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Phylogenetic study of the "Megaspiridae" tree snails reveals new families (Gastropoda, Orthalicoidea)

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Abstract. Orthalicoidea is a diverse Gondwanan clade, with over 2,000 species spread mainly throughout the Americas and with small branches living in Australia, New Zealand, and some other South Pacific islands, as well as a relict lineage in southern Africa. The latest phylogenetic study on this superfamily demonstrated that the family Megaspiridae was paraphyletic, with three separate branches, and that the family Orthalicidae remained unresolved as a polytomy. Here we present a new multi-marker molecular phylogenetic study of the Orthalicoidea, with greatly expanded sampling of Orthalicidae and the multiple branches of Megaspiridae, including the unique genus *Auris* Spix, 1827. Our results have many implications for the classification of the superfamily. Firstly, Megaspiridae is restricted to two genera (*Megaspira* Lea, 1836 and *Callionepion* Pilsbry & Vanatta, 1899) and four new families are described: Auriidae fam. nov. Salvador, La Pasta, Silva & Breure; Koridae fam. nov. Salvador, Cavallari & Breure; Orphaicidae fam. nov. Salvador, Rosa, Cavallari & Breure; and Paeniscutalidae fam. nov. Breure & Salvador. Thus, Orthalicoidea now contains 12 families, in a classification scheme that better reflects its diversity. In addition, the family Liguidae, previously considered synonymous with Orthalicidae, is here reestablished as subfamily Liguinae, sister to Orthalicinae. Furthermore, some changes in the taxonomy of genus- and species-level taxa are also proposed.

Key words. Land snails, molecular phylogenetics, Neotropics, Stylommatophora, taxonomy

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Introduction

The Neotropical region tops world biodiversity charts and includes the first (Brazil) and second (Colombia) most biodiverse countries in most terrestrial taxa (Butler 2016). To a large extent, knowledge of the Neotropical fauna, and land snails in particular, remains incipient to this day. The region's expected high biodiversity and vast territory naturally contribute to this scenario, especially considering the abundance of logistically difficult regions to survey (e.g. Amazon,

Andes, and Guiana Highlands) (Salvador 2019b; Salvador *et al.* 2024). Still, historical and socio-economic factors perhaps play a larger role in this situation, considering colonial history (e.g. Salvador 2019b), the chronic lack of sustained funding for science (e.g. Ciocca & Delgado, 2017; Lazcano, 2025) particularly during periods of instability such as the era of U.S.-backed "regime changes" into authoritarianism (e.g. Rabe 2015; Ramírez & Franco 2021), and the continuity of neocolonial practices in science that rarely involve the local scientific community or develop local infrastructure and expertise (e.g. Abreu *et al.* 2025).

For most Neotropical land snails, systematic classification and taxonomy, in many cases remain largely reliant upon important historical studies such as those by Henry A. Pilsbry (e.g. the *Manual of Conchology* series) and Zilch (1959–1960). Recent phylogenetic studies, therefore, have brought large changes in the classification of Neotropical snails (e.g. Sei *et al.* 2017; Calcutt *et al.* 2020; Salvador *et al.* 2020). One group that benefited from this approach was the superfamily Orthalicoidea Martens, 1860, commonly known as the tree snails. Orthalicoidea is a diverse Gondwanan clade, with over 2,000 species (in conservative estimates; Rosenberg 2014) spread mainly throughout the Americas, with small branches living in Australia, New Zealand, and some other South Pacific islands, as well as a relict lineage in southern Africa (Herbert & Mitchell 2009; Salvador *et al.* 2023). While the taxonomic studies of Breure (1978, 1979), Breure & Eskens (1981), and Breure & Schouten (1985) had already made much headways in the classification of Orthalicoidea (then known simply as Bulimulidae), numerous surprises came with the phylogenetic studies of Breure & Romero (2012) and Salvador *et al.* (2023), which have shed some light on the relationships of the major clades within this superfamily. On the other end of the scale, more focused studies on single genera or small groups of genera have also brought new insight into the taxa involved, such as Herbert & Mitchell (2009) for the African *Prestonella*, Köhler *et al.* (2025) for the Australian *Bothriembryon*, and Breure *et al.* (2024) for the Neotropical *Antidrymaeus*.

In any event, many questions, big and small, remain open. Notably, Megaspiridae was demonstrated to be paraphyletic, with three separate branches, by Salvador *et al.* (2023). However, those authors' sampling of "megaspirid" taxa was very restricted, and the relationships of its branches among themselves and with the rest of Orthalicoidea remained uncertain. Furthermore, Orthalicidae was a big polytomy in the study of Salvador *et al.* (2023), and very little could be extracted from those results. Finally, one genus of particular interest due to its unique morphology, *Auris* Spix, 1827, could not be included in the analyses of Breure & Romero (2012) and Salvador *et al.* (2023).

Here we present a new multi-marker molecular phylogenetic study of the Orthalicoidea, with greatly expanded sampling of Orthalicidae and the multiple scattered branches of non-monophyletic Megaspiridae; importantly, the genus *Auris* is included. Our results have implications for the classification of the superfamily and, therefore, we propose new taxa, new combinations, and new synonymies. Finally, we also provide anatomical and preliminary natural history data on *Auris*.

Materials and Methods

The material studied herein (for both molecular and anatomical analyses) came from the malacological collections of the following institutions: Museu de Zoologia da Universidade de São Paulo (MZSP, São Paulo, Brazil); Florida Museum of Natural History (UF, Gainesville, USA); and the private collection of Valentín Mogollón Ávila (VMA, Lima, Peru).

DNA extraction and amplification

A small tissue clip was obtained from the foot of each voucher specimen (Table 1) for DNA extraction, conducted using the QIAGEN DNeasy® Blood & Tissue Kit. The standard protocol for DNA extraction was followed, although adding a minor modification to the final step of the procedure: to improve concentration and increase yield, we used only one-quarter (50 µL) of the suggested amount of buffer AE and also included a repetition of the final step.

Following the studies of Breure & Romero (2012) and Salvador *et al.* (2023), four genetic markers were targeted: the barcoding fragment of the mitochondrial COI gene (primers LCO/HCO of Folmer *et al.* 1994); a fragment of the nuclear H3 gene (histone 3), (primers H3pulF and H3pul3 of Uit de Weerd & Gittenberger 2013); and a continuous fragment of nuclear DNA encompassing the 3′ end of the 5.8S rRNA gene, the ITS2 region, and the 5′ end of the 28S rRNA gene (amplified in two fragments using primers LSU-1/LSU-3 and LSU-2/LSU-5 of Wade & Mordan 2000, Wade *et al.* 2007).

PCR amplification protocols for all markers included an initial denaturation step at 96 °C (3 min) and a final extension step at 72 °C (5 min), differing in the cycles as follows. COI: 35 cycles of denaturation at 94 °C (30 s), annealing at 48 °C (COI) (1 min), and extension at 72 °C (2 min). H3: 40 cycles of denaturation at 95 °C (30 s), annealing at 57 °C

Table 1. Specimens sequenced for the present study, their GenBank accession numbers, locality where the specimens were collected, and registration number of the voucher specimens in natural history collections.

