The Sri Lankan endemic semi-slug *Ratnadvipia* (Limacoidea: Ariophantidae) and a new species from southwestern Sri Lanka

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Contents
Abstract 99
Introduction 99
Genus *Ratnadvipia* 100
Species descriptions 107
   *Ratnadvipia* irradians 107
   *Ratnadvipia* karui 117
Acknowledgements 125
References 125
Appendix I Abbreviations used in figures 126
Appendix II List of forest areas 126

Abstract The endemic Sri Lankan land-snail genus *Ratnadvipia* is reviewed and a new species is described. Detailed descriptions of the shell, external morphology of the animal, reproductive anatomy, spermatophore and radula of *Ratnadvipia* irradians and the new species are provided. Distributional data collected to date for the two species are reviewed. Both species are associated with the highly fragmented rain forests of Sri Lanka’s wet southwestern quarter. *R. irradians* is the most wide-ranging of Sri Lanka’s endemic land snails. It extends into the drier parts of the island and occurs in synanthropic habitats such as home gardens. The new species is largely restricted to the lowland rain forests of the southern part of the wet lowlands. Both species appear to be at least partly arboreal, but little is known of their ecology.

Key words *Ratnadvipia*, Ariophantidae, rainforest, land snail, Sri Lanka

Introduction

Sri Lanka is an integral part of the ancient Deccan Plate separated from the Indian mainland by the narrow and shallow Palk Strait. It has been repeatedly joined to the mainland, most recently during the last glacial period when global sea levels were lowered. Nevertheless, the island possesses a rich endemic snail fauna. The endemic species are mostly concentrated in the small fragments of rain forest remaining in the southwest of the island. Our extensive surveys of the land molluscan fauna suggest that it is highly threatened by fragmentation and transformation of forest habitats. The taxonomic status of the snail fauna needs significant revision and taxonomic diversity is far greater than was previously recognised (Naggs et al., 2003, 2005).

Five snail genera are currently considered to be endemic to Sri Lanka, the cyclophorid prosobranch *Aulopoma* and four stylommatophoran pulmonates. The stylommatophorans are the acavoids *Acavus* and *Oligospira*, and ariophantid limacoids *Ravana* and *Ratnadvipia*. *Ratnadvipia* (Godwin-Austen, 1899a) is a striking semi-slug commonly encountered in the rain forests of southwestern Sri Lanka.

Detailed investigations of the endemic snail fauna are needed in order to gain an understanding of what has given rise to this endemism and its significance for conservation. To this end we are currently engaged in several projects ranging from disseminating information in educational material such as faunal guides (Naggs & Raheem, 2000, 2002, 2003a, 2003b; Mordan et al., 2003) to the inclusion of Sri Lankan snails in molecular phylogenetic studies (Wade et al., 2001, in press). Here we investigate the morphology of *Ratnadvipia* concentrating on features of the reproductive organs that have proved of value in developing stylommatophoran systematics.
Godwin-Austen (1899a: 253) described *Ratnadvipa* in his review of the anatomical foundations for recognising genera within the ‘Zonitidae’, in which he focused on the reproductive organs proximal to the genital orifice. However, *Zonitidae sensu* Godwin-Austen was a broad Limacoidean group and was not used in the currently restricted sense. Earlier work on *Ratnadvipa* was based entirely on shell characters. Godwin-Austen (1899b) and later Blanford & Godwin-Austen (1908) also considered the external appearance of the body, the jaw and radula and were thus responsible for demonstrating homoplasy in similar shelled forms of limacoids from South and South-East Asia which represent different, local or regional radiations. Hausdorf (1998) carried out a review of morphological relationships within all limacoid families but the monophyly of the Ariophantidae *sensu* Hausdorf, or even that of genera in the Ariophantinae *sensu* Zilch 1959, has not been resolved.

The eastern geographical limit of the Ariophantinae has not been firmly established but it is primarily, if not entirely, a South Asian group and a significant component of the regional fauna, representing 30% of Sri Lanka’s stylommatophoran species (Naggs & Raheem, 2000). From our investigations of the Sri Lankan snail fauna it is clear that, in addition to systematic studies on relationships, there is an urgent need for taxonomic revisions and the publication of information on distributions before conservation issues can be addressed adequately. Unfortunately, Indian controls on the export of biological material for research currently hinder our investigating the relationships of the Sri Lankan snail fauna to that of India (Pethiyagoda, 2004).

**Genus Ratnadvipa**

*Genus Ratnadvipa* Godwin-Austen, 1899

**Type species**

*Vitrina irradians* Pfeiffer 1853 (by monotypy)

**Taxonomic history**

Pfeiffer (1853) cited the original description of *Vitrina irradians* as appearing in the 1851 *Proceedings of the Zoological Society of London*. This description, however, appeared later in number *ccxlvi* part *xx* of the 1852 *Proceedings* which were published in 1854 (Duncan, 1937) and the 1853 date has priority. Described from material in the Hugh Cuming collection, now in the Natural History Museum (NHM), London, the specimens were probably collected by either Fred or Edgar Layard, both of whom sent many land snails to London (Naggs, 1995, 1997). There are three specimens of *Vitrina irradians* from the Cuming collection in the collections of the Natural History Museum, London. These specimens do not possess a label in Pfeiffer’s handwriting, which is generally accepted as evidence confirming the type status of Pfeiffer’s species. However, they represent the only material of *Vitrina irradians* from the Cuming collection in the Natural History Museum London. These specimens do not possess a label in Pfeiffer’s handwriting, which is generally accepted as evidence confirming the type status of Pfeiffer’s species. However, they represent the only material of *Vitrina irradians* from the Cuming collection in the Natural History Museum and are possibly syntypes (Fig. 1, BMNH 20040004). All three specimens agree with the figure of Cuming material of *R. irradians* given in Reeve (1862). Reeve cites *R. irradians* as being figured in plate 13 of Pfeiffer 1854 but *R. irradians* was not included on the plate. Hanley & Theobald (1876) claim to figure type material in their work and their figure also agrees with the three Cuming specimens but is not sufficiently detailed to allow a specimen to be matched with the figure.

Theobald (1876, Section C, page 24) placed *V. irradians* in *Helicarion*, and this was followed by Nevill (1878), Clessin (1881) and Tryon (1885). Godwin-Austen (1899a) wrongly attributed *Vitrina irradians* to Benson and treated *Ratnadvipa* as a sub-genus but it is not clear in the original publication what the genus should be; Godwin-Austen (1899b) included *Ratnadvipa* in *Macrochlamys*. Blanford & Godwin-Austen
The Sri Lankan semi-slug *Ratnadvipia* (1908) followed Collinge (1901) in elevating *Ratnadvipia* to full generic rank. The name *Ratnadvipia* is drawn from the Sanskrit name for Ceylon derived from *ratna*, ‘a jewel’, and *dwipa*, ‘an island’ (Godwin-Austen, 1899a).

Preliminary studies of the reproductive anatomy of *Ratnadvipia* (Godwin-Austen, 1899b; Collinge, 1901) were followed by a highly detailed account in German of the histology and function of the different parts of the reproductive system (Woldt, 1932–33).

*Ratnadvipia* consists of two species: *Ratnadvipia irradians* (Pfeiffer, 1853) and *Ratnadvipia karui* sp. nov. described here. Blanford & Godwin-Austen (1908) provisionally placed *Vitrina edgariana* Benson 1853 in the genus *Ratnadvipia*. This was done purely on the basis of Benson’s description; Blanford and Godwin-Austen indicate that no specimens were available for examination. Two shells in the Natural History Museum, London, collected by Beddome are consistent with Benson’s description and are labelled as *Ratnadvipia edgariana*. Beddome’s specimens, however, are clearly not representatives of *Ratnadvipia* but examples of *Sattella* or a related taxon. As Benson’s description is unclear and his types cannot be traced, we consider *V. edgariana* to be a nomen dubium.

**External morphology of shell and animal**

Shell (Fig. 1) vitriniform, thin and depressed, with few whorls and ranging in colour from golden-brown to greenshoulder yellow. Adult shells with not more than about 3.5 whorls, the first 1.25–1.75 whorls densely lirated and the remaining whorls striated transversely with obsolete growth lines.

In life the animal (Fig. 2a–c, e) is much larger than the shell and slug-like, with a broad and well-developed mantle surrounding the shell on all sides and partly or wholly covering the shell. The adult animal is unable to retract into the shell and is highly variable in colour.

The dorsal part of the body, immediately behind and under the shell is flat, but it is sharply keeled posteriorly up to the extremity of the tail. Caudal extremity truncated and mucous pore large. Peripheral groove double. Sole of foot undivided.

**Morphology of the reproductive system**

Orientation of descriptive terms is with reference to the genital orifice as proximal. Figure 3 shows the reproductive system of adult *Ratnadvipia irradians* (a key to the abbreviations of the morphological terms used in all the figures is provided in Appendix 1). An amatorial organ or ‘dart sac’, one of the types of stimulators described by Hausdorf (1998), is present. It originates in the atrium and consists of a sheath, which distally takes the form of a hollow and highly muscular cylinder; the cylinder terminates proximally in a short, blunt papilla, which projects into the sheath. A retractor muscle originates in the columnellar muscle and inserts distally on the amatorial organ. The section of the amatorial organ proximal to the atrium may exhibit a sharp ‘s’-shaped bend.

