RAFFLES BULLETIN OF ZOOLOGY **62**: 115–123
Date of publication: 17 March 2014
http://zoobank.org/urn:lsid:zoobank.org:pub:4D5F3585-04B2-45AA-BA00-8795AEF68A83

On the land snail *Rhagada* Albers, 1860 (Gastropoda: Camaenidae) from across the Lesser Sunda Islands

Frank Köhler

Abstract. Six land snail species from across the Lesser Sunda Islands have so far been assigned to the camaenid genus *Rhagada* Albers, 1860. Previous taxonomic treatments have emphasised shell features, which were usually inferred from small series of specimens. Based on the study of newly collected, ethanol preserved material from various islands, I compared the penial anatomy of four species and analysed the mitochondrial differentiation of three. In addition, I completely review the previous literature on the Lesser Sunda species. Six previously named species are recognised as full species: *R. solorensis* (Martens, 1863) from Solor, *R. colona* (Martens, 1877) from Dana Island, *R. floresiana* (Martens, 1891) from Flores, *R. supracostulata* (Schepman, 1892) from Sumba, *R. marghitae* Falconieri, 1995 from Nusa Penida, and *R. setzeri* Maassen, 2009 from Alor. In addition, a new subspecies, *R. setzeri atauroensis* n. subsp. from Atauro Island, Timor-Leste, and a new species, *Rhagada abbasi* n. sp. from Lembata Island, are described based on morphological and molecular evidence.

Key words. Pulmonata, Stylommatophora, penial anatomy, shell, taxonomy, COI, 16S

INTRODUCTION

Land snails of the genus *Rhagada* Albers, 1860 are chiefly recognised by their typically medium sized shell with conspicuous, reddish-brown spiral banding on a brighter background of white to ochre colour. Having radiated extensively throughout the Kimberley and Pilbara regions in coastal Western Australia, *Rhagada* is amongst the most species-rich camaenid genera in Australia (Solem, 1985a, 1997; Johnson et al., 2004, 2012; Köhler, 2011). In the past, there has been controversy about the systematic placement of the *Rhagada* species from the Lesser Sunda Islands. Solem (1985a, 1997) was the first to revise the taxonomy of the Australian species comprehensively and considered the genus to be endemic to Australia. He further assumed that the Lesser Sunda species represented a separate group. This conclusion was based on observed differences in the genital anatomy between the Australian species and *Rhagada solorensis* (Martens, 1863) as illustrated by Wiegmann (1893). By contrast, Maassen (2009) reported the genital anatomy of the Lesser Sunda species *R. setzeri* Maassen, 2009 to be consistent with that of the Australian *Rhagada* species. Therefore, Maassen (2009) maintained the affiliation of the Lesser Sunda species with this genus. Recently, a molecular phylogenetic study has revealed that the Lesser Sunda species form a clade nested within the Australian radiation confirming that Lesser Sunda and Australian species are indeed congeneric (Köhler & Criscione, 2013). A molecular clock analysis suggested that the Lesser Sunda clade originated during the Plio-Pleistocene indicating that *Rhagada* may have radiated throughout the archipelago during the Pleistocene when lowered sea levels and narrower sea ways facilitated dispersal between islands (Voris, 2000).

While the controversy over the genus-level taxonomy has thus been resolved, the species-level taxonomy of the Lesser Sunda taxa has remained problematic due to an inconsistent use of names. Until today six nominal species were described from various islands. However, revising authors treated these names differently. Most previous treatments relied exclusively on shell characters with emphasis on features such as shell size, thickness, and sculpture. More recent studies of the Australian *Rhagada* species have demonstrated, however, that shell characters may be of little taxonomic utility. *Rhagada* species are known to possess a generally conserved shell with respect to shell size and shape while other shell features, such as colour, sculpture, and umbilical morphology, exhibit considerable intraspecific variability. In fact, many species cannot be unambiguously recognised by their shell alone (Köhler, 2011). Recently, a molecular study has revealed that the morphological diversification and levels of molecular genetic divergence are disconnected in *Rhagada* from the Australian Pilbara region. Shells from divergent mitochondrial clades may be morphologically conserved while other clades with low mitochondrial diversification revealed morphological divergence, which spanned almost that of the entire genus (Stankowski, 2011; Johnson et al., 2012). With shell features potentially being misleading, studies of additional characters, such as genital anatomy or molecular markers, are needed to resolve the taxonomy of the Lesser Sunda species. Based on a comprehensive review of all available literature as well as the examination of genital anatomy and mitochondrial differentiation of

---

Australian Museum, Research Branch, 6 College Street, Sydney, NSW 2010, Australia; Email: frank.koehler@austmus.gov.au

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

newly collected samples, I am summarising the taxonomic history of *Rhagada* species from the Lesser Sunda Islands and describe new taxa from Atauro and Lembata islands.

MATERIAL AND METHODS

Morphological studies. Morphological characters of adult shells (dimensions, colouration and sculpture) were assessed from adult specimens only, which were recognised by a completed apertural lip. Shells were measured with callipers precise to 0.1 mm. Characters measured were height (H = maximum dimension parallel to axis of coiling, including lip) and diameter (D = maximum dimension perpendicular to H, including lip). The number of whorls (W), including protoconch, was counted precise to 0.1 whorl as shown in Köhler (2011: Fig. 2). Dissections were performed by use of a stereo microscope and a drawing mirror.