Species	COI	H3	ITS2+28S	Voucher	Provenance
Anostoma octodentatum Fischer von Waldheim, 1807	PZ746034	PZ754683	PZ745247	MZSP 070505	Brazil, Ceará, Serra do Ibiapaba
Auris bilabiata (Broderip & Sowerby I, 1830)	—	OP381225	—	MZSP 069607	Brazil, Bahia, Alcobaça
Auris bilabiata (Broderip & Sowerby I, 1830)	PZ746035	PZ754694	PZ740969	MZSP 166707	Brazil, Bahia, Icaraí do Ranulfo
Koltrora pyrostoma Simone, 2024	—	PZ754695	PZ745242	MZSP 151789 [paratype]	Brazil, Bahia, Bom Jesus da Lapa
Koltrora pyrostoma Simone, 2024	—	PZ754696	PZ745243	MZSP 163500 [holotype]	Brazil, Bahia, Bom Jesus da Lapa
Kora arnaldoi Pena, 2024	PZ746042	PZ754701	PZ745252	MZSP 151890	Brazil, Minas Gerais, Januária
Kora ajar Simone, 2024	PZ746036	—	—	MZSP 151829 [paratype]	Brazil, Minas Gerais, Itacarambi
Kora ajar Simone, 2024	PZ746037	PZ754697	PZ745248	MZSP 151867 [paratype]	Brazil, Minas Gerais, Itacarambi
Kora ajar Simone, 2024	PZ746038	—	PZ745249	MZSP 163700 [holotype]	Brazil, Minas Gerais, Itacarambi
Kora corallina Simone, 2012	PZ746039	PZ754698	PZ745250	MZSP 167391	Brazil, Bahia, São Félix do Coribe
Kora jimenezi Simone, 2024	PZ746040	PZ754699	PZ745251	MZSP 152139 [paratype]	Brazil, Minas Gerais, Januária
Kora nigra Simone, 2015	PZ746041	PZ754700	PZ745244	MZSP 151828	Brazil, Minas Gerais, Itacarambi
Kora tupan Simone, 2024	PZ746031	PZ754702	PZ745253	MZSP 151817 [paratype]	Brazil, Minas Gerais, São João da Ponte, Gruta do Índio
Kora tupan Simone, 2024	PZ746032	—	PZ745254	MZSP 161200 [holotype]	Brazil, Minas Gerais, São João da Ponte, Gruta do Índio
Kora uhlei Simone, 2024	PZ746043	PZ754703	PZ745255	MZSP 164889 [paratype]	Brazil, Minas Gerais, Matias Cardoso
Kora uhlei Simone, 2024	PZ746033	PZ754704	PZ745256	MZSP 165720 [holotype]	Brazil, Minas Gerais, Matias Cardoso
Liguus fasciatus (Müller, 1774)	—	PZ754689	PZ745257	UF 449421	USA, Florida, Dade County
Quechua salteri (Sowerby III, 1890)	—	PZ754690	PZ745258	VMA 1700/2	Peru, Cajamarca, Sócota
Sultana labeo (Broderip, 1828)	—	PZ754691	PZ745259	VMA 1697/1	Peru, Amazonas, Molinopampa
Sultana labeo (Broderip, 1828)	PZ740695	PZ754692	PZ745260	VMA 1698/1	Peru, Amazonas, Molinopampa
Sultana liae Vega-Luz, 2021	PZ740696	PZ754693	PZ745261	VMA 1508/1 [paratype]	Peru, Amazonas, Yambrasbamba
Thaumastus foveolatus (Reeve, 1849)	—	PZ754685	—	VMA 1705/1	Peru, Junín, Canchamayo
Thaumastus magnificus (Grateloup, 1840)	PZ746044	PZ754686	PZ745262	MZSP 166216	Brazil, Minas Gerais, Parque Nacional do Itatiaia
Thaumastus nehringi (Martens, 1889)	PZ746045	PZ754684	PZ745245	MZSP 165584	Brazil, São Paulo, Atibaia, Estrada Municipal da Pedra Grande
Thaumastus robertsi Pilsbry, 1932	—	PZ754687	PZ745246	VMA 1237/1	Peru, Amazonas, Yambrasbamba
Thaumastus tiradentensis Pena, Coelho & Salgado, 1996	—	PZ754688	—	MZSP 090109b	Brazil, Minas Gerais, Mariana

(30 s), and extension at 72 °C (40 s). ITS2+28S: 40 cycles of denaturation at 95 °C (30 s), annealing at either 50 °C (ITS2 section) or 45 °C (28S section) (1 min), and extension at 72 °C (2 min). The success of the PCR step was visually assessed via agarose gel electrophoresis. Successful PCR products were then cleaned using ExoSAP-IT™ (Affymetrix Inc.) following the manufacturer's protocol. Samples were prepared for Sanger sequencing in plates and sent to Macrogen Europe (Amsterdam, The Netherlands).

The resulting sequences were visually quality-checked through Phred Quality Score of bases, and *de novo* assembled in Geneious Prime (v. 2025, Biomatters Ltd). The consensus sequences were extracted and uploaded to GenBank (Table 1).

Phylogenetic analysis

Our new sequences were then combined with those of previous studies (available from GenBank; Table 2) for the phylogenetic analysis. We included all taxa from families Amphibulimidae, Orthalicidae, and the non-monophyletic Megaspiridae that are available in the literature. For the other families (Bothriembryontidae, Tomogeridae, and the crown group Cyclodontinidae, Simpulopsidae, and Bulimulidae), we selected only a few representatives of each, including type genera of families and subfamilies (and type species as well whenever possible). One species of Strophocheilidae (*Catracca uhlei* Simone, 2022) was selected as the outgroup, following Breure & Romero (2012) and Salvador *et al.* (2023).

The sequences of each marker (COI, H3, and ITS2+28S) were aligned using the MAFFT plugin (Katoh *et al.* 2002; Katoh & Standley 2013) for Geneious Prime, using the default settings. The resulting alignments were visually proofed for inconsistencies. The ITS2 region is difficult to alignm at such a high taxonomic level, so the ITS2+28S alignment was run through Gblocks (Castresana 2000; Talavera & Castresana 2007) using the least restrictive settings, to eliminate poorly aligned and/or data-deficient positions that could add noise to the analyses. The alignments were then concatenated for analysis.

A Bayesian inference phylogenetic analysis was performed using MrBayes (v. 3.2.7, Ronquist *et al.* 2012) through the CIPRES Science Gateway (v. 3.3, Miller *et al.* 2015). Two concurrent analyses were run, each with 4 Markov chains of 70 million generations, using a generalised time reversible model, nst = 6, rates = invgamma, default priors; substitution model parameters were unlinked across the three markers (COI, H3, ITS2+28S). The first 20% of trees were discarded as "burn-in". MCMC convergence was assessed by examining the standard deviation of split frequencies (~0.002) and the potential scale reduction factor (PSRF = 1.0), as well as the trace plots (Ronquist *et al.* 2009).

Anatomical study and field observations

For the anatomical study, 10 museum specimens of *Auris bilabiata* (Broderip & Sowerby I, 1830) were dissected, belonging to specimen lot MZSP162441 (from Bahia, Alcobaça, collected in August 2017). August is the end of winter (although mean temperature is 22.8 °C) and the second driest month (both in precipitation and relative humidity) of the year in Alcobaça (Climate Data 2025). We expect the species' reproductive season to be from late October to December, that is, the spring and wettest months (Climate Data 2025), as egg laying was observed in December (TFM & FSS pers. obs.). Therefore, reported features of the reproductive tract might differ from specimens collected during other seasons.

For the conchological description, more specimens were analysed: MZSP007951 (1 shell, Minas Gerais, Teófilo Otoni, 1908); MZSP034383 (1 specimen, Minas Gerais, Bonfim, v/1993); MZSP123911 (2 shells, Bahia, iii/2009); MZSP129593 (6 shells, Espírito Santo, Anchieta); MZSP161901 (1 shell, Minas Gerais, Itaipé, v/2022); MZSP161951 (1 shell, Minas Gerais, Serra dos Aimorés, xii/2022); MZSP161982 (14 shells, Minas Gerais, Serra dos Aimorés, xii/2022); MZSP162441 (25 specimens, Bahia, Alcobaça, viii/2017); MZSP165177 (25 shells, Bahia, Alcobaça, v/2019); MZSP166706 (9 specimens, Bahia, Icaraí do Ranulfo, 2020); MZSP166707 (1 specimen, Bahia, Icaraí do Ranulfo, i/2024). A distinction is made between "specimen", which includes the whole animal, and "shell", which includes only the shell, without the soft parts.

