



**Monograph**

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**Revision of the land snail genus *Landouria* Godwin-Austen, 1918  
(Gastropoda, Camaenidae) from Java**

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**Abstract.** A revision of the land snail genus *Landouria* Godwin-Austin, 1918 (Camaenidae) from Java reveals that this group represents the most diverse land snail radiation on that island. Only six species of *Landouria* were recognized from Java in the last revision of the genus based on shell characters. Our investigation, which also considers the genitalia as well as DNA sequences, shows that the diversity in Java is much higher. Based on newly collected specimens as well as museum material, twenty-eight species of *Landouria* from Java are described and figured. To stabilize the nomenclature, neotypes are designated for *L. winteriana* (Pfeiffer, 1842) and *L. rotatoria* (Pfeiffer, 1842). Sixteen species are described as new to science, i.e., *L. naggsi* sp. nov., *L. parahyangensis* sp. nov., *L. nusakambangensis* sp. nov., *L. petrukensis* sp. nov., *L. tholiformis* sp. nov., *L. madurensis* sp. nov., *L. abdidalem* sp. nov., *L. sewuensis* sp. nov., *L. tonywhitteni* sp. nov., *L. sukoliloensis* sp. nov., *L. nodifera* sp. nov., *L. pacitanensis* sp. nov., *L. zonifera* sp. nov., *L. pakidulan* sp. nov., *L. dharmai* sp. nov. and *L. menorehensis* sp. nov. *Landouria conoidea* (Leschke, 1914) comb. nov., *L. intumescens* (Martens, 1867) comb. nov., *L. moussoniana* (Martens, 1867) comb. nov., *L. schepmani* (Möllendorff, 1897) comb. nov. and *L. leucochila* (Gude, 1905) comb. nov. are considered valid species of the genus *Landouria* for the first time. *Plectotropis kraepelini* Leschke, 1914 syn. nov. is considered a probable synonym of *L. winteriana* (Pfeiffer, 1842), *P. trichotrochium* Möllendorff, 1897 syn. nov. is a synonym of *L. epiplatia* (Möllendorff, 1897) and the preoccupied name *Helix squamulosa* Martens, 1867 syn. nov. is a synonym of *L. madurensis* sp. nov. We estimate that there are actually more than fifty species of *Landouria* in Java because many shell samples could not be classified and because no material is available from several regions of the island. A molecular phylogeny reveals that the species from Java do not form a monophyletic group, but that at least one species from Timor is nested within Javanese clades. This means that the Oriental *Landouria* crossed Wallace's line, the supposed border between the Oriental and Australo-Papuan regions, at least twice and supports the conclusion that Wallace's line does not represent a more severe barrier for terrestrial organisms than other straits through the archipelago. Within the Javanese clades, species from western and eastern Java are mixed, indicating frequent dispersals also within Java.

**Keywords.** Camaenidae, Indonesia, Java, *Landouria*, phylogeny.

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## Introduction

The Aegistini Kuroda & Habe, 1949 (Bradybaeninae Pilsbry, 1934 (1898), Camaenidae Pilsbry, 1895, in the sense of Bouchet *et al.* 2017, corresponding to *Aegista* Albers, 1850 in the sense of Hirano *et al.* 2014) are a highly diverse group of land snails, which is mainly distributed in East and Southeast Asia (Schileyko 2004; Hirano *et al.* 2014). In the Indo-Australian Archipelago, they are represented by species with a depressed, often angular or keeled, usually brownish-corneous shell with a wide umbilicus. Some of these species were placed in the East Asian group *Plectotropis* Martens, 1860 by Martens (1867). However, Wiegmann (1893) could not find a dart apparatus in two juvenile specimens of two species from Sumatra and Java, whereas a dart apparatus is present in the East Asian representatives of *Plectotropis* (Pilsbry 1895 in 1893–1895; Schileyko 2004). Rensch (1932) confirmed the lack of the dart apparatus in adult specimens from the Sunda Islands and suggested the transfer of species from the Indo-Australian Archipelago to *Landouria* Godwin-Austen, 1918. *Landouria* was established for species without a dart apparatus from the Himalayas, eastern India, Myanmar and Sri Lanka by Godwin-Austen (1918). Schileyko & Kuznetsov (1998) recognized that *Landouria* belongs to the Aegistinae Kuroda & Habe, 1949 despite the lack of the dart apparatus. They described additional species from the Himalayas and questioned the placement of the species from the Indo-Australian Archipelago in *Landouria*. However, Schileyko (2004) continued to include them with a question mark in *Landouria*. Páll-Gergely *et al.* (2013) described an additional species from southern China and questioned the placement of *L. radleyi* (Jousseume, 1894) from Sri Lanka in *Landouria*. The molecular phylogeny of Hirano *et al.* (2014) showed that *Landouria* belongs to the Aegistini and is the sister taxon of a group of high-spined species from the Ryukyu Islands and Taiwan, which were formerly erroneously included in the Chinese *Pseudobuliminus* Gredler, 1887 and which also lack a dart apparatus. Thus, the loss of the dart apparatus is probably a synapomorphy of this group and *Landouria*. However, Hirano *et al.* (2014) also showed that the dart apparatus was lost independently at least three times in the Aegistini. Hirano *et al.* (2014) suggested tentatively to include all species of the Aegistini in a single genus *Aegista*. This genus would include approximately 200 species distributed from Korea and Japan to India, Nepal and Indonesia, and would display a high disparity with regard to shell and genital morphology. We prefer to split this complex into smaller taxa to facilitate discussions of biogeography, character evolution and other aspects. Thus, we continue the use of the name *Landouria* for the clade of South Asian species with a depressed shell and without a dart apparatus. This opinion is shared by Köhler *et al.* (in press), who revised the species from Timor-Leste.

The earliest records of *Landouria* in Java date back to Pfeiffer (1842). Sixteen nominal species presumably belonging to *Landouria* had been described from Java until 1950. However, van Benthem Jutting (1950) considered only six of them valid in her revision based on shell characters. One additional species from Java has recently been described by Dharma (2015).

The study of recently collected material proved that many samples could not be unambiguously assigned to the species delimited by van Benthem Jutting (1950) based on shell characters. The anatomy of most of these species has remained unknown. Thus, we started a revision of the genus *Landouria* from Java by applying an integrative approach combining shell morphology, characters of the genitalia and DNA sequences. Our work revealed the most diverse land snail radiation on Java. We describe or redescribe 28 species here, but we consider it possible that there are about twice as many species of *Landouria* on Java.

## Material and methods

### Material, morphology and geographic data

This study is based on material from surveys by the first author in Java and surrounding islands in 2013–2015 as well as museum collections. Most living specimens were killed and preserved in alcohol without extracting the soft body from the shell. We usually made a small hole in the umbilical side at the beginning of the last whorl to sever the columellar muscle, so that at least the anterior part of the body with the taxonomically important distal genitalia could be extracted while keeping shell damage to a minimum.

The material is kept in the following institutions:

- AM = Australian Museum, Sydney, Australia
- BDJ = private collection of Bunjamin Dharma, Jakarta, Indonesia
- MZB = Museum Zoologicum Bogoriense, Bogor, Indonesia
- NHM = Natural History Museum, London, United Kingdom
- RMNH = Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden, the Netherlands
- SMF = Senckenberg Museum, Frankfurt, Germany
- ZMA = the former Zoologisch Museum, Amsterdam, the Netherlands (now in RMNH)
- ZMB = Museum für Naturkunde, Berlin, Germany
- ZMH = Zoological Museum of the University of Hamburg, Germany
- ZMZ = Zoological Museum Zürich, Switzerland

We measured the diameter (D) and height (H) of the shell, the diameter of the third whorl (D3W), the diameter of the inner edge of the umbilicus at the largest diameter of the shell (U), and the diameter (da) and height (ha) of the aperture with a digital calliper or an ocular micrometer (accurate to 0.1 mm) and counted the number of whorls with an accuracy of 0.25 whorls following the method described by Kerney & Cameron (1979). In the descriptions of the genitals, the terms proximal and distal refer to the position in relation to the gonad. Stacked images of shells were taken with the Passport Imaging System (Dun, Palmyra, VA, USA) with a Canon EOS 6D camera (Canon Inc., Tokyo, Japan) and processed with Helicon Focus (HeliconSoft, Kharkiv, Ukraine) and Adobe Photoshop (Adobe Systems Inc., San José, CA, USA) software.

In the lists of material examined, localities are ordered in provinces and listed from west to east. We specify for each locality whether we examined the genitalia of one or several specimens from that locality (det. anat. = anatomically determined). For newly designated name-bearing types, we specify the collector (leg. = collected by).

The International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999) is abbreviated as ICZN.

### DNA extraction, amplification and sequencing

Total genomic DNA was extracted from the foot muscle tissue of recently collected specimens stored in 70% ethanol (for voucher numbers see Table 1) using a slightly modified version of the protocol of Sokolov (2000) as described in Scheel & Hausdorf (2012).

Fragments of the mitochondrial 16S rDNA were amplified by polymerase chain reaction (PCR) using the primer pair 16Scs1 (Chiba 1999) plus 16S\_MN3R (Neiber *et al.* 2017). If the PCR with this primer combination was not successful, newly designed internal forward and reverse primers were used in combination with one of the above listed primers: 16S\_BF1 (5'-CCA TCR AAA AGT ATY WAG TAC-3')

**Table 1** (continued on next page). Museum catalogue numbers, DNA voucher numbers and GenBank accession numbers for the specimens and DNA sequences used in the molecular phylogenetic analyses. All localities in Java unless otherwise specified.

Taxon	Locality	Museum number	DNA voucher	GenBank accession number (16S rDNA)
<i>L. abdidalem</i> sp. nov.	Kulonprogo, Sibolong, near Kiskendo Cave (holotype)	MZB 21271	ZMH Extr 3928	MK608364
<i>L. ciliocincta</i>	Malang, Kondangmerak	MZB 19211	AYLAN16	MK608365
<i>L. epiplatia</i>	Bogor, Gunung Gede	ZMH 79946	AYLAN45	MK608366
<i>L. intumescens</i>	Tuban, Montong, Guwoterus, sumber Krawak	MZB 19207	AYLAN33	MK608367
<i>L. madurensis</i> sp. nov.	Madura Island, Sampang (holotype)	MZB 21432	AYLAN17	MK608368
<i>L. menorehensis</i> sp. nov.	Kulonprogo, Sibolong (holotype)	MZB 19201	AYLAN12	MK608369
<i>L. montana</i>	Timor-Leste, Tirsfu near Kampung Qeurema	AM C477070	–	MH521075 <sup>1</sup>
<i>L. montana</i>	Timor-Leste, Mundo Perdido Protected Area, Mt Laritame	AM C477047	–	MH521080 <sup>1</sup>
<i>L. nodifera</i> sp. nov.	Pati, Larangan Village (paratype)	MZB 21266	AYLAN8	MK608370
<i>L. omphalostoma</i>	China, Yunnan, Xiangyun Xian, entrance of the Qinghuadong	HNHM 98758	PGB-a	MH521068 <sup>1</sup>
<i>L. omphalostoma</i>	China, Yunnan, Xiangyun Xian, entrance of the Qinghuadong	HNHM 98758	PGB-b	MH521069 <sup>1</sup>
<i>L. pacitanensis</i> sp. nov.	Pacitan, Srau Beach (holotype)	MZB 21191	AYLAN35	MK608371
<i>L. rotatoria</i>	Bogor, Blok kancil (neotype)	MZB 19205	AYLAN39	MK608372
<i>L. sewuensis</i> sp. nov.	Gunung Kidul, Tepus, near Poktunggal Beach (paratype)	MZB 21269	AYLAN6a	MK608373
<i>L. sewuensis</i> sp. nov.	Gunung Kidul, Tepus, Mbajo Hill (holotype)	MZB 19255	AYLAN42	MK608374
<i>L. sewuensis</i> sp. nov.	Gunung Kidul, Tepus, Mbajo Hill (paratype)	MZB 19256	AYLAN5	MK608375
<i>L. sewuensis</i> sp. nov.	Gunung Kidul, Tepus, near Poktunggal Beach (paratype)	ZMH 79891	–	MK613237
<i>L. sukoliloensis</i> sp. nov.	Pati, Kayen, near Watu Payung (holotype)	MZB 19219	ZMH Extr 3931	MK613236
<i>L. sukoliloensis</i> sp. nov.	Pati, Sukolilo, Kedumulyo (paratype)	MZB 19222	AYLAN37	MK608376
<i>L. tholiformis</i> sp. nov.	Gunung Kidul, Tepus, near Poktunggal Beach (holotype)	MZB 17999	AYLAN14	MK608377
<i>L. timorensis</i>	Timor-Leste, Atauro Island, 1.5 km N of Beloi (paratype)	AM C468777a	–	MH521081 <sup>1</sup>

<sup>1</sup> Köhler *et al.* (in press).

**Table 1** (continued).

Taxon	Locality	Museum number	DNA voucher	GenBank accession number (16S rDNA)
<i>L. timorensis</i>	Timor-Leste, Atauro Island, Villa, 1.8 km WSW of Tua Coin Eco Village	AM C470449	–	MH521079 <sup>1</sup>
<i>L. tonywhitteni</i> sp. nov.	Grobogan, Taruman (holotype)	MZB 19214	AYLAN50	MK608378
<i>L. tonywhitteni</i> sp. nov.	Grobogan, Taruman (paratype)	MZB 21268	AYLAN28	MK608379
<i>L. winteriana</i>	Bogor, Cisarua	MZB 19235	AYLAN21	MK608380
<i>L. winteriana</i>	Padalarang, Gunung Pawon	MZB 19236	AYLAN24	MK608381
<i>L. zonifera</i> sp. nov.	Kulonprogo, Sibolong (holotype)	MZB 17727	AYLAN47	MK608382
<i>L. zonifera</i> sp. nov.	Kulonprogo, Jonggrangan	ZMH 140031	ZMH Extr 3929	MK608383
<i>L. sp.</i>	Timor-Leste, Manatuto District, 4.7 km E of Laclubar	AM C477078	–	MH521073 <sup>1</sup>
<i>Mandarina suenoae</i>	Japan, Chichijima Archipelago, Anijima	–	–	AY829638 <sup>2</sup>
<i>Euhadra peliomphala</i>	Japan, Izu Peninsula, Nagaoka	–	–	AF104053 <sup>3</sup>

<sup>1</sup> Köhler *et al.* (in press); <sup>2</sup> Davison & Chiba (2006); <sup>3</sup> Hayashi & Chiba (2000).

plus 16S\_MN3R, 16Scs1 plus 16S\_BR1 (5'-CAA AGC CTA RAC ACY GYG CA-3') or 16Scs1 plus 16S\_BR2 (5'-CAA AGC CTG GCC ACT RYG CA-3').

Amplifications were performed in 25 µL volumes containing 18.3 µL ddH<sub>2</sub>O, 2.5 µL Dream Taq™ Green Buffer (Thermo Fisher Scientific, Waltham, MA, USA), 1.0 µL of a dNTP mix (5 mM each), 1.0 µL of each primer (10 µM), 0.2 µL DreamTaq™ DNA polymerase (Thermo Fisher Scientific) and 1.0 µL of the template DNA under the following reaction conditions: an initial denaturation step at 94 °C for 2 min, 35–45 PCR cycles (94 °C for 30 s, 50 °C for 30 s, 72 °C for 30 s) and a final extension step at 72 °C for 5 min. Both strands of the amplified products were sequenced at MacroGen Europe Laboratory (Amsterdam, the Netherlands).

#### Phylogenetic analyses of DNA sequence data

Forward and reverse sequences were assembled using ChromasPro 1.7.4 (Technelysium, Tewantin, QLD, Australia). Obtained sequences were deposited in GenBank (for accession numbers see Table 1). Additionally, we included sequences from species of *Landouria* from the study of Köhler *et al.* (in press) as well as sequences of *Mandarina suenoae* Minato, 1978 (Davison & Chiba 2006) and *Euhadra peliomphala* (Pfeiffer, 1850) (Hayashi & Chiba 2000) as outgroups (see Table 1). The 16S rDNA sequences were aligned with MAFFT 7 (Katoh *et al.* 2017), using the Q-INS-i strategy and otherwise default settings.

An appropriate evolutionary model was selected with PartitionFinder 2.1.1 (Lanfear *et al.* 2016) conducting an exhaustive search, with the Bayesian information criterion to select among models and partitions. The models were limited to those available in MrBayes 3.2.6 (Ronquist *et al.* 2012) as well as those in GARLI 2.1 (Zwickl 2006). The PartitionFinder analysis suggested the HKY+I+G model.

Bayesian inference (BI) and maximum likelihood (ML) analyses were used to reconstruct phylogenetic relationships. The BI analysis was performed using MrBayes 3.2.6. Metropolis-coupled Monte Carlo Markov chain (MC<sup>3</sup>) searches were run with four chains in two separate runs, with 50 000 000 generations with default priors, trees sampled every 1000 generations under default heating using the evolutionary model as suggested by the PartitionFinder analyses. The first 50 000 generations of each run were discarded as a burn-in.

The ML analysis was performed using GARLI ver. 2.1 (<http://www.bio.utexas.edu/faculty/antisense/garli/Garli.html>), with the evolutionary model as suggested by PartitionFinder and otherwise default settings from the standard configuration file. Support values were calculated by bootstrapping with 1000 replications.

Bootstrap support (BS) values from the ML analysis, as well as posterior probabilities (PP) from the BI analysis, were mapped on the BI 50% majority rule consensus tree with SumTrees ver. 3.3.1, which is part of the DendroPy ver. 3.8.0 package (Sukumaran & Holder 2010).  $PP \geq 0.95$  and  $BS \geq 70$  were interpreted as positive support for nodes.

## Results

### *Molecular phylogeny*

The aligned 16S rDNA fragments had a length of 526 base pairs. The p-distances between 16S rDNA sequences of different species of *Landouria* from Java and Madura Island vary between 0.026 and 0.310 (Table 2) and reach up to 0.384 between the Indonesian species and *L. omphalostoma* Páll-Gergely & Hunyadi, 2013 from China. The high p-distances between the morphologically delimited species from Java (Table 2) support the conclusion that these populations really represent distinct species, even though some differ only in a few characters of the genitalia.

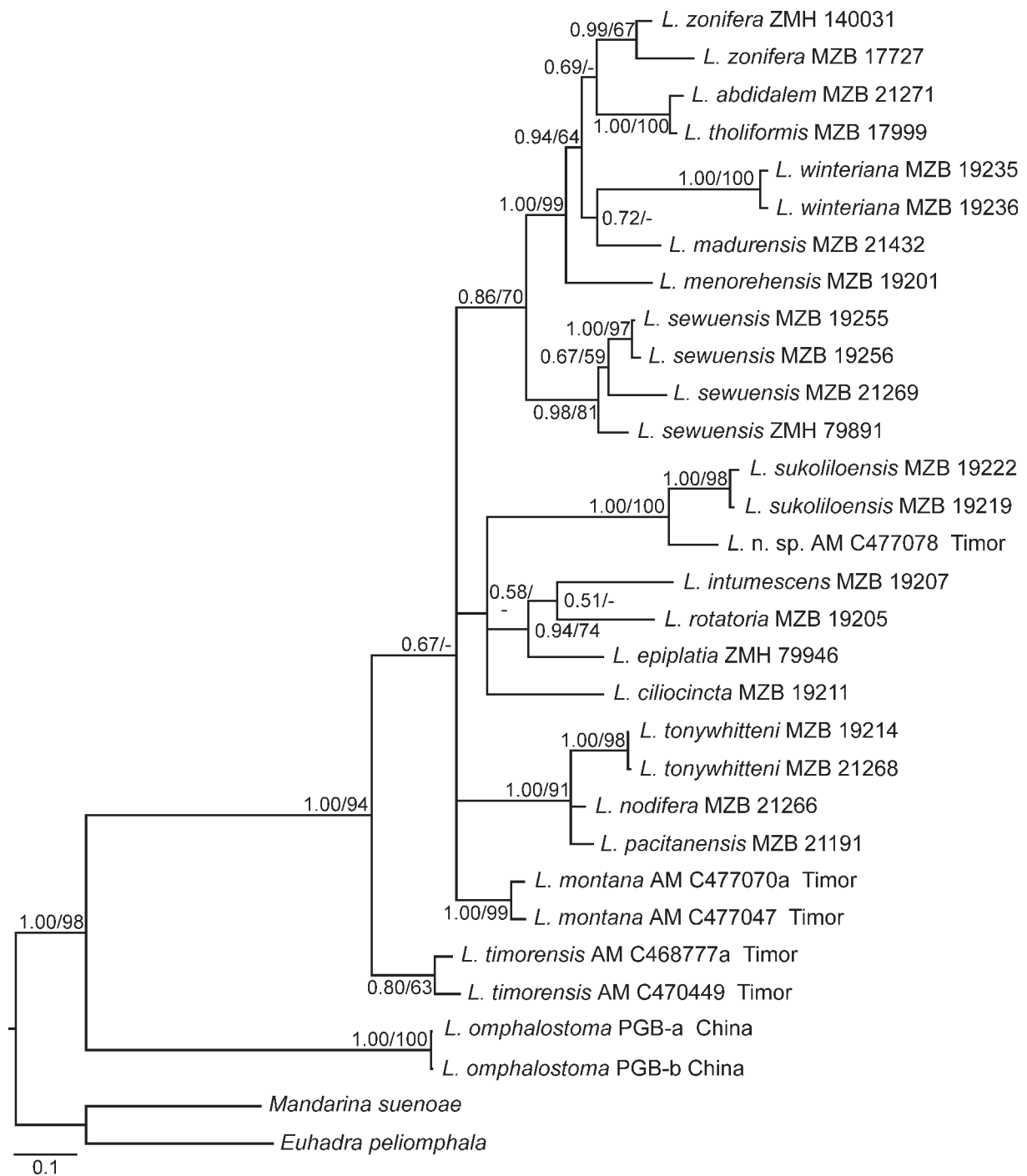
In the ML and BI analyses of the 16S rDNA sequences, *L. omphalostoma* from China represents the sister group of the Indonesian species of *Landouria* (Fig. 1). The Javanese species that are represented by several specimens form monophyletic groups in the 16S rDNA tree (Fig. 1). However, the species of *Landouria* from Java do not form a monophyletic group. At least *Landouria* sp. nov. (= *L. winteriana* (not Pfeiffer, 1842) in Köhler *et al.* in press) from Timor is nested within Javanese clades. The relationships of *L. timorensis*\* Köhler *et al.*, in press and *L. montana*\* Köhler *et al.*, in press from Timor and the Javanese clades are not resolved and it cannot be excluded that these two species from Timor form a clade. Nevertheless, Timor has been colonized at least twice. This means that the Oriental *Landouria* crossed Wallace's line, the supposed border between the Oriental and Australo-Papuan regions, at least twice. This supports the conclusion that Wallace's line does not represent a more severe barrier for terrestrial organisms than other straits through the archipelago (Hausdorf 2019). Within the Javanese clades, species from western and eastern Java are mixed, indicating frequent dispersals also within Java.

The three species that are characterized by the unusual node at the flagellum and/or a distinct penis coecum, *L. tonywhitteni* sp. nov., *L. nodifera* sp. nov. and *L. pacitanensis* sp. nov. form a clade. However, it remains unclear whether the node at the flagellum is a synapomorphy of *L. tonywhitteni* sp. nov. and *L. nodifera* sp. nov. (or was lost in *L. pacitanensis* sp. nov.) and whether the penis coecum is a synapomorphy of *L. nodifera* sp. nov. and *L. pacitanensis* sp. nov. (or was lost in *L. tonywhitteni* sp. nov.), because the relationships among these three species were not resolved.

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\* Note that the names *Landouria timorensis* and *L. montana* were not made available by the preliminary online version of Köhler *et al.* (in press) according to ICZN Art. 8.5.3, 9.9 and 21.8.3, and will only become available when the print version is published.





**Fig. 1.** Bayesian 50% majority rule consensus tree based on mitochondrial 16S rDNA sequences of species of *Landouria* Godwin-Austen, 1918 with *Mandarina suenoae* Minato, 1978 and *Euhadra peliomphala* (Pfeiffer, 1850) as outgroups. All species of *Landouria* in this tree are from Java except *L. omphalostoma* Páll-Gergely & Hunyadi, 2013 from China and *L. timorensis* Köhler *et al.* in press, *L. montana* Köhler *et al.* in press and *Landouria* sp. nov. (= *L. winteriana* (non Pfeiffer, 1842) in Köhler *et al.* (in press)) from Timor. Values at the nodes represent Bayesian posterior probabilities (left) and maximum likelihood bootstrap values (right). Numbers after taxon names correspond to MZB and ZMH catalogue numbers, AM catalogue numbers or GenBank accession numbers (see Table 1).



*Landouria ciliocincta* (Möllendorff, 1897) (Figs 83–84) and *L. menorehensis* sp. nov. (Fig. 88) share a whitish basic coloration of the shell, whereas the basic coloration of the shell is brownish-corneous in most species of *Landouria*. The molecular phylogeny indicates that the species with a whitish basic coloration of the shell do not form a clade and, thus, that the transition from a brownish-corneous to a whitish basic coloration of the shell occurred convergently in different clades of *Landouria*. Whereas the species with a brownish-corneous basic coloration of the shell usually live among debris on the forest floor, *L. menorehensis* sp. nov. lives on banana trees and on the leaves of snakefruit trees and the whitish basic coloration of the shell might be an adaptation to an arboreal life style.

### **Systematics**

Family Camaenidae Pilsbry, 1895

Subfamily Bradybaeninae Pilsbry, 1934 (1898)

Tribe Aegistini Kuroda & Habe, 1949

Genus *Landouria* Godwin-Austen, 1918

*Landouria* Godwin-Austen, 1918: 604 (type species by original designation: *Helix huttonii* Pfeiffer, 1842 (new name for *Helix orbicula* Hutton & Benson, 1838, not *H. orbicula* Orbigny, 1835)).

*Thaitropis* Schileyko, 2004: 1632, fig. 2104 (type species by original designation: *Helix goniochila* Pfeiffer, 1862 (= *Helix ptychostyla* Martens, 1860; see Schileyko 2011)).

### **Remarks**

Schileyko & Kuznetsov (1998) pointed out that the features of *Landouria* correspond to those of *Aegista* with the exception of the lack of a dart apparatus. Furthermore, they supposed that the dart apparatus might have been lost several times within the Aegistini, once in the Indian lineage and once in the lineage of the species from the Indo-Australian Archipelago and the Philippines. They argued that this hypothesis is also supported by the different structure of the flagellum, which bears external tubercles in the continental lineage but is indented in the Archipelagic lineage. The molecular phylogeny of Hirano *et al.* (2014) showed that the dart apparatus was actually lost at least three times within the Aegistini and other studies have shown that the loss of the dart apparatus is also a common homoplasy in other groups of the Helicoidea (Neubert 1998, 2014; Wade *et al.* 2007; Neiber & Hausdorf 2015; Neiber *et al.* 2017). However, the molecular phylogeny of Köhler *et al.* (in press) showed that the species of *Landouria* from the Sunda Islands form a clade with *L. omphalostoma* Páll-Gergely & Hunyadi, 2013 from China. The structure of the flagellum is variable in the species from the Asian mainland (Schileyko & Kuznetsov 1998; Páll-Gergely *et al.* 2013) as well as in those from the Indo-Australian Archipelago (see Köhler *et al.* in press and results below). Thus, there is no reason to assume an independent loss of the dart apparatus in the continental and Archipelagic lineages.