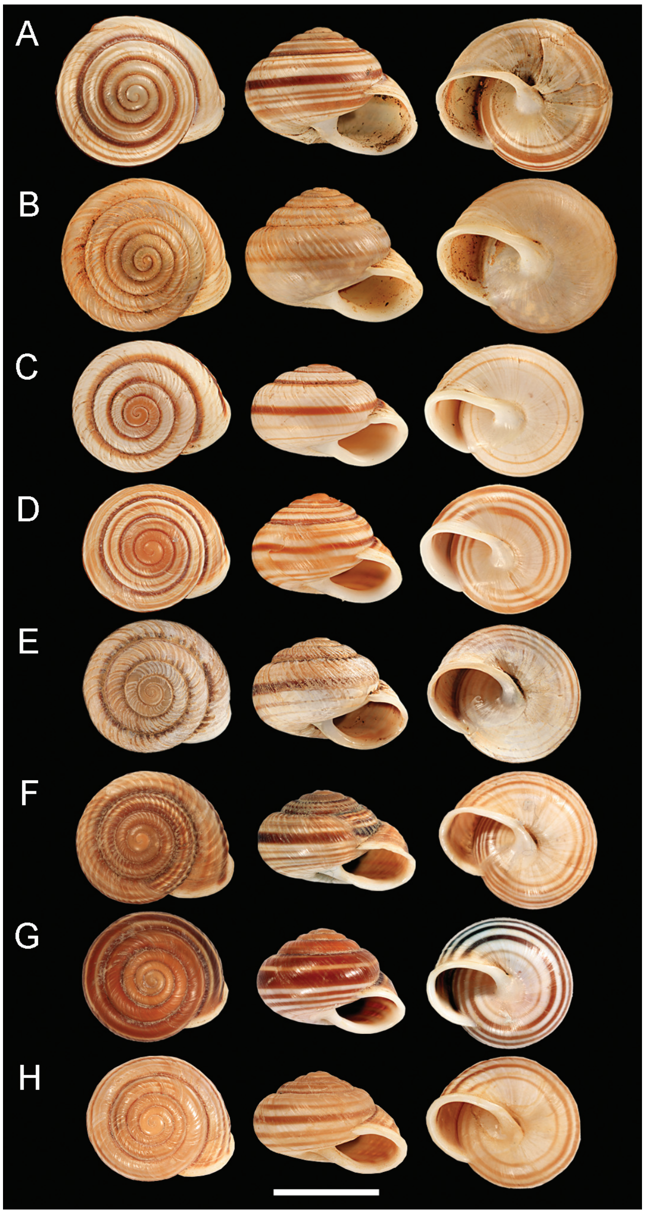

Fig. 1. Shells (1.5× of natural size). A, *Rhagada solorensis*, Solor Island, AM C.471154; B, *Rhagada setzeri setzeri*, Alor Island, AM C.471156; C, D, *Rhagada setzeri atauroensis* n. subsp., Atauro Island: C, Paratype AM C.468711; D, Paratype AM C.468709; E–H, *Rhagada abbasi* n. sp., Lembata Island: E, Holotype AM C.478280; F–H: Paratypes AM C.471153, showing variation in sculpture and colour pattern. Scale bar = 10 mm.

Material examined. This study is based on newly collected, ethanol-preserved samples and dry shells deposited in the Australian Museum (AM). Cited type material is deposited Museo di Storia Naturale, Milano, Italy (MSNM), the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (RMNH) and the Museum für Naturkunde, Berlin, Germany (ZMB).

Molecular methods and phylogenetic analyses. DNA was extracted from small pieces of foot muscle by use of a QIAGEN DNA extraction kit for animal tissue following the standard procedure of the manual. Fragments of the mitochondrial 16S rRNA gene (16S) and of the cytochrome c oxidase subunit 1 (COI) gene were amplified by PCR using the primer pairs: 16Scs1 (Chiba, 1999) and 16Sbd1 (Sutcharit et al., 2007), and L1490 and H2198 (Folmer et al., 1994), respectively. Reactions were performed under standard conditions with annealing temperatures/elongation times of 55°C/90 s for 16S and 50°C/60 s for COI. Both strands of purified PCR fragments were cycle sequenced by use of the PCR primers. Forward and reverse strands were corrected for misreads and merged into one sequence file using CodonCode Aligner v. 3.6.1 (CodonCode Corporation, Dedham, MA). COI sequences of identical length were obtained by trimming PCR primer sites from either end of the amplified fragment. These sequences were combined into one data set, which was inspected visually and translated into amino acid sequences to check for misreads. 16S sequence alignments were generated using MUSCLE as implemented in MEGA5 (Tamura et al., 2011). Uncorrected pair-wise genetic p-distances were calculated using MEGA5 under the option 'pair-wise deletion of gaps'. Phylogenetic relationships were estimated by running a 10,000,000 generations Metropolis-coupled Markov chain Monte Carlo (2 runs with each 4 chains, one of which was heated) as implemented by MrBayes vs. 3.2.1 (Ronquist & Huelsenbeck, 2003). A data partition was applied allowing model parameters to be estimated separately for each codon position of the COI gene and for 16S. Sampling rate of the trees was 1,000 generations. Generations sampled before the chain reached stationarity were discarded as burn-in (average standard deviation of split frequencies below than 0.01; Ronquist & Huelsenbeck, 2003) and the log likelihood of sampled trees reached a stationary distribution. The last 7,000 trees were employed to calculate the Bayesian consensus tree.

