Sri Lankan snail diversity: faunal origins and future prospects

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Abstract – Sri Lankan snails have a complex history that might be linked to events ranging from Mesozoic plate tectonics and climate change on a global scale to more recent regional climate change and human impact. The fauna could include ancient groups that may have been present in Pangaea, diversified in Gondwana and survived in Deccan Plate refugia at the K/T boundary and Pangaean taxa that arrived via Eurasia. Taxa could have been assimilated from continental fragments encountered during the northward rafting of the Deccan Plate. Fauna colonising immediately following Eurasian contact could have been a regional fauna associated with Tibetan plateau plate fragments. There may have been a brief period when an Arabian corridor was open to African faunas and there was likely to have been a succession of immigrants through the Assam corridor or through long distance dispersal. The presence of *Acavus* and *Oligospira* as endemic acavoids in Sri Lanka and the complete absence of acavoids from India as well as the presence of at least 10 species of *Corilla* and only one in India, give a greater potential Gondwanan identity to Sri Lanka's snail fauna. A similar pattern with *Tortulosa* may also have ancient origins. It is possible, but perhaps doubtful, that this picture has been sustained since the K/T boundary. A more likely explanation might be that during successive Deccan Trap lava flows Gondwanan snails survived as a small relict fauna in a southern Deccan Plate refuge and possibly a north eastern refuge. Snail faunas could have later dispersed across the intertrappean and supratrappean landscape from a refuge or refugia to be largely replaced in India by a subsequent combination of climate change and competition from a succession of colonizing species. A notable feature of the Sri Lankan snail fauna is the level of endemism and lack of shared components with India at the species level. A high level of endemism may have been present in the highland areas of Sri Lanka through the Cenozoic and earlier, and current endemism may be a mixture that includes Mesozoic elements. However, species turnover could be high and many of the current species could have become established in the Quaternary. Most of the Sri Lankan land snail species diversity and endemism is confined to forests in the wet zone of the Southwest. The maintenance of high levels of endemism and generation of high species diversity in a confined area through long periods is thought to be linked to the varied topography in Sri Lanka and the capacity for altitudinal faunal shifts in response to climate change. The remaining fragmented forests in a mosaic of transformed habitats no longer offer such capacity for altitudinal adjustment giving a poor prognosis for the long-term survival of the fauna.

Key words: Molluscan biodiversity; South Asia; evolutionary history; plate Tectonics; conservation biology

INTRODUCTION

We have been engaged in faunal surveys of Sri Lankan land snails for several years, particularly since 1999 with the launch of the three-year Darwin Initiative project *Land snail diversity in Sri Lanka* (Naggs *et al.*, 2005). With additional support from the Darwin Initiative we are in the early stages of working up these investigations under the project title *Land snails as models for biodiversity assessment in Sri Lanka*. Future prospects for the fauna appear to be starkly clear but faunal associations are poorly known and we can currently offer only a broad outline of events that may have given rise to Sri Lanka's modern snail fauna.

Sri Lanka is a relatively small component of the Deccan Plate separated from peninsular India by a shallow and narrow sea passage. There have repeatedly been land connections to India (Jacob, 1949) but Sri Lanka possesses a highly endemic snail fauna. The Deccan Plate has a long geological history and Sri Lanka possesses a central massif of Precambrian origin (Cooray, 1984). We examine the land snail fossil record in order to establish what global events in earth history might be relevant to

understanding land snail distribution. In addition to rafting of the Deccan Plate from Gondwana, contact with the Eurasian Plate, closure of the Tethys Ocean and elevation of the Himalaya, events at the K/T boundary, subsequent climate change and human influence are all likely to have had a profound impact on faunal composition.

Historical background to investigations of the Sri Lankan land snail fauna

Samuel Woodward (1856) was the first to recognise the distinctive composition of Sri Lanka's snail fauna. Based on land snail distribution information provided by William Benson, Woodward established Sri Lanka as a biogeographical province of the Indian region and, influenced by the work of Edward Forbes, he was also prescient in recognising the different geological context in which many of his provinces originated. Woodward (1856, p. 352) considered that: 'provinces are of various ages, and their origin is connected with former (often very remote) geological changes, and a different distribution of land and water over the surface of the globe'. Benson (1856) increased the total of 110 species listed by Woodward to 117 but considered that the Sri Lankan snail fauna was essentially Indian, being closely linked to that of the Western Ghats. Blanford (1864, p. 22) took the view that 'there can be no rational doubt that, with the further exploration of the South-Indian hills, the claims of those of Ceylon to be considered a distinct zoological province will vanish completely'. Mavinkurve *et al.* (2004) published a species list for Karnataka and Aravind *et al.* (2004 and this volume) and have recently carried out surveys in the Western Ghats but details of their work have yet to be published and current knowledge has progressed little since Blanford's time. The snail faunas of India and Sri Lanka undoubtedly share common origins but, in addition to a high level of endemism, Sri Lanka appears to possess a larger component of what are considered to be possible Gondwanan relicts. The occurrence of *Acavus* in Sri Lanka but not in India was of particular interest to early reviewers of the regional fauna (Woodward, 1856; Cooke, 1895).

Solem (1959, 1968, 1979a, 1979b, 1981a, 1981b, 1984) published extensively on the global historical biogeography of land snails and commented widely on the extent to which acavids in particular might be recognised as a southern relict group. Such narrative commentaries have been considered to be unscientific (Morrone and Crisci, 1995) and Solem's (1981a) review attracted particularly critical comment (Smith-Vaniz, 1981; Springer, 1981; Schuh, 1981). However, in his response Solem (1981b) expressed the view that the available morphological phylogenies were unstable and unsuitable bases for rigorous analysis of distributions. With the introduction of large taxa sets in the construction of molecular land snail phylogenetic trees (Wade *et al.*, 2001) the formulation of hypotheses can be justified on the basis that there is an increasing capacity for critically testing them.

Current issues and current investigations

Our investigations of the Sri Lankan land snail fauna (Naggs *et al.*, 2005) have reinforced rather than dispelled the notion that Sri Lanka is rich in endemic species (Table 1). Most of the approximately 250 described and currently recognised Sri Lankan species (Naggs and Raheem, 2000) are restricted to the wet zone of southwestern Sri Lanka. Many are confined to the mostly small remaining areas of fragmented rainforest where snail endemism is close to 100%, with exotic species appearing in only significantly disturbed forest and dominating only outside of forest habitats. Allopatric diversity within Sri Lankan snails is high, which is in keeping with some observations on tropical land snail faunas elsewhere (Solem, 1984). Different species within genera often occupy restricted ranges, most notably with different species occupying individual hills or ranges of hills.

Establishing phylogenies and genetic distances between Sri Lankan and the Western Ghats' snail taxa is clearly of critical importance for understanding the relationships, history and origins of the regional snail fauna. Unfortunately, Indian controls on the export of biological material for research (Pethiyagoda, 2004) currently prevent meaningful collaboration with Indian colleagues and hinder attempts to understand the relationships of the Sri Lankan snail fauna to that of India. Where investigations have been carried out on Western Ghats and Sri Lankan vertebrate and non-molluscan invertebrate groups (Bossuyt, 2004), the results show higher levels of endemism than had been expected from established taxonomy. Three of six groups exhibited Sri Lankan lineages nested within Indian lineages while three other groups required further data to confirm this relationship. The large number of snail taxa and the presence of a family level endemism in Sri Lanka that is absent from India is likely to offer valuable insight into the biotic history of this region.

