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A new species of *Landouria* Godwin-Austen, 1918 (Gastropoda: Stylommatophora: Camaenidae) from Myanmar

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Abstract. *Landouria intha*, new species, is described from Myanmar's Shan state. The new species possesses a relatively large, light reddish brown shell with a flat dorsal side, strongly keeled body whorl, wide umbilicus, and prominent periostracal folds (scales) on the shell surface. The reproductive anatomy is characterised by a long penis, a thin sheath around its very distal part, a very long flagellum with several nodes at the basal part, and multiple horizontally arranged nodes at the terminal part. The new species turned out to be the sister species of *L. omphalostoma* Páll-Gergely & Hunyadi in Páll-Gergely et al., 2013, from China on the mitochondrial tree of 16S rDNA sequences.

Key words. taxonomy, systematics, molecular phylogeny, 16S, anatomy, shell

INTRODUCTION

Aegista Albers, 1850, and *Plectotropis* Martens, 1860 (described in Albers & Martens, 1860), are genera of the Aegistini Kuroda & Habe, 1949, possessing depressed-conical or lenticular shells and well-developed dart apparatus, which consists of a dart sac and corresponding mucous glands. They are widely distributed in East and Southeast Asia including Japan, Taiwan, Eastern China, and islands of the Malay Archipelago (Schileyko, 2004). These two generic names have often been used interchangeably, or sometimes *Plectotropis* treated as a subgenus of *Aegista* (e.g., Minato, 1988; Hirano et al., 2014). The main difference between the two is the more rounded body whorl of *Aegista* versus the more strongly keeled body whorl of *Plectotropis*. However, this trait has developed multiple times during the history of the Aegistini (Hirano et al., 2014).

Godwin-Austen (1918) erected the genus *Landouria* for some species from the Himalaya region and Sri Lanka that lack a dart apparatus. Subsequently, Schileyko & Kuznetsov (1998) reported further species of *Landouria* from Nepal, and Páll-Gergely et al. (2013) described a species from Yunnan, China. This genus was also reported from Thailand recently (Boonngam et al., 2008; Tumpeesuwan & Tumpeesuwan, 2019). Furthermore, the genus *Thaitropis* Schileyko, 2004, believed to be a Thai endemic comprising two species, was found to be a synonym of *Landouria* (Nurinsiyah et al., 2019).

Rensch (1932) was the first to transfer "*Plectotropis*" species from the Sunda Islands to *Landouria* due to the lack of the dart apparatus. Recent studies showed that *Landouria* species inhabit Timor (Köhler et al., 2019), and this genus represents the most speciose land snail radiation in Java (Nurinsiyah et al., 2019). Although it is highly likely that *Aegista*-like species in the Himalaya region and Myanmar belong to *Landouria*, most species listed by Gude (1914b) have not been examined anatomically and are still listed as *Aegista* species (e.g., Ramakrishna et al., 2010).

Hirano et al. (2014) suggested including all species of the Aegistini as *Aegista* regardless of the presence or absence of a dart apparatus. However, in order to avoid creating a monster genus with over 200 species, we prefer to keep *Landouria* as a separate taxon, following recent publications (e.g., Köhler et al., 2019; Nurinsiyah et al., 2019).

Here we describe a new aegistoid species from Myanmar's Shan State, and confirm by means of genital anatomy and molecular phylogeny its position in *Landouria*.

MATERIAL AND METHODS

Determination of the number of shell whorls (precision to 0.25 whorl) follows Kerney & Cameron (1979: p. 13). The ethanol-preserved holotype was dissected under a Zeiss stereomicroscope, photographs were taken using a Keyence LHX5000 digital microscope. In the description of the reproductive system, we used the terms "proximal" and "distal" relative to the hepatopancreas.

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DNA extraction, amplification, and sequencing. Total genomic DNA was extracted and fragments of the mitochondrial 16S rDNA were amplified by polymerase chain reaction using the primer pair 16Scs1 (Chiba, 1999) plus 16S_MN3R (Neiber et al., 2017), and sequenced as described in Nurinsiyah et al. (2019). Forward and reverse sequences were assembled using ChromasPro 1.7.4 (Technelysium, Tewantin, Australia). Obtained sequences have been deposited in GenBank (accession numbers MT179757–MT179758).

