SPECIES DIVERSIFICATION IN A TROPICAL RAINFOREST LAND-SNAIL FAUNA

Final Report

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1. BACKGROUND

Terrestrial biological diversity is not distributed evenly across the globe, but is concentrated in the forested tropics (Myers *et al.*, 2000; Sechrest *et al.*, 2002; Mittermeier *et al.*, 2004). Our understanding of the evolutionary processes that have generated and maintained this diversity is poor, but such knowledge will be vital for conserving both the patterns and processes of diversity in the face of ongoing and future environmental change (Mace *et al.*, 2003; Moritz & McDonald, 2005).

Using land snails as a focal group and an approach centred on molecular systematics and community ecology, my 18-month fellowship aimed to investigate speciation and ecological diversification in two Sri Lankan rainforest snail genera, the pulmonate *Corilla* and the caenogastropod *Theobaldius*. In common with other taxa from other tropical rainforest regions (Moritz, *et al.*, 2000; Hall, 2005; Weir, 2006; Brumfield & Edwards, 2007; Elias *et al.*, 2009; Santos *et al.*, 2009), *Corilla* and *Theobaldius* are represented by distinct species assemblages in lowland and montane rainforest. The study had two broad objectives: first, to reconstruct the evolution of these distinct lowland and montane assemblages, and second, to explore the relationship between species diversification and niche evolution.

Work to date has been focussed on carrying out molecular and initial phylogenetic analyses on the two land-snail genera, *Corilla* and *Theobaldius*. In addition, I have been working on a major new taxonomic revision (Raheem *et al*., in press) on the land-snail fauna of the Western Ghats of India, as well two smaller related projects, one on the widespread Asian land snail *Macrochlamys*, and the other on the type collections of William Benson, the pioneering 19th century worker on Indian land snails. These taxonomic projects are of crucial relevance to my evolutionary research because of the close faunistic affinities between Sri Lanka and India, particularly the Western Ghats. A substantial share of the species richness of both the Sri Lankan and the Western Ghats snail faunas is made up of species belonging to shared genera. Thus, an indepth-understanding of land-snail diversification in Sri Lanka (or the Western Ghats) must necessarily involve studying diversification across several such genera and include representative taxa from both India and Sri Lanka. This is an area of research I hope to pursue in the near future in collaboration with other workers from the South Asian region. My taxonomic work, particularly my revision of the Western Ghats fauna, will provide an invaluable starting point and foundation for such work. Furthermore, it will have a much wider impact because of the fact that much of the pioneering work on the taxonomy of Asian land snails was done in South Asia and the Western Ghats in particular. Genera, for example, such as the pulmonate snail *Macrochlamys* and the caenogastropod *Pterocyclos*, which are speciose in Southeast Asia, were first described from India.

For the duration of my fellowship I was hosted by and based at the Royal Belgian Institute of Natural Sciences (RBINS) in Brussels. I was part of the research group led by Thierry Backeljau. During my time at RBINS I worked closely with Karin Breugelmans and benefitted from the expertise of several colleague, particularly Arantza Elejalde, Séverine Fourdrilis, Zoltan Nagy, Gontran Sonet, Vanya Prévot and Hilde Vrijders. Important collaborators outside RBINS included Fred Naggs (The Natural History Museum, London, NHM), Chris Wade (University of Nottingham), Richard Preece (University Museum of Zoology, Cambridge, UMZC) and Siran Deraniyagala (Archaeological Department, Sri Lanka).

My time at RBINS has allowed me to develop my role as an active member of the growing network of South and South East Asian land-snail researchers, whose research is being facilitated and supported by RBINS. Key researchers who belong to this network and carry out collaborative research include Prem Budha (University of Tribhuvan) from Nepal, Aravind Madhyastha (Ashoke Trust for Research in Ecology and the Environment, ATREE) from India, the research group led by Somsak Panha at Chulalongkorn University in Bangkok,Thailand, and myself from Sri Lanka.