Major land snail groups represented in Sri Lanka

Land snails are not a monophyletic group and there is clear evidence that at least seven gastropod groups made the transition from aquatic to terrestrial environments independently (Little, 1983, 1990). Stylommatophorans are the dominant group and they occupy all fully terrestrial habitat types occupied by land snails. In Sri Lanka they comprise about 65% of the snail fauna. Their success might be linked to their having made the transition to land directly from a saline environment (Little, 1983). The veronicellids are primitive pulmonate slugs;

Table 1 The four families holding the majority of Sri Lankan species. There are 23 'native' and 9 'non-native' Stylommatophoran families and 4 'native' prosobranch families. 250 species are currently recognised of which 104 are endemic to Sri Lanka. An additional 50+ endemic species are awaiting description. There are four named endemic genera *Acavus, Oligospira, Ravana* and *Aulopoma* and 3-4 additional endemic genera awaiting description

Genus	Number of Species		
	Endemic	Native	Total
Ariophantidae (34 species, 4 genera)			
Cryptozona	4	2	6
Euplecta	20	5	25
Ratnadvipia	2	–	2
Ravana*	1	–	1
Glessulidae (22 species, 1 genus)			
Glessula	18	4	22
Cyclophoridae (48 species, 10 genera)			
Cyclophorus	3	1	4
Aulopoma*	3	–	3
Cyathopoma	13	1	14
Japonia	3	–	3
Leptpoma	3	–	3
Leptopomoides	2	–	2
Micraulax	1	–	1
Scabrina	2	–	2
Theobaldius	12	–	12
Pterocyclus	3	2	5
Pupinidae (26 species, 1 genus)			
Tortulosa	26	–	26

little is known about their biology and the three species found in Sri Lanka are probably introduced (Mordan *et al.*, 2003). Prosobranch cyclophoroideans are the other major group in Sri Lanka, accounting for most of the remaining 35%. Having made the transition to land via freshwater (Little, 1983) their blood has a very low osmotic pressure and when active they require very high humidity to allow their renal system to function and produce very dilute urine. However, they can aestivate for long periods and are well adapted to the seasonal monsoon climates of South and Southeast Asia. The ellobiid *Pythia ceylanica* Pfeiffer lives above high tide in a fully terrestrial environment. Although the life cycle of *Pythia* seems to be independent of the sea, it lays eggs under damp logs (H. and A. Adams, 1858), it is only found in immediate proximity to the sea. *Truncatella ceylanica* Pfeiffer is the only representative of the Rissoidea in Sri Lanka that might be terrestrial but there is no published record of its habitat, which is probably at or just above high tide level.

The land snail fossil record

The fossil record offers the only direct evidence that places snail evolution within a geographical chronology. Solem (1979a) examined the biogeographic significance of land snail fossils on the basis of a review of the literature. However, the fossil record of land snails is very patchy, has been little and, it must be said, often poorly studied such

that identifications given and widely repeated in the literature cannot be accepted without critical re-examination. Such revision of the land snail fossil record is urgently needed but would be a major undertaking. We can only refer to a few examples that might be relevant to relationships with the Sri Lankan fauna. Homoplasy in shells is widespread and the lack of robust synapomorphies for shell characters is a major problem for assigning early fossil taxa to family level categories. We do not share Solem's (1978, 1981a, 1983a, 1985) view that early fossil land snails can be attributed to family level taxa with a high degree of confidence or that Late Palaeozoic fossils represented 'the obviously successful permanent colonisation of the land by snails' (Solem, 1981a p.200). These earliest known land snail fossils were contiguous in North America (Atoka Series of the Pennsylvanian) and Europe (Upper Carboniferous). The placement of some of these snails in contemporary stylommatophoran orders (Solem and Yochelson, 1979; Solem, 1983a) lacked a logical and factual basis (Naggs, 1997) and it seems possible that at least some of these early land snails were not directly related to modern snail groups. They may even represent an early colonisation of the land by gastropods that died out in the Late Permian or at the end-Permian extinctions, when life on earth came close to being extinguished (Benton and Twitchett, 2003).

From the last recorded appearance of these Palaeozoic fossils in the Lower Permian over 280 Ma

ago there is a gap of some 180 Ma before land snails reappear in the fossil record of the Cretaceous. Hallam and Wignall (1997) considered that biological recovery in the Mesozoic was slow and that it took 100 Ma for family-level diversity to recover to pre-Permian extinction levels. However, that we know nothing of early Mesozoic land snails is unlikely to be an indication that they were absent. It is clear that there is only a remote chance that specimens of land snail fossils will become preserved in situations where they will survive in the long term. Among the earliest known Mesozoic fossils are what appear to be a helicinid and a cyclophorid beautifully preserved in Myanmar (Burmese) amber and dated to between 90–100 Ma (Zherikhin and Ross, 2000; Grimaldi et al., 2002; Cruickshank and Ko, 2002). That such preservation represents extremely rare, chance events is further evidenced by the only Mesozoic land snail fossils recorded from the Deccan Plate that consist of just a few shells, all of which were found in shallow marine deposits mixed with a marine fauna (Stoliczka, 1867). These Deccan Plate land snail fossils, which have been widely overlooked, negate Solem's (1981a, p.201)

observation that 'the much later appearance of land snails in the fossil record from Gondwanan (Paleocene of both Patagonia and southwestern Africa) might be a real event rather than an imperfection in the fossil record'. The Deccan Plate specimens were presumably carried out to sea in floodwaters where they became incorporated in stable sedimentary deposits. They are all corilliform shells similar in appearance to Sri Lankan Corilla and dated between 90–67 Ma (Naggs, 1997).

What is now Central Europe has yielded a number of Late Cretaceous fossil land snails (Wenz, 1938; Zilch, 1959–1960; Hrubesch, 1965; Huckriede, 1967; Solem, 1979; Bandel and Riedel, 1994). Proterocorilla Hrubesch, of a similar age and a similar appearance to the Deccan Plate corilliform shells (Figure 1), is found in fossil assemblages of terrestrial gastropods from near Salzburg in Austria (Hrubesch, 1965). These deposits include cyclophoroideans such as Cyclomastoma Hrubesch, which has the distinctive appearance of modern pupinids. Thus as part of an ancient group, the wider relationships of the 25 modern pupinid species of Tortulosa Gray in Sri Lanka are of

Mid to Late Cretaceous corilliform and acavoid-form fossils

Paravitrea. Alberta, Canada. Russell 1929.

Vidaliella. Mallorca, Spain. Zilch 1960

Proterocorilla. Salzburg, Austria Hrubesch 1965

Gastrobulimius. Bakony Mountains, Hungary Bandel & Riedel 1994

Lychnus. Salzburg, Austria Hrubesch 1965

Modern Corilla

Modern Acavus
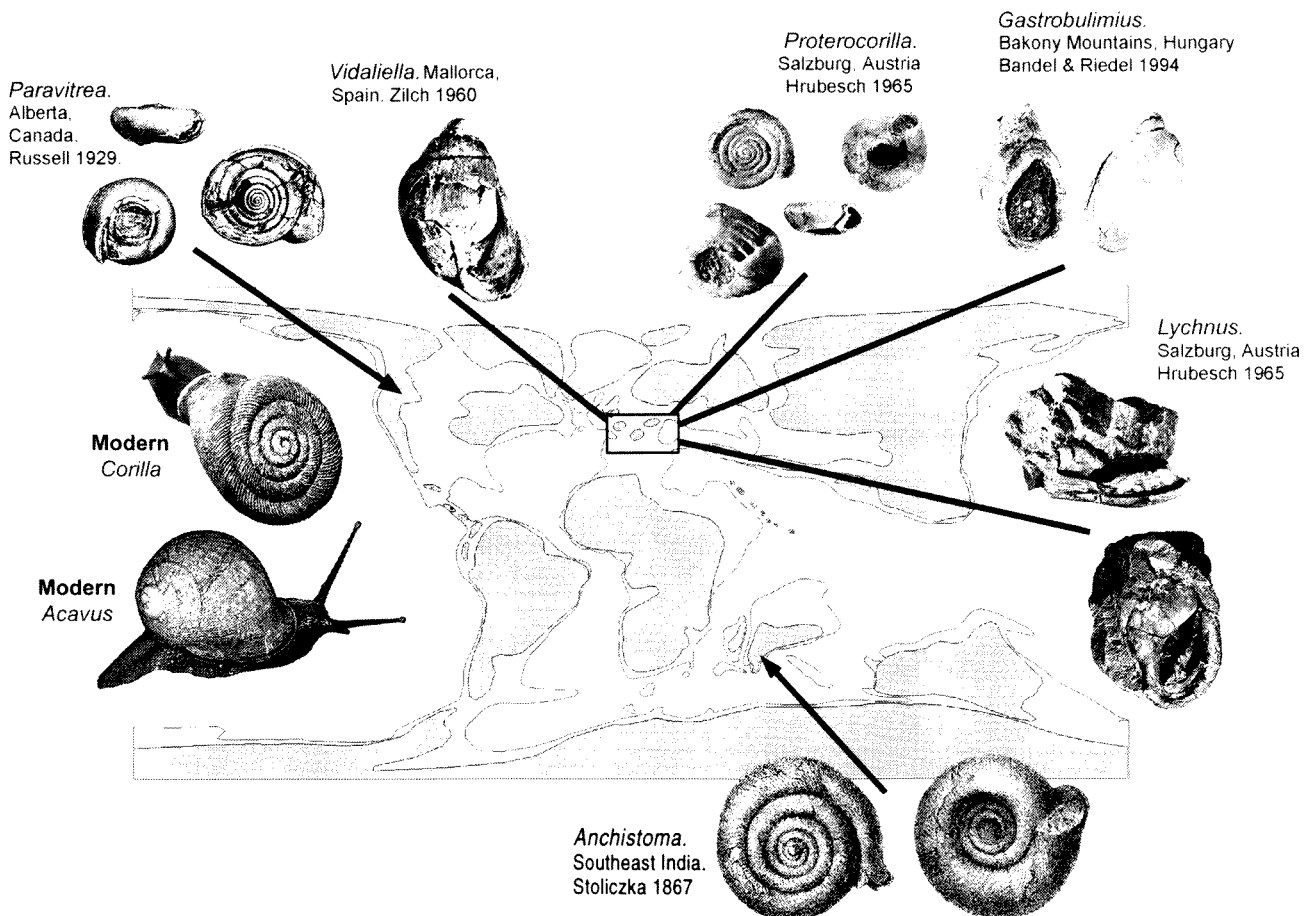
Anchistoma. Southeast India. Stoliczka 1867

