

TERRESTRIAL GASTROPODS OF THE MALDIVES, ALL OF WHICH ARE INVASIVE?

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Abstract Renewed collecting of land snails on various islands of the Maldives resulted in 23 new species records for that archipelago and a reconfirmation of 7 of the 9 species that had been listed for the region over a century earlier. Next to incidental records of single shells, populations of several species were recorded. Many species are well-known as invasive. Four species that were considered endemic to Sri Lanka are now also known from the Maldives, next to 10 additional, more widespread species that are shared. Therefore, Sri Lanka is hypothesised to be the main source of the Maldivian terrestrial molluscan fauna. A *Sitalinopsis* species that is known from 10 islands, belonging to 7 atolls, is described as new to science. It might be endemic to the Maldives albeit unlikely because of sea level fluctuations and occasional tsunamis that may have eradicated the terrestrial flora and fauna of the archipelago more than once in the geological past, counteracting time-consuming allopatric speciation.

Key words Land snails, new species, invasive species, *Sitalinopsis*, Maldives, biogeography.

INTRODUCTION

There are c. 1200 islands in the Maldivian archipelago, c. 1000 of which are uninhabited. They are part of the Laccadives-Chagos Ridge, extending over nearly 800 kilometers from north to south in the Indian Ocean, more than 600km SW of southern India and Sri Lanka. The chain of 19 atolls, which is 120km broad at its widest point, is formed from coral structures. There are no hills. The highest point, situated on Viligili in the Addu Atoll, reaches only 2.4m above sea level (Anonymous, 2010). Reliable data on the geological history of the archipelago, in particular the biologically most relevant data regarding the persistence of terrestrial habitats in the region, are not readily available. Kench and co-workers studied reef growth in the Maldives after the Pleistocene (Kench *et al.*, 2005, 2009) and have found that modern sea level was reached c. 4500 yr B.P. whereas an up to 0.5m higher sea level occurred around 3000–2000 years ago. During much of Pleistocene time sea-level was lower than at present, but during mid- to late-Pleistocene interglacial periods sea-levels might have risen to as much as c. 20m higher, at least in the Pacific Ocean (Brook, 2010: 219). It may be assumed that periodical increases in sea level and occasional devastating tsunamis have eradicated the non-marine species more than once in the geological past, so hampering time-consuming, allopatric speciation events. As a consequence, despite the

isolated position of the archipelago, a Maldivian terrestrial molluscan fauna with a high percentage of endemics is not to be expected.

The vegetation on the islands varies from a woody area with trees and shrubs (Fig. 1A–C) to a sterile sandy surface that is regularly artificially ‘cleaned’, with humus only in circles around some garden plants (Fig. 1D). These contrasting habitats were seen in the Addu Atoll (Gan) and South Malé Atoll (Bigadhoo) on the one hand, and on the islet of Eriyadu in the North Malé Atoll on the other hand. Usually parts of an island at least are covered by a rather monotonous vegetation of trees and some other plants. This applies to, for example Vilamendhoo in the South Ari Atoll, and Filitheyo in the North Nilandhe Atoll. Some islands have their own cultivated garden (Fig. 1E). For these gardens, soil may be imported, which might be a source of invasive species. Details on this are unknown. Outside the cultivated parts of the islands the surface layer of humus is only a few centimetres thick at most. Nearly always the cover is even thinner.

Hameed (2002: 11) stated that ‘Little is documented on the terrestrial invertebrate fauna of the Maldives’. The earliest and hitherto only article on non-marine molluscan species from some of the Maldivian islands was published over a century ago by Edgar A. Smith (1902). Mead (1961) and Muniappan (1987) published records for *Lissachatina fulica* from some islands, whereas Mitra *et al.* (2005) cited some of the species reported by Smith (1902) from the Maldives,

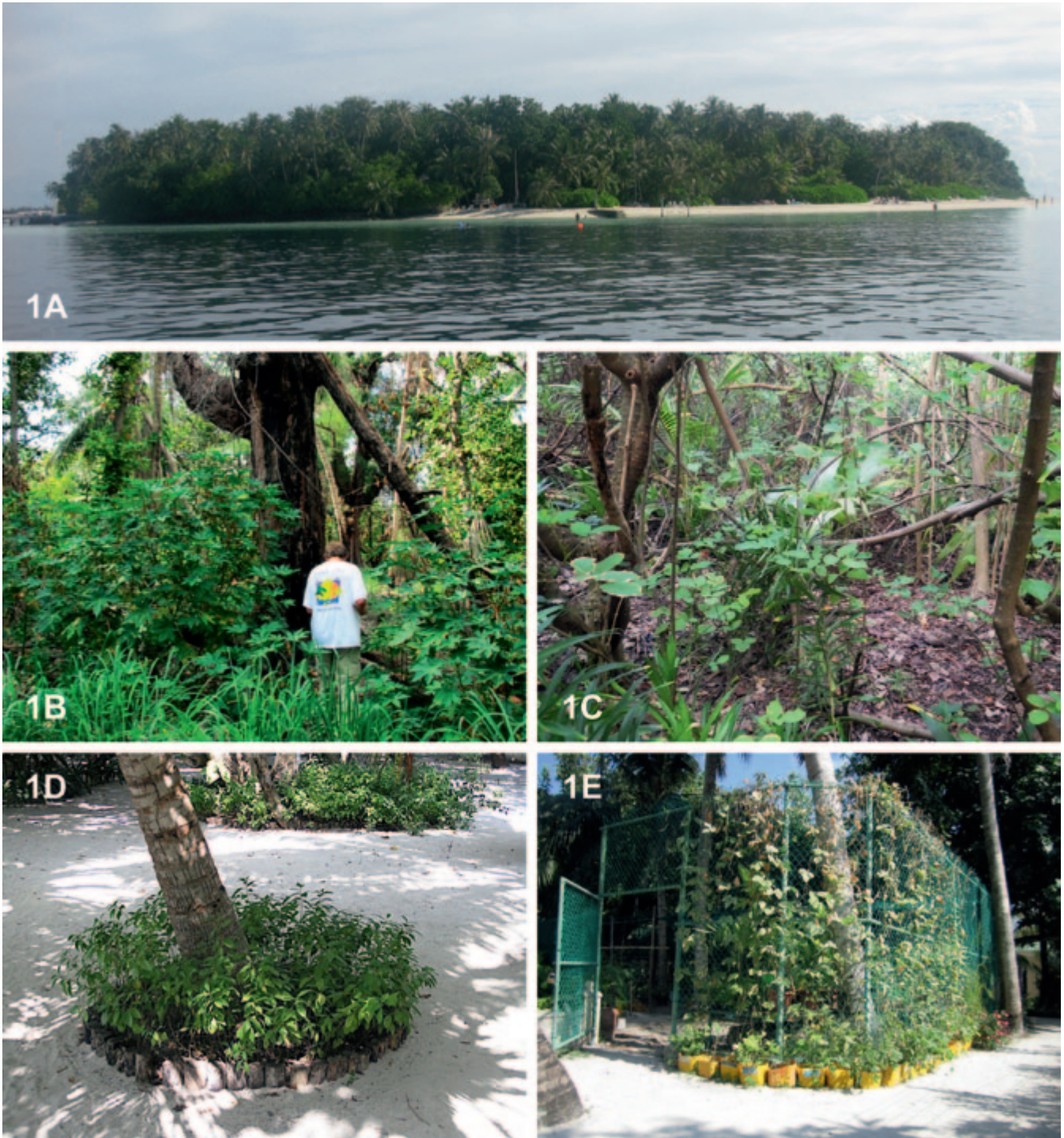


Figure 1 Habitats. **A, C**, South Malé Atoll, the island Biyadhoo (**A**), with a detail of the vegetation (**C**); **B**, Addu Atoll, S. Hithadhoo, old forest; **D, E**, North Malé Atoll, Eriyadu, where snails were found in small areas around trees (**D**) and in the clean garden (**E**).

without adding any further details. During the past decade, several islands have been investigated for terrestrial molluscs more or less thoroughly. For less than one percent of the islands some data are available now. The most promising uninhabited islands, where the most

undisturbed natural ecosystem will be found, have not been investigated. The largest gaps in geographical coverage of the archipelago (Fig. 2) are the Miladhunmadulu Atoll and the Thiladhunmathee Atoll in the northernmost part of the Maldives, north of 5°30'N, and the

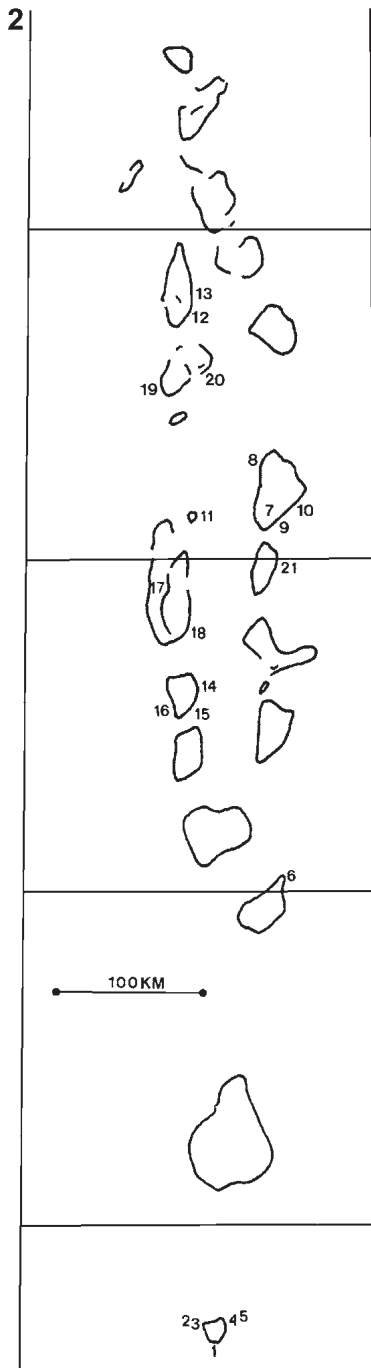


Figure 2 Simplified map of the Maldives, with abbreviated locality nos. **1–5** Addu Atoll: **1** Gan; **2** N. Hithadhoo; **3** S. Hithadhoo; **4** Hulhudhoo; **5** Midu. **6** Hadhdhunmathee Atoll: Isdhoo. **7–10** North Malé Atoll: **7** Bandos; **8** Eriyadu; **9a** Malé; **9b** Hulhule; **10** Lankanfinolhu. **11** North Ari Atoll: Kuramathi. **12–13** North Maalhosmadulu Atoll: **12a** Fainu; **12b** Inguradu (= Iguraidhoo); **13** Mahdu. **14–16** North Nilandhe Atoll: **14** Filitheyo; **15** Magoodhoo; **16** Nilandhoo. **17–18** South Ari Atoll: **17** N. Moofushi; **18** Vilamendhoo. **19–20a–c** South Maalhosmadulu Atoll: **19** Turadu; **20a–c** Heddufuri, Cumfinadu, and Reethi. **21** South Malé Atoll: Biyadhoo.

Huvadhoo Atoll, between the equator and 1°00'N, in the south.

In this article, the following questions are addressed: (1) what species have been recorded for the archipelago; (2) from which island[s]; (3) by live individuals or by one or more shells only; (4) what are the ranges of these species; (5) are all species known as invasive; (6) what, if any, main area of origin can be hypothesised for the Maldivian terrestrial molluscan fauna?

MATERIAL AND METHODS

The authors G. and R. visited several islands and gathered bottom material without any standardisation to be searched microscopically for micro-snails and shells. Larger specimens were collected on the spot. Some additional samples of shells were collected incidentally by others, in one case with marine material. Thus, the various localities are not all comparable regarding the species composition.

Few live animals were found. Some of these were used for DNA barcoding. When the individual was expected to be mature, it was used for dissection. The material is stored at Naturalis Biodiversity Center, Leiden, The Netherlands.

DNA extractions and PCR amplification were carried out as described by Groenenberg *et al.* (2011). For DNA barcoding purposes, partial *Cytochrome c oxidase subunit I* (COI) was sequenced using the primers of Folmer *et al.* (1994). Forward and reverse sequences were assembled and checked using Geneious v. 10.2.3 (Kearse *et al.*, 2012). That program was also used to calculate genetic distances (uncorrected p) in cases where the same species was collected from different localities. All sequences were submitted to GenBank under accession numbers MH626419–MH626446 to be available for other studies. Unless stated otherwise, GenBank Blast searches that are used here are nucleotide Blasts (BlastN).

While trying to locate the various islands mentioned by Smith (1902), it turned out that several geographic names have been changed over time. Apart from that, there may be more than one name in use for most islands and atolls. For that reason, all the names that we encountered are included in the following list of localities, with cross-references. For atolls, the names that are in bold type are used. Every single sample

has been given a code number that is used in the Systematics section. For every species, the Maldivian records are indicated by references to the atolls in question, with numbers referring to the separate islands.

The various taxa are dealt with in the sequence that is used by Bouchet *et al.* (2017). For all species, there are references to the original descriptions and to articles that are considered useful because of illustrations or otherwise. Full synonymies are not presented.

Geographic names

Addu Atoll (Seenu): Gan, Equator Village Resort, near tree trunks, 00°42'S 73°09'E, E.G. leg. 27.ii.2012 [1]; N. Hithadhoo (= Hitadu), shrubs near lake, 00°37'S 73°05'E, E.G. leg. 2.iii.2012 [2]; S. Hithadhoo, old forest (Fig. 1B), 00°37'S 73°05'E, E.G. leg. 2.iii.2012 [3]; Hulhudhoo, near harbour, mixed vegetation, 00°36'S 73°14'E, E.G. leg. 1.iii.2012 [4]; Midu (= Meedhoo), 00°35'S 73°14'E, Smith, 1902 [5].

Alifu Dhaalu, see South Ari Atoll

Alifu Alifu, see North Ari Atoll

Baa, see South Maalhosmadulu Atoll

Goidhoo Atoll, see South Maalhosmadulu Atoll

Hadhdhunmathee Atoll (Laamu): Isdhoo, 2°06'54"N 73°33'44"E, G. Schmelzer leg. 1991(ex colln A.J. de Winter) [6].

Kaafu, see North and South Malé Atoll

Laamu, see Hadhdhunmathee Atoll

North Ari Atoll (Alifu Alifu), Rasdhoo Atoll: Kuramathi, 4°16'N 72°59'E, F. Bagusche leg., iv.2014 [11].

North Maalhosmadulu (= North Mahlos) **Atoll** (Raa): Fainu, 5°28'00"N 73°01'00"E, Smith, 1902 [12a]; Inguradu (= Iguraidhoo), 5°28'00"N 73°01'00"E, Smith, 1902 [12b]; Mahdu (= North Mahlos Mahdu Atoll), 5°37'00"N 72°55'00", Smith, 1902 [13].

North Malé Atoll (Kaafu): Bandos Island, 4°17'N 73°29'E, E.G. leg. 25.i.2016 [7]; Eriyadu (Fig. 1D), 4°35'N 73°25'E, E.G. leg. 27.ii.2011 [8]; Malé, 4°11'N 73°31'E, Smith, 1902 [9a]; Hulhule (airport island), 4°12'N 73°32'E, E.G. leg. 28.ii.2011 [9b]; Lankanfinolhu, 4°17'N 73°33'E, B.T. Reijnen & S.E.T. van der Meij leg. v.2011 [10].