Dissections followed standard procedures with an incision along the mantle border to expose the pallial cavity, followed by a cut along the pallial cavity, alongside the lower digestive tract, up to the top of the spire. Specimens were dissected under 70% ethanol, using a Zeiss Stemi SV 11 stereomicroscope with a camera lucida. The pallial, reproductive, digestive, circulatory, excretory, and nervous systems were isolated, examined and described. For the descriptions of the nervous system, acronyms used for nerves were defined by their insertion (letters) and position from the anterior to posterior axis (numbers) (*cf.* La Pasta 2025, 2026). No assumptions of homology were made in the identification and numbering of these nerves. Illustrations made using a camera lucida were digitised using a scanner, and later vectorised and edited using Inkscape.

Table 2. Published genetic data used in the phylogenetic analysis. GenBank accession numbers, collection locality, and original references are provided. The asterisk (*) indicates the outgroup. Abbreviations of further collections not mentioned in the Materials and Methods section: ANSP, Academy of Natural Sciences of Drexel University (Philadelphia, USA); CMRP, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto (Ribeirão Preto, Brazil); IML, Instituto Miguel Lillo (Tucumán, Argentina); FMNH, Field Museum of Natural History (Chicago, USA); NMSA, KwaZulu-Natal Museum (Pietermaritzburg, South Africa); NZAC, New Zealand Arthropod Collection, Maanaki Whenua – Landcare Research (Auckland, New Zealand); RMNH, Naturalis Biodiversity Center, formerly Rijksmuseum van Natuurlijke Historie (Leiden, The Netherlands); UFAC, Universidade Federal do Acre (Rio Branco, Brazil); WAM, Western Australia Museum (Perth, Australia).

Species	COI	H3	ITS2+28S	Provenance	Reference
**Catracca uhlei* Simone, 2022	OP361014	OP381236	OP355600	Brazil, Minas Gerais, Vargem Grande	Salvador *et al.* 2023
Amphibulima pardalina Guppy, 1868	OP361000	OP381220	OP355588	Montserrat, Saint Peter, Hope, Hope Ridge	Salvador *et al.* 2023
Amphibulima patula (Bruguière, 1792)	OP361001	OP381221	OP355589	Dominica, Pagua Bay	Salvador *et al.* 2023
Anctus laminiferus (Ancey, 1888)	OP361002	OP381222	OP355590	Brazil, Piauí, Regeneração	Salvador *et al.* 2023
Antidrymaeus inusitatus (Fulton, 1900)	JF514648	—	HM027503	Costa Rica, Limón, south of Liverpool	Breure *et al.* 2010; Breure & Romero 2012
Bostryx edmundi Breure & Neubert, 2008	JF514622	JF514666	JF514730	Peru, Lima, between Yauyos and Magdalena	Breure & Romero 2012
Bothriembryon dux (L. Pfeiffer, 1861)	JF514643	JF514686	HM027490	Australia, Western Australia, Mt. Caitlin	Breure *et al.* 2010; Breure & Romero 2012
Bulimulus guadalupensis (Bruguière, 1789)	OP361008	OP381229	OP355595	Puerto Rico	Salvador *et al.* 2023
Burringtonia labrosa (Menke, 1828)	OP361013	OP381235	OP355599	Brazil, Espírito Santo, Sooretama, Trilha do Jequitibá	Salvador *et al.* 2023
Clessinia stelzneri (Doering, 1875)	JF514617	—	JF514726	Argentina, Córdoba, Dean Funes-Tulumba	Breure & Romero 2012
Cochlorina andradae La Pasta, Klautau & Oliveira, 2026	OP361015	OP381237	OP355601	Brazil, São Paulo, Praia Grande	Salvador *et al.* 2023 [as *C. aurisleporis*]
Corona pfeifferi (Hidalgo, 1869)	JF514654	—	HM027495	Peru, Loreto, Río Curany	Breure *et al.* 2010; Breure & Romero 2012
Corona regalis (Hupé, 1857)	MW033969	MW147744	MW035049	Brazil, Acre, Senador Guiomard, Fazenda Experimental Catuába	Lima *et al.* 2021
Corona regina (Bowdich, 1822)	OP361016	OP381242	OP355604	Brazil, Rondônia, Porto Velho, margins of Rio Madeira	Salvador *et al.* 2023
Cyclodontina gemellata (Ancey, 1904)	OP361017	OP381243	OP355605	Brazil, Goiás, Terezópolis de Goiás, Fazenda Santa Barbara	Salvador *et al.* 2023
Discoleus ameghinoi (Ihering, 1908)	KT371415	JF514698	JF514753	Argentina, Río Negro, Las Grutas [provenance of COI unknown]	Herbert & Mitchell 2009; Breure & Romero 2012
Drymaeus poecilus (d'Orbigny, 1835)	OP361026	OP381255	OP355615	Brazil, Mato Grosso, Itiquira	Salvador *et al.* 2023
Gaeotis flavolineata Shuttleworth, 1854	OP361030	OP381261	OP355621	Puerto Rico, Río Grande, Bosque Nacional del Caribe (El Verde)	Salvador *et al.* 2023
Gaeotis nigrolineata Shuttleworth, 1854	JF514659	JF514695	HM027509	Puerto Rico, El Yunque	Breure *et al.* 2010; Breure & Romero 2012
Hyperaulax rildeyi (E.A. Smith, 1890)	MN175954†	OP381262	OP355622	Brazil, Fernando de Noronha, Mirante	Salvador *et al.* 2023

Table 2. Continued.

Species	COI	H3	ITS2+28S	Provenance	Reference
Kara thompsonii (L. Pfeiffer, 1845)	JF514608	JF514713	HM027508	Ecuador, Azuay, San Francisco	Breure *et al.* 2010; Breure & Romero 2012
Kora rupestris Salvador & Simone, 2016	OP361031	OP381263	OP355623	Brazil, Minas Gerais, Parque Nacional Cavernas do Peruaçu, Lapa dos Brancos	Salvador *et al.* 2023
Leiostracus perlucidus (Spix, 1827)	JF514640	JF514716	JF514744	Brazil, São Paulo	Breure & Romero 2012
Liguus virgineus (Linnaeus, 1758)	—	OP381269	OP355630	Dominican Republic, Santiago, Yaque del Norte River, la Angostura, las Charcas	Salvador *et al.* 2023
Maoristylus hongii (Lesson, 1830)	MT163273	MT559984	MN567954	New Zealand, Far North District	Quenu *et al.* 2021
Megaspira elatior (Spix, 1827)	JF514610	JF514715	JF514721	Brazil, Rio de Janeiro, Serra de Macaé	Breure & Romero 2012
Megaspira robusta Pilsbry, 1904	OP361036	OP381270	OP355631	Brazil, Rio de Janeiro, Serra de Macaé	Salvador *et al.* 2023
Orthalicus floridensis Pilsbry, 1891	OP361039	—	OP355635	USA, Florida, Homestead	Salvador *et al.* 2023
Orthalicus ponderosus (Strebel & Pfeffer, 1882)	JF514655	—	HM027506	Mexico, Jalisco, Punta Perula	Breure *et al.* 2010; Breure & Romero 2012
Orthalicus pulchellus (Spix, 1827)	OP361040	—	OP355636	Brazil, São Paulo, Jardinópolis, Rio Pardo	Salvador *et al.* 2023
Orthalicus pulchellus (Spix, 1827)	—	OP381274	OP355637	Brazil, São Paulo, Ribeirão Preto, Campus USP-FFCLRP	Salvador *et al.* 2023
Orthalicus reses (Say, 1830)	OP361041	—	OP355638	USA, Florida, Miami	Salvador *et al.* 2023
Paeniscutalus crenellus (Philippi, 1867)	JF514609	JF514714	JF514720	Peru, Ancash, Macará	Breure & Romero 2012
Pellicula appendiculata L. Pfeiffer, 1848	—	OP381277	OP355641	Montserrat, Saint Peter, Hope, Hope Ridge	Salvador *et al.* 2023
Pellicula depressa (Rang, 1853)	—	OP381278	OP355642	Montserrat, Saint Georges, Jack Boy Hill, New Windward Estate	Salvador *et al.* 2023
Placostylus fibratus (Martyn, 1784)	MT163270	MT559980	MN567952	New Caledonia, Isle of Pines	Quenu *et al.* 2021
Plagiodontes multiplicatus (Doering, 1875)	JF514620	JF514664	HM027496	Argentina, Córdoba, Sierra de Cuniputo	Breure *et al.* 2010; Breure & Romero 2012
Plectostylus broderipii (G.B. Sowerby I, 1832)	OP361044	OP381280	OP355644	Chile, Los Ríos, Valdivia, Mehuin	Salvador *et al.* 2023
Plekocheilus breweri Breure & Schlögl, 2010	JF514657	JF514693	JF514751	Venezuela, Bolívar, Churi-tepui	Breure & Romero 2012
Plekocheilus lacerta (L. Pfeiffer, 1855)	OP361045	OP381259	OP355619	Brazil, Pará, Belém	Salvador *et al.* 2023
Plekocheilus nebulosus Breure, 2009	OP361046	OP381282	OP355646	Brazil, Amazonas, São Gabriel da Cachoeira, Pico da Neblina	Salvador *et al.* 2023
Plekocheilus vlceki Breure & Schlögl, 2010	JF514658	JF514694	HM027491	Venezuela, Bolívar, Churi-tepui	Breure *et al.* 2010; Breure & Romero 2012
Porphyrobaphe iostoma (G.B. Sowerby I, 1820)	JF514656	—	HM027500	Ecuador, Manabi, Puerto Lopez	Breure *et al.* 2010; Breure & Romero 2012