Phylogenetic analyses of DNA sequence data. We included sequences of *Landouria* species from China, Java, and Timor from the studies of Köhler et al. (2019) and Nurinsiyah et al. (2019) in addition to the newly obtained sequences of *Landouria intha*, new species, from Myanmar, as well as sequences of *Mandarina suenoae* Minato, 1978 (see Davison & Chiba, 2006) and *Euhadra peliomphala* (L. Pfeiffer, 1850) (see Hayashi & Chiba, 2000) as outgroups in the phylogenetic analyses. The 16S rDNA sequences were aligned with MAFFT 7 (Katoh et al., 2017) using the L-INS-i method.

An appropriate evolutionary model was selected based on an exhaustive search with PartitionFinder 2.1.1 (Lanfear et al., 2016) using the corrected Akaike Information Criterion. The models were limited to those available in MrBayes 3.2.6 (Ronquist et al., 2012).

Phylogenetic relationships were reconstructed by Bayesian Inference (BI) and Maximum Likelihood (ML) analyses. The BI analysis was performed using MrBayes 3.2.6. Two separate runs with four Metropolis-coupled Monte Carlo Markov chains with 50,000,000 generations each were conducted with default priors under default heating using the evolutionary model suggested by PartitionFinder. Trees were sampled every 1,000th generation and the trees for the first 12,500,000 generations of each run were discarded as a burn-in.

The ML analysis was performed using GARLI 2.01 (Zwickl, 2006) with the evolutionary model as suggested by PartitionFinder and default settings otherwise. Support values were calculated by bootstrapping with 1,000 replications.

Posterior probabilities (PP) from the BI analysis as well as bootstrap support (BS) values from the ML analysis were mapped on the BI 50% majority rule consensus tree with SumTrees, which is part of the DendroPy 4.4.0 package (Sukumaran & Holder, 2010).

Abbreviations.
AM: Australian Museum (Sydney, Australia)
D: shell diameter
HA: Collection András Hunyadi (Budapest, Hungary)
H: shell height
HNHM: Hungarian Natural History Museum (Budapest, Hungary)
MZB: Museum Zoologicum Bogoriense (Bogor, Indonesia)
NHM: The Natural History Museum (London, United Kingdom)
NHMUK: when citing NHM registered specimens
UMZC: University Museum of Zoology (Cambridge, United Kingdom)
ZMH: Zoological Museum of the University of Hamburg (Hamburg, Germany)

RESULTS

Molecular phylogeny. The alignment of the 16S rDNA fragments had a length of 496 base pairs. In the ML and BI analyses of the 16S rDNA sequences with the GTR+G+I model, *L. intha*, new species, from Myanmar was found to be the sister species of *L. omphalostoma* Páll-Gergely & Hunyadi in Páll-Gergely et al., 2013, from China (Fig. 1). The two *Landouria* species from the mainland (i.e., *L. intha*, new species, and *L. omphalostoma*) were the sister group of a clade including the *Landouria* species from Java and Timor.

TAXONOMY AND SYSTEMATICS

Camaenidae Pilsbry, 1895

Bradybaeninae Pilsbry, 1934 (1898)

Aegistini Kuroda & Habe, 1949

Landouria Godwin-Austen, 1918

Type species. *Helix huttonii* L. Pfeiffer, 1842, by original designation.

Landouria intha, new species
(Figs. 2–4)

Type material. Holotype (D: 19.4 mm, H: 6.8 mm) (HNHM 104442), Myanmar, Shan State, Pinlaung centre, SSW ca. 29 km – Laneli Bridge, Nam Pam, right side of rd., near "War Lee Kwey Cave (Resurgence)", 700 m a.s.l., 19.97547°N, 96.67076°E (locality codes: 2018/31 and 20181004C), coll. A. Hunyadi & J.U. Otani, 04 October 2018. Paratype (juvenile shell and body in ethanol) (HNHM 104443), same data as holotype; Paratypes (9 empty shells) (HA) (D: 16.7–18.8 mm, H: 5.1–6.5 mm), same data as holotype.