The penis is a simple cylindrical sheath enclosing a fleshy, cuboidal or conical penial papilla (Fig. 4). The penial papilla divides the penis into distinct proximal and distal regions; the lumen of these two regions is continuous. The inner wall of the proximal penis is ornamented with longitudinal and/or transverse rows of papillae. The inner wall of the distal penis is smooth apart from the two to three cylindrical pilasters that run along its entire length. These pilasters fuse proximally to form the penial papilla, which projects into the proximal penis. The outer surface of the penial papilla may be uneven or papillate; proximally it has an opening which may be wide and prominent or barely evident.

Externally the penis is encased in a highly muscular penial sheath. Use of the term penial tunica (Van Goethem, 1977) is preferred by Hausdorf (1998) on the basis that penial sheath is ambiguous, having been used by some authors for the penial wall. However, we consider that penial sheath is unacceptable for describing the penial wall; penial sheath is a widely used term in the sense that we adopt here, and its use should be clarified rather than abandoned. The penial sheath may or may not hold the posterior portion of the penis in a loop. The penis divides distally into two epiphallic branches: a straight and muscular epiphallic caecum, with a distal insertion of the penial retractor muscle, and the epiphallus, which terminates in a strongly bent or bluntly hooked part into which the vas deferens enters. Godwin-Austen (1899b), Collinge (1901), Godwin-Austen & Blanford (1908) andDasen (1933) refer to this bent terminal part of the epiphallus as the kalc-sac. The epiphallus is straight proximally and the distal penial sheath attaches to the epiphallus near its junction with the penis. The proximal part of the penial sheath is fused with the wall of the penis at the point where the penis opens into the genital atrium. The microstructure of the penial sheath was not investigated and it was not established if the wall of the penial sheath is continuous with the penial wall as in the achatinoid subulinid *Paroepas* (Naggs, 1994).

The female part of the reproductive system (Fig. 3a) consists of a simple cylindrical vagina and oviduct; at their junction is the gametolytic sac, the duct of which is very short or barely evident. Distally the oviduct passes first into an externally visible and wider-lumened glandular section, the capsular gland (Dasen, 1933) and then to the spermoviduct and prostate gland. The prostate gland empties proximally into the vas deferens. Continuous with the most distal section of the spermoviduct is the albumen gland, in which an externally simple fertilisation pouch (= spermatheca complex or carrefour region) is located (Fig. 3b), with a narrow duct leading to the convoluted hermaphrodite duct. On reaching the digestive gland, in which it becomes embedded, the hermaphrodite duct fans out into a series of ducts leading to the ovotestis.

**The spermatophore and its mechanism of transfer**

Godwin-Austen (1899b: 132–135) reviewed the form of ariophantid spermatophores and illustrated examples from *Austenia, Girasia, Mariaella, Macrochlamys, Bensonia, Cryptosoma (=Megaustenia), Sesara, Kalileia, Nilgiria (=Cryptozona), Euplecta and Ariophanta*. The spermatophore of *Ratnadvipia* (Fig. 5) is similar in its gross external morphology to the spermatophores of *Cryptosoma semirugata* (=Nilgiria tranquebarica) (Godwin-Austen, 1899b: Plate LXXI: fig. 3c, 3d) and *Ariophanta ligulata* (Dasen, 1933: fig. 8).
Figure 2  Live adults of *Ratnadvipia irradians* (a) and *R. karui* (b, c), egg cluster (d) and a medium-sized juvenile (e) of *R. karui* and a home garden (f) dominated by the trees *jak* *Artocarpus nobilis*, arecanut *Areca catechu* and mango *Mangifera indica* at Batuwangala, near Neluwa, Galle District, habitat of *R. irradians*. Photographs: D. Samarasinghe (a–c), H. Lokugamage (d, e) and D. Raheem (f).

*Ratnadvipia* it is a thick-walled, rigid and hollow tube and is anteriorly ornamented with a spike-like extension bearing an intricate arrangement of spines. The lumen of the spermatophore is widest at its anterior and median sections, becoming narrower posteriorly; the wall of the spermatophore is also less rigid posteriorly. Dasen’s (1933) study of the reproductive anatomy and behaviour of *Ariophanta ligulata* has shown that the spermatophore of *A. ligulata* when *in situ* in the epiphallus is positioned with the spiny anterior portion in the epiphallus and the smooth posterior part in the epiphallic caecum. In
Figure 3  Reproductive system of *Ratnadvipia irradians* from Ritigala SNR (a) and albumen gland of the holotype of *Ratnadvipia karui* from Gilimale-Eratne PR (b). Scale bars: a = 5 mm and b = 2 mm. See Appendix I for a key to the abbreviations for morphological terms used in the figures. Terminology for protected forest areas as indicated by the abbreviated extensions SNR, PR etc. is explained under ‘Distribution’ (p. 117).

*A. ligulata* when the penis is everted during copulation, the spiny anterior portion of the spermatophore emerges first. Figure 6 shows that the orientation of the spermatophore at its formation in the epiphallus and epiphallic caecum of *R. irradians* is similar to the orientation of the spermatophore in the male tract of *A. ligulata*. The spiny anterior part of the spermatophore is lodged in the epiphallus and the posterior part in the epiphallic caecum. This suggests that sperm is delivered through the vas deferens into the anterior spermatophore and, as with *A. ligulata*, the anterior part of the
spermatophore of *R. irradians* is the first to emerge during copulation. A comparison of Fig. 3a and Fig. 6 shows that the epiphallus and epiphallic caecum in *R. irradians* extend considerably to accommodate the spermatophore. The epiphallic caecum must lengthen even further during copulation, presumably by contraction of the penial retractor muscle, to allow the spermatophore to be drawn into the penis.

In *A. ligulata* the spermatophore is deposited by the erect penis of the donor into the oviduct of the recipient snail (Dasen, 1933). This mechanism is strikingly different to that described by Lind (1973) for *Helix pomatia*. In *H. pomatia* the spermatophore is deposited by the penis directly into the duct of the gametolytic sac of the recipient. The different manner in which the spermatophores of *Ariophanta ligulata* and *Helix pomatia* are deposited in the female tract is clearly reflected in the very different arrangement of the vagina, oviduct and gametolytic sac in these taxa. In *Helix pomatia* the highly elongated stalk of the gametolytic sac is the direct continuation of the vagina; the oviduct is a side branch of the vagina and has a slit-like opening (Lind, 1973). In *Ratnadvipia*, *Ariophanta* and *Euplecta* it is the wide-lumened oviduct that is directly continuous with the vagina; the gametolytic sac is a side branch and has a stalk with a noticeably narrower lumen.

Dasen's (1933) observations of the reproductive behaviour of *A. ligulata* do not include an account of the fate of the spermatophore after copulation. One spermatophore was recovered from the female tract of single representatives of each of the two species, *R. irradians* and *R. karui*. Figure 7 illustrates the orientation of the spermatophore from *R. karui in situ* in the female tract and shows the spiny anterior positioned proximally in the capsular gland and the smooth posterior part within the gametolytic sac. The spermatophore from the specimen of *R. irradians* was partially digested. In this spermatophore only the anterior portion remained intact, the greater part of it lodged in the gametolytic sac. We interpret this evidence to indicate that the spermatophore is initially inserted higher in the oviduct, allowing the posterior spermatophore to enter the gametolytic sac. As the posterior spermatophore is digested, the remaining anterior section would then be drawn down the oviduct, through the capsular gland and into the gametolytic duct and sac.

**Morphology of the foregut**

Patterns of digestive tract morphology can be of value in stylommatophoran systematics above species level and Tillier has demonstrated this for limacoids (1984) and for stylommatophora in general (1989). The general arrangement of the digestive tract of *Ratnadvipia irradians* was figured and briefly discussed by Collinge (1901). We will describe the digestive tract morphology of Sri Lankan ariophantids, including *Ratnadvipia*, in a separate paper. Here we describe only the gross
The Sri Lankan semi-slug *Ratnadvipia*

**Figure 5** Spermatophore of *Ratnadvipia irradians* from Gilimale-Eratne PR (a–c); (b) and (c) show lateral and upper views of the anterior portion. Note the single row of spines in (c).

structure of the foregut. This (Fig. 8) is composed of the buccal mass, containing the radula sac; the oesophagus, which is continuous with the posterior part of the buccal mass; and the paired salivary glands, which extend over the dorsal and lateral surfaces of the oesophagus. The paired salivary glands are asymmetric in their arrangement with the left salivary gland posterior to the right salivary gland. Anteriorly the left salivary gland generally has a very narrow connection to the posterior part of the right salivary gland. Sometimes the two glands are broadly contiguous. Anteriorly the salivary glands are connected to a pair of salivary ducts of unequal length, the left salivary duct being noticeably longer than the right duct. The salivary ducts enter the posterio-dorsal part of the buccal mass on either side of the oesophagus.

The radula (Fig. 9, 10) is broad with numerous teeth in each row; the formula is highly variable and the form of the central tooth and the inner laterals is also variable, both inter- and intraspecifically. The outer laterals and marginals are bicuspid. The total number of laterals and marginals varies from about 140 to about 350 teeth on each side of the central tooth.

The jaw (Fig. 10) is oxygnath and simple. It has a concave cutting edge, which may or may not exhibit a slight median projection.