Figure 1   Examples of Mid to Late Cretaceous fossils exhibiting a general corilliform and acavoid-form shape but for which affinities have not been clearly demonstrated. Shaded areas show continental land margins; black lines indicate current continental margins (after Scotese, 2001)

potential historical biogeographical interest. The supposed record of the modern Sri Lankan, South East Asian prosobranch cyclophorid genus 'Leptopoma' Pfeiffer in these Austrian deposits proves to be a stylommatophoran pulmonate of a form that we consider might be attributable to several groups. The example identified as Lychnus [Family: Anadromidae] by Hrubesch (1965) closely resembles the often robust and distinctive shells found in the strophocheilid and acavoid clade (Figure 1). It is possible that at least some of the genera included in the Anadromidae by Zilch (1960), such as Vidaliella Wenz belong in this group. The Late Cretaceous example of Gastrobulimus munieri (Hantken) from Ajka, Hungary figured by Bandel and Riedel (1994, pl. 16, figs 5–8) is an unusually well preserved specimen of these acavoid-form shells.

The mixture of marine, brackish and freshwater molluscs described from the Upper Jurassic and very early Cretaceous of Northwest Germany by Huckriede (1967) also appears to contain a number of terrestrial prosobranchs and stylommatophorans. An example is the holotype of Hydrobia cyprideae Huckriede, which has the general appearance of an achatinoid subulinid.

We consider that the current fossil record is so imperfect that few conclusions can be made about wider contemporary distributions in the Mesozoic. However, what appear to be several modern groups of land snails such as corilliform and acavoid-form taxa (Figure 1) were well established by the Late Mesozoic and this supports the hypothesis that they evolved much earlier when tectonic plates were coalesced into the supercontinent Pangaea.

Deccan plate tectonic events

The collision of the Deccan Plate with Asia has been described as the most profound tectonic event to have occurred in the past 100 Ma (Rowley, 1996). It may have given rise to the K/T extinctions and undoubtedly changed the course of evolution for the regional biota. Before any biotic interpretation can be considered for the Mesozoic and Cenozoic Deccan Plate it is necessary to examine current views on what geological events took place. The study of plate tectonics is a very dynamic discipline and the current flow of numerous publications demonstrates the rapid accumulation of knowledge in this field and also reveals the extent of disagreement and controversy.

The synthesis of data by Smith et al. (1994) gave a detailed atlas of Mesozoic and Cenozoic coastlines that continues to be a valuable source for tracking land connections. According to Smith et al. (1994), from the Middle to Late Jurassic some 180–160 Ma, the Tethys Ocean divided Pangaea into northern and southern landmasses but land routes may have existed in the western Tethyan area. If there were common elements in land snail faunas between Laurasia and Gondwana in the Early Cretaceous as, for example, might be extrapolated from corilliform taxa in the later Cretaceous fossil record, they could be attributed to dispersal or to vicariance. However, for much of the Cretaceous the Tethys appears to have presented a major obstacle to dispersal and it is likely that Laurasian and Gondwanan biotas largely followed independent paths. By 150 Ma the South American Plate and African Plate had largely separated from eastern Gondwana: Antarctica, combined Madagascar and Deccan with Seychelles, and Australian plates.

According to Smith et al. (1994) and Scotese (2001, 2002) from 130 Ma the Deccan Plate rafted across the Tethys Ocean before the northeastern Deccan Plate made land contact with Eurasia at about 30 Ma. However, it has been suggested that a land connection across the Kerguelen Plateau to Antarctica may have been in place as late as 80 Ma (Krause et al., 1997).

The Eurasian and Deccan Plates will have made submarine contact very much earlier (Beck et al., 1995). Klootwijk et al. (1992) suggest that contact was made by the K/T boundary at 65 Ma, a finding based on the greatly reduced rate of northern motion and associated with a causal link to Deccan Trap formation. Klootwijk et al. (1994) provide evidence that the northwestern Deccan Plate had made contact with Eurasia at or before the K/T boundary. Rowley (1996) dated an initial contact with Asia in the Lower Eocene (55–50 Ma) for the northwestern Deccan Plate and a Middle Eocene contact (50–45 Ma) in the northeast. However an anti-clockwise rotation of the Deccan Plate (Treloar and Coward, 1991) resulted in an uplift of the Tibetan plateau that started in the east about 40 Ma, 10 Ma before the initial land connection date given by Smith et al. (1994). This eastern uplift extended south to the Patkai and Brail ranges and Mizo and Chin hills to form an early high-altitude/climate barrier to dispersal. In addition, the sedimentary deposition record in the east indicates that shallow marine and brackish habitats extended north to the Himalayan foothills until the Late Miocene, further hindering early access to a Malaysian fauna through the Assam Corridor (Mannan, 2002). Although elevation of the Hindu Kush, Toba Kakar, Central Brahui and Kirthar ranges followed much later from about 20 Ma, there is little in the South Asian land snail fauna that shows a connection with current faunas to the west.

Thus the north/south/east/west Himalayan barrier to dispersal was established between the Late Eocene through the Oligocene to the Early Miocene (Chung et al., 1998). The regional climate is considered to be greatly influenced by the extent and height of the Himalaya and the Tibetan plateau but according to Zhiseng et al. (2001) the monsoon

climate only became established in the Late Miocene at about 9–8 Ma. Estimates of the northern extent of the Deccan Plate prior to collision have varied widely but with increasing palaeomagnetic data, crustal shortening between the Tethyan Himalaya and the Indian Shield has been estimated to be in the order of 1,500 km (Patzelt *et al.* 1996). Satellite magnetic data (Rajaram and Langel, 1992) is consistent with the view that the Tibetan plateau is made up of several tectonic fragments that were attached to Eurasia prior to the Deccan Plate collision. Thus when the land connection was made, the Eurasian fauna in immediate contact with the Deccan Plate could have been a regional fauna associated with Tibetan plateau plate fragments. In addition, there is evidence that a number of islands such as the Ladakh and Kohistan island arc were incorporated in the Deccan Plate during its northern trajectory (McKenna, 1995), introducing the possibility of faunal assimilation prior to Deccan Plate land contact with Eurasia.