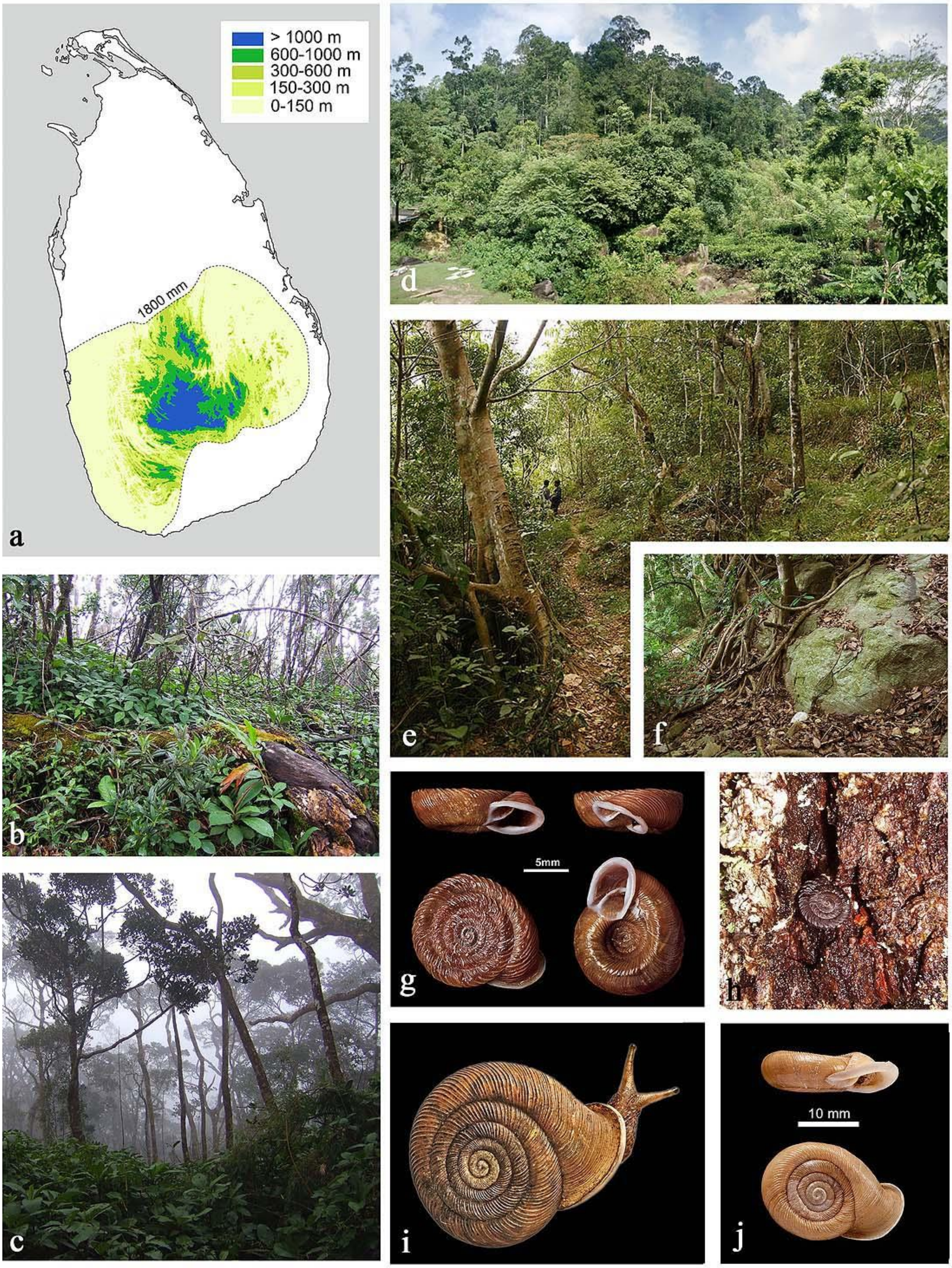

Figure 1. A, the distribution of *Corilla* in Sri Lanka extends across the region bounded by the 1800 mm rainfall isohyet (shaded in pale green through to blue). **B, C**, montane rainforest habitats of *C. beddomeae* and *C. erronea*. **D**, lowland rainforest habitat of *C. adamsi*. **E**, habitat of *C. colletti* in an area of abandoned tea that is returning to forest. **F**, habitat of *C. carabinata* among rocks and leaf litter in secondary moist monsoon forest. **G**, shell of *C. beddomeae* showing the angled periphery and wrinkled sculpture distinctive of this species. **H**, juvenile *C. beddomeae* feeding on decaying wood. **I**, adult *C. adamsi*. **J**, shell of *C. carabinata* showing the widely expanded and reflected lip characteristic of this snail.

2. SPECIES DIVERSIFICATION IN RAINFOREST LAND SNAILS

2.1 The Genus *Corilla*

The pulmonate land-snail genus *Corilla* is endemic to the Western Ghats and Sri Lanka and is represented by 1 Indian species, *C. anax*, and 10 Sri Lankan species. *Corilla* is considered to be a Gondwanan relict, Corilliform fossils dated to 60-90 MYA having been found in South India (Stolickzka, 1867; Naggs, 1997). The current species-level taxonomy for *Corilla* is based entirely on shell morphology, with key characters being shell size and form, shell sculpture, and the arrangement of the folds inside the mouth of the shell. Sri Lankan *Corilla* (**Fig. 1**) fall into two distinct species assemblages, a lowland rainforest assemblage (*Corilla adamsi*, *C. carabinata*, *C. colletti*, *C. lesleyae*) and a montane rainforest one (*Corilla beddomeae*, *C. erronea*, *C. fryae*, *C. gudei*, *C. humberti*, *C.odontophora*).

My work has focused on two main questions:

1) to what extent does DNA sequence data support the currently recognized species-level taxonomy, which is based on shell characters?

2) do lowland and montane taxa form phylogenetically-distinct clusters, reflecting sustained independent diversification within the lowland and montane zones?