North Nilandhe Atoll (Faafu): Filitheyo, 3°13'N 73°03'E, E.G. leg. 10.iii.2014 [14]; Magoodhoo, 3°05'N 72°58'E, agrifarm and playground, B.T. Reijnen & S.E.T. van der Meij leg. 27.11.2015 [15]; Nilandhoo, 3°03'N 72°53'E, B.T. Reijnen & S.E.T.

van der Meij leg. 27.11.2015 [16].

Rasdhoo Atoll, see North Ari Atoll

Seenu, see Addu Atoll

South Ari Atoll (Alifu Dhaalu): N. Moofushi, 3°53'N 72°44'E, A. Lugli leg. 9.viii.1994 (ex colln J. Delsing) [17]; Vilamendhoo, 3°38'N 72°58'E, E.G. leg. 17.iii.2009 [18].

South Maalhosmadulu (= South Mahlos = Goidhoo) **Atoll** (Baa): Turadu, 5°02'N 72°49'E, Smith, 1902 [19]; Heddufuri (= Hedufuri), 5°07'N 73°03'E, Smith, 1902 [20a]; Cumfinadu (= Kumfinadu), 5°08'N 73°03'E, Smith, 1902 [20b]; Reethi Beach, 5°15'N 73°10'E, E.G. leg. 24.i.2017 [20c]. All indicated as 20 in Fig. 2.

South Mahlos Atoll, see South Maalhosmadulu Atoll

South Malé Atoll (Kaafu): Biyadhoo (Fig. 1A, C), 3°56'N 73°27'E, E.G. leg. 26.i.2018 [21].

India, Laccadive Islands: Minikoi, 8°17'N 73°02'E, Smith, 1902 [22].

ABBREVIATIONS

AB – breadth of the aperture; AH – height of the aperture; B – shell breadth; H – shell height; NHMUK – The Natural History Museum, London; RMNH – Naturalis Biodiversity Center, Leiden.

SYSTEMATICS

CAENOCASTROPODA

Superfamily Cyclophoroidea Gray, 1847

Family Cyclophoridae Gray, 1847

Genus *Leptopomoides* G. Nevill, 1878

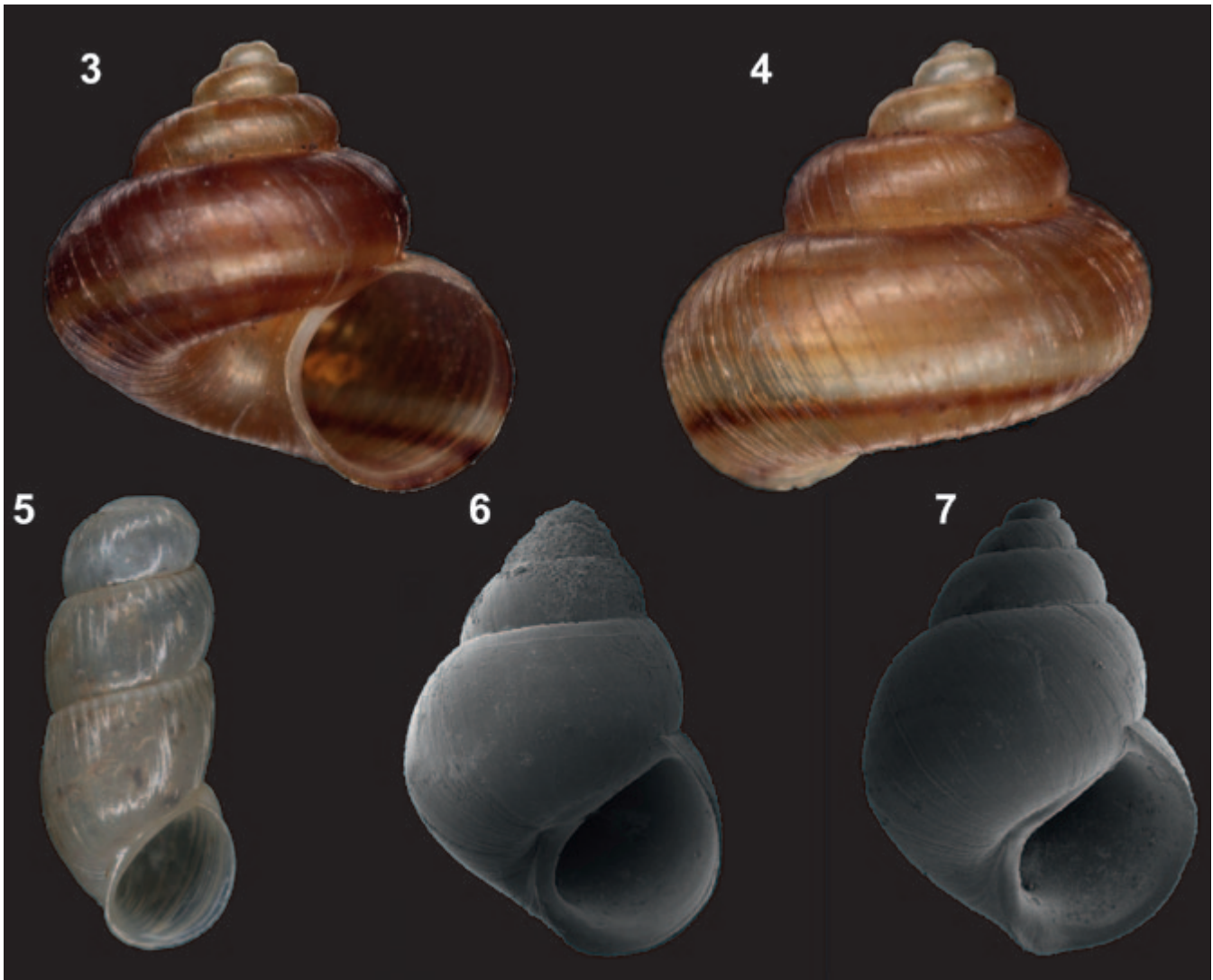
Leptopomoides halophilus (Benson, 1851) (Figs 3–4)

Cyclostoma halophilum Benson, 1851: 265. L. Pfeiffer, 1853: 241, pl. 31 figs 29–31. Reeve, 1862: pl. 8 sp. 49.

Leptopomoides halophilus; Gude, 1921: 20. Wenz, 1938: 455, fig. 1139 [as '*haliophilus*']. Naggs & Raheem, 2000: 159, fig. 190. Mitra *et al.*, 2005: 66.

Maldivian records Addu [1–5], North Malé [7–9], North Ari [11], North Maalhosmadulu [12], North Nilandhe [14, 15], South Ari [18], South Maalhosmadulu [19, 20c], South Malé [21].

Range Described by Benson (1851: 265) from "Point de Galle, Ceylon" [Sri Lanka] and hitherto



Figures 3–7 Caenogastropoda. 3–4 *Leptopomoides halophilus* (Benson, 1851), Vilamendhoo [18], both B= 5.1mm; 5 *Truncatella marginata* Küster, 1855, Hulhudhoo [4], H=5.4mm; 6 *Assimineea* spec. 1, Hulhudhoo [4], H=1.7mm; 7 *Assimineea* spec. 2, Bandos [7], H=2.4mm.

considered endemic to Sri Lanka (Naggs & Raheem, 2000: xi).

Shell Conical, about as high as broad, with 4–4½ very convex whorls; aperture circular, its edge neither reflected nor thickened. Umbilicus wide, measuring 1/6–1/7 of the total breadth. With fine growth lines that become more narrowly spaced and coarser towards the aperture and may be accentuated by low periostracal edges that are more or less regularly arranged; with some inconspicuous spiral lines above the periphery, c. five on the penultimate whorl. Colour and colour pattern variable: unicoloured pale greyish, brown or olive green, or with spiral banding, viz. a whitish band below the periphery, bordered by

a narrower, contrasting reddish brown band and sometimes more basally another reddish-brown spiral band. Operculum membranous, with concentric lines. Measurements (n > 50): H up to 4.6mm; B up to 5.1mm.

Notes Two shells from the type locality (RMNH305206) cannot be distinguished from the shells from the Maldives. Benson (1851: 265) apparently used the epithet *halo-philum* (salt-loving), because of the habitat of this species. Its type locality is sparsely vegetated, and close to the sea. The species is said to be accompanied there by two more species of terrestrial snails, viz. *Allopeas gracile* and *Gulella bicolor*. The proximity to the sea might make these snails prone to

transport by means of floating objects. The same three species were found together in 7 atolls of the Maldives.

Superfamily Truncatelloidea Gray, 1840
Family Truncatellidae Gray, 1840; subfamily
Truncatellinae Gray, 1840
Genus *Truncatella* Risso, 1826

Truncatella marginata Küster, 1855 (Fig. 5)

Truncatella marginata Küster, 1855: 12, pl. 2 figs 24–26. Griffiths & Florens, 2006: 68, pl. 18 fig. C. Muratov, 2010: 262, fig. 9. Gittenberger & van Bruggen, 2013: 238, fig. 2.

Truncatella teres L. Pfeiffer, 1856: 336.

Maldivian record Addu [4].

Range Muratov (2010: 262, fig. 9) refers to this allegedly amphibious species (p. 264) as having a 'coastal distribution from South Africa to the South Pacific'.

Shell Cylindrical, decollate, colourless, somewhat transparent; with radial ribs that are most prominent on the upper half of the whorls. Apertural lip continuous, thickened and reflected where it closed the umbilicus. With 4 whorls; B 2.4mm, H 5.5mm.

Notes Only a single, fresh, fully grown, decollate shell was found.

According to Herbert & Kilburn (2004: 97), *T. teres* Pfeiffer, 1856, is a synonym of *T. marginata*. Because of its habitat and the presence of an operculum, this species may be relatively easily transported over sea.

Family Assimineidae H. & A. Adams, 1856; subfamily Assimineinae H. & A. Adams, 1856
Genus *Assimineia* Fleming, 1828

From two localities a single assimineid-like shell is known. These shells are clearly not conspecific. Their generic classification is uncertain. We cannot exclude the possibility that these species are in fact marine.

Assimineia spec. 1 (Fig. 6)

Maldivian record Addu [4].

Shell Conical with slightly convex sides in profile and about 5 moderately convex whorls; with

a spiral thread shortly below the suture and irregular growth lines. Umbilicus closed by a prominent parieto-columellar callus, which continues, regularly curved towards the base of the shell. The apex is worn. Measurements: H 1.7mm.

Assimineia spec. 2 (Fig. 7)

Maldivian record North Malé [7].

Shell Conical with slightly convex sides in profile and 4 convex whorls; with growth lines that are crossed by much finer spiral striae. Apex smooth. Umbilicus closed by a prominent parieto-columellar callus, which forms a broadened part of the apertural lip at the base of its columellar part. Measurements: H 2.4mm.

Superorder Eupulmonata
Order Ellobiida
Superfamily Ellobioidea L. Pfeiffer, 1854
Family Ellobiidae L. Pfeiffer, 1854
Genus *Melampus* Montfort, 1810

Melampus fasciatus (Deshayes, 1830) (Fig. 14)

Auricula fasciata Deshayes, 1830: 90.

Melampus castaneus sensu Smith (1902: 144), not Megerle von Mühlfeld, 1816.

Melampus fasciatus; Raven & Vermeulen, 2007: 44, pl. 3 figs 24–26.

Maldivian record Addu[1], ?NorthMaalhosmadulu [12b] .

Range Widespread, from the Pacific islands and Australia, to Indonesia, Malaysia, Vietnam, and the Maldives (Cowie & Rundell, 2002: 146; Raven & Vermeulen, 2007: 44; Smith, 1902: 144).

Shell (n=5) Unmistakable shape, with a very large body whorl and a short, conical spire. Body whorl broadest near the insertion of the palatal edge of the aperture, narrowing abapically; with some brown spiral bands on a yellowish grey background. Aperture with a weak columellaris, a prominent lower parietal knob and a less conspicuous upper one with a parietal lamella in between, with 4 palatal, 3 parietal and 1 columellar tooth. With c. 10 whorls. The initial c. 4 whorls narrowly coiled and sculptured with both spiral riblets and incised radial lines, resulting in a reticulate surface. Radial



Figure 8 Pulmonata. *Laevicaulis alte* (Férussac, 1821), Vilamendhoo [18], length 5cm.

sculpturing becoming obsolete from about the 7th whorl on. Measurements (n=5): B 6.9–7.4mm; H 11.4–13.4mm.

Notes The species should be considered terrestrial because the snails occur ‘just above the high tide mark’ or sometimes further away from the coast (Raven & Vermeulen, 2007: 45).

According to Smith (1902: 144), this species was recorded ‘on the shore’. The original shells should be studied to reconfirm the identification.

Order Systellommatophora
Superfamily Veronicelloidea Gray, 1840
Family Veronicellidae Gray, 1840
Genus *Laevicaulis* Simroth, 1913

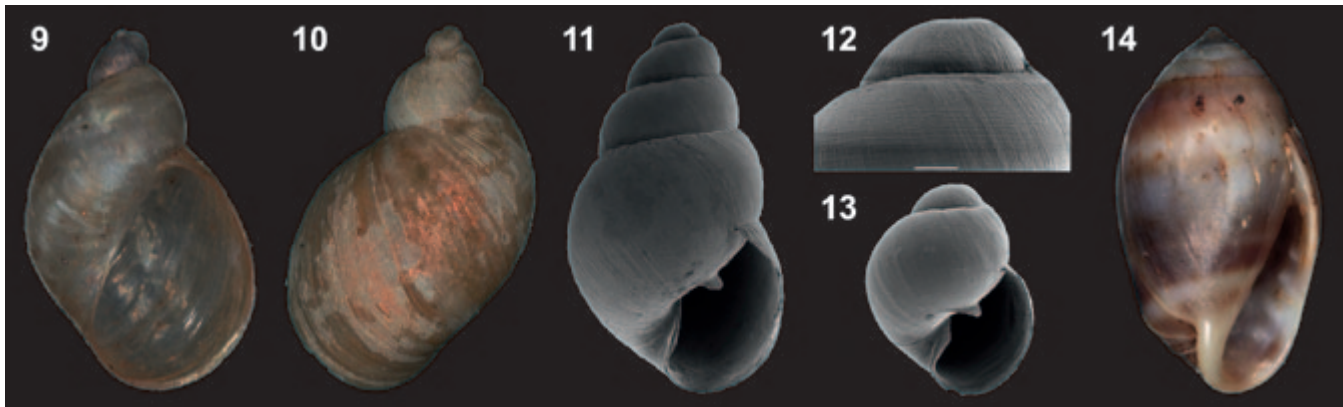
According to Gomes & Thomé (2004: 591) there are 8 species in this genus, all of which occurring in Africa. *Laevicaulis alte* is the only *Laevicaulis* species that is not restricted to that region.

Laevicaulis alte (Férussac, 1821) (Fig. 8)

Vaginulus alte Férussac, 1821a: 14.
Laevicaulis alte; Naggs & Raheem, 2000: 132, fig. 157. Gomes & Thomé, 2004: 590, 599, fig. 3. Herbert, 1997: 207, figs 12, 20, map 3.

Maldivian record South Ari [18].

