

Delineating *Paralaoma annabelli*, a Minute Land Snail Impacted by the 2019–2020 Wildfires in Australia

JUNN KITT FOON¹ , PETER T. GREEN^{2,3} , AND FRANK KÖHLER¹ 

¹ Australian Museum Research Institute,
Australian Museum, 1 William Street, Sydney NSW 2010, Australia

² Department of Environment and Genetics,
La Trobe University, Melbourne VIC 3086, Australia

³ Research Centre for Future Landscapes,
La Trobe University, Melbourne VIC 3086, Australia

ABSTRACT. The 2019–2020 megafires in eastern Australia have devastated large parts of the known distributional range of the minute land snail *Paralaoma annabelli*, prompting conservation concerns for this species. However, this species is poorly defined thus hampering its accurate identification and the delineation of its distribution. Most crucially, it has been questionable if and how *P. annabelli* could be distinguished from another Australian congener, *Paralaoma morti*. This systematic ambiguity posed a problem in assessing the impact of the 2019–2020 wildfires in Australia on this species. Herein, we demonstrate, based on comparative morphometrics as well as analyses of mitochondrial and nuclear DNA, that *P. annabelli* is indeed distinct from a second widespread species of *Paralaoma*, which is identified as *P. morti* by some workers. Yet, sequences of *P. morti* cluster closely with non-Australian sequences of the globally distributed species *P. servilis*. Therefore, the taxonomic status of *P. morti* in relation to *P. servilis* remains to be investigated.

Our comparative morphological analyses revealed that *P. annabelli* is significantly smaller than *P. morti*, has a significantly flatter shell, more elongated aperture, lower spire, and tighter coiling whorls. With the revised diagnosis of *P. annabelli*, we have delineated its distribution in New South Wales based on the examination of all available museum samples. We show that *P. annabelli* is primarily found at higher elevations in the Great Dividing Range while *P. morti* is widespread in eastern Australia. In addition, molecular phylogenetic analyses reveal that the genera *Pseudiotula*, *Iotula*, *Trocholaoma* and *Miselaoma*, all described based only on shell characteristics, form a single clade with the abovementioned species of *Paralaoma*. This reveals the inadequacies of a purely shell-based taxonomy in punctids and highlights the need for a more integrative approach to punctid systematics.

Introduction

In the aftermath of the 2019–2020 megafires in eastern Australia, which were unprecedented in both scale and severity (Boer *et al.*, 2020; Collins *et al.*, 2021), over 60 species of native Australian land snails were identified to

be of particular conservation concern, as substantial parts of their known distributions had been burnt by these fires (Hyman *et al.*, 2020; Marsh *et al.*, 2021; Legge *et al.*, 2022).

The minute punctid land snail *Paralaoma annabelli* Shea & Griffiths, 2010 endemic to south-eastern Australia, is one of the species of conservation concern, as up to 38%

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ORCID: Junn Kitt Foon, 0000-0001-7876-8384; Peter T. Green, 0000-0001-8845-8873; Frank Köhler, 0000-0001-7150-6509

Corresponding author: Junn Kitt Foon Junn.Foon@Australian.Museum

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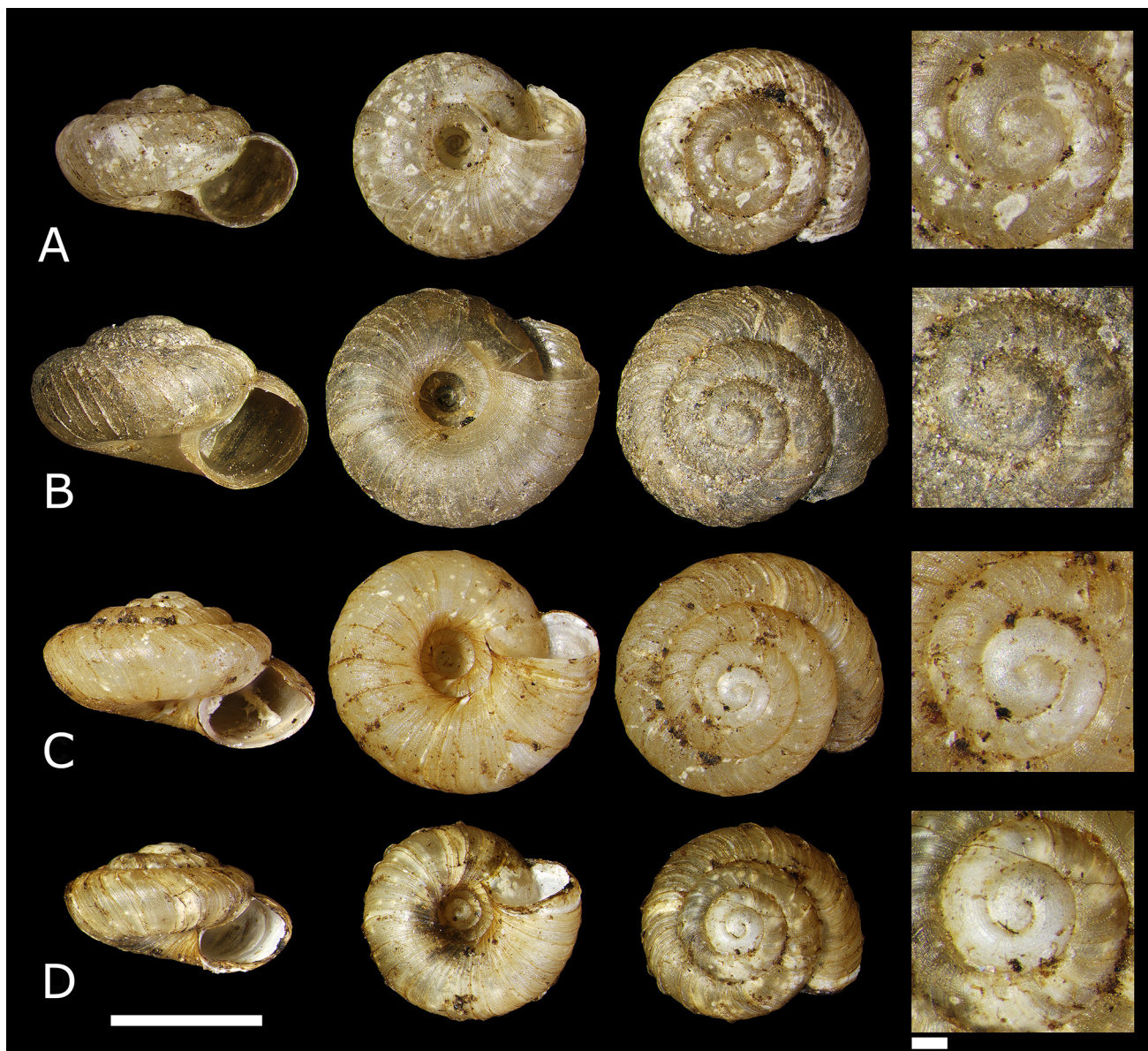


Figure 1. Shells of (A–B) *Paralaoma morti* and (C–D) *Paralaoma annabelli*: (A) lectotype, Darling Point (AM C.031181); (B) Woollahra, 1 km from lectotype locality of *P. morti* (AM C.347565); (C) holotype, Wombeyan Caves (AM C.353384); (D) Jenolan Caves (AM C.466715). Main scale bar = 1 mm. Inset scale bar = 100 μ m.