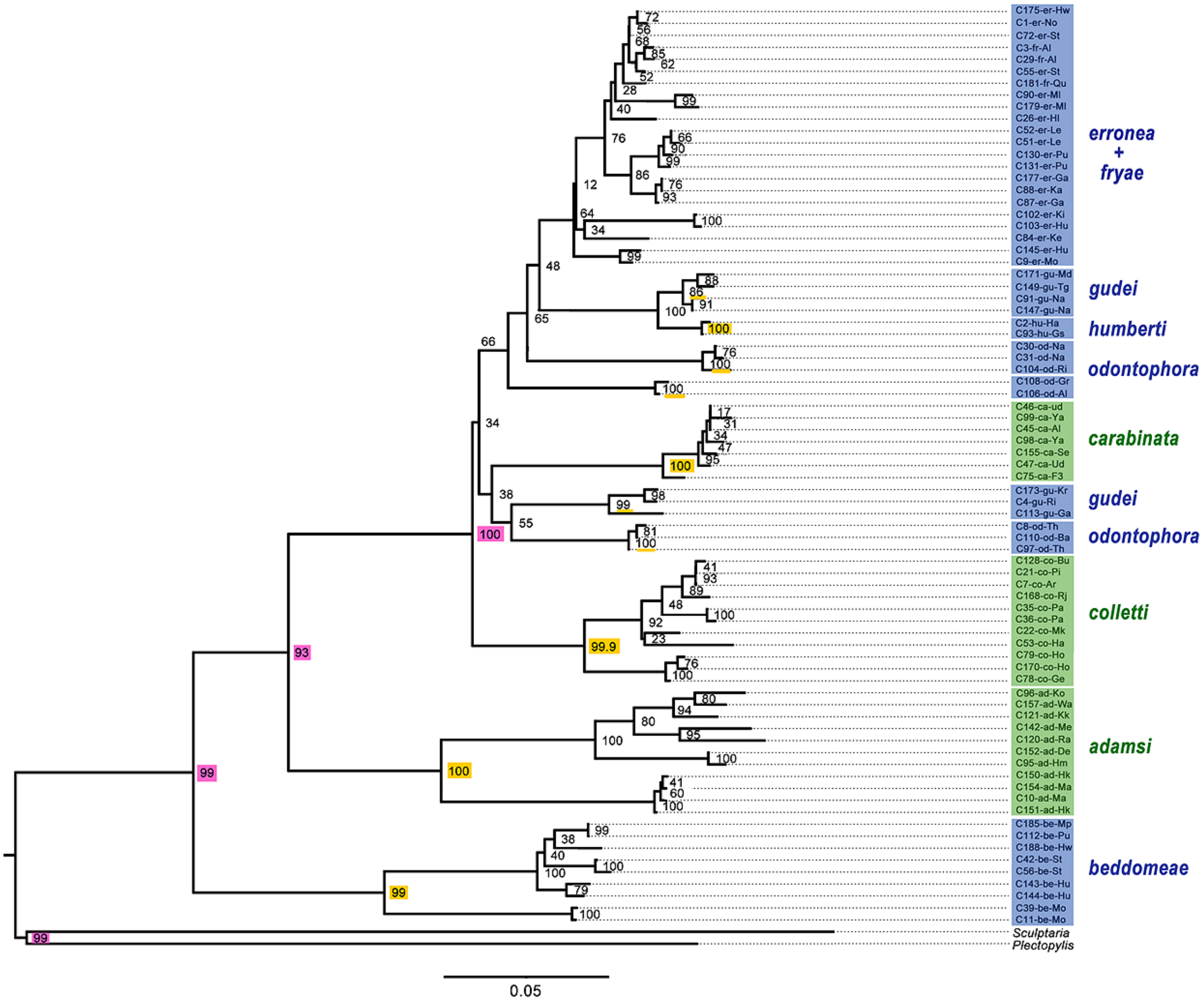

Figure 2. NJ tree for *Corilla* based on the complete 16S dataset (estimated by MEGA version 5.05, using 1000 bootstrap replicates, using Kimura 2-Parameter distances, both transitions and transversions, uniform rates among sites, and complete deletion of all gaps). *Corilla* is represented by 79 distinct haplotypes and the two outgroup taxa, *Sculptaria* and *Plectopylis*, by a single haplotype each. Lowland and montane taxa are shown in green and blue font (and shading) respectively.

Methods

Molecular phylogenetic analyses were largely focussed on three mitochondrial markers and the nuclear gene region ITS1 (ribosomal internal transcribed spacer). The mitochondrial markers were the protein-coding genes, cytochorome oxidase 1 (CO1, ~680 bp, Folmer *et al*., 1994) and NADH dehydrogenase 1 (ND1, ~470 bp, Quinteiro *et al.*, 2005), and the non-protein-coding 16S rRNA (~480 base pairs (bp), Simon *et al.*, 1994).

DNA has been extracted from approximately 140 individuals, representing 9 morphospecies of *Corilla* (*C.lesleyae* could not be traced) and 2 outgroup taxa, *Sculptaria* and *Plectopylis*. For 16S, a near-complete dataset of sequences has been generated, consisting of 77 haplotypes of *Corilla* and the two outgroup taxa, *Plectopylis* and *Sculptaria*. Partial datasets have been obtained for CO1, ND1 and ITS1 because of the difficulty experienced in successfully amplifying some taxa.

Sequence data was aligned using MAFFT version 7.023b (L-INS-i strategy). Model-testing was carried out using the programmes JModeltest (v. 2.1.4) and Partitionfinder (v. 1.1.1). Phylogenetic analyses were carried out using Neighbour-Joining (NJ, software: MEGA v. 5.05) and Bayesian (software: MrBayes v. 3.2.1) approaches.