K/T events on the Deccan Plate

The Chicxulub meteorite crater is widely considered to be the site of the impact that gave rise to K/T mass extinctions but this is hotly disputed and a period of volcanism is also claimed to have been responsible for these extinctions (McLean, 1985; Keller, 2001, 2003, 2004). Whether or not the Chicxulub meteorite was the primary cause, antipodal events on the Deccan Plate played a major role in extinctions at or around the K/T boundary. Massive outflows of low-viscosity lava, possibly from the Narmada fissure, spread over vast areas of the Deccan Plate. These lava flows are considered to have taken place within the relatively short period of about half a million years beginning near the end of the Cretaceous (Courtillot, 1999). Some flows, up to 30 m in thickness, extended over a vast area of the Deccan Plate (Figure 2). They were likely to have spread in excess of the 100 kph recorded for some modern lava flows (Cheminée, 2001), would have spread like tsunami of molten lava and rapidly obliterated any living organism in their path. Outliers of the Traps in Saurashra and in Rajamundry, Andhra Pradesh, indicate that the original lava coverage (Figure 2) extended across much of the Deccan Plate apart from the southern and northeastern margins (McLean, 1985; Baksi, 2001). The cause of these outflows has variously been attributed to passage of the Deccan Plate over a Réunion hot spot and to collision of the Deccan and Eurasian plates. It has also been suggested that the outflows may have been subjected to massive
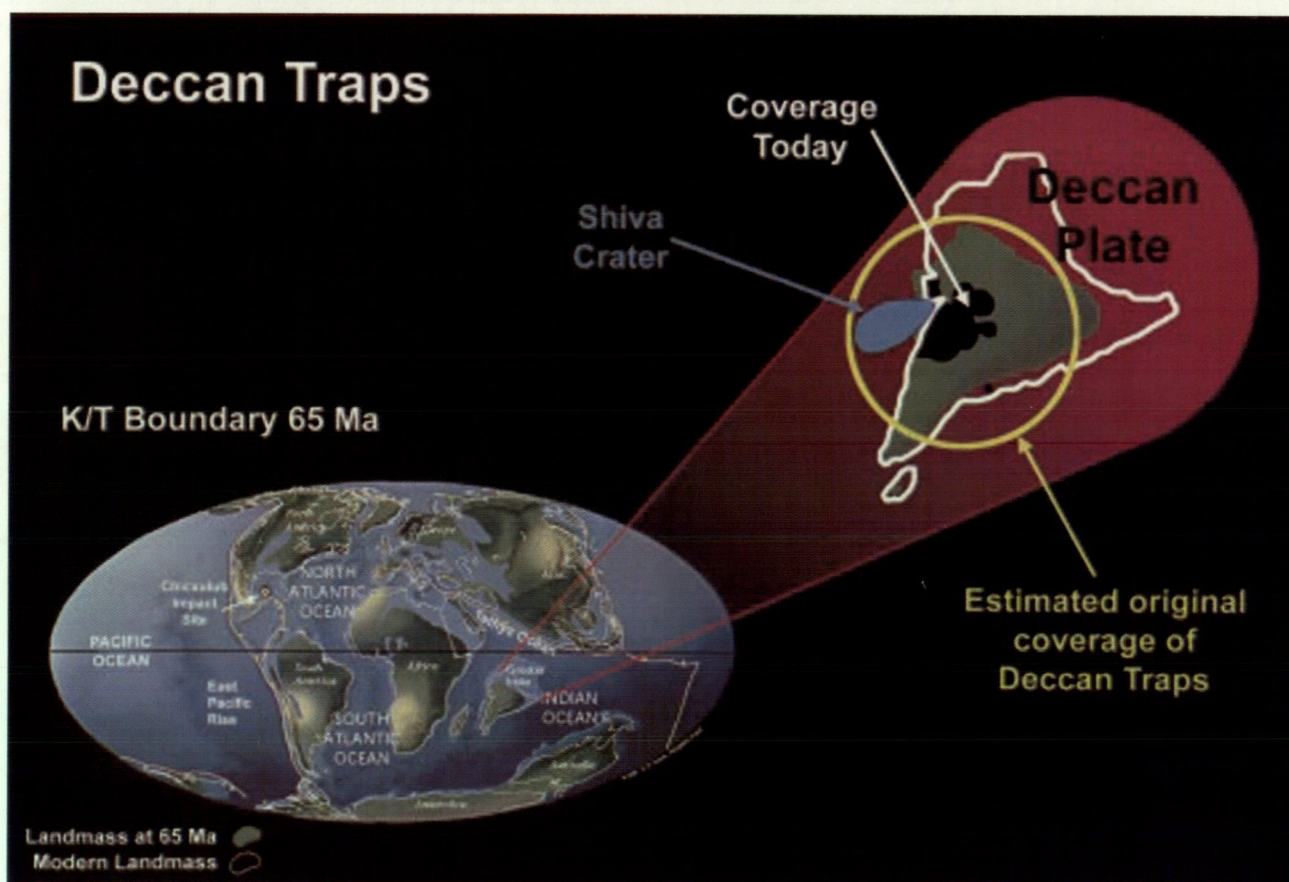

Figure 2   Current and estimated extent of Deccan Traps at 65 Ma. (World map at K/T boundary from Scotese, (2002), Deccan Plate after McLean (1985)).

Figure 3   The Western Ghats near Mahabaleshwar, Maharashtra, India, showing successions of Deccan Trap lava flows. Photograph: Pesh Framjee.

amplification if the Amirante Basin marks an impact site, the Shiva Crater, at the Deccan Plate/Seychelles Plate rift margin off Mumbai (Hartnady, 1986; Chatterjee, 1992, 1996). Whatever the cause, evidence of the magnitude of the Deccan Traps is very clear and river erosion through the Traps near Mahabaleshwar in the Western Ghats (Figure 3) reveals a succession of exposed lava flows that in some areas extend up to 1,500 m in depth. The magnitude of the Deccan Trap lava flows was such as to have inevitably caused significant global climate change and CO_2 outgassing that McLean (1985) considered sufficient to disrupt the Williams-Riley pump.

The remaining volume of Deccan Trap lava has been estimated at 10^6 km^3 (Krishnan, 1960) and the original volume as greater than 2.6×10^6 km^3 (Pascoe, 1964). A single lava flow ranging up to 30 m in depth could have amounted to 30,000 km^3 and been some 2,500 times greater than the Mount Laki flow. The Mount Laki flow was the largest eruption of this type in historical times, an estimated 12 km^3 that flowed from a 25 km fissure which opened near Mount Laki in Iceland in 1783. Emitted gases destroyed vegetation and up to 80% of the livestock died, as did a quarter of Iceland's human population. Global climate was affected and the winter of 1783–84 was particularly harsh in Europe (Courtillot, 1999). Even if figures for the Deccan Traps are gross overestimates it might be surprising if any of the Deccan Plate biota survived. However, as discussed below, there is clear evidence that a

Deccan Plate Gondwanan biota did survive. At the very least, Deccan Trap formation would have been a massive vicariant event isolating the southern and northeast extremities of the Deccan Plate and having a severe impact on the Seychelles Plate, which began rifting from the Deccan Plate at the end of the Cretaceous.

Deccan Plate biotic history

It has been widely considered that there is little evidence that the Deccan Plate was ever a major centre of biological endemism and this theme was the focus of a lively debate (Briggs, 1989, 2003; Patterson and Owen, 1991; Thewissen and McKenna, 1992; Rage and Jaeger, 1995; McKenna, 1995). The participants in this debate were in agreement about the reality of the lack of endemism but disagreed about the mechanism to explain it. One controversial issue has been the longitudinal trajectory of the Deccan Plate in the Late Triassic and Early Cretaceous. Based on palaeomagnetic and seafloor spreading data (Smith *et al.*, 1994; Scotese, 2001) the Deccan Plate clearly followed an isolated trajectory across the Indian Ocean. Based largely on an interpretation of the fossil record, Briggs (1989, 2003) has been a leading proponent of the view that the Deccan Plate followed a trajectory close to the African Plate that allowed biotic transfer. Patterson and Owen (1991) invoked an expanding earth model to explain the same faunal association. Chatterjee and Scotese (1999) suggested that a hypothesised Greater Somalia could have

provided a land route between the African and Deccan plates from about 70 Ma. However, no aspect of the modern Sri Lankan land snail fauna is suggestive of biotic transfer from Africa during rafting of the Deccan Plate.

A few taxonomic groups provide an impoverished Mesozoic fossil record for the Deccan Plate with conflicting evidence of faunal associations ranging from pan-tropical to Gondwanan (Briggs, 2003). Evidence of mammal and reptile faunas from the Late Cretaceous, when a high degree of endemism would be expected if the Deccan Plate was isolated, have been interpreted as being part of a cosmopolitan fauna (Krause et al., 1997; Raminder et al., 1996).

Briggs (2003, p. 384) stated "perhaps the most important consideration of all is the absence in the Indian fossil record of peculiar animals and plants that should have developed, had India undergone an extended period of isolation (millions of years) just before its contact with Eurasia. When continents or islands are well isolated for such extended periods of time, evolution invariably produces endemic species. If the isolation continues long enough, 30 Myr for example, a host of peculiar genera and families would be expected. The absence of such fossils in India, and the Asian-African relationships of its present fauna and flora, provide strong evidence that India did not take an isolated journey across the middle of the Indian Ocean."

Thewissen and McKenna (1992, p. 249) state that the Deccan Traps 'must have had a devastating impact on the biota of Indo Pakistan'. However, Briggs and others (Briggs, 1989, 2003; Patterson and Owen, 1991; Rage and Jaeger, 1995) seem to have given little consideration to the affect that events at the K/T boundary would have had on the Deccan Plate biota and its subsequent composition. Formation of the Deccan Traps must have taken a heavy toll on the rafted Deccan Plate biota while island assimilation and post Eurasian collision opened up access to a complex mixture of biotas so that unraveling the mixture requires critical investigation. The fact remains that a Deccan Plate Cretaceous fossil record is currently unknown for most systematic groups and further evidence must be sought from the modern biota. Evidence is accumulating of the survival of Gondwanan lineages on the Deccan Plate and Roelants et al. (2004) describe relict groups of frogs from both Sri Lanka and the Western Ghats. In addition, Gower et al. (2002) and Conti et al. (2002) demonstrate support for hypotheses of Deccan Plate origins and dispersal into Southeast Asia for caecilians and Crypteroniacea respectively. However, caution must be exercised in attributing origins to the Deccan Plate because of the possibility that Gondwanan elements could have arrived via other plate fragments.