Table 2. Continued.

Species	COI	H3	ITS2+28S	Provenance	Reference
Prestonella bowkeri (G.B. Sowerby III, 1890)	KF129392	JF514711	EU622021	South Africa, Glen Avon	Herbert & Mitchell 2009; Breure & Romero 2012
Protoglyptus luciae (Pilsbry, 1897)	JF514651	JF514712	JF514748	St. Lucia, Union Quarter	Breure & Romero 2012
Rhinus botocudus Simone & Salvador, 2016	OP361050	OP381287	OP355650	Brazil, Minas Gerais, Nanuque	Salvador *et al.* 2023
Simpulopsis decussata L. Pfeiffer, 1856	JF514639	JF514683	JF514743	Brazil, São Paulo, Santos	Breure & Romero 2012
Sultana sultana (Dillwyn, 1817)	OP361056	—	OP355656	Brazil, Pará, Altamira, Usina Hidrelétrica de Belo Monte	Salvador *et al.* 2023
Thaumastus largillierti (Philippi, 1845)	JF514611	JF514660	JF514722	Brazil, Minas Gerais, Mariana	Breure & Romero 2012
Thaumastus taunaisii (Férussac, 1822)	—	JF514699	JF514754	Brazil, Espírito Santo, Guarapari	Breure & Romero 2012 [as *T. achilles*]
Tomigerus corrugatus Ihering, 1905	MN175956†	OP381294	OP355658	Brazil	Salvador *et al.* 2023

Buccal masses were dissected; radulae and jaws were manually extracted without digestion and rinsed in distilled water. Pieces of the shell were extracted from the body whorl and visualised axially to investigate shell ultrastructure. Scanning electron micrographs (SEM) of shell sections, radulae, and jaws were performed using a JEOL-JSM-6390-LV at the Rudolf Barth Electron Microscopy Platform (Oswaldo Cruz Institute, Rio de Janeiro, Brazil). The material was sputter coated with gold before imaging with SEM.

Field observations of *Auris bilabiata* were conducted by TFM in Icaraí do Ranulfo, Nova Canaã, Bahia state, Brazil, during August and December of 2022, as part of a separate project (Macabeu 2023). We provide preliminary data here, but a full report on the species' natural history is in preparation (Macabeu *et al.* in prep.).

Results and Discussion

The phylogenetic tree was built with a total of 76 terminals plus the outgroup, and used concatenated sequences of 1818 bp (COI 670 bp, H3 267 bp, ITS2+28S 881 bp). The resulting tree showed good resolution, except for a single polytomy involving three families. The tree is depicted here in three parts to facilitate viewing and discussion, with branches collapsed accordingly in each figure (Figs 1–3). Also, to facilitate discussion, the main Clades (i.e. family-level taxa) are numbered 1–12.

Despite low support for some larger group arrangements, each family-level taxon has very strong support (PP = 1, except for Orthalicidae [PP = 0.99], and Bulimulidae [PP = 0.90]), and each lineage is distinctly separate from one another. This is similar to what is observed in other gastropod superfamilies with multiple family-level lineages with deep divergence (e.g. Wilke *et al.* 2013; Takano & Kano, 2014). We have all "Megaspiridae" genera represented in our tree (except the elusive *Callionepion* Pilsbry & Vanatta, 1899; see Salvador 2019a) and our results show that, instead of being the three sequential branches recovered by Salvador *et al.* (2023), "Megaspiridae" is actually five completely separate branches (Figs 1–3: Clades 3, 4, 5, 8, and 9). It is untenable to keep all these disparate branches under a polyphyletic family "Megaspiridae" and, thus, new family-level names are required, in line with the results of the phylogenetic analysis.

Below, we discuss the family-level clades in order. The discussion is followed by a Systematics section containing nomenclatural acts and other taxonomic information, including the anatomical description of *Auris bilabiata*.

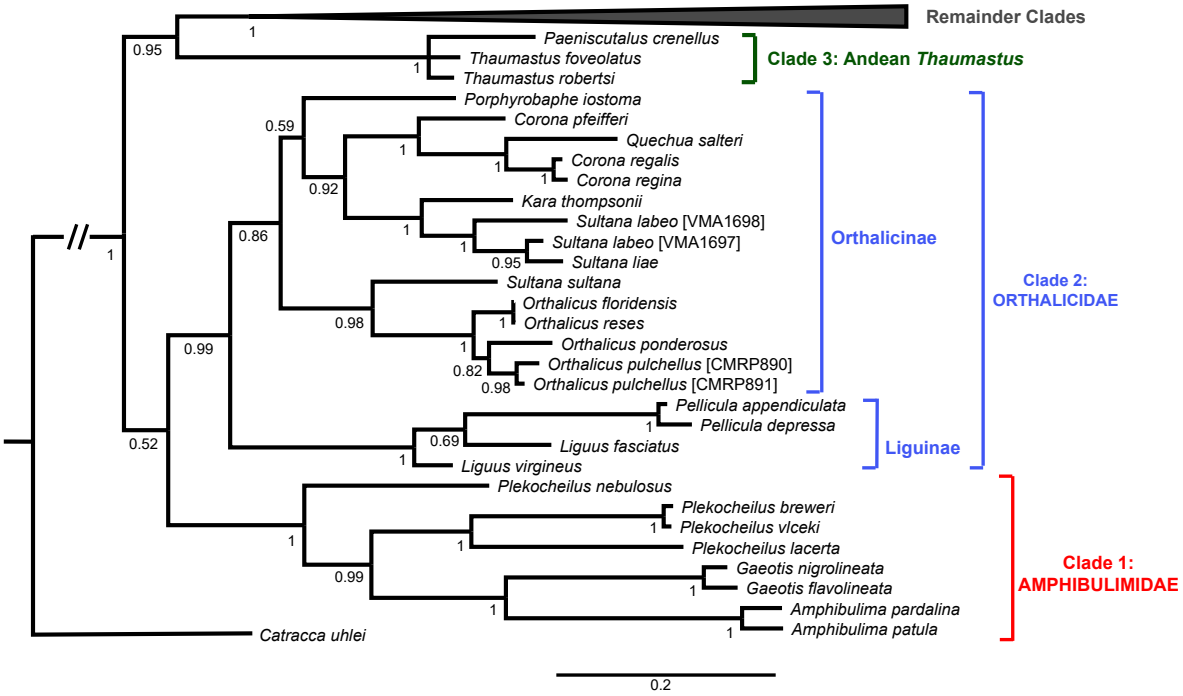

Figure 1. Bayesian inference phylogenetic tree (50% majority-rule consensus) based on the concatenated markers (COI, H3, ITS2+28S). The family-level clades are shown in different colours and the more derived clades are collapsed (see Figs 2, 3). Posterior probabilities are shown on nodes. Scale bar represents substitutions per site. See Tables 1 and 2 for more specific information on each species/specimen.