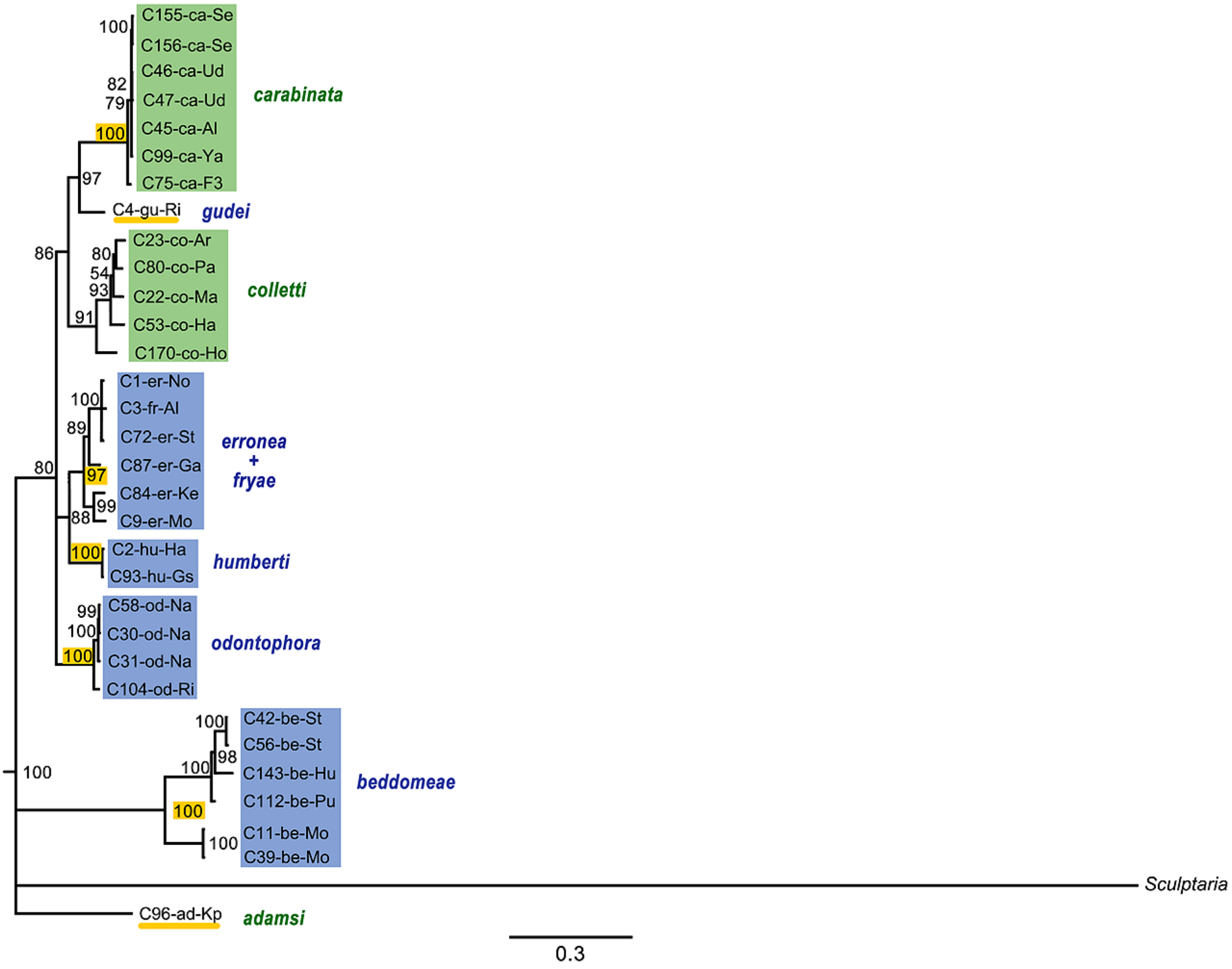

Figure 3. Bayesian tree for *Corilla* based on combined dataset for the genes16S (517 bp), ND1 (439 bp) and ITS1 (467 bp). *Corilla* is represented by 32 distinct haplotypes and the outgroup taxon, *Sculptaria*, by a single haplotype. Lowland and montane taxa are shown in green and blue font (and shading) respectively, and Bayesian posterior probability values are shown at the nodes. The tree was estimated using a partition scheme with 4 subsets: 1 (GTR+I+G model), 16S and ND1 (codon position 1); 2 (GTR+G model), ND1 (codon position 2); 3 (HKY+G model), ND1 (codon position 3); 4 (HKY+G model) ITS1; the analysis was run for 10 million generations (maximum standard deviation of split frequencies = 0.014, average PSRF for parameter values = 1.000).

Results

The NJ analysis of the complete 16S dataset (609 bp, 79 haplotypes) produced a tree (**Fig. 2**) that is basally resolved and shows *Corilla* to be monophylectic, with *C. beddomeae* sister to all the other species. In the sister clade of *C. beddomeae*, *C. adamsi* is sister to all the remaining species (*Corilla carabinata* clade); the relationships of these latter species is unresolved. Of the 9 morphospecies of *Corilla* studied, 5 are represented as well-supported clades: *C.*

adamsi, *C. beddomeae*, *C. carabinata*, *C. colletti* and *C. humberti*. The clade comprising *C. erronea* and *C. fryae* is not well supported, having a marginal bootstrap value of just over 70%. The relationship within the *Corilla carabinata* clade is currently unclear. The 16S Baysian tree (not figured) is less resolved, but not inconsistent with the results of the NJ tree. Note, however, that there is a well-supported montane clade consisting of *C. erronea*, *C. fryae*, *C. humberti* and some of the haplotypes of *C. odontophora* and *C. gudei*, and that the relationship of *C. erronea* and *C. fryae*, though unclear, does not contradict the NJ tree.

A concatenated NJ analysis of 33 haplotypes (32 haplotypes of *Corilla* and the outgroup *Sculptaria*) for the combined 16S-ND1-ITS1 dataset (1423 bp) yielded a basally unresolved tree (not shown), suggesting that the monophyly of Sri Lankan *Corilla* is only supported when a composite outgroup is used. However, 5 of the 9 morphospecies are represented as well-supported monophylectic taxa, and unlike the analyses of the 16S marker on its own, *C. erronea* and *C. fryae* together form one well-supported clade. A Bayesian analysis (**Fig. 3**) of the same dataset was largely consistent with this result. The key differences were that only 4 of the 9 morphospecies are represented as well-supported clades and these are not the same as in the NJ analysis. For the concatenated dataset, I also ran analyses of each of the three markers on their own, and these were consistent with results of the combined analysis.