Hirano *et al.* (2014) showed that *Landouria* is the sister taxon of a group of high-spired species from the Ryukyu Islands and Taiwan, which were formerly erroneously included in the Chinese *Pseudobuliminus* Gredler, 1887, which also lack a dart apparatus. Thus, the loss of the dart apparatus is probably a synapomorphy of this group and *Landouria*. *Landouria* differs from this group in the depressed conical or globular shell, which usually has periostracal scales or hairs. However, these character states are plesiomorphies that *Landouria* shares, e.g., with *Aegista*. Currently, no morphological apomorphies of *Landouria* are known.

Schileyko (2004) separated two species from Thailand in a distinct genus, *Thaitropis*. He considered a sharp constriction between the epiphallus and penis as the main diagnostic character of *Thaitropis*. We also found a similar constriction in *L. pacitanensis* sp. nov. and in a less drastic form in *L. intumescens*

(Martens, 1867) and *L. smimensis* (Mousson, 1848) from Java. There is a verge in the dilatation proximal of the constriction in *L. pacitanensis* sp. nov. Thus, the constriction is not situated between the epiphallus and penis, but within the penis. Schileyko did not find a verge, but there is also a small dilatation proximal of the constriction in the Thai species figured by Schileyko. Thus, we suppose that the constriction is also within the penis in the Thai species. As long as the phylogenetic relationships within *Landouria* are not better resolved and the genus is not further subdivided, we consider *Thaitropis* to be a synonym of *Landouria*. However, it is possible that the Southeast Asian species and the Himalayan species, to which the type species of *Landouria*, *L. huttonii* (Pfeiffer, 1842), belongs, form separate clades that might be classified at least as subgenera. In this case the name *Thaitropis* would be available for the Southeast Asian clade.

In the following, the species are ordered according to similarities to facilitate comparisons.

***Landouria winteriana* (Pfeiffer, 1842)**

Figs 2–3, 15, 29, 52; Tables 3–4

*Helix winteriana* Pfeiffer, 1842: 41 (“Java”).

?*Plectotropis kraepelini* Leschke, 1914: 211, figs 5–7 (“Tjibodas”). **Syn. nov.**

*Helix winteriana* – Philippi 1843 in 1842–1845: 23, pl. II.1, fig. 7. — Pfeiffer 1851 in 1849–1853: pl. 95, figs 1–2; 1852 in 1849–1853: 162. — Martens 1867: 264 (in part).

*Plectotropis sumatrana* var. *moussoniana* – Leschke 1914: 211. (not Martens, 1867)

*Landouria winteriana* – van Benthem Jutting 1950: 463 (in part).

*Landouria rotatoria* – van Benthem Jutting 1950: 461 (in part). — Smith & Djajasasmita 1988: 394, pl. 2 fig. 10. (not Pfeiffer, 1842)

*Landouria* cf. *rotatoria* – Köhler *et al.* in press: 6, figs 3A, 5 (in part). (not Pfeiffer, 1842)

**Diagnosis**

*Landouria winteriana* is characterized by a brownish-corneous, depressed conical, keeled shell with a wide umbilicus, a penis with a large globular bulge at the proximal end and a flagellum consisting of a crenated distal part and a short tapering proximal part.

**Material examined**

**Type material**

INDONESIA – **West Java** • 1 syntype of *Plectotropis kraepelini*; Cibodas; 6°45' S, 107°01' E; ZMH 98416 • neotype of *Helix winteriana* (designated here) (det. anat.) (voucher for *L. rotatoria* in van Benthem Jutting 1950); Padalarang, Gunung Masigit; 6°50' S, 107°26' E; 500 m a.s.l.; Jan. 1938; W.Ch. Voute leg.; measurements: D = 12.6 mm, H = 6.9 mm; ZMA 376193a.

**Other material**

INDONESIA – **West Java** • 1 spec. (det. anat.); Bogor, Cisarua, Halimun Salak National Park, 1166 m a.s.l.; 6°39'03" S, 106°27'15" E; MZB 19235 • 1 spec. (voucher for van Benthem Jutting 1950); Bogor, Gunung Salak; 1200 m a.s.l.; ZMA 407749 • 4 spec.; Bogor, Cigudeg, Sipahang Cave (in Gudawang cave complex), agroforestry; 6°27'00" S, 106°31'00" E; 91 m a.s.l.; MZB 17602 • 7 spec.; Bogor, Ciampea, limestone hill Gunung Cibodas, secondary forest; 6°33'05" S, 106°41'09" E; 296 m a.s.l.; MZB 19238 • 98 spec.; same data as for preceding; MZB 19239 • 11 spec.; same data as for preceding; MZB 19240 • 6 spec.; same data as for preceding; ZMH 133425 • 30 spec.; same data as for preceding; ZMH 133426 • 4 spec.; same data as for preceding; ZMH 133427 • 3 spec.; Bogor, Ciampea, limestone hill Gunung Cibodas, inside Si Panjang Cave; 6°33'09" S, 106°41'13" E; 357 m a.s.l.; MZB 19279 • 3 spec.; Bogor, Ciampea, limestone hill Gunung Cibodas, Si Ase (Si Gajah) cave mouth; 6°33'08" S, 106°41'14" E;

309 m a.s.l.; MZB 19249 • 1 spec. (voucher for *P. sumatrana* var. *moussoniana* in Leschke 1914); Ciampea; 6°33' S, 106°42' E; ZMH 20426 • 3 spec. (det. anat.); Bogor, Pabaton 25; 6°35'22" S, 106°47'33" E; ZMA 369719 • 2 spec. (vouchers for *P. sumatrana* var. *moussoniana* in Leschke 1914); Bogor; 6°36' S, 106°48' E; ZMH 20425 • 1 spec.; Bogor; 6°36' S, 106°48' E; 230 m a.s.l.; ZMA 407751 • >10 spec. (vouchers for van Benthem Jutting 1950); Bogor; 6°36' S, 106°48' E; 250 m a.s.l.; ZMA 407628 • 1 spec. (voucher for van Benthem Jutting 1950); Bogor, botanical garden; 6°36' S, 106°48' E; 250 m a.s.l.; ZMA 407750 • 2 spec.; Sukabumi, Jampangtengah, Ciareuy, bamboo plantation; 7°01'49" S, 106°48'26" E; 573 m a.s.l.; MZB 19248 • 1 spec. (voucher for van Benthem Jutting 1950); Lake of Cigombong, forest near lake; 6°45' S, 106°49' E; ZMA 407800 • 2 spec.; Sukabumi, Benda, Bodogol Nature Reserve at Gunung Pangrango, 800 m a.s.l.; 6°46'40" S, 106°51'26" E; ZMH 140032 • 2 spec. (vouchers for van Benthem Jutting 1950); Bogor, Gunung Pancar, 800 m a.s.l.; 6°35' S, 106°54' E; ZMA 407790 • 1 spec. (det. anat.); Bogor, saddle between Gunung Pancar and Gunung Paniisan; 6°35' S, 106°54' E; 500 m a.s.l.; ZMA 370986 • 5 spec.; Sukabumi, Nyalindung, near Bibijilan waterfall, secondary forest; 7°01'27" S, 106°54'21" E; 696 m a.s.l.; MZB 19247 • 7 spec.; Sukabumi, Nyalindung, Buniayu cave complex, Cipicung Cave, secondary forest; 7°02'10" S, 106°54'21" E; 755 m a.s.l.; MZB 19244 • 7 spec.; Sukabumi, Nyalindung, Buniayu, secondary forest; 7°02'12" S, 106°54'26" E; 795 m a.s.l.; MZB 19246 • 3 spec.; same data as for preceding; ZMH 133422 • 1 spec.; Sukabumi, Nyalindung, Buniayu, Altingia (Rasamala) Forest; 7°02'11" S, 106°54'35" E; 805 m a.s.l.; MZB 19245 • 1 spec. (det. anat.); Bogor, Megamendung; 6°38'35" S, 106°55'23" E; MZB 3618 • 2 spec. (vouchers for van Benthem Jutting 1950); Bogor, S of Cisarua; 6°41' S, 106°56' E; 800 m a.s.l.; ZMA 407712 • 2 spec. (vouchers for van Benthem Jutting 1950); same data as for preceding; ZMA 407719 • 1 spec. (voucher for *P. sumatrana* var. *moussoniana* in Leschke 1914); Cibodas; 6°45' S, 107°01' E; ZMH 20424 • 1 spec.; Padalarang, Rajamandala; 6°50' S, 107°21' E; ZMA 413757 • 1 spec. (voucher for van Benthem Jutting 1950); Jampang, limestone rock near Sukanegara; 7°01' S, 107°22' E; 1000 m a.s.l.; ZMA 407746 • 4 spec. (vouchers for van Benthem Jutting 1950); Garut; 7°01' S, 107°25' E; RMNH 309721 • 6 spec. (det. anat.); Padalarang, Gunung Masigit; 6°50' S, 107°26' E; 500 m a.s.l.; ZMA 376193 • many spec. (vouchers for van Benthem Jutting 1950); Padalarang, Gunung Pawon; 6°49' S, 107°26' E; 700 m a.s.l.; ZMA 407631 • 27 spec.; Padalarang, Gunung Pawon, shrubs and palm; 6°49'29" S, 107°26'12" E; 626 m a.s.l.; MZB 19237 • 28 spec.; Padalarang, Gunung Pawon, shrubs; 6°49'30" S, 107°26'13" E; 689 m a.s.l.; MZB 19243 • 15 spec.; same data as for preceding; ZMH 133422 • 1 spec.; Padalarang, Gunung Pawon, agroforestry; 6°49'31" S, 107°26'16" E; 697 m a.s.l.; MZB 19236 • 11 spec.; same data as for preceding; MZB 19254 • 4 spec.; Padalarang, bamboo; 6°49'36" S, 107°27'09" E; 784 m a.s.l.; MZB 19251 • 3 spec.; Padalarang, Gunung Hawu, agroforestry; 6°50'04" S, 107°27'31" E; 835 m a.s.l.; MZB 19291 • 36 spec.; Padalarang, Gunung Hawu, guava plantation; 6°50'07" S, 107°27'35" E; 787 m a.s.l.; MZB 19242 • 20 spec.; same data as for preceding; ZMH 133423 • 15 spec.; Padalarang, Gunung Hawu, agroforestry; 6°50'03" S, 107°27'46" E; 775 m a.s.l.; MZB 19241 • 8 spec.; same data as for preceding; ZMH 133424 • 4 spec. (vouchers for van Benthem Jutting 1950); Cibuluh near Cisurupan, slope of Papandayan; 7°21' S, 107°47' E; RMNH 309739 • 4 spec.; Cibuluh near Cikajang, slope of Papandayan; 7°21' S, 107°48' E; RMNH 309762 • 7 spec.; Tasikmalaya, Karangnunggal, surroundings of Kiara Jenggot Cave, agroforestry; 7°39'37" S, 108°06'55" E; 234 m a.s.l.; MZB 19250 • 3 spec.; Tasikmalaya, Setiawaras, near Sambawa Cave, agroforestry; 7°35'02" S, 108°10'58" E; 361 m a.s.l.; MZB 17789.

### Description

SHELL (Figs 2–3; Tables 3–4). Depressed conical, with 5–5.75 hardly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes sparse, mainly at periphery; tuberculate around umbilicus; brownish-corneous; body whorl keeled; aperture rounded rhombic; upper insertion of peristome descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, wide, comprising 29–51% of shell diameter, hardly obscured by columellar edge.



**Figs 2–5.** Shells of species of *Landouria* from Java. **2.** *L. winteriana* (Pfeiffer, 1842), West Java, Padalarang, Gunung Masigit (neotype of *Helix winteriana*, ZMA 376193a). **3.** *L. winteriana*, West Java, Cibodas (syntype of *Plectotropis kraepelini* Leschke, 1914, ZMH 98416). **4.** *L. conoidea* (Leschke, 1914), West Java, Bogor (syntype, ZMH 98144). **5.** *L. rotatoria* (Pfeiffer, 1842), West Java, Gunung Salak (neotype of *Helix rotatoria*, MZB 19205). Scale bar: 5 mm.

GENITALIA (Figs 15, 29; Table 4). Atrium short; penis long, distal part cylindrical, proximal part globularly dilated; without penis coecum; membranaceous sheath around distal part of penis connected with proximal part of epiphallus by tissue; penial retractor runs from diaphragm to middle part of short cylindrical epiphallus; flagellum moderately long, distal part broader, apically with some indentions, apical part tapering towards its apical end; without node; vas deferens narrow and long; vagina long; oviduct short; peduncle of bursa copulatrix subdivided into a broader, rapidly tapering distal part and a narrower, longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

### Remarks

*Landouria winteriana* and *L. rotatoria* are the oldest names for species of *Landouria* from the Indo-Australian Archipelago. Pfeiffer (1842) described both from Java without more exact locality data. Later, these names have been used for many different species from Java and other islands of the Indo-Australian Archipelago. Thus, it is important to clarify their identity. The original description of *H. winteriana* was based on material in Pfeiffer's own collection (Pfeiffer 1852 in 1849–1853). Pfeiffer's collection was acquired by H. Dohrn and his collection in the Stettin Museum was destroyed during the Second World War (Zilch 1967; Dance 1986). We could not locate type specimens of *H. winteriana* in other museums (e.g., the collection of von dem Busch in the Geosciences Collection of the University of Bremen, SMF, ZMH). Thus, a neotype has to be designated to clarify the taxonomic status and the type locality of *H. winteriana*.

We designate a specimen from Gunung Masigit near Padalarang in West Java (ZMA 376193a; Figs 2, 21), which agrees with the original description of Pfeiffer (1842) and the figures of Pfeiffer (1851 in 1849–1853: pl. 95, figs 1–2) in the depressed conical shell with an angular periphery and a wide umbilicus, as the neotype of *Helix winteriana* Pfeiffer, 1842. This specimen represents a species that is widespread in western Java, which was more intensively studied than other parts of Java in former times (and still today), so it is likely that the neotype actually belongs to the same species as the specimens described by Pfeiffer (1842).

Köhler *et al.* (in press) recently redescribed *L. winteriana* under the name *L. cf. rotatoria* (not Pfeiffer, 1842). The species from Timor named *L. cf. winteriana* by Köhler *et al.* (in press) is not closely related to *L. winteriana*. Although it is more closely related to species of *Landouria* from Java than to *L. timorensis* Köhler *et al.* in press or *L. montana* Köhler *et al.* in press from Timor (see Fig. 1; Köhler *et al.* in press: fig. 2), it is not identical with any of the species described here from Java, but probably represents a new species.

The only available syntype of *P. kraepelini* (Fig. 3) differs from usual *L. winteriana* in the smaller shell diameter at three whorls (4.0 mm vs 4.4–5.2 mm in other *L. winteriana*) and the slightly more pronounced keel. We suppose that *P. kraepelini* represents a small variety of *L. winteriana*. However, the specific identity of *P. kraepelini* and *L. winteriana* should be checked by an anatomical examination of specimens resembling the syntype of *P. kraepelini* from Cibodas, its type locality.

*Landouria winteriana* differs from *L. sukoliloensis* sp. nov. in the angular body whorl, the not convoluted distal part of the penis, the short epiphallus and the flagellum with a broader distal part with external indentions. This species occurs sympatrically with *L. petrukensis* sp. nov., from which it differs in the larger size and the angular, less sharply keeled periphery.

### Distribution

Anatomically determined samples of *L. winteriana* are known from Bogor Regency and Padalarang in the mountain region in West Java (Fig. 52). The shells from Tasikmalaya Regency resemble the

**Table 3** (continued on next 3 pages). Shell measurements for species of *Landouria* Godwin-Austen, 1918 (in mm). Abbreviations: D = shell diameter; D3W = diameter of the third whorl; da = diameter of the aperture; H = shell height; ha = height of the aperture; max = maximum; min = minimum; n = number of measured spec.; std = standard deviation; U = diameter of the umbilicus; W = number of whorls.

	D	D3W	H	da	ha	U	W	D/H	U/D	D/da	H/ha	da/ha
<i>Landouria winteriana</i> ; several localities; n = 20												
min	9.7	4.4	5.5	3.7	4.0	3.4	5	1.55	0.29	2.26	1.24	0.94
max	12.6	5.2	7.8	5.5	5.2	6.0	5.75	2.07	0.51	2.60	1.55	1.15
mean	11.8	4.8	6.7	5.0	4.8	4.1	5.3	1.76	0.35	2.39	1.41	1.04
std	0.7	0.2	0.6	0.4	0.3	0.7	0.2	0.11	0.06	0.08	0.08	0.05
<i>Landouria conoidea</i> ; Bogor; n = 3												
min	7.6	3.6	5.2	3.4	3.2	2.5	4.75	1.48	0.30	2.16	1.55	1.04
max	8.7	4.4	5.6	3.8	3.7	2.6	5	1.54	0.33	2.27	1.59	1.12
mean	8.1	4.1	5.3	3.6	3.4	2.5	4.9	1.52	0.31	2.23	1.57	1.07
std	0.5	0.4	0.3	0.2	0.2	0.1	0.1	0.03	0.01	0.06	0.02	0.04
<i>Landouria rotatoria</i> ; Gunung Gede; Gunung Salak; n = 22												
min	15.6	4.5	8.3	6.8	6.5	4.1	5.75	1.57	0.24	2.19	1.17	0.96
max	19.1	5.8	10.6	8.5	8.0	5.8	6.5	2.09	0.32	2.38	1.47	1.12
mean	17.4	5.1	9.5	7.6	7.2	5.0	6.1	1.85	0.29	2.28	1.31	1.06
std	0.8	0.3	0.6	0.4	0.4	0.5	0.2	0.12	0.02	0.05	0.08	0.04
<i>Landouria naggsi</i> sp. nov.; Sukabumi; n = 4												
min	11.6	4.2	8.5	5.0	4.9	3.3	6.25	1.21	0.28	2.07	1.55	0.92
max	14.0	5.0	10.6	5.8	6.1	4.7	7	1.37	0.33	2.40	1.99	1.16
mean	12.5	4.5	9.6	5.5	5.5	3.9	6.6	1.31	0.31	2.28	1.74	1.00
std	1.1	0.4	0.9	0.4	0.5	0.6	0.3	0.07	0.02	0.14	0.19	0.11
<i>Landouria epiplatia</i> ; Jampang; near Palabuhan Ratu Bay; n = 8												
min	11.8	4.5	5.7	4.4	4.1	3.8	5.25	2.03	0.30	2.61	1.02	1.03
max	17.0	5.7	6.9	6.2	6.0	7.3	6.25	2.94	0.43	2.74	1.41	1.19
mean	15.3	4.9	6.0	5.7	5.2	5.7	5.7	2.52	0.37	2.66	1.18	1.11
std	2.0	0.4	0.4	0.7	0.7	1.5	0.4	0.34	0.06	0.05	0.14	0.05
<i>Landouria parahyangensis</i> sp. nov.; Karangnunggal; n = 7												
min	14.7	4.3	8.4	5.3	5.5	5.8	6.5	1.69	0.39	2.55	1.42	0.95
max	16.9	5.0	9.3	6.3	6.2	7.4	7	1.94	0.45	2.82	1.60	1.10
mean	15.7	4.5	8.7	5.8	5.8	6.5	6.8	1.80	0.42	2.71	1.50	1.00
std	0.9	0.3	0.4	0.4	0.3	0.6	0.2	0.09	0.02	0.09	0.05	0.05
<i>Landouria nusakambangensis</i> sp. nov.; Nusa Kambangan Island; n = 8												
min	11.9	4.4	6.6	4.8	4.6	3.9	5.25	1.65	0.32	2.36	1.29	0.95
max	15.0	5.4	9.1	6.4	6.2	5.8	6	1.83	0.40	2.52	1.56	1.09
mean	13.5	4.9	7.9	5.6	5.4	4.9	5.7	1.72	0.36	2.43	1.46	1.03
std	1.3	0.3	0.8	0.6	0.6	0.8	0.3	0.07	0.03	0.05	0.09	0.05

**Table 3** (continued). Shell measurements for species of *Landouria* Godwin-Austen, 1918.

	D	D3W	H	da	ha	U	W	D/H	U/D	D/da	H/ha	da/ha
<i>Landouria petrukensis</i> sp. nov.; Karangbolong; <i>n</i> = 13												
min	8.1	3.7	5.2	3.6	3.4	2.2	4.75	1.49	0.24	2.05	1.35	1.02
max	9.8	4.3	6.3	4.6	4.1	3.3	5.5	1.79	0.37	2.44	1.63	1.18
mean	9.0	3.9	5.5	4.0	3.7	2.5	5.1	1.62	0.27	2.22	1.48	1.08
std	0.6	0.2	0.4	0.3	0.3	0.3	0.2	0.08	0.03	0.09	0.09	0.05
<i>Landouria tholiformis</i> sp. nov.; Gunung Kidul; <i>n</i> = 7												
min	13.0	4.2	7.4	5.1	4.9	4.5	6	1.77	0.32	2.40	1.37	1.00
max	14.4	4.5	7.8	5.8	5.7	5.6	6.25	1.88	0.40	2.57	1.52	1.06
mean	13.9	4.4	7.7	5.6	5.4	4.9	6.1	1.82	0.35	2.48	1.42	1.04
std	0.5	0.1	0.2	0.2	0.3	0.4	0.1	0.04	0.03	0.05	0.05	0.02
<i>Landouria abdidalem</i> sp. nov.; Kulonprogo; <i>n</i> = 11												
min	13.1	4.3	6.3	5.1	4.6	4.6	5.75	1.93	0.33	2.42	1.29	1.01
max	16.4	4.8	7.8	6.1	5.8	7.0	6	2.14	0.48	2.79	1.43	1.13
mean	14.0	4.5	6.9	5.5	5.1	5.4	5.9	2.03	0.38	2.56	1.35	1.07
std	0.9	0.2	0.5	0.3	0.4	0.8	0.1	0.07	0.04	0.10	0.04	0.04
<i>Landouria madurensis</i> sp. nov.; Madura Island; <i>n</i> = 3												
min	11.4	3.9	5.5	4.5	4.5	4.3	5.5	1.75	0.38	2.45	1.23	1.00
max	12.0	4.5	6.5	4.7	4.6	4.5	5.75	2.11	0.40	2.57	1.46	1.04
mean	11.6	4.1	5.9	4.6	4.5	4.4	5.7	1.98	0.39	2.52	1.31	1.02
std	0.3	0.3	0.5	0.1	0.1	0.1	0.1	0.20	0.01	0.06	0.13	0.02
<i>Landouria sewuensis</i> sp. nov.; several hills in Gunung Kidul; <i>n</i> = 8												
min	11.4	3.9	6.3	5.0	4.4	3.5	5.25	1.61	0.30	2.21	1.25	1.06
max	16.3	5.3	8.7	7.2	6.3	6.0	6	2.25	0.40	2.57	1.50	1.23
mean	13.7	4.6	7.2	5.9	5.2	4.9	5.7	1.90	0.36	2.35	1.39	1.12
std	1.8	0.5	0.7	0.8	0.6	0.8	0.3	0.20	0.03	0.12	0.09	0.05
<i>Landouria sukoliloensis</i> sp. nov.; Pati; Grobogan; <i>n</i> = 20												
min	10.4	3.6	6.0	4.7	3.9	2.5	5	1.60	0.22	2.04	1.26	1.04
max	12.3	4.6	7.4	5.6	4.8	4.8	5.75	1.93	0.41	2.46	1.67	1.20
mean	11.2	4.0	6.5	5.1	4.5	3.3	5.5	1.72	0.29	2.22	1.47	1.14
std	0.5	0.2	0.4	0.3	0.3	0.8	0.2	0.09	0.07	0.09	0.09	0.05
<i>Landouria tonywhitteni</i> sp. nov.; Grobogan; <i>n</i> = 10												
min	14.3	4.8	7.0	6.0	5.5	5.5	5.75	1.93	0.32	2.30	1.11	1.07
max	17.6	5.4	8.5	7.4	6.7	6.7	6	2.34	0.41	2.61	1.46	1.20
mean	16.1	4.9	7.5	6.6	6.0	5.9	5.8	2.14	0.37	2.43	1.27	1.11
std	1.0	0.2	0.4	0.4	0.4	0.4	0.1	0.16	0.03	0.08	0.10	0.04
<i>Landouria nodifera</i> sp. nov.; Pati; <i>n</i> = 13												
min	14.7	5.0	6.4	5.8	4.6	3.9	5	1.93	0.26	2.33	1.14	1.00
max	16.1	5.5	8.1	6.9	6.3	5.6	5.75	2.29	0.38	2.54	1.39	1.36
mean	15.2	5.3	7.2	6.3	5.8	4.8	5.5	2.12	0.32	2.42	1.24	1.09
std	0.4	0.1	0.5	0.3	0.4	0.4	0.2	0.10	0.03	0.07	0.07	0.09