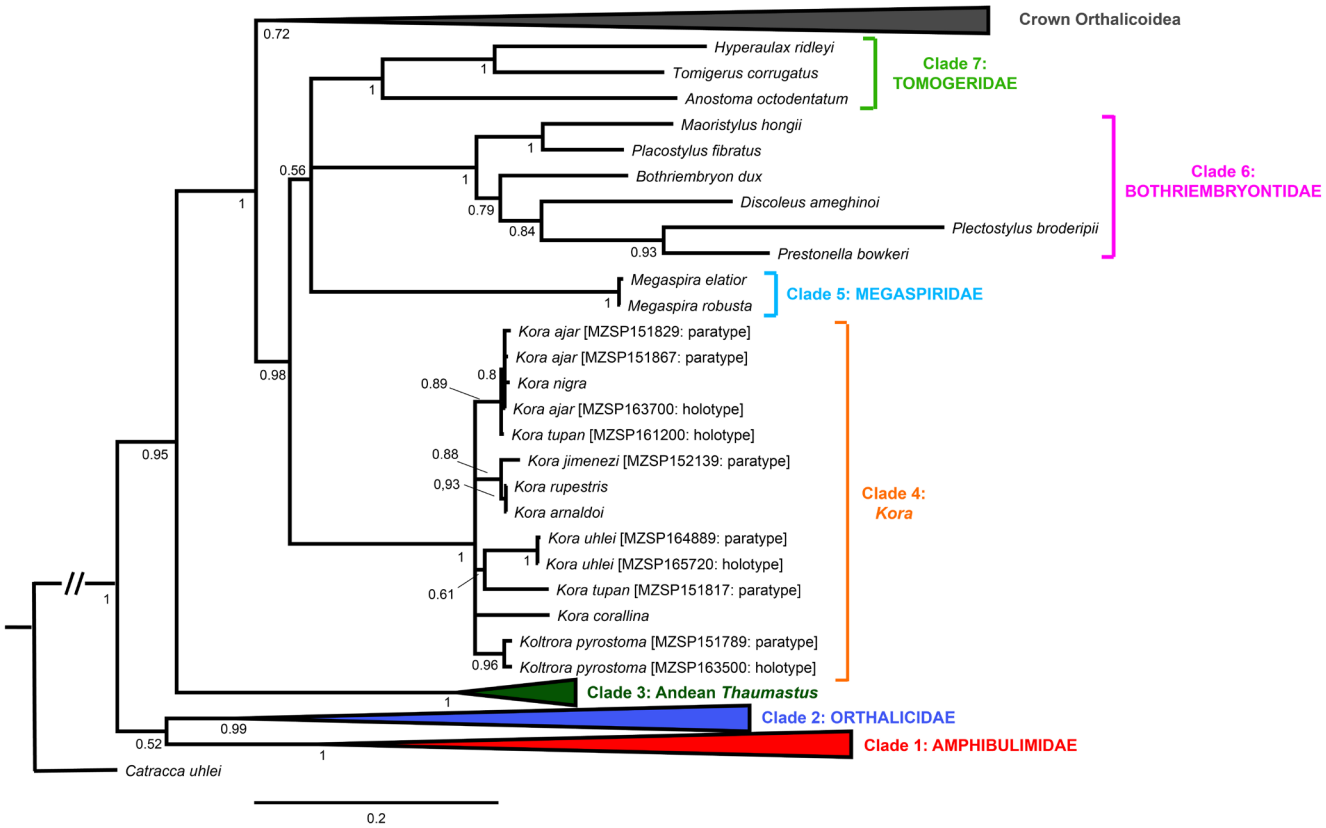

Figure 2. Phylogenetic tree showing the clades that were presented collapsed in Fig. 1. Other clades (from Fig. 1 as well as the Crown Orthalicoidea) are shown collapsed. Posterior probabilities are shown on nodes. Scale bar represents substitutions per site.

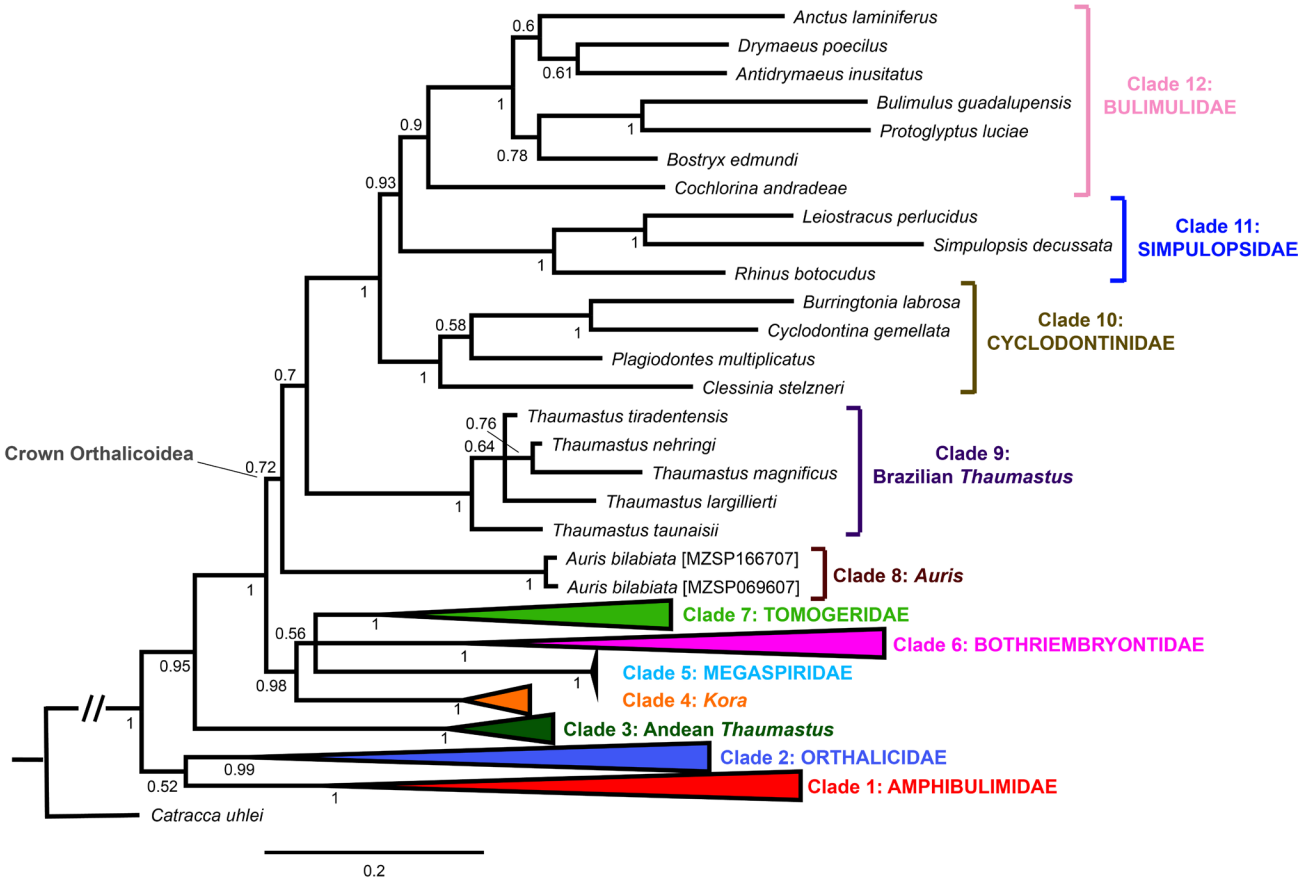

Figure 3. Phylogenetic tree showing the crown Orthalicoidea from Fig. 2. Other clades (from Figs 1 and 2) are shown collapsed. Posterior probabilities are shown on nodes. Scale bar represents substitutions per site.