Conclusions

The discrepancy between the results for the complete 16S dataset and the concatenated dataset may reflect the influence of differences in the level of sampling and the number of outgroup taxa. Clearly there is better resolution deeper in the tree when a composite outgroup is used - including a composite outgroup, in effect, accentuates the difference between the outgroup and the ingroup. The problem here, however, is that if the outgroup and ingroup are very different it may induce homoplasy.

These results support two key conclusions. First, they indicate that the current species-level taxonomy of *Corilla*, which is based on shell characters, is at least partly supported by molecular phylogenetic data (i.e. support for *C. beddomeae*, *C. carabinata* and *C. humberti* is shown in all analyses). Second, the analyses of the complete 16S dataset suggest that the diversification in the genus *Corilla* has involved climatic/habitat niche shifts between the montane and lowland zones on at least one occasion – *C. beddomeae* is montane and its sister clade a mixture of lowland and montane species.

I am currently working on a manuscript that integrates these findings with a synthesis of available published and unpublished data on morphological characters and species distributions (i.e. from material in the RBINS and other museum collections, the historical literature, other published and unpublished sources including my own extensive surveys). This paper will be submitted to the journal *Molecular Phylogenetics and Evolution*.

This study on the diversification of *Corilla* has been challenging for two reasons. First, I found it difficult and in some cases impossible to amplify the gene regions ND1 and ITS1 for certain species and/or populations. Second, the trees generated to date show a lack of basal resolution, and this most likely reflects the fact that they are based on too small a dataset. Both of these problems can be addressed by adopting a Next-Generation Sequencing (NG) approach, which is what I plan to do to take this research forward.

2.2 The Genus *Theobaldius*

The genus *Theobaldius* belongs to the land caenogastropod family Cyclophoridae. Though cyclophorids and other land caenogastropods constitute a substantial share of land-snail diversity in many tropical forest regions, data on the molecular systematics of these snails are scarce.

Theobaldius has a disjunct distribution in South and Southeast Asia. The main centre of diversity is Sri Lanka and the Western Ghats, but a handful of species also occur in Northeast India and on Sumatra and its satellite islands (Fulton, 1907; Gude, 1921; Laidlaw, 1957; Van Benthem Jutting, 1959). In Sri Lanka, *Theobaldius*, like *Corilla*, is represented by distinct assemblages of lowland and montane rainforest species. On the basis of shell morphology, *Theobaldius sensu lato* is represented by two distinct morphotypes: a depressed, discoid-shelled morphotype (characteristic of *Theobaldius annulatus* and similar species) and a morphotype with a raised, turbinate shell (characteristic of some species such as *T. bairdi*). Both of these morphotypes have a flat proteinaceous operculum, which is broadly similar to the operculum of *Cyclophorus*, but is strikingly different to that of *Aulopoma*; *Aulopoma* is unique among South Asian cyclophorid snails in having an operculum that sits like a tightly-fitting cap over the mouth of the shell.