**Phylogenetic relationships**

Godwin-Austen (1899b) indicated that *Ratnadvipia* was closely allied to three ariophantid taxa, the genus *Euplecta* and the species *Cryptozona chenui* and *Ariophanta dalyi*. Blanford & Godwin-Austen (1908) indicated that *Ratnadvipia* was similar to the South Indian ariophantid, *Indrella*. Godwin-Austen (1899b) also commented on the similarity of the radula and jaw of *Ratnadvipia irradians*, *Hemiplecta uter* Theobald and *H. humphreysiana* Lea. Molecular phylogenetic investigations of the Stylommatophora promise rapid progress in resolving relationships (Wade et al., 2001). Wade et al. (in press) have demonstrated that, among examined taxa, the ariophantids *Ratnadvipia*, *Cryptozona* and *Euplecta* form a distinct clade within the Limacoidea, supporting Godwin-Austen’s (1899b) morphological interpretations.

The genus *Euplecta* is represented in Sri Lanka by more than 20 described species. A distinctive character of this genus is that the penial sheath holds the distal penis in a loop by means of an opening in the penial sheath. This is strikingly similar to the form of the penis in some of the preserved specimens of *Ratnadvipia* examined by us. This arrangement of a ‘penial loop’ was not observed in the single specimen examined by Godwin-Austen (1899b) or the seven dissected by Collinge (1901). Godwin-Austen (1899b) likened the penis of *Ratnadvipia irradians* most closely to *Cryptozona chenui* and *Ariophanta dalyi*. He perceptively observed that if the distal penis, at the junction of the epiphallic caecum and the epiphallus, were greater in length, the penis would be folded into a loop comparable to that of *Euplecta*. Interestingly, Dasen (1933) has shown that several species of the Indian genus *Ariophanta*, have the penis folded in a loop. However, unlike in *Euplecta* and *Ratnadvipia*, this loop is held by a ‘...thin membranous investment...’ Dasen (1933), which envelopes the loop completely.

The penial loop is not evident in all the preserved specimens of *Ratnadvipia* examined by us (Fig. 11). Some individuals show a large and well-developed loop, which is external to the penial sheath, in others the loop is minute and is external to or concealed by the penial sheath and in others the penis shows no indication of a loop. In the latter cases it may or may not be possible to differentiate the penial sheath from the wall of the penis. The reason for this variation is unclear. One possible explanation may be that the form of the penial loop varies temporally or seasonally. Also, the presence or absence of the loop may at least be partly linked to the state of eversion of the penis. That the penial loop is absent in specimens of *Ratnadvipia* with a partially or fully everted penis is suggested by Dasen’s (1933) observations of the changes in the form of the penis in *Ariophanta* during copulation. The process of
eversion involves the straightening out of the loop: the distal penis pushes into the proximal penis so that the papillate inner wall of the proximal penis is everted exposing the penial papilla.

The Ariophantidae are one of several limacoid families that exhibit both distinct and indistinct foot furrows in different genera (Hausdorf, 1998). Godwin-Austen (1899b) and Blanford & Godwin-Austen (1908) recognised these character states and differentiated between Indian ariophantids with an ‘undivided’ sole and those with a ‘tripartite’ sole. *Macrochlamys, Girasia* and *Austenia*, for example, have the foot divided into a central tract and two lateral tracts; this tripartite sole is clearly visible to the naked eye. The sole of the foot of *Ratnadvipia*, *Euplecta* and *Cryptozona*, even when viewed under a dissecting microscope, shows no obvious differentiation.

Some preserved specimens of *Ratnadvipia, Euplecta* and *Cryptozona* show the foot contracted along a central line giving the appearance of what Blanford & Godwin-Austen (1908) describe as a ‘median groove’. This groove is not always evident, but Godwin-Austen (1899b) suggests that this kind of contraction may occur in life and may be an adaptation for an arboreal lifestyle. The little that is known on the ecology of *Ratnadvipia* indicates that it is at least partly arboreal. While some species of *Euplecta* are arboreal, *Cryptozona chenui*, a common and characteristic species of Sri Lankan lowland rainforest, is entirely ground-living.
Figure 7  Reproductive system of Ratnadvipia karui from Nakiyadeniya PR (paratype) with spermatophore in situ in the vagina and gametolytic sac. Scale bar = 5 mm.

Species descriptions

**Ratnadvipia irradians** (Pfeiffer 1853, page 3)  
Figs 1–6, 9–15, 18

**Material examined**


**Diagnosis**

Shell solid, but thin, with 3.5 rapidly increasing whorls and a raised spire. Mantle surrounds shell and is posteriorly a very narrow band, marked by two tongue-like extensions on either side. The mantle only partly covers the shell.

The inner proximal surface of the penis is ornamented with longitudinal papillate ridges.

**Distribution**

Endemic to Sri Lanka. Widespread in the forested lowlands of the wet and intermediate zones. Occurs in some synanthropic situations.
Description

SHELL. Shell (Figs 1, 12) vitriniform, imperforate or subperforate, thin, depressed and diaphanous, ranging in colour from rich golden brown to greenish yellow. Shell dimensions of 9 specimens: length 24.11–26.9 mm; width 17.4–20.69 mm; and height 13–15.91 mm. Adult shells approximately 3.5 whorls (using Kerney & Cameron’s (1979) method); whorls flattened above and increase rapidly; suture impressed. Spire slightly elevated or nearly planar, apex obtuse. Body whorl comparatively very large, rounded at the periphery, convex beneath. Aperture large, very oblique, lunately oval; peristome simple, thin, upper margin curved. Columellar margin curved, briefly reflected close to junction with body whorl.

The embryonic whorls, which comprise the first 1.5–1.75 whorls are densely and uniformly sculpted with spiral bands of short transverse lirations, recalling the sculpture on the embryonic whorls of some Euplecta species such as E. isabellina and E. colletti. The sculpture on the embryonic whorls is often worn and indistinct in adult shells giving the apex of the shell a worn, whitish appearance and this contrasts with the darker colour of the rest of the shell. The remaining whorls are striated irregularly with indistinct transverse growth lines and ornamented with short raised transverse lines arranged in spiral rows. These transverse lirations are similar to the sculpture on the embryonic whorls, but are of a much coarser quality; they are highly variable, being extensive on some shells and sparse or absent on others. In some adult shells these lirations are so worn as to be not apparent. Such specimens show quite prominent broad impressed spiral lines between the rows of worn transverse lirations; the transverse growth lines are also very conspicuous. The shell is smoother and more polished beneath. Adult shells are often very sparsely marked with a few scattered rows of short, longitudinal indentations, disposed obliquely, on the dorsal and ventral surface of the body whorl.

The measurements given by Pfeiffer (1853) for the Cumming material are: ‘Diam. maj. 18 ½ , min. 14, alt. 8 ½ mill’. It is not clear if the altitude corresponds to the height of the shell, the length of its axis or some other measurement. Pfeiffer (1853) also refers to a variety with a larger shell and a more elevated spire. The measurements given for this shell are ‘diam. maj. 25, min. 19, alt. 11 mill’. The measurements for minimum and maximum diameters correspond well with the width and length of some of the larger shells examined by us. For these shells the height ranges from about 13–15 mm and the axis between 8–9 mm. The type status of three specimens in the NHM from the H. Cuming collection is discussed above (page 100).

MANTLE, HEAD AND FOOT. Both the adults and juveniles of this species are highly variable in colour, ranging from pale pinkish white or pale yellow to dark steel grey or brownish black (Fig. 2a) with the fringe and sole of the foot often paler. Godwin-Austen (1899b) adopted a complex and sometimes confusing terminology for the different parts of the mantle of Indian ariophantids. He divided the mantle into left and right dorsal lobes (parts of the mantle lying immediately on the head and foot) and the left and right shell lobes (parts of the mantle resting immediately on the shell). We have adopted a different but simpler approach as no clear demarcation can be drawn between the four lobes identified by Godwin-Austen (1899b).

The mantle of R. irradians (Fig. 13) surrounds the shell on all sides. The most distinctive feature of the mantle is that posteriorly it is produced into two left and right tongue-like extensions, with a very narrow fringe of mantle in-between. The margin of the mantle resting on the shell is marked on its right side by a small but distinctly elongated tongue-like lobe (see Fig. 2a) lying immediately posterior to and a little above the pneumostome. Godwin-Austen (1899b) identified a similar lobe on the left anterior margin of the mantle, but this is not always present. The margin of the mantle is highly variable in form. In some specimens the mantle edge is ragged or possesses several lobes in addition to the tongue-like lobe on the right side. In other specimens the mantle margin is slightly indented in places and in others the edge is straight throughout and unmarked with lobes or indentations. In life the mantle can be extended to cover most of the shell, but it is more common to observe all growth stages of R. irradians with a large part of the shell exposed as in Fig. 2a.

The differentiation of the mantle posteriorly into distinct left and right extensions is evident from an early stage (Fig. 14).
The Sri Lankan semi-slug *Ratnadvipia*

Figure 9  
Radulae of *Ratnadvipia irradians* from Sembawatte OSF (a), Ritigala SNR (b), Kitulgala (c) and Batathota (d, e); (a) and (b) show the central teeth and the inner and outer laterals, (c) and (d) show the central and inner lateral teeth and (e) shows the marginal teeth.

This together with the more spherical, inflated appearance of the early whorls of this species allows for identification of most juvenile *R. irradians* in the field. Juveniles of *Satiella* are superficially similar, but possess a clear golden, depressed shell, a different arrangement to the mantle and a paler body with a well-defined thin greenish or brownish grey dorsal stripe. The smallest observed juveniles of *R. irradians* measure about 5 mm from tail tip to the anterior extremity of the head. Presumably this is the approximate size of juvenile *R. irradians* when they emerge from the eggs; this size corresponds well with the size of the eggs noted for other Sri Lankan ariophantid species (see below). At this stage juveniles possess a mantle which is very narrow posteriorly and are able to retract completely into the shell. Larger juveniles and adults, in contrast, are able to
retract into the shell only partially and the posterior part of the mantle is broader and more extensive and cannot be retracted.