of its range falls within the fire zone (Hyman *et al.*, 2020). However, taxonomic ambiguity renders an assessment of the fire impacts on this species difficult. The short and rather vague description of *P. annabelli* in Stanisic *et al.* (2010) is the only study to deal with this taxon. Yet, it is rather uninformative and not based on quantified shell traits, hampering its diagnostic value. This paucity of diagnostic characters has rendered the unambiguous discrimination of *P. annabelli* from other congeners difficult. According to Stanisic *et al.* (2010), there are two additional species of *Paralaoma* in New South Wales. The first species, *Paralaoma gelida* Iredale, 1941, is readily distinguished by having crowded radial ribs and a narrow to closed umbilicus. However, the shell of the second species closely resembles *P. annabelli* in shell size, shape, umbilical size and sculpture. This species was long referred to as *P. caputspinulae* (Reeve, 1852) (e.g., Smith, 1992; Stanisic *et al.*, 2010). However,

the name *P. caputspinulae* was synonymized with *P. servilis*, a global tramp species (Falkner *et al.*, 2002; Hausdorf, 2002; Christensen *et al.*, 2012; Gittenberger *et al.*, 2020). Because Stanisic *et al.* (2018) considered the Australian *Paralaoma* species as endemic to Australia and distinct from *P. servilis*, they revived the name *P. morti* (Cox, 1864) for this species, which up to then had been considered a synonym of *P. caputspinulae* (Smith & Kershaw, 1979; Smith, 1992). Stanisic *et al.* (2018) stated that *P. annabelli* differed from *P. morti* by having a smaller shell, wider umbilicus, and more strongly depressed shell shape. However, when we examined a large series of specimens from different localities throughout southern NSW, we observed considerable variation and extensive overlap in these shell characters within and between populations of *Paralaoma* snails, rendering an unequivocal discrimination between *P. annabelli* and *P. morti* challenging.

To test the shell-based species hypotheses of *P. morti* and *P. annabelli* of Stanisic *et al.* (2010, 2018), we herein reconstruct their evolutionary relationships by means of molecular phylogenetics, using both mitochondrial and nuclear DNA sequences. The phylogenetic trees are also used to evaluate the current taxonomy of several other punctid species from south-eastern Australia that were initially included as outgroup taxa. Secondly, we use statistical morphometrics to address the utility of the proposed diagnostic shell characters in distinguishing the two species *P. morti* and *P. annabelli*. Finally, by employing a refined species concept of *P. annabelli*, we delimit its current distribution more accurately based on the re-assessment of all samples in the Australian Museum collection. The results of this facilitated the assessment of the 2019–2020 bushfire impacts on *P. annabelli* (Decker *et al.*, 2023).

Materials and methods

Sample collection and processing

Specimens were picked from leaf litter collected at 328 sites in New South Wales and Victoria that were sampled during post-bushfire surveys between 2019 and 2021. Live specimens were preserved in 95% ethanol while dead specimens (shells) were cleaned and air dried. All specimens were identified to morphospecies based on the diagnoses given by Stanisic *et al.* (2010, 2018) as well as by comparison with types and topotypes in the Australian Museum (Fig. 1). All voucher specimens have been deposited in the Australian Museum malacology collection. Geographic abbreviations: *NP*, National Park; *NR*, Nature Reserve; *SF*, State Forest; *KCR*, Karst Conservation Reserve; *NSW*, New South Wales; *ACT*, Australian Capital Territory; *VIC*, Victoria.

Genomic DNA extraction and PCR

Ethanol-preserved specimens were air dried, photographed (Foon *et al.*, 2023a: figs 1–3), and then the entire specimen was used for DNA extraction. Overall, we used 10 specimens each of *P. annabelli* and *P. morti* that were collected at several different sites. In addition, we produced new sequences of *Paralaoma gelida*, *Pseudiotula eurysiana* Stanisic, 2010, *Iotula microcosmos* (Cox, 1868), *Miselaoma sinistra* (Gabriel, 1930) and *Trocholaoma parvissima* (Legrand, 1871) and included these in our molecular phylogenetic analyses (Foon *et al.*, 2023a: fig. 3). DNA was extracted using the QIAGEN DNA extraction kit for animal tissues following the manufacturer's protocol. Partial sequences of the two mitochondrial genes *cytochrome c oxidase subunit I* (COI) and 16S rRNA were amplified by PCR using the primer pairs L1490 and H2198 (Folmer *et al.*, 1994) as well as 16Sar and 16Sbr (Palumbi *et al.*, 1991), respectively. In addition, we sequenced the single copy nuclear marker intron 8 of the *embryonic lethality and abnormal visual system* gene (ELAV-I8) by PCR using the standard primers and PCR protocol given by Nekola *et al.* (2022). All strands of PCR fragments were purified with ExoSAP-IT (Applied Biosystems, Thermo Fisher Scientific) and cycle sequenced using the PCR primers.

Sequence and molecular phylogenetic analysis

Chromatograms were corrected for misreads and primer sites were pruned from the sequence reads before forward and reverse strands were combined to contigs using the software Sequencher vs 5.4 (Gene Codes Corporation, Ann Arbor, USA). Our sequence datasets included additional sequences available from GenBank (Table 1). 16S and ELAV-I8 sequences were aligned using the online MAFFT version 7 (Katoh *et al.*, 2002) available at <https://mafft.cbrc.jp/alignment/server> using iterative refinement methods. We then used the Guidance2 server (Sela *et al.*, 2015) to remove unreliably aligned regions (threshold: < 95% statistical support) in the 16S and ELAV-I8 sequence alignments. The final sequence alignments of the mitochondrial sequences of 16S and COI were concatenated into one partitioned dataset. Four partitions were designated: each one for the three codon positions in the COI fragment, and one for the 16S sequences.

We used the program IQ-TREE 2 (Minh *et al.*, 2020) to reconstruct the phylogenetic relationships by employing a Maximum Likelihood-based method of tree reconstruction. The best-fit model of sequence evolution was determined by using the integrated ModelFinder function (Kalyaanamoorthy *et al.*, 2017). Nodal support of the best ML tree was estimated by performing 10,000 Ultrafast Bootstraps (Minh *et al.*, 2013).

Shell morphometrics and comparative morphology

We measured up to 10 randomly selected, mature shells from each locality sequenced in this study (i.e., specimens found within a radius of no more than 200 m). In addition, we measured 10 paratypes of *P. annabelli* from the type locality. Types of *P. morti* were not suitable for measurement as the shells were either immature or damaged. Instead, we measured 10 shells from two populations found within 1 km distance from the type locality of *P. morti* (Foon *et al.*, 2023b: table 1). In total, we measured 40 specimens of *P. annabelli* from four populations and 39 specimens of *P. morti* from 6 populations. Each population was represented by 10 specimens for *P. annabelli* and 4–10 specimens for *P. morti*.

We measured and statistically assessed a range of quantitative size and shape characters following Horsák & Meng (2018). Measurements were done with the aid of the calibrated eyepiece graticule mounted on a Leica M165 C stereo microscope. For size, we measured shell width (SW), aperture width (AW), shell height (SH), body whorl height (BWH), aperture height (AH), umbilicus width (UW) and protoconch width (PW) (Fig. 2). We also counted the number of whorls as shown by Kerney & Cameron (1979). For shape characters, we calculated the aperture angle or elongation = ratio of aperture height to aperture width (AH/AW), ratio of umbilical width to shell width (UW/SW), ratio of shell width to shell height (SW/SH), rate of whorl expansion or coiling tightness = ratio of shell width to number of whorls (SW/NOW), ratio of umbilical width to number of whorls (UW/NOW), ratio of body whorl height to shell height (BWH/SH), ratio of aperture width to shell width (AW/SW), ratio of aperture height to shell height (AH/SH), ratio of aperture height to body whorl height (AH/BWH) and ratio of shell

Table 1. List of specimens used for the molecular phylogenetics study, with their GenBank registration numbers, voucher specimen accession numbers and localities. Specimens where species identification was found to be erroneous were marked with an asterisk.