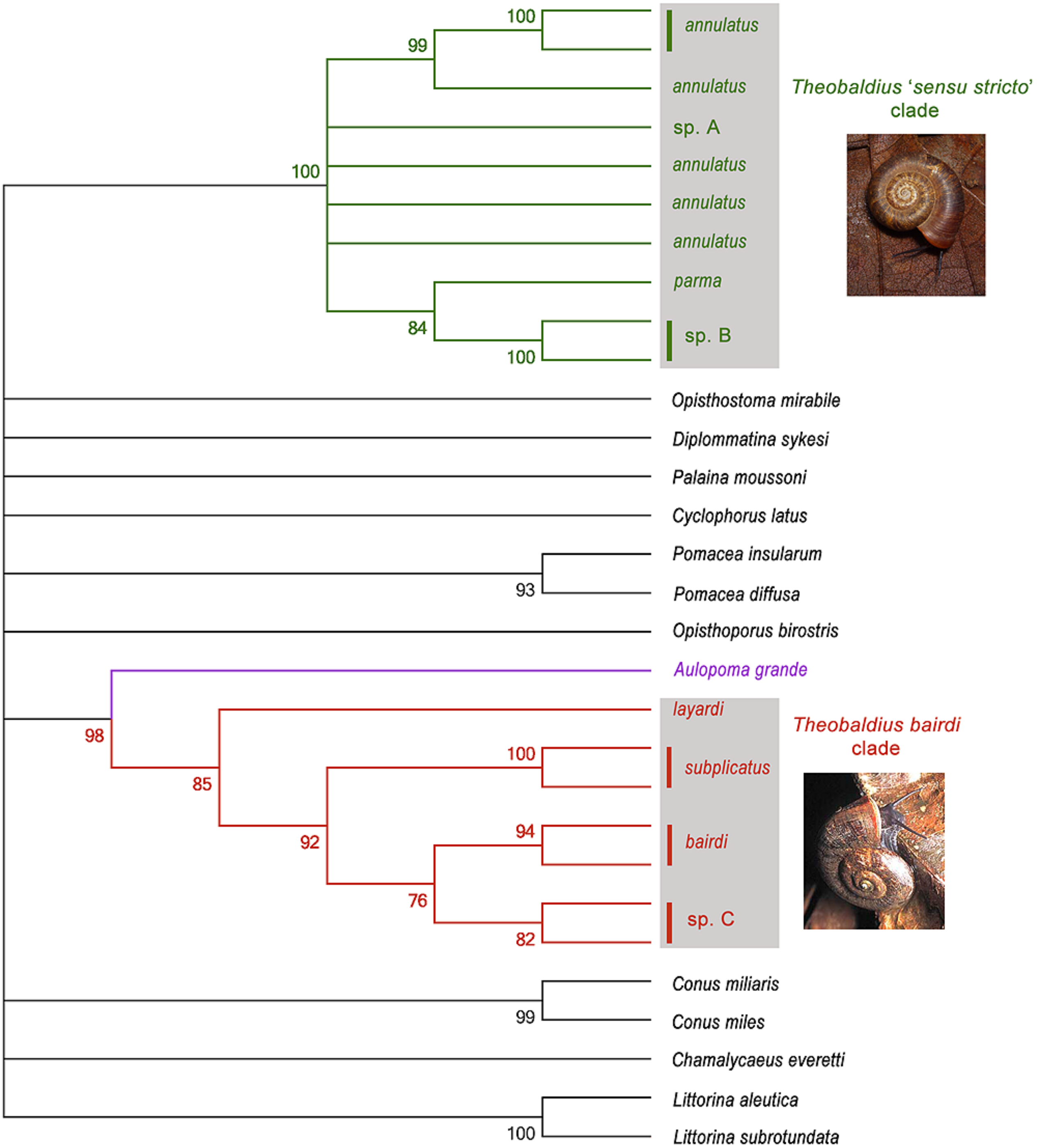

Figure 4. Neighbour-joining tree for *Theobaldius* and other caenogastropod snails based on the CO1 marker (estimated by MEGA version 5.05, using 1000 bootstrap replicates, using Kimura 2-Parameter distances, both transitions and transversions, uniform rates among sites, and complete deletion of all gaps). Only internal nodes with bootstrap values ≥ 70% are shown. Sequences for taxa shown in black font are mostly from Webster *et al.*, 2012 (now deposited in Genbank), apart from those for the outgroup taxa, *Littorina aleutica*, *L. subrotundata* and *Pomacea diffusa*, which are from Genbank.

Methods

Work to date has involved a preliminary exploration of the relationships between Sri Lankan members of the genus, and between *Theobaldius* and other tropical Asian land caenogastropods. I have generated sequence data for two markers, CO1 and 16S rRNA. Sequence data was aligned using MAFFT version 7.023b (L-INS-i strategy).

A preliminary NJ analysis (software: MEGA v. 5.05) was carried out using CO1 data (677 bp) for *Theobaldius* (17 haplotypes) and a range of other land caenogastropods (10 haplotypes representing *Aulopoma*, *Chamalycaeus*, *Cyclophorus*, *Diplommatina*, *Opisthoporus*, *Opisthostoma* and *Palaina*), with *Conus*, *Littorina* and *Pomacea* as outgroup taxa. Sequences for taxa other than *Theobaldius* and *Aulopoma* were largely obtained from Webster *at al.*

(2012) (these data are now available from Genbank); sequences for the outgroup taxa, *Littorina aleutica*, *L. subrotundata* and *Pomacea diffusa*, were obtained directly from Genbank (accession numbers HE590831, HE590844 and HQ908055).

Preliminary Results

The NJ anaylsis of the CO1 data yielded a tree with an unresolved basal branching pattern. Intriguingly, however, this tree raises the possibility of two alternative and contrasting scenarios. The first scenario is that all the *Theobaldius* species sampled fall into one clade comprising two well-supported sister clades, one clade containing the discoid-shelled species (the clade*Theobaldius* '*sensu stricto*' in **Fig. 4**), and the other containing the turbinate-shelled morphotype (the *Theobaldius bairdi clade* in **Fig. 4**) and its sister taxon, *Aulopoma*. In this case *Theobaldius* is paraphyletic. The second scenario is that the *Theobaldius* '*sensu stricto*' clade is not the sister of the clade composed of *Aulopoma* and the *Theobaldius bairdi* clade. In an effort to improve phylogenetic resolution I am currently generating new sequence data, both for *Theobaldius*, including data for species from outside South Asia, and for other tropical Asian cyclophorids.

3. TAXONOMY OF ASIAN LAND SNAILS

3.1 Taxonomic Revision of the Land-snail Fauna of the Western Ghats of India

The Western Ghats, the mountain chain running for 1600 km along the western coastline of India, has a phylogenetically-diverse land-snail fauna (64 genera in 23 pulmonate and caenogastropod families) dominated by endemic species (**Fig. 5**). Approximately 300 species have been described, and of this more than 70% are endemic to the Western Ghats; many of them belong to genera unique to the Western Ghats and Sri Lanka (Raheem *et al.*, in press). The study of the land snails of the Western Ghats, and of the wider South Asian region, has a long and rich history, extending back to the 18th century. Virtually all of our current knowledge of the diversity and distribution of the Western Ghats snail fauna is based on the publications and collections of 19th century and early 20th century workers, particularly William Benson, Louis Pfeiffer, William and Henry Blanford, Henry Godwin-Austen and Richard Beddome. The three volumes of *The Fauna of British India* series on land molluscs (Blanford and Godwin-Austen, 1908; Gude, 1914, 1921, abbreviated as the *FBI*) mark the culmination of this intense period of faunistic exploration. Published between 1908 and 1921, these volumes provide a synthesis and summary of the historical literature and data from shell collections, and include detailed synonymies. It is an essential work for anyone wishing to study the land-snail fauna of the Western Ghats, but it is nevertheless an incomplete aid to species identification. Many of the species descriptions in the *FBI* are only given in Latin, only a small number of the species are illustrated, and there are many inaccuracies and errors. Consequently, the *FBI* is of limited use as a species-identification tool on its own; access to type material or comprehensive reference shell collections is usually essential. However, although many of the early workers on Indian snails donated material directly to the Indian Museum in Calcutta (now Kolkata), most of the type material is in the U.K., at the Natural History Museum, London (NHM), and the University Museum of Zoology, Cambridge (UMZC).

