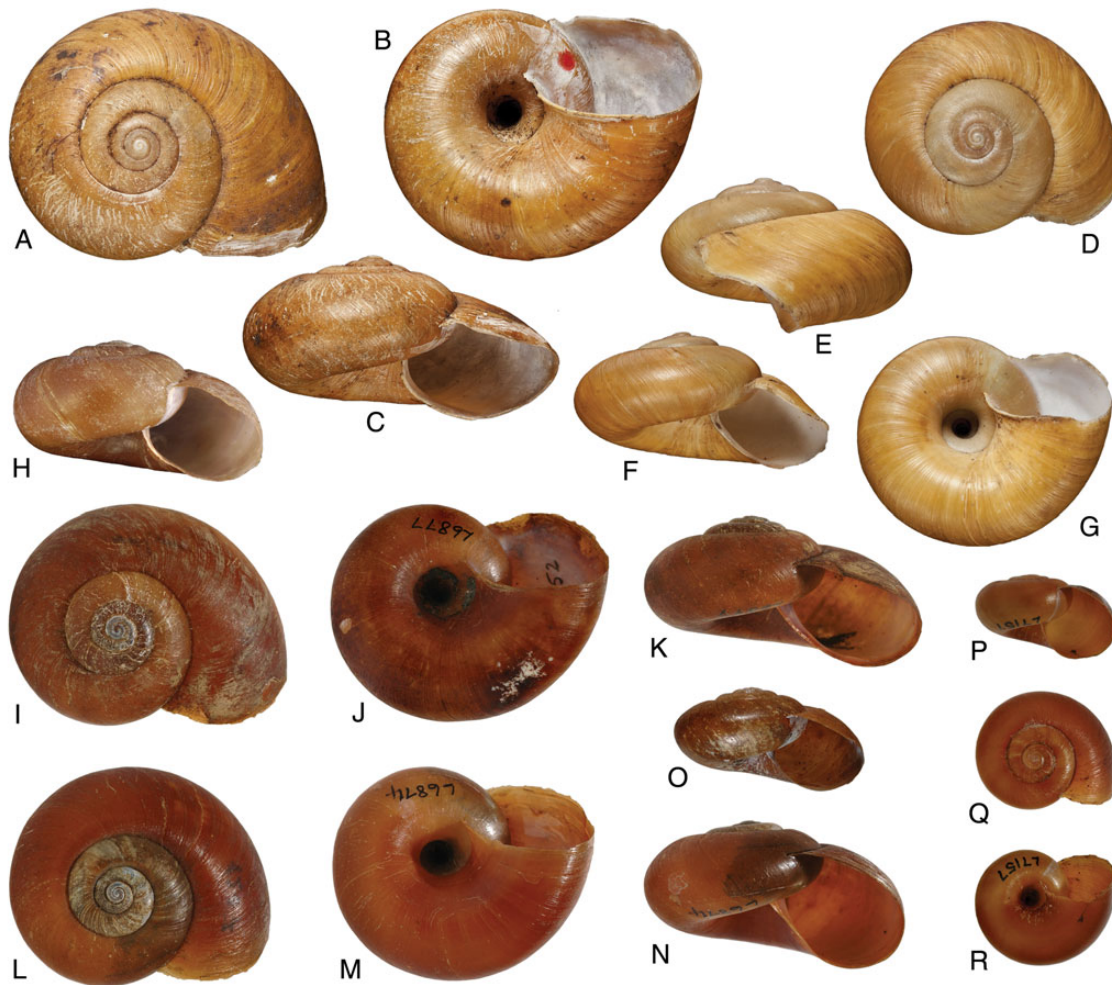
Family	Species	P1	P2	GenBank acc. no.	Museum reg. no.	Locality
Acavidae	<i>Acavus phoenix</i> (Pfeiffer, 1854)	–	–	AY014083*	–	–
Acavidae	<i>Ampelita capuroni</i> Fischer-Piette <i>et al.</i> , 1974	x	x	KP230505	NMSA L7303	Maromizaha Forest, Andasibe, Madagascar
Acavidae	<i>Ampelita lamarei</i> (Pfeiffer, 1853)	x	x	KP230504	NMSA L7348	Msoala Peninsula, Madagascar
Acavidae	<i>Ampelita milloti</i> Fischer-Piette, 1952	x	x	KP230503	NMSA L7195	Tsingy Beanka, Belitsaka, Madagascar
Rhytididae	<i>Austrorhytida capillacea</i> (Férussac, 1832)	x	x	KP230506	MV F193250	Yarra Range, Vic., Australia
Caryodidae	<i>Brazieresta larreyi</i> (Brazier, 1871)	x	x	KP230507	QM Mo64447	Coffs Harbour, NSW, Australia
Bulimulidae	<i>Bulimulus sporadicus</i> (Orbigny, 1835)	–	–	AY841299*	–	–
Rhytididae	<i>Capitina calcicola</i> Herbert & Moussalli, 2010	x	x	KP230527	NMSA W3369	Gansbaai, W Cape, South Africa
Caryodidae	<i>Caryodes dufresnii</i> (Leach, 1815)	–	–	AY014086*	–	–
Chlamydephoridae	<i>Chlamydephorus gibbonsi</i> Binney, 1879	x	x	KP230508	NMSA W9298	Port Shepstone, KZN, South Africa
Acavidae	<i>Clavator obtusatus</i> (Gmelin, 1791)		x	KP230509	NMSA L7542	Elenza, S of Ampanihy, Madagascar
Acavidae	<i>Clavator eximius</i> (Shuttleworth, 1852)	x	x	KP230510	NMSA L7154	Maromizaha Forest, Andasibe, Madagascar
Acavidae	<i>Clavator griffithsjonesi</i> Emberton 1999	x	x	KP230511	NMSA L7192	Tsingy Beanka, Belitsaka, Madagascar
Achatinidae	<i>Cochlitoma zebra</i> (Bruguière, 1789)	x	x	KP230512	NMSA W8920	De Hoop, W Cape, South Africa
Rhytididae	<i>Delos coresia</i> (Gray, 1850)	x	x	KP230514	MV F193257	Raglan, New Zealand
Dorcasidae	<i>Dorcasia alexandri</i> Gray, 1838	–	–	AY014079*	–	–
Caryodidae	<i>Hedleyella falconeri</i> (Gray, 1834)	x	x	KP230515	MV F193247	Border Ranges, NSW, Australia
Acavidae	<i>Helicophanta goudotiana</i> (Férussac, 1839)	x	x	KP230517	NMSA L7048	Tsingy Beanka, Belitsaka, Madagascar
Acavidae	<i>Helicophanta ibaraoensis</i> (Angas, 1879)	x	x	KP230516	NMSA L7166	Maromizaha Forest, Andasibe, Madagascar
?	<i>Helix covani</i> Smith, 1879	x	x	KP230513	NMSA L7157	Maromizaha Forest, Andasibe, Madagascar
Acavidae	<i>Leucotaenius favanii</i> (Lamarck, 1822)		x	KP230518	NMSA L7453	Beantsiva, S of Ampanihy, Madagascar
Acavidae	<i>Leucotaenius proctori</i> (Sowerby, 1894)	–	–	AY014085*	–	–
Strophocheilidae	<i>Megalobulimus oblongus</i> (Müller, 1774)	--	–	AY014078*	–	–
Rhytididae	<i>Nata dumeticola</i> (Benson, 1851)	x	x	KP230520	NMSA W3210	Langebaan, W Cape, South Africa
Rhytididae	<i>Nata vernicosa</i> (Krauss, 1848)	x	x	KP230521	NMSA W9130	Kap River Nat. Res., E Cape, South Africa
Rhytididae	<i>Natalina cafra natalensis</i> Herbert & Moussalli, 2010	x	x	KP230519	NMSA W8663	Pietermaritzburg, Shepstone, KZN, South Africa
Bothriembryontidae	<i>Placostylus eddytonensis</i> (Pfeiffer, 1855)	–	–	AY841297*	–	–
Bothriembryontidae	<i>Prestonella bowkeri</i> (Sowerby, 1889)	x	x	KP230522	NMSA W9367	Glen Avon, Somerset East, E Cape, South Africa
Rhytididae	<i>Prolesophanta dyeri</i> (Petterd, 1879)	x	x	KP230523	MV108 (tissue only)	Saxton, Vic., Australia
Pupillidae	<i>Pupoides myoporinae</i> (Tate, 1880)	x	x	KP230524	MV F183547	Ned's Corner, Vic., Australia
Rhytididae	<i>Rhytida greenwoodi greenwoodi</i> (Gray, 1850)	x	x	KP230525	MV F193251	Raglan, New Zealand
Rhytididae	<i>Schizoglossa novoseelandica</i> (Pfeiffer, 1862)	x	x	KP230526	MV F193252	Raglan, New Zealand
Rhytididae	<i>Strangesta gawleri</i> (Brazier, 1872)	x	x	KP230528	MV F193253	Mt Lofty, SA, Australia
Rhytididae	<i>Tasmaphena lamproides</i> (Cox, 1868)	x	x	KP230529	MV F193254	Wilson's Promontory, Vic., Australia
Rhytididae	<i>Terrycarlessia turbinata</i> Stanistic, 2010	x	x	KP230530	MV F193249	Green Mountain, NSW, Australia
Camaenidae	<i>Thersites novaehollandiae</i> (Gray, 1834)	x	x	KP230531	MV F193248	Comboyne, NSW, Australia
Dorcasidae	<i>Trigonephrus globulus</i> (Müller, 1774)	–	–	AY014081*	–	–
Dorcasidae	<i>Trigonephrus porphyrostoma</i> (M & P, 1891)	x	x	KP230532	NMSA W225	Grootderm, Alexander Bay, N Cape, South Africa
Rhytididae	<i>Victaphanta atramentaria</i> (Shuttleworth, 1852)	x	x	KP230533	MV F193255	Sylvia Creek, Vic., Australia
Rhytididae	<i>Victaphanta milligani</i> (Pfeiffer, 1853)	x	x	KP230534	MV F193256	Frog Flats, Tasmania, Australia