REPRODUCTIVE SYSTEM

**Penis.** The general external form of the penis is as described above for the genus (Figs 3, 6). The penial loop may or may not be evident (Fig. 11). When present, the penial loop may be prominent and large or minute, and it may or may not be completely enveloped by the penial sheath.

The internal surface of the proximal part of the penis (Fig. 4) is marked along most of its length by longitudinal rows of irregular papillate ridges; in places the ridges give way to rows of individual papillae. The relative extent of the papillate ridges and the individual papillae vary from individual to individual, as does the form of the papillae. The penial wall close to the junction of the penis with the genital atrium is thickened and free of ridges or papillae; the prominence of this proximal thickening varies greatly between individuals. There appears to be little difference in the appearance of the inner surface of the proximal penis between specimens exhibiting a penial loop and specimens lacking a penial loop.

**Figure 10** Marginal teeth of *Ratnadvipia irradians* from Ritigala SNR (a) and jaw of *R. irradians* from Sembawatte OSF (b) and Monerakelle OSF (c).

**Figure 11** Examples of the penis of *Ratnadvipia irradians* from Ritigala SNR (a), Batathota (b) and Monerakelle OSF (c) and *R. karui* from Gilimale-Eratne PR (d, holotype) and Nakiyadeniya PR (e, paratype). The dotted area indicates the portion of the penial sheath which is visibly distinguishable from the wall of the penis. In (a) the penial loop is concealed within the penial sheath; in (b) the penial loop is not evident (note that the penial sheath and the wall of the penis cannot be differentiated); in (c) and (d) the penial loop is clearly visible and external to the penial sheath; and in (e) the penial loop is not evident but the penial sheath can be differentiated from the penis. Scale bar = 3 mm.
Gametolytic sac. The gametolytic sac (Figs 3, 6) is variable in form. In a range of taxa the gametolytic sac has been shown to be distorted by its contents and individuals with an opaque sac, usually lined with a layered red pigment, to have mated at least once, whereas those with transparent sacs indicate virgins (Tompa, 1984; Naggs, 1994). In *R. irradians* the gametolytic sac may be a spherical inflated bag or more asymmetric in shape; it may be opaque or semi-transparent; and it may or may not possess a short, barely discernible duct.

Spermatophore. Two spermatophores were recovered from *R. irradians* (Fig. 5): one fully intact spermatophore from the male tract of the Gilimale-Eratne specimen (see page 106) and one partially digested example from the gametolytic sac of the Monerakelle specimen (in both specimens the gametolytic sac was large, transparent and rather flaccid with milky, granular contents). Both spermatophores exhibit a single row of spines arranged along the axis of the spike on the anterior part of the spermatophore. This may be a species-specific character.

Radula and Jaw. The central tooth may be bluntly unicuspid, sharply unicuspid or bicuspid (Figs 9, 10). The band of inner laterals, ranging from 17–27 teeth, are also variable in form. All but the last two to three inner laterals are unicuspid, the cusp being bluntly or sharply pointed or quadrangular. The last two to three inner laterals are faintly bicuspid. The outer laterals and marginals, including the outer marginals, are uniformly and evenly bicuspid. Godwin-Austen (1899b) recorded 204 outer laterals and marginals on each side of the radula he examined. The total number of outer laterals and marginals vary from 116 to more than 170 in the four radulae we examined, it being difficult to count the outer marginals which are very closely pressed together towards the margin. In the specimens examined by us the outer marginals are not as stated by Godwin-Austen (1899b) minute and unicuspid, but as with the outer laterals and other marginals they are large and evenly bicuspid. Godwin-Austen’s dissected specimen is not available for examination.

There is some variation in the form of the inner laterals. In the Kitulgala specimen with the unequal number of inner laterals on the left and right sides of the radula, the first and third teeth on the right side exhibit a very broad, blunt quadrangular cusp; the other inner laterals are bluntly unicuspid, with a narrower, rounded cusp. In the specimen from Ritigala SNR (protected forest areas are indicated by the abbreviated extensions FR, PR, SNR etc.; see under ‘Distribution’ (page 117) for a complete list of terms) the 17th tooth on the left side is very small in comparison to the other inner laterals which are large and uniformly unicuspid.

The following formulae are for the four specimens examined (for the purposes of direct comparison all the radula counts were carried out in the area of greatest width):

<table>
<thead>
<tr>
<th>Location</th>
<th>Formula</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kitulgala</td>
<td>120+, 19. 1. 21. 120+</td>
</tr>
<tr>
<td>Ritigala</td>
<td>116. 23. 1. 23. 116</td>
</tr>
<tr>
<td>Sembawatte</td>
<td>160+, 22. 1. 22. 160+</td>
</tr>
<tr>
<td>Batathota</td>
<td>170+, 17. 1. 17. 170+</td>
</tr>
</tbody>
</table>
Another specimen (from Monerakelle OSF) with a partly damaged radula was also examined; the number of inner laterals was 27. The formula of Godwin-Austen’s specimen was: 204. 23. 1. 23. 204.

The jaw in *R. irradians* (Fig. 10) has a simple concave cutting edge, which may or may not bear a very slight median projection. In some specimens the jaw is more arched and has a strongly concave edge, whereas in other specimens the jaw is only slightly curved and its cutting edge only slightly concave.

**Distribution**

Pfeiffer (1853) briefly notes the habitat of *R. irradians* as ‘in insula Ceylon’. Godwin-Austen (1899b) lists two localities: Kegalle at 600 ft (O. Collett) and the Botanical Gardens at Peradeniya (Freeman). Blanford & Godwin-Austen (1908) indicate that the habitat of this species is ‘South-western Ceylon’. They also refer to some specimens of *R. irradians* in the NHM collections said to be from Southern India; these specimens are no longer traceable. We agree with Blanford & Godwin-Austen (1908) in considering this a doubtful locality for *R. irradians*, which should be considered as endemic to Sri Lanka, until conclusive evidence of its presence in Southern India is obtained.

Apart from a handful of unpublished records in the NHM collections, the distributional data presented above represent all that was known about the distribution of *R. irradians* until
1995 when we began carrying out preliminary surveys of land-snail diversity in Sri Lanka. Climatically Sri Lanka can be divided into three zones: the wet, dry and intermediate zones. Different workers have delimited these zones in different ways. We have followed the system adopted by Legg & Jewell (1995). According to this system the wet zone, lying in the southwest and south-central part of the island, is delimited by the 2500 mm rainfall isohyet, while the 1800 mm rainfall isohyet represents the boundary between the intermediate and dry zones. As emphasised by Legg & Jewell (1995) these isohyets provide a general idea of the distribution of Sri Lanka’s major natural forest types in relation to climate, but should not be treated as precise boundaries demarcating one climatic zone from another.

The distributional data gathered on *R. irradians* since 1995 (Fig. 15) shows that its range encompasses much of the wet zone and extends into the wetter or more elevated parts of the intermediate and dry zones. In the wet zone it occurs from 60 m in the wet lowlands through to altitudes of over 1900 m on the higher slopes of Sri Lanka’s Central Highlands. On the basis of current information, *Ratnadvipia irradians* is the most wide-ranging endemic land snail with a distribution centred in the wet zone. Other wide-ranging endemic ‘wet zone’ snails such as *Acavus phoenix* and *Oligospira polei* have a narrower altitudinal range in the wet zone and are absent from the eastern part of the intermediate zone.

*R. irradians* is essentially a forest species, but in the wet zone and parts of the intermediate zone it often occurs in moist or well-wooded home gardens (Fig. 2f). Sri Lanka’s wet and intermediate zone home gardens represent a centuries-old and characteristic human-influenced non-forest habitat. The older and floristically more diverse home gardens are structurally similar to forests, with a well-developed ground flora, understorey, subcanopy and main canopy. Geographically wide-ranging studies of home gardens both in the wet and intermediate zones are needed to assess the conservation importance of these habitats for endemic land snails such as *R. irradians*.

The distribution of *R. irradians* in the wet zone is generally associated with the range of two of the three characteristic natural vegetation types of the wet zone. These are lowland rain forest, which occurs from sea level to 1200 m and lower montane rain forest, which extends from 1200–1500 m (terminology and altitudinal limits follow Whitmore (1990)). *R. irradians* is a common species of the largely degraded lowland rain forests of the southern part of the wet lowlands. It occurs in some of the smallest lowland rain forest fragments (≤50 acres in total extent) which remain intact e.g. Batugodavila and Gangodakanda forests in this part of the wet zone.

Sri Lanka’s Central Highlands are composed of an extensive central hill country, sometimes known as the Central Massif, and two small outlying massifs, the Rakwana massif to the south and the Knuckles massif to the north. It is only in the western part of the Central Massif that *R. irradians* ranges into upper montane rainforest, the characteristic forest type at elevations above 1500 m. Here, along the high forested range extending from Adam’s Peak in the north to the Meeriyakota ridge in the east, *R. irradians* has been recorded to an upper limit of 1961 m. It appears to be absent from the eastern and northern part of the Central Highlands, which are characterised by higher mean elevation than the western sector of the Central Highlands.