Figure 5. **A**, the Indian Peninsula, showing the location of the Western Ghats (red shading). Approximately 70% of species found in the Western Ghats are endemic to it. **B**, caenogastropod (*Mychopoma*, *Opisthostoma*, *Pearsonia* and *Tortulosa*) and pulmonate (*Glessula, Perrottetia, Indrella* and *Euplecta*) land-snail genera of the Western Ghats.

To address this issue, I have recently completed a fully-illustrated taxonomic revision of the land snails of the Western Ghats (Raheem *et al.*, in press), in collaboration with Fred Naggs (NHM), Richard Preece (UMZC), and Aravind Madhyastha of the Ashoka Trust for Ecology and Environment in Bangalore (India). Our objective has been to produce a taxonomically-updated, fully-illustrated revision of the land-snail species described to date from the Western Ghats. Given that there has been little taxonomic revisionary work on the fauna since the publication of the last volume of the *FBI* in 1921, our revision is based almost entirely on the species listed in the *FBI*. In essence it is an initial attempt to critically evaluate and clarify the nomenclature and taxonomy of the taxa within a modern systematic framework and to provide some details of their geographical distribution. The revision evaluates the status of 337 land-snail taxa (299 species and 38 forms), including all those listed from the Western Ghats in the *FBI*, and will be the first publication to include colour images (see **Fig. 6** for an example of a plate) and specimen data of type material for all the Western Ghats taxa alongside distributional data from the original literature, much of which dates back to the 19th century or earlier. Photographic images of the types of most Western Ghats land snails have not been published before, and this in combination with all the data extracted from specimen labels and historical literature will make this a major contribution to advancing knowledge on the land-snail fauna of South Asia. This revision marks the first major publication of the research network involving South and Southeast Asian land-snail workers, which is being developed and facilitated by RBINS.


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FIGURE 1. A. *Cyclophorus altivagus* Benson, 1854, neotype, UMZC. **B-D.** *Cyclophorus indicus* (Deshayes, 1834), Museum of Natural History, Paris, lectotype (**B**), and paralectotypes (**C**, **D**). **E.** *Cyclophorus jerdoni* (Benson 1851), lectotype, UMZC. **F.** *Cyclophorus nilagiricus* (Benson, 1852), lectotype, UMZC.

Figure 6. An example of a plate from the new revision of the Western Ghats land-snail fauna (Raheem *et al.*, in press), illustrating type specimens of species belonging to the caenogastropod genus *Cyclophorus*.

The revision, which is currently in press, will be published as a special issue of the journal *Tropical Natural History* (http://www.biology.sc.chula.ac.th/TNH) and will be available in open-access online and print formats. We will also develop this revision into an interactive database, which will be accessible at http://www.nhm.ac.uk/tropicalsnails.

3.2. Benson Collection at the University Museum of Zoology, Cambridge

The UMZC and the NHM in London hold most of the non-marine molluscs collected and described by William Benson (1803-1870) in the early 19th century, much of it from the Indian Subcontinent. Benson's collections at Cambridge and NHM contain many potential types. I am currently involved in a project, led by Richard Preece at UMZC, to document and illustrate all this material in a forthcoming publication. The project is funded by Trinity College, University of Cambridge, through the Isaac Newton Trust. As with my work on the Western Ghats land-snail fauna this publication will make freely available for the first time colour images and specimen data of Benson's type material. This will be an important contribution to the study of tropical Asian land snails because Benson described many species from South and Southeast Asia and was far ahead of his time in meticulously studying the geographical distribution of the snails he collected.

3.3. Nomenclature of the genus *Macrochlamys*

The species-rich genus *Macrochlamys sensu* Godwin-Austen (1883-1888, pp. 76-92, 97-122, 209-215, 1899, pp. 87-90, 136-137, 151-170) and Blanford and Godwin-Austen (1908, pp. 77-141) is indigenous to and widespread in South and Southeast Asia. The name *Macrochlamys* was first introduced but not made available (see ICZN, 1999, Articles 10-12) by Benson in 1832 (p. 13). Benson stated "a new genus of the Helicidae, separated by me from Helix, in consequence of the wide departure of the animal from the type of that genus". Later in the same volume (p. 76) the species *Macrochlamys indicus* Benson was mentioned, but again neither *Macrochlamys* nor *indicus* were made available and the description was limited to the difference between the new species and *Helix*. The current generic concept of *Macrochlamys* dates from Godwin-Austen (1883, pp. 76-92, 97-122), who denoted *Macrochlamys indica* Benson in Godwin-Austen (1883, p. 97, pl. 18, figs. 1-8b, pl. 21, fig. 1, pl. 25, figs. 9, 10) as the type species. Although the generic concept of *Macrochlamys sensu* Godwin-Austen (1883) is well-defined, there are two available names that have priority over it: *Macrochlamys* Gray 1847 (p. 169) and *Orobia* Albers 1860 (pp. 57). The type species of both of these names is the poorly-known *Helix vitrinoides* of Deshayes (1831, p. 26), of which the locality is unknown and the type no longer traceable. *H. vitrinoides*, as described by Deshayes, has a small, imperforate shell, but imperforate-shelled species are rare among South Asian *Macrochlamys sensu* Godwin-Austen 1883 - only 6 of the 116 species listed in the *FBI* (Blanford and Godwin-Austen, 1908) are imperforate and these may not be correctly attributed to *Macrochlamys sensu* Godwin-Austen. Some authors, such as Stoliczka (1871, pp. 246-247) and Blanford and Godwin-Austen (1908, pp. 95, 97, 99, 132), have argued that the Indian taxon or taxa referred to as *H. vitrinoides* by Gray and Albers is not the *H. vitrinoides* of Deshayes. Given the widespread distribution of *Macrochlamys* in the Asian tropics, this complex nomenclatural puzzle needs to be resolved, and I am currently working with Fred Naggs (NHM) on a solution, which we hope to have in press very shortly.