\*Sequences downloaded from GenBank (Wade *et al.* 2006). P1 = primer pair LSU1 and LSU3, P2 = primer pair LSU2 and LSU4. Institutions for registered voucher specimens: NMSA, KwaZulu-Natal Museum, South Africa; MV, Museum Victoria, Australia; QM, Queensland Museum, Australia. Family assignments follow Bouchet *et al.* (2005).

remains thin and unreflected even in the largest shells and it is usually only weakly descendant at the suture. The adapical surface of adult whorls bears fine, close-set, collabral riblets crossed by even finer and more close-set spiral threads; together these elements interact to produce a fine, obliquely reticulate microsculpture (Fig. 3C); in places the spiral sculpture may render the riblets microscopically granular. The sculpture is weaker on the base, but distinct again in the umbilical region.

The embryonic shell is small and spirally striate (see below). The coloration is more or less uniform, rich chestnut brown in fresh specimens, fading to tan or yellowish-brown in older material.

Specimens from southern localities within the range of the species (i.e. the granitic Andringitra Massif and environs) have shells with a slight peripheral angulation (Fig. 1O), but in other respects they closely resemble material from sites to the north.



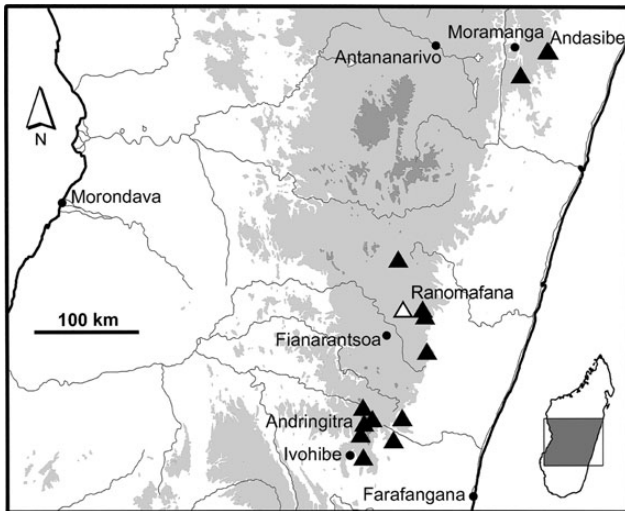
**Figure 1.** *Helix covani* Smith, 1879. **A–C.** NHMUK supposed ‘type’ (1882.3.4.9), diameter 44.5 mm. **D–G.** holotype, diameter 35.40 mm, NHMUK (1882.3.4.8). **H.** Anevoka, subadult, diameter 34.8 mm (ANSP A16399). **I–K.** Andasibe, diameter 39.0 mm (NMSA L6877). **L–N.** Ranomafana, subadult, diameter 36.7 mm (NMSA L6874). **O.** Andringitra area, SW of Ankarimbelo, diameter 27 mm (NMSA L9340). **P–R.** Andasibe, juvenile, diameter 19.7 mm (NMSA L7157).

*Type material:* Smith’s original description was based on a single specimen from ‘Madagascar’, with a diameter of 36 mm (Smith, 1879), but he subsequently obtained additional material from Rev. W.D. Cowan collected at Ankafana (Smith, 1882), the largest of which measured 45 mm in greatest diameter. The type lot in NHMUK (1882.3.4.8–9) contains three specimens, of which the largest has a greatest diameter of 44.5 mm, and the locality is given as Ankafana. This largest specimen has a red dot in the aperture indicating it to be the ‘type’ (Fig. 1A–C). However, it is evident that the subsequently acquired material was simply added to the original material; the dimensions of the shells indicate that the largest specimen was not the original singleton and thus it cannot be considered the holotype. The other two specimens are both within one millimetre of the maximum diameter given in the original description [one (with complete lip) measures 36 × 30 mm, the other (with broken lip) 35.4 × 29.5 mm, J. Ablett, personal communication, vi/2013]. Shell dimensions therefore do not help resolve which of these specimens was the original singleton and since the original description was not accompanied by an illustration, both appear to be candidate holotypes. However, Smith (1879: 338) stated in his description that the peristome was “subsimpler; its upper margin prominent in the middle” (our emphasis) and that the columellar edge was “slightly thickened, expanded and reflexed”.

These observations, particularly the former, clearly apply to one of the candidate holotypes (with broken lip, dimensions 35.4 × 29.5 mm) more than the other. We therefore feel confident in considering this to be the original singleton and thus the holotype (Fig. 1D–G). It has now been separated as NHMUK 1882.3.4.8 and the other two specimens (NHMUK 1882.3.4.9) are no longer regarded as type specimens.

*Type locality:* Madagascar (ex Rev. W.D. Cowan), later given as Ankafana, Betsileo Province [= Ankafina-Tsarafidy, NW of Ranomafana, c. 21.2°S, 47.2°E] (Smith, 1882).