Clades 1 and 2: Amphibulimidae and Orthalicidae

Clades 1 and 2 together are the sister taxon to all other Orthalicoidea (Fig. 1). They represent, respectively, families Amphibulimidae and Orthalicidae. Each family is well supported on its own (PP= 1 and 0.99, respectively), but their relationship as sister taxa remains contentious (PP= 0.52), similar to the findings of Salvador *et al.* (2023).

In Amphibulimidae, there are no further updates from the study of Salvador *et al.* (2023), as we did not succeed in DNA extraction for additional representatives of this clade. All the subclades inside this family are strongly supported (PP = 0.99 or 1) (Fig. 1) and *Plekocheilus* is paraphyletic, as already known, and needs further revision.

The phylogenetic tree of Salvador *et al.* (2023) showed a large polytomy inside Orthalicidae. Our expanded sampling resulted in a much better resolution within this family (Fig. 1), which allows for some taxonomic changes. Firstly, Orthalicidae is split into two clades: one with strong support (PP = 1) and one with lower support (PP = 0.86). Given their seemingly old split and distance from one another, they are potentially meaningful at the subfamily level (similar to Bothriembryontidae and Bulimulidae, which are the two other orthalicoid families to contain subfamilies; see Salvador *et al.* 2023). The first clade includes colourful snails of the genus *Liguus* Montfort, 1810 (type species *L. virgineus* (Linnaeus, 1758)) and translucent semi-slugs of the genus *Pellicula* Fischer, 1856 (type species *P. depressa* (Rang, 1835)). There is already a name available in the literature for this clade: Liguidae Pilsbry, 1891, which is here reestablished as a subfamily, Liguinae Pilsbry, 1891. The second clade, naturally, represents the Orthalicinae.

It is worthwhile to note that *Liguus* is paraphyletic (Fig. 1) and will need further study. Notably, *Liguus* is paraphyletic pending the inclusion of *Pellicula* semi-slugs; this situation is very similar to what was seen between the Bulimulidae genera *Drymaeus* Albers, 1850 and *Peltella* Gray, 1855 (Breure & Romero, 2012; Salvador *et al.* 2023). This seems to be a case of convergence of colourful tree snails giving rise to semi-slugs in distinct families and places (Liguinae in the Caribbean and Peltellinae in Brazil) and warrants further study.

Within the Orthalicinae, we observe a split (Fig. 1) with a clade (PP = 0.98) formed by *Orthalicus* Beck, 1837 and *Sultana* Shuttleworth, 1856 as sister to a clade (PP = 0.59) formed by the remaining terminals. Given the lack of support for the last clade, this relationship is still open to debate. In any event, some conclusions can be extracted from it. Firstly, *Quechua salteri* (Sowerby III, 1890), the type species of *Quechua* Strebel, 1910, is nested within genus *Corona* Albers, 1850 (type species *C. regina* (Bowdich, 1822)) (PP = 1; Fig. 1); thus, *Quechua* can be considered a junior synonym of *Corona*. The close similarity of shell morphology of both genera (e.g. Breure & Ablett, 2015) is in line with this finding. The four species of *Quechua* must then be reclassified as: *Corona olmosensis* (Zilch, 1954) **comb. nov.**; *Corona salteri* (Sowerby III, 1890) **comb. nov.**; *Corona taulisensis* (Zilch, 1953) **comb. nov.**; *Corona tetrica* (Haas, 1951) **comb. nov.** Secondly, *Sultana labeo* and *Sultana liae* are far removed from the type species of the genus, *S. sultana* (Dillwyn, 1817) (which is the sister taxon to *Orthalicus*; Fig. 1). They form a strongly supported clade (PP = 1) with *Kara thompsonii* (Pfeiffer, 1845), the type species of the genus *Kara* Strebel, 1910 (Fig. 1). Thus, these two species are transferred to the genus *Kara*, resulting in the new combinations *Kara labeo* (Broderip, 1828) **comb. nov.** and *Kara liae* (Vega-Luz, 2021) **comb. nov.** We also note that *Kara labeo* comb. nov. is rendered paraphyletic by *Kara liae* comb. nov., with distant branches (Fig. 1), and this matter will require further investigation in the future.

Clade 3: Andean *Thaumastus* and *Paeniscutalus*

Within the large clade formed by all orthalicoideans except Amphibulimidae and Orthalicidae (PP = 0.95), the first lineage to branch off is Clade 3 (Fig. 1). Clade 3 is strongly supported (PP = 1) and very distant from its sister group (PP = 1) containing the remaining Orthalicoidea lineages and the bulk of the superfamily's biodiversity.

Clade 3 contains specimens of Andean *Thaumastus* spp. from Peru, as well as the monotypic *Paeniscutalus* Wurtz, 1947. Even though we could not procure a sample of the type species of *Thaumastus* Martens, 1860 (*T. hartwegi* (Pfeiffer, 1846), from Ecuador) for our analysis, we hypothesise it would be placed here, as the other *Thaumastus* spp., from southeast and southern Brazil, form a clearly distinct and unrelated group (Clade 9; Fig. 3). Considering its position in the tree and distance to other lineages, Clade 3 is a family-level branch. We describe the new family in the Systematics section below.

Clade 3 is sister to a strongly supported clade (PP = 1) containing two main branches: the first branch is strongly supported (PP = 0.98), formed by Clades 4–7. The second branch includes the Crown Orthalicoidea, but has low support (PP = 0.72), and contains Clades 8–12.

Clade 4: *Kora* and *Koltrora*

The genera *Kora* Simone, 2012, and *Koltrora* Simone, 2024 together form a distinct strongly supported (PP = 1) lineage from the remaining orthalicoidean branches. It is the sister taxon (PP = 0.98) to a polytomous clade (PP = 0.56) including three families: Tomogeridae (PP = 1), Bothriembryontidae (PP = 1), and the actual Megaspiridae (PP = 1). The lack of support (PP = 0.56) for this polytomous clade leaves the possibility of a different arrangement of this entire clade open. Considering its relationship to other lineages, it is clear that the *Kora+Koltrora* branch is a family-level taxon and is described as a new family in the Systematics section below.

The internal arrangement of Clade 4 consists of a large polytomy (Fig. 2), with each branch generally representing a single species (see synonymisations below). This includes *Kora* spp. and the monotypic genus *Koltrora*. We believe this is due to our choice of markers, as both H3 and 28S are better suited for resolving deeper taxonomic relationships and COI and ITS2 were not enough to solve such closely related taxa. The addition of further variable markers such as 16S and ITS1 should be helpful, though disentangling the detailed relationship of each species inside this clade is beyond the scope of this study. In any event, the present data strongly support that the monotypic *Koltrora* is synonymous with *Kora*, which is supported by the extensive similarities in shell and anatomical features (Simone 2024). This results in the new classification of the former's single species as *Kora pyrostoma* (Simone, 2024) **comb. nov.**

By the phylogenetic tree (Fig. 2) and genetic similarity (Table 3), it can also be seen that four *Kora* spp. described in 2024 (*Kora arnaldoi* Pena, 2024, *Kora jimenezi* Simone, 2024, *Kora ajar* Simone, 2024, and *Kora tupan* Simone, 2024) are conspecific with earlier taxa and must be synonymised.