Possible Gondwanan associations in the South Asian snail fauna

In addition to the very limited fossil evidence, several modern distributions strongly indicate that a number of land snail groups may have been present in Gondwana. The current distribution of bulimulids, and acavoid-strophocheilids suggests that they may have been widely distributed in Gondwana. Prestonella has recently been confirmed as an African representative of the Bulimulidae (Herbert and Mitchell, 2004), which occur in South America and Australia but no bulimulids are known from the Deccan Plate. The Charopidae: Punctoidea, are a southern group but the Punctoidea, as currently conceived, are not monophyletic and includes northern discids, while the relationships of northern Punctidae such as Punctum Morse and other punctoid groups are unknown (Wade et al., in press). With tiny snails, such as many of the Punctoidea, long distance wind borne dispersal is likely to be involved in their distribution, as evidenced by their occurrence on remote oceanic islands. Inclusion of the Deccan Plate genera Ruthvenia Gude and Thysanota Albers within the Charopidae needs to be verified.

Solem's (1981a) view that land snails were probably absent from Gondwana can be discounted on the basis of evidence from the fossil record (Stoliczka, 1867; Smith et al., 2004) and it is likely that a rich snail fauna was present. A few snails do occur in the Western Ghats and a significant number are present in Sri Lanka that are potentially of Gondwanan origin. In addition to the undoubted influx of taxa from Eurasia, it is possible that Gondwanan snails successfully dispersed into Eurasia from the Deccan Plate. However, potential Gondwanan taxa are more difficult to recognise in northern India. Candidates include Schistoloma Kobelt (Pupinidae: Pupinellinae), discussed below, which ranges from northeast India to Sumatra, Borneo and the Philippines, and groups related to Alycaeus Gray (Cyclophoridae: Cyclophorinae), which occur from Madagascar, through parts of the Western Ghats to northeast India and Southeast Asia. However, a greater understanding of phylogenetic relationships of snails in the region is needed before an attempt can be made to untangle Indo-Malaysian faunal origins.

The extent to which other land fragments, including additional fragments of Gondwana, might have been incorporated into the Eurasian land mass and contributed to the region's faunal composition is unknown. However, if for example, Ladakh and Kohistan island fragments were incorporated into the Deccan Plate after the K/T boundary, they could have transferred a significant faunal component to a remnant Deccan Plate Gondwanan fauna impoverished or eliminated by Deccan Trap flows. Furthermore, any distinct fauna

from the continental fragments considered to make up the Tibetan plateau (Rajaram and Langel, 1992) could have entered into the Deccan Plate before being locally eliminated by climate change following elevation of the Tibetan plateau.

Possible Sri Lankan links with Madagascan snails

The rafting Deccan Plate is likely to have possessed a diverse snail fauna but because of the devastating effect of the Deccan Trap lava flows its composition prior to the K/T boundary might have been closer to that of modern Madagascar rather than to that of modern India. Between 95–84 Ma the Madagascan Plate separated from the Deccan Plate and there might appear to be interesting common elements with the Sri Lankan fauna. For example, *Cyathopoma* Blanford, a species of which was also described from the Congo (Pilsbry, 1919), the helicarionid *Kaliella* Blanford, and the ariophantids *Macrochlamys* Benson and *Sitala* Adams. However, some of these groups are widely distributed and current genera are likely to be composed of several distinct groups. For example, our examination of the anatomy of supposed *Macrochlamys* from Sri Lanka shows it to belong to a different group allied to *Eurychlamys*. The species diversity structure of the current snail faunas is radically different. Whereas there are no acavids in India and two genera of acavids totaling six or seven species in Sri Lanka, modern acavoids are strongly represented in Madagascar (Van Bruggen, 1980a). There are also a large number of Pomatiasids in Madagascar, which on the Deccan Plate are limited to five localised Indian species of *Cyclotopsis* Blanford. An additional pomatiasid species, *Revoilia hinduorum* (Blanford), occurs in coastal areas of Kathiawar in Gujarat and has been associated with species of *Revoilia* Bourguignat from the Arabian Peninsula (Neubert, 1998).

With 77 described species and an estimated species diversity of at least 250, *Kalidos* Gude Ariophantidae, is a highly diverse group in Madagascar (Emberton, 2002b). The Ariophantinae: Ariophantidae: Limacoidea are the most species diverse stylommatophoran subfamily in Sri Lanka and our initial studies show that additional Sri Lankan limacoid taxa probably belong here. Hausdorf (1988) took a significant step forward in applying a consistent phylogenetic analysis to the Limacoidea but inadequate morphological autapomorphies in this cosmopolitan group made it difficult to establish family-level identities and relationships. Within the Ariophantidae, Hausdorf recognised the likelihood of a sister relationship between the Madagascan (?), South Asian and Southeast Asian Macrochlamydinae, the Tonkin semi-slug Ostracolethinae and the Ariophantinae. Although widely reported in the literature from Southeast Asia east to New Guinea, it is unclear to what extent the Ariophantinae occur outside of southern India and Sri Lanka where *Euplecta* Semper, *Cryptozona* Mörch and *Ratnadvipia* Godwin-Austen, form a distinct clade (Wade *et al.*, in press). The relationships between African, Madagascan and Asian Ariophantinae/Urocyclidae is currently unclear. Emberton and Rakotomalala (1996, p. 566) suggest that *Kalidos* Gude might be 'synonymous with an Indian ariophantid' while Hausdorf placed the African Urocyclidae as a sister group to the Ariophantidae. Wade *et al.* (in press) consider that in their molecular tree the radiation of the Limacoidea was probably part of an early Cenozoic stylommatophoran radiation. This would seem to allow only for a Laurasian origin for the group and dispersal to southern distributions. If this proves to be the case then the group would seem to be capable of both rapid dispersal and rapid evolution, including that of the endemic Sri Lankan genera *Ratnadvipa* and *Ravana* Godwin-Austen. However, it is of interest to note that urocyclids are present in the earliest fossil land snail faunas recorded from East Africa and supposed extant species of *Trochonanina* Mousson and *Thapsia* Albers are recorded from beds dated at 22 Ma (Pickford, 1995).

In the only wide ranging review of cyclophoroidean anatomy, Tielecke (1940) examined the nervous and reproductive system, phylogeny and distribution of taxa and grouped *Tortulosa* and *Schistoloma* in the Pupinellinae: Pupinidae. The Pupinellinae are potentially of Deccan/Madagascan Plate origin and the Madagascan *Madecataulus* Fisher-Piette and Bedoucha, appears to belong in this group. On the Deccan Plate five Indian species and the 25 Sri Lankan species of *Tortulosa* Gray exhibit a similar shell form to *Madecataulus*. *Tortulosa* generally exhibits a single basal notch on the peristome that is the termination of an internal basal canal, and a corresponding external basal keel. *Tortulosa eurytrema* (Pfeiffer) exhibits an additional suprapalatal canal similar to the sutural canal found in *Madecataulus*, which also exhibits a basal canal. *Madecataulus* was synonymised with *Boucardicus* in the Alycaeinae (Emberton and Pearce, 1999) and incorporated as part of a supposed massive endemic radiation of *Boucardicus* in Madagascar (Emberton, 2002a). Emberton and Rakaotomalala (1996, p. 566) state that 'closer scrutiny may determine that the Madagascan *Boucardicus* is a synonym of the Indian Asian *Alycaeus*'. The Madagascan/South Asian/Southeast Asian distribution of *Alycaeus* and related genera, which Tielecke (1940) placed in the Cyclophorinae, includes the Western Ghats but the group is not represented in Sri Lanka. The status and relationships of *Boucardicus sensu* Emberton (2002) clearly need further investigation. From NE India

and extending across into SE Asia *Schistoloma* also possesses a very similar shell form to *Tortulosa* and *Madecataulus*. *Schistoloma* generally exhibits a basal keel but internally, opposite to the keel, there is only a slight depression and the distinctive notch that is found in *Tortulosa* and *Madecataulus* does not interrupt the peristome. If the Pupinellinae are of Gondwanan origin, the discontinuous distribution of *Tortulosa* and *Schistoloma* could originate from the vicariant event of Deccan Trap formation.