*Other material examined:* Toamasina Prov.: Anevoka, 10.3 km W. of turnoff to Fanovana on Antananarivo–Tamatave [Toamasina] road (18.956°S, 48.478°E), 900 m a.s.l., primary gallery forest, 23/ix/1990, (ANSP A16399, KCE147); 12 km E of Andasibe (O. Griffiths coll.); Andasibe area, Maromizaha Forest (18.96159°S, 48.49176°E), primary rainforest, c. 1,000 m a.s.l., juvenile alive in decaying tree stump, leg. L. Davis, D. Herbert, A. Moussalli, R. Randalana & D. Stuart-Fox, 10/x/2006 (NMSA L7157); near Anamalazoatra [Andasibe] (18.962°S, 48.492°E), primary rain forest, 1990s, (NMSA L6877). Fianarantsoa Prov.: Andalrandranobe, 7.5 km N of Ambatofitorahana (20.7695°S, 47.1917°E), 1600 m a.s.l., upland forest, logged but never clear-cut, burned at edges, 25/ix/1990, (ANSP 16400, KCE154);



**Figure 2.** Map of central Madagascar showing distribution of *Helix covani* Smith, 1879; each triangle represents one or more records; hollow triangle indicates type locality. Contours at 1,000 and 1,500 m.

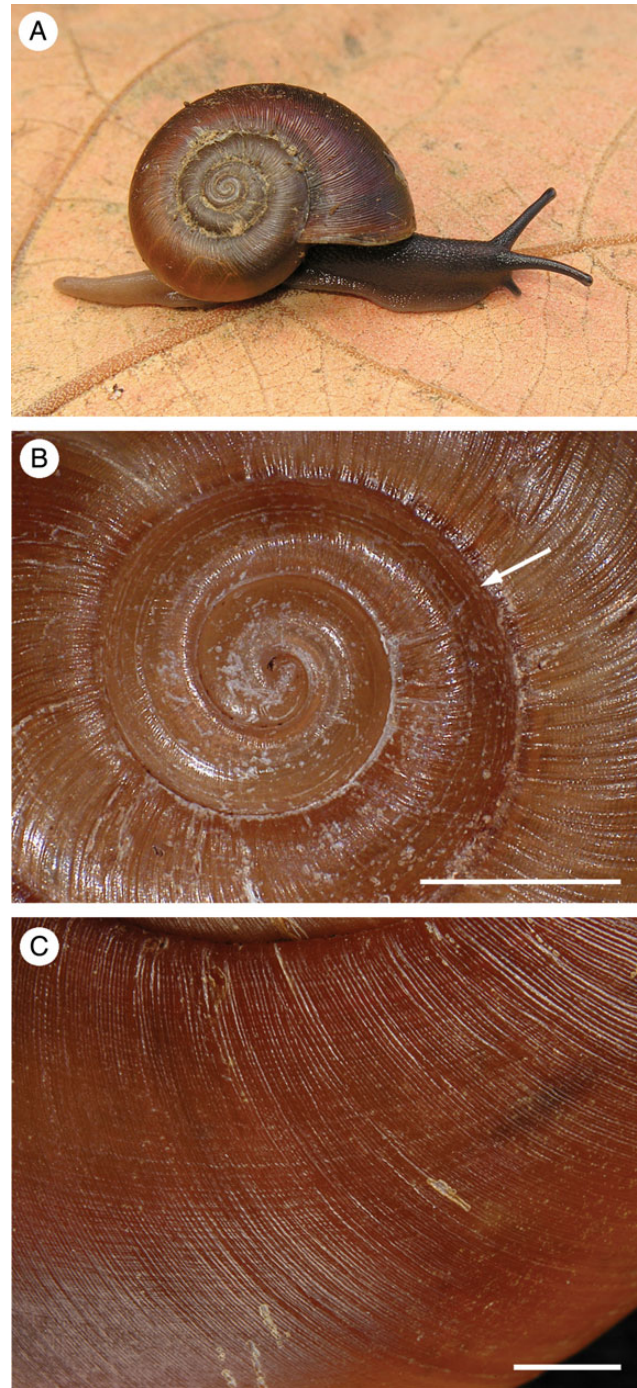
Ranomafana region, E of Fianarantsoa (21.323°S, 47.396°E), on ground and in dead leaves, 1990s, (NMSA L6874); Andrambavato, along railway line, ca 37 km E of Fianarantsoa (21.567°S, 47.458°E) (O. Griffiths coll. A636); Ambatobe, SW of village of Ankarimbelo, SE of Ambalavao (22.15722°S, 47.22464°E), 771 m a.s.l., in remnant montane forest on ridge top, xi/2012, (ex O. Griffiths Colln A4125) (NMSA L9340); Ankarimbelo area, 15 km SE of Andringitra Reserve (22.360°S, 47.158°E), c. 800 m a.s.l., dense mountain rainforest, 1997–2012 (NMSA L6881, L7148, L7149, L9280).

*Additional locality records* (material not examined): Toamasina Prov.: Forêt entre Moramanga et Anosibe [c. 19.2°S, 48.3°E], 800 m a.s.l. (Fischer-Piette, 1952). Fianarantsoa Prov.: Ranomafana Region: Ranomafana National Park, main trail system, 20–50 m along trail X (21.2555°S, 47.42083°E), 900 m a.s.l., rainforest, on ground, 26/x/1990 (ANSP 391638, KCE286). Andringitra Region: Forêt de Fivavona [Fivanona], Andringitra [ca 22.05°S, 46.88°E], 1949 (Fischer-Piette, 1952); summit of Anjavidilava [c. 22.15°S, 46.96°E] (Fischer-Piette *et al.*, 1994); Ambavahola [Ambavahala, c. 22.15°S, 46.95°E] (Fischer-Piette *et al.*, 1994); Sahanambo-Sahatena [W edge of Andringitra Reserve, c. 22.19°S, 46.84°E], (Fischer-Piette *et al.*, 1994); Forêt de la Vakoana, Andringitra [c. 22.19°S, 46.89°E], 1949 (Fischer-Piette, 1952); W slopes of l'Andrianony range, [c. 22.28°S, 46.86°E] (Fischer-Piette *et al.*, 1994); Forêt d'Amindramiova, 1,700–2,000 m a.s.l., Andringitra, 1949 (Fischer-Piette, 1952); Pic d'Hivohibe [Ivohibe, c. 22.48°S, 46.88°E], 2,100 m a.s.l., (Fischer-Piette & Garreau de Loubresse, 1965).

*Distribution* (Fig. 2): Recorded only from the highlands of central Madagascar, from the Andasibe [Perinet] area east of Moramanga (Toamasina Prov.), south to the Andringitra Massif and Ivohibe area (Fianarantsoa Prov.), a distance of c. 450 km.

*Habitat*: Primary rainforest at altitudes from 800 to 2,100 m. Little microhabitat data available, but evidently ground-dwelling, perhaps favouring rotting tree stumps (R. Randalana, personal communication).