**Table 3** (continued). Shell measurements for species of *Landouria* Godwin-Austen, 1918.

	D	D3W	H	da	ha	U	W	D/H	U/D	D/da	H/ha	da/ha
<i>Landouria pacitanensis</i> sp. nov.; Pacitan; n = 16												
min	10.6	3.4	6.2	4.1	4.1	3.0	5.25	1.57	0.28	2.16	1.19	0.93
max	14.7	4.8	8.2	6.2	5.8	4.8	6	2.18	0.34	2.65	1.56	1.17
mean	13.1	4.4	7.1	5.4	5.2	4.0	5.7	1.84	0.31	2.39	1.36	1.04
std	1.4	0.4	0.6	0.6	0.5	0.6	0.3	0.18	0.02	0.12	0.09	0.06
<i>Landouria intumescens</i> ; Tuban; Bojonegoro; Surabaya; n = 20												
min	11.6	4.2	6.1	5.5	4.7	2.8	5	1.50	0.22	2.10	1.22	0.98
max	14.1	5.3	8.7	6.4	6.2	4.5	5.75	1.98	0.34	2.33	1.60	1.19
mean	13.2	4.7	7.5	5.9	5.5	3.6	5.3	1.76	0.27	2.21	1.38	1.09
std	0.7	0.3	0.6	0.2	0.4	0.4	0.2	0.13	0.03	0.06	0.10	0.05
<i>Landouria moussoniana</i> ; Wonosari; n = 6												
min	10.2	4.0	5.5	4.2	4.1	2.7	5	1.73	0.37	2.60	1.52	0.99
max	12.0	4.4	6.7	4.6	4.6	4.6	6.25	1.81	0.38	2.74	1.57	1.05
mean	11.1	4.2	6.3	4.5	4.4	3.7	5.7	1.77	0.38	2.67	1.54	1.02
std	0.3	0.3	0.1	0.3	0.1	0.0	0.2	0.06	0.01	0.10	0.04	0.05
<i>Landouria schepmani</i> ; Sukapura; Gunung Bungbulang; n = 2												
lectotype	10.9	4.3	6.2	4.6	4.2	2.3	5.25	1.76	0.21	2.36	1.48	1.11
paralectotype	10.5	4.3	6.1	4.7	4.1	2.2	5	1.72	0.21	2.23	1.49	1.15
<i>Landouria monticola</i> ; Gunung Cikuray; Java; n = 5												
min	8.5	3.7	5.3	3.7	3.0	1.6	4.5	1.49	0.18	2.12	1.49	1.05
max	9.5	5.0	6.0	4.1	3.9	2.1	5.25	1.60	0.25	2.32	2.00	1.37
mean	9.0	4.4	5.8	4.0	3.4	1.8	4.8	1.56	0.21	2.25	1.73	1.21
std	0.4	0.5	0.3	0.2	0.4	0.2	0.4	0.04	0.03	0.08	0.23	0.14
<i>Landouria smimensis</i> ; several localities; n = 14												
min	6.3	3.6	4.1	3.1	3.1	1.3	4.5	1.28	0.18	1.78	1.21	0.92
max	11.9	4.4	8.4	5.3	5.1	3.3	5.5	1.64	0.32	2.63	1.65	1.08
mean	8.2	3.8	5.6	3.8	3.7	2.0	4.9	1.48	0.25	2.17	1.49	1.01
std	1.8	0.2	1.2	0.7	0.7	0.7	0.4	0.09	0.04	0.19	0.13	0.05
<i>Landouria leucochila</i>												
holotype	16.3	5.8	8.5	6.9	4.8	4.9	5.25	1.92	0.30	2.36	1.79	1.45
<i>Landouria zonifera</i> sp. nov.; Kulonprogo; n = 2												
min	12.5	3.9	6.9	4.8	5.4	5.0	5.5	1.73	0.40	2.32	1.28	0.89
max	13.2	4.8	7.6	5.7	5.6	5.3	5.75	1.81	0.40	2.61	1.37	1.02
mean	12.8	4.3	7.2	5.2	5.5	5.1	5.6	1.77	0.40	2.47	1.32	0.95
std	0.5	0.6	0.5	0.6	0.1	0.2	0.2	0.06	0.00	0.20	0.06	0.09
<i>Landouria ciliocincta</i> ; several localities; n = 9												
min	12.4	3.8	6.0	5.7	5.6	3.1	5	1.86	0.22	2.08	1.07	1.03
max	15.6	4.5	8.3	7.1	6.5	4.1	6	2.12	0.30	2.27	1.29	1.10
mean	13.6	4.3	7.0	6.2	5.8	3.7	5.4	1.94	0.27	2.18	1.21	1.07
std	1.0	0.2	0.7	0.4	0.3	0.3	0.3	0.09	0.03	0.06	0.07	0.03



**Table 3** (continued). Shell measurements for species of *Landouria* Godwin-Austen, 1918.

	D	D3W	H	da	ha	U	W	D/H	U/D	D/da	H/ha	da/ha
<i>Landouria pakidulan</i> sp. nov.; Pangandaran; Nusa Kambangan Island; <i>n</i> = 4												
min	12.5	4.6	6.9	5.7	5.4	3.0	5.25	1.70	0.24	2.05	1.20	1.05
max	14.0	4.7	8.1	6.8	6.1	4.1	5.5	1.86	0.30	2.18	1.43	1.17
mean	13.4	4.6	7.4	6.3	5.7	3.6	5.4	1.81	0.27	2.13	1.30	1.10
std	0.7	0.0	0.5	0.5	0.3	0.4	0.1	0.07	0.02	0.07	0.10	0.05
<i>Landouria dharmai</i> sp. nov.; Tulungagung, Popoh												
holotype	9.9	3.9	7.2	5.3	4.5	1.8	5.5	1.39	0.18	1.88	1.57	1.17
<i>Landouria davini</i> ; Baturraden, Pancuran Tujuh												
holotype	12.4	5.7	7.1	5.0	4.8	3.6	5	1.73	0.29	2.48	1.48	1.04
<i>Landouria menorehensis</i> sp. nov.; Kulonprogo, Sibolong; <i>n</i> = 9												
min	12.4	4.3	8.3	5.9	5.5	2.2	5.25	1.31	0.16	1.85	1.33	0.98
max	14.5	5.2	10.4	7.5	7.3	3.0	5.75	1.51	0.24	2.08	1.61	1.19
mean	13.4	4.6	9.3	6.8	6.3	2.5	5.5	1.44	0.19	1.96	1.48	1.09
std	0.7	0.3	0.7	0.6	0.6	0.2	0.1	0.06	0.02	0.08	0.10	0.06

anatomically determined samples from Bogor Regency and Padalarang. However, their specific identity has to be checked anatomically. In addition, we have anatomically determined a sample from Rakata Island (3 spec. (vouchers for Smith & Djajasasmita 1988), Krakatau Islands, 6°08'46" S, 105°26'23" E, MZB 9354).

*Landouria winteriana* has also been recorded from Thailand to the Philippines and the Maluku Islands (Martens 1867; Rensch 1932; van Benthem Jutting 1941, 1950; Vermeulen & Whitten 1998; Boonngam *et al.* 2008). Besides on Java, *L. winteriana* might occur on Sumatra, but records from other islands refer to other species.

***Landouria conoidea*** (Leschke, 1914) comb. nov.  
Figs 4, 6, 53; Tables 3–4

*Plectotropis conoidea* Leschke, 1914: 212, figs 8–9 (“Buitenzorg”).

*Landouria rotatoria* – van Benthem Jutting 1950: 461 (in part). (not Pfeiffer, 1842)

**Diagnosis**

*Landouria conoidea* is characterized by a small, conical, sharply keeled shell with tubercles all over the shell surface.

**Material examined**

**Syntypes**

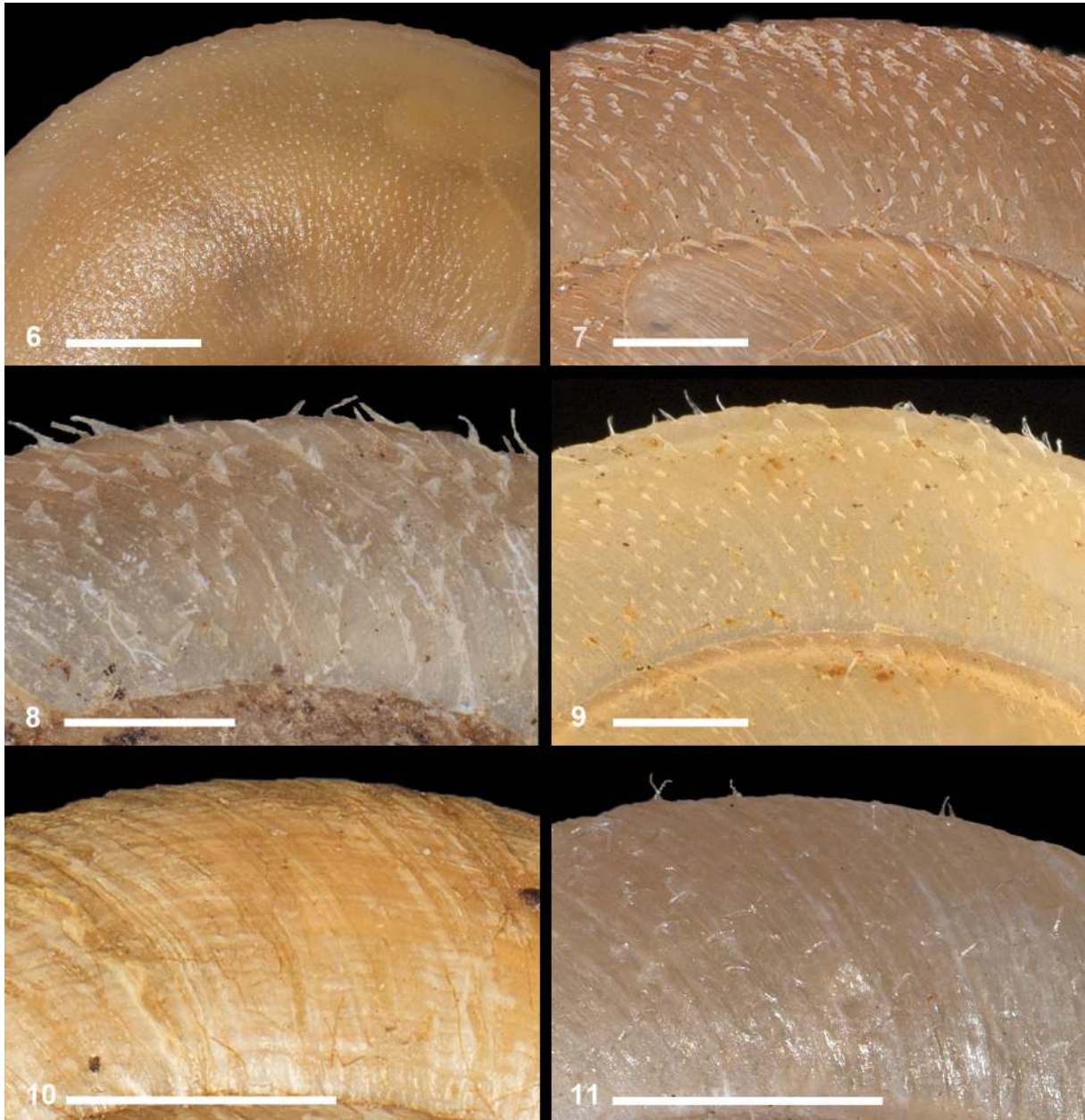
INDONESIA • 8 spec.; West Java, Bogor; 6°36' S, 106°48' E; ZMH 98144.

**Other material**

INDONESIA • 10 spec.; West Java, Bogor; 6°36' S, 106°48' E; ZMH 98145.

## Description

SHELL (Figs 4, 6; Tables 3–4). Conical, with 4.75–5 slightly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side without distinct incised spiral lines, umbilical side with indistinct spiral lines; with tubercles all over shell surface that carry scaly processes or hairs mainly at periphery; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled at beginning;



**Figs 6–11.** Shell sculpture of species of *Landouria* from Java (umbilical side of shell in 6; apical side in 7–11). **6.** *L. conoidea* (Leschke, 1914), West Java, Bogor (syntype, ZMH 98144). **7.** *L. tholiformis* sp. nov., Yogyakarta, Gunung Kidul, Tepus, near Poktunggal Beach (holotype, MZB 17999). **8.** *L. madurensis* sp. nov., East Java, Madura Island, Sampang, Nepa Monkey lowland rainforest (paratype, MZB 19209). **9.** *L. pacitanensis* sp. nov., East Java, Pacitan, Srau Beach (paratype, ZMH 148510). **10.** *L. monticola* van Benthem Jutting, 1950, West Java, Gunung Cikuray (paratype, SMF 8880). **11.** *L. smimensis* (Mousson, 1848), East Java, Tosari (ZMA 390881). Scale bars: 1 mm.

aperture almost circular; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus hardly eccentric, wide, comprising 30–43% of shell diameter, hardly obscured by columellar edge.

GENITALIA. Unknown.

### Remarks

*Landouria conoidea* differs from *L. winteriana*, which occurs in the same region in West Java, in the smaller shell diameter (7.6–8.7 mm vs 9.7–12.6 mm in *L. winteriana*), the higher shell form (D/H 1.48–1.54 vs 1.55–2.07 in *L. winteriana*), the more pronounced keel and the presence of tubercles all over the shell surface (Fig. 6).

With regard to the conical shell form, *L. conoidea* resembles *L. naggsi* sp. nov. (Fig. 25), from which it differs in the less elevated (D/H 1.48–1.54 vs 1.21–1.37 in *L. naggsi* sp. nov.), smaller shell (D 7.6–8.7 mm vs 11.6–14.0 mm in *L. naggsi* sp. nov.) with fewer whorls (4.75–5 vs 6.25–7 in *L. naggsi* sp. nov.), the more pronounced keel and the shell sculpture consisting of tubercles vs longish scales in *L. naggsi* sp. nov.

### Distribution

*Landouria conoidea* is so far known only from Bogor in West Java (Fig. 53).

#### *Landouria rotatoria* (Pfeiffer, 1842)

Figs 5, 12–14, 16, 30, 54; Tables 3–4

*Helix rotatoria* Pfeiffer 1842: 38 (“Java”).

*Plectotropis leucomphala* Möllendorff, 1897: 66 (“Java”; more exactly (Zilch 1966): “W-Java: Gunung Gedeh (4000’)”).

*Plectotropis leucomphala* f. *subfasciata* Möllendorff, 1897: 67 (“Java”; more exactly (Zilch 1966): “W-Java: Gunung Gedeh (3000’)”).

*Plectotropis leucomphala* f. *castanea* Möllendorff, 1897: 67 (“Java”; more exactly (Zilch 1966): “W-Java: Gunung Salak”).

*Helix rotatoria* – von dem Busch in Philippi 1842 in 1842–1845: 10, pl. I.4, fig. 5. — Pfeiffer 1851 in 1849–1853: pl. 95, figs 3–5; 1852 in 1849–1853: 163.

*Helix (Plectotropis) rotatoria* – Boettger 1890: 144. — Martens 1892: 234. — Wiegmann 1893: 166, pl. 12, figs 11–14.

*Landouria rotatoria* – van Benthem Jutting 1950: 461 (in part). — Zilch 1966: 294, pl. 7, figs 3–5 (in part).

### Diagnosis

*Landouria rotatoria* is characterized by a large, depressed conical, keeled shell, a penis with a small globular bulge at the proximal end and an externally smooth, longish lemon-shaped flagellum.

### Material examined

#### Type material

INDONESIA – **West Java** • neotype of *Helix rotatoria* (designated here) (det. anat.); Bogor, Blok kancil, Gunung Salak, Halimun Salak National Park; 6°44'42" S, 106°42'46" E; 1166 m a.s.l.; 17 Jun. 2015; A.S. Nurinsiyah, I. Fauziah, T. Setiadi and Y. Prasetyo leg.; measurements: D = 17.0 mm, H = 9.5 mm; MZB 19205 • holotype of *Plectotropis leucomphala* f. *castanea*; Gunung Salak; 6°44' S,

106°42' E; SMF 8916 • holotype of *Plectotropis leucomphala* f. *subfasciata*; Gunung Gede; 6°47' S, 106°59' E; ca 900 m a.s.l.; SMF 8914 • holotype of *Plectotropis leucomphala*; Gunung Gede; 6°47' S, 106°59' E; ca 1200 m a.s.l.; SMF 8912.

#### Other material

INDONESIA • 4 spec.; Java; SMF 24221 • 3 spec.; same data as for preceding; ZMB 47683 • 3 spec.; same data as for preceding; ZMB 47684 • 1 spec., same data as for preceding; ZMH 17719 • 5 spec.; same data as for preceding; ZMH 17720 • 4 spec.; same data as for preceding; ZMH 17721 • 3 spec.; same data as for preceding; ZMH 17722. – **West Java** • 2 spec. (vouchers for van Benthem Jutting 1950); Gora S of Bogor; RMNH 309846 • 7 spec. (vouchers for Boettger 1890); Bogor, Gunung Salak; 6°44' S, 106°42' E; SMF 8917 • 3 spec. (vouchers for Boettger 1890); same data as for preceding; SMF 24200 • 4 spec. (vouchers for Boettger 1890); same data as for preceding; SMF 24204 • 2 spec. (vouchers for Boettger 1890); same data as for preceding; ZMA 407645 • 4 spec. (vouchers for van Benthem Jutting 1950); Bogor, Situ Gunung, S slope of Mt Gede, forest; 6°50' S, 106°55' E; 1000 m a.s.l.; ZMA 407632 • 6 spec.; Gunung Gede; 6°47' S, 106°59' E; ZMA 407630 • 2 spec.; same data as for preceding; ZMA 407690 • 9 spec.; Gunung Gede; 6°47' S, 106°59' E; ca 900 m a.s.l.; SMF 8915 • 16 spec.; Gunung Gede; 6°47' S, 106°59' E; ca 1200 m a.s.l.; SMF 89136 • 3 spec.; Gunung Gede; 6°47' S, 106°59' E; ca 1500 m a.s.l.; ZMB 46035.

#### Description

SHELL (Figs 5, 12–14; Tables 3–4). Depressed conical, with 5.75–6.5 slightly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes sparse, mainly at periphery; tuberculate around umbilicus; brown or brownish-corneous; body whorl keeled; aperture rounded rhombic; upper insertion of peristome descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, wide, comprising 24–32% of shell diameter, hardly obscured by columellar edge.

GENITALIA (Figs 16, 30; Table 4). Atrium short; penis long, distal part cylindrical, with a small globular bulge at proximal end, without penis coecum; membranaceous sheath around distal part of penis connected with epiphallus by tissue; penial retractor runs from diaphragm to proximal part of cylindrical epiphallus; flagellum moderately long, very broad, without node, tapering at its proximal end; vas deferens narrow and long; vagina long; oviduct long, very broad, proximally tapering; peduncle of bursa copulatrix subdivided into a globular distal part, a proximally tapering middle part and a narrower and longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

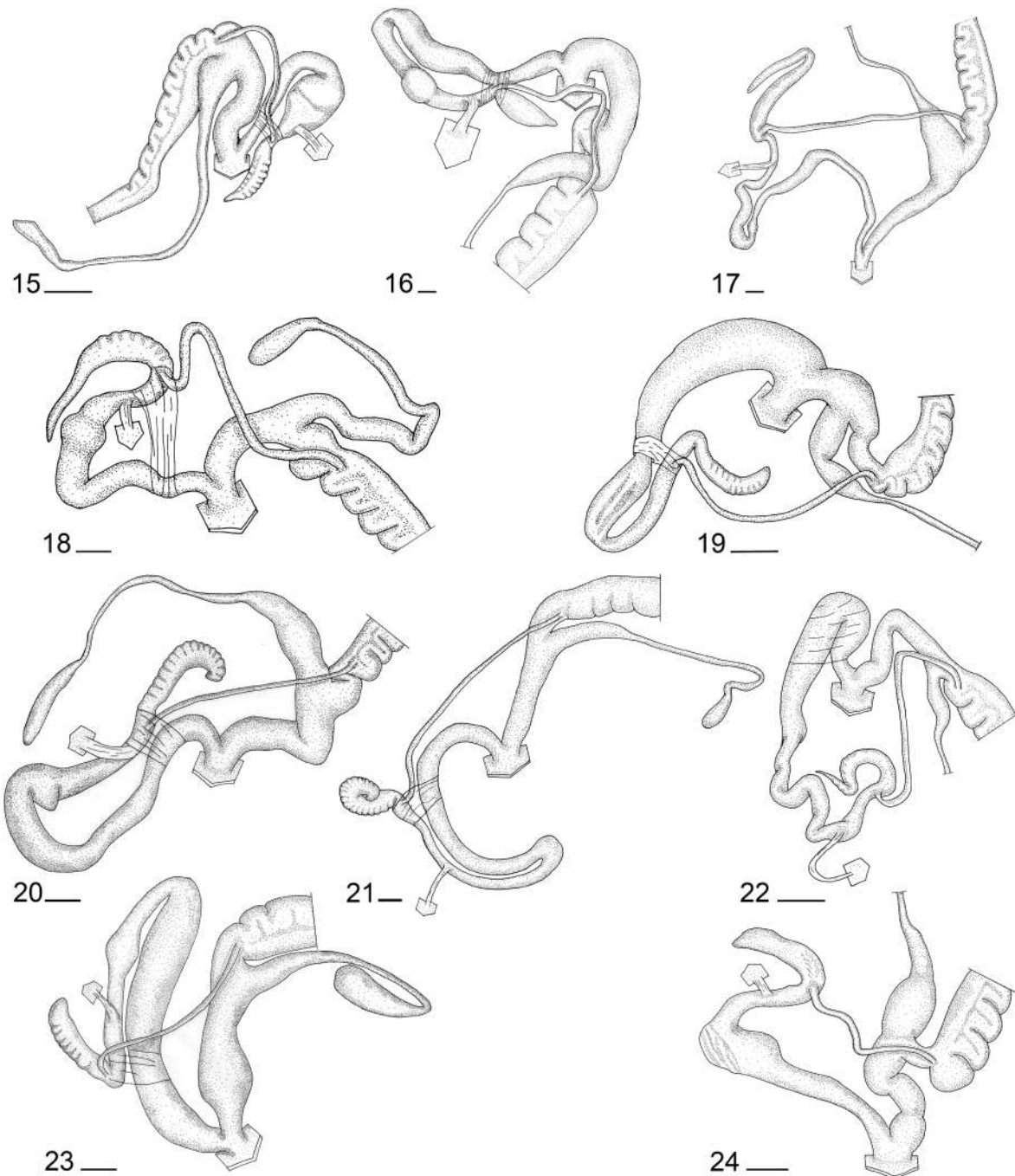
#### Remarks

The name *Helix rotatoria* goes back to von dem Busch and is often cited with von dem Busch (in Philippi 1842 in 1842–1845: 10, pl. I.4, fig. 5) as author. However, von dem Busch cited Pfeiffer (1842), who made the name available first (see also remarks under *L. winteriana*). Pfeiffer (1842) described the species based on specimens from von dem Busch and specimens he got from Winter. The material from Winter was in Pfeiffer's own collection (Pfeiffer 1852 in 1849–1853), which was destroyed during the Second World War (see *L. winteriana*). A part of the collection of von dem Busch is kept in the

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**Figs 12–14** (opposite page). Shells of *Landouria rotatoria* (Pfeiffer, 1842) from Java. **12**. West Java, Gunung Gede (holotype of *Plectotropis leucomphala* Möllendorff, 1897, SMF 8912). **13**. West Java, Gunung Salak (holotype of *P. leucomphala* f. *castanea* Möllendorff, 1897, SMF 8916). **14**. West Java, Gunung Gede (holotype of *P. leucomphala* f. *subfasciata* Möllendorff, 1897, SMF 8914). Scale bar: 5 mm.





**Figs 15–24.** Genitalia of species of *Landouria* from Java. **15.** *L. winteriana* (Pfeiffer, 1842), West Java, Padalarang, Gunung Masigit (neotype, ZMA 376193a). **16.** *L. rotatoria* (Pfeiffer, 1842), West Java, Gunung Salak, 1166 m a.s.l. (neotype, MZB 19205). **17.** *L. epiplatia* (Möllendorff, 1897)?, West Java, Bogor, Gunung Gede (ZMH 79946). **18.** *L. nusakambangensis* sp. nov., Central Java, Nusa Kambangan Island, nature monument Gligir (holotype, ZMA 412298a). **19.** *L. petrukensis* sp. nov., Central Java, Karangbolong, way to Petruk Cave (holotype, MZB 19203). **20.** *L. tholiformis* sp. nov., Yogyakarta, Gunung Kidul, Tepus, near Poktunggal Beach (holotype, MZB 17999). **21.** *L. abdidalem* sp. nov., Yogyakarta, Kulonprogo, Sabrang Kidul (holotype, MZB 17664). **22.** *L. madurensis* sp. nov., East Java, Madura Island, Sampang, Nepa Monkey lowland rainforest (paratype, MZB 19209). **23.** *L. sewuensis* sp. nov., Yogyakarta, Gunung Kidul, Tepus, Mbajo Hill (holotype, MZB 19255). **24.** *L. sukoliloensis* sp. nov., Central Java, Kayen, near Watu Payung (holotype, MZB 19219). Scale bars: 1 mm.

**Table 4** (continued on next 3 pages). Diagnostic characteristics of the species of *Landouria* Godwin-Austen, 1918 from Java. Characteristics most important for distinguishing similar taxa are printed in bold.