Description of the shell (Fig. 2A). D: 16.7–19.4 mm, H: 5.1–6.8 mm. Colour light reddish brown. Shell depressed, dorsal side flat, consisting of 5.25–5.5 slightly convex whorls. Body whorl with strong, sharp keel, with slight furrow below and above keel. Protoconch (Fig. 2B) consisting of 1.75 whorls, almost smooth, with very fine radial ribbing and slight indication of spiral striation along the suture. Teleoconch roughly, irregularly wrinkled without any traces of spiral striation. Radial wrinkles with additional, scale-like, triangular periostracal folds (scales) (Fig. 2C–E). Aperture quadrangular due to the prominent keel, upper insertion of peristome slightly descending. Peristome lighter in colour than the rest of the shell, strongly expanded, slightly reflected, discontinuous; parietal callus only indicated by slight

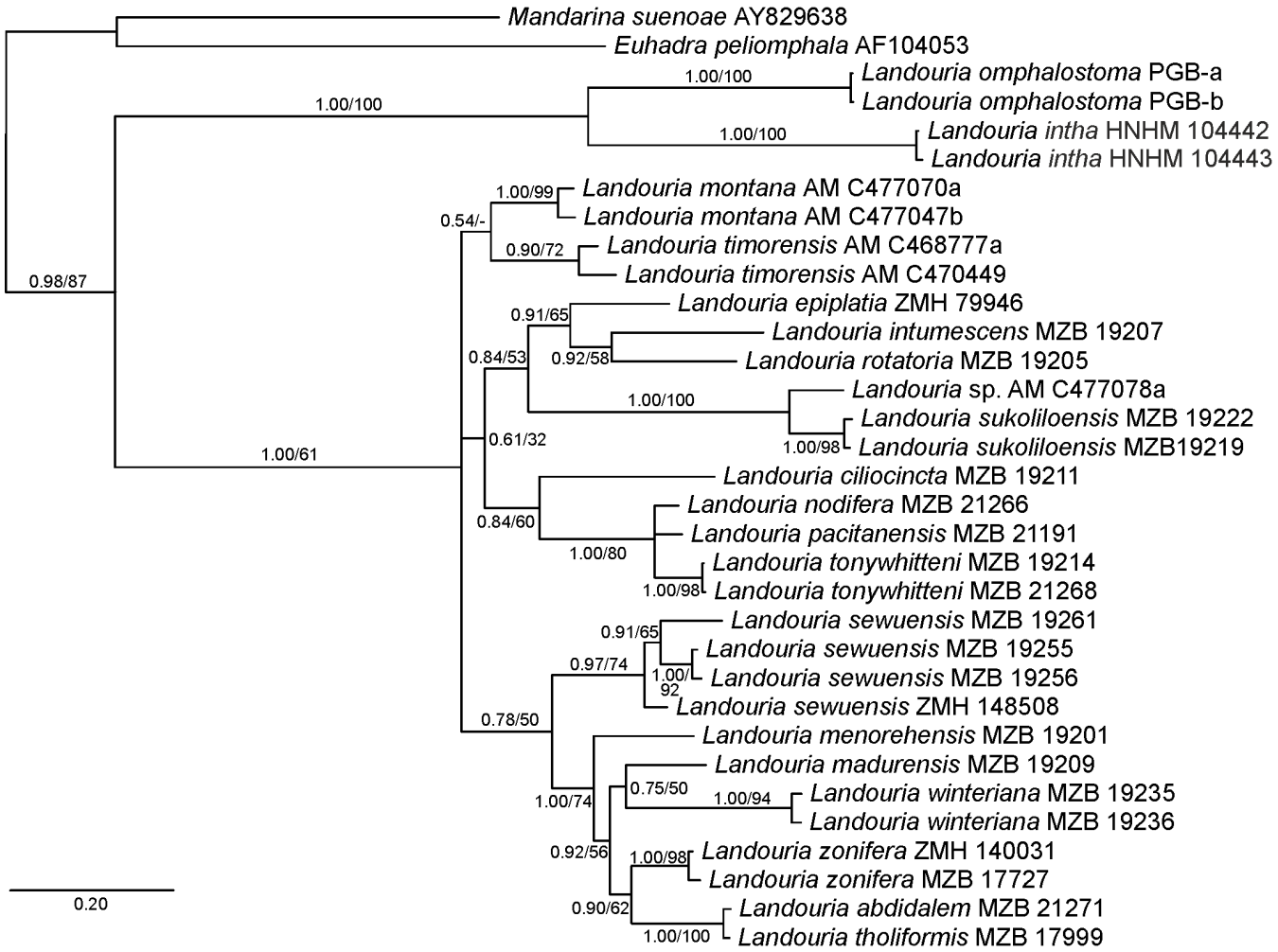

Fig. 1. Bayesian 50% majority rule consensus tree based on mitochondrial 16S rDNA sequences of *Landouria* species, and *Mandarina suenoae* and *Euhadra peliomphala* as outgroups. Values at the nodes represent Bayesian posterior probabilities (left) and maximum likelihood bootstrap values (right). Numbers after taxon names correspond to museum catalogue numbers or GenBank accession numbers.

transparent calcareous layer. Umbilicus open, relatively wide, funnel-shaped, occupying ca. one third of the shell's width.