SYSTEMATICS

Camaenidae Pilsbry, 1895

Rhagada Albers, 1860

Rhagada Albers, 1860 [in Martens & Albers]: 108–109 (type species *Helix reinga* Pfeiffer, 1846 by original designation); Pilsbry, 1890: 185–191, 1894: 135–136; Martens, 1891: 235–236; Preston, 1908: 120, 1914: 13; Hedley, 1916: 69–70; Rensch,

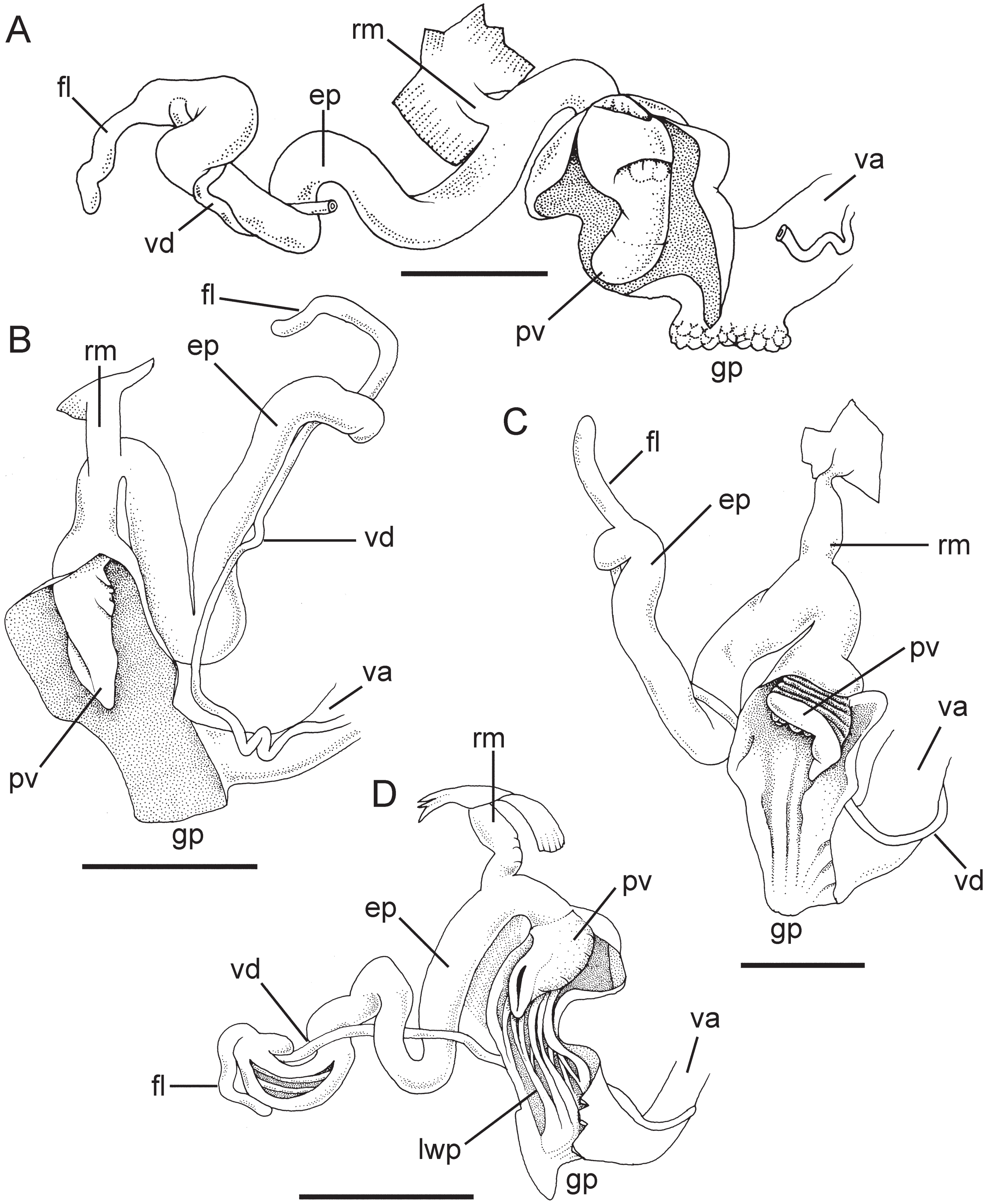

Fig. 2. Penial anatomy, with penial chamber opened showing internal anatomy. A, *Rhagada solorensis*, Solor Island, AM C.471154; B, *Rhagada marghitae*, Nusa Penida AM C.327851; C, *Rhagada setzeri atauroensis* n. subsp., Atauro Island, holotype AM C.478282; D, *Rhagada abbasi* n. sp., Lembata Island, holotype AM C.478280. Abbreviations: ep = epiphallus; fl = epiphallic flagellum; gp = genital pore; lwp = longitudinal wall pilaster; pv = penial verge; rm = penial retractor muscle; va = vagina; vd = vas deferens. Scale bars = 2 mm.

1931: 94–95, Iredale, 1938: 112–113, 1939: 58–63; Solem, 1985a: 875–919, 1985b: 143–136, 1991: 217–218, 1997: 1663–1789; Solem & McKenzie, 1991: 247–263; Johnson & Black, 1991: 367–374; Withers et al., 1997: 599–611; Falconieri, 1995: 81–84; Vermeulen & Whitten, 1998: 127–128; Johnson et al., 2004: 341–355; 2006: 45–50; Maassen, 2009: 65–69; Köhler, 2011: 270–287; Stankowski, 2011: 756–769, 2013: 2726–2741; Johnson et al., 2012: 316–327; Köhler & Criscione, 2013: 1971–1982.

Bellrhagada Iredale, 1938: 114, 1939: 71–72 (type species *Rhagada plicata* Preston, 1914, by original designation).

Tumegada Iredale, 1939: 62 (type species *Helix convicta* Cox, 1876, by original designation).