Range Gomes & Thomé (2004: 599, fig. 3) summarised the distributional data on *Laevicaulis alte*, the ‘tropical leatherleaf’. Apart from its native range in Africa, it is widespread as an invasive species in the Oriental and Australian biogeographical regions, ranging from India in the west to Hawaii in the east, with the southernmost records in E. Australia and New Caledonia. The horticultural industry may have increased its distribution, as has been shown for Hawaii (Cowie *et al.*, 2008). It is also known from Sri Lanka (Naggs & Raheem, 2000: 132, fig. 157).



Figures 9–14 Pulmonata. **9–10** *Succinea ceylanica* L. Pfeiffer, 1855. **9** S. Hithadhoo [3], $2\frac{3}{8}$ whorls, H=9.6mm; **10** Vilamendhoo [18], $2\frac{3}{4}$ whorls, H=7.3mm. **11–13** *Elasmias manilense* (Dohrn, 1863), Vilamendhoo [18]; **11** H=2.65mm, **12** scale bar=0.1mm, **13** H=1.0mm. **14** *Melampus fasciatus* (Deshayes, 1830), Gan [1], H=13.5mm.

External shape The finely granulated mantle of this slug is light chestnut brown, with a light yellowish median line, that is frequently interrupted on the anterior half of the body. The tripartite sole is light beige.

Notes A short rain shower on Vilamendhoo activated two slugs of this species, which can easily be overlooked, during dry periods especially. No additional specimens were collected later on. Obviously, this is an invasive species. No other species of invasive slugs are known from the Maldives.

Order Stylommatophora

Superfamily Achatinoidea Swainson, 1840

Family Achatinidae Swainson, 1840; subfamily

Achatininae Swainson, 1840

Genus *Lissachatina* Bequaert, 1950

Lissachatina fulica (Férussac, 1821)

Helix (*Cochlitoma*) *fulica* Férussac, 1821b: 53, 1821c: 49.

Achatina fulica; Naggs & Raheem, 2000: 98, fig. 124.

Lissachatina fulica; Raheem *et al.*, 2014: 115, 219 fig. C.

Maldivian records Addu [1, 3], North Malé [7].

Range Circumtropical, but originally from East Africa.

Shell Very large, over 5cm high, with an ovoid last whorl and a slender conical spire, with brown, irregular, radial streaks on a light background.

Notes Alan J. Kohn collected *L. fulica* in 1957 in the Addu Atoll, on Gan and Hithadhoo (Mead, 1961: 11, 191). This species has also been reported from the island of Malé, North Malé Atoll (Muniappan, 1987). The occurrence in these 2 atolls was confirmed by the authors, but nowhere else in the additional 7 atolls that have been surveyed now the ‘giant African snail’ was found. It is a remarkable fact that this icon of invasiveness has not expanded its known range in the Maldives.

Subfamily Subulininae P. Fischer & Crosse, 1877
Genus *Subulina* Beck, 1837

Subulina octona (Bruguière, 1798) (Fig. 26)

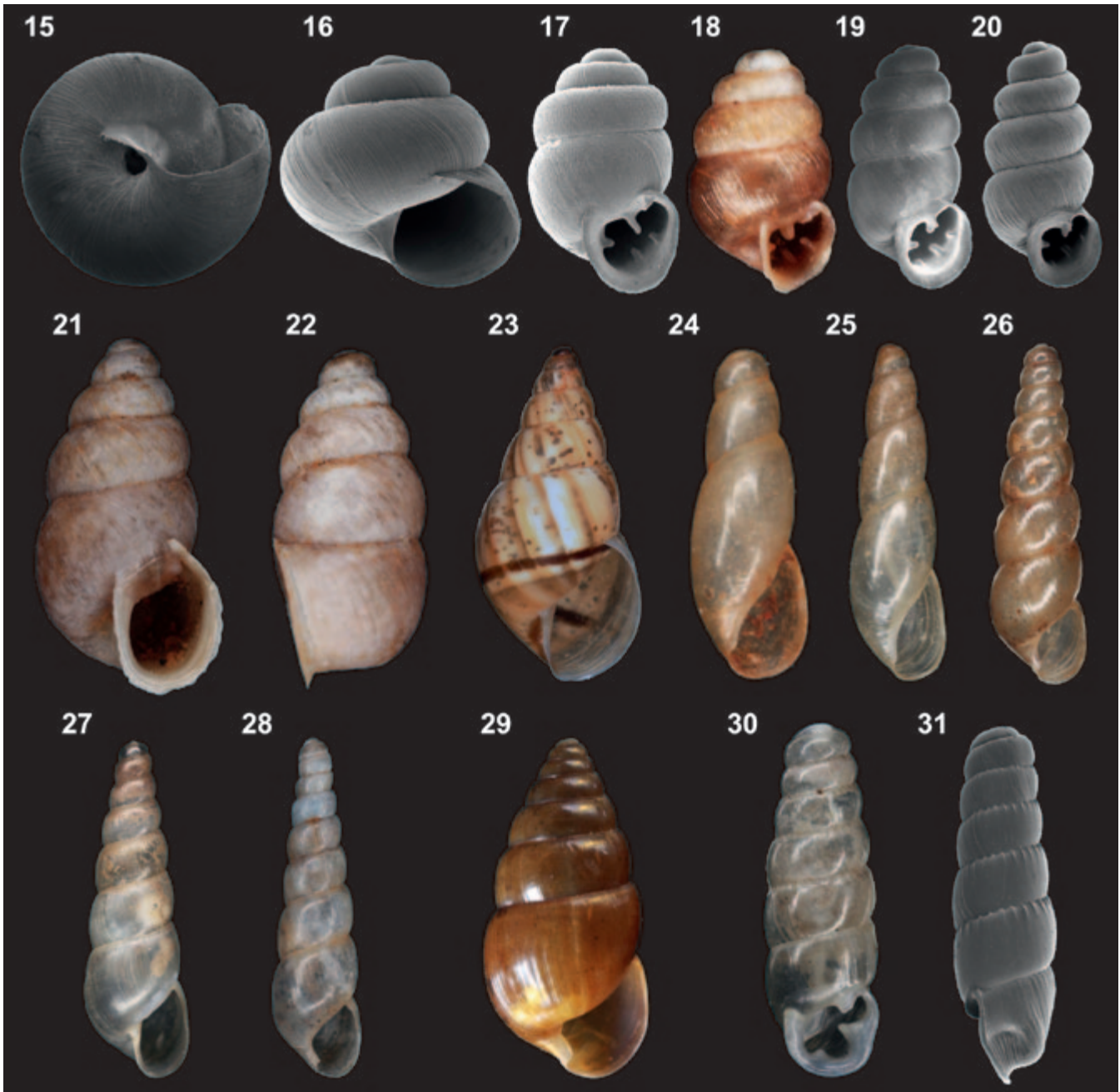
Bulimus octonus Bruguière, 1789: 325.

Subulina octona; Naggs & Raheem, 2000: 92, fig. 115a, b. Brook, 2010: 191. Raheem *et al.*, 2014: 116, 220 fig. B, C.

Maldivian records Addu [3, 4], North Ari [11], North Malé [7, 8, 10], North Nilandhe [14], South Ari [18], South Maalhosmadulu [20c], South Malé [21], Hadhdhunmathee [6].

Range The native range of this species might be tropical South America; it is widespread, worldwide in the tropics and subtropics and in hot-houses in Europe and North-America (Raheem *et al.*, 2014: 117). The horticultural industry may have increased its distribution (Cowie *et al.*, 2008).

Shell Very slender conical, with a broad apex and a truncated columella, whitish to light



Figures 15–31 Pulmonata. **15** *Pupisoma (Ptychopatala) circumlitum* Hedley, 1897, Kuramathi [11], B=1.4mm. **16** *Pupisoma (Ptychopatala) dioscoricola* (C.B. Adams, 1845), Vilamendhoo [18], H=1.6mm. **17** *Insulipupa mooreana* (E.A. Smith, 1894), Vilamendhoo [18], H=1.8mm. **18** *Nesupupa (Indopupa) spec.*, Reethi [20c], H=1.5mm. **19** *Gastrocopta servilis* (Gould, 1843), N. Moofushi [17], H=2.1mm. **20** *Gastrocopta mimula* (Benson, 1853), Vilamendhoo [18], H=2.4mm. **21–22** *Pupoides coenopictus* (Hutton, 1834), Magoodhoo [15], H=4.6mm. **23** *Rachis punctata* (Anton, 1839), Bandos [7], H=15.1mm. **24** *Cecilioides balanus* (Reeve, 1850), Lankanfinolhu [10], H=2.6mm. **25** *Ceciloides bensoni* Gude, 1914, Bandos [7], H=5.5mm. **26** *Subulina octona* (Bruguière, 1798), Biyadhoo [21]. **27** *Allopeas gracile* (Hutton, 1834), Eriyadu [8], H=8.2mm. **28** *Prosopeas spec.*, Magoodhoo [15], H=8.0mm. **29** *Glessula nitens* (Gray, 1825), Bandos [7], H=16.9mm. **30–31** *Gulella (Huttonella) bicolor* (Hutton, 1834). **30** Filitheyo [14], H=5.1mm; **31** Vilamendhoo [18], SEM photo, H=4.7mm.

yellowish, glossy, with dense obsolete irregular growth lines. Largest shell, 9 whorls (n=50): 16.5×4.0mm.

Molecular data Single specimens from two islands in the North Malé Atoll, viz. Eriyadu [8] and Lankanfinolhu [10], were used for

sequencing. Their COI sequences are identical and turned out to be most similar to a sequence for *S. octona* from Sonsorol island, Palau (Fontanilla *et al.*, 2017) (MF415357; sequence identity 98%), situated c. 7000km east of the Maldives.

GenBank accession numbers: MH626444, Eriyadu [8]; MH626445, Lankanfinolhu [10].

Genus *Allopeas* H.B. Baker, 1935

Allopeas gracile (Hutton, 1834) (Fig. 27)

Bulimus gracilis Hutton, 1834: 84, 93.

Opeas gracile; Gude, 1914: 355.

Allopeas gracile; Naggs & Raheem, 2000: 93, fig. 116a, b. Brook, 2010: 189. Gittenberger & van Bruggen, 2013: 254, 261 fig. 16. Raheem *et al.*, 2014: 117, 220 fig. 73 D (lectotype), E–F (paralectotypes).

Maldivian records Addu [1–5], Hadhdhunmathee [6], North Ari [11], North Maalhosmadulu [12a, 13], North Malé [7, 8, 9b, 10], North Nilandhe [14, 15, 16], South Ari [18], South Maalhosmadulu [20a, 20c], South Malé [21]. Laccadive Islands [22].

Range The native range of this widespread circumtropical species is unknown. For a more detailed account, see Raheem *et al.* (2014: 117).

Shell Very slender conical, columella not truncated, whitish; teleoconch with rather coarse growth lines and minute sutural papillae.

Molecular data For a specimen from the Addu Atoll, Gan [1], and two specimens from the South Ari Atoll, Vilamendhoo [18], COI sequences were acquired. Those from Vilamendhoo are identical and differ only 1.1% from the one from Gan. With a maximum sequence identity of 84% (Subulinidae spec., MF983683), no sequence in GenBank is very similar to *A. gracile*. However, a Blast search using the translated amino acid sequence (BlastP) did result in 99% identity with *Allopeas clavulinum* (Potiez & Michaud, 1838) (ADU33896.1). Apparently, the nucleotide sequences are so mutationally saturated that a genus level match cannot be made. The data did not enable a better insight regarding the phylogenetic relationships of *Allopeas*.

GenBank accession numbers: MH626423, Gan [1]; MH626421, 626422, Vilamendhoo [18].

Notes See the notes with *Leptopomoides halophilus*.

Genus *Prosopeas* Mörch, 1876

Prosopeas sp. (Fig. 28)

Maldivian record North Nilandhe [15].

Range Unknown.

Shell After the cylindrical 2¾ whorls of the smooth protoconch, the 6 teleoconch whorls increase very slowly but gradually in breadth. Whorls flattened, but separated by a deeply incised suture; glossy, with rather coarse, dense growth lines. The basal border of the aperture is missing, so that the columellar side of the aperture cannot be described; the curvature of the remaining part of the columella, however, suggests that it has been truncated below.

The shell, which may not be fully grown, is 2.1mm broad and has been 8.0+? mm high.

Notes The generic assignment of this species is uncertain.

Subfamily Glessulinae Godwin-Austen, 1920

Genus *Glessula* Martens, 1860

Glessula nitens (Gray, 1825) (Figs 29, 33)

Achatina nitens Gray, 1825: 415.

Glessula nitens; Pilsbry, 1908: 55, pl. 6 figs 1, 2. Gude, 1914: 404. Naggs & Raheem, 2000: 77, fig. 101a, b.

Maldivian record North Malé [7].

Range Hitherto considered endemic to Sri Lanka (Naggs & Raheem, 2000: vii).

Shell Yellowish brown, very glossy, with more or less irregular, blunt growth lines and very fine spiral striae, which are hardly or not visible in most specimens; apex smooth. With 7–7½ whorls. Columella prominently truncate below. Measuring (n=25) up to 16.6×8.3 and 16.9×7.9mm.

Genital tract (Fig. 33) Vas deferens not broadened where it is connected to the small, cylindrical, S-shaped epiphallus, and widening to over twice its diameter towards its insertion at the spermoviduct. Flagellum with five, parallel,

Family Ferussaciidae Bourguignat, 1883
Genus *Cecilioides* Ferussac, 1814

The genus is not reported from Sri Lanka. The species are notoriously difficult to identify conchologically. Our restricted material does not allow a profound analysis.

Cecilioides balanus (Reeve, 1850) (Fig. 24)

Achatina balanus Reeve, 1850: pl. 20 fig. 109.

Cecilioides (*Geostilbia*) *balanus*; Pilsbry, 1908: 46, pl. 4 figs 60, 61.

Cecilioides balanus; Raheem *et al.*, 2014: 115, 219, fig. D (lectotype), E, F (paralectotypes).

Maldivian record North Malé [10].

Range According to Raheem *et al.* (2014: 116) this species is restricted to the Indian subcontinent.

Shell Very slender, with a broad apex and 3½ whorls that hardly increase in breadth; light yellowish brown, glossy, somewhat transparent, with obsolete growth lines. Apertural edge broadly rounded below, with a prominently truncated columellar callus. Palatal edge protruding (side view). A juvenile and a shell that might be fully grown were found, the latter measuring 2.6×0.9mm.

Note The shells agree reasonably well with the figures of the lectotype and paralectotypes of this species.

Cecilioides bensoni Gude, 1914 (Fig. 25)

Caecilioides (*Geostilbia*) *bensoni* Gude, 1914: 375, fig. 121.

Cecilioides bensoni; Raheem *et al.*, 2014: 116, 220 fig. 73A (holotype).

Maldivian record North Malé [7].

Range According to Raheem *et al.* (2014: 116) *C. bensoni* is endemic to India.

Shell Very slender conical from the relatively broad apex on, transparent; up to 5 slightly convex, whitish whorls. Aperture obliquely rounded basally, palatal side vertical, nearly straight; columellar border thickened to shortly above the basal edge, where the callus is obliquely narrowed, resulting in hardly a truncation.