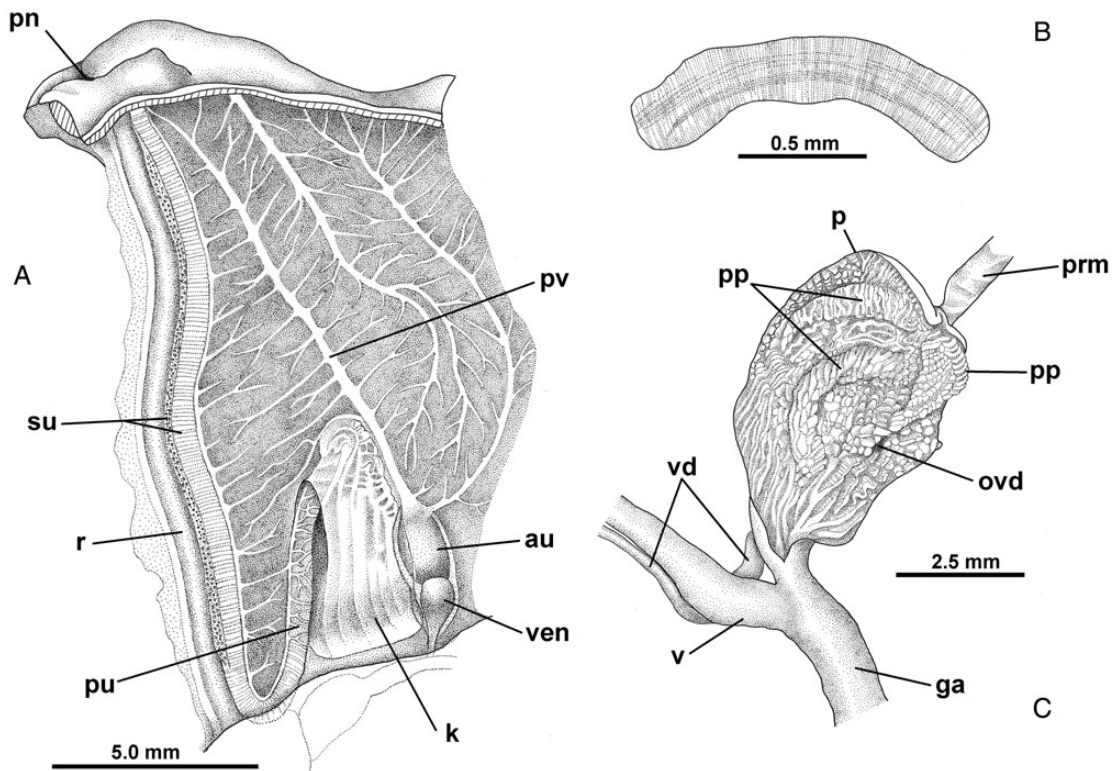
*Living animal* (Fig. 3A): Head and neck dark charcoal-grey to black, tail paler brown; skin texture finely granular, lacking strong grooves dorsally and on tail; peripodial groove also



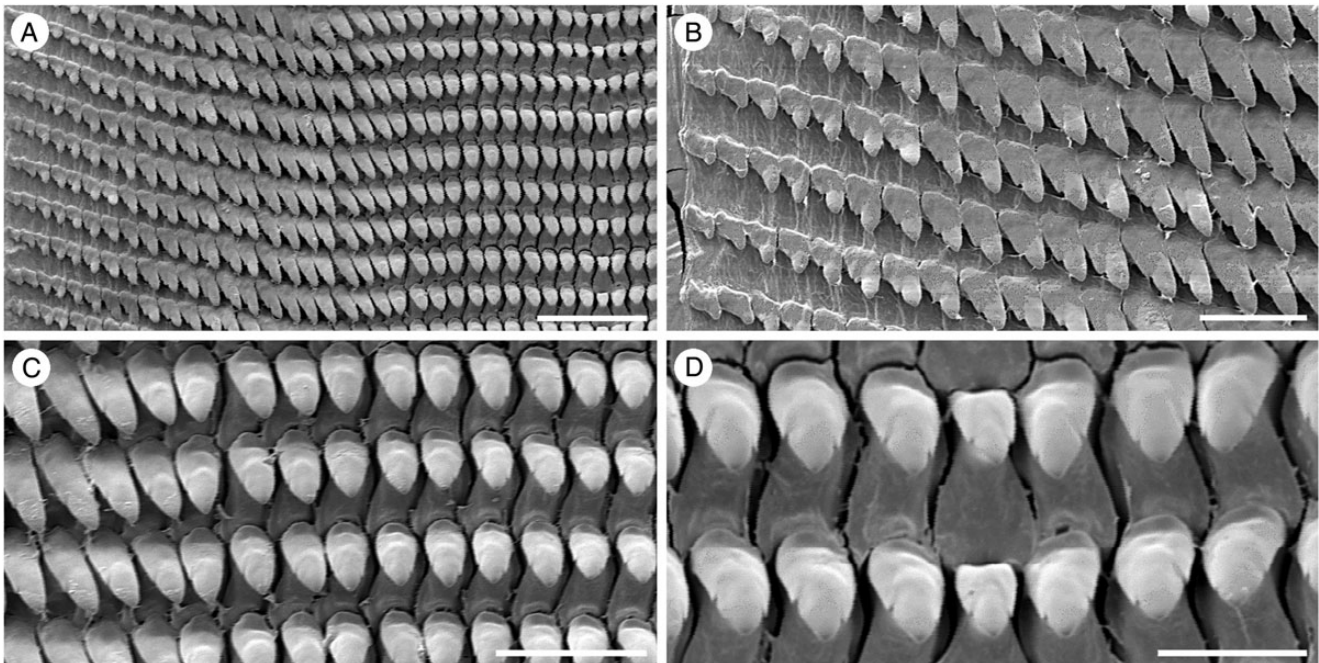
**Figure 3.** *Helix covani* Smith, 1879. **A.** Living animal, juvenile, shell diameter 19.7 mm, Andasibe area, Maromizaha Forest (NMSA L7157). **B.** Embryonic shell of the same specimen, arrow indicates start of teleoconch (NMSA L7157). **C.** Microsculpture on last adult whorl (NMSA L6877). Scale bars: **B** = 2.0 mm; **C** = 2.5 mm.

lacking, but a deep, slit-like channel extends around anterior pedal margin, on either side of opening of anterior pedal mucous gland; tentacles relatively stout; tail slender, uniformly tapering to bluntly rounded tip, lacking caudal pit and horn; neck region not conspicuously elongated; oral region lacking labial palps; genital pore ventral to and just posterior to right optic tentacle; foot sole undivided.

*Embryonic shell* (Fig. 3B): c. 1.5 relatively narrow whorls; sculptured with close-set microscopic axial threads and coarser,



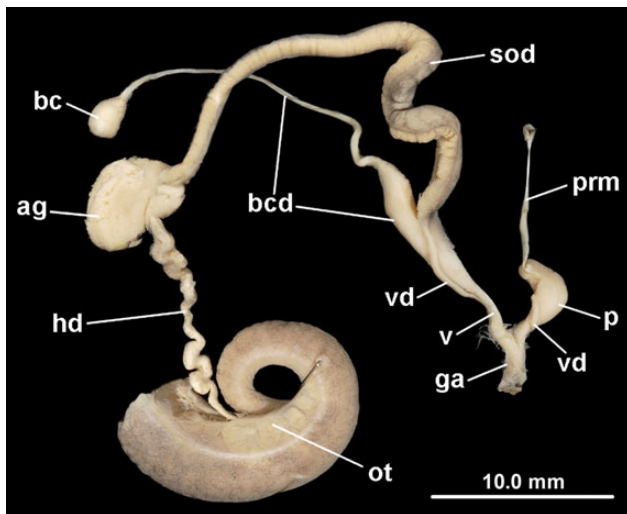
**Figure 4.** *Helix covani* Smith, 1879. **A.** Pulmonary anatomy (NMSA L7157). **B.** Jaw (NMSA L7157). **C.** Internal structure of penis (ANSP A16399). Abbreviations: au, auricle; ga, genital atrium; k, kidney; ovd, opening of vas deferens; p, penis; pn, pneumostome; pp, penis pilaster; prm, penial retractor muscle; pu, primary ureter; pv, pulmonary vein; r, rectum; su, secondary ureter; v, vagina; vd, vas deferens; ven, ventricle.