*R. irradians* has also been recorded from a number of forested sites in and around the Knuckles Conservation Area (Knuckles CA). The Knuckles CA encompasses the main ranges and foothills of the Knuckles massif, lying to the northeast of the main part of the Central Highlands. The Knuckles CA is characterised by high variation in altitude and climate and is floristically very diverse. Surveys carried out by K.B. Ranawana and his team of over 100 separate sites in the main ranges and foothills in and around the Knuckles CA have shown that *R. irradians* is confined to more moist rainforest sites between altitudes of 1141–1498 m. *R. irradians* is recorded from a very small and windswept home garden in the village of Pitawala at about 740 m. However, Ranawana’s data suggests that it may be very sparsely distributed or absent from the extensive areas of drier forests below about 1000 m on the eastern side of the Knuckles massif and from the small area of montane rainforest above 1500 m on the main ridges.

*R. irradians* occurs in scattered populations across the eastern part of the intermediate zone. The natural vegetation in this part of the intermediate zone is composed of hilly islands of moist monsoon forest with large intervening low-lying areas of drier grasslands, open woodlands or savannah. *R. irradians* appears to be confined to some of the islands of moist hilly forest above an altitude of about 400 m. Further surveys of this part of Sri Lanka are likely to show that *R. irradians* is widely distributed across the forested hills, which are a ubiquitous feature of this part of Sri Lanka.

The two most isolated populations of *R. irradians* occur well inside the dry zone on the forested hill tops of Galgiriyakanda and Ritigala. The dry zone is characterised by a dry, strongly seasonal climate and vegetation composed of dry monsoon forest, thornscrub and grassland. Unlike the surrounding countryside, the higher slopes of Galgiriyakanda and Ritigala are climatically and vegetationally distinct. The vegetation of Ritigala, for example, has a strong wet-zone element; 34.3% of the 329 flowering plants species recorded from Ritigala are otherwise confined to the lowland and lower montane rainforests of the wet zone (Jayasuriya, 1984). All of these wet-zone species are restricted to the forest on the moist higher slopes of Ritigala. The high ridge of Galkiriyakanda, which lies about 35 km southwest of Ritigala and is biologically little known, may also be an isolated outpost of the wet zone. The essentially wet zone land-snail taxa such as *Ratnadvipia*, *Acavus*, *Oligospira* and *Satiella* are locally confined to the higher slopes of Galkiriyakanda and are not found on the lower slopes and in the surrounding dry lowlands in the immediate vicinity.

Field observations of *R. irradians* indicate that the species is at least partly arboreal. Though the adults are most often to be observed on the ground amongst leaf litter, they are sometimes encountered on low vegetation. Juvenile *R. irradians*, in contrast, are only rarely found on the ground; as a general rule they are found on the leaves of trees and understorey plants.
Figure 15  Distribution of Ratnadvipia irradians. The wet zone (solid line) is delimited by the 2500 mm isohyet and the 1800 mm isohyet (broken line) represents the boundary between the intermediate and dry zones. Individual sites from which this species has been recorded are denoted by crosses and towns or villages by filled circles. Closed-canopy natural forest cover is shown in dark grey; the distribution of forest cover is based on the 1:50000-scale forest map by Legg & Jewell (1995). The current extent of occurrence of the species, extrapolated from the available distributional information is shown in pale grey.

**Distributional records:** Wahakotte (7°43.0′N, 80°35.0′E), J.H. Ponsonby, BMNH; Nalanda (7°39.5′N, 80°38.0′E), R. Winkworth, 1925, BMNH; 579 m, Haragama (7°14.7′N, 80°42.5′E), R. Winkworth, 1925, BMNH; 183 m, Kegalla (7°15.0′N, 80°20.5′E), O. Collett, BMNH; 488 m, Royal Botanical Gardens, Peradeniya (7°15.5′N, 80°36.0′E), c. 1898, BMNH; 1280 m, Maha Uva Estate (7°3.8′N, 80°52.5′E), F. Naggs, 1996; 457 m, Resthouse garden, Kitulgala (6°59.7′N, 80°24.3′E), F. Naggs, 1996; 457 m, Kandy (1500 ft.) (6°18.3′N, 80°38.7′E), c. 1901, BMNH; 155 m, Mulatiyana FR
The Sri Lankan semi-slug *Ratnadvipia* is a species found in various locations across Sri Lanka. The image includes a figure showing upper (a) and lower (b) views of the shells of *R. karui* from the Gilimale-Eratne PR (holotype, a–c) and Nakiyadeniya PR (paratype, d), with a partly worn ostracum of (c) and (d) respectively.

Locations where the Sri Lankan semi-slug *Ratnadvipia* has been found include:

- Peak Wilderness Sanctuary, Kondurugala, Peak Wilderness Sanctuary (6° 54.5’N, 81° 22.7’E), 1995; 510–695 m, Rijitigala SNR (8° 6.8’N, 80° 39.4’E), 1995; 130 m, Bandarakelle forest, Kitulgala (6° 59.6’N, 80° 24.0’E), 1995; 545 m, Sembawatte OSF (7° 2.0’N, 80° 26.2’E), 1995; 620 m, Uda Pawana Ella, Peak Wilderness Sanctuary (6° 47.6’N, 80° 27.6’E), 1998; 1285 m, Kodyiyadaputhena, Peak Wilderness Sanctuary (6° 48.5’N, 80° 28.0’E), 1998; 240 m, Sudagala, Gilimale-Eratne PR (6° 48.5’N, 80° 23.1’E), 1998; 350 m, Palabadda, Peak Wilderness Sanctuary (6° 46.8’N, 80° 27.1’E), 1998; 285–380 m, Batadomba Lena, Gilimale-Eratne PR (6° 46.5’N, 80° 23.5’E), 1998; 158–355 m, Kospelaketiya, Kanneliya FR (6° 14.8’N, 80° 20.9’E), 1998; 330 m, Pimburukanda, Nakiyadeniya PR (6° 12.9’N, 80° 22.9’E), 1998; 155–495 m, Hangarankanade, Kanneliya FR (6° 16.1’N, 80° 20.2’E), 1998; 125 m, Annasigetakanda, Kanneliya FR (6° 14.9’N, 80° 20.1’E), 1998; 75–330 m, Lavalvarukakanda, Kanneliya FR (6° 16.4’N, 80° 20.9’E), 1998; 165–265 m, Kodikande, Kanneliya FR (6° 15.2’N, 80° 21.8’E), 1998; 195–210 m, Manamaladolakanda, Kanneliya FR (6° 15.3’N, 80° 22.4’E), 1998; 165 m, Gabendidolakanda, Nakiyadeniya PR (6° 10.4’N, 80° 23.1’E), 1998; 937–1067 m, Dotagalala, Bamburabotuwa FR (6° 41.4’N, 80° 36.2’E), 1998; 799–980 m, Dehenakande, Peak Wilderness Sanctuary (6° 45.7’N, 80° 30.0’E), 1998; 1553 m, Ratkande, Peak Wilderness Sanctuary (6° 47.1’N, 80° 31.1’E), 1998; 918–1038 m, Kondurugala, Peak Wilderness Sanctuary (6° 44.7’N, 80° 32.8’E), 1998; 763 m, Asamanakande, Bamburabotuwa FR (6° 39.0’N, 80° 35.4’E), 1998; 1829 m, above Moray Estate, Peak Wilderness Sanctuary (6° 48.4’N, 80° 30.5’E), 1998; 790–1025 m, Bathborakande, Peak Wilderness Sanctuary (6° 53.6’N, 80° 27.8’E), 1998; 465 m, Sevalagala, Kelani Valley PR (6° 56.0’N, 80° 26.7’E), 1998; 850–1110 m, Kiripanagala, Kelani Valley PR (6° 55.7’N, 80° 27.6’E), 1998; 1748–1961 m, Doturugala, Peak Wilderness Sanctuary (6° 46.5’N, 80° 32.6’E), 1998; 1795 m, Gavarawewa Patana, Peak Wilderness Sanctuary, 6° 46.8’N, 80° 33.7’E), 1998; 760 m, Gannoruwa forest (7° 17.2’N, 80° 35.8’E); 565 m, Udawattakele FR (7° 18.0’N, 80° 38.5’E), 1995; 753 m, Udawattakele FR (7° 14.9’N, 80° 37.0’E); 1248 m, Hantane forest (7° 13.7’N, 80° 38.3’E); 450 m, Vijayanahela OSF (7° 17.5’N, 81° 22.6’E); 738–844 m, Madigala OSF (7° 18.1’N, 81° 16.0’E); 501 m, Velibela OSF (6° 52.9’N, 81° 26.9’E); 424 m, Kitulhela OSF (6° 59.6’N, 81° 27.8’E); 1053–1119 m, Monerakelle OSF (6° 53.2’N, 81° 23.4’E); 610 m, Doluwakanda PR (7° 36.9’N, 80° 24.7’E); 906 m, Neugalkanda PR (7° 36.9’N, 80° 34.2’E); 1013 m, Opolagala OSF (7° 36.5’N, 80° 41.8’E); 396–463 m, Galgiriya PR (7° 56.2’N, 80° 22.9’E); 223 m, Malagalla, Kanneliya FR (6° 17.6’N, 80° 21.7’E); 623 m, Hinidunkande, Habarakada PR (6° 19.9’N, 80° 17.8’E); 232 m, Dediyagala FR (6° 11.2’N, 80° 24.6’E); 273 m, Gabendidolakande, Nakiyadeniya PR (6° 10.3’N, 80° 23.0’E); 360 m, Malambe, Malambe FR (6° 14.5’N, 80° 18.8’E); 405 m, Pimburukanda, Nakiyadeniya PR (6° 12.3’N, 80° 22.8’E); 380 m, Murutukanda OSF (6° 49.2’N, 81° 11.0’E); 1120 m, Handapan Ella OSF (6° 26.7’N, 80° 34.8’E); 183 m, Kospelaketiya, Kanneliya FR (6° 15.0’N, 80° 20.8’E); 140 m, Kombala-Kottawa PR (6° 5.7’N, 80° 20.3’E); 165 m,
Figure 17  Early whorls and sculpture of the shells of adult Ratnadvipia karui from Gilimale-Eratne PR (a and c, paratype) and juvenile R. karui (b). The white arrow indicates the approximate point of termination of the protoconch. The white box in (a) indicates the area of the shell shown in (c); note the oblique rows of indentations in (c).