	D (in mm)	H (in mm)	whorls	D/H	U/D	shell periphery	shell coloration	scale sculpture	spiral lines on apical side	penis	penis coecum	flagellum	node at flagellum
<i>L. winteriana</i>	9.7–12.6 (mean 11.8)	5.5–7.8 (mean 6.7)	5–5.75 (mean 5.3)	1.55–2.07 (mean 1.76)	0.29–0.51 (mean 0.35)	<b>keeled</b>	brownish- corneous	scaly processes sparse, at periphery	indistinct	with large globular bulge at proximal end	absent	distal part crenated, proximal part short	absent
<i>L. conoidea</i>	<b>7.6–8.7</b> (mean <b>8.1</b> )	5.2–5.6 (mean 5.3)	4.75–5 (mean 4.9)	<b>1.48–1.54</b> (mean <b>1.52</b> )	0.30–0.33 (mean 0.31)	sharply keeled	brownish- corneous	<b>tubercles all over teleoconch</b>	not discernible	?	?	?	?
<i>L. rotatoria</i>	<b>15.6–19.1</b> (mean <b>17.4</b> )	8.3–10.6 (mean 9.5)	5.75–6.5 (mean 6.1)	1.57–2.09 (mean 1.85)	0.24–0.32 (mean 0.29)	keeled	<b>brown</b>	scaly processes sparse, at periphery	indistinct	with small globular bulge at proximal end	absent	longish lennon- shaped	absent
<i>L. naggsi</i> sp. nov.	11.6–14.0 (mean 12.5)	8.5–10.6 (mean 9.6)	6.25–7 (mean 6.6)	<b>1.21–1.37</b> (mean <b>1.31</b> )	<b>0.28–0.33</b> (mean <b>0.31</b> )	<b>angular</b>	brownish- corneous	<b>scaly processes all over teleoconch</b>	not discernible	?	?	?	?
<i>L. epiplatia</i>	11.8–17.0 (mean 15.3)	5.7–6.9 (mean 6.0)	5.25–6.25 (mean 5.7)	<b>2.03–2.94</b> (mean <b>2.52</b> )	<b>0.30–0.43</b> (mean <b>0.37</b> )	sharply keeled	brownish- corneous	scaly processes sparse, at periphery	indistinct	very long, with small bulge at proximal end	absent	very long, tapering towards proximal end	absent
<i>L. para- hyangensis</i> sp. nov.	14.7–16.9 (mean 15.7)	<b>8.4–9.3</b> (mean <b>8.7</b> )	<b>6.5–7</b> (mean <b>6.8</b> )	<b>1.69–1.94</b> (mean <b>1.80</b> )	<b>0.39–0.45</b> (mean <b>0.42</b> )	sharply keeled	brownish- corneous	scaly processes sparse, at periphery	not discernible	?	?	?	?
<i>L. nusakam- bangensis</i> sp. nov.	11.9–15.0 (mean 13.5)	6.6–9.1 (mean 7.9)	5.25–6 (mean 5.7)	1.65–1.83 (mean 1.72)	<b>0.32–0.40</b> (mean <b>0.36</b> )	<b>keeled</b>	brownish- corneous	scaly processes sparse, at periphery	indistinct	with small globular bulge at proximal end	absent	distal part slightly crenated, proximal part long	absent
<i>L. petrukensis</i> sp. nov.	<b>8.1–9.8</b> (mean <b>9.0</b> )	5.2–6.3 (mean 5.5)	4.75–5.5 (mean 5.1)	1.49–1.79 (mean 1.62)	0.24–0.37 (mean 0.27)	sharply keeled	brownish- corneous	<b>scaly processes all over teleoconch</b>	indistinct	divided by narrowing into long, cylindrical distal part and slightly dilated proximal part	absent	slightly crenated, abruptly tapering at proximal part	absent
<i>L. tholiformis</i> sp. nov.	13.0–14.4 (mean 13.9)	7.4–7.8 (mean 7.7)	6–6.25 (mean 6.1)	<b>1.77–1.88</b> (mean <b>1.82</b> )	0.32–0.40 (mean 0.35)	sharply keeled	brownish- corneous	<b>scaly processes all over teleoconch</b>	indistinct	slightly broader proximally	short	crenated, slightly longer than epiphallus	absent

**Table 4** (continued). Diagnostic characteristics of the species of *Landouria* Godwin-Austen, 1918 from Java.

	D (in mm)	H (in mm)	whorls	D/H	U/D	shell periphery	shell coloration	scale sculpture	spiral lines on apical side	penis	penis coecum	flagellum	node at flagellum
<i>L. abdidalem</i> sp. nov.	13.1–16.4 (mean 14.0)	6.3–7.8 (mean 6.9)	5.75–6 (mean 5.9)	<b>1.93–2.14</b> (mean <b>2.03</b> )	0.33–0.48 (mean 0.38)	sharply keeled	brownish- comeous	scaly processes sparse, at periphery	indistinct	long and narrow, without proximal buldge	absent	<b>crenated, shorter than epiphallus</b>	absent
<i>L. madurensis</i> sp. nov.	11.4–12.0 (mean 11.6)	5.5–6.5 (mean 5.9)	5.5–5.75 (mean 5.7)	1.75–2.11 (mean 1.98)	<b>0.38–0.40</b> (mean <b>0.39</b> )	sharply keeled	brownish- comeous	<b>scaly processes protruding into hairs</b>	no spiral lines	long, divided into longer, broader distal and shorter, narrower proximal part	absent	long, broadest in middle part, gradually tapering towards proximal end, slightly crenated	absent
<i>L. sewuensis</i> sp. nov.	11.4–16.3 (mean 13.7)	6.3–8.7 (mean 7.2)	5.25–6 (mean 5.7)	1.61–2.25 (mean 1.90)	0.30–0.40 (mean 0.36)	sharply keeled	brownish- comeous	scaly processes sparse, at periphery	indistinct	with globular swelling at proximal end	absent	<b>broad, with two rows of tubercles</b>	absent
<i>L. sukotilo-</i> <i>ensis</i> sp. nov.	10.4–12.3 (mean 11.2)	6.0–7.4 (mean 6.5)	5–5.75 (mean 5.5)	1.60–1.93 (mean 1.72)	0.22–0.41 (mean 0.29)	sharply keeled	brownish- comeous	scaly processes sparse, at periphery	indistinct	slightly dilated at proximal end	absent	abruptly tapering at proximal end, not distinctly crenated	absent
<i>L. tonywhitteni</i> sp. nov.	14.3–17.6 (mean 16.2)	7.0–8.5 (mean 7.5)	5.75–6 (mean 5.8)	1.93–2.34 (mean 2.15)	0.32–0.41 (mean 0.37)	sharply keeled	brownish- comeous	radial scaly processes	indistinct	divided into long, cylindrical distal part and dilated proximal part	absent	short, broadest at base, not distinctly crenated	<b>present</b>
<i>L. nodifera</i> sp. nov.	14.7–16.1 (mean 15.2)	6.4–8.1 (mean 7.2)	5–5.75 (mean 5.5)	1.93–2.29 (mean 2.12)	0.26–0.38 (mean 0.32)	sharply keeled	brownish- comeous	scaly processes sparse, at periphery	indistinct	divided into cylindrical distal and dilated proximal part	<b>present</b>	moderately long, tuberculated	<b>present</b>
<i>L. pacitanensis</i> sp. nov.	10.6–14.7 (mean 13.1)	6.2–8.2 (mean 7.1)	5.25–6 (mean 5.7)	1.57–2.18 (mean 1.84)	0.28–0.34 (mean 0.31)	sharply keeled	brownish- comeous	scaly processes sparse, at periphery	indistinct	<b>divided by narrowing into long distal and short proximal section</b>	<b>present</b>	moderately long, not crenated	absent



**Table 4** (continued). Diagnostic characteristics of the species of *Landouria* Godwin-Austen, 1918 from Java.

	D (in mm)	H (in mm)	whorls	D/H	U/D	shell periphery	shell coloration	scale sculpture	spiral lines on apical side	penis	penis coecum	flagellum	node at flagellum
<i>L. intumescens</i>	11.6–14.1 (mean 13.2)	6.1–8.7 (mean 7.5)	5–5.75 (mean 5.3)	1.50–1.98 (mean 1.76)	0.22–0.34 (mean 0.27)	sharply keeled	brownish- corneous	without scaly processes	indistinct	divided by narrowing into long distal and short proximal section	absent	distal part crenated, proximal part short	absent
<i>L. moussoniana</i>	10.2–12.0 (mean 11.1)	5.5–6.7 (mean 6.3)	<b>5–6.25</b> (mean <b>5.7</b> )	1.73–1.81 (mean 1.77)	<b>0.37–0.38</b> (mean <b>0.38</b> )	keeled	brownish- corneous	?	indistinct	?	?	?	?
<i>L. schepmani</i>	10.5–10.9	6.1–6.2	5–5.25	1.72–1.76	<b>0.21</b>	<b>sharply keeled</b>	brownish- corneous	no scales discernible	distinct	?	?	?	?
<i>L. monticola</i>	<b>8.5–9.5</b> (mean <b>9.0</b> )	5.3–6.0 (mean 5.8)	4.5–5.25 (mean 4.8)	1.49–1.60 (mean 1.56)	<b>0.18–0.25</b> (mean <b>0.21</b> )	<b>keeled</b>	yellowish or brownish- corneous	no scales discernible	distinct	?	?	?	?
<i>L. smimensis</i>	6.3–11.9 (mean 8.2)	4.1–8.4 (mean 5.6)	4.5–5.5 (mean 4.9)	1.28–1.64 (mean 1.48)	0.18–0.32 (mean 0.25)	<b>angular or rounded</b>	brownish- corneous	<b>hair-like processes</b>	indistinct	<b>long, gradually tapering towards its proximal end</b>	absent	<b>slightly crenated, gradually tapering towards proximal end</b>	absent
<i>L. leucochila</i>	<b>16.3–17.5</b>	8.5–9.5	5.25	1.92	0.30	<b>angular</b>	<b>yellowish</b>	<b>scaly processes all over teleoconch</b>	indistinct	?	?	?	?
<i>L. zonifera</i> sp. nov.	12.5–13.2 (mean 12.8)	6.9–7.6 (mean 7.2)	5.5–5.75 (mean 5.6)	1.73–1.81 (mean 1.77)	0.40	keeled	<b>corneous with brownish zone at periphery</b>	scaly processes sparse, at periphery	indistinct	slightly dilated at proximal end	absent	<b>slightly crenated, more than twice as long as epiphallus</b>	absent
<i>L. ciliocincta</i>	12.4–15.6 (mean 13.6)	6.0–8.3 (mean 7.0)	5–6 (mean 5.4)	<b>1.86–2.12</b> (mean <b>1.94</b> )	0.22–0.30 (mean 0.27)	<b>keeled</b>	<b>whitish- corneous with brownish band at periphery</b>	scaly processes sparse, at periphery	indistinct	with small bulge at proximal end	absent	<b>short, very broad, tapering towards proximal end</b>	absent

**Table 4** (continued). Diagnostic characteristics of the species of *Landouria* Godwin-Austen, 1918 from Java.

	D (in mm)	H (in mm)	whorls	D/H	U/D	shell periphery	shell coloration	scale sculpture	spiral lines on apical side	penis	penis coccum	flagellum	node at flagellum
<i>L. pakidulan</i> sp. nov.	12.5–14.0 (mean 13.4)	6.9–8.1 (mean 7.4)	5.25–5.5 (mean 5.4)	<b>1.70–1.86</b> (mean <b>1.81</b> )	0.24–0.30 (mean 0.27)	angular	whitish, with reddish- brown band at periphery	without scaly processes	indistinct	short, with large bulge at proximal end	absent	moderately long, almost smooth, gradually tapering near proximal end	absent
<i>L. dharmai</i> sp. nov.	9.9	7.2	5.5	1.39	0.18	angular	whitish, with reddish- brown band at periphery	not observed	indistinct	?	?	?	?
<i>L. davini</i>	11–14.8	7.1–10.3	5–5.5	<b>1.41–1.67</b>	0.29	angular	whitish- corneous, with one reddish- brown band above and one below periphery	without scaly processes	indistinct	?	?	?	?
<i>L. menoreh- ensis</i> sp. nov.	12.4–14.5 (mean 13.4)	8.3–10.4 (mean 9.3)	5.25–5.75 (mean 5.5)	1.31–1.51 (mean 1.44)	0.16–0.24 (mean 0.19)	rounded	whitish, with distinct brown band above periphery	without scaly processes	indistinct	short, distal part cylindrical, proximal part slightly dilated	absent	long, broad	absent

Geosciences Collection of the University of Bremen. However, we could not locate type specimens of *H. rotatoria* in this collection or in other museums (e.g., SMF, ZMH). Thus, a neotype must be designated to clarify the taxonomic status and the type locality of *H. rotatoria*.

According to the original description of Pfeiffer (1842), *H. rotatoria* is a brown, sharply keeled, large species with a diameter of 16 mm. There are several sharply keeled species in Java and some reach a diameter of 16 mm. The figures of Pfeiffer (1851 in 1849–1853: pl. 95, figs 3–5) show a specimen with a rather high spire (D/H ratio 1.82). The species that best fits the figure occurs on Gunung Salak and Gunung Gede south of Bogor in West Java (compare the shell of the holotype of *P. leucomphala* Moellendorff, 1897 (Fig. 12) with Pfeiffer 1851 in 1849–1853: pl. 95, figs 3–5). Thus, we designate an anatomically examined specimen from Gunung Salak in West Java (MZB 19205; Fig. 5) as the neotype of *Helix rotatoria* Pfeiffer, 1842.

The same species was later described by Möllendorff (1897) as *Plectotropis leucomphala* with two colour varieties, *P. leucomphala* f. *subfasciata* and *P. leucomphala* f. *castanea*. *Plectotropis leucomphala* was synonymized with *L. rotatoria* by van Benthem Jutting (1950).

*Landouria rotatoria* differs from *L. winteriana* (Figs 2–3), which also occurs on Gunung Salak, and from *L. epiplatia* (Figs 26–28, 31), which also occurs on Gunung Gede, in the larger, more intensively brownish coloured shell and an externally smooth, longish, lemon-shaped flagellum.

### Distribution

*Landouria rotatoria* is endemic to Gunung Salak and Gunung Gede south of Bogor in West Java (Fig. 54). It has also been recorded from other Sunda Islands, as well as the Philippines (Martens 1867; Rensch 1932, 1934; van Benthem Jutting 1941, 1950; Vermeulen & Whitten 1998), but these records refer to other species.

### *Landouria naggsi* sp. nov.

[urn:lsid:zoobank.org:act:4EF9E468-DDEF-460D-939C-7D9C86254CF4](https://zoobank.org/act:4EF9E468-DDEF-460D-939C-7D9C86254CF4)

Figs 25, 52; Tables 3–4

### Diagnosis

*Landouria naggsi* sp. nov. is characterized by an angular, tightly coiled, high conical shell with scales all over the teleoconch.

### Etymology

*Landouria naggsi* sp. nov. is named in honour of the British malacologist Fred Naggs, who brought the authors of this study together.

### Material examined

#### Holotype

INDONESIA • holotype; West Java, Cibitung, near Cikaso Waterfall, teak agroforestry; 7°21'41" S, 106°37'10" E; 47 m a.s.l.; 5 Jul. 2015; A.S. Nurinsiyah and T. Setiadi leg.; D = 11.8 mm, H = 9.8 mm; MZB 20424.

#### Paratypes

INDONESIA – **West Java** • 1 spec.; Cibitung, near Cikaso Waterfall, riparian (high shrubs); 7°21'40" S, 106°37'05" E; 61 m a.s.l.; MZB 20426 • 1 spec.; same data as for preceding; ZMH



148184 • 3 spec.; same data as for holotype; MZB 20425 • 2 spec.; same data as for holotype; ZMH 148183.

### Description

SHELL (Fig. 25; Tables 3–4). Conical, with 6.25–7 slightly convex whorls; protoconch almost smooth; teleoconch with irregular wrinkles; incised spiral lines not discernible; scales all over teleoconch; tuberculate around umbilicus; brownish-corneous; body whorl angular; aperture oval; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus hardly eccentric, wide, comprising 28–33% of shell diameter, hardly obscured by columellar edge.

GENITALIA. Unknown.

### Remarks

*Landouria naggsi* sp. nov. resembles *L. parahyangensis* sp. nov. (Fig. 48), from which it differs in the smaller (D 11.6–14.0 mm vs 14.7–16.9 mm in *L. parahyangensis* sp. nov.), higher conical (D/H: 1.21–1.37 vs 1.69–1.94 in *L. parahyangensis* sp. nov.), less sharply keeled shell with a narrower umbilicus (U/D 0.28–0.33 vs 0.39–0.45 in *L. parahyangensis* sp. nov.) and in having scales all over the teleoconch.

With regard to the conical shell form *L. naggsi* sp. nov. resembles *L. conoidea* (Leschke, 1914) (Fig. 4). For differences, see remarks under that species.

### Distribution

*Landouria naggsi* sp. nov. is known only from the surroundings of Cikaso Waterfall in Sukabumi Regency (Fig. 52).

### *Landouria epiplatia* (Möllendorff, 1897)

Figs 17, 26–28, 31, 55; Tables 3–4

*Plectotropis epiplatia* Möllendorff, 1897: 67 (“Java”; more exactly (Zilch 1966): “W-Java: Djampang (2000’”).

*Plectotropis trichotrochium* Möllendorff, 1897: 67 (“Java”, more exactly (Zilch 1966): “W-Java: Djampang (2000’), s. Susabuni [sic]”). **Syn. nov.**

*Landouria epiplatia* – van Benthem Jutting 1950: 466, fig. 82. — Zilch 1966: 293, pl. 7, fig. 2.

*Landouria rotatoria* – van Benthem Jutting 1950: 461 (in part) . — Zilch 1966: 294, pl. 7, fig. 6 (in part). (not Pfeiffer, 1842)

### Diagnosis

*Landouria epiplatia* is characterized by a brownish, sharply keeled, almost disc-like shell with an only slightly elevated spire and a very wide umbilicus.

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**Figs 25–28** (opposite page). Shells of species of *Landouria* from Java. **25.** *L. naggsi* sp. nov., West Java, Cibitung, near Cikaso Waterfall (holotype, MZB 20424). **26.** *L. epiplatia* (Möllendorff, 1897), West Java, Jampang (lectotype of *Plectotropis epiplatia*, SMF 8909). **27.** *L. epiplatia*, West Java, Jampang (lectotype of *Plectotropis trichotrochium* Möllendorff, 1897, SMF 8918). **28.** *L. epiplatia?*, West Java, Bogor, Gunung Gede (ZMH 79946). Scale bar: 5 mm.

## Material examined

### Type material

INDONESIA – **West Java** • lectotype of *Plectotropis epiplatia* (designated by Zilch 1966); Jampang; 7°03' S, 106°48' E; ca 600 m a.s.l.; SMF 8909 • 1 paralectotype of *Plectotropis epiplatia*; same data as for preceding; SMF 8910 • lectotype of *Plectotropis trichotrochium*; same data as for preceding; SMF 8918.

### Other material

INDONESIA • 1 spec.; Java; ZMB 47682. – **West Java** • 4 spec.; 5 km from Palabuhan Ratu Bay; 7°00' S, 106°35' E; SMF 96542 • 2 spec.; Jampang; 7°03' S, 106°48' E; ca 600 m a.s.l.; SMF 8911 •



**Figs 29–47.** Flagella of species of *Landouria* from Java. **29.** *L. winteriana* (Pfeiffer, 1842), West Java, Padalarang, Gunung Masigit (neotype, ZMA 376193a). **30.** *L. rotatoria* (Pfeiffer, 1842), West Java, Gunung Salak, 1166 m a.s.l. (neotype, MZB 19205). **31.** *L. epiplatia* (Möllendorff, 1897)?, West Java, Bogor, Gunung Gede (ZMH 79946). **32.** *L. nusakambangensis* sp. nov., Central Java, Nusa Kambangan Island, nature monument Gligir (holotype, ZMA 412298a). **33.** *L. petrukensis* sp. nov., Central Java, Karangbolong, way to Petruk Cave (holotype, MZB 19203). **34.** *L. tholiformis* sp. nov., Yogyakarta, Gunung Kidul, Tepus, near Poktunggal Beach (holotype, MZB 17999). **35.** *L. abdidalem* sp. nov., Yogyakarta, Kulonprogo, Sabrang Kidul (holotype, MZB 17664). **36.** *L. madurensis* sp. nov., East Java, Madura Island, Sampang, Nepa Monkey lowland rainforest (paratype, MZB 19209). **37.** *L. sewuensis* sp. nov., Yogyakarta, Gunung Kidul, Tepus, Mbajo Hill (holotype, MZB 19255). **38.** *L. sukoliloensis* sp. nov., Central Java, Kayen, near Watu Payung (holotype, MZB 19219). **39.** *L. tonywhitteni* sp. nov., Central Java, Taruman Village, near Sendang Sedayu (holotype, MZB 19214). **40.** *L. nodifera* sp. nov., Central Java, Larangan Village, Lanang Spring (holotype, MZB 19227). **41.** *L. pacitanensis* sp. nov., East Java, Pacitan, near Srau Beach (MZB 19231). **42.** *L. intumescens* (Martens, 1867), East Java, Guwoterus (MZB 19207). **43.** *L. smimensis* (Mousson, 1848), East Java, Tosari (ZMA 390881). **44.** *L. zonifera* sp. nov., Yogyakarta, Kulonprogo, Sibolong (holotype, MZB 17727). **45.** *L. ciliocincta* (Möllendorff, 1897), East Java, Malang, Kondangmerak (MZB 19211). **46.** *L. pakidulan* sp. nov., Central Java, Nusa Kambangan Island, nature monument Gligir (holotype, ZMA 417011a). **47.** *L. menorehensis* sp. nov., Yogyakarta, Kulonprogo, Sibolong (holotype, MZB 19201). Scale bar: 1 mm.

2 spec. (vouchers for van Benthem Jutting 1950); Sukabumi; 6°55' S, 106°55' E; ZMA 407610 • 1 spec. (det. anat.; see remarks); Bogor, Gunung Gede; 6°46' S, 106°59' E; ZMH 79946.

### Description

**SHELL** (Figs 26–28; Tables 3–4). Almost disc-like, with 5.25–6.25 hardly convex whorls; protoconch almost smooth; teleoconch with irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes sparse, mainly at periphery; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture rounded rhombic; upper insertion of peristome slightly descending; peristome expanded, slightly reflexed and slightly thickened; umbilicus almost concentric, very wide, comprising 30–43% of shell diameter, hardly obscured by columellar edge.

**GENITALIA** (Figs 17, 31; Table 4). Atrium short; penis very long, with a small bulge at proximal end containing a short penis papilla; without penis coecum; membranaceous sheath around distal part of penis connected with epiphallus by tissue; penial retractor runs from diaphragm to proximal part of cylindrical epiphallus; flagellum very long, broadest in its middle part, without node, tapering towards its proximal end; vas deferens narrow and long; vagina long; oviduct short, broad; peduncle of bursa copulatrix subdivided into a broader, abruptly tapering distal part and a narrower, longer proximal part. Right ommatophoral retractor runs between penis and vagina.

### Remarks

*Landouria epiplatia* was described from Jampang in West Java. However, there are several places called Jampang in West Java, two among them being more important ones: Jampang Kulon and Jampang Tengah in Sukabumi Regency. Jampang Kulon is at ca 300 m a.s.l., Jampang Tengah is at ca 500 m a.s.l. and closer to Sukabumi, the locality given by van Benthem Jutting (1950). Thus, we suppose that Jampang Tengah is the type locality.

*Plectotropis trichotrochium* Möllendorff, 1897 (Fig. 27) was synonymized with *L. rotatoria* by van Benthem Jutting (1950) and Zilch (1966). However, in contrast to *L. rotatoria*, the spire of the single specimen on which *P. trichotrochium* was based is hardly elevated. We suppose that the holotype of *P. trichotrochium* is a subadult specimen of *L. epiplatia* that formed a slightly expanded peristome at a premature stage. The specimen is furthermore characterized by stronger radial wrinkles and more distinct incised spiral lines than is usual in *L. epiplatia*. Nevertheless, its occurrence at the type locality of *L. epiplatia* also indicates that it is an aberrant specimen of that species. As first revisers (ICZN 1999: Art. 24), we determine precedence of the name *Plectotropis epiplatia* Möllendorff, 1897 over *Plectotropis trichotrochium* Möllendorff, 1897.

The description of the genitalia is based on a single subadult specimen from Gunung Gede (ZMH 79946; Figs 17, 31), which differs from typical *L. epiplatia* in the slightly tighter coiled, more elevated spire. The available material is insufficient to decide whether this specimen falls within the variability of *L. epiplatia* or represents a distinct species.

### Distribution

*Landouria epiplatia* is known from the northern part of Sukabumi Regency in West Java and its range might extend to Gunung Gede (Fig. 55).

*Landouria parahyangensis* sp. nov.

urn:lsid:zoobank.org:act:41EEB2F2-7781-4D19-9F62-34316F374749

Figs 48, 54; Tables 3–4

**Diagnosis**

*Landouria parahyangensis* sp. nov. is characterized by a sharply keeled, tightly coiled conical shell with a very wide umbilicus.

**Etymology**

*Landouria parahyangensis* sp. nov. is named after its occurrence in the mountainous region Parahyangan. In the Sundanese language, the name ‘Parahyangan’ means ‘the abode of hyangs (gods)’, which were supposed to reside in the mountain tops.

**Material examined**

**Holotype**

INDONESIA • holotype; West Java, Karangnunggal, surroundings of Pasir Taraje Cave, agroforestry; 7°39'58" S, 108°07'01" E; 243 m a.s.l.; 4 Jul. 2014; A.S. Nurinsiyah and T. Setiadi leg.; D = 15.0 mm, H = 8.4 mm; MZB 20429.

**Paratypes**

INDONESIA – **West Java** • 3 spec.; Karangnunggal, surroundings of Kiara Jenggol Cave, agroforestry; 7°39'37" S, 108°06'55" E; 234 m a.s.l.; MZB 20431 • 10 spec.; Karangnunggal, near Sela Dower Cave, agroforestry and bamboo; 7°40'00" S, 108°07'00" E; 237 m a.s.l.; MZB 20428 • 5 spec.; same data as for preceding; ZMH 148186 • 3 spec.; same data as for holotype; MZB 20430 • 3 spec.; same data as for holotype; ZMH 148187 • 1 spec.; Karangnunggal, surroundings of Liang Cai, agroforestry and shrubs; 7°40'01" S, 108°07'03" E; 237 m a.s.l.; ZMH 148185 • 1 spec.; Tasikmalaya, Karangnunggal, mouth of Bojong Cave, agroforestry; 7°40'12" S, 108°07'12" E; 240 m a.s.l.; MZB 20427.

**Description**

SHELL (Fig. 48; Tables 3–4). Conical, with 6.5–7 hardly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; without distinct incised spiral lines; scaly processes sparse, only at periphery; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture rounded rhombic; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus hardly eccentric, wide, comprising 39–45% of shell diameter, hardly obscured by columellar edge.

GENITALIA. Unknown.

**Remarks**

*Landouria parahyangensis* sp. nov. resembles *L. epiplatia* (Figs 26–28) with regard to the wide umbilicus. It differs from *L. epiplatia* in the less sharply keeled, higher, conical shell (H 8.4–9.3 mm vs 5.7–6.9 mm in *L. epiplatia*; D/H 1.69–1.94 vs 2.03–2.94 in *L. epiplatia*) with more whorls (6.5–7

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**Figs 48–51** (opposite page). Shells of species of *Landouria* from Java. **48.** *L. parahyangensis* sp. nov., West Java, Karangnunggal, surroundings of Pasir Taraje Cave (holotype, MZB 20429). **49.** *L. nusakambangensis* sp. nov., Central Java, Nusa Kambangan Island, nature monument Gligir (holotype, ZMA 412298a). **50.** *L. petrukensis* sp. nov., Central Java, Karangbolong, way to Petruk Cave (holotype, MZB 19203). **51.** *L. tholiformis* sp. nov., Yogyakarta, Gunung Kidul, Tepus, near Poktunggal Beach (holotype, MZB 17999). Scale bar: 5 mm.





vs 5.25–6.25 in *L. epiplatia*). *Landouria parahyangensis* sp. nov. also resembles *L. naggsi* sp. nov. (Fig. 25). For differences, see remarks under that species.

### Distribution

*Landouria parahyangensis* sp. nov. is endemic to the Karangnunggal karst area in West Java (Fig. 54).

### *Landouria nusakambangensis* sp. nov.

[urn:lsid:zoobank.org:act:3F1A3273-1ECA-4D55-B350-AC9FE593D6AD](https://zoobank.org/act:3F1A3273-1ECA-4D55-B350-AC9FE593D6AD)

Figs 18, 32, 49, 52; Tables 3–4

*Landouria rotatoria* – van Benthem Jutting 1941: 310 (in part). (not Pfeiffer, 1842)

### Diagnosis

*Landouria nusakambangensis* sp. nov. is characterized by a brownish-corneous, keeled shell, a penis with a small globular bulge at the proximal end and a flagellum consisting of a crenated distal part and a long tapering proximal part.

### Etymology

*Landouria nusakambangensis* sp. nov. is named after its occurrence on Nusa Kambangan Island.

### Material examined

#### Holotype

INDONESIA • holotype (det. anat.); Central Java, Nusa Kambangan Island, Nature Monument Gligir; 7°44' S, 108°53' E; 15–16 Feb. 1927; P.F. Franck leg.; D = 14.9 mm, H = 9.1 mm; ZMA 412298a.