species	voucher number	locality	data source	COI	16S	ELAV-I8
<i>Punctum minutissimum</i> (Lea, 1841)	BIOUG14034-B10	Kejimkujik NP, Nova Scotia, Canada	J. R. deWaard, NCBI BioProject PRJNA472144	MF545143	—	—
<i>Punctum californicum</i> Pilsbry, 1898	NMNZ M.328402	Presidio, San Francisco, USA	Salvador <i>et al.</i> (2020)	MN792621	MN756746	—
<i>Punctum randolphii</i> (Dall, 1895)	NMNZ M.328401	Pemberton, British Columbia, Canada	Salvador <i>et al.</i> (2020)	MN792622	MN756748	—
<i>Punctum pygmaeum</i> (Draparnaud, 1801)	NMW.Z.2017.008.00537	Monmouth, UK	Salvador <i>et al.</i> (2020)	MN812719	MN756747	—
<i>Paralaoma servilis</i> (Shuttleworth, 1852)	BIOUG27664-E06	Nechako Plateau, Canada	J. R. deWaard, NCBI BioProject PRJNA472144	MG421241	—	—
<i>Paralaoma servilis</i> (Shuttleworth, 1852)	BIOUG27664-E05	Nechako Plateau, Canada	J. R. deWaard, NCBI BioProject PRJNA472144	MG422548	—	—
<i>Paralaoma servilis</i> (Shuttleworth, 1852)	BIOUG27664-E07	Nechako Plateau, Canada	J. R. deWaard, NCBI BioProject PRJNA472144	MG422687	—	—
<i>Laoma leimonias</i> (Gray, 1850)	OZD Lalem-1	Kaihu, New Zealand	Salvador <i>et al.</i> (2020)	MN792602	MN756729	—
<i>Phrixgnathus celia</i> Hutton, 1883	OZD Pheel-1	Stewart Island, New Zealand	Salvador <i>et al.</i> (2020)	MN792620	MN756745	—
<i>Paralaoma servilis</i> (Shuttleworth, 1852)	OZD Paser-2	Colac Bay, New Zealand	Salvador <i>et al.</i> (2020)	MN792615	MN756739	—
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010	AM C.589836 (L562)	Bimberi NR, NSW, Australia	this study	OP404171	OP407541	OP408013
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010	AM C.589838 (L566)	Mt York, NSW, Australia	this study	OP404175	OP407545	OP408017
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010	AM C.589841 (L570)	Brindabella NP, NSW, Australia	this study	OP404179	OP407549	OP408021
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010	AM C.589843 (L572)	Brindabella NP, NSW, Australia	this study	OP404181	—	OP408023
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010	WS195S9 (L640)	Mt Wong SF, Nunniong, VIC, Australia	this study	OP404186	OP407555	—
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010	AM C.589842 (L571)	Brindabella NP, NSW, Australia	this study	OP404180	OP407550	OP408022
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010	AM C.586203 (L564)	Grand Canyon, Blue Mountains NP, NSW, Australia	this study	OP404173	OP407543	OP408015
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010	AM C.589837 (L565)	Grand Canyon, Blue Mountains NP, NSW, Australia	this study	OP404174	OP407544	OP408016
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010	AM C.589839 (L568)	Victoria Creek Cascades, Blue Mountains NP, NSW	this study	OP404177	OP407547	OP408019
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010	WS301S1.1 (L641)	Cochrane Lake, SE Forest NP, NSW, Australia	this study	OP404187	OP407556	OP408026
<i>Trocholaoma parvissima</i> (Legrand, 1871)	AM C.588441 (L646)	Goodmans Gully, Kosciuszko NP, NSW, Australia	this study	OP404190	OP407559	OP408029
<i>Iotula microcosmos</i> (Cox, 1868)	AM C.589907 (L636)	Carrai SF, NSW, Australia	this study	OP404182	OP407551	—
<i>Paralaoma morti</i> (Cox, 1864)*	AM C.589945 (L638)	Carrai SF, NSW, Australia	this study	OP404184	OP407553	OP408024
<i>Miselaoma sinistra</i> (Gabriel, 1930)	AM C.589948 (L647)	Goodmans Gully, Kosciuszko NP, NSW, Australia	this study	OP404191	OP407560	OP408030
<i>Paralaoma gelida</i> Iredale, 1941	AM C.588470 (L648)	Brindabella NP, NSW, Australia	this study	OP404192	OP407561	—
<i>Pseudiotula eurysiana</i> Stanisic, 2010	AM C.589908 (L637)	Gibraltar Range NP, NSW, Australia	this study	OP404183	OP407552	—
<i>Iotula microcosmos</i> (Cox, 1868)	AM C.589952 (L649)	Gibraltar Range NP, NSW, Australia	this study	OP404193	OP407562	—
<i>Iotula microcosmos</i> (Cox, 1868)	AM C.589949 (L650)	Kanangra Boyd NP, NSW, Australia	this study	OP404194	OP407563	—
<i>Paralaoma annabelli</i> Shea & Griffiths, 2010*	AM C.589947 (L645)	Terrace Creek, Jenolan KCR, NSW, Australia	this study	OP404189	OP407558	OP408028
<i>Pseudiotula eurysiana</i> Stanisic, 2010	AM C.589950 (L652)	Mt Irvine, NSW, Australia	this study	—	OP407565	OP408032
<i>Pseudiotula eurysiana</i> Stanisic, 2010	AM C.589951 (L651)	Mt Coricudgy. Coricudgy SF, NSW, Australia	this study	—	OP407564	OP408031
<i>Paralaoma morti</i> (Cox, 1864)	AM C.589946 (L639)	Hat Head NP, NSW, Australia	this study	OP404185	OP407554	OP408025
<i>Paralaoma morti</i> (Cox, 1864)	AM C.586232 (L560)	Jenolan Road, Jenolan KCR, NSW, Australia	this study	OP404169	OP407539	OP408011
<i>Paralaoma morti</i> (Cox, 1864)	AM C.594138 (L644)	Jenolan Caves, Jenolan KCR, NSW, Australia	this study	OP404188	OP407557	OP408027
<i>Paralaoma morti</i> (Cox, 1864)	AM C.588429 (L561)	Cooleman Cave, Bimberi NR, NSW, Australia	this study	OP404170	OP407540	OP408012
<i>Paralaoma morti</i> (Cox, 1864)	AM C.588484 (L563)	Namadgi NP, ACT, Australia	this study	OP404172	OP407542	OP408014
<i>Paralaoma morti</i> (Cox, 1864)	AM C.588490 (L567)	Yarrangobilly Caves, Kosciuszko NP, NSW	this study	OP404176	OP407546	OP408018
<i>Paralaoma morti</i> (Cox, 1864)	AM C.589835 (L559)	Wollemi NP, NSW, Australia	this study	OP404168	OP407538	OP408010
<i>Paralaoma morti</i> (Cox, 1864)	AM C.589840 (L569)	Victoria Creek Cascades, Blue Mountains NP, NSW	this study	OP404178	OP407548	OP408020

Table 2. Summary statistics of shell size and shape metrics for *P. annabelli* and *P. morti*. Measurements are in millimetres except for the number of whorls. *AH/AW*, *UW/SW*, *SW/SH*, *SW/NOW*, *UW/NOW*, *BWH/SH*, *AW/SH*, *AH/SH*, *AH/BWH* and *SH/NOW*. Significant p-values with Bonferroni correction ($p \leq 0.003$) are underlined. The magnitude of effect size indicated by asterisks: large (**), moderate (*), small (no asterisk). Abbreviations: *SW*, shell width; *AH*, aperture height; *UW*, umbilicus width; *NOW*, number of whorls; and *PW*, protoconch width.