4. OTHER PROJECTS

4.1 Biotic Impacts of Forest Fragmentation

My doctoral research was focussed on the impact of habitat fragmentation and degradation on community structure (Raheem *et al.*, 2008, 2009), and during the course of my BELSPO Fellowship I have contributed to a major new database that draws together primary data on biotic responses to forest fragmentation from studies across the world. This ground-breaking relational database, called BIOFRAG, will facilitate comparative study of the effects of forest fragmentation across a wide range of taxa and study sites. A description of the database will be presented in a forthcoming paper (Pfeifer *et al.*, in press) in the journal *Ecology and Evolution*.

5. PUBLICATIONS IN PRESS

Raheem, D.C., Taylor, H.T., Ablett, J., Preece, R.C., Aravind, N.A. and Naggs, F. In press. A Systematic Revision of the Land Snails of the Western Ghats of India. *Tropical Natural History*, Supplement.

Pfeifer, M., Lefebvre, V., Gardner, T.A., Arroyo-Rodriguez, V., Baeten, L., Banks-Leite, C., Barlow, J., Betts, M.G., Brunet, J., Cerezo, A., Cisneros, L.M., Collard, S., D'Cruze, N., da Silva Motta, C., Duguay, S., Eggermont, H., Eigenbrod, F., Hadley, A.S., Hanson, T.R., Hawes, J.E., Heartsill Scalley, T., Klingbeil B.T., Kolb, A., Kormann, U., Kumar, S., Lachat, T., Lakeman, Fraser P., Lantschner, V., Laurance, W.F., Leal, I.R., Lens, L., Marsh, C.J., Medina-Rangel, G.F., Melles, S., Mezger, D., Oldekop, J.A., Overal, W.L., Owen, C., Peres, C.A., Phalan, B., Pidgeon, A.M., Pilia, O., Possingham, H.P., Possingham, M.L., **Raheem, D.C.**, Ribeiro, D.B., Ribeiro Neto, J.D., Robinson, W.D., Robinson, R., Rytwinski, T.4, Scherber, C., Slade, E.M., Somarriba, E., Stouffer, PC., Struebig, M.J., Tylianakis, J.M., Tscharntke, T., Tyre A.J., Urbina Cardona, J.N., Vasconcelos, H.L., Wearn, O., Wells K., Willig, M.R., Wood, E., Young, R.P., Bradley, A,V., and Ewers, R.M. In Press. BIOFRAG – A new database for analysing Biodiversity responses to forest fragmentation. *Ecology and Evolution.*

6. MEETINGS ATTENDED

April-May 2013 - I attended an intensive 2-week course, Computational Molecular Evolution, which was held at the Wellcome Trust Genome Campus at Hinxton, near Cambridge, UK.

July 2013 - I gave a presentation of my research on the systematics and diversification of the land-snail genus *Corilla* at the World Congress of Malacology, which was held in Ponta Delgada in the Açores, Portugal.

7. CURRENT AND FUTURE PLANS

Manuscripts in Preparation

In order to complete the research carried out during the course of my fellowship, I will have the following manuscripts published or in press by the end of this year: a) an analysis of the systematics and evolution of Sri Lankan *Corilla* based on the datasets outlined in this report; b) an analysis of the systematics and evolution of the genus *Theobaldius* and related caenogastropod taxa from the Asian region which will incorporate the data presented in this paper, as well as new data; and c) a paper on the nomenclature of *Macrochlamys*, as outlined above. As outlined above, I will also be co-authoring a publication on the Benson type specimens at the UMZC and NHM – this will also be in press by the end of the year.

Aftermath and Future Projects

As laid out in my Mid-term Report, the most important task on my return to Sri Lanka will be to prepare and publish a synthesis of all the currently available distributional data on the Sri Lankan land-snail fauna by integrating data from recent and historical collections and surveys of the extant fauna with data from palaeo-ecological excavations. This will involve substantial taxonomic study of fossil snail material from recent and ongoing excavations by my collaborators at the Archaeological Department in Sri Lanka.

In terms of future projects, I am particularly keen to utilise NGS approaches in my research on molecular systematics and evolution. I am currently in the early stages of taking this forward with a study, in collaboration with Thierry Backeljau, on the diversification of *Corilla* using NGS. I am also keen to extend the scope of my evolutionary research to explore a range of different issues. I am particularly interested in exploring the relationship between the Sri Lankan and Indian land-snail faunas, and between the South and Southeast Asian biotas and this work will necessarily involve extensive collaboration, particularly with workers from the Asian region, such as Prem Budha (Tribuvhan University, Nepal), Aravind Madhyastha (ATREE, India) and Somsak Panha (Chulalongkorn University, Thailand Thailand), who are key members of the network of South and Southeast Asian land-snail researchers being fostered and supported by RBINS.

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