Description of the genitalia (Figs. 3, 4). Atrium short. Penis very long, without penial caecum, with membranaceous sheath around very distal part of penis. Penis internally (Fig. 4A) with a few fine longitudinal folds that become slightly stronger towards penial verge. Penial verge (Fig. 4B, C) small, rather conical, slightly irregular, opens terminally. Epiphallus approximately as long as penis, internally also with weak longitudinal folds. Retractor muscle slender, inserts at the middle of epiphallus. Flagellum (Fig. 4E) very long, broadest at its base, with a few nodes at the basal part, and multiple horizontally arranged nodes at the terminal part. Vas deferens narrow and long. Vagina slightly longer than penis, internally with longitudinal, occasionally serrate folds (Fig. 4D). Peduncle of bursa copulatrix subdivided into a strongly thickened base, internally with elevated, irregular, longitudinal folds, and a slender, much longer proximal part; spermoviduct longer then vagina, albumen gland also very long, elongated.

Differential diagnosis. This new species differs from all *Aegista*, *Landouria*, and *Plectotropis* species described from Myanmar and India by the flat apical side, the wide umbilicus, and the relatively large, permanent periostracal folds covering the entire surface.

The most similar species is *Plectotropis nutans* Gude, 1914 (described in Gude, 1914a; Fig. 5) (material examined: 3 syntypes [NHMUK 1906.3.3.68], Habiang, Garo Hills, Assam, coll. Godwin-Austen), which has a slightly elevated spire resulting in a low conical shape, a much narrower umbilicus, and no deciduous periostracal folds, but is finely spirally striated and irregularly, finely wrinkled.

Plectotropis akowtongensis (Theobald, 1859) (material examined: 6 shells [NHMUK 1906.2.2.130], Pegu, Thyet Myo, coll. W.T. Blanford; 2 shells [NHMUK], Pegu; 5 shells [NHMUK 1909.3.15.24], Akoutong, Pegu; 1 shell, [NHMUK 1910.6.33.1921], Pegu; 1 shell [NHMUK 1903.7.1.394], Akoukthoung, on Irrawady, Pegu, coll. Godwin-Austen; 2 shells [NHMUK], Thayet Myo, Burmah, coll. Salisbury) is much smaller, paler in colour, has a low dome-shaped dorsal side and a narrower umbilicus, but is somewhat similar in sculpture. Namely, the shell surface is very finely scaly. Fine periostracal folds, which are nevertheless much smaller than those of the new species, are also present near