	SW	AW	SH	BWH	AH	UW	NOW	PW	AH/AW	UW/SW	SW/SH	SW/NOW	UW/NOW	BWH/SH	AW/SW	AH/SH	AH/BWH	SH/NOW	
<i>Paralaoma annabelli</i> (n = 40)																			
median	1.66	0.71	0.90	0.71	0.51	0.41	3.38	0.45	0.73	0.25	1.84	0.48	0.12	0.78	0.42	0.58	0.74	0.26	
interquartile range	0.33	0.12	0.11	0.13	0.13	0.16	0.38	0.06	0.09	0.05	0.11	0.07	0.04	0.04	0.04	0.06	0.06	0.03	
<i>Paralaoma morti</i> (n = 39)																			
median	1.91	0.84	1.13	0.91	0.67	0.46	3.25	0.51	0.81	0.24	1.66	0.57	0.14	0.80	0.44	0.60	0.72	0.34	
interquartile range	0.23	0.13	0.19	0.16	0.13	0.13	0.44	0.07	0.09	0.04	0.18	0.11	0.04	0.04	0.04	0.07	0.08	0.07	
Wilcoxon test results																			
W statistic	292	264	160	78	131	490	919	386	320	743	1270	205	432	478	662	624	858	104	
p-value	<u>1.72E-06</u>	<u>3.97E-07</u>	<u>1.17E-09</u>	<u>5.57E-09</u>	<u>1.92E-10</u>	<u>0.0044</u>	<u>0.163</u>	<u>1.02E-04</u>	<u>6.6E-06</u>	0.72	<u>1.63E-06</u>	<u>1.69E-08</u>	<u>5.93E-04</u>	<u>0.00316</u>	0.249	0.127	0.447	<u>3.23E-11</u>	
effect size	0.539	0.571	0.685	0.776	0.717	0.321	0.157	0.438	0.508	0.408	0.54	0.635	0.387	0.333	0.13	0.172	0.0861	0.747	
	***	***	***	***	**	*		*	**	**	**	*	*	*				**	

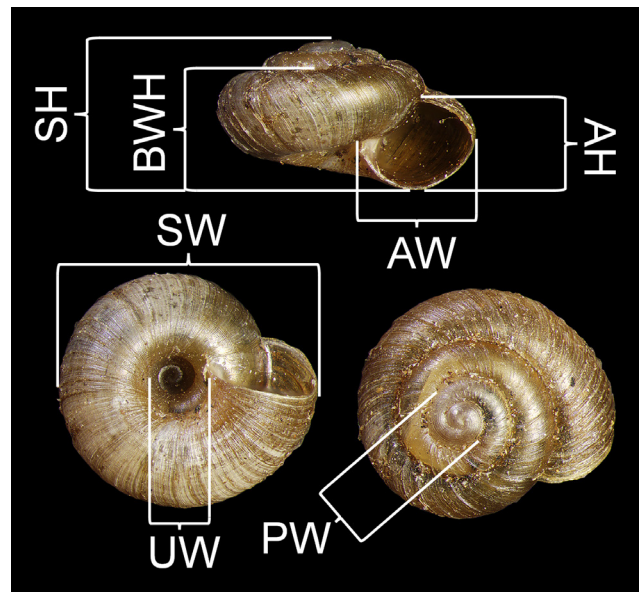


Figure 2. Shell dimensions measured. Abbreviations: *SW*, shell width; *AW*, aperture width; *SH*, shell height; *BWH*, body whorl height; *AH*, aperture height; *UW*, umbilicus width; and *PW*, protoconch width.

height to number of whorls (*SH/NOW*) (Horsák & Meng, 2018). We also recorded the qualitative character presence or absence of radial periostracal folds. We restricted our measurements to specimens with three or more whorls, where the slight inward expansion of the peristome at the umbilicus is assumed to indicate that the specimens are mature (Roth, 1985; Horsák & Meng, 2018). We employed the Shapiro-Wilk’s Test to test if measured metrics were normally distributed. The observed trends for each measured metric were assessed using the Wilcoxon Rank Sum Test for significance. To control for the study’s error rate, we adopt a conservative approach by setting the significant p-value at 0.003 based on a Bonferroni correction for the 18 tests of measured metrics. All statistical analyses were undertaken in the R statistical environment version 4.1.2 (R Core Team, 2022). We used comparison of shell parameters to test the hypotheses that *P. annabelli* has a smaller and flatter shell with a wider umbilicus than *P. morti* and that both species differ in shell shape. We also tested whether both species differed in tightness of whorl coiling, the height of body whorl relative to shell height, the width of the aperture relative to shell width, and the length of the aperture relative to shell height.

Reconstructing species distributions

To delineate the distribution of each species, we re-examined all relevant samples (labelled as *P. annabelli*, *P. servilis*, *P. caputspinulae* and *P. morti*) in the dry collection of the Australian Museum by employing our revised species diagnoses. The geo-referenced collecting sites were used to generate distribution maps for both species.