Kora ajar and *K. tupan* are synonyms of *Kora nigra* Simone, 2015. There are minimal genetic differences between them, *c.* 1.5% or less in the COI marker (Table 3), much less than the usual 4% cut-off. Furthermore, the morpho-anatomical differences given by Simone (2024) are all from very plastic characters, which are known to widely vary intraspecifically. These include basic conchological features (e.g. shell height/width, degree of opening of the umbilicus) (e.g. Salvador *et al.* 2018, 2026; Proćków *et al.* 2022), as well as confounding and unreliable anatomical

Table 3. COI sequence identity (%) between species of *Kora*, for the 618 bp for which information was available for all species, with values rounded to the first decimal place. The asterisk (*) indicates the type species. Unfortunately, we could not obtain COI data for *Koltrora pyrostoma*.

***Kora* spp.**	***K. arnaldoi***	***K. ajar* [holotype]**	***K. ajar* [paratype]**	***K. ajar* [paratype]**	***K. corallina****	***K. jimenezi* [paratype]**	***K. nigra***	***K. rupestris***	***K. tupan* [holotype]**	**K. tupan [paratype]**	***K. uhlei* [holotype]**	***K. uhlei* [paratype]**
K. arnaldoi	—	92.6	92.6	92.7	89.3	96.9	92.2	100	92.9	91.3	91.4	91.3
K. ajar [holotype]	92.6	—	99.0	99.8	89.8	90.8	99.7	92.6	99.0	89.8	91.9	91.7
K. ajar [paratype]	92.6	99.0	—	98.9	89.8	90.8	98.7	92.5	98.4	90.0	91.6	91.4
K. ajar [paratype]	92.7	99.8	98.9	—	90.0	90.9	99.5	92.7	99.2	90.0	92.1	91.9
*K. corallina**	89.3	89.8	89.8	90.0	—	88.2	89.5	89.3	90.4	87.2	87.7	87.9
K. jimenezi [paratype]	96.9	90.8	90.8	90.9	88.2	—	90.4	96.9	91.1	90.5	90.1	90.0
K. nigra	92.2	99.7	98.7	99.5	89.5	90.4	—	92.2	98.7	89.8	91.9	91.7
K. rupestris	100	92.6	92.5	92.7	89.3	96.9	92.2	—	92.9	91.3	91.4	91.3
K. tupan [holotype]	92.9	99.0	98.4	99.2	90.4	91.1	98.7	92.9	—	90.3	91.6	91.4
K. tupan [paratype]	91.3	89.8	90.0	90.0	87.2	90.5	89.8	91.3	90.3	—	90.3	90.1
K. uhlei [holotype]	91.4	91.9	91.6	92.1	87.7	90.1	91.9	91.4	91.6	90.3	—	99.8
K. uhlei [paratype]	91.3	91.7	91.4	91.9	87.9	90.0	91.7	91.3	91.4	90.1	99.8	—

minutiae: minor differences in positioning (e.g. "in the middle third") of muscle attachments and gland apertures, and features of reproductive tract that may not only vary intraspecifically within populations and across habitats, but also seasonally in the same individual (e.g. "small curve at the end of the hermaphrodite duct", penis length) (e.g. Emberton 1985; Doums *et al.* 1998; Baur & Baur 2016; den Duijn *et al.* 2025). Simone (2024) had already noted the major similarities across these three taxa in shell and aperture shape, as well as in anatomical characters known to be of greater significance in taxonomy, such as jaw (considered particularly important in Orthalicoidea taxonomy; Breure 1979) and reproductive tract (e.g. inner longitudinal fold in the epiphallus). These three taxa also form a monophyletic clade in the morphological tree of Simone (2024). Furthermore, the distributions of *K. nigra* and *K. ajar* overlap, and if *K. tupan* is added, the entire area covers around only a narrow strip (*c.* 200 km long) of largely the same type of transitional biome (Simone 2024). Considering all the above, it is safe to conclude that *K. ajar* and *K. tupan* are junior synonyms of *K. nigra*.

Pena (2024) described *Kora arnaldoi* from a locality in the vicinity of previous records of *Kora rupestris* Salvador & Simone, 2016 (Salvador & Simone 2021). That author provided a thorough comparison with specimens that she assigned to *K. rupestris*, but which in fact belonged to *K. nigra*, also known from the area (Salvador & Simone 2021). Thus, in effect, *K. arnaldoi* was a redescription of *K. rupestris* by another name. While this is visible from the shells (Salvador & Simone 2016, 2021; Pena 2024), the 100% genetic similarity between them leaves little doubt that these two taxa are synonymous (Table 3). *Kora jimenezi* is more genetically distinct from both, but still within the known cut-off for intraspecific variation in the COI barcoding marker (*c.* 3%; Table 3). The shell is the same in size and shape (although some specimens of *K. jimenezi*, including the holotype, are wider; Simone 2024); the situation with anatomical differences is similar to what was described above for *K. nigra* and its synonyms, and this taxon occurs in sympatry with the other two taxa (Salvador & Simone 2016, 2021; Pena 2024; Simone 2024). Considering all the above, we conclude that *K. arnaldoi* and *K. jimenezi* are junior synonyms of *K. rupestris*.

The paratype of *K. tupan*, however, was recovered separately from the holotype and seems to be a separate branch of *Kora* (Fig. 2). It was recovered as the sister group to *Kora uhlei* Simone, 2024 and conchologically, this paratype of *K. tupan* (see Simone 2024: fig. 16H–J) is indeed more similar to *K. uhlei*. It could perhaps represent a new species. Its COI sequence has some differences (Table 3), including a 12-bp insertion (the insertion does not influence the phylogenetic analysis), which is unique to it in the whole

genus. We are not sure if this is taxonomically significant or if it might represent other circumstances at play with this specimen (e.g. being a hybrid). So, for now, we just refer to it as *Kora* aff. *uhlei*.

Clade 5: Megaspiridae *sensu stricto*

Clades 5, 6, and 7 form a polytomous clade (PP = 0.56), although each family within it is strongly supported (PP = 1) (Fig. 2). One of these families is Megaspiridae, though in a much more restricted sense. As all other putative Megaspiridae (*sensu* Salvador *et al.* 2023) have been "scattered" through the tree (Clades 3, 4, 8, and 9), the actual family Megaspiridae is here restricted to *Megaspira* Lea, 1836. To which we also include the morphologically similar *Callionepion* Pilsbry & Vanatta, 1899, of which only historical shells are known (see Salvador 2019a).

Clades 6 and 7: Bothriembryontidae and Tomogeridae

Both Tomogeridae and Bothriembryontidae are strongly supported (PP = 1). These families were not the focus of this study, and only select taxa were included (favouring type genera and type species when possible) to give structure to the tree and to help unveil the relationships of the taxa of interest. Still, there is one notable result involving these clades that warrants further discussion.

In the phylogenetic tree of Salvador *et al.* (2023), these were sequentially branching clades, with Tomogeridae branching out before Bothriembryontidae, with well-supported nodes all over. However, here they appear in a polytomy with Megaspiridae (Fig. 2), which together with Clade 4 (*Kora*), is sister to crown Orthalicoidea (Clades 8–12). A close relationship between Tomogeridae and Bothriembryontidae should be investigated further in future studies, including from a morphoanatomical perspective.

Clade 8: *Auris*

Auris Spix, 1827 has typically been classified in the Bulimulidae even though, within the Orthalicoidea, members of this genus have possibly the most unique combination of shell morphology (meringue-shaped) and head–foot morphology (with a long spear-like "tail"). We could not obtain specimens of *Auris* for our previous study (Salvador *et al.* 2023) and hypothesised it would be more closely related to the Bothriembryontidae and Tomogeridae rather than the Bulimulidae. Our results (Fig. 3) showed that neither is exactly the case: *Auris* forms its own distinct family-level lineage (PP = 1), separate from everything else, and positioned within crown Orthalicoidea as the sister (but with low support, PP = 0.72) to a clade containing Clades 9–12 (i.e. Brazilian "*Thaumastus*", Cyclodontinidae, Simpulopsidae, and Bulimulidae). This relationship with the crown Orthalicoidea, but not strictly close to Bulimulidae per se, is also observed in the anatomical features of members of the genus (see Systematics section below).