#### Paratypes

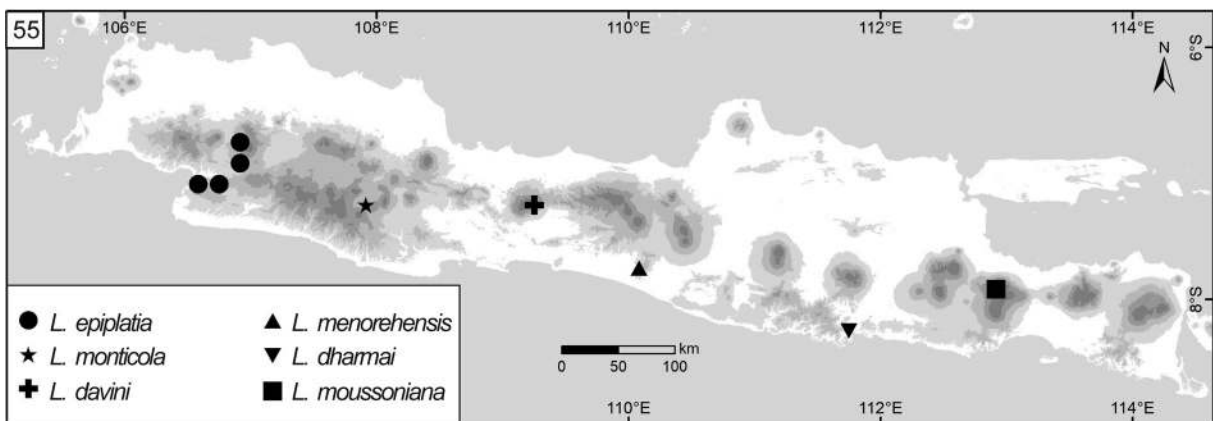
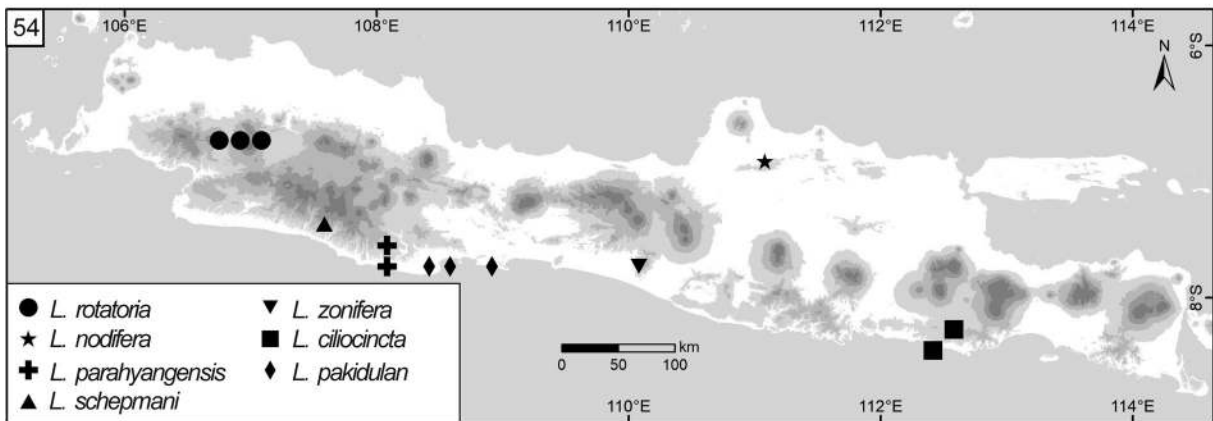
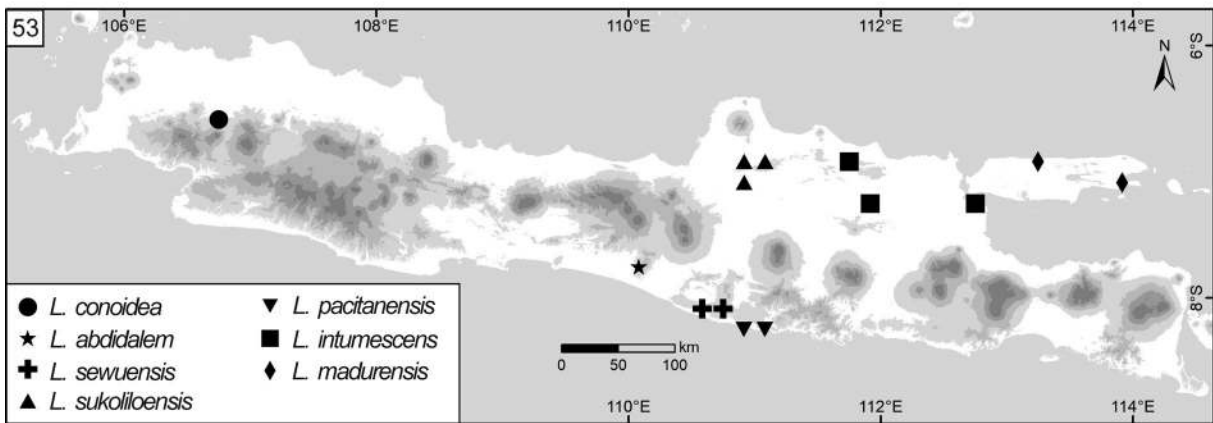
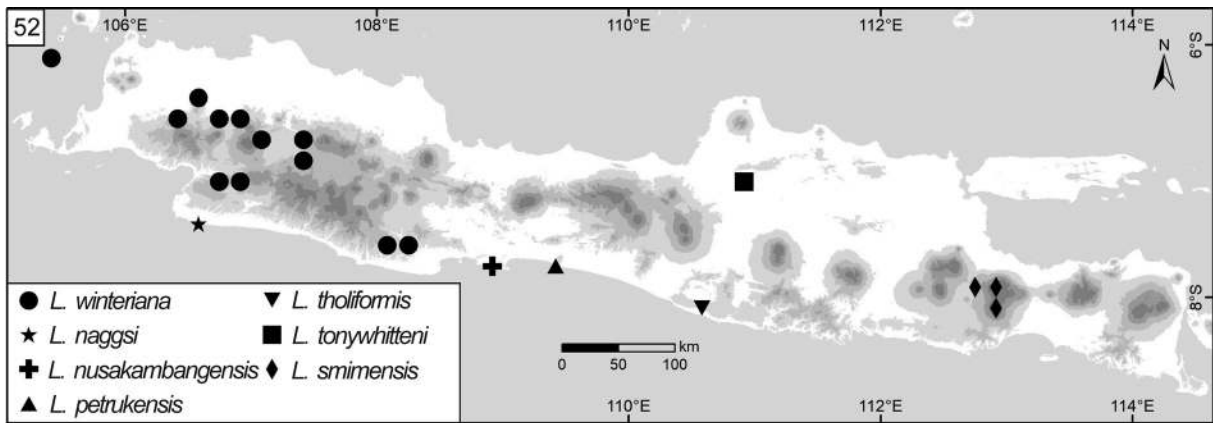
INDONESIA • 7 spec. (vouchers for van Benthem Jutting 1941); same data as for holotype; ZMA 412298 • 16 spec. (vouchers for van Benthem Jutting 1941); same data as for holotype; ZMA 410726 • 6 spec. (vouchers for van Benthem Jutting 1941); Nusa Kambangan Island; 7°44' S, 108°53' E; ZMA 407622.

### Description

SHELL (Fig. 49; Tables 3–4). Depressed conical, with 5.25–6 hardly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines and a granular sculpture; scaly processes sparse, mainly at periphery; tuberculate around umbilicus; brownish-corneous; body whorl keeled; aperture rounded rhombic; upper insertion of peristome descending; peristome expanded, reflexed and thickened; umbilicus slightly eccentric, wide, comprising 32–40% of shell diameter, hardly obscured by columellar edge.

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**Figs 52–55** (opposite page). Distribution of species of *Landouria* in Java (10' grid). **52.** *L. winteriana* (Pfeiffer, 1842), *L. naggsi* sp. nov., *L. nusakambangensis* sp. nov., *L. petrukensis* sp. nov., *L. tholiformis* sp. nov., *L. tonywhitteni* sp. nov., *L. smimensis* (Mousson, 1848). **53.** *L. conoidea* (Leschke, 1914), *L. abdidalem* sp. nov., *L. sewuensis* sp. nov., *L. sulkoliloensis* sp. nov., *L. pacitanensis* sp. nov., *L. intumescens* (Martens, 1867), *L. madurensis* sp. nov. **54.** *L. rotatoria* (Pfeiffer, 1842), *L. nodifera* sp. nov., *L. parahyangensis* sp. nov., *L. schepmani* (Möllendorff, 1897), *L. zonifera* sp. nov., *L. ciliocincta* (Möllendorff, 1897), *L. pakidulan* sp. nov. **55.** *L. epiplatia* (Möllendorff, 1897), *L. monticola* van Benthem Jutting, 1950, *L. davini* Dharma, 2015, *L. menorehensis* sp. nov., *L. dharmai* sp. nov., *L. moussoniana* (Martens, 1867).



GENITALIA (Figs 18, 32; Table 4). Atrium short; penis long, becoming broader proximally; with a small globular bulge at proximal end; without penis coecum; membranaceous sheath around distal part of penis connected with proximal part of epiphallus by tissue; penial retractor runs from diaphragm to proximal part of cylindrical epiphallus; flagellum moderately long, broader distal part usually slightly crenated, proximal part tapering towards its proximal end, without node; vas deferens narrow and long; vagina long; oviduct short, broad, proximally tapering; peduncle of bursa copulatrix subdivided into a broader, cylindrical distal part and a narrower, longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

### Remarks

*Landouria nusakambangensis* sp. nov. resembles *L. winteriana*, from which it differs in the slightly more distinct keel, the smaller globular bulge at the proximal end of the penis and a longer tapering proximal part of the flagellum. In shell shape and the keeled body whorl, *L. nusakambangensis* sp. nov. also resembles *L. rotatoria*, from which it differs in the smaller shell (D 11.9–15.0 mm vs 15.6–19.1 mm in *L. rotatoria*) with a wider umbilicus (U/D 0.32–0.40 vs 0.24–0.32 in *L. rotatoria*).

*Landouria nusakambangensis* sp. nov. occurs sympatrically with *L. pakidulan* sp. nov. (Fig. 85), from which it can easily be distinguished by the brownish, keeled shell.

### Distribution

*Landouria nusakambangensis* sp. nov. is known only from Nusa Kambangan Island (Fig. 52).

### *Landouria petrukensis* sp. nov.

[urn:lsid:zoobank.org:act:32D7E6E9-561F-4E05-95D2-66295BFD6C5E](https://zoobank.org/act:32D7E6E9-561F-4E05-95D2-66295BFD6C5E)

Figs 19, 33, 50, 52; Tables 3–4

### Diagnosis

*Landouria petrukensis* sp. nov. is characterized by a rather high, sharply keeled shell with small scales all over the teleoconch, a penis that is divided into a long, broad, cylindrical distal part and a slightly dilated proximal part by a narrow point and a flagellum, which is broadest near its proximal end.

### Etymology

*Landouria petrukensis* sp. nov. is named after its occurrence in the surroundings of Petruk Cave in Karangbolong.

### Material examined

#### Holotype

INDONESIA • holotype (det. anat.); Karangbolong, way to Petruk Cave; 7°42' S, 109°24' E; 78 m a.s.l.; 5 Aug. 2014; A.S. Nurinsiyah, F.L.H. Irsyad, F.J. Sari and E. Nurlaela leg.; D = 8.7 mm, H = 5.2 mm; MZB 19203.

#### Paratypes

INDONESIA – **Central Java** • 6 spec.; Karangbolong, near Petruk Cave, agroforestry; 7°42'17" S, 109°23'59" E; 78 m a.s.l.; MZB 19273 • 2 spec.; same data as for preceding; ZMH 133409 • 1 spec.; same data as for preceding; MZB 19204 • 5 spec.; Karangbolong, near Petruk Cave, agroforestry; 7°42'19" S, 109°24'02" E; 78 m a.s.l.; MZB 19265 • 4 spec.; same data as for preceding; ZMH 133417 • 4 spec.; Karangbolong, wall and surroundings of Petruk Cave; 7°42'21" S, 109°24'03" E; 104 m a.s.l.; MZB 19266 • 3 spec.; same data as for preceding; MZB 19267 • 5 spec.; Karangbolong, near Petruk Cave,

agroforestry; 7°42'18" S, 109°24'05" E; 138 m a.s.l.; MZB 19274 • 1 spec.; same data as for preceding; ZMH 133407 • 23 spec.; Karangbolong, Adiraja Hill, agroforestry; 7°42'48" S, 109°24'05" E; 168 m a.s.l.; MZB 19271 • 4 spec.; Karangbolong, Adiraja Hill, teak plantation; 7°42'50" S, 109°24'05" E; 166 m a.s.l.; MZB 19275 • 3 spec.; same data as for preceding; ZMH 133414.

### Description

SHELL (Fig. 50; Tables 3–4). Depressed conical, with 4.75–5.5 hardly convex whorls; protoconch almost smooth; teleoconch with irregular wrinkles, apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes all over teleoconch; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture oval; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, wide, comprising 24–37% of shell diameter, hardly obscured by columellar edge.

GENITALIA (Figs 19, 33; Table 4). Atrium short; penis divided by a narrowing into a long, broad cylindrical distal part and a slightly dilated proximal part, without penis coecum; membranaceous sheath around distal part of penis connected with proximal part of epiphallus by tissue; flagellum moderately long, broadest near its proximal end, where it rapidly tapers, slightly crenated, without node; vas deferens narrow and long; vagina short, distally dilated; oviduct longer, proximally hardly tapering; peduncle of bursa copulatrix subdivided into a broader, cylindrical distal part and a narrower, longer proximal part. Right ommatophoral retractor runs between penis and vagina.

### Remarks

With regard to the presence of scales all over the teleoconch, *L. petrukensis* sp. nov. resembles *L. tholiformis* sp. nov. (Fig. 51) and *L. madurensis* sp. nov. (Fig. 57). It differs from both species in the smaller (D 8.1–9.8 mm vs 13.0–14.4 mm in *L. tholiformis* sp. nov. and 11.4–12.0 mm in *L. madurensis* sp. nov.), more depressed shell (D/H 1.49–1.79 vs 1.77–1.88 in *L. tholiformis* sp. nov. and 1.75–2.11 in *L. madurensis* sp. nov.) with fewer whorls (4.75–5.5 vs 6–6.25 in *L. tholiformis* sp. nov. and 5.5–5.75 in *L. madurensis* sp. nov.), an on average narrower umbilicus (U/D 0.24–0.37 vs 0.32–0.40 in *L. tholiformis* sp. nov. and 0.38–0.40 in *L. madurensis* sp. nov.) and in the penis that is divided by a constriction into a long, broad, cylindrical distal part and a slightly dilated proximal part.

We could only investigate the anatomy of the holotype, from Karangbolong in southern Central Java (MZB 19203). There are several samples from other regions of Central Java, West Java and Banten with similar shells. Thus, it is possible that this species is more widely distributed, but the identity of the samples from other regions must be confirmed anatomically.

### Distribution

*Landouria petrukensis* sp. nov. is known from Karangbolong in southern Central Java (Fig. 52).

#### *Landouria tholiformis* sp. nov.

[urn:lsid:zoobank.org:act:C083E997-420A-4CAA-8A67-088C02177B83](https://zoobank.org/urn:lsid:zoobank.org:act:C083E997-420A-4CAA-8A67-088C02177B83)

Figs 7, 20, 34, 51–52; Tables 3–4

### Diagnosis

*Landouria tholiformis* sp. nov. is characterized by a brownish-corneous, sharply keeled shell with scaly processes all over the shell, with a bulge at the proximal end of the penis forming a short coecum, and a crenated flagellum, which tapers abruptly at its proximal end.

### Etymology

*Landouria tholiformis* sp. nov. is named after its dome-shaped shell (Latin: ‘tholus’ = ‘dome’, ‘forma’ = ‘shape’; used as an adjective).

### Material examined

#### Holotype

INDONESIA • holotype (det. anat.); Gunung Kidul, Tepus, near Poktunggal Beach, agroforestry; 8°08'42" S, 110°37'52" E; 137 m a.s.l.; 9 Aug. 2014; A.S. Nurinsiyah, F.L.H. Irsyad, F.J. Sari and E. Nurlaela leg.; D = 8.7 mm, H = 5.2 mm; MZB 17999.

#### Paratypes

INDONESIA • 8 spec.; Yogyakarta, Gunung Kidul, Tepus, Pego Hill, agroforestry; 8°06'10" S, 110°37'50" E; 230 m a.s.l.; MZB 19299.

### Description

**SHELL** (Figs 7, 51; Tables 3–4). Depressed conical, with a dome-shaped spire, with 6–6.25 slightly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes all over shell; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture rounded rhombic; upper insertion of peristome descending; peristome expanded, reflexed and thickened; umbilicus slightly eccentric, wide, comprising 32–40% of shell diameter, hardly obscured by columellar edge.

**GENITALIA** (Figs 20, 34; Table 4). Atrium short; penis long, becoming slightly broader proximally, with a bulge at proximal end forming a short coecum; membranaceous sheath around distal part of penis connected with epiphallus by tissue; penial retractor runs from diaphragm to proximal part of cylindrical epiphallus; flagellum moderately long, broadest in its middle part, crenated, without node, abruptly tapering at its proximal end; vas deferens narrow and long; vagina moderately long; oviduct short, broad, proximally tapering; peduncle of bursa copulatrix subdivided into a broader, almost cylindrical distal part that abruptly passes into a narrower and longer proximal part that ends in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

### Remarks

*Landouria tholiformis* sp. nov. clusters in the phylogeny (Fig. 1) with *L. abdidalem* sp. nov. (Fig. 56). It differs from that species in the more depressed (D/H 1.77–1.88 vs 1.93–2.14 in *L. abdidalem* sp. nov.), less sharply keeled shell with scaly processes all over the teleoconch (Fig. 7), in the flagellum, which is slightly longer than the short epiphallus, and in having a bulge at the proximal end of the penis (perhaps this is an individual abnormality).

*Landouria tholiformis* sp. nov. occurs sympatrically with *L. sewuensis* sp. nov. (Fig. 58), from which it differs in the less sharply keeled shell with a dome-shaped spire, a more distinct granular microsculpture, with scaly processes all over the shell (Fig. 7) and less distinct spiral lines at the umbilical side, the bulge at the proximal end of the penis that forms a short coecum, and a narrow, crenated flagellum. The flagellum of *L. sewuensis* sp. nov. is broader than that of *L. tholiformis* sp. nov. and equipped with two rows of tubercles. There is a globular bulge in the distal part of the vagina in *L. sewuensis* sp. nov. which is absent in *L. tholiformis* sp. nov.

### Distribution

*Landouria tholiformis* sp. nov. is endemic to the Gunung Sewu karst region in Gunung Kidul Regency (Fig. 52).

*Landouria abdidalem* sp. nov.

[urn:lsid:zoobank.org:act:B91C66B0-56B9-40EB-800E-4C321959C0B2](https://zoobank.org/urn:lsid:zoobank.org:act:B91C66B0-56B9-40EB-800E-4C321959C0B2)

Figs 21, 35, 53, 56; Tables 3–4

**Diagnosis**

*Landouria abdidalem* sp. nov. is characterized by a sharply keeled shell, a long and narrow penis and epiphallus, and a crenated flagellum, which is shorter than the epiphallus and abruptly tapering at its proximal end.

**Etymology**

The name of the species is derived from the Javanese expression ‘Abdi Dalem’ (used as a noun in apposition). Abdi Dalem is a person who devotes himself to serve the Keraton of Yogyakarta (Yogya Palace) and the Sultan.

**Material examined**

**Holotype**

INDONESIA • holotype (det. anat.); Yogyakarta, Kulonprogo, Jatimulyo, near Kiskendo Cave; 7°44'53" S, 110°07'53" E; 700 m a.s.l.; 25 Aug. 2017; B. Hausdorf leg.; D = 13.4 mm, H = 6.8 mm; MZB 21271.

**Paratypes**

INDONESIA – **Central Java** • 1 spec. (det. anat.); Purworejo, Donorejo, near Seplawan Cave, shrubs and limestone rock; 7°45'52" S, 110°05'46" E; 700 m a.s.l.; MZB 17733 • 3 spec.; same data as for preceding; MZB 17732 • 5 spec.; same data as for preceding; MZB 19314 • 4 spec.; same data as for preceding; ZMH 133410 • 1 spec.; same data as for preceding; ZMH 133421 • 10 spec.; Yogyakarta, Kulonprogo, Jatimulyo, near Kiskendo Cave; 7°44'53" S, 110°07'53" E; 700 m a.s.l.; ZMH 140026 • 1 spec. (det. anat.); Yogyakarta, Kulonprogo, Sabrang Kidul, snakefruit plantation; 7°44'38" S, 110°07'55" E; 730 m a.s.l.; MZB 17664 • 7 spec.; same data as for preceding; MZB 19253.

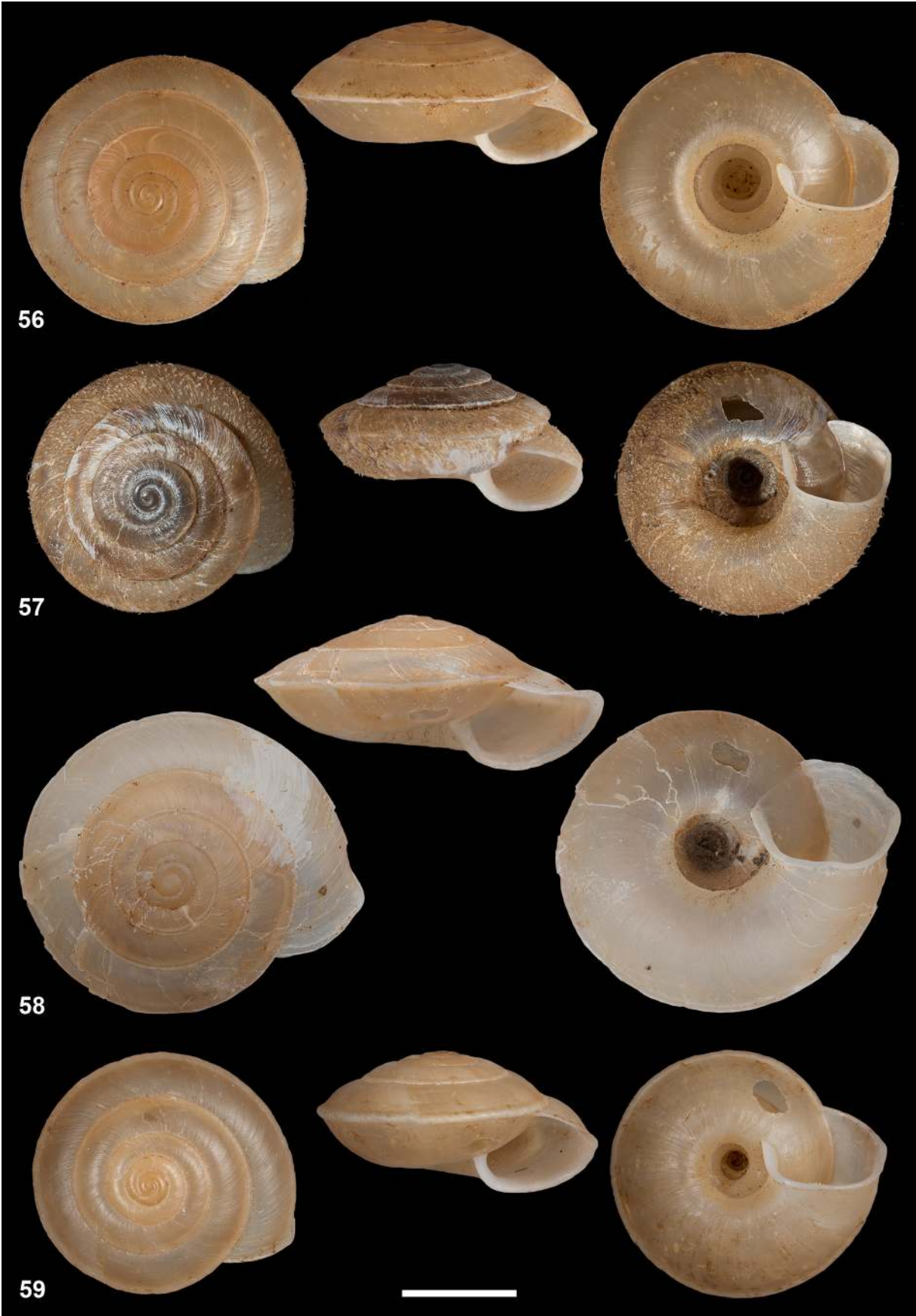
**Description**

SHELL (Fig. 56; Tables 3–4). Depressed conical, with 5.75–6 hardly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes sparse, mainly at periphery and at umbilical side; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture rounded rhombic; upper insertion of peristome descending; peristome expanded, reflexed and thickened; umbilicus hardly eccentric, wide, comprising 33–48% of shell diameter, hardly obscured by columellar edge.

GENITALIA (Figs 21, 35; Table 4). Atrium short; penis long, becoming slightly broader proximally, without penis coecum; membranaceous sheath around distal part of penis connected with the epiphallus by tissue; penial retractor runs from diaphragm to proximal part of cylindrical epiphallus; flagellum shorter than epiphallus, broadest in its middle part, without node, abruptly tapering towards its blunt proximal end, crenated; vas deferens narrow and long; vagina long; oviduct shorter, broad, proximally tapering; peduncle of bursa copulatrix subdivided into a broader, spindle-shaped distal part and a narrower, longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

**Remarks**

With regard to the shell, *L. abdidalem* sp. nov. resembles *L. tholiformis* sp. nov. (Fig. 51), with which it clusters in the molecular phylogeny (Fig. 1). For differences, see remarks under that species. The range





of *L. abdidalem* sp. nov. overlaps with that of *L. zonifera* sp. nov. For differences, see remarks under that species. Furthermore, the range of *L. abdidalem* sp. nov. overlaps with that of *L. menorehensis* sp. nov. (Fig. 88) from which it can easily be distinguished by the sharply keeled, depressed conical, brownish-corneous shell.

### Distribution

*Landouria abdidalem* sp. nov. is endemic to the Menoreh Hills (Fig. 53).

### *Landouria madurensis* sp. nov.

[urn:lsid:zoobank.org:act:024A8B78-91C2-49CA-8721-C0B8CCC46982](https://zoobank.org/urn:lsid:zoobank.org:act:024A8B78-91C2-49CA-8721-C0B8CCC46982)

Figs 8, 22, 36, 53, 57; Tables 3–4

*Helix squamulosa* Martens, 1867: 266, pl. 13, fig. 10 (“Insel Madura (an der Nordostseite von Java), bei Sumanap”) (objective junior synonym of *Helix squamulosa* Mousson, 1856). **Syn. nov.**

*Helix squamulosa* – Pfeiffer 1871 in 1870–1876: pl. 117, figs 13–15; 1872 in 1870–1876: 41.

*Landouria squamulosa* – van Benthem Jutting 1941: 311.

### Diagnosis

*Landouria madurensis* sp. nov. is characterized by a sharply keeled shell with longish scales all over the teleoconch, a wide umbilicus, a long penis, which is divided into a longer, broader distal and a shorter, narrower proximal part, and a long flagellum, which gradually tapers towards its proximal end.

### Etymology

*Landouria madurensis* sp. nov. is named after its occurrence on Madura Island.

### Material examined

#### Holotype

INDONESIA • holotype (det. anat.); East Java, Madura Island, Sampang, Nepa Monkey lowland rainforest; 6°54'01" S, 113°12'08" E; 17 m a.s.l.; 14 May 2014; A.S. Nurinsiyah and T. Setiadi leg.; D = 11.4 mm, H = 6.5 mm; MZB 21432.

#### Paratypes

INDONESIA • 1 spec.; same data as for holotype; MZB 19209 • 4 spec.; same data as for holotype; MZB 19210 • 1 spec.; same data as for holotype; ZMH 133408 • 4 spec.; same data as for holotype; ZMH 133437 • 2 spec. (also syntypes of *H. squamulosa*); Sumenep (see Martens 1867: 267); 7°01' S, 113°52' E; ZMB 7155.

### Description

SHELL (Figs 8, 57; Tables 3–4). Depressed conical, with 5.5–5.75 hardly convex whorls; protoconch almost smooth; teleoconch with irregular wrinkles; without distinct incised spiral lines; longish scales

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**Figs 56–59** (opposite page). Shells of species of *Landouria* from Java. **56.** *L. abdidalem* sp. nov., Yogyakarta, Kulonprogo, Sabrang Kidul (holotype, MZB 17664). **57.** *L. madurensis* sp. nov., East Java, Madura Island, Sampang, Nepa Monkey lowland rainforest (holotype MZB 21432). **58.** *L. sewuensis* sp. nov., Yogyakarta, Gunung Kidul, Tepus, Mbajo Hill (holotype, MZB 19255). **59.** *L. sukoliloensis* sp. nov., Central Java, Kayen, near Watu Payung (holotype, MZB 19219). Scale bar: 5 mm.

all over teleoconch; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture rounded rhombic; upper insertion of peristome descending; peristome expanded, reflexed and thickened; umbilicus slightly eccentric, very wide, comprising 38–40% of shell diameter, hardly obscured by columellar edge.