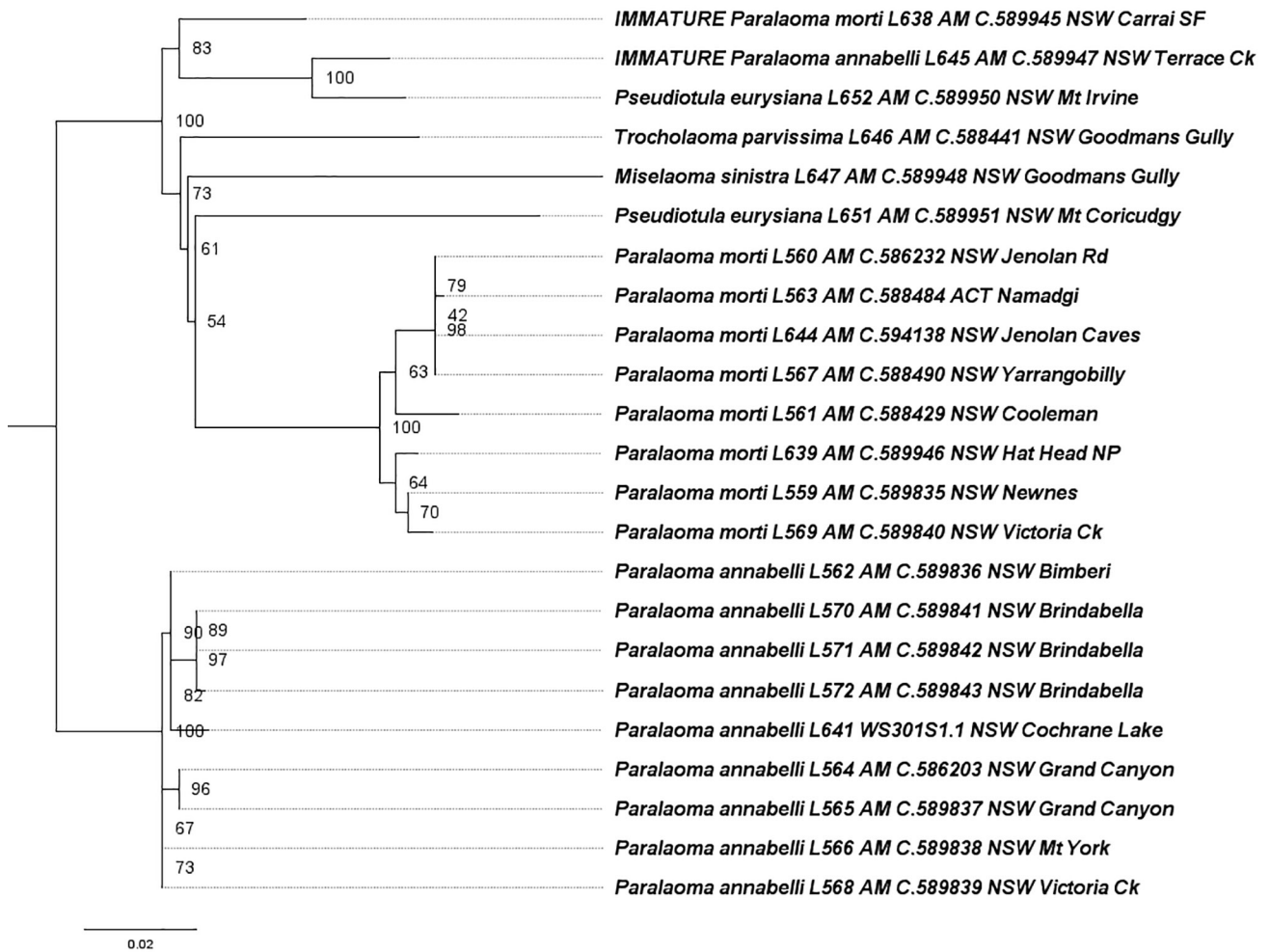


Figure 4. Best Maximum Likelihood tree based on analysis of ELAV-I8 sequences. Numbers on branches indicate nodal support based on 10,000 ultra-fast bootstrap replicates. Scale bar indicating 2% of modelled sequence divergence. Note that the species for the immature specimens were misidentified (L638 = *Iotula microcosmos* misidentified as *P. morti*; L645 = *Pseudiotula euryisiana* misidentified as *P. annabelli*).

The dataset for ELAV-I8 contained 23 sequences. The length of aligned ELAV-I8 sequences was 705 base pairs. The taxa included in the in-group are *Paralaoma morti*, *Pseudiotula euryisiana*, *Iotula microcosmos*, *Miselaoma sinistra* and *Trocholaoma parvissima*. No ELAV-I8 sequences are available for any of the GenBank samples (i.e., *Laoma leimonias*, *Phrixgnathus celia*, *Paralaoma gelida*, *Punctum* spp.). Therefore, *Paralaoma annabelli* sequences were treated as an outgroup based on the topology of the phylogenetic tree for the mitochondrial sequence dataset.

The topology of the tree based on the nuclear marker was generally consistent with that of the mitochondrial tree: *P. annabelli* and *P. morti* formed two distinct clades in the best Maximum Likelihood tree for ELAV-I8 with high statistical support (Fig. 4), one sequence of *P. annabelli* formed the sister group of *Pseudiotula euryisiana* (sample L645) and another (sample L638) formed the sister group of the clade containing L645, while *Paralaoma* was rendered non-monophyletic by the inclusion of the other punctid genera.

Comparative shell morphology

Material examined included a set of types and topotypes for both species (Fig. 1). Each population was represented by at least one sequenced specimen except for the types. A

comparison of the number of whorls for the material examined shows no significant difference between the two species, hence all samples are considered to be mature (Fig. 5H, Table 2).

Shapiro-Wilk's Test revealed that 10 shell metrics (shell height, number of whorls, protoconch width, UW/SW, SW/SH, UW/NOW, BWH/SH, AW/SW, AH/SH and SH/NOW) were not normally distributed. Considering this, the Wilcoxon Rank Sum Test for significance with Bonferroni correction was used to assess the observed trends for each shell metric.

Our measurements showed that *P. annabelli* differs from *P. morti* in having a significantly smaller shell (height and width), narrower protoconch, shorter body whorl, as well as smaller aperture (height and width), although there is some size overlap between the species (Figs. 5A–G, Table 2).

Paralaoma annabelli does not differ from *P. morti* in umbilicus width (Fig. 5A, Table 2) and umbilicus width adjusted to the shell width (UW/SW) (Figs. 6I, 7J, Table 2). *Paralaoma annabelli* has significantly more whorls per millimetre of umbilicus width (UW/NOW) compared to *P. morti* (Figs 5I, 7A, Table 2).

On shell shape, the ratio of shell width to shell height (SW/SH) showed that *P. annabelli* has a significantly flatter shell compared to the more globular shell of *P. morti* (Figs 6A, 7B, Table 2). Comparisons of the ratio of aperture height

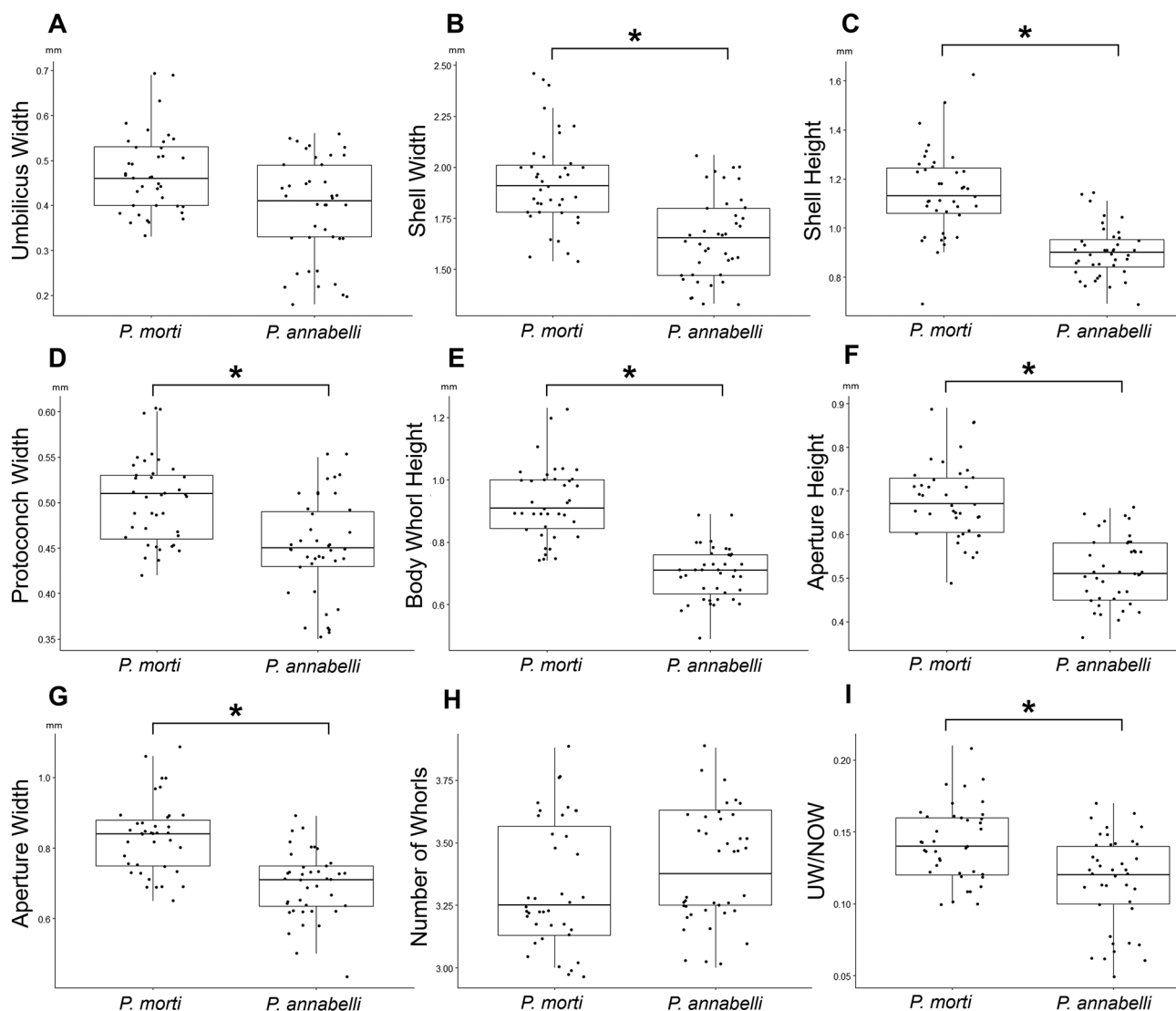


Figure 5. Boxplots showing comparisons between *Paralaoma annabelli* and *Paralaoma morti* in size and shape metrics: (A) Umbilicus width, (B) Shell width, (C) Shell height, (D) Protoconch width, (E) Body whorl height, (F) Aperture height, (G) Aperture width, (H) Number of whorls, and (I) UW/NOW. Asterisk above pairwise comparisons of the two species indicate significant difference ($p \leq 0.003$) with a Wilcoxon Rank Sum Test with Bonferroni correction.