Taxonomic history. Solem (1985a) synonymised *Bellrhagada* and *Tumegada*. There are about 35 species in Western Australia, which are comparatively well-known. Six nominal species have so far been described from the Lesser Sunda Islands. Rensch (1931) grouped the species known at the time into two polytypic species (so-called "Rassenkreise") based on shell features. He considered *R. colona* (Martens, 1877) and *R. supracostulata* (Schepman, 1892) as subspecies of the Australian "*R. plectilis* (Benson, 1853)" (= *Plectorhagada plectilis*) for having a small shell with strong axial ribs. However, *P. plectilis* has since been shown to be part of a different genus (Solem, 1997). Rensch (1931) also recognised a second polytypic species, *R. solorensis* (Martens, 1863) with its subspecies *R. solorensis floresiana* (Martens, 1891), as a distinct species for its larger shell and faint axial ribs. Subsequently, Maassen (2009) reinstated *R. colona* and *R. supracostulata* as full species but maintained the subspecies arrangement for *R. solorensis* and *R. s. floresiana* without explanation. In addition, he described a new species from Alor island, *R. setzeri* Maassen, 2009. Earlier, Falconieri (1995) also described a new species from Nusa Penida, *R. marghitae*. However, this description was apparently overlooked subsequently. Except for the description of *R. setzeri*, all taxonomic decisions were based on shell features only. Characters considered particularly relevant for the taxonomy of *Rhagada* species were shell size, development of axial ribs, and closure of umbilicus.

Diagnosis. Shell small to medium-sized (D = 9–25 mm), subglobose with moderately to strongly elevated, exceptionally also low spire; umbilicus frequently concealed by greatly expanded callus, occasionally forming a chink or narrowly open; protoconch smooth to weakly sculptured by radial ridgelets or ribs; teleoconch with faint to well-developed sculpture of axial ridgelets or ribs, mostly on upper sector of whorls; whorls separated by shallow suture; periphery well-rounded to weakly angulated. Shell colour generally variable, background whitish or brownish horn, with well-developed, red subsutural, peripheral and frequently additional, thinner spiral bands. Eversible head wart between ommatophores. Penis without penial sheath, with well-developed, long and coiled epiphallus with flagellum of variable length; penial retractor muscle attached at epiphallus; epiphallus opens to lumen of penial chamber through large, cone-shaped verge with characteristic sperm groove. Bursa copulatrix short to long, simple to kinked (based on Köhler, 2011).

Rhagada solorensis (Martens, 1863)

Helix solorensis Martens, 1863: 179 (from 'Lamakera, Solor', 8° 25' 60" S, 123° 10' 00" E; nine syntypes ZMB Moll. 5587, not seen).

Helix (*Rhagada*) *solorensis* – Martens, 1891: 235.

Rhagada solorensis solorensis – Rensch, 1931: 95, Maassen, 2009: 66 (partim).

Material examined. AM C.471154 (Indonesia, Solor Island, 3 wet, 2 dry).

Taxonomic history. Representing the first named non-Australian species, *R. solorensis* has continuously been maintained as a distinct species in previous taxonomic treatments. Vermeulen & Whitten (1998) and Maassen (2009) reported *R. solorensis* from Bali and Nusa Penida, apparently unaware of the description of *R. marghitae* from these islands. In fact, Maassen's (2009) report of *R. solorensis* is entirely based on material of *R. marghitae*. Rensch (1931) and Maassen (2009) assigned *R. floresiana* as a second subspecies for its similar shell. However, Rensch (1931) indiscriminately lumped together most Lesser Sunda species while Maassen (2009) confused *R. solorensis* and *R. marghitae*. The proposals of both authors are therefore not well-substantiated. In light of generally widespread narrow-range endemism in *Rhagada* (Köhler, 2011; Johnson et al., 2012), I prefer maintaining the original treatment of Martens (1863, 1891) and consider *R. solorensis* as endemic to Solor Island. Populations from other islands should not be lumped with *R. solorensis* in absence of evidence from comparative studies. Consequently, *R. floresiana* is also maintained as a distinct species endemic to Flores.

Diagnosis. Shell comparatively large (D = 16–19 mm; Table 1), smooth or with fine axial ribs only, umbilicus forming a chink or narrowly open, peripheral band particularly well-developed (Fig. 1A) (Martens, 1891). Penis with large, smooth penial verge with rounded tip, epiphallus with short flagellum (Fig. 2A).

Comparative remarks. Shells figured by Maassen (2009) from Nusa Penida are misidentified specimens of *R. marghitae*. Most typical characteristic is smooth penial verge with rounded tip.

Rhagada colona (Martens, 1877)

Helix colona Martens, 1877: 272, pl. 1, figs 4, 5 (from 'Dana Island, SW of Timor', centre at 10° 58' 59.35" S, 122° 52' 5.86" E; eight syntypes ZMB Moll. 26629, not seen)

Rhagada plectilis colona – Rensch, 1931: 95.

Taxonomic history. While Rensch (1931) treated *R. colona* as subspecies of the Australian species *Plectorhagada plectilis* based on a similar shell, Maassen (2009) maintained it as a distinct species. Museum material from Savu Island has also been assigned to this species under an unpublished variety name (ZMB Moll. 52292).

Diagnosis. Shell comparatively small, smooth, umbilicus forming a chink (Martens, 1877; Maassen, 2009). Genitalia unknown.

Table 1. Shell measurements for N shells of different *Rhagada* species and subspecies. H = height; D = diameter; W = no. of whorls.

Species	Island	N	H	D	W
R. solorensis	Solor	4	10.7–12.0 (11.3 ± 0.5)	16.0–17.4 (16.7 ± 0.5)	4.6–4.8 (4.7 ± 0.1)
R. setzeri atauroensis n. subsp.	Atauro	17	8.9–11.0 (9.8 ± 0.6)	13.0–15.9 (14.6 ± 0.8)	4.3–5.0 (4.6 ± 0.2)
R. marghitae	Nusa Penida	8	9.3–10.0 (9.7 ± 0.3)	14.2–15.5 (14.9 ± 0.4)	4.5–5.0 (4.8 ± 0.2)
R. abbasi n. sp.	Lembata	20	8.5–10.8 (9.3 ± 0.5)	13.4–15.0 (14.1 ± 0.4)	4.3–5.0 (4.6 ±0.2)
		1	10.3	14.7	4.7

Remarks. Poorly characterised by reference to shell features; comparative study of anatomical and molecular characters required to confirm status.