Lavalvarukanda, Kanneliya FR (6°15.3′N, 80°20.5′E); 290 m, Manamadalakanda, Kanneliya FR (6°14.9′N, 80°22.4′E); 457 m, Kalukanda, Kanneliya FR (6°16.7′N, 80°21.1′E); 219 m, Homadola, Nakiyadeniya PR (6°11.8′N, 80°22.3′E); 232 m, Awugagalakanda, Auwegalakanda OSF (6°22.5′N, 80°17.1′E); 253 m, Kondagala, Kanneliya FR (6°14.1′N, 80°23.8′E); 170 m, Olu Dola, Dediyagala FR (6°11.1′N, 80°26.0′E); 236 m, Kekirikanda, Dediyagala FR (6°12.6′N, 80°24.7′E); 310 m, Viharakanda, Mulatiravana FR (6°11.5′N, 80°32.4′E); 220 m, Viharekele FR (6°6.6′N, 80°36.5′E); 76 m, Home garden, Batuwangala, Neluwa FR (6°22.4′N, 80°23.3′E); 90 m, Home garden, Pansalagodaheena, Dediyagala (6°9.6′N, 80°25.9′E); 780 m, Rammalakanda FR (6°15.2′N, 80°37.9′E); 220 m, Home garden, Ehelakanda, Mawarala (6°13.0′N, 80°36.0′E); 72 m, Gangodakanda forest (6°8.6′N, 80°31.2′E); 23 m, Getara forest, Oliyangankele FR (6°5.0′N, 80°32.4′E); 100 m, Kudaludolakanda forest (6°11.3′N, 80°30.7′E); 250 m, Home garden, Panapola (6°26.0′N, 80°27.9′E); 560 m, Wanduragala ridge, Sinharaja NHWA (6°23.6′N, 80°28.9′E); 540 m, Wewagama, Delgoda PR (6°27.1′N, 80°23.6′E); 588 m, Illumbeekanda, Sinharaja NHWA (6°25.4′N, 80°33.6′E); 394 m, Nawalakanda, Waratalgoda PR (6°30.5′N, 80°19.8′E); 728 m, Dothalugala, Delgoda PR (6°24.9′N, 80°33.4′E); 151 m, Pallekumbura, Morapitiya-Runakanda PR (6°28.5′N, 80°19.2′E); 595 m, Denihena, Morapitiya-Runakanda PR (6°28.5′N, 80°20.8′E); 461 m, Dothalankanda, Morapitiya-Runakanda PR (6°29.8′N, 80°20.2′E); 210 m, Batugodavila forest, Hidigalla (6°27.5′N, 80°17.9′E); 448 m, Giguruwa Ihala, Sinharaja NHWA (6°21.5′N, 80°29.5′E); 520 m, Kohila Arambé, Sinharaja NHWA (6°22.5′N, 80°29.9′E); 1065 m, Kurulugala, Sinharaja NHWA (6°23.9′N, 80°33.1′E); 1017 m, Hinjipitigala, Sinharaja NHWA (6°23.7′N, 80°31.6′E); 160 m, Wattekelewa forest (6°8.6′N, 80°22.8′E); 60 m, Tawalama forest (6°20.3′N, 80°19.4′E); 351 m, Warukandeniya, Sinharaja NHWA (6°23.2′N, 80°24.7′E); 1275 m, Between Nawanagalagala and Loolwatta, Knuckles CA (7°19.2′N, 80°51.6′E); 1141 m, Dankanda-Midland Top Division, Knuckles CA (7°31.4′N, 80°43.5′E); 1498 m, Hunuasgiriya, Campbell’s Land FR (7°23.3′N, 80°42.4′E); 1380 m, Knuckles Peaks, Knuckles CA (7°23.7′N, 80°48.0′E); 1298 m, Walpalamulla-Kaluphanna, Knuckles CA (7°27.1′N, 80°47.4′E); 741 m, Home garden, Pitawela, near Illukkumbura, Knuckles CA (7°32.0′N, 80°45.3′E); 1203 m, Udagaldebokka-Bunueluwa, Knuckles CA (7°25.2′N, 80°53.7′E); 1150 m, Walpalamulla-Bambaragalakanda, Knuckles CA (7°29.8′N, 80°45.8′E).

All records dated 1995 collected by D. Raheem and those dated 1998 collected by D. Raheem, T. O. Butterworth and those dated 1998 collected by D. Raheem, T. O. Butterworth and C. Inglis. Distributional information obtained from the reference collections of the Natural History Museum, London are indicated as ‘BMNH’. The remaining distributional records, unless otherwise indicated, were gathered by D. Raheem largely during the Darwin Initiative Project ‘Land-Snail Diversity in Sri Lanka’ (1999–2002). The only exceptions are the records from the Knuckles CA and Campbell’s Land FR, which were collected by K.B. Ranawana and his Darwin Initiative team from the University of Peradeniya.
The Sri Lankan semi-slug *Ratnadvipia*

Forest names follow the Forest register of the Forest Department, Government of Sri Lanka (source: Green & Gunawardena, 1997). Forests are designated as FR = Forest Reserve, PR = Proposed Reserve, OSF = Other State Forest, NHWA = National Heritage Wilderness Area, CA = Conservation Area or SNR = Strict Natural Reserve unless otherwise stated.

*Ratnadvipia karui* (sp. nov.)
Figs 2–3, 7–8, 16–26

Material examined
Unless otherwise indicated all examined samples are preserved single specimens.

Type material

Other material

Diagnosis
Shell partly membranaceous, elongately oval, spire flat, 2.5 rapidly increasing whorls. Mantle continues as a broad band around shell and generally covers all or nearly all of the shell.

Inner surface of the proximal penis ornamented in some specimens with a proximal band of longitudinal papillate ridges and a distal zone of dentate transverse ridges; some specimens with an extensive proximal thickening and a distal zone of papillate and/or smooth longitudinal ridges.

Distribution: Endemic to Sri Lanka and restricted to the lowland rainforests of the southern part of the wet lowlands.

Description
**SHELL.** Shell (Figs 16, 17) vitriform; thin, highly depressed and planar, varying in colour from golden yellow to deep golden-brown. Shell dimensions of four specimens: length 19.16–22.21 mm; width 11.2–14.66 mm; and height 6.55–8.62 mm. Unlike in *R. irradians* the shell is highly membranaceous and strikingly glossy and polished in appearance. The shell is more solid dorsally, but the thin, limp membrane which constitutes the ventral or basal part of the shell is very delicate and is likely to dry up, shrivel and disintegrate very rapidly once the shell and animal are separated. The ostracum of some fully formed shells is sometimes heavily worn, giving the shell a very transparent appearance. The ostracum is whitish in colour and when intact gives the shell an opaque appearance. When the ostracum is...
abraded the transparent quality of the periostracum is clearly apparent. In the holotype (Fig. 16) the ostracum has almost entirely eroded away and the inner surface of the periostracum is marked by transverse rows of indistinct wrinkles. Due to the abraded state of the ostracum the very regular sculpture on the inner surface of the shell is clearly visible through the shell’s external surface. This sculpture may be very pronounced, but is often sparse or not evident.

Adult shells usually possess about 2.5 whorls. The whorls increase more rapidly than in *R. irradians* (Fig. 18) and when viewed from above *R. karui* has a more elongate shell than *R. irradians*. The spire is planar or noticeably concave in profile; the apex is obtuse and flattened. The more elongate form of the adult shell of *R. karui* is clearly evident by the time the first 1.25 whorls have been developed because of the very rapid expansion of the whorls; in *R. irradians* the expansion of the early whorls is relatively gradual. Whorl for whorl *R. karui* is larger than *R. irradians* and this is clearly apparent when the early whorls of the two species are compared. The embryonic shell, which comprises the first 1.25 whorls, is densely and intricately lirated as in *R. irradians* (Fig. 18). The remaining whorls are striated with indistinct transverse growth lines, but the spiral rows of short transverse lirations characteristic of *irradians* are absent. As in *R. irradians*, however, there are a few oblique rows of short and parallel transverse indentations on the dorsal and ventral surfaces of the
body whorl of the adult shell. These indentations are usually concentrated in the terminal half of the body whorl.