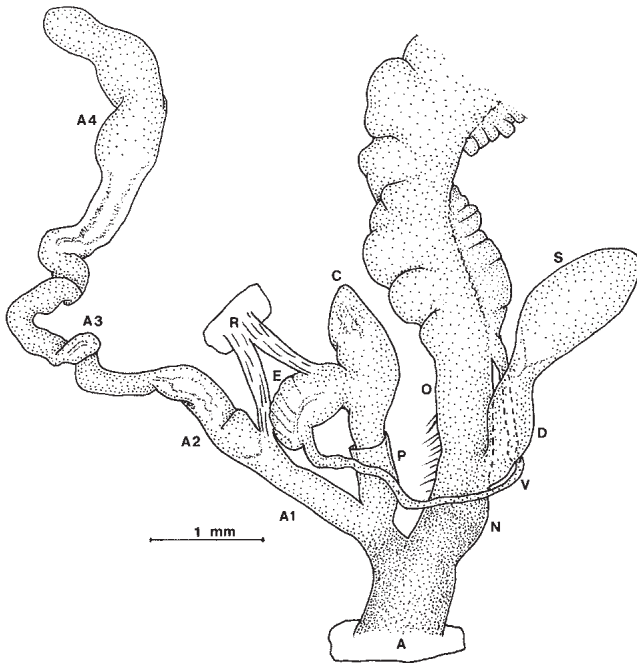


Figure 32 Genital tract of *Rachis punctata* (Anton, 1839), Hulhule [9b]; RMNH mol. slide 1156. A – atrium genitale; A1–A4 – sections of the penial appendix; C – penial caecum; D – pedunculus; E – epiphallus, with septa in the lumen; N – vagina; O – oviductus; P – penis, partly covered by a sheath; R – retractor muscles; S – spermatheca; V – vas deferens.

equally large and tightly connected fingerlike structures on a broader, large basal part. Penis hammer-like, with a proximal part that increases in size to double its width from the genital atrium on, and a transverse, large, elliptical distal part with the flagellum, the epiphallus and the penial retractor muscle inserting close to each other at one side. Vagina very short, hardly discernible as such. Bursa copulatrix not clearly differentiated from its broad duct. Oviduct little shorter than half the length of the bursa copulatrix. Uterus with 4 embryos.

Notes This species is only known from the North Malé Atoll, Bandos [7], where it is very common. It was not possible to decide with certainty between *Glessula nitens* and *G. ceylanica* (L. Pfeiffer, 1845) on the basis of the data in the literature. These nominal taxa refer to species that are conchologically very similar, if not identical. The oldest name is selected here.

For additional data regarding the structure of the genitalia in Glessulinae, see Budha *et al.* (2017).

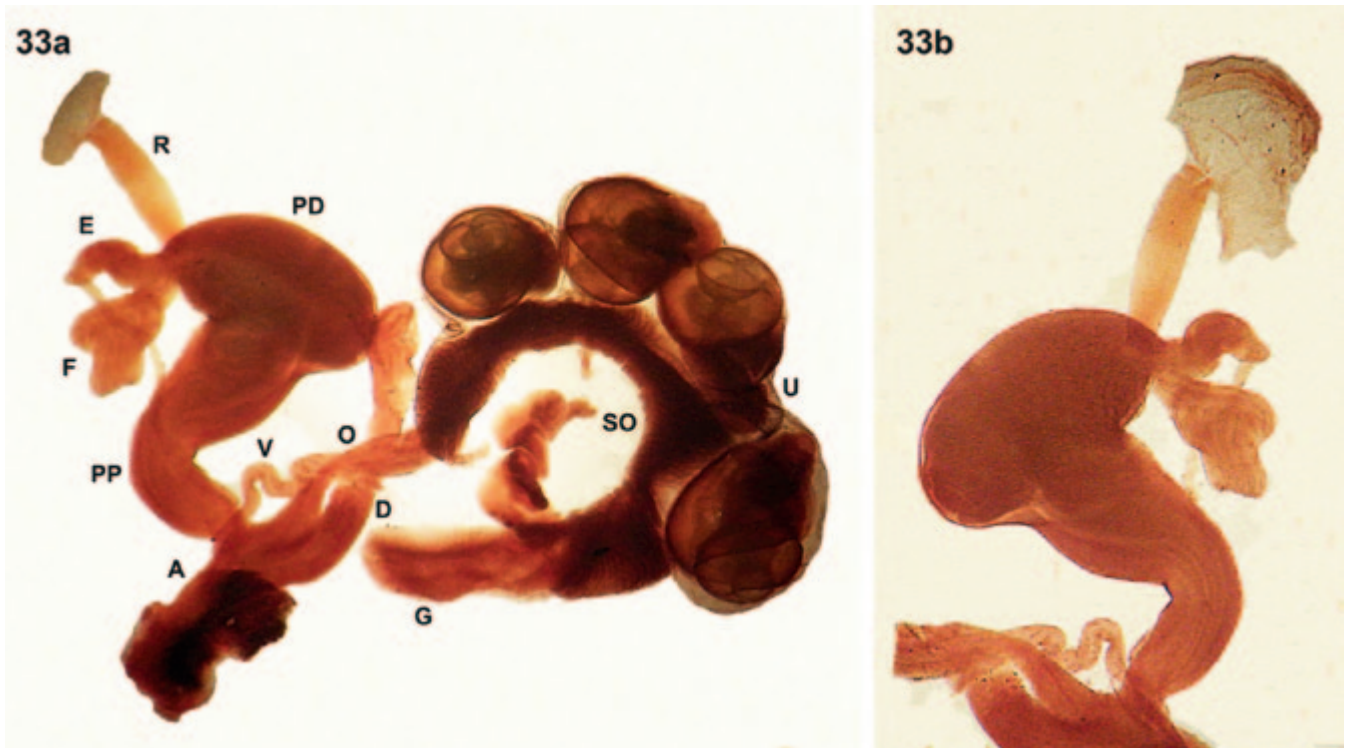


Figure 33 Genital tract (a) of *Glessula nitens* (Gray, 1825), Bandos [7], with a detail of the male part (b); RMNH mol. slide 1173. A – atrium genitale; D – pedunculus; E – epiphallus; F – flagellum; G – glandula albuminifera; O – oviductus; PD – penis distalis; PP – penis proximalis; R – retractor muscle; S – spermatheca; SO – spermoviductus; U – uterus; V – vas deferens.

Notes Two of the four shells found on Bandos are relatively large and two are small. Because the large ones have $\frac{3}{4}$ whorl more than the smaller ones, we consider all shells conspecific.

In the holotype of *C. bensoni*, the aperture seems to be damaged; its whorls are slightly more flattened than in the four shells that are reported here. Its dimensions, H. 4.6mm, are close to those of our material, with the smallest shell 3.5×1.1mm (4¼ whorls) and the largest one 5.5×1.4mm.

Superfamily Streptaxoidea Gray, 1860
Family Streptaxidae Gray, 1860
Genus *Gulella* L. Pfeiffer, 1856

Gulella (Huttonella) bicolor (Hutton, 1834) (Figs 30–31)

Pupa bicolor Hutton, 1834: 86, 93.

Gulella bicolor; Naggs, 1989: 165. Naggs & Raheem, 2000: 102, fig. 130a, b.

Gulella (Huttonella) bicolor; Brook, 2010: 192. Rowson & Herbert, 2016: 82.

Maldivian records Addu [1–4], Hadhdhunmathee [6], North Ari [11], North Malé [7, 8, 9b, 10], North Nilandhe [14, 15], South Ari [18], South Maalhosmadulu [20c], South Malé [21].

Range A well-known invasive species that is widespread in Asia, Africa and elsewhere in tropical areas. Its precise native range is unknown. The horticultural industry may have increased its distribution (Cowie *et al.*, 2008).

Shell Subcylindrical, with 6¼–7½ whorls; the final two to three whorls often not increasing in breadth anymore. Protoconch glossy. Apical whorls more convex than the more basal ones; whitish and transparent when fresh, with a sculpture of vague growth lines and prominent, radially elongated but short, sutural papillae, which continue as riblets only on the final half of the body whorl.

Aperture with a conspicuous parieto-palatal sinus, which is bordered by a short, straight, protruding parietalis and an equally long palatalis with a slightly concave rim; both lamellae contact the apertural border in front. The palatalis

is not a solid lamella; it corresponds with a very prominent indentation on the final quarter of the body whorl. Shortly behind the strongly thickened and reflexed, ring-like apertural lip, there is a small roundish basal denticle; deeper inside still, the prominent, close to vertical, slightly curved columellaris is about as long and prominent as the parietalis and palatalis.

Rather variable in measurements ($n > 50$): B 1.2–1.9mm; H 3.9–6.4.

Molecular data For specimens of three atolls COI sequences were acquired. The sequences for the Addu Atoll, Gan [1] and the South Ari Atoll, Vilamendhoo [18], are nearly identical (99.8%), but the COI for the North Malé Atoll, Eriyadu [8], differs by c. 8%. A specimen from Sri Lanka (Rowson *et al.*, 2011: GenBank HQ328167) is very similar (99%) to the latter.

GenBank accession numbers: MH626427, Gan [1]; MH626425, Vilamendhoo [18]; MH626426, Eriyadu [8].

Notes See the notes with *Leptopomoides halophilus*.

Superfamily Succineoidea Beck, 1837
Family Succineidae Beck, 1837;
Genus *Succinea* Draparnaud, 1801

The generic assignment of the Succineidae is impossible on the basis of only shell characters. The subfamily, either Succineinae Beck, 1837, or Catinellinae Odhner, 1950, is equally uncertain.

Succinea ceylanica L. Pfeiffer, 1855 (Figs 9–10)

Succinea ceylanica L. Pfeiffer, 1855: 298. Naggs & Raheem, 2000: 131, fig. 156a, b.

Succinea vitrea; Smith, 1902: 142. Not L. Pfeiffer, 1855. Gude, 1914: 455. Raheem *et al.*, 2014: 58, 179 fig. 32F (lectotype), 180 fig. 33A (paralectotype).

Maldivian records Addu [3], North Malé [7–10], North Maalhosmadulu [12], North Nilandhe [14, 15], South Ari [18], South Maalhosmadulu Atoll [20c], South Malé [21], Laccadive Islands [22].

Range Hitherto considered endemic to Sri Lanka. Taking into account that the identification is poorly-based, the actual range is equally uncertain.

Shell Body whorl very large; the aperture measuring c. 65% of the total shell height. Spire very short,

measuring 8–11% of the total height. With up to $2\frac{3}{4}$ convex whorls; light yellowish brown, densely covered with partially rather coarse growth lines. The largest shell (Addu Atoll, Hithadhoo; $n > 50$) is 9.5mm high and 5.8mm broad.

Molecular data No specimens for dissection were available, but dry tissue from inside a shell could be used for a molecular analysis. The resulting COI sequence was compared with a dataset on worldwide Succineidae by Brenden Holland, who found that the 'closest match is to *modesta/manuana* from the S. Pacific (Samoa & Marquesas)', being 'not very close' however (pers. comm., May 12, 2010). We found a maximum sequence identity of 87%. See also Rundell *et al.* (2004: 250, 251, figs 3,4, clade C). The generic assignment of these species is unclear. The Maldivian succineid is provisionally classified in *Succinea*.

GenBank accession number: MH626446.

Notes Gude (1914: 455), who studied the specimens collected by the Stanley Gardiner Expedition in the British Museum, accepted Smith's identification as *S. vitrea* for the Maldivian shells, which are supposed to "belong to a rather slender form, pale greenish corneous, and almost transparent". Pfeiffer (1855: 298) indicated a shell height of 12mm for *S. vitrea* from Calcutta, and only 7.5mm for *S. ceylanica* from Sri Lanka. According to a figure published by Raheem *et al.* (2014: fig. 32F), the measurements of the lectotype of *S. vitrea* are: H=11.6mm, B=6.6mm, spire=1.4mm (= 8% of H), AH=7.0mm (= 61% of H). A paralectotype of *S. vitrea* (Raheem *et al.*, 2014: fig. 33A) measures: H=10.6mm, B=8.4mm, spire=0.85mm (= 8% of H), AH=7.1mm (= 67% of H). Two figures of *S. ceylanica* from Sri Lanka (Naggs & Raheem, 2000: fig. 156a, b) show shells with the following measurements: H=6.2mm, B=3.7mm, spire=0.6mm, AH=4.0mm, and H=10.5mm, B=5.8mm, spire=1.65mm, AH=5.8mm. The largest *Succinea* shell from the Maldives measures 9.5×5.8mm, but nearly all other specimens are (much) smaller. In a sample of 66 shells from the Ari Atoll, Vilamendhoo, for example, the largest shell is only 8.7mm high. The data in the literature do not allow to differentiate between *Succinea vitrea* and *S. ceylanica* in shape. The many (> 100) *Succinea* shells from various islands of the Maldives that are at our disposal are as small as *S. ceylanica*.

Superfamily Pupilloidea Turton, 1831

The subdivision of this superfamily is still largely unclear (Hausdorf, 2007: 1481).

Family Pupillidae Turton, 1831
Genus *Pupoides* L. Pfeiffer, 1854

Pupoides coenopictus (Hutton, 1834) (Figs 21–22)

Pupa coenopicta Hutton, 1834: 85.

Pupoides coenopictus; Naggs & Raheem, 2000: 1, fig. 2. Raheem *et al.*, 2014: 61, 182 figs C (lectotype), D, E (paralectotypes). Ali & Hausdorf, 2017: 2, figs 3–4.

Maldivian record North Nilande [15].

Range Most recently, Ali & Hausdorf (2017: 3) summarised the wide range of this species, which is known from arid regions of the Cape Verde Islands and Africa, including Egypt, eastwards to India and Sri Lanka. According to Mordan *et al.* (2003: 4) it 'has been introduced into many other parts of the tropics'.

Shell Slender conical with slightly convex sides, light brown, with 5 convex whorls with growth lines only. Apertural lip broadly reflected and flattened; interrupted by a thin callus at the parietal side, with a small angular knob. Umbilicus very narrow. Measurements (n=2): H 4.6mm; B 2.3mm.

Family Achatinellidae Gulick, 1873
Subfamily Auriculellinae Odhner, 1921
Genus *Elasmias* Pilsbry, 1910

Elasmias manilense (Dohrn, 1863) (Figs 11–13)

Tornatellina manilensis Dohrn, 1863: 160.

Tornatellina natunensis Smith, 1894: 458, pl. 16 fig. 7.

Elasmias manilense; Solem, 1988: 469, figs 14, 19.

Maldivian records North Ari [11], North Nilandhe [14, 16], South Ari [18], South Malé [21].

Range Overlooking the Maldivian record by Smith (1902: 144), Solem (1988: 470) reported this species from Australia, the Philippines, Java, and Papua, Port Moresby. It is not known from Sri Lanka.

Shell Shell elongated ovoid, with moderately convex sides; shell height is 7/4 its breadth (n=3). Protoconch finely pitted on top, changing into a wrinkly sculpture of spiral and radial lines. Teleoconch with less prominent, dense, spiral striae and coarser, irregular growth lines

Aperture with a regularly curved, palatal border, which is neither thickened nor reflected and gradually passes into the basal border; the latter reaches further than the columellar axis before it passes with a blunt angle into the lamella-like, thickened, columellar border, which is not connected to the parietal side of the aperture, but continues inside the shell as a low columellar lamella. The prominent parietalis is hardly 1/2 whorl long; it is also developed in juvenile shells (Fig. 13), so that, apparently, while growing in front it is dissolved at its inner end. Umbilicus closed. Broadest shell (apical part missing): 2.0mm. Corresponding height (based on H=7/4B): 3.5mm.