GENITALIA (Figs 22, 36; Table 4). Atrium short; penis long, divided into a longer, broader distal and a shorter, narrower proximal part, without penis coecum; membranaceous sheath around distal part of penis connected with proximal part of epiphallus by tissue; penial retractor runs from diaphragm to middle part of cylindrical epiphallus; flagellum long, broadest in its middle part, gradually tapering towards its proximal end, slightly crenated, without node; vas deferens narrow and long; vagina cylindrical, long; oviduct shorter, proximally hardly tapering; peduncle of bursa copulatrix subdivided into a broader, cylindrical distal part and a narrower, longer proximal part. Right ommatophoral retractor runs between penis and vagina.

### Remarks

*Landouria madurensis* sp. nov. differs from the neighbouring *Landouria intumescens* in the presence of longish scales all over the teleoconch (Fig. 8), a wider umbilicus (U/D 0.38–0.40 vs 0.22–0.34 in *L. intumescens*) and a relatively long vagina (P:V 2.1 vs 2.4–3.9 in *L. intumescens*).

A second, more conical species of *Landouria* without longish scales and with a narrower umbilicus, of which only juveniles were found, lives sympatrically with *Landouria madurensis* sp. nov. in Nepa Monkey lowland rainforest on Madura Island.

### Distribution

*Landouria madurensis* sp. nov. is endemic to Madura Island (Fig. 53).

### *Landouria sewuensis* sp. nov.

[urn:lsid:zoobank.org:act:2E324442-51A9-4897-9635-22666EF0E037](https://zoobank.org/urn:lsid:zoobank.org:act:2E324442-51A9-4897-9635-22666EF0E037)

Figs 23, 37, 53, 58; Tables 3–4

*Landouria* cf. *rotatoria* – Köhler *et al.* in press: 6 (in part). (not Pfeiffer, 1842)

### Diagnosis

*Landouria sewuensis* sp. nov. is characterized by a brownish-corneous, sharply keeled shell with a wide umbilicus, a penis that is divided into a long, broad distal and a short, narrow proximal part with a globular bulge at its proximal end, a broad flagellum with two rows of broad tubercles and a globular bulge in the distal part of the vagina.

### Etymology

*Landouria sewuensis* sp. nov. is named after its occurrence in the Gunung Sewu karst region.

### Material examined

#### Holotype

INDONESIA • holotype (det. anat.); Gunung Kidul, Tepus, Mbajo Hill, natural forest; 8°08'33" S, 110°40'59" E; 249 m a.s.l.; 8 Aug. 2014; A.S. Nurinsiyah, F.L.H. Irsyad, F.J. Sari and E. Nurlaela leg.; D = 15.1 mm, H = 7.1 mm; MZB 19255.

**Paratypes**

INDONESIA – **Central Java** • many spec.; Yogyakarta, Gunung Kidul, Kemadang: Pantai Baron; 8°07'43" S, 110°32'54" E; 20 m a.s.l.; ZMH 140024 • 2 spec. (det. anat.); Gunung Kidul, Tepus, Cemara Udang Hill, secondary forest; 8°08'55" S, 110°36'37" E; 39 m a.s.l.; MZB 19261 • 1 spec.; same data as for preceding; ZMH 133418 • many spec.; Gunung Kidul, Tepus, rock above Poktunggal Beach; 8°09'23" S, 110°37'22" E; 10 m a.s.l.; ZMH 140025 • 1 spec. (det. anat.); Gunung Kidul, Tepus, Pego Hill, agroforestry; 8°06'10" S, 110°37'50" E; 230 m a.s.l.; MZB 19259 • 1 spec. (det. anat.); Gunung Kidul, Tepus, Pego Hill, agroforestry; 8°06'10" S, 110°37'51" E; 244 m a.s.l.; MZB 19258 • 1 spec.; Gunung Kidul, Tepus, near Poktunggal Beach, agroforestry; 8°08'42" S, 110°37'52" E; 137 m a.s.l.; MZB 21269 • 3 spec. (det. anat.); same data as for preceding; MZB 19260 • 3 spec.; same data as for preceding; ZMH 79891 • 1 spec. (det. anat.); Gunung Kidul, Tepus, Mbajo Hill, natural forest; 8°08'32" S, 110°40'58" E; 281 m a.s.l.; MZB 19257 • 1 spec.; same data as for preceding; ZMH 133419 • 1 spec. (det. anat.); Gunung Kidul, Tepus, Mbajo Hill, natural forest; 8°08'33" S, 110°40'59" E; 258 m a.s.l.; MZB 19256.

**Description**

**SHELL** (Fig. 58; Tables 3–4). Depressed conical, with 5.25–6 hardly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes, if present, at periphery; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture rounded rhombic; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, wide, comprising 30–40% of shell diameter, hardly obscured by columellar edge.

**GENITALIA** (Figs 23, 37; Table 4). Atrium short; penis long, distal part broad, shorter proximal part narrow, with a globular swelling at proximal end; without penis coecum; membranaceous sheath around distal part of penis connected with proximal part of epiphallus by tissue; penial retractor runs from diaphragm to middle of cylindrical epiphallus; flagellum moderately long, broad, with two rows of broad tubercles at margin, tapering towards its proximal end; without node; vas deferens narrow and long; vagina long, distally globularly dilated, constriction towards its middle, becoming broader again towards its proximal end; oviduct short, broad, proximally tapering; peduncle of bursa copulatrix subdivided into a broader, cylindrical distal part and a narrower, longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

**Remarks**

The shell of *L. sewuensis* sp. nov. cannot be reliably distinguished from those of *L. sukoliloensis* sp. nov. (Fig. 59) or *L. intumescens* (Figs 72–74). *Landouria sewuensis* sp. nov. differs from these species in the division of the penis into a long, broad distal and a short, narrow proximal part with a globular bulge at its proximal end, the broad flagellum with two rows of broad tubercles and the globular bulge in the distal part of the vagina.

*Landouria sewuensis* sp. nov. occurs sympatrically with *L. tholiformis* sp. nov. (Fig. 51). For differences, see remarks under that species.

A sequence of *L. sewuensis* sp. nov. was included in the phylogenetic analysis of Köhler *et al.* (in press: fig. 2; ZMH 79891; erroneously labelled “Sumatra”) under the name *L. cf. rotatoria* (not Pfeiffer, 1842).

**Distribution**

*Landouria sewuensis* sp. nov. is endemic to the Gunung Sewu karst region in Gunung Kidul Regency (Fig. 53).

*Landouria sukoliloensis* sp. nov.

[urn:lsid:zoobank.org:act:74853E9E-ECA0-4182-8CB2-FD09A4CD903C](https://doi.org/10.21203/rs.3.rs-2700000/v1)

Figs 24, 38, 53, 59; Tables 3–4

*Landouria winteriana* – Nurinsiyah 2015: 32. (not Pfeiffer, 1842)

### Diagnosis

*Landouria sukoliloensis* sp. nov. is characterized by a brownish-corneous, sharply keeled shell, a penis that is dilated at its proximal end and a flagellum that is not crenated, but abruptly tapering at its proximal end.

### Etymology

*Landouria sukoliloensis* sp. nov. is named after its occurrence in the Sukolilo Karst.

### Material examined

#### Holotype

INDONESIA • holotype (det. anat.); Central Java, Pati, Kayen, near Watu Payung; 6°55'59" S, 110°55'34" E; 110 m a.s.l.; 16 Aug. 2014; A.S. Nurinsiyah, F.L.H. Irsyad, F.J. Sari and E. Nurlaela leg.; D = 11.7 mm, H = 6.1 mm; MZB 19219.

#### Paratypes

INDONESIA – **Central Java** • 7 spec. (det. anat.); Grobogan, Taruman Village, near Sendang Sedayu, agroforestry; 7°00'52" S, 110°51'29" E; 20 m a.s.l.; MZB 19221 • 1 spec.; same data as for preceding; ZMH 133432 • 5 spec.; Grobogan, Taruman Village, near Sendang Sedayu, agroforestry; 7°00'52" S, 110°51'29" E; 23 m a.s.l.; MZB 19216 • 2 spec.; same data as for preceding; ZMH 133435 • 13 spec.; same data as for holotype; MZB 19218 • 9 spec.; same data as for holotype; ZMH 133433 • 10 spec.; Pati, Kayen, near Watu Payung; 6°56'00" S, 110°55'34" E; 115 m a.s.l.; MZB 19225 • 4 spec.; same data as for preceding; ZMH 133429 • 21 spec. (det. anat.); Pati, Sukolilo, Kedumulyo, Wareh Cave, agroforestry; 6°55'41" S, 110°57'37" E; 73 m a.s.l.; MZB 192229 • 15 spec.; same data as for preceding; ZMH 133431 • 7 spec.; Pati, Sukolilo, Kedumulyo, Wareh Cave, agroforestry; 6°55'41" S, 110°57'38" E; 53 m a.s.l.; MZB 19223 • 4 spec.; same data as for preceding; ZMH 133430.

#### Other material

INDONESIA – **Central Java** • 3 spec.; Grobogan, Sedayu, surroundings of Macan Cave, agroforestry and shrubs; 6°58'30" S, 110°57'03" E; 363 m a.s.l.; MZB 19252 • 3 spec.; Pati, Kayen, Brati, Nggoboyo Spring, agroforestry; 6°54'58" S, 111°01'54" E; 89 m a.s.l.; MZB 19232 • 3 spec.; Pati, Tambakromo, Larangan, Lanang Spring, secondary forest; 6°54'19" S, 111°03'22" E; 100 m a.s.l.; MZB 19226 • 2 spec.; Pati, Tambakromo, Larangan, Lowo Cave, secondary forest; 6°54'19" S, 111°03'24" E; 112 m a.s.l.; MZB 19230 • 1 spec.; Pati, Tambakromo, Kedunglawah, Ngencek Spring, agroforestry; 6°54'05" S, 111°03'57" E; 110 m a.s.l.; MZB 19262.

### Description

SHELL (Fig. 59; Tables 3–4). Depressed conical, with 5–5.75 hardly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles, indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes sparse, mainly at periphery; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture rounded rhombic; upper insertion of peristome slightly descending; peristome expanded, slightly reflexed and thickened; umbilicus slightly eccentric, wide, comprising 22–41% of shell diameter, hardly obscured by columellar edge.

GENITALIA (Figs 24, 38; Table 4). Atrium short; penis long, cylindrical, dilated at its proximal end, without penis coecum; membranaceous sheath around distal part of penis connected with proximal part of epiphallus by tissue; penial retractor runs from diaphragm to middle part of almost cylindrical epiphallus; flagellum moderately long, broadest in its middle part, abruptly tapering at its proximal end, not crenated, without node; vas deferens narrow and long; vagina long, often constricted near atrium; oviduct short, broad, proximally tapering; peduncle of bursa copulatrix subdivided into a broader distal part and a narrower, longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

### Remarks

*Landouria sukoliloensis* sp. nov. cannot be distinguished from *L. sewuensis* sp. nov. and *L. intumescens* by shell characters. It differs from these species in the penis that is dilated at its proximal end and in the flagellum, which is not crenulated but abruptly tapers at its proximal end.

*Landouria sukoliloensis* sp. nov. differs from *L. tonywhitteni* sp. nov. (Fig. 60), with which it occurs sympatrically, in the smaller (D 10.4–12.3 mm vs 14.3–17.6 mm in *L. tonywhitteni* sp. nov.), higher shell (D/H 1.60–1.93 vs 1.93–2.34 in *L. tonywhitteni* sp. nov.), the dilatation at the proximal end of the penis and the lack of a globular node at the flagellum.

### Distribution

*Landouria sukoliloensis* sp. nov. is endemic to Sukolilo Karst (Fig. 53).

### *Landouria tonywhitteni* sp. nov.

[urn:lsid:zoobank.org:act:59260748-3438-411F-82B4-14A7847AFA58](https://zoobank.org/act:59260748-3438-411F-82B4-14A7847AFA58)

Figs 39, 52, 60, 63; Tables 3–4

### Diagnosis

*Landouria tonywhitteni* sp. nov. is characterized by having a strongly depressed conical, brownish-corneous, sharply keeled shell and a penis that does not become distinctly broader towards its proximal end, the lack of a coecum at the proximal end of the penis and the presence of a node at the base of the flagellum.

### Etymology

*Landouria tonywhitteni* sp. nov. is named in honour of the late British naturalist Tony Whitten (1953–2017), who dedicated his life to the conservation of karst habitats and especially the snails that inhabit these habitats.

### Material examined

#### Holotype

INDONESIA • holotype (det. anat.); Central Java, Grobogan, Taruman, near Sendang Sedayu; 7°00'52" S, 110°51'29" E; 20 m a.s.l.; 16 Aug. 2014; A.S. Nurinsiyah, F.L.H. Irsyad, F.J. Sari and E. Nurlaela leg.; measurements: D = 17.6 mm, H = 7.6 mm; MZB 19214.

#### Paratypes

INDONESIA – **Central Java** • 9 spec.; same data as for holotype; MZB 19217 • 5 spec.; same data as for holotype; ZMH 133434 • 9 spec. (det. anat.); Grobogan, Taruman, near Sendang Sedayu; 7°00'52" S, 110°51'29" E; 23 m a.s.l.; MZB 19215 • 1 spec.; same data as for preceding; MZB 21268 • 5 spec.; same data as for preceding; ZMH 133436.



**Figs 60–62.** Shells of species of *Landouria* from Java. **60.** *L. tonywhitteni* sp. nov., Central Java, Taruman Village, near Sendang Sedayu (holotype, MZB 19214). **61.** *L. nodifera* sp. nov., Central Java, Larangan Village, Lanang Spring (holotype, MZB 19227). **62.** *L. pacitanensis* sp. nov., East Java, Pacitan, Srau Beach (holotype, MZB 21191). Scale bar: 5 mm.

**Description**

SHELL (Fig. 60; Tables 3–4). Depressed conical, with 5.75–6 hardly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct spiral lines, umbilical side with indistinct incised spiral lines; with radial scaly processes; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture rhombic; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, wide, comprising 32–41% of shell diameter, hardly obscured by columellar edge.

GENITALIA (Figs 39, 63; Table 4). Atrium short; penis long, consisting of a long, cylindrical distal part covered by an additional sheath, which is connected by muscular tissue to proximal part of epiphallus and a dilated proximal part containing a short penial papilla; without penis coecum; penial retractor runs from diaphragm to distal part of long, narrow epiphallus; flagellum short, broadest at its base, where it is equipped with a globular node, tapering towards its proximal end, not distinctly crenated; vas deferens narrow and long; vagina long; peduncle of bursa copulatrix subdivided into a slightly broader, cylindrical distal part and a narrower, longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

**Remarks**

*Landouria nodifera* sp. nov., *L. tonywhitteni* sp. nov., *L. pacitanensis* sp. nov., *L. sewuensis* sp. nov. and *L. intumescens* share strongly depressed, brownish-corneous, sharply keeled shells. These species cannot be reliably distinguished by shell characters. *Landouria tonywhitteni* sp. nov. shares a node at the base of the flagellum with *L. nodifera* sp. nov., from which it differs in the lack of a coecum at the proximal end of the penis and in having a penis that does not become broader towards its proximal end.

**Distribution**

*Landouria tonywhitteni* sp. nov. is endemic to Sukolilo Karst (Fig. 52), where it occurs sympatrically with *L. sukoliloensis* sp. nov.

*Landouria nodifera* sp. nov.

[urn:lsid:zoobank.org:act:36465425-2C50-4721-9B73-3719E2D4A78A](https://zoobank.org/act:36465425-2C50-4721-9B73-3719E2D4A78A)

Figs 40, 54, 61, 64; Tables 3–4

*Landouria rotatoria* – Nurinsiyah 2015: 32 (in part). (not Pfeiffer, 1842)

**Diagnosis**

*Landouria nodifera* sp. nov. is characterized by a strongly depressed conical, brownish-corneous, sharply keeled shell and a penis that becomes broader towards its proximal end, the presence of a coecum at the proximal end of the penis and a node at the base of the flagellum.

**Etymology**

*Landouria nodifera* sp. nov. is named after the node at its flagellum (Latin: ‘nodus’ = ‘node’, ‘ferre’ = ‘to carry’; used as an adjective).

**Material examined****Holotype**

INDONESIA • holotype (det. anat.); Central Java, Pati, Larangan Village, Lanang Spring; 6°54'19" S, 111°03'22" E; 100 m a.s.l.; 15 Aug. 2014; A.S. Nurinsiyah, F.L.H. Irsyad, F.J. Sari and E. Nurlaela leg.; measurements: D = 15.0 mm, H = 7.0 mm; MZB 19227.

### Paratypes

INDONESIA – **Central Java** • 1 spec.; same data as for holotype; MZB 19233 • 6 spec.; same data as for holotype; MZB 19228 • 5 spec.; same data as for holotype; ZMH 133428 • 9 spec. (det. anat.); Pati, Larangan Village, Lowo Cave; 6°54'19" S, 111°03'24" E; 112 m a.s.l.; MZB 19229 • 1 spec.; same data as for preceding; MZB 21266.

### Description

**SHELL** (Fig. 61; Tables 3–4). Depressed conical, with 5–5.75 hardly convex whorls; protoconch almost smooth; teleoconch with irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes sparse, mainly at periphery; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture rhombic; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, wide, comprising 26–38% of shell diameter, hardly obscured by columellar edge.

**GENITALIA** (Figs 40, 64; Table 4). Atrium short; penis long, consisting of a cylindrical distal part covered by an additional sheath, connected by muscular tissue to proximal part of epiphallus, and a dilated proximal part containing a short penial papilla; inside proximal part of penis with longitudinal pilasters, which pass into a more complex sculpture in distal part of penis; at proximal end of penis with a blunt penis coecum; penial retractor runs from diaphragm to distal part of epiphallus, which tapers proximally; flagellum moderately long, broadest in its middle part, where it is equipped with a node, tapering towards its proximal end; vas deferens narrow and long; vagina long; peduncle of bursa copulatrix subdivided into a broader, cylindrical distal part and a narrower, longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

### Remarks

*Landouria nodifera* sp. nov., *L. tonywhitteni* sp. nov., *L. pacitanensis* sp. nov., *L. sukoliloensis* sp. nov., *L. sewuensis* sp. nov. and *L. intumescens* share strongly depressed, brownish-corneous, sharply keeled shells. These species cannot be reliably distinguished by shell characters. *Landouria nodifera* sp. nov. shares having a coecum at the proximal end of the penis with *L. pacitanensis* sp. nov., from which it differs in the lack of the narrow constriction subdividing the penis of *L. pacitanensis* sp. nov. and the presence of a node at the base of the flagellum. *Landouria nodifera* sp. nov. shares having a node at the base of the flagellum with *L. tonywhitteni* sp. nov., from which it differs in the presence of the coecum at the proximal end of the penis and the proximally broader penis.

### Distribution

*Landouria nodifera* sp. nov. is endemic to Sukolilo Karst (Fig. 54).

#### *Landouria pacitanensis* sp. nov.

[urn:lsid:zoobank.org:act:E0076893-CF05-4D23-A1E0-402A2DE7F0EF](https://zoobank.org/urn:lsid:zoobank.org:act:E0076893-CF05-4D23-A1E0-402A2DE7F0EF)

Figs 9, 41, 53, 62, 65; Tables 3–4

### Diagnosis

*Landouria pacitanensis* sp. nov. is characterized by a strongly depressed conical, brownish-corneous, sharply keeled shell and a penis with a distinct constriction between its distal and its proximal part, and the presence of a coecum at the proximal end of the penis.

### Etymology

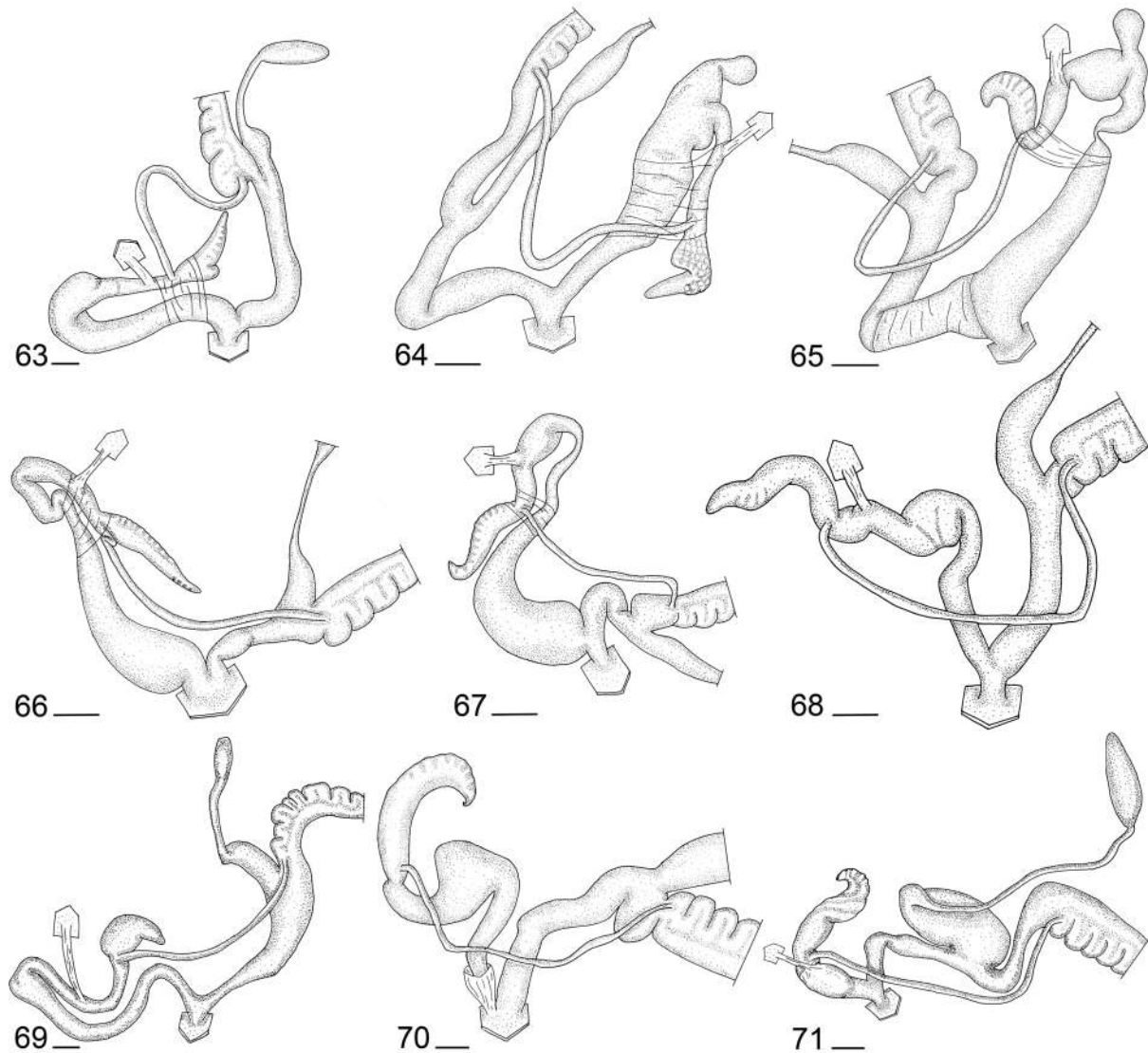
*Landouria pacitanensis* sp. nov. is named after its occurrence in the Pacitan Regency.



**Material examined**

**Holotype**

INDONESIA • holotype (det. anat.); East Java, Pacitan, Srau Beach; 8°15'01" S, 110°59'46" E; 60 m a.s.l.; 10 Aug. 2014; A.S. Nurinsiyah, F.L.H. Irsyad, F.J. Sari and E. Nurlaela leg.; measurements: D = 12.7 mm, H = 7.1 mm; MZB 21191.



**Figs 63–71.** Genitalia of species of *Landouria* from Java. **63.** *L. tonywhitteni* sp. nov., Central Java, Taruman Village, near Sendang Sedayu (holotype, MZB 19214). **64.** *L. nodifera* sp. nov., Central Java, Larangan Village, Lanang Spring (holotype, MZB 19227). **65.** *L. pacitanensis* sp. nov., East Java, Pacitan, near Srau Beach (MZB 19231). **66.** *L. intumescens* (Martens, 1867), East Java, Guwoterus (MZB 19207). **67.** *L. smimensis* (Mousson, 1848), East Java, Tosari (ZMA 390881). **68.** *L. zonifera* sp. nov., Yogyakarta, Kulonprogo, Sibolong (holotype, MZB 17727). **69.** *L. ciliocincta* (Möllendorff, 1897), East Java, Malang, Kondangmerak (MZB 19211). **70.** *L. pakidulan* sp. nov., Central Java, Nusa Kambangan Island, nature monument Gligir (holotype, ZMA 417011a). **71.** *L. menorehensis* sp. nov., Yogyakarta, Kulonprogo, Sibolong (holotype, MZB 19201). Scale bars: 1 mm.

### Paratypes

INDONESIA – **East Java** • 7 spec.; Pacitan, Srau Beach; 8°14'58" S, 110°59'42" E; 78 m a.s.l.; MZB 19304 • 4 spec.; same data as for preceding; ZMH 148511 • 6 spec.; same data as for holotype; MZB 19234 • 11 spec.; same data as for holotype; MZB 21270 • 4 spec.; same data as for holotype; ZMH 148510 • 6 spec.; same data as for holotype; ZMH 148513.

### Other material

INDONESIA – **East Java** • 1 spec. (det.anat.); Pacitan, near Srau Beach; 8°13'55" S, 111°00'54" E; 217 m a.s.l.; MZB 21267 • 11 spec.; same data as for preceding; MZB 19231 • 5 spec.; same data as for preceding; ZMH 148509 • 4 spec.; same data as for preceding; ZMH 148512 • 7 spec.; Pacitan, near Srau Beach; 8°13'54" S, 111°00'55" E; 223 m a.s.l.; MZB 21192 • 5 spec.; same data as for preceding; ZMH 148507.

### Description

**SHELL** (Figs 9, 62; Tables 3–4). Depressed conical, with 5.25–6 slightly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes sparse, mainly at periphery; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture almost circular; upper insertion of peristome descending; peristome expanded, reflexed and slightly thickened; umbilicus hardly eccentric, wide, comprising 28–34% of shell diameter, hardly obscured by columellar edge.

**GENITALIA** (Figs 41, 65; Table 4). Atrium short; penis long, consisting of a long, cylindrical and very muscular distal part covered by an additional sheath, which is connected by muscular tissue to proximal part of epiphallus, and a dilated proximal part; distal and proximal parts of penis separated by a narrow constriction; penial papilla indistinct; inside proximal part of penis with longitudinal pilasters, which pass into a more complex sculpture in distal part of penis; at proximal end of penis with a blunt penis coecum; penial retractor runs from diaphragm to proximal part of epiphallus, which tapers proximally; flagellum moderately long, broadest in its middle part, without node, gradually tapering towards its proximal end; vas deferens narrow and long; vagina long; peduncle of bursa copulatrix subdivided into a broader, cylindrical distal part and a narrower, longer proximal part.