Acavids

Sri Lankan acavids have been widely considered as components of a relict Gondwanan fauna on the Deccan Plate (Bruggen, 1980b; Mead, 1985; Nordsieck, 1986; Emberton, 1990; Neubert, 1998). This is primarily because of the current distribution of acavoids but, in addition, their powers of dispersal are considered to be low because of their disproportionately large eggs and the lowered chance of passive dispersal by wind. While considering that acavoids were the one group for which a Gondwanan distribution might be valid, Solem (1981a, p. 214) added that 'all of the taxa which show a Gondwanian distribution can be interpreted equally well as remnants from a Pangean fauna'. Solem (1968) presented a detailed case based on the principle adopted by Darlington (1957) that primitive species were found remote from centres of origin whereas derived taxa occupied areas at the centre of origin. This so-called evolutionary biogeography paradigm was followed to support Solem's view that the Acavoid/ Strophocheilid clade was a group of Laurasian origin that dispersed to southern continents and subsequently became extinct in the north. Solem was also viewing biogeography from the perspective of fixed continents though he later recognised the potential of plate tectonic events for understanding land snail distributions (Solem, 1979).

Solem (1981a, p. 207, fig. 5.4) showed a distribution for the acavoids that took a wide sweep east and north of Madagascar and extended north and east of the Seychelles to encompass south and southeast peninsular India. With its brightly coloured attractive shells *Acavus* has long been a prized item for shell collectors and museums around the world have numerous unlocalised examples and occasionally locality information outside of Sri Lanka that is almost certainly erroneous. For example, *Acavus haemastoma* (Linnaeus) from Sivaganga, Tamil Nadu, India (Satyamurti, 1960) would need to be confirmed by additional supporting evidence. In the North Gallery at the Royal Botanic Gardens, Kew one of the 832 paintings by Marianne North of her travels around the world depicts the Sri Lankan endemic *Acavus phoenix* (Pfeiffer), supposedly from Singapore. However, there are no verified records of acavoids in Asia outside of Sri Lanka.

Supported by his mistaken assertion that the Paleocene provided the earliest land snail fossil record from Gondwana, Solem repeatedly returned to his earlier theme of a northern origin for all land snail taxa. A northern origin for some currently supposed Gondwanan land snail taxa cannot be discounted. A number of extant disjunct plant distributions in southern continents have been attributed to dispersal directly from the boreotropics or indirectly from one southern plate to another via the boreotropics (Davis *et al.*, 2002; Givnish and Renner, in press). It is not clear if tropical forest Eurasian biotas would have been present in the Eurasian contact zone of a Mid to Late Oligocene land connection with the Deccan Plate. In any case, acavoids are not restricted to the tropics or to wet climates; the extant Australian acavoid fauna extends into the temperate climate of Tasmania and African acavoids occur in arid environments. The likelihood that acavoids crossed the Deccan Plate from Eurasia to die in their tracks and survive only in Sri Lanka without also occurring in southeast Asia seems remote. However, Wade *et al.* (in press) show a neighbour joining molecular tree and Bayesian tree for the Stylommatophora in which *Acavus* falls in a weakly supported group with the enigmatic northern carnivorous slug *Testacella* and a long branch linking to the Charopidae. This lends tenuous support to a possible northern origin for *Acavus* but the lack of structure at the base of the Wade *et al.*, trees means that this relationship is likely to change under different analyses or when different genes are examined. However, other acavoids in the trees are linked with the exclusively southern Rhytididae and *Corilla*.

Solem (1968) hypothesised the dispersal of acavoids from a northern origin to southern Africa, Madagascar, the Seychelles, Australia and South America. This might appear untenable in the context of plate tectonic events, the basal position of acavoids within the Stylommatophora (Wade *et al.*, 2001) and the high diversity of acavoids in the isolated land mass of Madagascar. However, because of incongruent timings between the supposed origin of taxa and plate tectonic events, the mechanism of long-distance dispersal has been restored as a more likely explanation for supposed Gondwanan distributions in many plant groups (Givnish and Renner, in press, and presentations and discussion at a Royal Society, London, meeting in March 2004, to be published). In addition, the presence of chameleons in Madagascar, one of the few extant terrestrial vertebrate groups thought to have distributions congruent with Gondwanan origins, has been attributed to repeated long-distance dispersal from Africa (Raxworthy *et al.*,

2002). Chameleons are not considered to be sufficiently ancient to exhibit a shared African and Madagascan divergence pattern that would have to predate the rifting of Africa and South America from the rest of Gondwana at 150 Ma if vicariant origins were to be invoked to explain their distribution. Nevertheless, land snails are different in having extant groups with Gondwanan distributions that appear to have a fossil record extending into the Mesozoic. There are also a large number of snail taxa that might be investigated. In particular, more acavoid and corilliform taxa need to be included in a molecular phylogeny to demonstrate the history of these groups.

Corilliform groups

Corilliform taxa are of particular interest because of the record of corilliform shells from the Mesozoic Deccan Plate and Western Eurasia (Figure 1). Solem (1981a, p. 206, fig. 5.3) showed the distributions of two geographical groups of corilliform taxa that he included within the Corillidae. *Sculptaria* Pfeiffer, a West African group and a group including *Corilla* Adams and *Plectopylis* Benson were shown as being continuously distributed over much of South and mainland Southeast Asia. However, this pattern is misleading. The African group consists of several species of *Sculptaria* in Namibia and an additional *Sculptaria* on Bioko (Fernando Poo), an island in the Gulf of Guinea that is part of the African Plate. In Asia *Corilla* is confined to ten species in Sri Lanka and a single species, *Corilla anax* Benson, confined to the Anamalai Hills in the southern Western Ghats of Tamil Nadu and Kerala. There is a discontinuity of some 2,500 km between *Corilla* and *Plectopylis*; *Plectopylis* extends from NE India east through Myanmar, northern Thailand and into China, where it ranges north and east as far as the East China Sea coastal islands and southern Japan. Within the general range of *Plectopylis* are several shell forms that may represent distinct genera: *Endothyrella* Zilch, *Chersaecia* Gude, *Endoplon* Gude, *Sinicola* Gude, *Amphicoelina* Haas, and possibly *Stegodera* Martens, although *Stegodera* is probably a camaenid (Pilsbry, 1905; Richardson, 1985). The systematic position of *Craterodiscus pricei* from northeastern Queensland is controversial but placement within the Corillidae on anatomical criteria (Tillier, 1989; Stanisic, 1998) or within the Camaenidae (Solem, 1973) was not supported in a molecular phylogeny where *Craterodiscus* came within the Limacoidea (Wade *et al.*, 2001).

The internal anatomy has been described for *Sculptaria, Corilla*, and *Plectopylis* (Stoliczka, 1871; Semper, 1873; Pilsbry 1894; Degner, 1923; Solem, 1973; Tillier, 1989; Emberton, 1991) but most corilliform groups are known only from their shells. *Sculptaria* and *Corilla* share similar anatomical features in their reproductive and renal systems

(Tillier, 1989) that justify their association in the Corillidae. In particular they share an arrangement of the gametolytic sac and duct in which the duct is long and narrow with a distal branching into a flagellum and separate narrow duct to the gametolytic sac. Missing from the example of *Sculptaria collaris* Pfeiffer figured by Tillier (1989), a gametolytic flagellum had presumably broken off of the specimen that he examined. In *Plectopylis* the gametolytic duct is short relative to that of *Corilla* and expands into a long gametolytic sac and there is an accessory organ branching from the vagina. The small central radula tooth has been compared to that of subulinids and the v-shaped central elements of the jaw have been compared to bulimulids (Pilsbry, 1894). The external similarity of the shells of *Corilla* and *Plectopylis* is remarkable but shells of *Plectopylis* possess internal lamellae that are aligned transversely whereas, when present in *Corilla*, lamellae are more or less aligned with the suture. *Plectopylis* and *Corilla* share a number of plesiomorphic characters (Tillier, 1989) but on current evidence there seems to be little basis for including *Plectopylis* within the Corillidae. There is a clear need to include *Plectopylis* within a molecular phylogeny and historical biogeographical interpretations cannot include *Plectopylis* until its phylogenetic relationships are more firmly established. The current uncertainty serves to emphasise that homoplasy in shells might not be resolved or even recognised in the fossil record.