MANTLE, HEAD AND FOOT. In life the dorsal surface of the adult animal of \textit{R. karui} (Fig. 2) ranges in colour from a bright ochre yellow to rufous orange or brown. The brilliant yellow or orange of some adults fades to a dull and pale pinkish cream or greyish white on preservation. A distinctive character of this species is the scattering of irregular dark spots on the head, sides and margins of the foot, the mantle and/or the tail. The spotting may be very plentiful, sparse or rarely absent and may take the form of fine specks or large irregular blotches. \textit{R. karui} occasionally produces a clear, brilliant orange-red mucous on being handled. Juveniles are generally a dark steel grey, pale bluish or yellowish grey, or greyish white, with the fringe and sole of the foot paler. Some juveniles exhibit black eye retractor muscles that impart two distinctive black dorsal bands from the tip of the tentacles to the mantle edge and possess a single band of dark grey dorsal pigmentation that extends from the distal mantle to the tip of the tail. Similar patterns of pigmentation
are found in some juveniles of *R. irradians* and *Satiella* and occur widely in the stylommatophora.

The mantle of *Ratnadvipia karui* (Fig. 19) is very different to that of *R. irradians*. Unlike in *R. irradians* the mantle is posteriorly not produced into two extensions, but effectively continues as a broad band right around the shell, the band of mantle being broadest anteriorly and laterally and less broad posteriorly. The edge of the mantle possesses a large and very conspicuous lobe on its right side, just posterior to and above the pneumostome. In preserved specimens this lobe covers all or part of the early whorls and a small part of the body whorl of the shell. This lobe is clearly evident in the adult and juvenile of *R. karui* in Fig. 2 (b and e); note also the very prominent pneumostome in the adult in Fig. 2b. Apart from this large lobe the edge of the mantle is smooth and unmarked by indentations. In life the edges of the mantle can be extended so that the entire shell is covered and this condition is often observed in the field and is characteristic of both adults and juveniles (Fig. 2c).

Juvenile specimens of *R. karui* (Fig. 2e, Fig. 20) are generally easy to identify in the field. Both the snail and the shell have a flat, very elongated appearance; the mantle surrounds the shell as a broad continuous band; and the mantle often covers the shell completely or almost completely, with just a thin sliver of shell being exposed along the line of contact of the margins of the mantle. Occasionally it may be difficult to differentiate between the smallest juveniles (measuring 5–7 mm from head to tail tip) of *R. karui* and *R. irradians* with the naked eye. Examination of the shells under a dissecting microscope, however, will show the very different protoconch of the two species (Fig. 18c–d).

**REPRODUCTIVE SYSTEM**

**Penis.** As in *R. irradians* some specimens exhibit a penial loop, other specimens do not (Figs 7, 11, 21). Both the holotype and paratype from Gilimale-Eratne PR exhibit a prominent and well-developed penial loop; other specimens, such as the example from Nakiyadeniya PR, lack a penial loop. However,
The Sri Lankan semi-slug Ratnadvipia

unlike *R. irradians*, the internal surface of the proximal penis in *R. karui* specimens with a penial loop (Fig. 22a) is very different to those without a penial loop. In the holotype and paratype of *R. karui* from Gilimale-Eratne PR the proximal penis is distally ornamented with about five to twelve parallel irregular and wavy transverse ridges. Proximally, these transverse ridges give way to a broad zone of longitudinal papillate ridges and/or longitudinal rows of papillae; these longitudinal ridges and papillae are similar in form to those of *R. irradians*. As in *R. irradians* the part of the penis just proximal to its junction with the genital atrium is marked by a thickened or swollen penial wall. At the meeting point of the longitudinal ridges with this proximal thickening, the ridges are smoother with little or no papillae.

The internal structure of the penis of specimens lacking a penial loop (Fig. 22b–c) is very different. The inner surface of the proximal penis is composed largely of the plain proximal thickening of the penial wall bordered distally by a narrow band of longitudinal ridges. These ridges are smooth and cylindrical proximally and become markedly papillate distally and immediately around the penial papilla.

In *R. irradians* the internal surface of the penis (Fig. 4) shows a uniform arrangement irrespective of the presence or absence of a penial loop. *R. karui*, in contrast, exhibits two clearly distinct arrangements to the inner surface of the penis, which our preliminary investigations have shown to be associated with the presence or absence of the penial loop. Further study is needed to establish if the two penial forms in *R. karui* correspond to different stages of growth and reproductive development or if they have taxonomic significance.

**Gametolytic sac.** As in *R. irradians* the gametolytic sac (Figs 7, 21) is variable in form. In the holotype and paratype from Gilimale-Eratne PR the gametolytic sac is an asymmetric and inflated hooked sac with an opaque appearance, which is connected to the oviduct by a very short but discernible narrow-lumened duct. In other specimens, such as the one from Nakiyadeniya PR, the gametolytic sac is a symmetrical, transparent elongated bag; the duct is not discernible.

**Spermatophore.** Only one spermatophore (Fig. 23) was recovered from the six specimens of *R. karui* examined. It is smaller but similar in general form to the spermatophore of *R. irradians* (Fig. 5). However, it exhibits a very distinctive arrangement of spines on the anterior spike. In *R. karui* there are two rows of spines positioned along the axis of the spike; one row is long, with large spines. This runs along the entire length of the spike’s axis and resembles the single row of spines found in *R. irradians*, the second row is very small, with small spines and is confined to the anterior tip of the spermatophore. The complex arrangement of grooves and channels on the internal surface of the bent proximal portion of the epiphallus corresponds exactly with the arrangement of spines on the anterior spike of the spermatophore. The internal structure of the bent part of the epiphallus in several of the specimens was clearly visible through the wall of the epiphallus. The epiphallus of specimens with and without a penial loop were examined and in all the gross morphology of the inner surface of the epiphallus corresponded to a spermatophore bearing two rows of spines anteriorly, one long row of large spines and one short row of smaller spines. The wall of the part of the epiphallus of *R. irradians* is more opaque, so that the internal structure of the epiphallus is not clearly visible. Additional detailed examinations of the spermatophores and the structure of the epiphallus of *R. irradians* and *R. karui* are needed to establish whether the differences we have observed are constant at the specific level.

**Egg.** The egg (Fig. 2d) is a translucent white, oval with pointed ends and longitudinal sulcations. It is soft and measures approximately 7 mm in length and 4 mm in width. The egg of *R. karui* is similar to Collett’s description (Blanford & Godwin-Austen, 1908) of the egg of *Cryptozona chenui*. We have also observed a similar egg-form in *Euplecta*. 
The egg of *R. irradians* is not known, but *Cryptozona*, *Euplecta* and *Ratnadvipia* form a distinct clade (Wade et al., in press) and it seems likely that all species in this group will possess similar eggs.

Radula and Jaw. In *R. karui* (Fig. 24) the central tooth may be unicuspid or tricuspid, the cusps being blunt or sharp, elongated or small. Two of the three specimens examined show unevenly bicuspid laterals and marginals. In the Habarakada example all the laterals and marginals are uniform. In the example from Gilimale-Eratne PR the first six laterals are only faintly bicuspid; thereafter and up to and including the 18th lateral there is a transition from evenly to unevenly bicuspid teeth. The complete formula for these specimens is shown below:

- Paratype from Gilimale-Eratne: 350+, 1. 350+
- Habarakada: 330+, 1. 330+

In the third specimen (Fig. 25), which is from Nakiyadeniya PR, the arrangement of the teeth is similar to *R. irradians*; the first 38–40 inner laterals are sharply unicuspid and are followed by evenly bicuspid outer laterals and marginals. The formula is:

200 + . 40. 1. 40. 200 +.

A comparison of the figures above with those for *R. irradians* suggest that the radula of *R. karui* may exhibit more teeth per row than *R. irradians*, but also that there is some degree of overlap between the two species. The bicuspid inner laterals of *R. karui* are very distinctive, but their diagnostic value needs further clarification. The specimen of *R. karui* with *irradians*-like unicuspid inner laterals indicates that there is considerable intraspecific variation in the form of the inner laterals in *R. karui*.

The jaw of *R. karui* (Fig. 25) is very similar to that of *R. irradians*. It is simple and has a concave cutting edge. Two specimens were examined and in both the curve of the jaw and the concavity of the cutting edge is very gentle; one specimen has a slight median projection to the cutting edge.

Distribution

The distributional information available for *R. karui* (Fig. 26) indicates that it is almost exclusively confined to the tropical lowland rain forests of the wet zone and occurs across altitudes from 60–938 m. On the basis of current data it is clear that, unlike *R. irradians*, *R. karui* is exclusively a forest species. A recent preliminary study of village home gardens in the Kalutara, Galle and Matara districts has shown that *R. karui* does not occur in home gardens although it may be common in natural forests in close proximity to gardens (<0.5 km away). Interestingly *R. karui*, like *R. irradians*, can survive in very small forest fragments (e.g. Hingalgodawatta, Yattapatha, Batugodavila and Tawalama) ranging from two to five acres...
in total and is common in larger forests subjected to high disturbance such as intensive selective felling in the recent past (e.g. Kanneliya FR).

The known range of *R. karui* falls within the southern part of the range of *R. irradians*, so that *R. karui* across its range is sympatric with *R. irradians*. The distributional data suggest that *R. karui* has a restricted distribution in the lowland wet zone. We have not recorded it, for example, from Mulatiyana FR and adjacent forests along the southern boundary of the wet zone which have been relatively well sampled. *R. karui* does not occur in the lower montane rain forests of the eastern sector of Sinharaja NHWA and the contiguous Handapan Ella OSF. It is also apparently absent from the lowland rain forests around Kitulgala and Maliboda, which lie on the northern edge of the Peak Wilderness Sanctuary. *R. karui* is a common species, however, about 12 km to the south of Maliboda, in Gilimale-Eratne PR.