to aperture width (AH/AW) showed that *P. annabelli* has a significantly more elongated aperture perpendicular to the coiling axis compared to *P. morti*, indicating that *P. annabelli* has a trochoidal shell compared to the turbinated shelled *P. morti* (Figs 6H, 7I, Table 2). Comparisons of the ratio of shell height to the number of whorls (SH/NOW) also showed that the shell of *P. annabelli* has a significantly flatter spire compared to the taller spired *P. morti* (Figs 6C, 7D, Table 2).

Comparisons of the ratio of shell width to the number of whorls (SW/NOW) showed that *P. annabelli* has a significantly more tightly coiled whorl compared to *P. morti* (Figs 6B, 7C, Table 2). *Paralaoma annabelli* does not differ from *P. morti* in the ratio of body whorl relative to shell height (BWH/SH), aperture width to shell width (AW/SW), aperture height to shell height (AH/SH) and aperture height to body whorl height (AH/BWH) (Figs 6D–G, 7E–H, Table 2).

The examined populations of both *P. annabelli* and *P. morti* exhibited a mix of shells with and without periostracal folds (Table 3).

Table 3. The number of examined *Paralaoma annabelli* and *Paralaoma morti* specimens with and without radial periostracal folds.

character	number of specimens
<i>Paralaoma annabelli</i>	
has radial periostracal folds	26
no radial periostracal folds	14
<i>Paralaoma morti</i>	
has radial periostracal folds	19
no radial periostracal folds	20

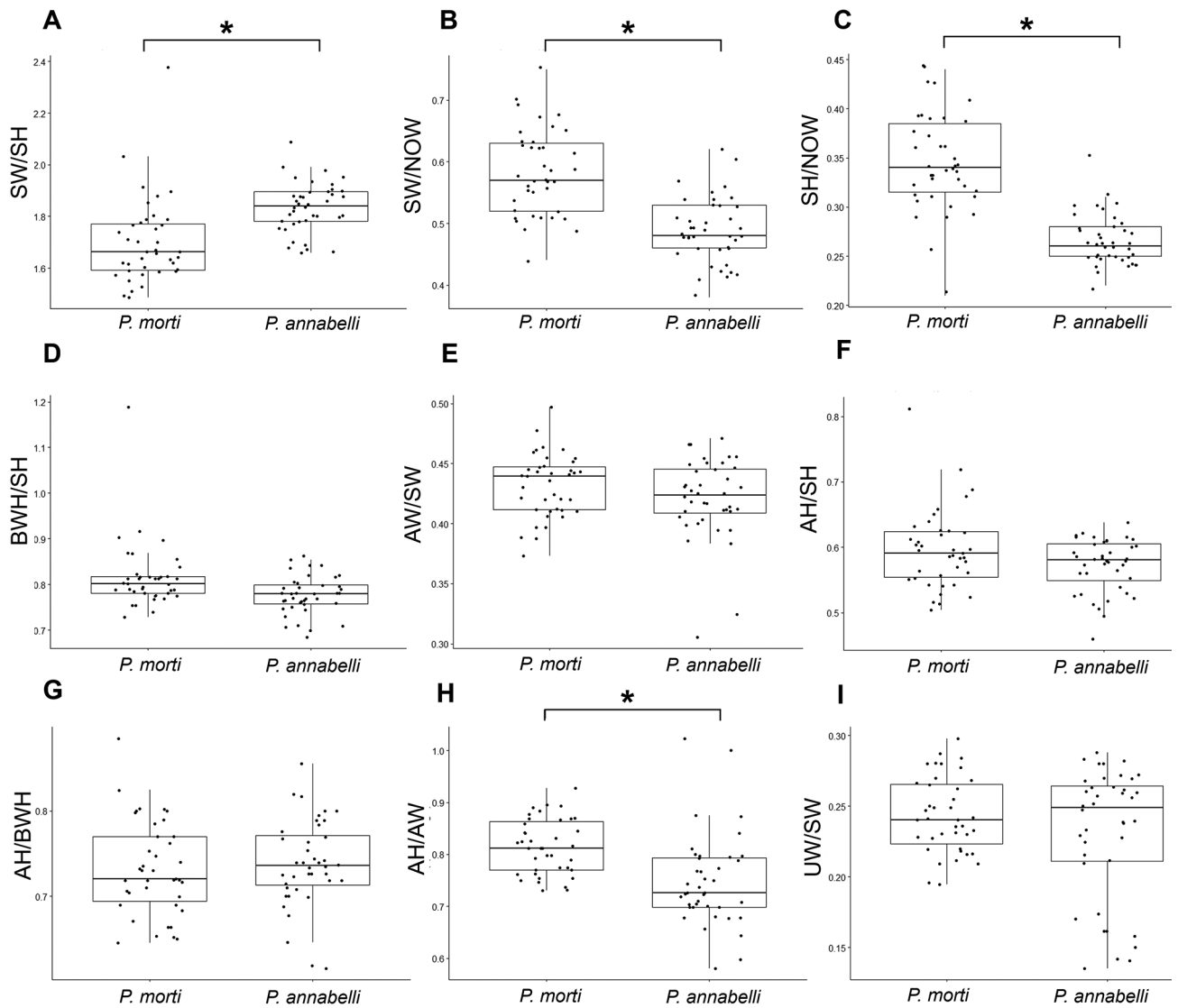


Figure 6. Boxplots showing comparisons between *Paralaoma annabelli* and *Paralaoma morti* in shape metrics: (A) SW/SH, (B) SW/NOW, (C) SH/NOW, (D) BWH/SH, (E) AW/SW, (F) AH/SH, (G) AH/BWH, (H) AH/AW, and (I) UW/SW. Asterisk above pairwise comparisons of the two species indicate significant difference ($p \leq 0.003$) with a Wilcoxon Rank Sum Test with Bonferroni correction.

Species distributions

Based on the shell characters that we identified to be diagnostic, we checked the identification of all available samples in the Australian Museum collection. In total, we reviewed and confirmed the identity of more than 605 specimens in 70 lots for *P. annabelli*, and more than 9980 specimens in 862 lots for *P. morti* (including lots labelled as *P. caputspinulae* and *P. servilis*) (Foon *et al.*, 2023b: table 2). Based on this material, we mapped the distribution of both species (Fig. 8). *Paralaoma annabelli* occurs along the Great Dividing Range south of Warrumbungle in New South Wales, as well as scattered localities in Victoria. Meanwhile, *P. servilis* has a wide distribution across New South Wales, southern Queensland, and Victoria.