Notes According to Smith (1902: 144), the form from the Natuna Islands cannot be distinguished from the species described by Dohrn (1863).

Family Cerastidae Wenz, 1923

See Mordan (1992) for an analysis of the morphology and the phylogeny of the 'Cerastinae'.

Genus *Rachis* Albers, 1850

Rachis punctata (Anton, 1839) (Fig. 23)

Bulimus punctatus Anton, 1839: 42.

Rachis punctata; Mordan, 1992: 13, fig. 21A

Rachis punctatus; Naggs & Raheem, 2000: 7, 8, fig. 11a, b. Mordan *et al.*, 2003: 4. Raheem *et al.*, 2014: 68, 186 fig. A.

Maldivian records Addu [1, 3], North Malé [7, 8, 9b, 10], South Maalhosmadulu [13, 19, 20, 21]. North Nilandhe [14–16], North Maalhosmadulu [12a, 13], South Maalhosmadulu [20c], Laccadive Islands [21].

Range Raheem *et al.* (2014: 68) report this species from India and Sri Lanka, the Laccadive Islands, and East and West Africa.

Shell Slender conical, apart from the apical part with straight sides; up to 6 1/2 moderately convex whorls. Initial half protoconch whorl blackish

brown, following whorls light yellowish brown with irregular, darker radial banding, numerous dark dots and a narrow, prominent, spiral band shortly below the periphery. Apertural edge neither clearly thickened nor reflected. Umbilicus very narrowly open. Largest shell (n=28): 15.2 × 7.1mm.

Genital tract (Fig. 32) Penis with a very prominent caecum; its proximal half covered by a sheath. Penial appendix long, with four parts that can only vaguely be distinguished at the outside; its proximal quarter (1) is about as broad as the penis, the adjoining part (2) is shorter and equally broad, the longest part (3) is the narrowest and the large, elongated bursa (4), is the broadest. The structure of the lumen, made visible in a transparent specimen, can also be used to distinguish the four parts; in between (1) and (2) there is a papilla, whereas part (3) has a narrower lumen than the other parts. Epiphallus short and broad, with some septa in the lumen, which can externally be recognised. The two retractor muscles, inserting near the papilla of the penial appendix and near the proximal end of the epiphallus, are nearly entirely separate. Both vagina and oviduct nearly twice as broad as the penis and about equally long. Pedunculus as long as the penis and slightly broader, with a large, oval bursa.

Molecular data For specimens from two localities in the North Malé atoll COI sequences were acquired, which are identical. The data did not enable a better insight regarding the higher systematics of the Cerastidae.

GenBank accession numbers: MH626437, Eriyadu [8]; MH626438, Hulhule [9b].

Notes According to Gude (1914: 277), some shells from the South Mahlos Atoll have an "indication of a second band" below the usual infra-peripheral band

Family Gastrocoptidae Pilsbry, 1918
Genus *Gastrocopta* Wollaston, 1878

Gastrocopta servilis (Gould, 1843) (Fig. 19)

Pupa servilis Gould, 1843: 356, pl. 16 fig. 14.
Gastrocopta servilis; Pilsbry, 1916: 70, pl. 14 figs 4–7.
Wu *et al.*, 2007: 147 fig. 13, 148. Brook, 2010: 186.

Maldivian record South Ari [17].

Range Pilsbry (1916: 72) still considered *G. servilis* a common Antillean species and (1917: 127) dealt with *Pupa lienardiana* Crosse, 1873, *P. seignaciana* Crosse & P. Fischer, 1879, *P. tripunctum* Morelet, 1882, and *P. microscopia* von Martens, 1898, from the Indian Ocean as separate species, though not unreservedly because of the conspicuous similarity with *G. servilis*. Later on, *G. servilis* was considered to be very widespread on the Pacific islands, in Indonesia, the Philippines and Australia (Solem, 1988: 483; Brook, 2010: 186). We doubtfully accept the record for the South China Sea (Wu *et al.*, 2007), since the figured shell has very convex whorls, whereas the apertural denticles cannot be seen. The horticultural industry may have increased its distribution, as has been shown for Hawaii (Cowie *et al.*, 2008). The species has not been reported from islands in the Indian Ocean before.

Shell Spindle-shaped, with 4½–5 convex whorls. Teleoconch with obsolete growth lines and a few more prominent ones. Aperture obliquely oval, broadly interrupted at the parietal side; with a prominent, twisted parieto-angularis, a prominent columellaris, and three denticles on the outer lip, of which the middle one is the largest. Measurements (n=11): H 2.1–2.4mm; B 1.0–1.1mm.

Notes The single record refers to 11 bleached specimens found among marine shells.

Gastrocopta mimula (Benson, 1853) (Fig. 20)

Pupa mimula Benson, 1853: 95.

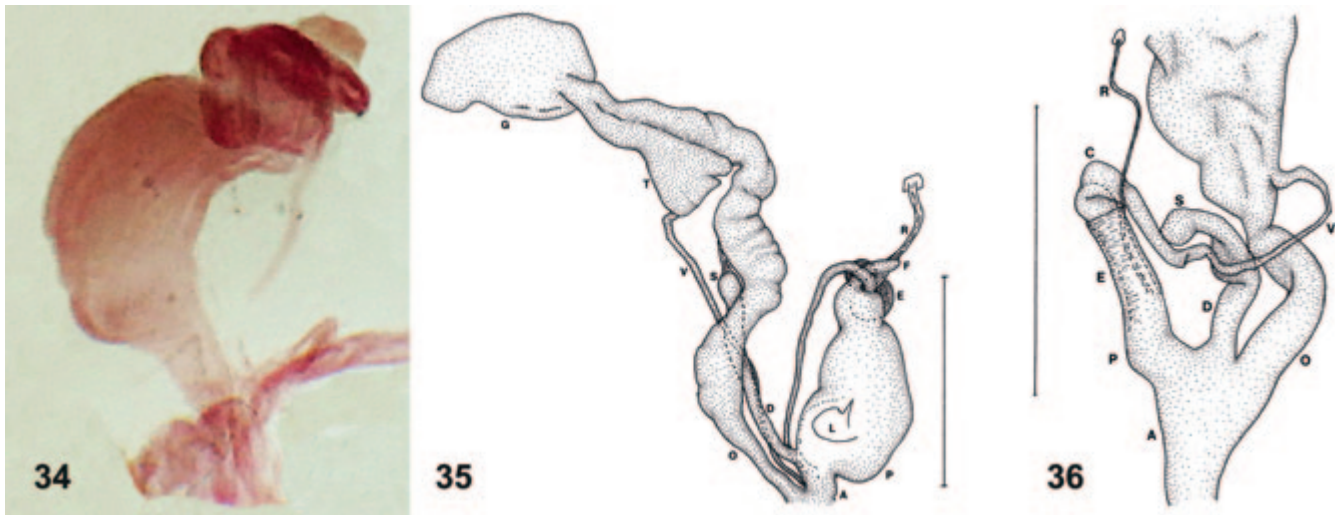
Gastrocopta mimula; Pilsbry, 1917: 134, pl. 23 figs 16, 17.

Gastrocopta (*Gastrocopta*) *mimula*; Naggs & Raheem, 2000: 2, fig. 3.

Maldivian records Addu [1, 3, 4], North Malé [7–10], South Ari [18], South Maalhosmadulu Atoll [20c], South Malé [21].

Range Hitherto considered endemic to Sri Lanka.

Shell Spindle-shaped, with 4½–4¾ very convex whorls that are separated by a deeply incised suture. Teleoconch with coarse growth lines. Aperture roundish with a nearly continuous edge; with a prominent, twisted parieto-angularis, a



Figures 34–36 Euconulidae, genitalia. A – atrium genitale; C – caecum; D – pedunculus; E – epiphallus, covered by a sheath in *Sitalinopsis maldivensis*; F – flagellum; G – glandula albuminifera; L – dart-like structure; O – oviductus; P – penis; R – retractor muscles; S – spermatheca; SO – spermoviductus; T – prostata; V – vas deferens. **34** *Liardetia (Belopygmaeus) doliolum* (L. Pfeiffer, 1846), Biyadhoo [21], RMNH mol. slide 1171; **35** *Liardetia (Liardetia) samoensis* (Mousson, 1865), Vilamendhoo [18], RMNH mol. slide 1154; **36** *Sitalinopsis maldivensis* spec. nov., Reethi [20c], RMNH mol. slide 1153.

prominent columellaris, and three denticles on the outer lip, of which the middle one is the largest.

Notes Pilsbry (1917: 135) considered this species ‘somewhat related to *G. klunzingeri*’, probably because of the very convex whorls with irregularly spaced rather coarse axial striae.

Family Valloniidae Morse, 1864
Genus *Pupisoma* Stoliczka, 1873
Subgenus *Ptychopatula* Pilsbry, 1889

We follow Bouchet *et al.* (2017: 364) in classifying *Pupisoma* provisionally in Valloniidae.

Shells of *Pupisoma* species can easily be overlooked or confused with juvenile specimens of other species. Two species of this genus are known from Sri Lanka, both of which with globular shells that are similar to those of the Maldivian species, but without spiral lines (Pilsbry, 1920: 22) and for that reason classified in the nominate subgenus. The shells differ additionally by being imperforate.

Pupisoma (Ptychopatula) circumlitum Hedley, 1897 (Fig. 15)

Pupisoma circumlitum Hedley, 1897: 44, pl. 11 figs 1–3 (= Pilsbry, 1920: pl. 3 figs 14–16); Vermeulen & Whitten, 1998: 82, 145.

Pupisoma (Ptychopatula) circumlitum; Gittenberger & van Bruggen, 2013: 245, fig. 7.

Maldivian record North Ari [11].

Range Known from Tanzania (the islet of Misali off Pemba island, Zanzibar), peninsular Malaysia, Indonesia, and Australia (Gittenberger & van Bruggen, 2013: 247).

Shell (n=10) Similar to the next species, but smaller, more depressed, and with a wider umbilicus, that measures c. 1/10 of the total shell breadth. All specimens from the North Ari Atoll are more or less seriously damaged or (very) juvenile. Therefore, reliable measurements of Maldivian shells cannot be provided.

Notes See Gittenberger & van Bruggen (2013: 245–248) for additional data.

Pupisoma (Ptychopatula) dioscoricola (C.B. Adams, 1845) (Fig. 16)

Helix dioscoricola C.B. Adams, 1845: 16.

Helix orcula Benson, 1850: 251.

Pupisoma orcula; Pilsbry, 1920: 31, pl. 2 figs 1–5.

Adam, 1957: 24, fig. 18. Brook, 2010: 188.

Pupisoma (Ptychopatula) dioscoricola; Hausdorf, 2007: 1483, figs 1, 2, 6.

Maldivian records Addu [2–4], North Malé [7, 8, 10], North Nilandhe [14, 15], South Ari [18], South Maalhosmadulu [20c], South Malé [21].

Range Circumtropical when *P. dioscoricola* and *P. orcula* are considered synonyms (Hausdorf, 2007).

Shell Shell globose-conical, yellowish brown, translucent when fresh, with up to c. 3 very convex whorls that are separated by a deeply incised suture; looking juvenile to the unexperienced eye. About as high as broad. Aperture without teeth, with a broadly reflected columellar border, which partly to nearly completely covers the narrow umbilicus; outer lip neither thickened nor reflected. Protoconch granular. Teleoconch with irregular growth-lines and relatively prominent spiral lines. Breadth and height 1.9mm or less.

Molecular data A COI sequence of a specimen from the North Malé Atoll, Eriyadu [8], was acquired, but did not enable a better insight regarding the higher systematics of the Pupilloidea.

GenBank accession number: MH626436.

Notes Gude (1914: 34) mentioned that “*P. orcula*” is found on both native and cultivated shrubs and trees, and may have reached its unusually large range by being carried with plants. Hausdorf (2007: 1489), while hesitantly (‘genetic studies’ can always contradict a synonymy) synonymising *Helix dioscoricola* and *H. orcula*, considered this a widespread, i.e. circumtropical species, ‘most frequent in lowland forest .. up to 2100m altitude’. E.G. found live animals of this species together with *Insulipupa mooreana* attached to large leaves below the bushes growing only a few meters from the sandy beach. This observation suggests that this species might expand its range in an archipelago attached to (floating) objects like leaves or twigs.

Family Vertiginidae Fitzinger, 1833

The subfamilies Vertigininae Fitzinger, 1833, and Nesopupinae Steenberg, 1925, are not supported in a molecular phylogeny analysis (Gittenberger & van Bruggen, 2013: 240). The following vertiginid species could be classified into the latter.

Genus *Insulipupa* Pilsbry & Cooke, 1920

Regarding the generic status, see Gittenberger & van Bruggen, 2013: 241.

Insulipupa mooreana (E.A. Smith, 1894) (Fig. 17)

Pupa mooreana E.A. Smith, 1894: 97, pl. 7 fig. 25.
Gastrocopta mooreana; Pilsbry, 1917: 160, pl. 30 fig. 4; 1921: 230, pl. 24 figs 6, 7.
Nesopupa mooreana; Solem, 1988: 477, 574 figs 33–37.

Maldivian records Addu [1–3], North Ari [11], North Malé [7–10], North Nilandhe [14,15], South Ari [18], South Maalhosmadulu [20c], South Malé [21].

Range ‘*Nesopupa*’ *mooreana* is considered endemic to Australia by Solem (1988: 478). It is not known from Sri Lanka for instance. Its actual range is unclear.

Shell Shell subcylindrical to more or less elongated ovoid. Proto- and entire teleoconch pitted; teleoconch additionally with few wrinkled vague growth lines. Aperture with five teeth. Parietalis lamellar, most prominent; angularis straight, very oblique, more or less obsolete and hardly or not connected to the apertural border; columellaris straight, about half as high as the parietalis; two short palatales, the upper one of which is the least prominent and more denticle-like. Measurements (n > 50): H 1.8–2.1mm; B 1.0–1.2mm

Molecular data Specimens from three localities were used for sequencing. Two COI sequences of animals from the South Ari Atoll, Vilamendhoo [18], and one from the Addu Atoll, Gan [1], are similar (sequence divergence ~2.2%), but differ clearly from that of the North Malé Atoll, Lankanfinolhu [10] (sequence divergence ~ 10.0%). This cannot be considered a direct consequence of geographical distances because the nearest localities are not the most similar ones in COI sequences. The localities [10] and [18] are only c. 100km apart, whereas [1] is situated c. 500km away from [10] and [18].

GenBank accession numbers: MH626428, 626429, South Ari Atoll, Vilamendhoo [18]; MH626430, North Malé Atoll, Lankanfinolhu [10]; MH626431, Addu Atoll, Gan [1].

Notes The shells are clearly different from *Nesopupa (Indopupa) cinghalensis* (Gude, 1914) in microsculpture and general shape (see Naggs & Raheem, 2000: 2, fig. 4). They are most similar to the specimens figured as *Nesopupa mooreana* by Solem (1988: 574 figs 33–37). *Insulipupa malayana* (Issel, 1874) differs by a more prominent angularis and less prominent palatales (Gittenberger & van Bruggen, 2013: 241, 242 fig. 4a).