### Remarks

*Landouria nodifera* sp. nov., *L. tonywhitteni* sp. nov., *L. pacitanensis* sp. nov., *L. sukoliloensis* sp. nov., *L. sewuensis* sp. nov. and *L. intumescens* share strongly depressed, brownish-corneous, sharply keeled shells. These species cannot be reliably distinguished by shell characters. *Landouria pacitanensis* sp. nov. shares a coecum at the proximal end of the penis with *L. nodifera* sp. nov., from which it differs in the long and very muscular distal part of the penis, which is separated from the proximal part of the penis by a very narrow constriction, the insertion of the penial retractor close to the distal end of the epiphallus and the lack of a node at the base of the flagellum.

The populations from the surroundings of Srau Beach differ in shell size and shape. The populations closer to the beach are smaller (D 10.6–12.7 mm vs 13.7–14.7 mm) and more elevated (D/H 1.57–1.83 vs 1.70–2.18) than those from further inland.

### Distribution

*Landouria pacitanensis* sp. nov. is endemic to the Pacitan Regency in East Java (Fig. 53).

***Landouria intumescens* (Martens, 1867) comb. nov.**

Figs 42, 53, 66, 72–74; Tables 3–4

*Helix intumescens* Martens, 1867: 263, pl. 13, fig. 10 (“bei Surabaya und dem benachbarten Grisse ... im Tengergebirge bei Wonosari”) (in part?).

*Landouria winteriana* – van Benthem Jutting 1950: 463 (in part). (not Pfeiffer, 1842)

**Diagnosis**

*Landouria intumescens* is characterized by a medium-sized, brownish-corneous, depressed conical, sharply keeled shell and a penis that is divided by a constriction into a long distal and a short proximal section and a flagellum with a broad, crenated distal part and a short and narrow proximal part.

**Material examined**

**Lectotype**

INDONESIA • lectotype (here designated); East Java, Surabaya; 7°20' S, 112°45' E; E. von Martens leg.; measurements: D = 13.4 mm, H = 8.2 mm; ZMB 5160a.

**Paralectotypes**

INDONESIA • 7 spec.; same data as for lectotype; ZMB 5160.

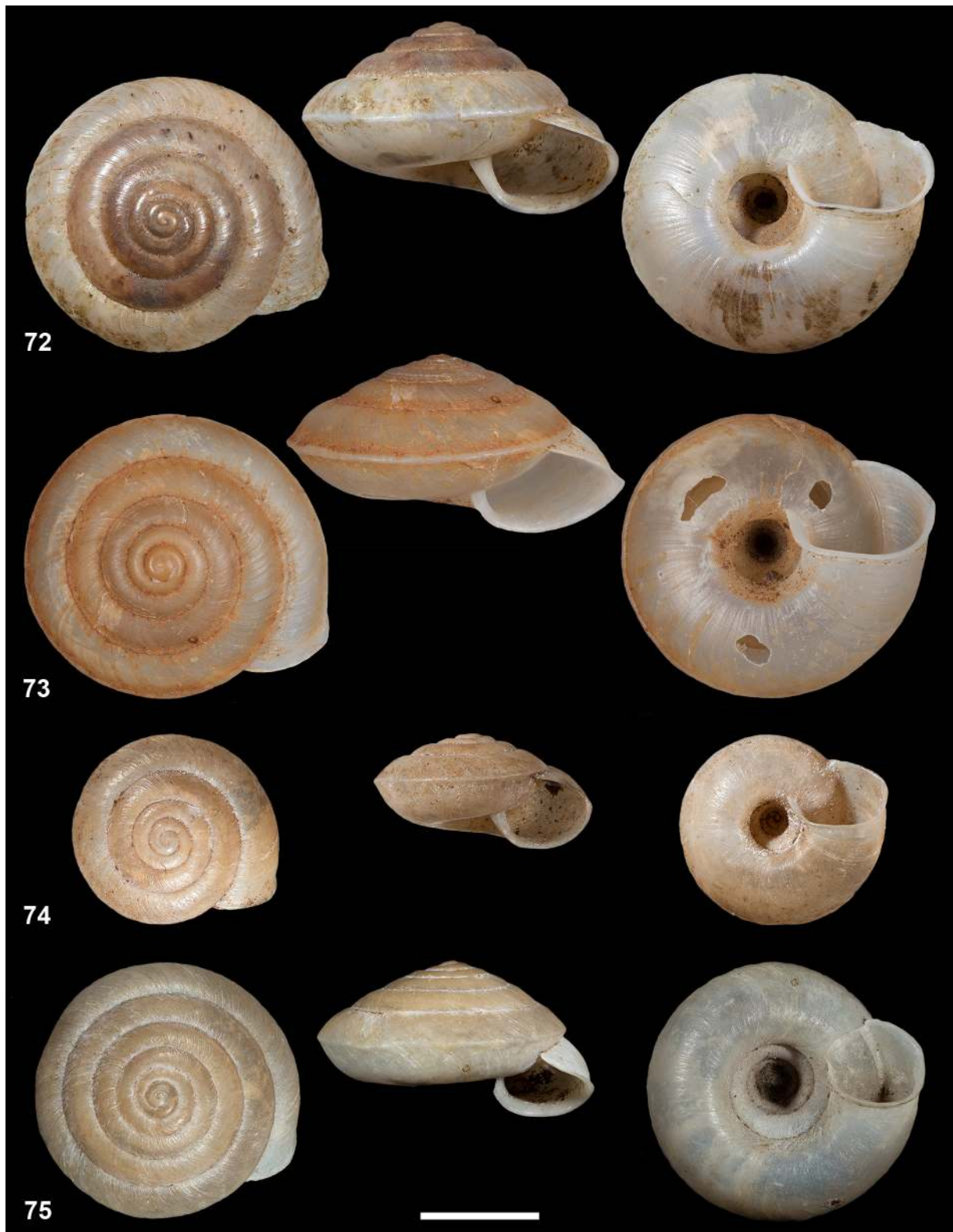
**Other material**

INDONESIA – **East Java** • 2 spec. (det. anat.); Tuban, Montong, Guwoterus, teak and agroforestry; 6°57'56" S, 111°47'56" E; 122 m a.s.l.; MZB 19208 • 11 spec. (det. anat.); Tuban, Montong, Guwoterus, sumber Krawak, secondary forest; 6°57'50" S, 111°48'20" E; 147 m a.s.l.; MZB 19206 • 1 spec.; same data as for preceding; MZB 19207 • 8 spec.; same data as for preceding; ZMH 133438 • 20 spec.; Bojonegoro, Dander, Sumberarum, mouth of Lawa Cave; 7°16'30" S, 111°51'09" E; 117 m a.s.l.; MZB 19284 • 10 spec.; same data as for preceding; ZMH 1334110 • 1 spec.; Bojonegoro, Dander, Sumberarum, mouth of Sumur Cave; 7°16'08" S, 111°51'41" E; 72 m a.s.l.; MZB 19263 • 4 spec.; same data as for preceding; MZB 19316 • 8 spec.; same data as for preceding; ZMH 133415.

**Description**

**SHELL** (Figs 72–74; Tables 3–4). Depressed conical, with 5–5.75 slightly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; without scaly processes; tuberculate around umbilicus; brownish-corneous, some with a light brownish band at periphery; body whorl sharply keeled; aperture rounded rhombic; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, wide, comprising 22–34% of shell diameter, hardly obscured by columellar edge.

**GENITALIA** (Figs 42, 66; Table 4). Atrium short; penis long, distal part cylindrical, broad, tapering proximally, separated from proximal part by a constriction before bend in penis, proximal part slightly dilated at its proximal end, without penis coecum; membranaceous sheath around distal part of penis connected with proximal part of epiphallus by tissue; penial retractor runs from diaphragm to middle part of short, cylindrical epiphallus; flagellum moderately long, broadest near its distal end, slightly crenated, without node, proximal part narrow, almost cylindrical; vas deferens narrow and long; vagina long, distally broad, proximally narrow; oviduct shorter, proximally tapering; peduncle of bursa copulatrix subdivided into a broader, cylindrical distal part and a narrower, longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.



**Figs 72–75.** Shells of species of *Landouria* from Java. **72.** *L. intumescens* (Martens, 1867), East Java, Surabaya (lectotype, ZMB 5160a). **73.** *L. intumescens*, East Java, Guwoterus (MZB 19207). **74.** *L. intumescens?*, East Java, Wonosari (paralectotype, ZMB 230704). **75.** *L. moussoniana* (Martens, 1867), East Java, Wonosari (syntype, ZMB 109902). Scale bar: 5 mm.

**Remarks**

Martens (1867: 263, pl. 13, fig. 10) proposed the name *H. intumescens* for a medium-sized morph from Surabaya, which he figured, but also included a smaller morph from Wonosari in the Tengger Mountains in the nominal taxon. To fix the name for the morph from Surabaya, we designate the specimen figured by Martens (1867: pl. 13, fig. 10; see Fig. 72) as the lectotype.

We examined specimens from Tuban Regency anatomically; they agree in shell characters with the morph from Surabaya. The specific identity of these specimens with *L. intumescens* must be proven by an anatomical examination of specimens from Surabaya.

Whether the smaller paralectotypes of *H. intumescens* from Wonosari in the Tengger Mountains (ZMB 230704; Fig. 74) are conspecific with *L. intumescens* must also be proven by an anatomical examination.

*Landouria intumescens* cannot be reliably distinguished from *L. winteriana* by shell characters. However, the shells of *L. intumescens* usually differ from those of *L. winteriana* in the larger diameter (11.6–14.1 mm vs 9.7–12.6 mm in *L. winteriana*) and in the relatively narrower umbilicus, which comprises 22–34% of the shell diameter in *L. intumescens* vs 29–51% in *L. winteriana*. *Landouria intumescens* also differs from *L. winteriana* in the penis, which becomes narrow towards its proximal end, whereas it ends proximally in a globular dilatation in *L. winteriana* (Fig. 15).

**Distribution**

*Landouria intumescens* is known only from northern East Java (Fig. 53).

***Landouria moussoniana*** (Martens, 1867) comb. nov.  
Figs 55, 75; Tables 3–4

*Helix sumatrana* var. *moussoniana* Martens, 1867: 266 (“Oestliches Java, im Tengergebirge bei Wonosari”).

*Landouria rotatoria* – van Benthem Jutting 1950: 461 (in part). (not Pfeiffer, 1842)

**Diagnosis**

*Landouria moussoniana* is characterized by a tightly coiled, keeled shell with a hardly eccentric, very wide umbilicus.

**Material examined****Syntypes**

INDONESIA • 6 spec.; East Java, Wonosari; 7°54' S, 112°49' E; ZMB 109902.

**Description**

**SHELL** (Fig. 75; Tables 3–4). Depressed conical, with 5–6.25 slightly convex whorls; protoconch almost smooth; teleoconch with irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes not observed; tuberculate around umbilicus; brownish-corneous; body whorl keeled; aperture oval; upper insertion of peristome hardly or distinctly descending; peristome expanded, reflexed and slightly thickened; umbilicus very wide, comprising 37–38% of shell diameter, hardly obscured by columellar edge.

**GENITALIA.** Unknown.

### Remarks

Martens (1867) recorded *L. moussoniana* from Wonosari in the Tengger Mountains together with *L. smimensis* and another form of *Landouria* that he included in his *L. intumescens*. *Landouria moussoniana* differs from *L. intumescens* in having a more tightly coiled, less sharply keeled shell with a wider umbilicus (U/D 0.37–0.38 vs 0.22–0.34 in *L. intumescens*).

### Distribution

*Landouria moussoniana* is endemic to the Tengger Mountains in East Java (Fig. 55).

### *Landouria schepmani* (Möllendorff, 1897) comb. nov.

Figs 54, 76; Tables 3–4

*Plectotropis schepmani* Möllendorff, 1897: 68 (“Java”, more exactly (van Benthem Jutting 1950; Zilch 1966): “Bungbulan, 1500 feet”).

*Landouria winteriana* – van Benthem Jutting 1950: 463 (in part). — Zilch 1966: 294, pl. 7, fig. 7 (in part). (not Pfeiffer, 1842)

### Diagnosis

*Landouria schepmani* is characterized by a depressed conical, sharply keeled shell with distinct incised spiral lines but no discernible scales, and a narrow umbilicus.

### Material examined

#### Lectotype

INDONESIA • lectotype (designated by Zilch 1966); West Java, Sukapura, Gunung Bungbulang; 7°27' S, 107°36' E?; ca 450 m a.s.l.; SMF 8877.

#### Paralectotype

INDONESIA • 1 spec.; same data as for lectotype; SMF 8878.

### Description

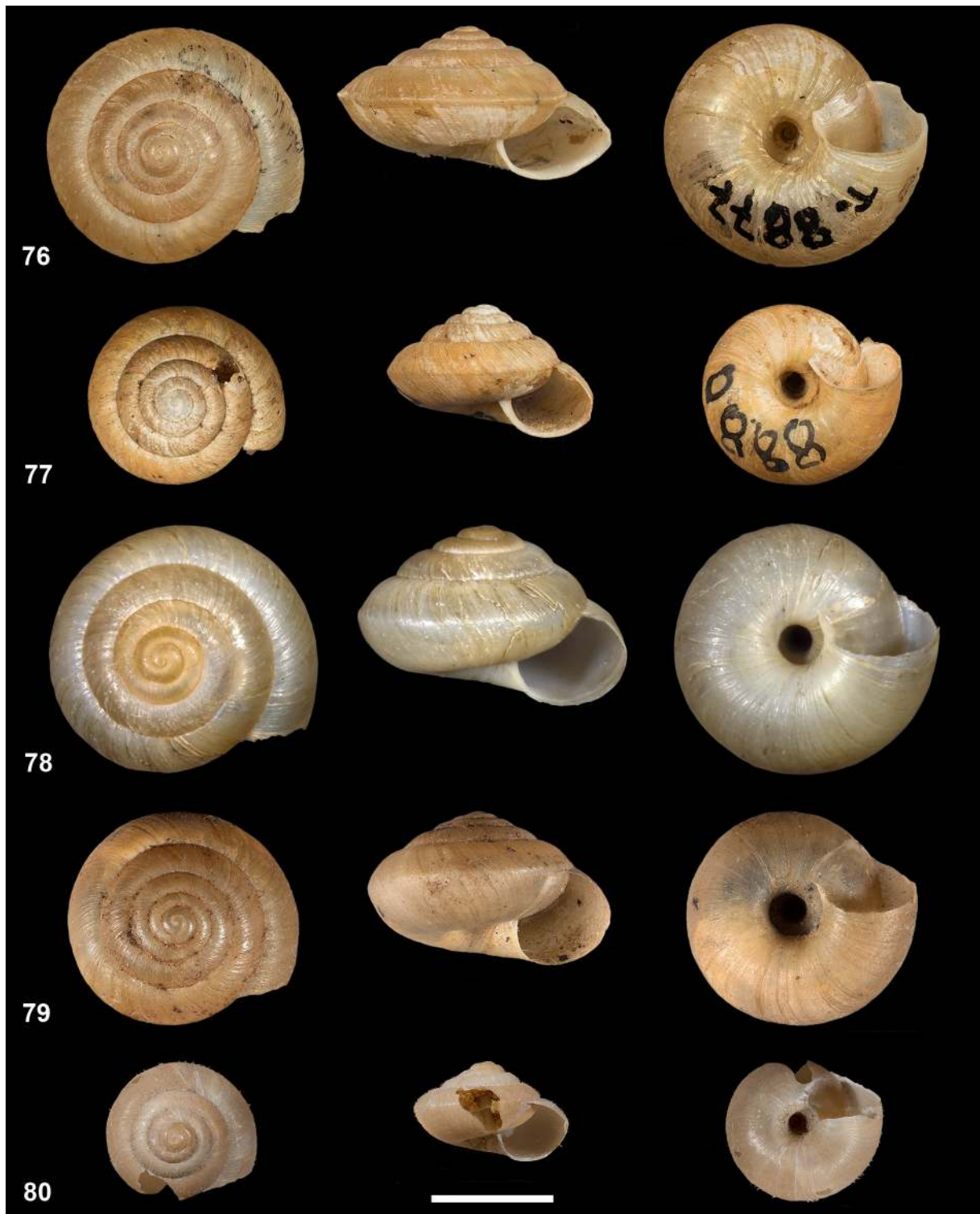
SHELL (Fig. 76; Tables 3–4). Depressed conical, with 5–5.25 slightly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles and distinct incised spiral lines; no scales discernible; tuberculate around umbilicus; brownish-corneous; body whorl sharply keeled; aperture rounded rhombic; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, wide, comprising 21% of shell diameter, hardly obscured by columellar edge.

GENITALIA. Unknown.

### Remarks

Van Benthem Jutting (1950) and Zilch (1966) synonymized *L. schepmani* with *L. winteriana*. However, *L. schepmani* differs from *L. winteriana* in having a sharply keeled, more conical shell with distinct incised spiral lines and a narrower umbilicus (U/D 0.21 vs 0.29–0.51 in *L. winteriana*).

According to the original label, the type locality is Sukapura, Gunung Bungbulan. Van Benthem Jutting (1950: 465) listed a Bungbulan south of Gunung Papandayan (7°27' S, 107°36' E). It is not clear whether this is the Bungbulan of Fruhstorfer, because there are also several other localities called Bungbulan in the former Sukapura Regency. For example, there is a Gunung Bungbulang, now called Gunung



**Figs 76–80.** Shells of species of *Landouria* from Java. **76.** *L. schepmani* (Möllendorff, 1897), West Java, Sukapura, Gunung Bungbulang (lectotype, SMF 8877). **77.** *L. monticola* van Benthem Jutting, 1950, West Java, Gunung Cikuray (paratype, SMF 8880). **78.** *L. smimensis* (Mousson, 1848), East Java, Gunung Semeru, ca 1200 m a.s.l., 8°06' S, 112°55' E (syntype of *Helix smimensis*, ZMZ 508598). **79.** *L. smimensis*, East Java, Nongkojajar (holotype of *Plectotropis tenggerica* Schepman, 1912, ZMA 174453). **80.** *L. smimensis*, East Java, Tosari (ZMA 390881). Scale bar: 5 mm.

Banguang, in West Java at 7°12' S, 108°05' E. Thus, the distribution area of *L. schepmani* remains dubious.

### Distribution

*Landouria schepmani* is known only from “Gunung Bungbulan” in West Java (Fig. 54; see Remarks).

### *Landouria monticola* van Benthem Jutting, 1950 Figs 10, 55, 77; Tables 3–4

*Landouria monticola* van Benthem Jutting, 1950: 469, fig. 85 (“Mt. Tjikorai, 2500–2800 m”).

*Landouria monticola* – Zilch 1966: 294.

### Diagnosis

*Landouria monticola* is characterized by a conical, keeled shell with distinct incised spiral lines, but no discernible scales, and a narrow umbilicus.

### Material examined

#### Type material

INDONESIA • 2 paratypes; Java; SMF 8879. – **West Java** • 3 paratypes; Gunung Cikuray; 7°19' S, 107°52' E; 2500 m a.s.l.; SMF 8880 • 1 paratype (or holotype?); Gunung Cikuray, summit; 7°19' S, 107°52' E; 2800 m a.s.l.; ZMA 407615.

#### Other material

INDONESIA • 1 spec.; West Java, Gunung Cikuray; 7°19' S, 107°52' E; 2400 m a.s.l.; ZMB 46038.

### Description

SHELL (Figs 10, 77; Tables 3–4). Conical, with 4.5–5.25 convex whorls; protoconch almost smooth; teleoconch with irregular wrinkles and distinct incised spiral lines; no scales discernible; not tuberculate around umbilicus; yellowish or brownish-corneous; body whorl keeled; aperture oval; upper insertion of peristome hardly descending; peristome slightly expanded, not reflexed and slightly thickened; umbilicus hardly eccentric, narrow, comprising 20–25% of shell diameter, hardly obscured by columellar edge.

GENITALIA. Unknown.

### Remarks

*Landouria monticola* resembles *L. schepmani* (Fig. 76), in which it was apparently included by Möllendorff (1897). It differs from that species in the smaller (D 8.5–9.5 mm vs 10.5–10.9 mm in *L. schepmani*), higher conical (D/H 1.49–1.60 vs 1.72–1.76 in *L. schepmani*), less sharply keeled shell.

The holotype of *L. monticola* could not be traced in the RMNH/ZMA collection. Van Benthem Jutting (1950) reported *L. monticola* from several regions in West, Central and East Java. We examined a juvenile paratype of *L. monticola* from Gunung Kawi in East Java (ZMA 137804), which differs from the paratypes from Gunung Cikuray in the smoother shell with a narrower umbilicus. We doubt that this specimen is conspecific with the paratypes of *L. monticola* from Gunung Cikuray. The identity of the populations from high mountain regions in Central Java with *L. monticola* must also be checked.



### Distribution

Currently only the populations from Gunung Cikuray in West Java are included in *L. monticola* (Fig. 55). Records from other regions of Java (van Benthem Jutting 1950) and from Sumatra (Heryanto 2013) probably refer to other species.

***Landouria smimensis*** (Mousson, 1848)  
Figs 11, 43, 52, 67, 78–80; Tables 3–4

*Helix smimensis* Mousson, 1848: 266 (“Java”; more exactly (Mousson 1849): “Smim, 4000”).

*Helix smironensis* Mousson, 1850: 177 (unjustified emendation).

*Helix smiruensis* Martens, 1867: 268 (unjustified emendation).

*Plectotropis tenggerica* Schepman, 1912: 233, pl. 10, figs 9–11 (“Nongkodjadjar”).

*Helix smimensis* – Mousson 1849: 21, pl. 2, fig. 10.

*Plectotropis* sp. – Schepman 1915: 19.

*Landouria smironensis* – van Benthem Jutting 1950: 467 (in part).

### Diagnosis

*Landouria smimensis* is characterized by a small, depressed conical shell with hairs and a usually slightly angular body whorl, a long penis, which gradually tapers towards its proximal end, and a slightly crenated, gradually tapering flagellum.

### Material examined

#### Type material

INDONESIA – **East Java** • holotype of *P. tenggerica*; Nongkojajar; 7°54' S, 112°49' E; ZMA 174453 • 2 syntypes of *H. smimensis*; Gunung Semeru; 8°06' S, 112°55' E; ca 1200 m a.s.l., ZMZ 508598.

#### Other material

INDONESIA • 23 spec. (vouchers for Martens 1867); Java; ZMB 4062 • 1 spec. (voucher for van Benthem Jutting 1950); Java; ZMB 67043. – **East Java** • 3 spec. (vouchers for van Benthem Jutting 1950); Nongkojajar, near waterfall; 7°54' S, 112°49' E; ZMA 407685 • many spec. (vouchers for van Benthem Jutting 1950); same data as for preceding; ZMA 407681 • 7 spec.; Nongkojajar, near Baron; 7°54' S, 112°49' E; ZMA 407686 • 2 spec. (vouchers for van Benthem Jutting 1950) (det. anat.); Tosari; 7°53' S, 112°54' E; ca 1800 m a.s.l.; ZMA 390881.

### Description

**SHELL** (Figs 11, 78–80; Tables 3–4). Depressed conical, with 4.5–5.5 convex whorls; protoconch almost smooth; teleoconch irregularly striated, with indistinct incised spiral lines; with hair-like processes; not tuberculate around umbilicus; brownish-corneous; body whorl slightly angular or rounded; aperture oval; upper insertion of peristome hardly descending; peristome sharp; umbilicus slightly eccentric, narrow, comprising 18–32% of shell diameter, hardly obscured by columellar edge.

**GENITALIA** (Figs 43, 67; Table 4). Atrium short; penis long, gradually tapering towards its proximal end; without penis coecum; surrounded by a membranaceous sheath connected to proximal epiphallus by tissue; penial retractor runs from diaphragm to middle part of cylindrical epiphallus; flagellum moderately long, narrow, broadest in its middle part, without node, gradually tapering towards its proximal end, slightly crenated; vas deferens narrow and long; vagina broad and short; oviduct short, proximally slightly tapering; peduncle of bursa copulatrix subdivided into a broad abruptly tapering distal part and a narrower and longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

### Remarks

The original spelling of the species name was *Helix smimensis* Mousson, 1848. This was not an inadvertent error, such as a lapsus calami or printer's error, because this spelling was also used later by Mousson (1849). Thus, *H. smimensis* is the correct original spelling according to ICZN, Article 32. The name was intentionally changed to *H. smironensis* by Mousson (1850) and to *H. smiruensis* by Martens (1867). Both names are unjustified emendations, which are available with these authors and dates, and which are junior objective synonyms of *H. smimensis* (ICZN, Art. 33). According to ICZN, Article 33.2.3.1, an unjustified emendation may be deemed to be a justified emendation, if it is in prevailing usage. *Helix smiruensis* was used by Tryon (1887), Leschke (1914) and Rensch (1932), *L. smironensis* by van Benthem Jutting (1950) and Vermeulen & Whitten (1998), the incorrect subsequent spelling *Landouria* cf. *smiroensis* by Boonngam *et al.* (2008) and the correct original spelling *L. smimensis* by Köhler *et al.* (in press). Thus, there is no prevailing usage of any of the emendations and the correct original spelling should be used.

The voucher specimen for *L. tenggerica* of Rensch (1934) from Gunung Lawu, 2400 m a.s.l. (ZMB 76086) is tuberculate around the umbilicus and is a juvenile of a different species.

### Distribution

*Landouria smimensis* is known from the Tengger Mountains in East Java (Fig. 52). It has also been recorded from other mountains in Central and East Java (Rensch 1934), Lombok (Rensch 1932), Bali (Vermeulen & Whitten 1998) and Thailand (Boonngam *et al.* 2008), but these populations probably represent separate species.

### *Landouria leucochila* (Gude, 1905) comb. nov.

Fig. 81; Tables 3–4

*Plectotropis leucochila* Gude, 1905: 14, pl. 3, figs 1a–c (“Java”).

*Landouria rotatoria* – van Benthem Jutting 1950: 461 (in part). (not Pfeiffer, 1842)

### Diagnosis

*Landouria leucochila* is characterized by a large, depressed conical, yellowish shell with an angular body whorl, a wide umbilicus and scales all over the teleoconch.