Discussion

The identity of *Paralaoma annabelli*

Paralaoma annabelli has been described for having a smaller shell, wider umbilicus, and more strongly depressed shell than a congener in mainland Australia for which the name *P. morti* was suggested (Stanisic *et al.*, 2010, 2018). However, no objective data has been available to confirm the accuracy of this comparison. We subjected this initial species hypothesis to rigorous tests using objective evidence from shell morphometrics and molecular phylogenetics. We found that *P. annabelli* can indeed be distinguished by means of shell morphometrics from the other widespread Australian *Paralaoma* species. Moreover, its distinctiveness is solidly corroborated by analyses of both mitochondrial and nuclear DNA sequences as both species form well differentiated (by means of basal branch length) and well-supported (by means of bootstrapping) clades in phylogenies based on analyses of independent sequence datasets.

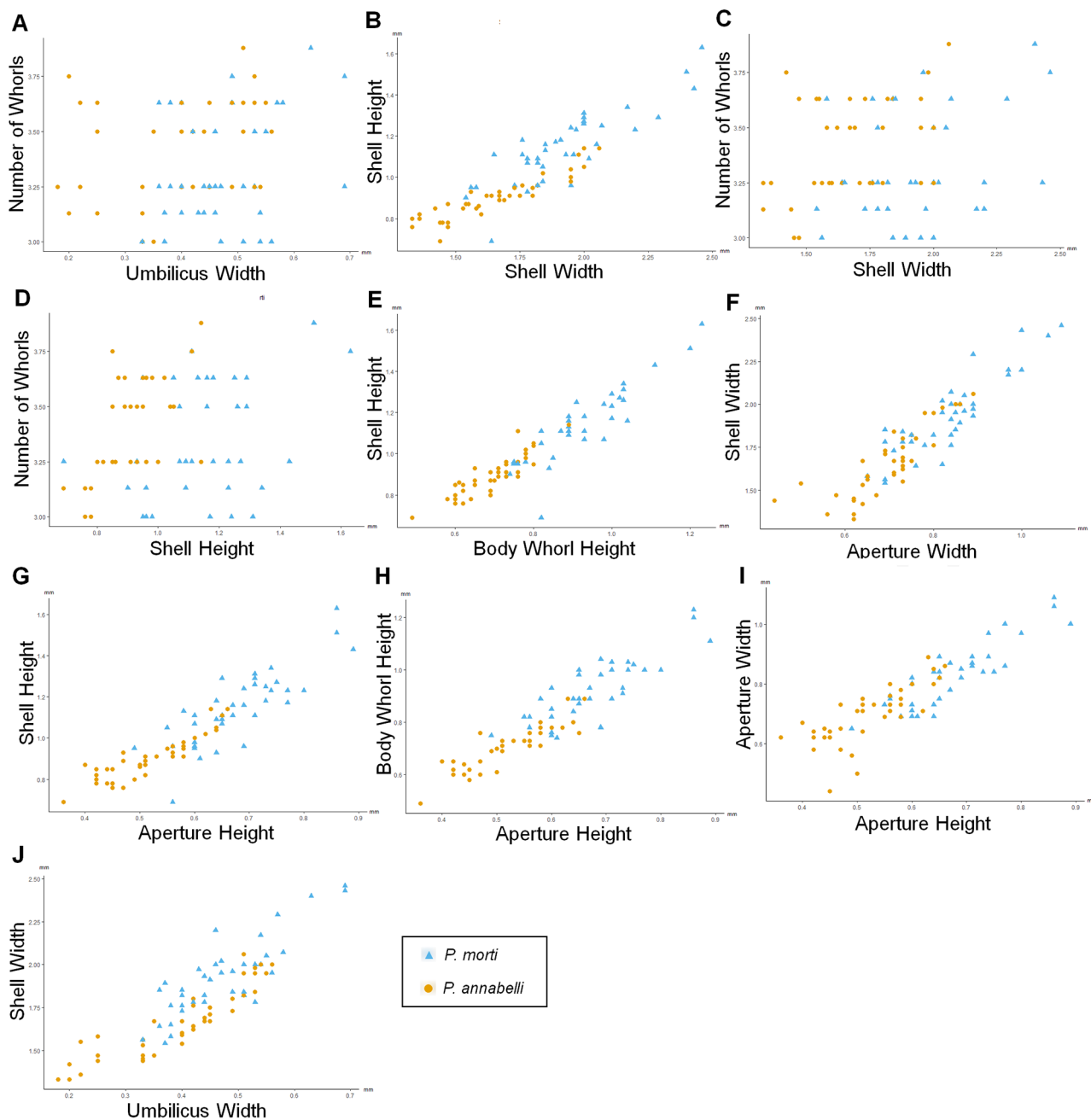


Figure 7. Scatterplots of shell shape metrics for *Paralaoma annabelli* and *Paralaoma morti*: (A) AH/AW, (B) UW/SW, (C) SW/SH, (D) SW/NOW, (E) UW/NOW, (F) BWH/SH, (G) AW/SW, (H) AH/SH, (I) AH/BWH, and (J) SH/NOW.

Based on our data, we demonstrate that the shell of adults of *P. annabelli* is smaller than that of the second species (referred to by some as *P. morti*). However, we also show that *P. annabelli* does not have a wider umbilicus in absolute size as well as when related to shell width. The key shell shape characters that differentiate *P. annabelli* from *P. morti* are summarized in Table 4. In contrast with studies of non-Australian *Paralaoma* species (e.g., Fonseca & Thomé, 1995; Goulstone & Brook, 1999), we found that the ribbed radial periostracal folds are not diagnostic, since this character state varies within species. The intraspecific variation in periostracal fold development was noted by Cox (1868), and similar observations have been made also for *P. servilis* (Roth, 1986; Neubert, 1998). While our empirical study shows that the proposed shell characters for diagnosing

Table 4. The main differences in shell characters between *Paralaoma annabelli* and *Paralaoma morti*.

character	<i>P. annabelli</i>	<i>P. morti</i>
shell shape (SW/SH; AH/AW)	flat; trochoidal	globular; turbinate
aperture (AH/AW)	more elongated	less elongated
spire (SH/NOW)	flatter	taller
coiling (SW/NOW)	tighter coil	looser coil
body whorl (BWH/SH)	shorter	taller

P. annabelli and *P. morti* are supported with statistical significance, field identification of specimens to these species remains difficult due to intraspecific variation. Moreover, correct identifications require mature shells since immature