**Figure 5.** *Helix covani* Smith, 1879, radula (NMSA L7157). **A.** Half row. **B.** Outer marginal teeth. **C.** Lateral-marginal transition zone. **D.** Rachidian and inner lateral teeth. Scale bars: **A** = 150 µm; **B** = 50 µm; **C** = 100 µm; **D** = 25 µm.

relatively widely spaced incised spiral striae; junction between embryonic shell and teleoconch often not well defined and sculpture similar before and after. Diameter *c.* 4.0 mm.

*Pulmonary anatomy* (Fig. 4A): Mesurethrous. Kidney elongate-triangular, cardiac edge almost twice length of pericardium; renal pore near anterior extremity, opening into primary ureter,



**Figure 6.** *Helix covani* Smith, 1879, reproductive tract, Anevoka, 10.3 km W of turnoff to Fanovana on Antananarivo–Tamatave road (ANSP A16399). Abbreviations: ag, albumen gland; bc, bursa copulatrix; bcd, bursa copulatrix duct; ga, genital atrium; hd, hermaphrodite duct; ot, ovotestis; p, penis; prm, penial retractor muscle; sod, spermoviduct; v, vagina; vd, vas deferens.

the early part of which is covered with a hood-like flap, but is thereafter an open conduit running along right side of kidney to posterior of pulmonary cavity where it turns sharply forward to become secondary ureter that runs anteriorly alongside rectum to pneumostome; wall of secondary ureter divided into two distinct, parallel tracts. Lining of pulmonary cavity well vascularized, veins conspicuous against dark pigmentation of cavity lining; pulmonary vein with side branches on both sides, and with a lateral branch on left joining it close to pericardium.

*Jaw* (Fig. 4B): Present; comprising a single curved plate, with a slight mid-line bulge on ventral margin; surface smooth, but with numerous fine, scratch-like, vertical striations (aulacognathous) and fewer, curved, longitudinal lines.

*Buccal mass and radula* (Fig. 5): Buccal mass relatively small, spherical to ovate, situated almost entirely anterior to circum-oesophageal nerve ring.

Radula comparatively short and broad, length 6.87 mm, width 2.0 mm (subadult specimen, shell diameter 34.8 mm, ANSP A16299), with *c.* 170, more or less straight, transverse rows of teeth, each with *c.* 87 teeth; formula 1 + 20 + 23, but transition from lateral to marginal teeth gradual with no precise distinction between the series. Rachidian with elongate, roundly trigonal base-plate and shaft; cusp triangular, somewhat smaller than that of neighbouring laterals, with dominant mesocone and single small ectocone on each side, appearing almost monocuspid. Laterals with an asymmetrical, sinuously rectangular base-plate and shaft, bearing roundly trigonal cusp; cusp flat or broadly rounded basally (anteriorly), bluntly pointed apically and essentially monocuspid, although some teeth (particularly the inner ones) retain weak endocone and slightly more basal ectocone. Cusps of inner marginal teeth similar to laterals but somewhat more elongate and angled toward midline of radula, becoming progressively shorter and with progressively more prominent ectocone toward edge of radula; outer marginals reduced, bearing small mesocone and laterally expanded ectocone.

*Genital system* (Figs 4C, 6): Distal reproductive tract relatively simple, lacking auxiliary structures (e.g. dart sac, accessory glands, appendages and stimulatory organs). Penis relatively

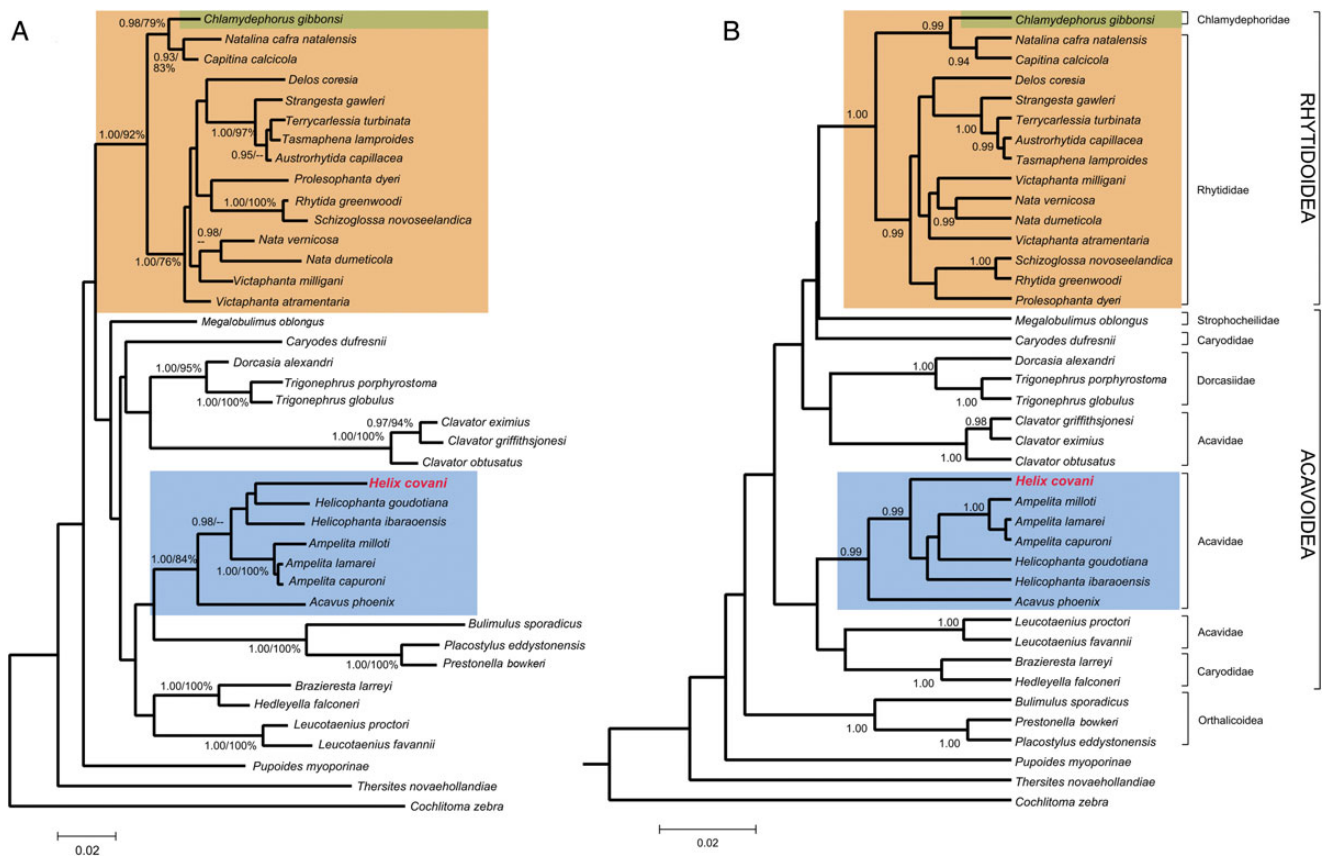
short, clavate, broader and curved apically, narrowing basally towards junction with genital atrium; no epiphallus or flagellum evident, retractor muscle attached to penis tip. Retractor muscle of optic tentacle passes between penis and spermoviduct. Vas deferens distinct, not convoluted; from its origin at base of spermoviduct it runs beside free oviduct and vagina to the angle between vagina and penis at which point it is embedded in loose connective tissue; from this angle it is closely adherent curving around and up penis, inserting approximately halfway along penis on its opposite side. Inner lining of penis with three longitudinal pilasters in clavate apical region (Fig. 4C), separated by papillate intervals; crests of pilasters with close-set, transverse folds; basal region with finer longitudinal ridges; opening of vas deferens a simple foramen lacking swollen rim, papilla or verge of any kind. Vagina of moderate length, proximally slender near its junction with genital atrium, distally more swollen near origin of bursa copulatrix duct. Proximal region of bursa copulatrix duct markedly swollen, but remainder long and slender, terminating in small, ovate bursa copulatrix (gametolytic sac). Free oviduct short. Spermoviduct long, distally sinuous, tapering progressively toward albumen gland, divided into distinct prostatic and oviducal portions. Albumen gland roundly reniform; hermaphrodite duct convoluted, thinner in mid region; ovotestis present as several distinct lobes, embedded in upper whorl of digestive gland.