### Material examined

#### Holotype

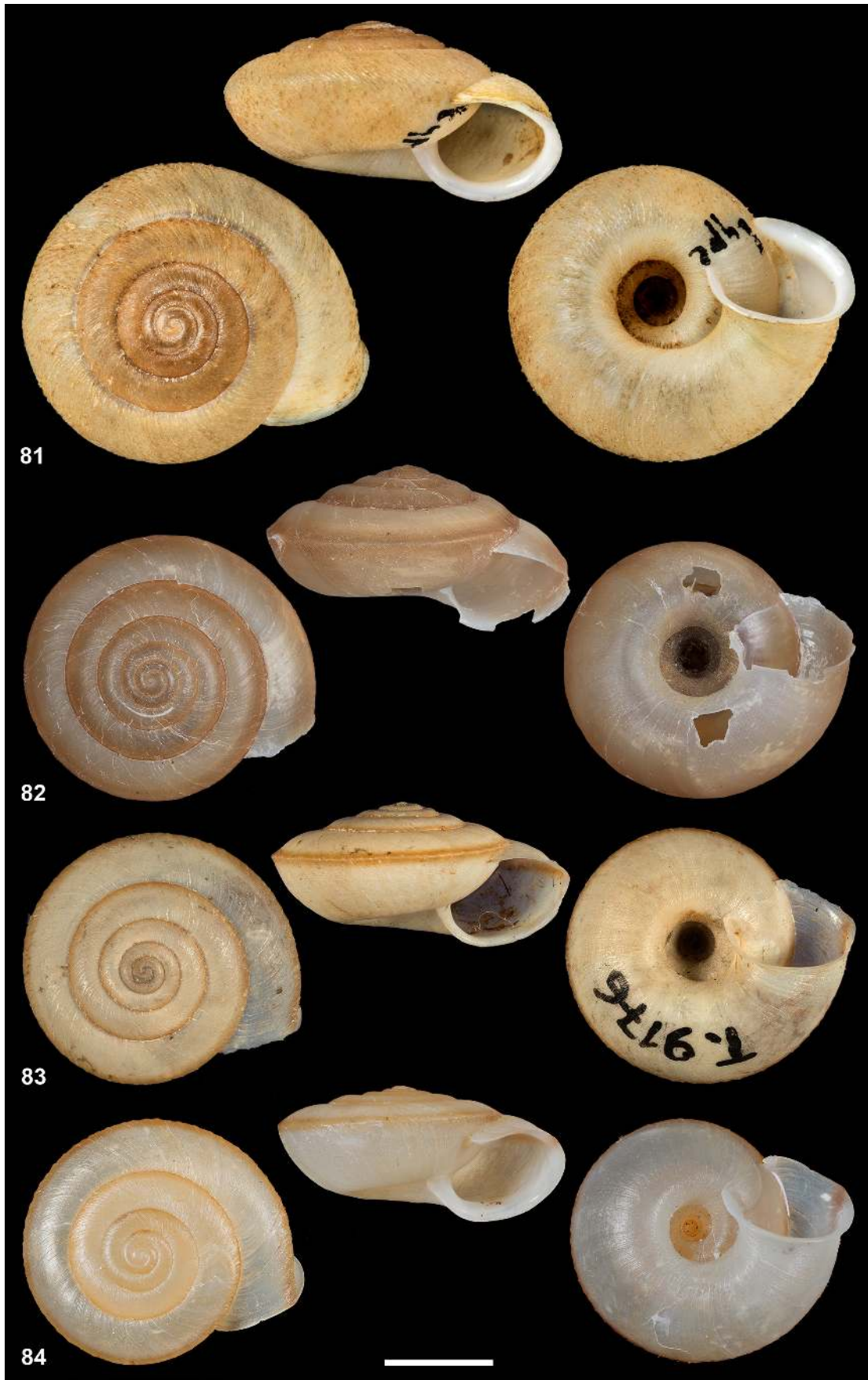
INDONESIA • holotype; Java; NHM 1922.8.29.87.

### Description

SHELL (Fig. 81; Tables 3–4). Depressed conical, with 5.25 hardly convex whorls; protoconch almost smooth; teleoconch with irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes all over teleoconch; tuberculate around umbilicus;

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**Figs 81–84** (opposite page). Shells of species of *Landouria* from Java. **81.** *L. leucochila* (Gude, 1905), Java (holotype, NHM 1922.8.29.87). **82.** *L. zonifera* sp. nov., Yogyakarta, Kulonprogo, Sibolong (holotype, MZB 17727). **83.** *L. ciliocincta* (Möllendorff, 1897), East Java, Zuider Mountains (lectotype, SMF 9176a). **84.** *L. ciliocincta*, East Java, Malang, Kondangmerak, protected forest (MZB 19211). Scale bar: 5 mm.



yellowish; body whorl angular; aperture oval; upper insertion of peristome descending; peristome expanded, reflexed and distinctly thickened; umbilicus eccentric, wide, comprising 30% of shell diameter, hardly obscured by columellar edge.

GENITALIA. Unknown.

### Distribution

The type locality and the distribution of *L. leucochila* in Java remain unknown.

*Landouria zonifera* sp. nov.

[urn:lsid:zoobank.org:act:81A2A657-B12B-43BE-B19D-22AE36E2525C](https://doi.org/10.21203/rs.3.rs-2220362/v1)

Figs 44, 54, 68, 82; Tables 3–4

### Diagnosis

*Landouria zonifera* sp. nov. is characterized by a keeled, corneous shell with a brownish zone at the periphery, a wide umbilicus and a flagellum that is more than twice as long as the short epiphallus.

### Etymology

*Landouria zonifera* sp. nov. is named after the brownish zone at its shell periphery (Latin: ‘zona’ = ‘zone’, ‘ferre’ = ‘to carry’; used as an adjective).

### Material examined

#### Holotype

INDONESIA • holotype (det. anat.); Yogyakarta, Kulonprogo, Sibolong, snakefruit plantation; 7°44'44" S, 110°08'02" E; 716 m a.s.l.; 9 Jan. 2013; A.S. Nurinsiyah and T. Setiadi leg.; D = 13.2 mm, H = 7.6 mm; MZB 17727.

#### Paratypes

INDONESIA • 1 spec.; Yogyakarta, Kulonprogo, Sibolong, Sibolong Hill, agroforestry; 7°45'00" S, 110°07'00" E; 721 m a.s.l.; MZB 17762 • 13 spec.; same data as for holotype; MZB 17720 • 1 spec.; same data as for holotype; ZMH 133420 • 4 spec.; Kulonprogo, Jonggrangan; 7°44'20" S, 110°08'32" E; 730 m a.s.l.; ZMH 140031.

### Description

SHELL (Fig. 82; Tables 3–4). Depressed conical, with 5.5–5.75 hardly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles and indistinct incised spiral lines; scaly processes sparse, mainly at periphery; tuberculate around umbilicus; corneous with a brownish zone at periphery; body whorl keeled; aperture rounded rhombic; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, wide, comprising 40% of shell diameter, hardly obscured by columellar edge.

GENITALIA (Figs 44, 68; Table 4). Atrium short; penis long, cylindrical, slightly dilated at proximal end, without penis coecum; membranaceous sheath around distal part of penis connected with proximal part of epiphallus by tissue; penial retractor runs from diaphragm to proximal part of short, cylindrical epiphallus; flagellum more than twice as long as epiphallus, broadest near its proximal end, then abruptly tapering, slightly crenated, without node; vas deferens narrow and long; vagina very long, cylindrical; oviduct shorter, broad, proximally tapering; peduncle of bursa copulatrix subdivided into a broader,

cylindrical distal part and a narrower, longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

### Remarks

*Landouria zonifera* sp. nov. clusters in the molecular phylogeny (Fig. 1) with *L. abdidalem* sp. nov. (Fig. 56) and *L. tholiformis* sp. nov. (Fig. 51). *Landouria zonifera* sp. nov. and *L. abdidalem* sp. nov. have overlapping ranges. *Landouria zonifera* sp. nov. differs from *L. abdidalem* sp. nov. in the smaller (D 12.5–13.2 mm vs 13.1–16.4 mm in *L. abdidalem* sp. nov.), more depressed (D/H 1.73–1.81 vs 1.93–2.14 in *L. abdidalem* sp. nov.), corneous shell with a brownish zone at the periphery, the shorter penis and a flagellum that is more than twice as long as the short epiphallus. Furthermore, *Landouria zonifera* sp. nov. occurs sympatrically with *L. menorehensis* sp. nov. (Fig. 88) from which it can easily be distinguished by the keeled, depressed conical, corneous shell with a brownish zone at the periphery.

### Distribution

*Landouria zonifera* sp. nov. is endemic to the Menoreh karst area (Fig. 54).

### *Landouria ciliocincta* (Möllendorff, 1897)

Figs 45, 54, 69, 83–84; Tables 3–4

*Plectotropis ciliocincta* Möllendorff, 1897: 67 (“Java”; more exactly (Zilch 1966): “O-Java: Zuider-Gebirge”).

*Landouria ciliocincta* – van Benthem Jutting 1950: 466 (in part). — Zilch 1966: 293, pl. 7, fig. 1 (in part). — Dharma 2015: 8, figs 2, 4 (in part). — Nurinsiyah *et al.* 2016: 559.

### Diagnosis

*Landouria ciliocincta* is characterized by a whitish, almost disc-like, keeled shell with an only slightly elevated spire, a reddish-brown band at the angular periphery and a wide umbilicus, a long, cylindrical penis with a small bulge at its proximal end, and a short, very broad flagellum, which tapers towards its proximal end.

### Material examined

#### Lectotype

INDONESIA • lectotype (designated by Zilch 1966); East Java, Zuider (Southern) Mountains; SMF 9176a.

#### Paralectotype

INDONESIA • 1 spec.; same data as for lectotype; SMF 9716b.

#### Other material

INDONESIA – **East Java** • 1 spec. (voucher for Dharma 2015); Malang, Ngliyep; 8°23' S, 112°25' E; near sea level; BDJ • 1 spec. (det. anat.) (voucher for Nurinsiyah *et al.* 2016); Malang, Kondangmerak, nature/protected forest; 8°23'22" S, 112°31'02" E; 51 m a.s.l.; MZB 19211 • 1 spec. (voucher for Nurinsiyah *et al.* 2016); Malang, Kondangmerak, nature/protected forest; 8°23'21" S, 112°31'05" E; 100 m a.s.l.; MZB 17645 • 2 spec.; Tengger Mountains; ZMB 45408.

### Description

SHELL (Figs 83–84; Tables 3–4). Almost disc-like with slightly elevated spire, with 5–6 moderately convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles, indistinct incised

spiral lines and sparse scaly processes, mainly at periphery; tuberculate around umbilicus; whitish-corneous with a brownish band at periphery; body whorl keeled; aperture rounded rhombic; upper insertion of peristome descending; peristome expanded, reflexed and thickened; umbilicus slightly eccentric, wide, comprising 22–30% of shell diameter, hardly obscured by columellar edge.

GENITALIA (Figs 45, 69; Table 4). Atrium short; penis long, cylindrical, with a small bulge at its proximal end, without penis coecum; membranaceous sheath around distal part of penis connected with flagellum by tissue; penial retractor runs from diaphragm to middle part of cylindrical epiphallus; flagellum short, very broad, without node, tapering towards its proximal end; vas deferens narrow and long; vagina long; oviduct short, broad, proximally tapering; peduncle of bursa copulatrix subdivided into a broad, proximally tapering distal part and a narrower, longer proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

### Remarks

*Landouria ciliocincta* shares with *L. pakidulan* sp. nov. and *L. menorehensis* sp. nov. the whitish shell with a brown band at the periphery. For differences, see remarks under *L. pakidulan* sp. nov.

### Distribution

*Landouria ciliocincta* is known from Malang Regency in East Java (Fig. 54). Records from other areas of Java (Oostingh 1923; van Benthem Jutting 1941, 1950; Zilch 1966; Dharma 2015) and from Sumatra (van Benthem Jutting 1959; Heryanto 2013) probably refer to other species.

### *Landouria pakidulan* sp. nov.

[urn:lsid:zoobank.org:act:D059D3B1-85D9-4760-B9F2-ABC24A7735ED](https://doi.org/10.21203/rs.3.rs-2611111/v1)

Figs 46, 54, 70, 85; Tables 3–4

*Landouria ciliocincta* – van Benthem Jutting 1941: 310 (in part); 1950: 466 (in part). — Dharma 2015: 8 (in part). (not Möllendorff, 1897)

### Diagnosis

*Landouria pakidulan* sp. nov. is characterized by a whitish, depressed conical shell with a reddish-brown band at the angular periphery and a wide umbilicus, a short penis with a large bulge at the proximal end and a moderately long, almost smooth flagellum, which tapers abruptly near its proximal end.

### Etymology

*Landouria pakidulan* sp. nov. (from the Sundanese and Javanese word ‘pakidulan’ meaning ‘southern’) is named after its occurrence in southern Java.

### Material examined

#### Holotype

INDONESIA • holotype (det. anat.) (voucher for *L. ciliocincta* in van Benthem Jutting 1941, 1950); Central Java, Nusa Kambangan Island, Nature Monument Gligir; 7°44' S, 108°53' E; 15.–16 Feb. 1927; P.F. Franck leg.; D = 12.5 mm, H = 6.9 mm; ZMA 417011a.

#### Paratypes

INDONESIA – **West Java** • 2 spec.; Pangandaran, Green Canyon; 7°44' S, 108°27' E; MZB 14067 • 1 spec.; Pangandaran Nature Reserve; 7°42' S, 108°39' E; MZB 6162. – **Central Java** • 2 spec. (vouchers for *L. ciliocincta* in van Benthem Jutting 1941, 1950); same data as for holotype; ZMA 417011.



**Figs 85–88.** Shells of species of *Landouria* from Java. **85.** *L. pakidulan* sp. nov., Central Java, Nusa Kambangan Island, nature monument Gligir (holotype, ZMA 417011a). **86.** *L. dharmai* sp. nov., East Java, Tulungagung, Popoh (holotype, MZB 21272). **87.** *L. davini* Dharma, 2015, Central Java, Baturraden, Pancuran Tujuh, Gunung Slamet (holotype, MZB 17063). **88.** *L. menorehensis* sp. nov., Yogyakarta, Kulonprogo, Sibolong (holotype, MZB 19201). Scale bar: 5 mm.

## Description

**SHELL** (Fig. 85; Tables 3–4). Depressed conical, with 5.25–5.5 slightly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes not observed; tuberculate around umbilicus; whitish with a reddish-brown band at periphery; body whorl angular; aperture oval; upper insertion of peristome slightly descending; peristome expanded, reflexed and thickened; umbilicus eccentric, wide, comprising 24–30% of shell diameter, hardly obscured by columellar edge.

**GENITALIA** (Figs 46, 70; Table 4). Atrium short; penis short, almost cylindrical, with a large bulge at proximal end, without penis coecum; membranaceous sheath around distal part of penis; penial retractor not observed; epiphallus cylindrical, short; flagellum moderately long, broadest in its middle part, abruptly tapering near its proximal end, almost smooth, without node; vas deferens narrow and long; vagina long; oviduct short, broad, proximally tapering; peduncle of bursa copulatrix subdivided into a broad, abruptly tapering distal part and a narrower, longer proximal part. Right ommatophoral retractor runs between penis and vagina.

## Remarks

*Landouria pakidulan* sp. nov. shares with *L. menorehensis* sp. nov. and *L. ciliocincta* the whitish shell with a brown band at the periphery. *Landouria pakidulan* sp. nov. differs from *L. menorehensis* sp. nov. in the more depressed shell (D/H 1.70–1.86 vs 1.31–1.51 in *L. menorehensis* sp. nov.) with an angular body whorl and a wider umbilicus that comprises 24–30% of the shell diameter (vs 16–24% in *L. menorehensis* sp. nov.). The holotype and only anatomically examined specimen of *Landouria pakidulan* sp. nov. (Figs 70, 85) differs from *L. menorehensis* sp. nov. (Figs 71, 88) in the triangular dilation at the proximal end of the penis. More specimens must be examined to corroborate that this is a species specific character and not an individual aberration. *Landouria pakidulan* sp. nov. differs from *L. ciliocincta* in the less depressed shell (D/H 1.70–1.86 vs 1.86–2.12 in *L. ciliocincta*), the shorter penis and epiphallus, and the longer flagellum.

## Distribution

*Landouria pakidulan* sp. nov. is known from southern Java from Pangandaran in West Java and Nusa Kambangan Island in Central Java (Fig. 54).

### *Landouria dharmai* sp. nov.

[urn:lsid:zoobank.org:act:B4620BC6-38C3-4E3D-AA72-46B82D2D1CB8](https://doi.org/10.21203/rs.3.rs-10000000)

Figs 55, 86; Tables 3–4

*Landouria ciliocincta* – Dharma 2015: 8, pl. 1, fig. 3 (in part). (not Möllendorff, 1897)

## Diagnosis

*Landouria dharmai* sp. nov. is characterized by a conical, whitish shell with a reddish-brown band at the angular periphery and a moderately wide umbilicus.

## Etymology

*Landouria dharmai* sp. nov. is named in honour of the Indonesian malacologist Bunjamin Dharma, who discovered this species.

## Material examined

### Holotype

INDONESIA • holotype (voucher for *L. ciliocincta* in Dharma 2015: pl. 1, fig. 3); East Java, Tulungagung, Popoh; 8°16' S, 111°48' E; B. Dharma leg.; MZB 21272.



### Description

SHELL (Fig. 86; Tables 3–4). Conical, with 5.5 slightly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes not observed; tuberculate around umbilicus; whitish with a reddish-brown band at periphery; body whorl angular; aperture oval; upper insertion of peristome descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, moderately wide, comprising 18% of shell diameter, hardly obscured by columellar edge.

GENITALIA. Unknown.

### Remarks

*Landouria dharmai* sp. nov. differs from *L. ciliocincta* (Figs 83–84), in which it was included by Dharma (2015), in the smaller (D 9.9 mm vs 12.4–15.6 mm in *L. ciliocincta*), higher conical (D/H 1.39 vs 1.86–2.12 in *L. ciliocincta*), less sharply keeled shell with a narrower umbilicus (U/D 0.18 vs 0.24–0.30 in *L. ciliocincta*).

### Distribution

*Landouria dharmai* sp. nov. is endemic to Tulungagung Regency in East Java (Fig. 55).

### *Landouria davini* Dharma, 2015

Figs 55, 87; Tables 3–4

*Landouria davini* Dharma, 2015: 9, figs 5–7 (“Pancuran Tujuh, Baturraden, Mt. Slamet, Central Jawa, 720 m alt.”).

### Diagnosis

*Landouria davini* is characterized by a depressed conical, whitish shell with one brown band above and one below the angular periphery.

### Material examined

#### Holotype

INDONESIA • holotype; Central Java, Baturraden, Pancuran Tujuh, Gunung Slamet; 7°18'36" S, 109°13'05" E; 720 m a.s.l.; MZB 17063.

#### Paratypes

INDONESIA – **Central Java** • 1 spec.; Pondok Pakis, Bojong Tegal, Gunung Slamet; 7°11'56" S, 109°11'56" E; 2200 m a.s.l.; BDJ • 1 spec.; Pondok Buncis, Bojong Tegal, Gunung Slamet; 7°13'04" S, 109°12'00" E; 1600 m a.s.l.; MZB 17066 • 3 spec.; same data as for holotype; MZB 17064 • 3 spec.; same data as for holotype; SMF 341605 • 3 spec.; same data as for holotype; RMNH 329337 • 3 spec.; same data as for holotype; BDJ • 1 spec.; Baturraden, Perhutani, Gunung Slamet; 7°18' S, 109°14' E; 800 m a.s.l.; MZB 17065.

#### Other material

INDONESIA • 1 spec.; Central Java, Gunung Slamet; MZB 15425.

### Description

SHELL (Fig. 87; Tables 3–4). Depressed conical, with 5–5.5 slightly convex whorls; protoconch almost smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; scaly processes not observed; tuberculate around umbilicus; whitish-

corneous with one reddish-brown band or a broader brownish zone above and one below periphery; body whorl angular; aperture oval; upper insertion of peristome slightly descending; peristome expanded, reflexed and slightly thickened; umbilicus slightly eccentric, moderately wide, comprising 29% of shell diameter, hardly obscured by columellar edge.

GENITALIA. Unknown.

### Distribution

*Landouria davini* is endemic to Gunung Slamet (800–2200 m a.s.l.) in Central Java (Fig. 55).

### *Landouria menorehensis* sp. nov.

[urn:lsid:zoobank.org:act:E09F6255-8F7A-49E7-A3BC-E5B795EE2015](https://doi.org/10.21203/rs.3.rs-2611111/v1)

Figs 47, 55, 71, 88; Tables 3–4

### Diagnosis

*Landouria menorehensis* sp. nov. is characterized by a whitish, globose shell with a distinct brown band above the rounded periphery and a moderately narrow umbilicus.

### Etymology

*Landouria menorehensis* sp. nov. is named after its occurrence in the Menoreh karst area.

### Material examined

#### Holotype

INDONESIA • holotype (det. anat.); Yogyakarta, Kulonprogo, Sibolong, agroforestry; 7°44'52" S, 110°08'12" E; 687 m a.s.l.; 8 Jan. 2013; A. Nurinsiyah leg.; measurements: D = 13.4 mm, H = 8.6 mm; MZB 19201.

#### Paratypes

INDONESIA – **Central Java, Yogyakarta** • 1 spec.; Kulonprogo, Sibolong, agroforestry along the way to Sibolong Hill; 7°45'00" S, 110°07'00" E; 721 m a.s.l.; ZMH 133441 • 2 spec.; same data as for preceding; ZMH 133442 • 1 spec.; same data as for preceding; ZMH 133443 • 12 spec. (det. anat.); Kulonprogo, Sibolong, agroforestry; 7°44'44" S, 110°08'02" E; 716 m a.s.l.; MZB 17686 • 9 spec.; same data as for preceding; MZB 17702 • 5 spec.; same data as for preceding; ZMH 133311 • 1 spec. (det. anat.); Kulonprogo, Sibolong, snakefruit plantation; 7°44'44" S, 110°08'02" E; 716 m a.s.l.; MZB 17724 • 1 spec.; same data as for preceding; MZB 17725 • 2 spec. (det. anat.); Kulonprogo, Sibolong, near Kiskendo Cave, shrubs; 7°44'50" S, 110°08'09" E; 721 m a.s.l.; MZB 17644 • 1 spec.; same data as for preceding; ZMH 133444 • 6 spec.; same data as for holotype; MZB 19202 • 3 spec.; same data as for holotype; ZMH 133439 • 1 spec.; same data as for holotype; ZMH 133440 • 2 spec.; Kulonprogo, Sibolong, agroforestry; 7°44'51" S, 110°08'12" E; 673 m a.s.l.; MZB 18039 • 1 spec.; same data as for preceding; ZMH 133445 • 2 spec.; Kulonprogo, Jonggrangan; 7°44'20" S, 110°08'32" E; 730 m a.s.l.; ZMH 140034.

### Description

SHELL (Fig. 88; Tables 3–4). Slightly depressed conical-globose, with 5.25–5.75 convex whorls; protoconch smooth; teleoconch with fine, irregular wrinkles; apical side with indistinct incised spiral lines, umbilical side with more distinct spiral lines; without scaly processes; whitish with a distinct brown band above periphery; body whorl rounded; aperture almost circular; upper insertion of peristome distinctly descending; peristome expanded, reflexed and thickened; umbilicus slightly eccentric, moderately narrow, comprising 16–24% of shell diameter, hardly obscured by columellar edge.

GENITALIA (Figs 47, 71; Table 4). Atrium short; penis short, distal part cylindrical, proximal part slightly dilated, without penis coecum; membranaceous sheath around penis connected with proximal part of epiphallus by tissue; penial retractor runs from diaphragm to distal part of short epiphallus; flagellum long, broadest in its middle part, almost smooth, without node, tapering towards its proximal end; vas deferens narrow and long; vagina long; oviduct short; peduncle of bursa copulatrix subdivided into a short, broad distal part and a narrow and long proximal part, ending in an elongate oval bursa beside albumen gland. Right ommatophoral retractor runs between penis and vagina.

### Remarks

*Landouria menorehensis* sp. nov. shares with *L. pakidulan* sp. nov. and *L. ciliocincta* the whitish shell with a brown band at the periphery. For differences, see remarks under *L. pakidulan* sp. nov.

### Distribution

*Landouria menorehensis* sp. nov. is endemic to the Menoreh karst area (Fig. 55).

### Discussion

This revision of the species of *Landouria* from Java and adjacent islands based on newly collected specimens as well as museum material, revealed that this group represents the most diverse land snail radiation on Java. Only six species of *Landouria* were recognized from Java in the last revision of the genus based on shell characters by van Benthem Jutting (1950). Since then, only one additional species from Java has been described (Dharma 2015). Our investigation considering also the genitalia as well as DNA sequences recognized twenty-seven species of *Landouria* from Java and adjacent islands based on the available material. The p-distances between the 16S rDNA sequences of different species of *Landouria* from Java and Madura Island varied between 2.6% and 31.0% (Table 2). Especially the upper limit of variation is high in comparison with the variation of interspecific distances between 16S rDNA sequences in some other helicoid radiations, e.g., 0.9–18.7% in *Mandarina* Pilsbry, 1894 (Camaenidae; note that these are corrected distances; uncorrected p-distances would even be lower; Chiba 1999), 4.0–12.9% in *Kimberleytrachia* Köhler, 2011 (Camaenidae; p-distances; Criscione & Köhler 2014), 0.8–19.5% in *Xerocrassa* Monterosato, 1892 (Geomitridae; p-distances; Sauer & Hausdorf 2012), 1.4–33.5% in *Leptaxis* Lowe, 1852 (Hygromiidae; corrected distances; van Riel *et al.* 2005), and 10.7%–15.9% in *Fruticocampylaea* Kobelt, 1871 (Hygromiidae; p-distances; Walther *et al.* 2016). The high distances between the morphologically delimited species from Java (Table 2) support the conclusion that these populations really represent distinct species, even though some differ only in a few characters of the genitalia.

Most of these species are endemic to small areas within Java. Some of the species that have been described from Java have also been recorded from other islands of the Indo-Australian Archipelago, the Philippines and from Thailand (Martens 1867; Rensch 1932; van Benthem Jutting 1941, 1950, 1959; Vermeulen & Whitten 1998; Heryanto 2013; Boonngam *et al.* 2008). It is possible that *Landouria winteriana* actually also occurs in Sumatra, but most of the other records are probably misidentifications as a result of the similarity of the shells. Thus, a comprehensive revision of the genus in the Indo-Australian Archipelago is necessary.

In Java, the highest diversity of species of *Landouria* (19 species) can be found in the lowlands (below 500 m a.s.l.). The diversity decreases with increasing altitude. Only five species occur at altitudes above 1000 m a.s.l., and only *L. monticola* and *L. davini* are known from altitudes above 2000 m a.s.l. Most species of *Landouria* occur either in karst areas or on volcanoes. Seventeen species are restricted to karst areas and seven are restricted to volcanoes. Only three species, *L. winteriana*, *L. epiplatia* and

*L. ciliocincta*, were found in karst areas as well as on volcanoes. Nine species have been recorded from western Java (Banten and West Java), 14 from the central part of Java (Yogyakarta and Central Java) and only six species from East Java. Two species were found both in western and central Java.

Most species are allopatric, but some have overlapping ranges. There are several syntopic occurrences of two species. Most species live in the litter layer in rain forests and do not show special microhabitat preferences. One exception is *L. minorehensis* sp. nov., which has an arboreal life style. This suggests that the radiation is predominantly non-adaptive, like that of several other land snail groups (Gittenberger 1991; Cameron *et al.* 1996; Hausdorf 2000; Parmakelis *et al.* 2005; Sauer & Hausdorf 2009; Jordaens *et al.* 2009).

From large areas of Java, we had only shells which could not be accurately identified, or no samples at all. Thus, we suppose that the actual number of species is much higher than the one recorded here. We consider it not unlikely that there are more than 50 species of *Landouria* in Java.

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