Only a thorough revision of the genus *Nesopupa* and the most closely related genera can bring more clarity here.

Some live snails were found attached to large leaves only a few meters from the beach (see also *Pupisoma (Ptychopatalula) dioscoricola*).

Genus *Nesopupa* Pilsbry, 1900

Subgenus *Indopupa* Pilsbry & Cooke, 1920

Nesopupa (Indopupa) spec. (Fig. 18)

Maldivian record South Maalhosmadulu [20c].

Shell Ovoid, light brown, with 4¼ convex whorls; protoconch granular, teleoconch with prominent, dense radial riblets and faint spiral striae. Aperture triangular with rounded corners; with (1) a very prominent parietalis and a straight, low angularis, (2) a prominent columellaris, and (3) two moderately prominent palatal lamellae, the upper one of which corresponding with an indentation of the shell wall. Palatal border of the aperture not regularly curved, i.e. protruding above the middle (side view). Umbilicus open. Measurements (n=1): H 1.5mm, B 0.9mm.

Notes Only a single specimen is known. The shell looks fresh, but there are no remains of the soft parts of the animal inside. The species is provisionally classified with *Nesopupa (Indopupa)*. *Nesopupa (Indopupa) cinghalensis* (Gude, 1914), described by Gude (1914: 286, fig. 103) as *Pupilla cinghalensis* after a single shell from Sri Lanka is at least similar in size and the ovoid shape. This is not obvious from the original drawing by Gude, showing a cylindrical shell, but see Naggs & Raheem (2000: 2, fig. 4).

Superfamily Trochomorpoidea Mörch, 1864

Family Euconulidae H.B. Baker, 1928

Subfamily Microcystinae Thiele, 1931

In agreement with Baker (1938), Bouchet *et al.* (2017: 365) accepted Euconulinae H.B. Baker,

1928, and Microcystinae Thiele, 1931, as subfamilies. This view is neither supported nor contradicted by our preliminary molecular data.

Genus *Microcystina* Mörch, 1872

Microcystina spec. (Figs 37, 39, 49)

Maldivian records Addu [3, 4], North Ari [11], North Malé [7, 8], North Nilandhe [14, 15], South Ari [18], South Maalhosmadulu [20c], South Malé [21].

Shell Shell discoid, with up to 3½ whorls, light yellowish brown and transparent. Whorls moderately convex; in fully grown shells, the final part of the suture, i.e. bordering the body whorl, may be accompanied by a narrow concave zone so that the suture itself is very shallow (Fig. 37). Aperture regularly elliptical, apart from the broad parietal side, H/B c. ¾. Umbilicus gradually widening, measuring c. 1/12 B, with an umbilical protrusion. Initial part of the protoconch with c. 20 spiral rows of micro-pits, which become granular spiral lines further on and on the teleoconch (Fig. 49). Largest shell (n=50): 3½ whorls, 1.6×0.9mm.

Molecular data For a specimen of the North Malé Atoll, Hulhule [9b], a COI sequence was acquired. The most similar sequence in GenBank (MH626433) is that of *Microcystina rowsoni* Gittenberger & van Bruggen, 2013, from the islet of Misali off Pemba island, Zanzibar, Tanzania, differing 5.8%.

GenBank accession numbers: MH626434, Hulhule [9b].

Notes This species recalls several *Microcystina* species of the Indo-Malayan region, including the Pacific islands. Its generic classification is confirmed by the molecular data. It is beyond the scope of this article to deal with all these, incompletely described (without SEM data) nominal taxa. Geographically close and similar in shape and colour is for example '*Macrochlamys? atoma* Blanford, 1905', which was described from the banks of the Gadavari river and is considered endemic to India by Raheem *et al.* (2014: 104). The four syntypes that are illustrated by Raheem *et al.* (2014: 104, 213 fig. 66B), are slightly larger than the shells from the Maldives, measuring 1.5–1.65mm in breadth, and have an umbilicus that is only 1/14 B in diameter. There may be

additional differences but the four syntypes are mounted together on a sheet of paper with either the dorsal or the ventral surface uppermost. Therefore, a frontal view and data on the micro-sculpture are not available.

Two *Microcystina* species are known from Sri Lanka, viz. *M. bintennensis* Godwin-Austen, 1899, and *M. lita* Sykes, 1898, both of which are considerably larger than the Maldivian species.

Genus *Liardetia* Gude, 1913

The three *Liardetia* species that are known from the Maldivian Islands have similar low-conical shells with a more or less conspicuously angular periphery in juvenile specimens; the periphery is more rounded in fully grown shells. We refrain from a subgeneric classification, as is used by Baker (1938) and Zilch (1959) because it can only be based on the genital morphology, which is unknown for many species that are conchologically similar. Vermeulen *et al.* (2015) lumped *Liardetia* and *Kaliella*. Here we use the generic name *Kaliella* for species with a more or less high conical shell and a sharp peripheral angle or keel.

Liardetia doliolum can be recognised most easily by its characteristic sculpture, but the other *Liardetia* species cannot always be recognised with certainty from the data in the literature.

1a. Spire with prominent radial riblets (Fig. 52); basal spiral lines obsolete (Fig. 42): *Liardetia doliolum*.

1b. Spire with fine radial and spiral striae: 2.

2a. Shell glossy, protoconch whorls less quickly increasing in breadth (Fig. 58); basal spiral lines much more widely spaced than their own width (Fig. 48): *Liardetia scandens*.

2b. Shell silky, protoconch whorls more quickly increasing in breadth, flattened (Fig. 55); basal spiral lines very dense, hardly more widely spaced than their own width (Fig. 45): *Liardetia samoensis*.

Liardetia doliolum (L. Pfeiffer, 1846) (Figs 40, 42, 43, 46, 52)

Helix doliolum L. Pfeiffer, 1846a: 41.

Liardetia (Belopygmaeus) doliolum; H.B. Baker, 1938: 27, pl. 3 figs 6–8, pl. 9 fig. 9, pl. 14 fig. 9. Solem, 1988: 549, 597 fig. 175, 599 figs 181, 182.

Liardetia doliolum; Hoong, 1995: 102.

Kaliella doliolum; Vermeulen *et al.*, 2015: 102 fig. 74, 105. Phung *et al.*, 2018: 5.

Maldivian records North Malé [7], North Nilandhe [14], South Malé [21].

Range Known from Vietnam, Indonesia, Philippines, Australia and several Pacific islands (Solem, 1988: 550; Vermeulen *et al.*, 2015: 106). Singapore (Hoong, 1995: 102), peninsular Malaysia (Phung *et al.*, 2018: 5) and the Maldives (this article) are the westernmost records. Its precise native range is unknown. The horticultural industry may have increased its distribution (Cowie *et al.*, 2008).

Shell Depressed conical, with a blunt peripheral angle, light brown. Proto- and teleoconch with very prominent radial riblets and nearly obsolete, densely spaced spiral lines. The riblets are increasingly less prominent on the shell base towards the umbilicus; in fully grown specimens, they may be reduced on about the final quarter of the shell. The aperture is relatively lower than in *L. samoensis* and *L. scandens* (AH/AW < 0.6). There is a small protrusion of the columellar edge towards the umbilicus. Largest shell (n=50): 4½ whorls, 2.5×3.2mm.

Genital tract (n=1) A specimen with 3¼ whorls was dissected. The male parts were left in situ, so that the precise structure of the epiphallus remains unclear. A comparison with the impressively detailed figure of the genitals of this species as published by Baker (1938: pl. 3 fig. 8) supports the identification of this species.

Notes Hoong (1995: 103) mentioned that the snails were 'most often attached to decaying leaves of *Plumeria* and *Acacia*.'

Liardetia samoensis (Mousson, 1865) (Figs 35, 38, 41, 45, 55)

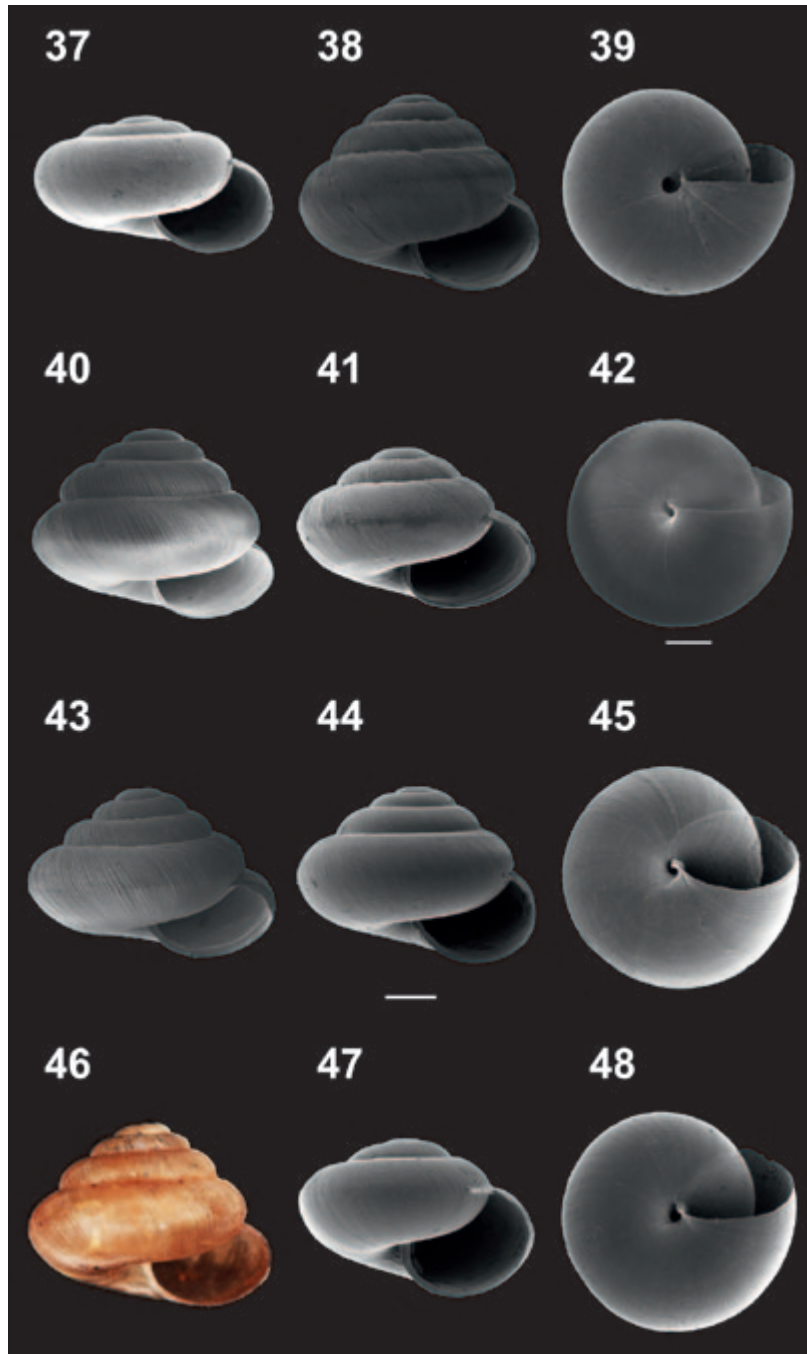
Helix striolata Pease, 1860: 439. Not C. Pfeiffer, 1828: 28.

Nanina samoensis Mousson, 1865: 165.

Sitala vagata E.A. Smith, 1902: 142 ("Minikoi, Laccadive Islands").

Kaliella vagata E.A. Smith, 1902: 142 ("Minikoi, Laccadive Islands"). Blanford & Godwin-Austen, 1908: 264.

Liardetia (Liardetia) striolata; H.B. Baker, 1938: 22, pl. 3 figs 4, 5; pl. 9 figs 5, 6; pl. 14 fig. 12.



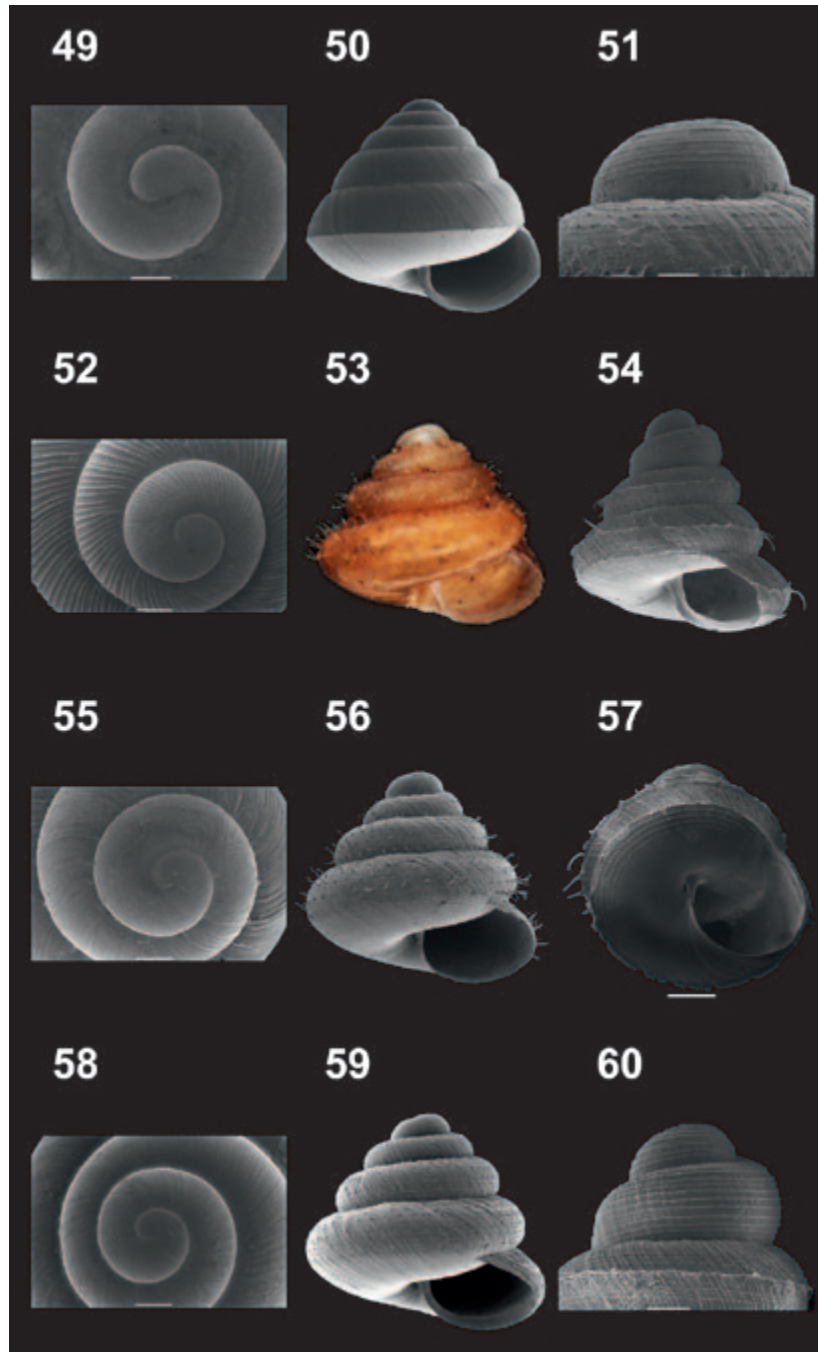
Figures 37–48 Euconulidae. **37, 39** *Microcystina* spec., Vilamendhoo [18]. **37** B=1.36mm; **39** B=1.35mm. **38, 41, 45** *Liardetia samoensis* (Mousson, 1865), Vilamendhoo [18]. **38** B=2.6mm; **41** B=2.1; **45** B=2.75. **40, 42, 43, 46** *Liardetia doliolum* (L. Pfeiffer, 1846) **40, 42, 43, 46** *Liardetia doliolum* (L. Pfeiffer, 1846). **40** Bandos [7], B=2.95mm; **42, 43** Filitheyo [14], **42** B=2.5mm, **43** B=2.6mm; **46** Biyadhoo [21], H=3.1mm. **44, 47, 48** *Liardetia scandens* (Cox, 1871), Vilamendhoo [18]. **44** B=2.33mm; **47** 1.6mm; **48** 2.4mm.