#### Molecular analyses

Sequences were obtained for all samples using the primer pair LSU2/LSU4, while only a subset was obtained using LSU1/LSU3 (Table 1). Sequences varied in length due to indels, ranging from 816 to 834 bp. Four minor indel regions were removed due to alignment ambiguity. A total of 812 bp were unambiguously aligned and used in the analyses. Both likelihood and Bayesian analyses provided strong support (support defined as bootstrap probability BS > 75, posterior probability PP > 0.95) for the monophyly of the superfamily Rhytidoidea (Fig. 7, orange boxes) and also for a clade encompassing a subset of Madagascan acavids plus *Acaeus phoenix* (Pfeiffer, 1854) from Sri Lanka (Fig. 7, blue boxes). However, the family Rhytididae is paraphyletic, with *Chlamydephorus* Binney, 1879 (Fig. 7, green boxes) being sister to a clade encompassing the South African genera of large carnivorous snails, *Natalina* Pilsbry, 1893 and *Capitina* Watson, 1934. The phylogenetic analyses provided little resolution of relationships between the major lineages traditionally referred to the Acaevidae. It is clear, however, that the family contains considerable phylogenetic diversity, with the genera *Leucotaenius* Martens, 1860 and *Clacator* Martens, 1860 representing deeply divergent lineages. Of particular interest in terms of the present study is the phylogenetic position of *H. covani*. The analyses clearly support the acavid affinities of this taxon, with a close and strongly supported relationship to the Madagascan acavid genera *Ampelita* and *Helicophanta* Férussac, 1821.

## DISCUSSION

The morphological characters shown by *Helix covani* strongly contradict referral of the species to the Rhytididae. The most conspicuous of these relate to the carnivorous mode of life of rhytidids. First, whereas a jaw is absent in rhytidids, an aulacognathous jaw is present in *H. covani*. Second, the elongate, enlarged and highly muscular buccal mass typical of rhytidids is absent. Instead the buccal mass of *H. covani* is relatively small and ovate or spherical, rather than elongate. Third, the radula of *H. covani* is relatively short and delicate, with polyglossate dentition typical of a herbivore, differing greatly from the long, beloglossate radula of rhytidids (Powell, 1930; Kondo, 1943; Herbert & Moussalli, 2010).



**Figure 7. A.** MrBayes and **B.** relaxed clock BEAST trees based on 28S rRNA sequences and GTR+G model of sequence evolution. *Helix covani* clusters in a strongly supported clade with Madagascan and Sri Lankan acavids (blue boxes). The Rhytididae (orange boxes) is paraphyletic and includes the chlamydephorid slugs (green boxes). Nodal support values represent posterior probabilities followed by RAXML bootstrap in the MrBayes tree (supported topology was consistent between analyses) and posterior probability in the relaxed BEAST tree. Only posterior probabilities greater 0.95 and bootstrap probabilities greater than 75% are shown. *Pupoides myoporinae*, *Thersites novaehollandiae* and *Cochlitoma zebra* were collectively constrained as the outgroup.

These features alone are sufficient to indicate that *H. covani* cannot be referred to the Rhytididae, but additional characters from other organ systems are also concordant with this view. In the pulmonary cavity, the morphology of the primary ureter is noteworthy, since in *H. covani* this is only covered over for a short distance beyond its origin at the anterior of the kidney, whereas in rhytidids the primary ureter is closed for its entire length (Watson, 1934; Kondo, 1943; Tillier, 1989; Schileyko, 2000; Herbert & Moussalli, 2010). Characters of the external soft anatomy, namely the relatively short neck region and the absence of a pair of longitudinal grooves along the dorsal mid-line of the neck, are atypical of a rhytidid. Features of the distal reproductive tract are less informative, since these are relatively simple, lacking specialized accessory structures both in rhytidids and acavids, as they are in *H. covani*.

This rejection on morphological grounds of Emberton's (1990) hypothesis concerning the rhytidid affinity of *H. covani* is confirmed by our molecular data. The molecular evidence unequivocally supports the long-held view that *H. covani* belongs within the Acavidae and suggests close affinity to the Madagascan genera *Ampelita* and *Helicophanta*. Further comparative re-evaluation of the morphological characters in the light of this provides additional support for the molecular evidence. Certainly the gross morphology of the buccal mass is consistent with that of a herbivore, as is the morphology of the radula mentioned above and its fine, polyglossate dentition. Moreover the essentially monocuspid form of the cusps of the lateral teeth, with quadrate but somewhat sinuous base-plates is

very similar to that depicted for acavids in general and *Ampelita* species by Pilsbry (1895, in 1893–5), Fischer-Piette (1950, 1952) and Fischer-Piette & Garreau de Loubresse (1965). The aulacognathous jaw likewise accords with an acavid relationship (Schileyko, 1999) and is similar to that illustrated for *Helicophanta* (Fischer-Piette, 1950) and *Ampelita* (Schileyko, 1999). The basally hooded, but otherwise open, primary ureter is also a feature found in *Ampelita* (Tillier, 1989).

In terms of the distal reproductive tract, the features described above for *H. covani* are entirely consistent with those of *Ampelita* (Emberton, 1990; Schileyko, 1999)—accessory structures are absent, the duct of the bursa copulatrix is swollen basally, the penis is short and clavate with the retractor muscle attached close to its apex, the vas deferens is adherent to the penis, and an epiphallus is absent.

When referring *H. covani* to *Ampelita* for the first time, Pilsbry was unable to find any features that linked the species with any of his *Ampelita* species groups (Pilsbry, 1890, in 1990–91). Instead he chose to treat it in a cluster of ungrouped species and later placed it in a group of its own (Pilsbry 1894, in 1893–95). As currently interpreted, *Ampelita s. l.* is a speciose taxon, now including over 90 species, few of which have been examined morphologically. Based on the characters used by Emberton (1990) in his subgeneric revision of the genus, *H. covani* would belong in an unresolved grouping representing *Ampelita s. s.* However, this is due more to the fact that it does not possess the defining autapomorphic characters of the other subgenera, rather than to any meaningful synapomorphies it shares with *Ampelita s. s.* The



morphological observations presented here demonstrate that *H. covani* possesses a number of features that set it apart from most of the species currently referred to *Ampelita s. s.* These include the relatively small size of the embryonic shell and its rather coarse spiral striae, the microscopically reticulate sculpture of the last adult whorl, and the limited reflection and thickening of the peristome at maturity. In terms of the reproductive tract, the absence of a papilla or verge in the penis also differs from the situation in other species for which such data are available (Schileyko, 1999; Griffiths & Herbert 2013), but since this is so few, it is largely uninformative from a phylogenetic perspective.