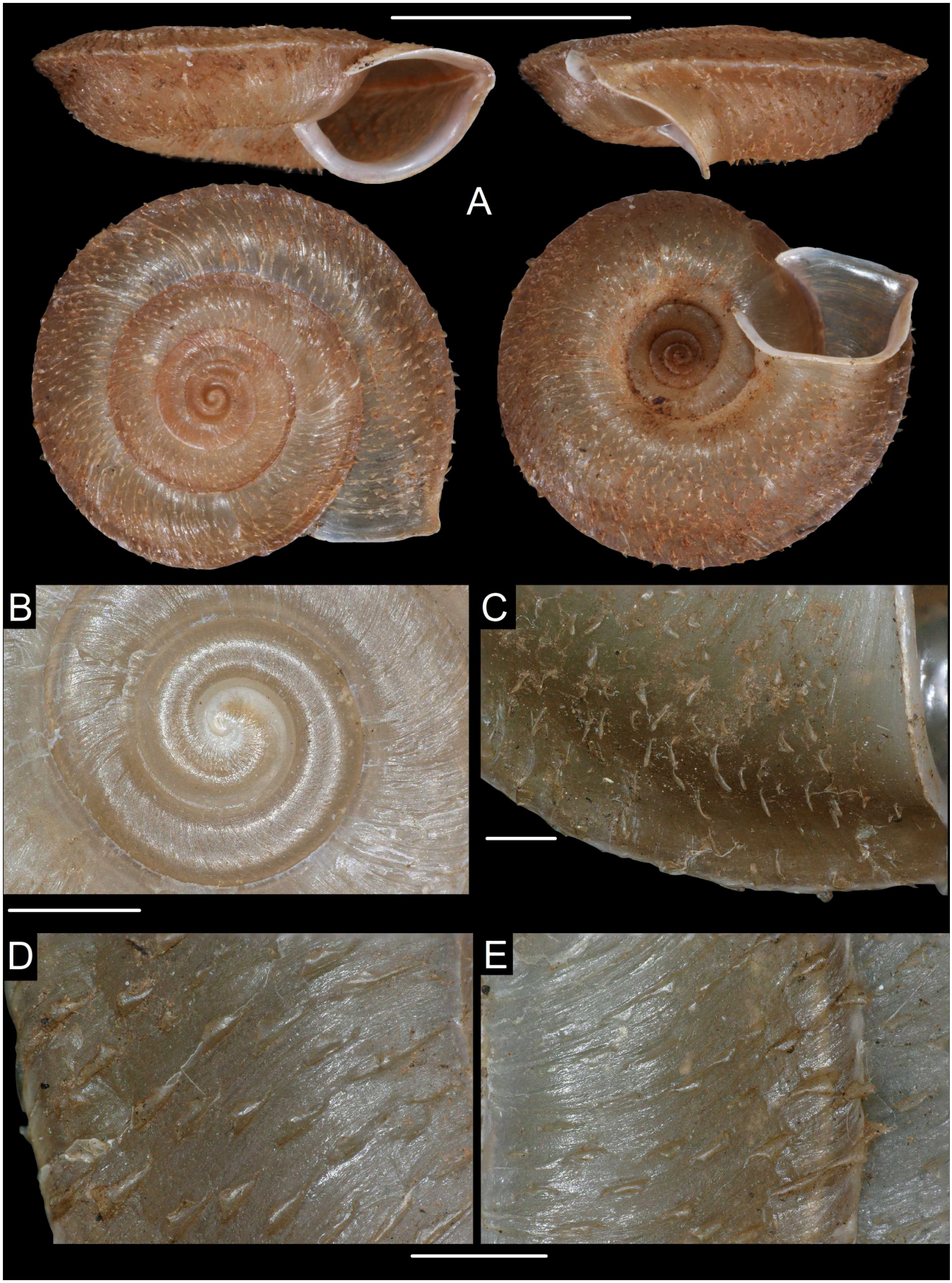

Fig. 2. Holotype of *Landouria intha*, new species (HNHM 104442). Scale bar for A = 10 mm, B–E = 1 mm.