Additional groups with possible Gondwanan or other Mesozoic origins

Glessula Martens has a modern distribution centered in South Asia and is potentially of Deccan Plate origin, its radiations in northeast India and Sri Lanka are linked by a number of species through the Western Ghats and Eastern Ghats. The range extends from northeast India into Myanmar, one species reaches Thailand and a single species occurs in Sumatra and Java. *Glessula* has a distinct and complex epiphallic structure and spermatophore formation, unique for achatinoids, and was placed in its own family, the Glessulidae by Godwin-Austen (1920). Earlier classifications assumed that *Glessula* is an African and Indian group (Pilsbry, 1910) a faunal affinity for which a Gondwanan or later origin through the Arabian corridor or long-distance dispersal might be hypothesised. However, the close similarity in shell form between African groups and *Glessula* seems likely to be the result of homoplasy. *Pseudoglessula* Boettger is an African genus in which the penial caecum has the same arrangement as in African *Subulina* Beck with a distal retractor insertion (Solem and Van Bruggen, 1976). On this basis *Pseudoglessula* belongs in the Subulinidae; in the Glessulidae the spermatophore forms in a free flagellum, which is distinct from the

penial caecum of *Pseudoglessula*. Again, although the shell of the African group *Neoglessula* Pilsbry, suggests a close affinity with South Asian *Glessula*, the limited anatomical information available (Odhner, 1932) suggests that this is not the case. Wade *et al.* (2001) show *Glessula* on a long branch linked to *Zootecus* Westerlund, the circum-Mediterranean *Rumina* Risso, and tropical African *Xerocerastus* Kobelt and Möllendorff, none of which are obviously related to *Glessula* on known anatomical criteria. *Zootecus* is a synanthropic genus likely to be dispersed by human agency and little interpretive value might be derived from its unusual distribution. It ranges across desert latitudes and extends from Atlantic islands east across North Africa, through the Middle East and across Central India to the dry zone of central Myanmar and is also found in the dry zone of Sri Lanka. The inclusion of a wider range of achatinoid taxa in molecular studies is likely to provide information on relationships that will allow a clearer understanding of *Glessula*.

Gastrocopta Wollaston is widely distributed and its range, which includes Sri Lanka, has been interpreted to have become established in the Middle Jurassic (Stworzewicz, 1993). However, the derived position in the molecular tree given by Wade *et al.* (2001) indicates that the Vertiginidae evolved later than supposed Mesozoic groups such as acavoids.

Several species in Sri Lanka and two in southern India represent the total range for the beautiful arboreal camaenid snail *Beddomea* Nevill. *Amphidromus* Albers, which ranges from northeast India, through Myanmar, Thailand, Malaysia and Indo-China to the Philippines and Australia (Solem, 1983b) and *Papuina* Martens from New Guinea are arboreal camaenids thought to be related to *Beddomea*. However, their relationships are not well established and with a supposed fossil record for camaenids extending into the Mesozoic (Solem, 1978; Smith *et al.*, 2004) we have no measure of what might account for this distribution.

Influence of climate

Following a land connection of the Arabian Plate with Eurasia in the Early Miocene there was a brief period when a wetter climate might have allowed an African forest land snail faunal route into Asia and into the Deccan (Neubert, 1998; Whybrow and Hill, 1999). However, apart from the possible example of *Zootecus*, which in any case lives in arid habitats, there is nothing to indicate that an African element might have entered through this route as far as Sri Lanka.

Plate tectonic land connections had a major impact on global climate (Haug, 2004) but were irrelevant as new land routes for South Asian distributions that have arisen since the Late Tertiary. Plant fossils through the Miocene and Pliocene, approximately 25–2 Ma ago, indicate that tropical wet evergreen forests were present throughout much of the peninsular region. Nowhere in India currently receives rainfall throughout the year but, although there seems to be a trend towards increased seasonality, some areas of the Sri Lankan wet zone do receive some rainfall every month. The closest comparable environments are those of Southeast Asia in Sumatra, peninsular Malaysia, Java and Borneo. However, we are not aware of Sri Lankan land snail groups that occur in Southeast Asia but not in India. For example, in *Philalanka* Godwin-Austen, the distribution appears to be determined largely by current climate but corresponds with wet and seasonally wet tropical Asian climates ranging from Sri Lanka and southern India through peninsular Malaysia and into the Sunda archipelago and east as far as New Ireland. Such generic distributions generally involve distinct species and probably predate current climate regimes but, with the current lack of knowledge of relationships and genetic distance between species, it is impossible to recognise when such patterns became established.

Confinement of many peninsular endemics to the Western Ghats could have arisen in the Quaternary by a combination of increased aridity in much of the Peninsula and temperature change. Ashton and Gunatilleke (1987) cite evidence of temperature depression of about 2°C at the height of the last glaciation in the south Indian region and less than 5°C at the highest altitudes. A scenario can be hypothesised in which, following on earlier Indo-Malaysian faunal immigrations through the Assam corridor, the peninsular tropical snail fauna, including any surviving Gondwanan elements, was impoverished with increasing latitude during glacial episodes. This may have led to the total extinction of a tropical snail fauna in North and Central India in glacial periods. With the opening up of a Malaysian faunal bridge in the Northeast in inter-glacials, a Recent Malaysian fauna was likely to have became established as the dominant element in the Himalayan region and extended into continuous forest through the Brahmaputtra valley and into the then forested Gangetic plains.

During glacial episodes, higher-altitude taxa may have had a temporary pathway from the Himalaya in Northeast India through the Vindhya-Satpura ranges to the Eastern and Western Ghats, a route which formed the basis of the Satpura hypothesis (Hora, 1949). The presence of Himalayan taxa in isolated high-altitude refugia in southern peninsular India might be explained by this hypothesised route and be examples of what has been described as the genetic legacy of the Quaternary ice ages (Hewitt, 2000). However, such lowering of temperatures seem insufficient to

account for a continuous link across the intervening lowlands separating the Central Highlands of Sri Lanka from the Western Ghats. It is particularly difficult to explain this as a mode of dispersal to Sri Lanka where taxa do not also occur in peninsular India.

Thus the presence in Sri Lanka of *Landouria* Godwin-Austen and a clausiliid, possibly *Phaedusa* Adams, which are absent from peninsular India, is not adequately explained by this mechanism. The Clausiliidae are primarily a northern group only represented in southern continents by *Nenia* Adams in South America and *Macroptychia* Boettger, in Africa, while *Sabaeola* Lindholm occurs on the Arabian Plate. *Phaedusa* is a Himalayan group and the only South Asian clausiliid recorded south of the Himalaya, *Clausilia ceylanica* Benson was known only from Fort McDonald, the type locality, which was a nineteenth century wooden structure at about 1,400 m in the Nuwara Eliya District, Sri Lanka. The fort is long gone and we have not found *P. ceylanica* at the site but in 1999 we discovered a population living on the bark of exotic trees at the western edge of Hakgala Botanical Gardens. *P. ceylanica* has not been recorded from natural forest and it seems likely to be a recent introduction. However, it has not been recognised outside of Sri Lanka and the nearest phaedusids are over 2,500 km away. A similar discontinuity occurs with the camaenid *Landouria radleyi* (Jousseaume), which also occurs in Nuwara Eliya District but is found in natural forest habitat. The only other known species of *Landouria* occur over 3,000 km away in Himalayan northeast India and northwestern Myanmar, including the type species *Landouria huttoni* (Pfeiffer), which Godwin-Austen (1918) described as being almost identical to *L. radleyi*.

Impact of exotic gastropod species

Introduced gastropod species have a major impact on Sri Lanka's farm and horticultural production. They may occur at very high densities and, although there are relatively few exotic species, because of the extent of transformed habitats the biomass of exotic species seems likely to exceed that of native gastropods. Species such as *Laevicaulis altae* (Férussac), *Pupoides coenopictus* (Hutton) and *Zootecus insularis* (Ehrenberg) have long been established in Sri Lanka and may have been introduced through trade with Arabia and East Africa, whereas *Bradybaena similaris* (Férussac) was possibly introduced by trade with Indonesia or Malaysia. The introduction of *Lissachatina fulica* (Bowdich) in about 1900 is well documented (Naggs, 1997). However, exotic species from temperate regions were not recorded in the early twentieth century *Fauna of British India, Mollusca* series, and remained unrecognised in Sri Lanka until our investigations established their significant presence in higher

altitudes (Naggs *et al.*, 2003; Mordan *et al.*, 2003; Naggs, 2004). The predatory gastropods *Eustreptaxis kibweziensis* (Smith) from East Africa and *Euglandina rosea* (Férussac) from Florida, were introduced into Peradeniya in the 1950s in an ill-advised attempt to control *Lissachatina fulica* (Mead, 1979). Individuals of *E. kibweziensis* are occasionally found but the introduction of *E. rosea* was apparently unsuccessful and none have been recorded since their release. Introduced predatory gastropods, particularly *E. rosea* have had a devastating impact on the snails of oceanic islands and many native species have become extinct. However, the land snail faunas of oceanic islands are generally founded on a few colonising species and the subsequent species radiations have not been tested against the rigorous competition of an established fauna. Oceanic island snail faunas are therefore likely to be less resilient and more vulnerable to extinction when exposed to invasive exotic species, particularly with such voracious predators as *E. rosea*.