Our molecular data do not resolve the position of *H. covani* within the Madagascan *Ampelita–Helicophanta* clade but, given that our analyses are preliminary, being based on a single marker and with limited sampling of acavid diversity, this is not unexpected. The drawing of conclusions concerning systematic relationships within the Acavidae is beyond the scope of this study. Only two of the four currently recognized subgenera of *Ampelita* (Emberton, 1990) are represented in the phylogeny, namely *Ampelita s. s.* and *Xystera* Emberton, 1990. Little definitive progress can be made in this regard until morphological and molecular data are available for a broader spectrum of species. For the present, therefore, we propose that *H. covani* be referred to *Ampelita s. l.*, pending the availability of a more representative dataset and a more robust analysis.

Although peripheral to the question at hand, two additional features of interest in our molecular phylogeny are worthy of comment. The first is the paraphyly of the Rhytididae resulting from the sister-group relationship of chlamydephorid slugs and the larger South African rhytidid genera (*Natalina* and *Capitina*). The close relationship of chlamydephorid slugs and rhytidid snails has long been recognized (Watson, 1915), but the two families have been maintained as separate entities by the majority of authors (e.g. Bouchet *et al.*, 2005). Tillier (1989), however, believed that chlamydephorids, like the New Zealand genus *Schizoglossa* Hedley, 1892, were simply limaciform rhytidids, and considered them a subfamily within the Rhytididae. Our phylogeny provides the first molecular evidence in support of this. The second noteworthy point is the lack of resolution concerning the position of other Madagascan genera traditionally referred to the Acavidae, namely *Leucotaenius* and *Clavator*. Wade *et al.* (2006) have already commented on this in respect of *Leucotaenius* and our results indicate that the relationships of *Clavator*, though well supported as a generic entity, are similarly not resolved. That *Clavator* appears to be distant and deeply divergent from the main acavid clade supports the view that it may warrant recognition as a distinct family (Thiele, 1931; Schileyko, 1999). However, it is apparent that the 28S rRNA gene is not able to resolve deeper relationships within the Acavoidea and clarification of these issues will require the use of additional markers or a genomic approach. These additional perspectives will be explored in greater detail as part of a broader scale study of Gondwana-wide relationships within and between the Acavoidea and Rhytidoidea.

In conclusion, it is clearly evident from morphological study of the soft parts that *Helix covani* is not referable to the family Rhytididae. The assertion that the family is represented in Madagascar (Emberton, 1990) is therefore unfounded. Based on our current knowledge, the Madagascan malacofauna includes no members of the Rhytididae. All indications (morphological and molecular) strongly suggest that *H. covani* is referable to the Acavidae. Thus although the malacofauna of Madagascar has clear family-level Gondwanan links with that of the Seychelles and Sri Lanka (family Acavidae), such links with Africa appear to be absent. Only at the deeper, more ancient, superfamily-level do links of this nature become apparent (Acavoidea: including Acavidae and Dorcasiidae).

## ACKNOWLEDGEMENTS

We acknowledge in particular Linda Davis (NMSA) for her help in the field and for preparing the anatomical drawings of dissected specimens. In addition, we thank Roger Randalana and Devi Stuart-Fox (University of Melbourne) for assistance in the field and Bema Andriamamonjy of Biodiversity Conservation Madagascar for logistical support. Jon Ablett (NHMUK) kindly supplied photographs of NHMUK type material and we thank Gary Rosenberg and Paul Callomon for the loan of ANSP specimens. Andrew Hugall kindly provided sequence data for *Brazieresta larreyi* and Gary Barker supplied tissue samples for New Zealand species. Our gratitude is also extended to the authorities in the Ministère de l'Environnement, des Eaux et Forêts et du Tourisme, Madagascar, for permission to collect material (permit numbers 173/06 and 205/09) and to Mireille Saory (Ministère de l'Environnement, des Eaux et Forêts et du Tourisme), Hajanirina Ramino (Tsimbazaza Museum) for their co-operation in this regard. SEM facilities were made available by the Centre for Electron Microscopy, University of KwaZulu-Natal, Pietermaritzburg. This research was supported by a grant to DH from the National Research Foundation (NRF) of South Africa (GUN 81078) and facilitated by Biodiversity Conservation Madagascar. Research permits for additional samples used in molecular phylogeny: Ezemvelo KZN Wildlife (4674 and OP 5180/2012), Western Cape Nature (L5628759 and AAA007-00021-0035), NSW-NPWS (SL101119), QLD-NPWS (TK12586613) and VIC (10004328).

## REFERENCES

- BOUCHET, P., FRÝDA, J., HAUSDORF, B., PONDER, W., VALDES, A. & WARÉN, A. 2005. Working classification of the Gastropoda. Part 2 (pp. 240–284). In: Classification and nomenclator of gastropod families (P. Bouchet & J-P. Rocroi). *Malacologia*, **47**: 1–397.
- BRUGGEN, A.C. VAN 1980. Gondwanaland connections in the terrestrial molluscs of Africa and Australia. *Journal of the Malacological Society of Australia*, **4**: 215–222.
- BRUGGEN, A.C. VAN 1981. The African element among the terrestrial molluscs of the island of Madagascar. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C*, **84**: 115–129.
- BRUGGEN, A.C. VAN 1994. *Semper aliquid novi ex Africa*. Instituut voor Evolutionaire en Ecologische Wetenschappen, Rijksuniversiteit Leiden.
- CHEVALLIER, H. 1964. Catalogue des exemplaires de Crosse et Fischer correspondant aux planches des mollusques de Madagascar. *Journal de Conchyliologie*, **104**: 29–34.
- CROSSE, H. & FISCHER, P. 1889. Histoire naturelle des mollusques, Atlas. In: *Histoire physique, naturelle et politique de Madagascar*, Vol. 25 (A. Grandidier, eds), pp. 1–26. Paris.
- DRUMMOND, A.J., SUCHARD, M.A., XIE, D. & RAMBAUT, A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**: 1969–1973.
- EMBERTON, K.C. 1990. Acavid land snails of Madagascar: subgeneric revision based on published data (Gastropoda: Pulmonata: Stylommatophora). *Proceedings of the Academy of Natural Sciences of Philadelphia*, **142**: 101–117.
- FISCHER-PIETTE, E. 1950. Mollusques terrestres de Madagascar genre *Helicophanta*. *Journal de Conchyliologie*, **90**: 82–106.
- FISCHER-PIETTE, E. 1952. Mollusques terrestres de Madagascar genre *Ampelita*. *Journal de Conchyliologie*, **92**: 5–62, pls 1–4.
- FISCHER-PIETTE, E., BLANC, C.P., BLANC, F. & SALVAT, F. 1994. *Faune de Madagascar*. 83. *Gastéropodes terrestres pulmonés*. Muséum National d'Histoire Naturelle, Paris.
- FISCHER-PIETTE, E. & GARREAU DE LOUBRESSE, N. 1965. Mollusques terrestres de Madagascar. Famille Acavidae. *Journal de Conchyliologie*, **104**: 129–160, pls 7–9.