Liardetia samoensis; Hoong, 1995: 103.

Liardetia (Liardetia) samoensis; Brook, 2010: 206.

Maldivian records Addu [1, 2, 4], North Malé [7, 8, 10], North Nilandhe [14], South Ari [18], South Maalhosmadulu [20c].

Range Widespread on islands in the Pacific Ocean (Baker, 1938: 23; Solem, 1978: 43; Brook, 2010: 206). Additionally in Singapore (Hoong, 1995: 103) and on islands of the Maldives (this article) and Laccadives (E.A. Smith, 1902: 142) in the Indian Ocean.



Figures 49–60 Euconulidae. **49** *Microcystina* spec., Vilamendhoo [18], scale bar 0.1mm. **50** *Kaliella barrakporensis* (Pfeiffer, 1853), Bandos [7], B=2.85mm. **51, 53, 56, 59** *Sitalinopsis maldivensis* spec. nov., **51, 56** (holotype), **59** Vilamendhoo [18]; **53** Biyadhoo [21]; **51** apex, scale bar 0.1mm; **53, 56** shells with hairs, **53** H=1.6mm, **56** H=1.75mm, **59** shell with hair-scars, H=1.79mm. **52** *Liardetia doliolum* (L. Pfeiffer, 1846), Filitheyo [14], apex, scale bar 0.1mm. **54, 57, 60** *Sitalinopsis conulus* (Blanford, 1865). Malaysia, Sabah, Interior Province, Simbaluyon limestone hill, 4 43 15.3 116 34 13.3; 338m alt.; M. Schilthuizen leg., 21–26.v.2011 (RMNH.MOL 333912). **55** *Liardetia samoensis* (Mousson, 1865), Vilamendhoo [18], apex, scale bar 0.1mm. **58** *Liardetia scandens* (Cox, 1871), apex, Vilamendhoo [18], scale bar 0.1mm.

Shell Conical with a more or less conspicuous peripheral angle, light brown with a silky gloss. Protoconch whorls more flattened than in the other Maldivian *Liardetia* species, with numerous,

narrowly spaced spiral lines and more prominent radial riblets. The spiral lines continue on the teleoconch above the periphery, where irregular, about equally strong growth lines form the

radial sculpture; the shell base has conspicuous spiral lines, which are less widely spaced than in *L. scandens*, and a much less conspicuous radial sculpture. The aperture is relatively higher than in *L. doliolum* (AH/AW=c. 0.7). There is a small protrusion of the columellar edge towards the umbilicus. Largest shell (n=50): 4½ whorls, 2.5×3.1mm.

Genital tract (n=1) Genital atrium very short. Penis sack-like, bulbous, inserting next to the pedunculus at a short, elongated part of the atrium, with a large penial dart inside. There is no vagina. The structure of the tortuous epiphallus and its transition to the vas deferens was not entirely clarified. There is a slender, cylindrical flagellum. Pedunculus and spermatheca not differentiated, together forming a slender, elongated tube.

The admirably precise figure of the genital tract of this species published by Baker (1938: pl. 3 fig. 5) agrees very well with our less detailed figure. We did not notice a penial sheath, which is reported by Baker (1938: 24).

Radula (n=1) (Fig. 61) The central tooth can be distinguished by its symmetrical basal plate, which has supportive ridges at both sides. The five lateral teeth are also tricuspid and very similar except for their asymmetrical basal plates, which have a supportive ridge at only one side. The sixth lateral tooth is intermediate in shape, resembling the marginal teeth in shape. Most of the 27 marginal teeth have three cusps, but there are some with four; the teeth near the border of the radula are more irregular, with smaller cusps.

These results are in agreement with Baker's description of the radula of this species (1938: 24).

Molecular data For a specimen from the South Ari Atoll, Vilamendhoo [18], a COI sequence was acquired. It did not enable a better understanding of the phylogenetic relationships of *Liardetia*.

GenBank accession number: MH626432, Vilamendhoo [18].

Notes There have been at least four syntypes of *Sitala* or *Kaliella vagata* in The Natural History Museum, London, glued on a piece of cardboard (NHMUK 1902.4.18.6–9). One of these shells is missing, demonstrating its former presence by

only an imprint in remains of glue, one is broken and loose, whereas two shells are still fixed.

Liardetia scandens (Cox, 1871) (Figs 44, 47, 48, 58)

Helix scandens Cox, 1871: 645.

Kaliella tenuisculpta Möllendorff, 1893: 69.

Liardetia (*Liardetia*) *tenuisculpta*; H.B. Baker, 1938: 25, pl. 2 figs 17, 18; pl. 9 fig. 7.

Liardetia scandens; Solem, 1988: 550, 597 fig. 176, 599 figs 183, 184.

Kaliella scandens; Vermeulen *et al.*, 2015: 101, 102 fig. 72. Phung *et al.*, 2018: 5.

Maldivian records Addu [2, 3, 4], North Malé [8], North Nilandhe [14], South Ari [18].

Range Widespread, from the Pacific and Australia westwards to Indonesia, Malaysia, Vietnam and Thailand (Vermeulen *et al.*, 2015: 104).

Shell Conical with an inconspicuous peripheral angle, smaller than the other Maldivian *Liardetia* species. Darker brown than *L. samoensis* and *L. doliolum*, more glossy, protoconch whorls with c. 15 spiral threads that are separated by broad interspaces, and additionally more irregular, about equally strong radial lines. The spiral sculpture continues on the teleoconch, which has diagnostic, prominent, widely spaced spiral lines on the base. The aperture is relatively higher than in *L. doliolum* (AH/AB=c. 0.7). The umbilical region has hardly any protrusion of the columellar edge towards the umbilicus, which is slightly larger than in the other *Liardetia* species. Largest shell (n=29): 4⅛ whorls, 2.0×2.5mm.

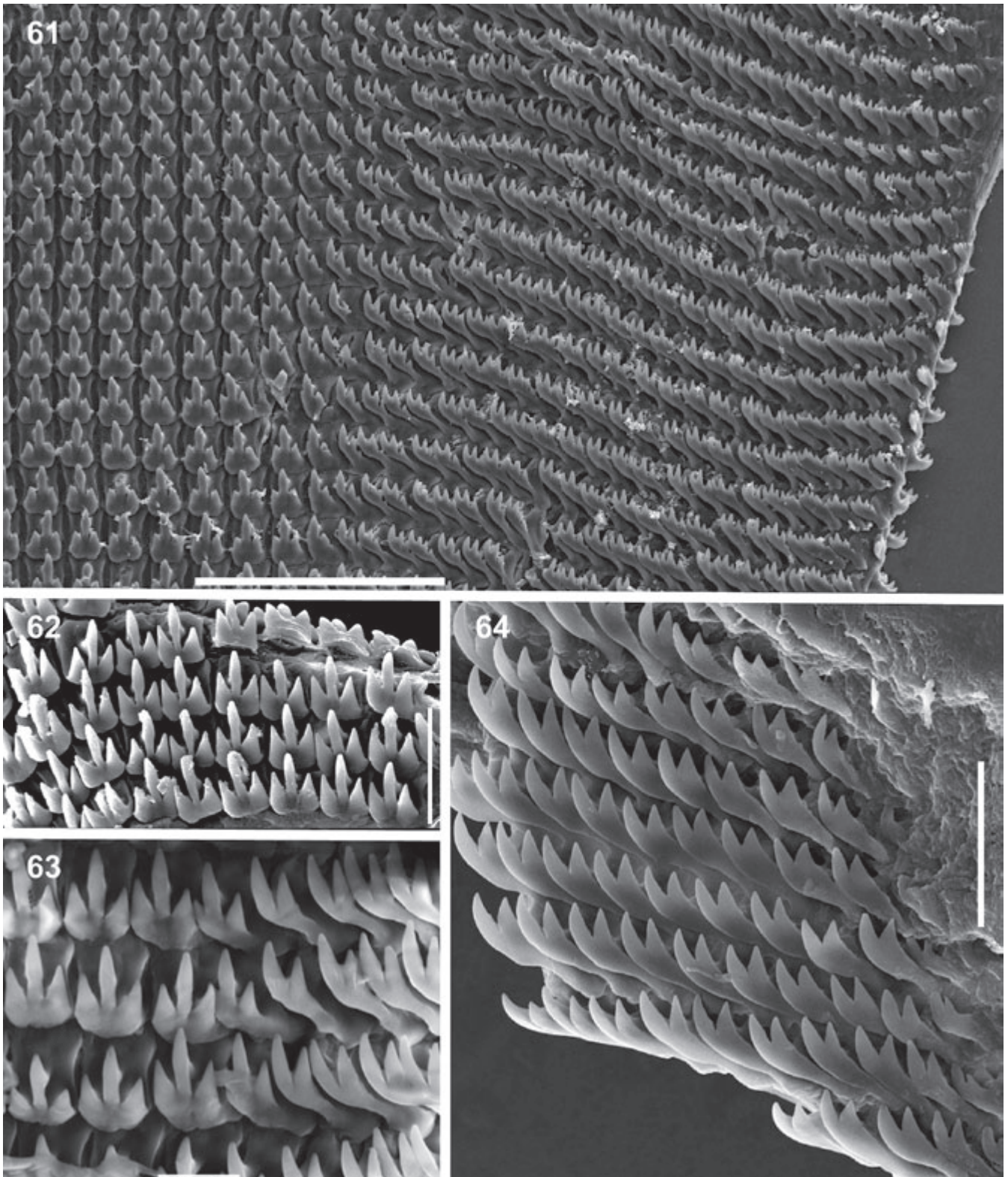
Notes *Liardetia scandens* is not mentioned by Baker (1938). Both Solem (1988: 550) and Vermeulen *et al.* (2015: 101) indicate a maximum shell breadth of 3.6mm for this species. However, Solem (1988: 551) also refers to "two size classes in most collections of *L. scandens*", viz. "2.3–2.6 mm" and 3.0–3.3mm shells"

Genus *Kaliella* Blanford, 1863

Kaliella barrakporensis (Pfeiffer, 1853) (Fig. 50)

Helix barrakporensis Pfeiffer, 1853: 59.

Kaliella barrakporensis; Raheem *et al.*, 2014: 77, 192 fig. 45 B, C (syntypes). Vermeulen *et al.*, 2015: 96, 98 fig. 70. Phung *et al.*, 2018: 5.



Figures 61–64 Radulae. **61** *Liardetia (L.) samoensis* (Mousson, 1865), Vilamendhoo [18], symmetrical central tooth with one lateral at the left and a complete half row at the right side, scale bar 50µm. **62–64** *Sitalinopsis maldivensis* spec. nov., Reethi [20c]. **62** central part of the radula, central tooth with 2 laterals at the left and 5 at the right side, scale bar 10µm; **63** transition between laterals and marginal, scale bar 5µm; **64** border of the radula, with regularly bicuspid marginals, scale bar 10µm.

Maldivian record North Malé [7].

Range Widespread in South Asia where it might be native; also known from other parts of the tropics where it may have been introduced with plants, as in hot-houses in temperate countries (Raheem *et al.*, 2014: 77; Vermeulen *et al.*, 2015: 99).

Shell Conical with slightly convex sides, little broader than high; light corneous brown, with a silky gloss, transparent. Protoconch with inconspicuous radial and spiral lines. Teleoconch above the sharp peripheral ridge with very fine radial lines and little less prominent, equally densely spaced spiral lines; below the periphery with more widely spaced and slightly more prominent spiral threads and an inconspicuous radial sculpture. The spiral sculpture is most clearly seen on the gold-coated shell, but it is too fine to be discernible on the photograph (Fig. 50). Columellar border of the aperture curved towards the narrowly open umbilicus. Largest shell (n=6): 5½ whorls, 3.3×3.1mm.

Notes *Schwammeria rumbangensis* (E.A. Smith, 1895), from Kalimantan, Indonesia, which was found in the Zoo of Vienna, has a very similar shell, so that it might be confused with *K. barrakporensis*. It differs conchologically most clearly by the closed umbilicus and slightly more flattened whorls (Schileyko, 2010).

Genus *Sitalinopsis* Thiele, 1931

Sitalinopsis Thiele, 1931: 612. Type species (monotypy): *S. conulus* (Blanford, 1865) (Figs 54, 57, 60). *Queridomus* Iredale, 1937: 322. Type species (monotypy): *Q. grenvillei* (Brazier, 1876).

Without referring to *Sitalinopsis*, Vermeulen *et al.* (2015: 75) provisionally consider *Queridomus* a junior synonym of *Thysanota* Albers, 1860, whereas *S. conulus* and *S. grenvillei* are regarded as congeneric, as was suggested previously by Solem (1988: 552), and is accepted also here. As a consequence, *Sitalinopsis* is a senior synonym of *Queridomus*. The type species of *Thysanota*, viz. *Helix guerini* L. Pfeiffer, 1842, is characterised by shells that are much larger than in *Queridomus* and *Sitalinopsis* species, differing additionally by the regularly curved, instead of angular, whorls of the spire (Raheem *et al.*, 2014: 189 fig. 42BC;

Zilch, 1959: 220, fig. 781). Furthermore, when *Helix crinigera* Benson, 1850, belongs to *Thysanota* indeed, as is suggested by its shell shape, size and sculpture, the structure of the radulae places *Sitalinopsis* as defined here and *Thysanota* far apart. According to Godwin-Austen (1907: 190, pl. 112 fig. 2), the central tooth and the adjoining ten lateral teeth are unicuspid in *Thysanota crinigera*. In *S. maldivensis* at least the central tooth and the adjoining laterals are prominently tricuspid (Fig. 63).

Solem (1988: 553) apparently planned to report about the radular structures of *Queridomus*, but never did so. He published a detailed description of the genital tract of '*Queridomus*' *grenvillei* (Brazier, 1876), type species of the originally monotypic genus *Queridomus* Iredale, 1937.

The genital tract of the Maldivian species is similar to that of *S. grenvillei*, what supports our interpretation of *Sitalinopsis*.

Our sequence data indicate that *Sitalinopsis* and *Liardetia* are closely related, and can be classified in the same subfamily.

Sitalinopsis maldivensis spec. nov. (Figs 36, 51, 53, 56, 59, 62, 63)

Type locality South Ari Atoll, Vilamendhoo [18].