Rhagada floresiana (Martens, 1891)

Helix (*Rhagada*) *floresiana* Martens, 1891: 235–236, pl. 14, figs 13, 14 (from 'Flores, Maumere', 8° 37' 12" S, 122° 13' 12" E; 3 syntypes ZMB Moll. 44732, not seen).
Rhagada solorensis floresiana – Rensch, 1931: 95, Maassen, 2009: 66 (partim).

Taxonomic history. Martens (1891) recognised *R. solorensis* as distinct by its thinner, more turreted shell, less thickened columellar lip and slightly different colour. This taxon has subsequently been treated as a subspecies of *R. solorensis* by Rensch (1931) and Maassen (2009) based on shell features. I prefer following the original concept and maintaining *R. floresiana* as a distinct species (see also under *R. solorensis*). Genitalia were figured by Wiegmann (1893), who noted that in this illustration the insertion of the penial retractor was missing.

Diagnosis. Shell comparatively large (D = 16–19 mm), smooth or with fine axial ribs only, umbilicus forming a chink or narrowly open, peripheral band particularly well-developed (Martens, 1891).

Comparative remarks. Shell similar to *R. solorensis*; species poorly defined by shell characters only; comparative study of anatomical and molecular characters required to confirm status.

Rhagada supracostulata (Schepman, 1892)

Helix supracostulata Schepman, 1892: 150, pl. 6, fig. 1 (from 'Sumba island', 9° 40' 0" S, 120° 0' 0" E; 15 syntypes RMNH 57062, not seen)
Rhagada plectilis supracostulata – Rensch, 1931: 95.
Rhagada supracostulata – Maassen, 2009: 66.

Taxonomic history. Known only from dry shells studied by Schepmann (1892) and Maassen (2009); not seen by the present author.

Diagnosis. Shell comparatively small, umbilicus forming a chink, most specimens with distinct basal ridge. Genitalia unknown (Maassen, 2009).

Comparative remarks. Poorly defined by shell characters only; comparative study of anatomical and molecular characters required to confirm status.

Rhagada marghitae Falconieri, 1995

Rhagada marghitae Falconieri, 1995: 81–84, figs 1, 2 (from 'Nusa Penida, Pura Batu Medau'; holotype MSNM 22635, not seen)
Rhagada solorensis (partim) – Vermeulen & Whitten, 1998: 127, fig. 129.
Rhagada solorensis solorensis – Maassen, 2009: 66 (partim).

Material examined. AM C.327851 (Indonesia, Nusa Penida, Goa Giri Putri, 8° 45' N, 115° 30' E, 5 wet).

Taxonomic history. Apparently not aware of Falconieri's description, this species was subsumed under *R. solorensis* by Vermeulen & Whitten (1998) and Maassen (2009). The original description focuses on characters exhibited by several species but provides little information permitting the recognition of this species.

Diagnosis. Shell moderately large (D = 14–15.5 mm), with fine axial growth lines, umbilicus forming a chink or narrowly open. Penial verge smooth with pointed tip and well-developed sperm groove, inner penial wall smooth, epiphallus with moderately long flagellum (Fig. 2B).

Comparative remarks. Confused with *R. solorensis* by Vermeulen & Whitters (1998) and Maassen (2009), who depicted shells of this species as *R. solorensis*. Most typical characteristics are smooth, pointed penial verge and smooth inner penial wall.

Rhagada setzeri setzeri Maassen, 2009

Rhagada setzeri Maassen, 2009: 66–69, figs 13–16 (from 'Alor Island, near the airport', 8° 15' 0" S, 124° 45' 0" E; holotype RMNH 113381).

Material examined. AM C.471156 (Indonesia, Alor Island, 3 dry).

Diagnosis. Shell comparatively large (D = 16–19 mm), with usually well-developed axial ribs, umbilicus closed. Penis with long epiphallus, short flagellum, inner penial anatomy unknown (based on Maassen, 2009).

Comparative remarks. Comparatively large shell with well-developed axial sculpture and closed umbilicus is most characteristic. Well-differentiated from *R. solorensis* and *R. abbasi* n. sp. in a molecular phylogeny based on mitochondrial COI and 16S sequences (Fig. 3). Specimens from Atauro Island differ by consistently smaller shell, weaker sculpture, narrowly open umbilicus but are differentiated by comparatively low genetic distances (Table 2); therefore being recognised as distinct subspecies.

Rhagada setzeri atauroensis n. subsp.
(Figs. 1C, D, 2C)

Type locality. Timor-Leste, Atauro Island, 2.6 km NW of Beloi, 8° 12' 08.3" S, 125° 35' 31.9" E.

Holotype. AM C.478282 (dissected specimen, wet, shell destroyed).

Paratypes. AM C.468712 (type locality, 23 wet), AM C.468711 (near Makadade, 8° 12' 42.3" S, 125° 34' 54.9" E, 20 wet, 5 dry), AM C.468709 (northern tip of Atauro, 8° 07' 56.3" S, 125° 37' 59.4" E, 7 wet, 8 dry), AM C.470222 (2.6 km NNW of Beloi, 8° 12' 30.3" S, 125° 36' 19.9" E, 4 dry).

Etymology. Named for Atauro Island.

Description. Shell moderate in size (D = 13–19 mm; Table 1), with faint to well-developed axial ribs, umbilicus forming a chink or narrowly open. Penial verge with circular folds, penial wall with weakly developed longitudinal pilasters, epiphallus with short flagellum (Fig. 2C).

Comparative remarks. Differs from the nominate form by smaller shell, weaker ribs, more vivid colouration, not completely closed umbilicus. Both island forms are separated by comparatively low genetic distances of about 4% in COI and 2% in 16S (Table 2). Because low genetic differentiation might indicate incomplete reproductive isolation, the Atauro Island populations are described as a subspecies of *R. setzeri* rather than being recognised as a full species. *Rhagada setzeri* is well-differentiated from *R. solorensis* and *R. abbasi* n. sp. by means of genetic distances of 12–16% in COI and 8–9% in 16S.