Nearly all of Sri Lanka’s remaining lowland rain forest is restricted to the southern part of the wet zone and it is the highly fragmented forests of this area which represents the core of the current range of *R. karui*. Important forest areas in the southern part of the wet lowlands which have yet to be surveyed and are likely to contain populations of *R. karui* include Dellawa PR in Galle District and Karawita PR, Kiribatgala OSF, and Delwela PR and its contiguous forests in Ratnapura District.

Like *R. irradians* this species is at least partly arboreal. The adults of *R. karui* have been observed on the ground and on low vegetation and the juveniles almost exclusively on the leaves of shrubs and trees. Studies of the ecology of *R. karui* and *R. irradians* are needed to establish whether these species spend most of their life on the forest floor or in above-ground vegetation and if the latter, how far up into the forest canopy they move.

**Distributional records:** 61 m, in small boggy forest near Ratnapura Resthouse, Ratnapura (6°40.9′N, 80°24.2′E); F. Naggs and P.B. Karunarathne, 1996; 68 m, Induruwu, Gilimale-Eratne PR (6°45.6′N, 80°25.6′E), 1998; 333 m, Sudagala, Gilimale-Eratne PR (6°48.3′N, 80°23.2′E), 1998; 285–380 m, Batadomba Lena, Gilimale-Eratne PR (6°46.5′N, 80°23.5′E), 1998; 130 m, Holmanwala, Kanneliya FR (6°15.5′N, 80°21.3′E), 1998; 155–495 m, Hangaranakande, Kanneliya FR (6°16.1′N, 80°20.2′E), 1998; 125 m, Annasigetakanda, Kanneliya FR (6°14.9′N, 80°20.1′E), 1998; 75–330 m, Lavalvaruvakanda, Kanneliya FR (6°16.4′N, 80°20.9′E), 1998; 265 m, Kodikande, Kanneliya FR (6°15.2′N, 80°21.8′E), 1998; 165 m, Galbendidolakanda, Nakiyadeniya PR (6°10.4′N, 80°23.1′E), 1998; 195–210 m, Manamaladolakanda, Kanneliya FR (6°15.3′N, 80°22.4′E), 1998; 195 m, Dediyagala FR (6°10.4′N, 80°25.5′E), 1998; 938 m, Dehenakande, Peak Wilderness Sanctuary (6°45.6′N, 80°30.3′E), 1998; 223 m, Malgalla, Kanneliya FR (6°17.6′N, 80°21.7′E); 400–623 m, Hinnidumkanda, Habarakada PR (6°19.9′N, 80°17.8′E); 232 m, Dediyagala, Dediyagala FR (6°11.2′N, 80°24.6′E); 273 m, Galbendidolakanda, Nakiyadeniya PR (6°10.3′N, 80°23.0′E); 360 m, Malamunure FR (6°14.5′N, 80°18.8′E), 2000; 183 m, Kospelaketiya, Kanneliya FR (6°15.0′N, 80°20.8′E); 210 m, Katukitulakanda, Kanneliya FR (6°17.8′N, 80°20.3′E); 410 m, Kalubowitiyana OSF (6°19.5′N, 80°24.9′E); 103 m, Beraliya (Kudagala) PR (6°15.8′N, 80°11.7′E); 165 m, Lavalvaruvakanda, Kanneliya FR (6°15.3′N, 80°20.5′E); 240 m, Harankahapatha, Kalugala PR (6°28.6′N, 80°14.1′E); 219 m, Homadola, Nakiyadeniya PR (6°11.8′N, 80°22.3′E); 232 m, Awudagalakanda, Auwegalakanda OSF (6°22.5′N, 80°17.1′E); 253 m, Kondagala, Kanneliya FR (6°14.1′N, 80°23.8′E); 170 m, Olu Dola, Dediyagala FR (6°11.1′N, 80°26.0′E); 236 m, Kekirikanda, Dediyagala FR (6°12.6′N, 80°24.7′E); 113 m, Hingalagodawatta forest (6°19.5′N, 80°19.7′E); 560 m, Wanduragala ridge, Sinharaja NHWA (6°23.6′N, 80°28.9′E); 592 m, Paththinigala, Sinharaja NHWA (6°24.1′N, 80°24.6′E); 717 m, Koskulana, Sinharaja NHWA (6°23.2′N, 80°28.0′E); 780 m, Sinhagala, Sinharaja NHWA (6°24.3′N, 80°26.6′E); 540 m, Wewagama, Delgoda PR (6°27.1′N, 80°23.6′E); 728 m, Dothalagala, Delgoda PR (6°24.9′N, 80°23.4′E); 441 m, Pitakele, Delgoda PR (6°26.7′N, 80°22.5′E); 151 m, Pallekumbura, morapiyita-Runakanda PR (6°26.8′N, 80°19.2′E); 120 m, Yattapatha forest, (6°26.0′N, 80°17.3′E); 461 m, Dothalanka, Morapiyita-Runakanda PR (6°29.8′N, 80°20.2′E); 314 m, Kalugala PR (6°27.8′N, 80°14.2′E); 472 m, Katukitulakanda.
Figure 26  Distribution of *Ratnadvipia karui* in Sri Lanka. The wet zone (solid line) is delimited by the 2500 mm isohyet and the 1800 mm isohyet (broken line) represents the boundary between the intermediate and dry zones. Individual sites from which this species has been recorded are denoted by crosses and towns or villages by filled circles. Closed-canopy natural forest cover is shown in dark grey; the distribution of forest cover is based on the 1:50000-scale forest map by Legg & Jewell (1995). The projected extent of occurrence of the species, extrapolated from the available distributional information, is shown in pale grey. The numbers refer to the forest numbers of forest areas as listed in the Forest register of the Forest Department, Government of Sri Lanka (see Appendix I).
Moratipitiya-Runakanda PR (6°26.1′N, 80°20.7′E); 210 m, Batugodavila forest, Hedigalla (6°27.5′N, 80°17.9′E); 448 m, Giguruwa Ihala, Sinharaja NHWA (6°21.5′N, 80°29.5′E); 60 m, Tawalamata forest (6°20.3′N, 80°19.4′E); 351 m, Warukandeniya, Sinharaja NHWA (6°23.2′N, 80°24.7′E); 285 m, Batadomba Lena, Gilimale-Eratne PR (6°46.5′N, 80°23.5′E).

All records dated 1998 collected by D. Raheem, T.O. Butterworth and C. Inglis. All other distributional records unless otherwise indicated were gathered largely during the Darwin Initiative Project ‘Land-snail Diversity in Sri Lanka’ 1999–2002 by D. Raheem.

Etymology

In recognition of his friendship and the inspiration he provided to Sri Lankan field naturalists Ratnadvipia karui has been named after the well-known Sri Lankan naturalist G.P.B. Karunaratne (1931–1996), who was known to his friends and colleagues as ‘Karu’.

Acknowledgements

We thank the Darwin Initiative (DEFRA) for funding the 1999–2002 project Land-snail diversity in Sri Lanka (grant no. 162/08/214) and for current post-project funding of Land snails as models for biodiversity assessment in Sri Lanka (grant no. EI DPO 1), which, with initial support from The Natural History Museum, London, Special Funds, has allowed this study to be undertaken. We wish to express our gratitude to Tom Butterworth and Cheryl Inglis who carried out surveys with D. Raheem and were involved with research between 1995 and 1999, when much of the examined material was obtained. These studies were made possible through funding by Fauna and Flora International, the University of London, The John Swire 1989 Charitable Trust, The National Science Foundation (Sri Lanka), Imperial College, London, The British Council (Colombo Branch, Sri Lanka), the Royal Geographical Society, the British Ecological Society and the Percy Sladen Memorial Fund. We would like to thank the Forest Department and Department of Wildlife Conservation, Sri Lanka, for permission to carry out this work. Yasantha Mapatuna and Lalitha Kariyawasam of the Department of National Museums, Colombo, Sri Lanka provided invaluable support in making the Darwin Initiative surveys and taxonomic research work a success. Kithsiri Ranawana led the University of Peradeniya group for the 1999–2002 Darwin Initiative surveys and provided distribution data for the Knuckles Conservation Area. We are also extremely grateful to Rohan Pethiyagoda for his support and assistance at various stages of our work in Sri Lanka. Peter Mordan commented on the manuscript and other members of staff of the Natural History Museum, London, kindly provided their expertise: Alex Ball with scanning electron microscopy; Harold Taylor with photography and graphic design; and Jim Chimonides with mapping of species distributions, rainfall and forest cover. Harish Gaonkar and Brigitte Grimm assisted with German translations.

References


Clessin, S. 1881. Nomenclator Heliceorum Viventium, Cassellis, Sumpibus Theodori Fischi.


Appendix I

**Abbreviations used in figures**

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<tr>
<th>Abbreviation</th>
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<tr>
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Appendix II

**List of forest areas**

The following is a list of forest areas highlighted in Fig. 26. Forest names and numbers follow the Forest register of the Forest Department, Government of Sri Lanka (source: Green & Gunawardena, 1997). The forests are designated as FR = Forest Reserve, PR = Proposed Reserve, OSF = Other State Forest or NHWA = National Heritage Wilderness Area, unless otherwise stated.

For the purposes of administration some of the larger individual forest fragments were divided into two or more protected areas by the Forest Department during the early part of the twentieth century; such forest fragments are indicated below by an asterisk. For example, the forest isolate of which Kanneliya FR forms the northern sector has its southern part divided into western and eastern portions known respectively as Nakiyadeniya PR and Dediyagala FR. For convenience, in Fig. 26 we have indicated forest fragments composed of several such constituent protected areas with the number of one of the constituent parts.

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