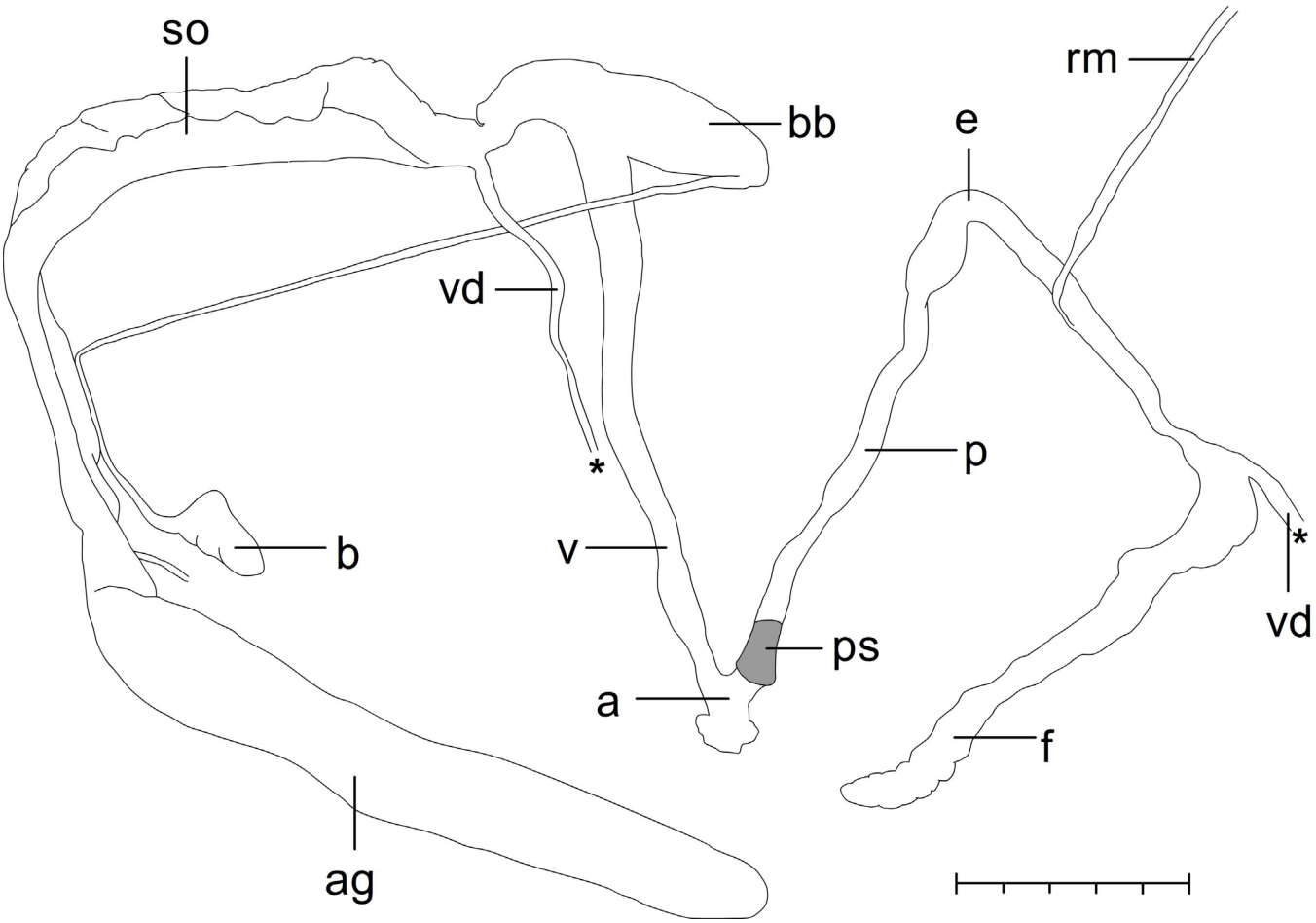

Fig. 3. Reproductive anatomy of the holotype of *Landouria intha*, new species (HNHM 104442). Abbreviations: a, atrium; ag, albumen gland; b, bursa of the bursa copulatrix; bb, base of the peduncle of bursa copulatrix; e, epiphallus; f, flagellum; p, penis; ps, penial sheath (indicated with grey shading); rm, retractor muscle; so, spermoviduct; v, vagina; vd, vas deferens. Asterisks indicate originally conjoined ends. Scale bar = 5 mm.

the suture and the keel in fresh shells. Even in live collected specimens the folds were largely lost, indicating that these are not permanent in *Plectotropis akowtongensis*.

Aegista phayrei (Theobald, 1859) (material examined: 4 shells [NHMUK 1906.2.2.274], Ava, Myaleit doung, coll. Godwin-Austen; 1 shell [NHMUK], Ava, Burmah, coll. Godwin-Austen; 6 shells [NHMUK], Ava, coll. H.F./W.F. Blanford) also has an elevated spire, much narrower umbilicus, and blunter keel, but its sculpture is roughly, irregularly covered by scale scars.

Aegista oldhami (Benson, 1859) (photos examined: 1 syntype [UMZC I_104645], Ava) is smaller and lighter in colour, has a slightly elevated spire, blunter keel, and its dorsal side is finely scaly, while the ventral side is practically smooth.

Aegista tapeina (Benson, 1836) (material examined: 2 shells [NHMUK], E. Frontier of Bengal; 2 adult + 2 juvenile shells [NHMUK], Theria Ghat, coll. Godwin-Austen) has a slightly elevated spire, a narrower umbilicus and a blunter keel than the new species. Sculpture of the first sample is very finely scaled, whereas that of the second sample is matte, finely reticulated on the ventral side, and has some scales inside the umbilicus and near the keel and suture.

The Chinese and Japanese *Plectotropis* species (e.g., *P. gerlachi* (Martens, 1881), *P. vulgivaga* (Schmacker & O. Boettger, 1890)) are strikingly similar to the new species in terms of shell shape and sculpture. However, the Japanese/Taiwanese species usually have prominent, long periostracal folds on the keel, whereas the new species is uniformly scaled on its entire surface.