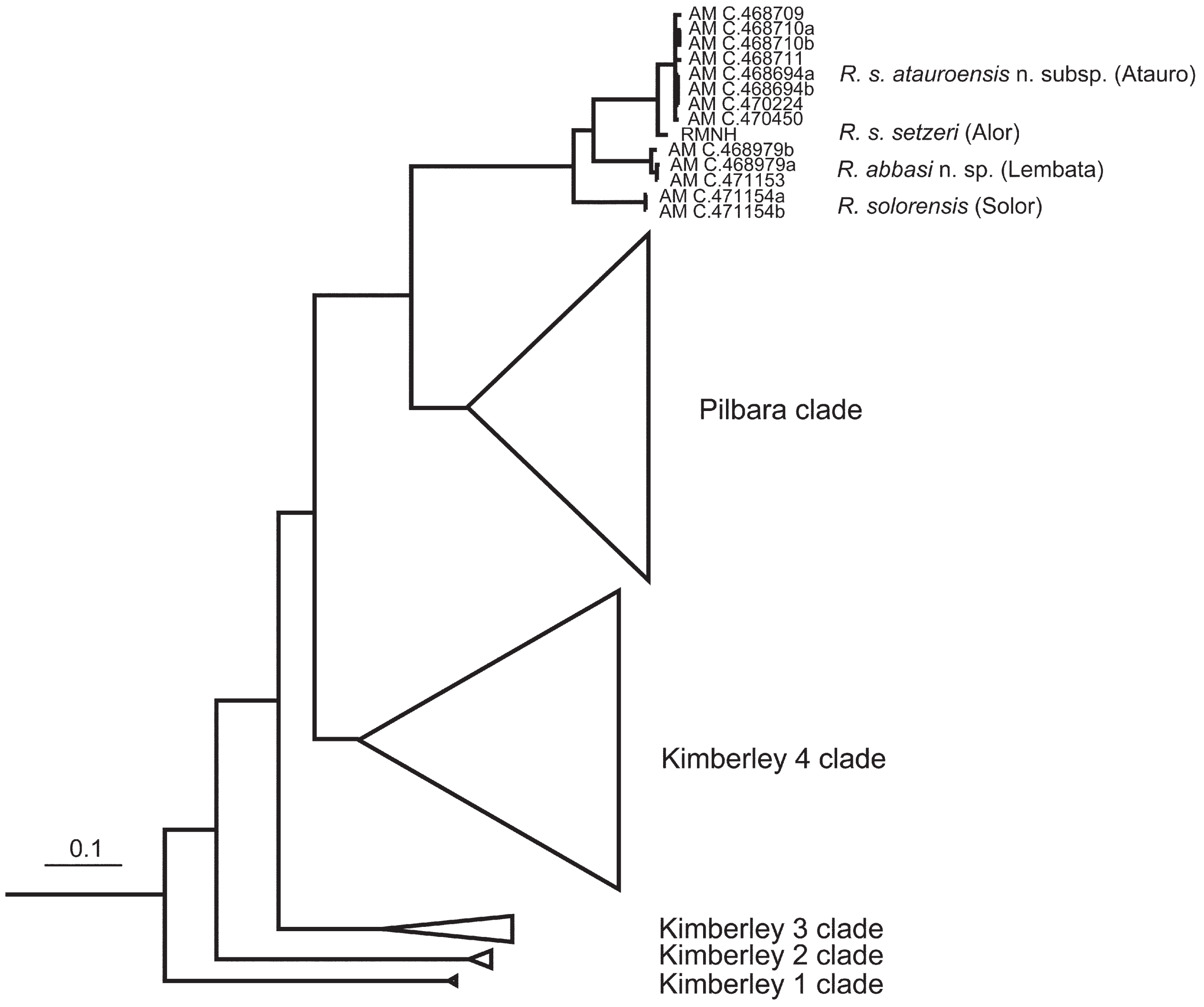

Fig. 3. Bayesian consensus phylogram based on analyses of concatenated 16S and COI sequences, adapted from Köhler & Criscione (2013). Lesser Sunda species *Rhagada solorensis*, *R. setzeri setzeri*, *R. setzeri atauroensis* n. subsp., and *R. abbasi* n. sp. form the sister clade of *Rhagada* from the Australian Pilbara. Clades from the Australian Kimberley and Pilbara regions collapsed; outgroup pruned from tree; see Köhler & Criscione (2013) for further details.

Table 2. Estimates of evolutionary divergence by means of uncorrected p-distances (base differences per site) within and between species in the mitochondrial gene fragments COI and 16S.

	Gene	*R. solorensis*	*R. setzeri*	*R. atauroensis*	*R. abbasi*
R. solorensis					
	COI	0.00	0.14	0.16	0.12
	16S	0.00	0.09	0.09	0.08
R. setzeri					
	COI		–	0.04	0.11
	16S		–	0.02	0.09
R. atauroensis					
	COI			0.01	0.12
	16S			0.01	0.09
R. abbasi					
	COI				0.01
	16S				0.01

Rhagada abbasi n. sp.

(Figs 1E–H, 2D)

Type locality. Indonesia, Nusa Tenggara Timur Province, Lembata Island (= Lomblem), –8° 25' S, 123° 28' E.

Holotype. AM C.478280 (dissected specimen, wet).

Paratypes. AM C.471153 (4 wet, 7 dry), AM C.468979 (2 wet, 5 dry), AM C.478281 (50 dry), ZMB 117967 (50 dry).

Etymology. In honour of John Abbas, Jakarta, who kindly provided material from Lembata and Solor.