- GERLACH, J. 1995. The taxonomic affinities of the genus *Priodiscus* (Mollusca: Gastropoda: Streptaxidae). *Journal of Conchology*, **35**: 357–368.
- GRIFFITHS, O. & HERBERT, D. 2008. Les mollusques terrestres et dulçaquicoles. In: *Paysages naturels et biodiversité de Madagascar* (S.M. Goodman, eds), pp. 227–247. Muséum National d'Histoire Naturelle, Paris.
- GRIFFITHS, O.L. & HERBERT, D.G. 2013. 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. *African Invertebrates*, **54**: 1–48.
- HERBERT, D.G. & MOUSSALLI, A. 2010. Revision of the larger cannibal snails (*Natalina s.l.*) of southern Africa—*Natalina s. s.*, *Aforhytida* and *Capitina* (Mollusca: Gastropoda: Rhytididae). *African Invertebrates*, **51**: 1–132.
- HUELSENBECK, J.P. & RONQUIST, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**: 754–755.
- KOBELE, W. 1909. Die Molluskenausbeute der erlangerschen Reise in Nordost-Afrika. Zweite Abteilung Verzeichnis der aus Afrika bekannten Binnenconchylien. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **32**: 53–97.
- KONDO, Y. 1943. Anatomical studies on three species of *Ouagapia* (Pulmonata, Agnatha, Paryphantidae). *Occasional Papers of the Bernice P. Bishop Museum*, **17**: 229–248.
- MOUSSALLI, A., HERBERT, D.G. & STUART-FOX, D. 2009. A phylogeny of the cannibal snails of southern Africa, genus *Natalina sensu lato* (Pulmonata: Rhytididae): assessing concordance between morphology and molecular data. *Molecular Phylogenetics and Evolution*, **52**: 167–182.
- PEARCE, T.A. 2003. Gastropoda, terrestrial snails. In: *The natural history of Madagascar* (S.M. Goodman & J.P. Benstead, eds), pp. 529–574. University of Chicago Press, Chicago.
- PILSBRY, H.A. 1890–91. Helicidae, Vol. 4. *Manual of Conchology*, Ser. 2, Vol. 6. Academy of Natural Sciences, Philadelphia. Pp 1–64, pls 1–15 [27 May, 1890]; pp 65–128, pls 16–30 [12 Aug. 1890]; 129–192, pls 31–47 [16 Dec. 1890]; pp 193–324, pls 48–69 [1 May, 1891].
- PILSBRY, H.A. 1893–95. Helicidae, Vol. 7. *Manual of Conchology*, Ser. 2, Vol. 9. Academy of Natural Sciences, Philadelphia. Pp 1–48, pls 1–14 [16. Nov. 1893]; pp 49–112, pls 15–28 [19 March, 1894]; pp 113–160, pls 29–40 [27, July, 1894]; pp 161–336, i–xlvii, pls 41–71 [2 Feb. 1895]; index 1–126 [April, 1895].
- PILSBRY, H.A. 1919. A review of the land mollusks of the Belgian Congo chiefly based on the collections of the American Museum Congo Expedition, 1909–1915. *Bulletin of the American Museum of Natural History*, **40**: 1–370.
- POWELL, A.W.B. 1930. The Paryphantidae of New Zealand: their hypothetical ancestry, with descriptions of new species and a new genus. *Records of the Auckland Institute and Museum*, **1**: 17–56.
- RAMBAUT, A. & DRUMMOND, A.J. 2007. Tracer v1.4: MCMC trace analyses tool. <http://beast.bio.ed.ac.uk/Tracer>. Accessed 20 June 2008.
- RICHARDSON, C.L. 1989. Streptaxacea: a catalog of species. Part II; Ammonitellidae, Chlamydephoridae, Haplotrematidae, Rhytididae, Systrophiiidae. *Tryonia*, **18**: i, 1–154.
- RONQUIST, F. & HUELSENBECK, J.P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**: 1572–1574.
- SCHILEYKO, A.A. 1999. Treatise on Recent terrestrial pulmonate molluscs. Part 4. Draparnaudiidae, Caryodidae, Macrocyclidae, Acavidae, Clavatoridae, Dorcasiidae, Sculpitariidae, Corillidae, Plectopylidae, Megalobulimidae, Strophocheilidae, Cerionidae, Achatinidae, Subulinidae, Glessulidae, Micractaeonidae, Ferrussaciidae [sic]. *Ruthenica*, **Suppl. 2**: 436–564.
- SCHILEYKO, A.A. 2000. Treatise on Recent terrestrial pulmonate molluscs. Part 6. Rhytididae, Chlamydephoridae, Systrophiiidae, Haplotrematidae, Streptaxidae, Spiraxidae, Oleacinidae, Testacellidae. *Ruthenica*, **Suppl. 2**: 729–880.
- SMITH, B.J. 1998. Family Rhytididae. In: *The southern synthesis. Fauna of Australia*. Vol. 5, part B. *Mollusca* (P.L. Beesley, G.J.B. Ross & A. Wells, eds), pp. 1091–1093. CSIRO Publishing, Melbourne.
- SMITH, E.A. 1879. Descriptions of two species of Helicidae from Madagascar. *Journal of Conchology*, **2**: 337–339.
- SMITH, E.A. 1882. A contribution to the molluscan fauna of Madagascar. *Proceedings of the Zoological Society of London*, **1882**: 375–389.
- SOLEM, A. 1959. Systematics and zoogeography of the land and fresh-water Mollusca of the New Hebrides. *Fieldiana: Zoology*, **43**: 1–359.
- STAMATAKIS, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**: 2688–2690.
- TAMURA, K., PETERSON, D., PETERSON, N., STECHER, G., NEI, M. & KUMAR, S. 2011. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, **28**: 2731–2739.
- THIELE, J. 1911. Mollusken der deutschen Zentral-Afrika-Expedition. *Wissenschaftliche Ergebnisse der deutschen Zentral-Afrika-Expedition, 1907–1908*. Band 3, Zoologie I, pp. 175–214. Klinkhardt & Biermann, Leipzig.
- THIELE, J. 1931. *Handbuch der systematischen Weichtierkunde*. Vol. 2, pp. 376–778. Fischer, Jena.
- THOMPSON, J.D., HIGGINS, D.G. & GIBSON, T.J. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. *Nucleic Acids Research*, **22**: 4673–4680.
- TILLIER, S. 1989. Comparative morphology, phylogeny and classification of land snails and slugs (Gastropoda: Pulmonata: Stylommatophora). *Malacologia*, **30**: 1–303.
- VERDCOURT, B. 1958. Descriptions of two new taxa of *Tayloria* Bgt. together with a synopsis of the genus. *Revue de Zoologie et de Botanique Africaine*, **58**: 267–276.
- WADE, C.M. & MORDAN, P.B. 2000. Evolution within the gastropod molluscs: using the ribosomal RNA gene cluster as an indicator of phylogenetic relationships. *Journal of Molluscan Studies*, **66**: 565–570.
- WADE, C.M., MORDAN, P.B. & NAGGS, F. 2006. Evolutionary relationships among the pulmonate land snails and slugs (Pulmonata, Stylommatophora). *Biological Journal of the Linnean Society*, **87**: 593–610.
- WATSON, H. 1915. Studies on the carnivorous slugs of South Africa. *Annals of the Natal Museum*, **3**: 107–267.
- WATSON, H. 1934. *Natalina* and other South African snails. *Proceedings of the Malacological Society of London*, **21**: 150–193.