Etymology. The specific epithet refers to the Intha people inhabiting the environment of the closely situated Inle lake. It is used as a noun in apposition.

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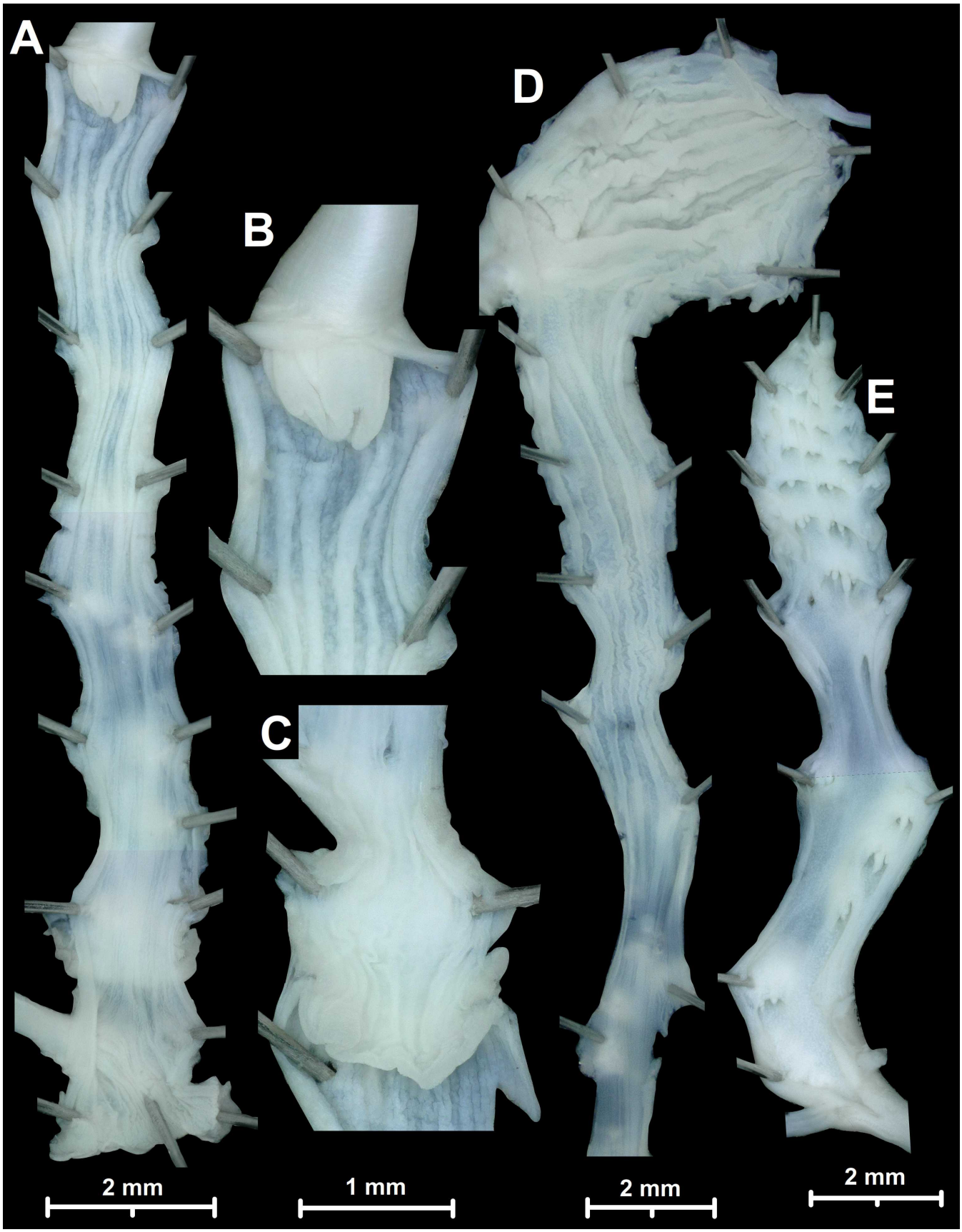

Fig. 4. Inner structure of genital organs of *Landouria intha*, new species (holotype, HNHM 104442). A, penis; B, penial papilla; C, penial papilla opened; D, vagina and base of bursa copulatrix; E, flagellum.

Fig. 5. Syntype of *Plectotropis nutans* Gude, 1914, NHMUK 1906.3.3.68. Scale bar = 10 mm.

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