Description. Shell moderate in size (D = 15–15 mm; Table 1), broadly subglobose, with variable reddish-brown banding on whitish to creamish background, with sculpture of faint to well-developed axial ribs, umbilicus forming a chink, lip thickened, slightly reflected (Fig. 1E–H). Penial verge smooth with pointed tip and well-developed sperm groove, inner penial wall with well-developed longitudinal pilasters, epiphallus with longitudinal pilasters along inner wall, short flagellum (Fig. 2D).

Comparative remarks. Shell smaller than *R. solorensis*, *R. floresiana*, and *R. setzeri setzeri*, but similar to. *R setzeri atauroensis*. Most typical features are smooth penial verge with pointed tip and well-developed longitudinal pilasters of penial wall. Well-differentiated from *R. solorensis* and *R. setzeri* in a molecular phylogeny based on mitochondrial COI and 16S sequences (Fig. 3).

Discussion. Previous taxonomic treatments of Lesser Sunda species were predominantly based on shell characters, which were usually inferred from small series of specimens. The better known Australian *Rhagada* species were shown to have rather conserved shells with regard to general shape and size while exhibiting considerable variation in shell sculpture, umbilical morphology and colour (Köhler, 2011; Johnson et al., 2012). Extreme amounts of intraspecific variation in shells were observed in some island populations, but are governed by strong selection in an extreme environment (Stankowski, 2011, 2013). By contrast, the species from the Lesser Sunda Islands remain poorly documented in terms of available study material. However, where large numbers of specimens are available for study (i.e., *R. setzeri atauroensis*), the intraspecific variation of shells was found to correspond well with levels observed in Australian species. There is no reason to assume that other Lesser Sunda species exhibit much lower amounts of intraspecific variability. Consequently, traditionally emphasised shell characters, such as sculpture, umbilical morphology and banding pattern, may be of little taxonomic utility.

Recent studies in Australian camaenids, including *Rhagada*, showed that comparative penial anatomy (Fig. 2) may provide valuable taxonomic information even in species that possess conserved shells (e.g., Köhler & Johnson, 2012; Criscione & Köhler, 2013a, 2013b). The penial anatomy of two already described species (*R. solorensis*, *R. marghitae*) and two new taxa (*R. setzeri atauroensis* n. sp., *R. abbasi* n. sp.) provided useful taxonomic information complementing the shell-based taxonomy. Molecular phylogenetic analyses based on mitochondrial sequences of the COI and 16S genes showed that *Rhagada* species from the Lesser Sunda Islands form a clade, which represents the sister group of all known species from the Australian Pilbara region (Fig. 3; Köhler & Criscione, 2013). Amongst these species, *R. setzeri atauroensis* forms the sister group of *R. setzeri setzeri* from Alor. Both species are differentiated by mean p-distances of 4% in COI and 2% in 16S (Table 2). Other species are differentiated by p-distances of 11–16% in COI and 8–9% in 16S. These distances correspond well with amounts of interspecific variation found in Australian *Rhagada* species (about 4%; Johnson et al., 2012) as well as other camaenid genera, such as *Exiligada* (about 3%; Criscione et al., 2012) and *Amplirhagada* (about 6%; Köhler & Johnson, 2012). However, extreme intraspecific distances of up to 10% have occasionally also been observed in camaenid snails (Chiba, 1999; Criscione & Köhler, 2013a).

Progress has been made towards a more complete documentation of the diversity of *Rhagada* across the

Lesser Sunda Islands. However, complete sampling on all Lesser Sunda Islands is required to address the remaining taxonomic issues and to improve our understanding of the evolution of this group throughout the entire archipelago.

ACKNOWLEDGEMENTS

Special thanks are due to John Abbas and Vince Kessner for providing study material. Field work in Timor-Leste was conducted with permission from Manuel Mendes, Director for Protected Areas and National Parks, Ministry of Agriculture and Fisheries, Dili. Thanks are also due to Michael Shea (Sydney) for producing anatomical drawings and to Francesco Criscione (Sydney) for help with DNA work.

LITERATURE CITED

Chiba S (1999) Accelerated evolution of land snails *Mandarina* in the oceanic Bonin Islands: evidence from mitochondrial DNA sequences. Evolution, 53: 460–471.

Criscione F & Köhler F (2013a) Conserved shell disguises diversity in *Mesodontrachia* land snails from the Australian Monsoon Tropics (Gastropoda: Camaenidae). Zoologica Scripta, 42: 389–405.

Criscione F & Köhler F (2013b) Six new species of *Australocosmica* Köhler, 2011 from the Kimberley Islands, Western Australia (Mollusca: Pulmonata: Camaenidae). Zootaxa, 3608: 101–115.

Criscione F, Law ML & Köhler F (2012) Land snail diversity in the monsoon tropics of Northern Australia: revision of the genus *Exiligada* Iredale, 1939 (Mollusca: Pulmonata: Camaenidae), with description of 13 new species. Zoological Journal of the Linnean Society, 166: 689–722.

Falconieri A (1995) *Rhagada marghitae* species nova. World Shells, 14: 81–84.

Folmer O, Black M, Hoeh W, Lutz R & Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology, 3: 294–299.

Hedley C (1916) A preliminary index of the Mollusca of Western Australia. Journal of the Royal Society of Western Australia, 1: 1–77.

Iredale T (1938) A basic list of the land Mollusca of Australia. Part III. Australian Zoologist, 9: 83–124.

Iredale T (1939) A review of the land Mollusca of Western Australia. Records of the Western Australian Museum and Art Gallery, 2: 1–88.

Johnson MS & Black R (1991) Growth, survivorship, and population size in the land snail *Rhagada convicta* Cox, 1870 (Pulmonata: Camaenidae) from a semiarid environment in Western Australia. Journal of Molluscan Studies, 57: 367–374.