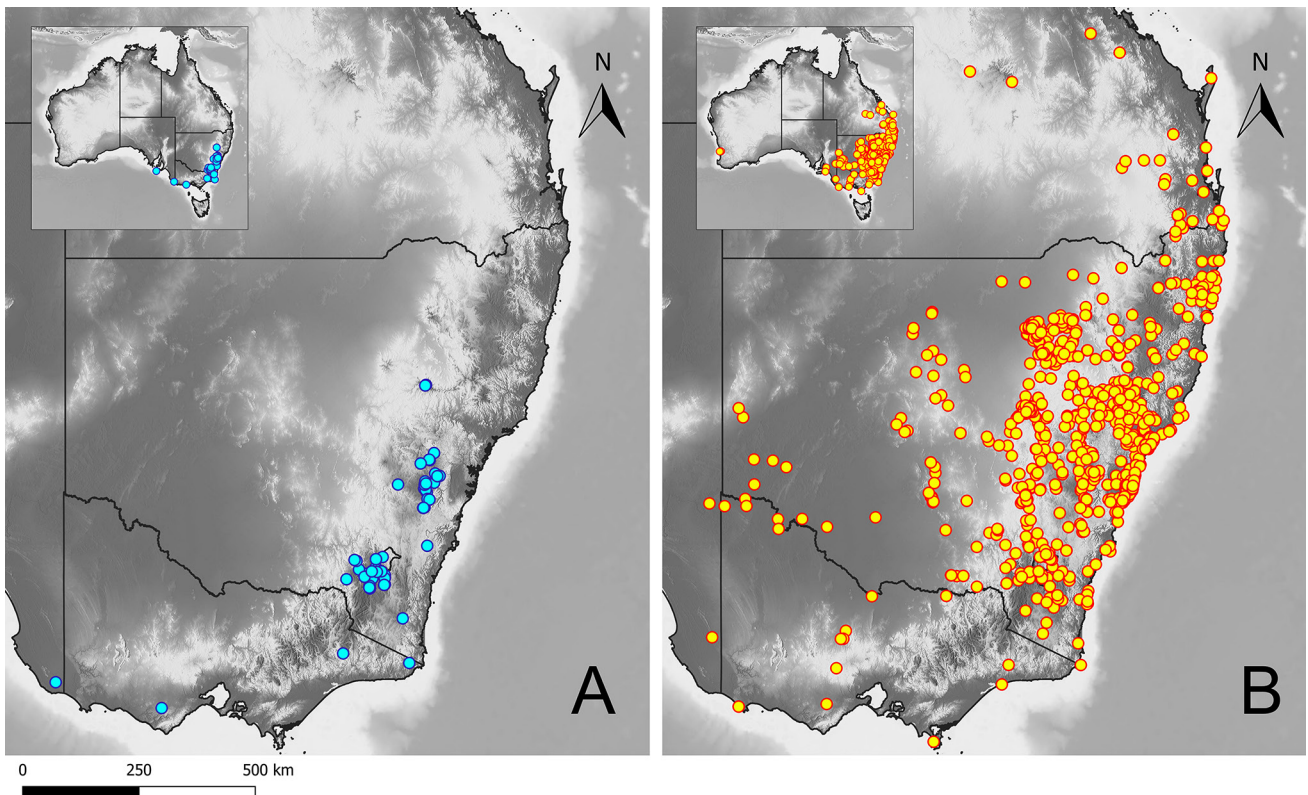


Figure 8. Examined and verified occurrence records of (A) *P. annabelli* and (B) *P. morti* from the Australian Museum dry collection. Main maps showing records in NSW, Queensland and Victoria. Insets showing all of Australia. Source of base map: Hans Braxmeier, maps-for-free.com.

specimens do not exhibit sufficient diagnostic features. The species for two immature specimens were misidentifications (L638 = *Iotula microcosmos* misidentified as *P. morti*; L645 = *Pseudiotula eurysiana* misidentified as *P. annabelli*; see Fig. 1; Foon *et al.*, 2023a: fig. 3).

On the taxonomy of *Paralaoma morti* and other Australian congeners

The failings of purely shell-based taxonomy become evident when considering the taxonomic history of Australian punctids, which presents us with a litany of subjective treatments based on expert opinion rather than hard evidence (Nekola & Horsák, 2022).

For example, 14 nominal species described from eastern Australia have earlier been synonymized with a single name, *P. caputspinulae*, by Smith (1992). Stanisic *et al.* (2010) maintained Smith's synonymies under *P. caputspinulae* for all *Paralaoma* species in NSW and Queensland except for *P. annabelli* and *P. gelida*. When it became apparent that *P. caputspinulae* is now widely regarded as just another synonym of the globally distributed *P. servilis* (Falkner *et al.*, 2002; Hausdorf, 2002; Christensen *et al.*, 2012; Gittenberger *et al.*, 2020), Stanisic *et al.* (2018) reintroduced the name *P. morti* for a species supposedly endemic to the eastern Australian mainland and distinct from *P. servilis*. This was based on the supposed difference between *P. morti* (with “either whitish grey, creamy yellow or yellowish-brown shells with the upper part of the whorl weakly to strongly shouldered”) and *P. servilis* (being smaller and “waxy bronze to dark brown coloured”). However, this distinction does not

fully account for the range of morphological variation in *P. servilis* (e.g., Roth, 1986; Neubert, 1998; Christensen *et al.*, 2012) nor that of *P. morti*.

GenBank sequences of just two non-Australian populations of *P. servilis* from Canada and New Zealand fall within the sequence cluster formed by the Australian *P. morti*, revealing amounts of sequence diversification that may well be within the range of intraspecific mitochondrial diversification. Based on this observation and the obvious similarity in shell characters, the treatment of *P. morti* as a species distinct from *P. servilis* remains hypothetical. To resolve the taxonomic relationships of both taxa, it will be necessary to sample the global structure of the *P. servilis* gene pool and to conduct a comprehensive conchometric analysis of both taxa.

Stanisic *et al.* (2018) used a similar argument to reinstate three other nominal species from Australia as accepted species: *P. mucooides*, *P. stabilis* and *P. hobarti*. In light of the present findings, it is evident that the taxonomy of these taxa also requires critical revision.

Delimiting the distributions of *P. annabelli* and *P. morti* in south-eastern Australia

Based on the revised occurrence records, *P. annabelli* within NSW appears to be restricted to the higher elevations of the Great Dividing Range from Warrumbungle in the north to the Australian Alps in the south, as well as scattered localities at lower elevations in Victoria (Fig. 8). In contrast, *P. morti* has a much wider distribution across all elevations and biomes of variable aridity in New South Wales, southern Queensland, Victoria and elsewhere in Australia (Fig. 8).

While we identified several samples in south-western Victoria and South Australia as morphologically akin to *P. annabelli*, we consider the identity of these specimens provisional pending a critical review of *Paralaoma* species in Australia, in particular the status of the closely similar taxa *P. mucoides* (Tenison-Woods, 1879) and *P. stabilis* Iredale, 1937a.

In contrast, *P. morti* is a wide-ranging and ecologically adaptable species in Australia that inhabits a range of different habitat types. We note that our map is based on material from the Australian Museum only, which is biased towards New South Wales. It is likely that *P. morti* is more widespread across Australia than currently recognized (Stanisic *et al.*, 2018).

Phylogenetic relationships of Australian punctids are at odds with current genus-level classification

The mitochondrial and nuclear phylogenies produced herein consistently reveal that Australian punctids assigned to different genera other than *Paralaoma* fall in between the two species *P. annabelli* and *P. morti*.

These genera, *Trocholaoma* Iredale, 1937b (type species: *Helix spiceri* Petterd, 1879 accepted as *Trocholaoma parvissima*), *Iotula* Iredale, 1941 (type species: *Helix microcosmos* Cox, 1868), *Miselaoma* Iredale, 1933 (type species: *Helix weldii* Tenison-Woods, 1877), and *Pseudiotula* Stanisic, 2010 (type species: *Pseudiotula eurysiana*), were all described based on shell characters and without proper cladistic or phylogenetic analysis. All these genera are either monotypic or contain few, highly similar, species (Stanisic *et al.*, 2010, 2018). We conclude that shell characters such as sinistrality, umbilical width, coiling tightness, shell sculpture, as well as spire height and shape are unsuitable to support the current recognition of these taxa as independent evolutionary lineages at the level of the genus group.

Considering the ambiguity of currently studied taxonomic characters in *Paralaoma* and Australian punctids in general, we recommend an integrative approach towards solving their taxonomy (Dayrat, 2005; Padial *et al.*, 2010). Future studies should statistically reassess the shell-based hypotheses of all punctid taxa and complement them with molecular phylogenetics as has been done here and for other taxa (e.g., Horsáková *et al.*, 2020; Horsáková *et al.*, 2022). A geographically comprehensive sampling for these punctid taxa, including at type localities, will also be required to clarify the variation of characters within and between taxa at the species and genus level. In addition, reproductive anatomy, radula, fine protoconch and teleoconch sculpture as well as other characters should be critically assessed for their potential use as diagnostic characters, as has been done in some punctoid taxa (e.g., Climo, 1980; Solem, 1983; Fonseca & Thomé, 1995; Climo *et al.*, 2019).

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