In intensively cultivated areas there are few, if any, native species but in more complex habitats, such as traditional village home gardens, there is a mixture of exotic and native species in varying proportions. At least in the short-term, introduced terrestrial gastropods rarely invade native environments (Hausdorf, 2002). However, there are exceptions and *Deroceras* Rafinesque has been recorded as an introduced alien in South Africa where it has invaded pristine indigenous habitats (Herbert and Kilburn, 2004). A major question for the long-term is the extent to which exotic species will interact with the native biota (Naggs *et al.*, 2003). The way in which exotic genera such as *Cochlicopa* Risso, *Oxychilus* Fitzinger, *Deroceras*, *Arion* Férussac and *Milax* Gray have become rapidly established in Sri Lankan and other tropical highland areas during the past fifty years or so seems likely to be a significant and irreversible evolutionary event. Although these gastropods are thought of as being temperate species at least some probably evolved in, and are therefore likely to be well adapted to, tropical highland habitats. *Cochlicopa, Oxychilus* and *Milax* occur as fossils in the British Palaeogene and Preece (1982) considered that what appear in modern faunas to be two largely discrete tropical and temperate faunal elements co-existed in a wet and warm, frost-free climate in the Palaeogene of Britain that has no modern equivalent. Earlier work suggested that this mixed fauna was the result of a depositional mixture of autochthonous tropical elements and allochthonous higher altitude faunas from adjacent upland regions. Although the taxa examined by Preece probably were sympatric, it seems likely that there was a component of this fauna that extended into higher altitudes and may have been confined to higher altitudes in the warmer episodes of the

Palaeogene. With the marked cooling of higher latitude climates at the end of the Eocene a number of frost tolerant groups, which probably evolved in northern high latitude/higher altitude tropical climates of the Early Palaeogene, survived in Europe through the Eocene/Oligocene boundary. It is from Europe and through human agency that they appear to have become re-established in higher altitude tropical habitats for the first time since the end of the Eocene.

Species level endemism in Sri Lankan snails

The high level of snail endemism in Sri Lanka and the Western Ghats is suggestive of a period of isolation that could date back well into the Tertiary and beyond. Little is known about the time scale in which new land snail species and genera might become established. There is clearly no set time period in which individual lineages at species level might diverge and there seems to be little understanding of the time scale in which whole faunas might diverge at species level. The best-known Miocene land snail fauna is that recorded from the Early Miocene to the Holocene of Kenya, a period spanning over 22 Ma (Verdcourt,1963; Pickford, 1995). All of this fauna can be attributed to extant genera, and many to extant species or to species similar to extant species. This suggests that for land snail faunas to show a completely different species level taxonomy, a period of isolation exceeding 22 Ma might be needed: a time scale well on the way to the 30 Ma contact date of the Deccan and Eurasian land connection. Speciation in small isolated oceanic islands can occur much more rapidly than appears to be the case with continental faunas and islands just a few million years old can establish a high level of species and generic endemism. But, as with the impact of exotic species, a fauna based on the radiation of a few colonising species on oceanic islands is probably an inappropriate model for a continental island fauna such as that of Sri Lanka.

However, it is possible that conservative shell forms in the fossil record can mask dynamic species turnover. This is supported by preliminary molecular investigations of *Acavus*, which show that all *Acavus* species are closely related. A 580 bp fragment of the LSU gene, primers LSU-2 and LSU-5 (Wade *et al.*, in press), have been sequenced for *A. phoenix, A. haemastoma, A. superbus* and an unidentified juvenile *Oligospira* species. The 4 specimens examined display very low levels of variation (less than 1%) which indicate that not only are *Acavus* species closely related but that *Oligospira* would be considered to be con-generic on these molecular criteria (Hudelot, pers. com.).

That *Acavus* species are closely related was supported from investigations carried out following fieldwork in 1995 by D. Raheem and T. Butterworth

(Imperial College, University of London Expedition Report 1997, *A Survey of land mollusc diversity in south-western Sri Lanka*. 22 pp). *Acavus* specimens from this survey formed the basis of an undergraduate project (Raheem, D., 1997. *An Investigation into the Taxonomy and Systematics of the Genus Acavus (Pulmonata: Acavidae)*, Imperial College, University of London, undergraduate report. 54 pp). This work demonstrated that *Acavus* species exhibit allopatric and largely contiguous distributions with evidence of narrow hybridization zones. For example, the penial morphology of specimens from Haycock, a hill in Galle District, was intermediate between that of *A. haemastoma* and *A. superbus* (Pfeiffer). Haycock is situated on the eastern edge of the currently known range of *A. haemastoma* and a few miles northwest of Kanneliya, which lies on the southern boundary of *A. superbus*. In addition, species level differences were identified in what had earlier been considered to be two forms of *Acavus phoenix*, including different spermatophores, and one of these 'forms' was subsequently described as *Acavus phoenix castaneus* Hausdorf and Perera (2000).

Although this pattern of closely related species is also consistent with a single colonization event, a close relative of *Acavus* has not been identified outside of Sri Lanka (Wade *et al.*, 2001). The three or four extant species of *Acavus* and three species of *Oligospira* are probably recent branches from a single lineage that has tenuously survived since the Mesozoic. As discussed above (p. 20), we take the view that a distribution confined to Sri Lanka and plate tectonic history supports a Gondwanan origin for *Acavus* and *Oligospira*. However, from molecular evidence it has yet to be established if this lineage was confined to the Deccan Plate or entered through Laurasia and the possibility of an origin from other continental fragments is a further complication. Although *Acavus* might be regarded as a living fossil in terms of its shell form, general morphology and physiology, it is dynamic at the biological species level.

The question of how high levels of diversity and endemism are sustained over long periods of time in a relatively confined area is central to the debate about rainforests as centres of biological diversity and the focus of conservation effort. Many biologists consider that rainforests are the most important reservoirs of global terrestrial biological diversity, that the forests and their diversity are rapidly disappearing and that current extinctions are at levels unprecedented since the K/T boundary. However, there is a counter argument that tropical biotas are just as dynamic as temperate ones in terms of the time scale of shifting ranges and mixing of faunas. There is clear evidence of major shifts in areas of tropical forests in Quaternary Africa, South America and Southeast

Asia (Flenley, 1979) but this argument has been perversely extended to make the case that loss of tropical forest is not a major issue for loss of biodiversity. With proselytizing fervour Stott (1999, 2001) has gone so far as to claim that concern about loss of tropical forest diversity is not only misplaced but amounts to a northern conspiracy constraining development in the South. Many conservation groups in the South are unlikely to agree. While many tropical faunas may have undergone considerable mixing with new combinations established during different climatic episodes, high local endemism might be interpreted as evidence that some restricted areas have sustained high levels of diversity for long periods of time. Forest loss in these isolated hotspots results in an irreversible loss of biological diversity and the forest fragmentation that has occurred in Sri Lanka must have inevitably resulted in land snail extinctions. In the Darwin Initiative surveys carried out between 1999 and 2002, 35–40% of the sampled taxa were undescribed and we can only conclude that a significant number of taxa have become extinct in the past two hundred years of forest loss without having been described. Nevertheless, our initial observations suggest that even the smallest fragments of forest can be important for conservation as reservoirs of snail diversity that might be sustainable in the short and medium term.

Whereas Quaternary faunal shifts in high latitudes have largely been latitudinal, in low latitudes corresponding shifts in topographically diverse areas have largely been altitudinal. Thus the varied physical geography of Sri Lanka would have allowed biotic shifts in distribution along altitudinal gradients to accommodate past climate change such as occurred in the Quaternary (Deraniyagala, 1992; Premathilake and Risberg, 2003). This partitioning of local faunas and isolation into small populations through altitudinal distribution changes in the Quaternary is analogous to the southern refugia in Europe that have been considered to be both reservoirs of diversity and to provide a mode of speciation (Hewitt, 2000). Such altitudinal shifts will not be possible with future climate change in Sri Lanka because forests are reduced to many small fragments; in the absence of forest corridors there is little capacity for biotic distribution shifts. Whatever the concerns might be about human-induced global warming it should be remembered that we are currently in an interglacial phase of the Quaternary and climate change is inevitable on a time-scale of thousands of years. This is an instant in the lifetime of species and there is no evidence that snails can adapt in situ to different climate regimes on this time scale: in order to survive distributions have to shift. Some Sri Lankan endemic snails thrive within the mosaic of transformed habitats, particularly in traditional village home gardens and as long as such home gardens survive they may serve as corridors for some native species. However, in the absence of forest corridors that would allow population shifts, the long-term future for much of Sri Lanka's land snail fauna is bleak.

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