Johnson MS, Hamilton ZR & Fitzpatrick J (2006) Genetic diversity of *Rhagada* land snails on Barrow Island. Journal of the Royal Society of Western Australia, 89: 45–50.

Johnson MS, Hamilton ZR, Murphy CE, MacLeay CA, Roberts B & Kendrick PG (2004) Evolutionary genetics of island and mainland species of *Rhagada* (Gastropoda: Pulmonata) in the Pilbara Region, Western Australia. Australian Journal of Zoology, 52: 341–355.

Johnson MS, Hamilton ZR, Teale ROY & Kendrick PG (2012) Endemic evolutionary radiation of *Rhagada* land snails (Pulmonata: Camaenidae) in a continental archipelago in northern Western Australia. Biological Journal of the Linnean Society, 106: 316–327.

Köhler F (2011) The camaenid species of the Kimberley Islands, Western Australia (Stylommatophora: Helicoidea). Malacologia, 54: 203–406.

Köhler F & Criscione F (2013) Plio-Pleistocene out-of-Australia dispersal in a camaenid land snail. Journal of Biogeography, 40: 1971–1982.

Köhler F & Johnson MS (2012) Species limits in molecular phylogenies: a cautionary tale from Australian land snails (Camaenidae: *Amplirhagada*). Zoological Journal of the Linnean Society, 165: 337–362.

Maassen WJM (2009) A new *Rhagada* species from Alor Island, Lesser Sunda Islands, Indonesia (Gastropoda, Pulmonata, Camaenidae). Miscellanea Malacologica, 3: 65–69.

Martens E von (1891) Landschnecken des Indischen Archipels In: M. Weber (ed.) Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien. Band 2. Brill, Leiden. Pp. 209–263, pls. XII–XIV.

Martens E von & Albers JC (1860) Die Heliceen nach natuerlicher Verwandtschaft. 2. Ausgabe. Engelmann, Leipzig, 394 pp.

Pilsbry HA (1890) Helicidae, Vol. IV. Manual of Conchology, Structural and Systematic, with Illustrations of the Species. Second Series: Pulmonata. Conchological Section, Academy of Natural Sciences, Philadelphia. Pp. 1–324, pls. 1–69.

Pilsbry HA (1894) Helicidae, Vol. VII. Manual of Conchology, Structural and Systematic, with Illustrations of the Species. Second Series: Pulmonata. Conchological Section, Academy of Natural Sciences, Philadelphia. Pp. 1–366, pls. 1–71.

Preston HB (1908) Description of a new species of *Rhagada* from Western Australia. Proceedings of the Malacological Society of London, 8: 120.

Preston HB (1914) Description of new species of land and marine shells from the Montebello Island, Western Australia. Proceedings of the Malacological Society of London, 11: 13–18.

Rensch B (1931) Die Molluskenfauna der Kleinen Sunda-Inseln Bali, Lombok, Sumbawa, Flores und Sumba. I. Zoologische Jahrbücher. Abteilung für Systematik Ökologie und Geographie der Tiere, 61: 361–396.

Ronquist F & Huelsenbeck JP (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

Schepman MM (1892) Land and freshwater shells collected by Dr. H. Ten Kate in Soemba, Timor, and other East-Indian Islands. Notes from the Leyden Museum 14: 145–160.

Solem A (1985a) Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). V. Remaining Kimberley genera and addenda to the Kimberley. Records of the Western Australian Museum, Supplement 20: 707–981.

Solem A (1985b) Simultaneous character convergence and divergence in Western Australian land snails. Biological Journal of the Linnean Society, 24: 143–136.

Solem A (1991) Land snails of Kimberley rainforest patches and biogeography of all Kimberley land snails. In: McKenzie NL, Johnston RB & Kendrick PG (eds.) Kimberley Rainforests of Australia. Surrey Beatty & Sons and Department of Conservation and Land Management Western Australia, Canberra. Pp. 145–246.

Solem A (1997) Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). VII. Taxa from Dampierland through the Nullabor. Records of the Western Australian Museum, Supplement 50: 1461–1906.

Solem A & McKenzie NL (1991) The composition of land snail assemblages in Kimberley rainforests. In: McKenzie, NL, Johnston RB & Kendrick PG (eds.) Kimberley Rainforests of Australia. Surrey Beatty & Sons and Department of Conservation and Land Management Western Australia, Canberra. Pp. 247–263.

Sutcharit C, Asami T & Panha S (2007) Evolution of whole-body enantiomorphy in the tree snail genus *Amphidromus*. Journal of Evolutionary Biology, 20: 661–672.

Stankowski S (2011) Extreme, continuous variation in an island snail: local diversification and association of shell form with the current environment. Biological Journal of the Linnean Society, 104: 756–769.

Stankowski S (2013) Ecological speciation in an island snail: evidence for the parallel evolution of a novel ecotype and maintenance by ecologically dependent postzygotic isolation. Molecular Ecology, 22: 2726–2741.

Tamura K, Peterson D, Peterson N, Stecher G, Nei M & Kumar S (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony Methods. Molecular Biology and Evolution, 28: 2731–2739.

Vermeulen JJ & Whitten AJ (1998) Fauna Malesiana. Guide to the Land Snails of Bali. Backhuys Publishers, Leiden. Pp. 1–164.

Voris HK (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. Journal of Biogeography, 27: 1153–1167.

Wiegmann F (1893) Beiträge zur Anatomie der Landschnecken des Indischen Archipels. In: M. Weber (ed.) Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien. Band 3. Brill, Leiden. Pp. 112–259.

Withers P, Pedler S & Guppy M (1997) Physiological adjustments during aestivation by the Australian land snail *Rhagada tescorum* (Mollusca: Pulmonata: Camaenidae). Australian Journal of Zoology, 45: 599–611.