Type series (paratypes unless stated otherwise) Addu Atoll, Hulhudhoo [4], RMNH340247/16 shells; North Ari Atoll, Kuramathi [11], RMNH340248/1 shell; North Malé Atoll, Lankanfinolhu [10], RMNH340249/1 shell, Bandos [7], RMNH340250/28 shells, Eriyadu [8], RMNH340251/2 shells; North Nilandhe Atoll, Filithayo [14], RMNH340252 /28 shells, Magoodhoo [15], RMNH340253/1 shell; South Ari Atoll, Vilamendhoo [18], RMNH340254/shell, holotype (Fig. 56), RMNH340255/50 shells, RMNH gen. slide 1172; South Maalhosmadulu, Reethi [20c], RMNH340256/39, RMNH gen. slide 1153; South Malé Atoll, Biyadhoo [21], RMNH340257/47 shells.

Range Only known from the Maldivian archipelago, where it is among the most widespread and common species.

Shell Shell conical, about as high as broad. Protoconch with 7–11 prominent spiral ridges, which are much more widely spaced than their

own width, and a faint, irregular radial sculpture. Teleoconch above the periphery densely covered by very oblique, rather coarse, irregular growth lines, much sharper spiral ridges, and four spiral rows of hairs that are up to 1.4mm long, or hair-scars in weathered specimens. Body whorl with c. 10 spiral ridges above the periphery and the same number on the shell base; halfway towards the narrow umbilicus the relatively prominent spiral ridges become obsolete and are replaced by a dense pattern of spiral striae. Below the suture the whorls have a straight zone, followed abapically by a very convex part. Aperture broad and low, the columellar edge curved towards the narrow umbilicus; with a prominently thickened columellar and basal border in only a few specimens (Fig. 59). Largest shell (n=50): 5 whorls, 2.2×2.2mm.

Sitalinopsis maldivensis differs from *S. grenvillei* and *S. conulus* most conspicuously by the evenly curved periphery of the shell, and the presence of four rows of hairs.

Genital tract (n=2) (Fig. 36) Genital atrium nearly as long as the epiphallus. Epiphallus narrower than the penis, with a sheath covering more than half its length, and a broad, inconspicuous caecum at the transition to the vas deferens. Penis very short, its retractor muscle runs under the epiphallus sheath. Pedunculus slightly narrower than the epiphallus, inserting at the genital atrium, so that there is no vagina; spermatheca elongated and somewhat longer than the pedunculus. Oviduct about as long as the combined penis and epiphallus.

Sitalinopsis grenvillei, as described and illustrated by Solem (1988: 552, 600, figs 191, 192) seems to differ mainly by the presence of a vagina and a double-walled epiphallus instead of an epiphallus with a sheath which is not closed at its distal end.

Radula (n=1) (Figs 62–64) The central tooth can be distinguished by its symmetrical basal plate, which has supportive ridges at both sides. The five lateral teeth are also tricuspid and very similar except for their asymmetrical basal plates, which have a supportive ridge at only one side. The sixth lateral tooth is more obliquely elongated and intermediate in shape with the c. 25 marginal teeth, all of which are regularly bicuspid, also close to the border of the radula.

Despite the intention to do so (Solem, 1988: 553), the radula of *S. grenvillei* has not been described.

Molecular data For specimens of two atolls three COI sequences were acquired. The sequences from the Addu Atoll, Hulhudhoo [4], and the South Ari Atoll, Vilamendhoo [18], are identical. The most similar (88%) sequence in GenBank is that of *Pristiloma chersinella* (Dall, 1886), a species of Zonitidae, Vitreinae, from western USA, which cannot be considered closely related for any other reason.

GenBank accession numbers: MH626441, Hulhudhoo [4]; MH626439, 626440, Vilamendhoo [18].

Notes The two species of the genus *Sitalinopsis* that are known, are widespread. Vermeulen *et al.* (2015: 76) report '*Thysanota conula*' from a wide range in SE Asia, including India, Vietnam, peninsular Malaysia and Sabah, Indonesia southwards to Java, and Philippines eastwards to Halmahera. These authors consider *Sitala fimbriosa* Quodras & Von Moellendorff, 1894, from the Philippines, *Sitala elatior* Bavay & Dautzenberg, 1908, from Vietnam, and *Thysanota elegans* Preston, 1909, from Sri Lanka, synonyms of *Nanina conula*, which was described from India. *Sitalinopsis grenvillei* is known from limestone hills near the coast in Vietnam, Sabah and Australia (Vermeulen *et al.*, 2015: 77).

It is unknown whether *Sitalinopsis maldivensis* evolved in the Maldivian archipelago. Because of its conspicuous shell characters, which reduce the possibility of overlooking an earlier description, we here describe it as new to science.

Derivation of name Even if this species once proves not to be endemic for the Maldivian islands, it deserves the epithet *maldivensis*, being one of the most widespread and common species in the archipelago.

Superfamily Helicarionoidea Bourguignat, 1877

Family Ariophantidae Godwin-Austen, 1888;

subfamily Ariophantinae Godwin-Austen, 1888

Genus *Euplecta* C. Semper, 1870

Euplecta indica (L. Pfeiffer, 1846)

Helix indica L. Pfeiffer, 1846b: 66.

Euplecta malabarica Blanford, 1901: 250, pl. 25 fig. 5.

Euplecta indica var. *malabarica*; Smith, 1902: 142. Raheem *et al.*, 2014: 100, 210, fig. 63C (lectotype). *Euplecta indica*; Blanford & Godwin-Austen, 1908: 60. Mitra *et al.*, 2005: 238 ('Maldives'). Raheem *et al.*, 2014: 100, 210 fig. 63A (lectotype), B (paralectotype).

Maldivian record North Maalhosmadulu [12a].

Range According to Raheem *et al.* (2014: 100) this species has been 'introduced to the Maldivian Islands' and is native to Sri Lanka and the central and southern Western Ghats in India

Shell Depressed globular, with a peripheral keel and a minute umbilicus. Relatively large. The lectotype measures: B 20mm, H 12mm.

Notes We have not seen any specimens of this species. Blanford & Godwin-Austen (1908: 61) refer to it as 'doubtless introduced with plants'.

Genus *Ariophanta* Des Moulins, 1829

Ariophanta bombayana (Grateloup, 1840)

Helix bombayana Grateloup, 1840: 161.

Ariophanta belangeri 'var. *bombayana*' Raheem *et al.*, 2014: 89, 201 fig. D (neotype).

Maldivian records North Maalhosmadulu [12a], North Malé [9a], South Maalhosmadulu [20c].

Range According to Raheem *et al.* (2014: 89) this taxon may be native to the 'eastern coastal region of South India'.

Shell A worn, colourless, depressed globular shell with 4½ whorls and a narrow umbilicus (<10% B), measuring 23.2×17.0mm, might belong here.

Notes Smith (1902: 143) and Blanford & Godwin-Austen (1908: 36) considered this an introduced species. Smith (1902: 143) mentioned that *Helix belangeri* Deshayes, 1834, and *Helix bombayana* are considered synonyms by Blanford (1901: 245), but did not accept that view. Raheem *et al.* (2014: 88, 200 fig. 53F, and 2014: 89, 201 fig. 54A–C) illustrated the lectotype and paralectotypes of *Helix belangeri* of Deshayes (1834: 413, pl. 1 figs 1–3). A further analysis regarding the taxonomic status of these nominal taxa lies beyond the scope of this article.

DISCUSSION

Smith (1902) reported 9 species of terrestrial gastropods from the Maldives, only two of which, viz. *Euplecta indica* and *Ariophanta belangeri*, were not found again during our recent investigations, more than a century later on. Now 32 species of terrestrial gastropod are listed for the archipelago. The fact that Smith (1902) did not mention 23 species that are reported as new for the archipelago here, cannot be seen as an argument in favour of recent introductions. Most of our new records are about very small snails that may have been overlooked during the Mr Stanley Gardiner's expedition in 1899–1900, which was not primarily malacologically oriented.

There are conspicuous differences in the rareness of the various species (Table 1). Most of the 15 species that were found on only one island are represented by less than five shells, viz. *Truncatella marginata* (1 shell), *Assimineia* spec. 1 (1), *Assimineia* spec. 2 (1), *Nesopupa* spec. (1), *Pupoides coenopictus* (2), *Cecilioides balanus* (2), *Cecilioides bensoni* (4), and *Prosopoeas* spec. (1). It is unclear whether these species live or have ever lived somewhere in the Maldivian archipelago. This also applies to *Gastrocopta servilis*, 11 shells of which were found on the beach among marine molluscs. These records allow only the conclusion that these species, at least their shells, could reach the Maldives. Both *Kaliella barrakporensis* and *Pupisoma (Ptychopatulula) circumlitum* are also known from only a single island, but by somewhat larger samples, i.e. 6 and 10 shells, respectively.

For *Laevicaulis alte*, *Melampus fasciatus* and *Glessula nitens*, which are all known from only a single island, live animals were observed, indicating that these species belong to the recent Maldivian malacofauna. Data regarding the occurrence of *Euplecta indica*, additional to Smith (1902: 142), are not known. Most, i.e. 15 of 17, species that are recorded from more than one Maldivian island, have been observed alive there (Table 1). Only for *Ariophanta belangeri*, which was not found again, details about its actual occurrence are not known.

Seven of the most common species, viz. *Allopeas gracile* (9 atolls, 20 islands), *Gulella bicolor* (8 atolls, 15 islands), *Liardetia samoensis* (5 atolls, 9 islands), *Liardetia scandens* (3 atolls, 5 islands), *Pupisoma dioscoricola* (6 atolls, 11 islands), *Rachis*

Table 1 Species recorded in the Maldives, alive (+) or as shells only (-), that are also known from Sri Lanka (SL+) or Australia (A+)

	alive	atolls	islands	SL	A
<i>Leptopomoides halophilus</i> (Benson, 1851)	+	8	16	+	-
<i>Truncatella marginata</i> Küster, 1855	-	1	1	-	-
<i>Assimineea</i> spec. 1	-	1	1	-	-
<i>Assimineea</i> spec. 2	-	1	1	-	-
<i>Melampus fasciatus</i> (Deshayes, 1830)	+	1	1	+	+
<i>Laevicaulis alte</i> (Férussac, 1821)	+	1	1	+	+
<i>Lissachatina fulica</i> (Férussac, 1821)	+	2	3	+	+
<i>Subulina octona</i> (Bruguière, 1798)	+	8	11	+	+
<i>Allopeas gracile</i> (Hutton, 1834)	+	9	20	+	+
<i>Prosopeas</i> spec.	-	1	1	-	-
<i>Glessula nitens</i> (Gray, 1825)	+	1	1	+	-
<i>Cecilioides balanus</i> (Reeve, 1850)	-	1	1	-	-
<i>Cecilioides bensoni</i> Gude, 1914	-	1	1	-	-
<i>Gulella bicolor</i> (Hutton, 1834)	+	8	15	+	+
<i>Succinea ceylanica</i> L. Pfeiffer, 1855	'+'	7	11	+	-
<i>Pupoides coenopictus</i> (Hutton, 1834)	-	1	1	+	-
<i>Elasmias manilense</i> (Dohrn, 1863)	-	4	5	-	+
<i>Rachis punctata</i> (Anton, 1839)	+	6	16	+	-
<i>Gastrocopta servilis</i> (Gould, 1843)	-	1	1	-	+
<i>Gastrocopta mimula</i> (Benson, 1853)	+	5	10	+	-
<i>Pupisoma</i> (<i>Ptychopatula</i>) <i>dioscoricola</i> (C.B. Adams, 1845)	+	6	11	-	+
<i>Pupisoma</i> (<i>Ptychopatula</i>) <i>circumlutum</i> Hedley, 1897	-	1	1	-	+
<i>Insulipupa mooreana</i> (E.A. Smith, 1894)	+	7	13	-	+
<i>Nesopupa</i> spec.	-	1	1	?	?
<i>Microcystina</i> spec.	+	7	10	?	?
<i>Liardetia doliolum</i> (L. Pfeiffer, 1846)	+	3	3	-	+
<i>Liardetia samoensis</i> (Mousson, 1865)	+	5	9	-	-
<i>Liardetia scandens</i> (Cox, 1871)	+	4	6	-	+
<i>Kaliella barrakporensis</i> (Pfeiffer, 1853)	-	1	1	+	-
<i>Sitalinopsis maldivensis</i> spec. nov.	+	7	10	-	-
<i>Euplecta indica</i> (L. Pfeiffer, 1846)	-	1	1	+	-
<i>Ariophanta belangeri</i> (Deshayes, 1834)	?	3	3	-	-

punctata (6 atolls, 16 islands), *Subulina octona* (8 atolls, 11 islands), and maybe also *Elasmias manilense* (4 atolls, 5 islands), are considered invasive or anthropophilic species (Solem, 1978, 1988; Christensen & Kirch, 1981; Cowie, 2001; Cowie & Rundell, 2002; Hausdorf, 2007; Wu *et al.*, 2007; Brook, 2010; Brook *et al.*, 2010; Raheem *et al.*, 2014). They belong to the 'tropical tramps' or 'culture snails' of the 'atoll fauna' in the terminology of Solem (1959: 209). Some of these species may have reached their present ranges by hitchhiking with humans in prehistoric times, as is suggested for example for *Pupisoma* (*Ptychopatula*) *dioscoricola*, *Liardetia samoensis* and *Allopeas gracile* by Brook (2010: 215). Three species that are about equally common in the Maldivian archipelago, viz. *Gastrocopta mimula* (5 atolls, 10

islands), *Succinea ceylanica* (7 atolls, 11 islands), and *Leptopomoides halophilus* (8 atolls, 16 islands) are hitherto considered endemic to Sri Lanka, like *Glessula nitens*. The range of *Microcystina* spec. (7 atolls, 10 islands) cannot be indicated because of the unclear taxonomy of the *Microcystina* species. The remarkably common *Sitalinopsis maldivensis* (7 atolls, 10 islands) is not known from outside the Maldivian archipelago; it might be a Maldivian endemic.

The fact that 14 species are known from both the Maldives and Sri Lanka, 4 of which hitherto considered endemic to Sri Lanka (Table 1), supports the view that the molluscan fauna of the Maldives is most closely related to that of Sri Lanka, located c. 1000km east of the Maldives. The main tracks of tropical storms and water

currents (Times Atlas, 1968: pls 3, 4) suggest that Sri Lanka might be the source of at least a part of the Maldivian molluscan fauna, which may be considered instable because of the very low Maldivian islands and the occurrence of tsunamis in the area. The endemic *Sitalinopsis maldivensis* might be the sister species of *S. conulus*, which is represented in Sri Lanka (see above). Only 10 species are known from both the Maldives and the Western Ghats of India, situated about as far from the Maldives as Sri Lanka, but these species are either widespread or poorly known (*Cecilioides* spec.). No less than 13 species that have been recorded for the Maldives are shared with Australia (Table 1), but those species are widespread.

Despite the incomplete sampling, something like a Maldivian terrestrial molluscan fauna emerges from the data, with several species that are widespread in the archipelago. Apart from *Lissachatina fulica*, *Subulina octona*, *Rachis punctata*, *Glessula nitens*, *Euplecta indica* and *Ariophanta bombayana*, the terrestrial snails are small to very small, with shell heights or breadths of much less than 1cm. Small size may have facilitated their transport over large distances.

The molecular data are much too fragmentary to allow for any reconstruction of the history of the Maldivian malacofauna, with single or multiple introductions of species. It would be worthwhile to investigate some of the uninhabited islands to get more insight about human interference in gastropod distributions.

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