Clade 9: Brazilian "*Thaumastus*"

The Brazilian "*Thaumastus*" form an entirely distinct branch (PP = 1) in crown Orthalicoidea, sister to (albeit with negligible support; PP = 0.7) a large group formed by Clades 10–12 (Fig. 3) and widely separated from the Andean *Thaumastus* (Clade 3; the type species *T. hartwegi* is not present in our phylogeny, but hypothesised to be in this clade, as explained above). Therefore, the Brazilian "*Thaumastus*" must be reallocated to another genus. Luckily, there is already one name available in the literature, *Orphaicus* Schaufuss, 1869. Its type species is *Helix taunaisii* Férussac, 1822, which is present in our tree and belongs to Clade 9 (Fig. 3; Table 2). Reclassifying the Brazilian "*Thaumastus*" in *Orphaicus* results in multiple new combinations and a new family must be erected to house it (see Systematics section below).

Considering that both Clades 8 and 9 are endemic to Brazil, one biogeographic implication is that the crown Orthalicoidea clade has its origins in Brazil and eventually expanded elsewhere: Cyclodontinidae mostly to the southern cone of South America, Simpulopsidae to the north, and Bulimulidae pretty much everywhere: to Central and North America, the Caribbean, and the Galapagos Islands, and with a high present-day diversity in the Andes.

Clades 10–12: Cyclodontinidae, Simpulopsidae, and Bulimulidae

Like Clades 6 and 7 above, these families were not the focus of this study and only a representative sampling (favouring type genera and type species when possible) was included. Still, an interesting result can be observed. In Salvador *et al.* (2023), Cyclodontinidae was the sister taxon of Bulimulidae, and Simpulopsidae was sister to both. Here, the positions are inverted (Fig. 3): Cyclodontinidae is sister to a clade (with moderate to low support, PP = 0.93) formed by Simpulopsidae and Bulimulidae. This arrangement would be intuitively more in line with knowledge of morphoanatomical similarities between Simpulopsidae and basal Bulimulidae (e.g. protoconch sculpture). However, our taxon sampling of these families was restricted here by design (extracted from the more ample sampling of Salvador *et al.* 2023, who recovered well-supported clades), so we cannot take these results at face value. Still, this is an interesting result, and this issue merits further investigation.

Systematics

Below, we provide the description of new taxa, as well as some additional revisions, updates and remarks on other known taxa. Only the former "Megaspiridae" branches are treated in this section.

Superfamily Orthalicoidea

Family Auriidae Salvador, La Pasta, Silva & Breure fam. nov.

ZooBank identifier. urn:lsid:zoobank.org:act:351AC287-9130-47DA-9143-BDF3F76D93AE

Type and only genus. *Auris* Spix, 1827.

Diagnosis. Broadly oval-bulimoid shell; suture well marked and well impressed; teleoconch sculptured by well-spaced sinuous axial ribs at least on second and third whorls, with a wave-like appearance; protoconch smooth; peristome strongly thickened, expanded, and reflected.

Head-foot very elongated; tail-end progressively narrows towards the tip, becoming spear-shaped; lateral margins of the foot can extend in very thin "flaps". Jaw smooth with completely indistinguishable fused plates. Ovotestis with one or two small lobes; talon slightly spiralised; unlobed uterus; very short epiphallus; flagellum longer than penis; bursa copulatrix as wide as bursa duct.

Discussion. According to our results (Fig. 3), *Auris* forms a lineage of its own, apart from all other branches of Orthalicoidea. When considering the phylogenetic tree topology alongside the unique morphology of both shell and soft parts of *Auris*, the description of a separate family to allocate this genus becomes necessary. Members of *Auris* and Auriidae fam. nov. can be immediately recognized from other Orthalicoidea by their bulky meringue-shaped shell (Fig. 4) and their very elongated head-foot, which progressively narrows towards the tip, forming a spear-shaped "tail" (Fig. 5A–C).

Genus *Auris* Spix, 1827

Auris Spix *in* Spix & Wagner 1827: 13.

Bulimus (*Pachyotus*) Beck 1837: 56. [Non *Pachyotus* Gray, 1831, Chiroptera].

Type species. *Bulimus melastomus* Swainson, 1820.

Common name. English: meringue snail. Portuguese: caracol-suspiro.

Included species. According to Salvador *et al.* (2024): *A. bernardii* (Pfeiffer, 1856); *A. bilabiata* (Broderip & Sowerby I, 1830); *A. brachyplax* Pilsbry, 1896; *A. chrysostoma* (Moricand, 1836); *A. egregia* (Jay, 1836); *A. illheocola* (Moricand, 1836); *A. inornata* Simone & Amaral, 2021; *A. melastoma* (Swainson, 1820); *A. nigrilabris* Pilsbry, 1896.

Distribution. Brazil: Sergipe, Bahia, Minas Gerais, Espírito Santo, and Rio de Janeiro states.

Biome. Atlantic Forest, although there are also populations in areas of transition between the Atlantic Forest and both the Caatinga and Cerrado biomes.

Discussion. There is a good amount of confusion in the usage of names among the "oldest" species of *Auris*, as well as potential synonymy among its "newer" species (late-19th century onwards). While revising the entire genus is beyond the scope of this study, we provide a full anatomical description of the most commonly found species, *A. bilabiata* (the one sequenced for this study).

Auris bilabiata (Broderip & Sowerby I, 1830)

Figures 4–9

Bulinus bilabiatus Broderip & Sowerby I 1830: 49, pl. 40, figs 1, 2 [type locality: "Brasiliâ"].

Helix maximiliana "A. Férussac" Moricand 1836: 431.

Helix maximiliana var. *melanostoma* Moricand 1836: 431 [type locality: "Ilheos"]. **Not** *Auris melanostoma* [sic] (Swainson, 1820), misspelling of *Auris melastoma* (Swainson, 1820) by authors. **Not** *Auris melanostoma* (Wagner, 1827), synonym of *Auris melastoma* (Swainson, 1820).

Helix maximiliana var. *minor* Moricand 1836: 431 [type locality: "Ilheos"].

Type locality. Brazil (Broderip & Sowerby I 1830).

Type material. Unknown.

Description. Shell (Fig. 4): large (height *c.* 40–45 mm; width *c.* 25–30 mm), with *c.* 5½ whorls, dextral, broadly oval-bulimoid; body whorl *c.* ¾ of shell height; apex blunt; spire angle *c.* 50–60°. Colour white to pink; orange around parietal callus. Periostracum thin. Suture well marked, well impressed, almost perpendicular to columellar axis. Protoconch white, *c.* 1½ whorls, smooth (Fig. 4m). Teleoconch sculptured by strong axial lirae (very strongly marked near suture) and well-spaced, sinuous opisthocline axial ribs. Aperture ovate, *c.* ½ of shell height and ⅔ of shell width; parietal callus present; columellar fold present. Peristome white, expanded, reflected, with a secondary ridge running through its length (hence "*bilabiata*"). Umbilicus rimate. Shell ultrastructure composed of an external periostracum less than 5 μm thick followed by four calcified layers (Fig. 4n): the first, and outermost layer, is amorphous, *c.* 30 μm thick; both second and third layers crossed-lamellar, each *c.* 60 μm thick; fourth and innermost layer amorphous, *c.* 5 μm thick.

Figure 4. *Auris bilabiata*, shell, MZSP162441. **A–D**, Specimen with pinkish shell, in apertural, dorsal, umbilical, and apical views, respectively. **E–H**, Specimen with broader shell, in apertural, dorsal, umbilical, and apical views, respectively. **I–L**, Specimen with whitish shell, in apertural, dorsal, umbilical, and apical views, respectively. **M**, SEM micrograph of the protoconch microsculpture (image cropped from micrograph of whole shell). **N**, SEM micrograph showing ultrastructure of the layers of a shell fragment in cross-section.

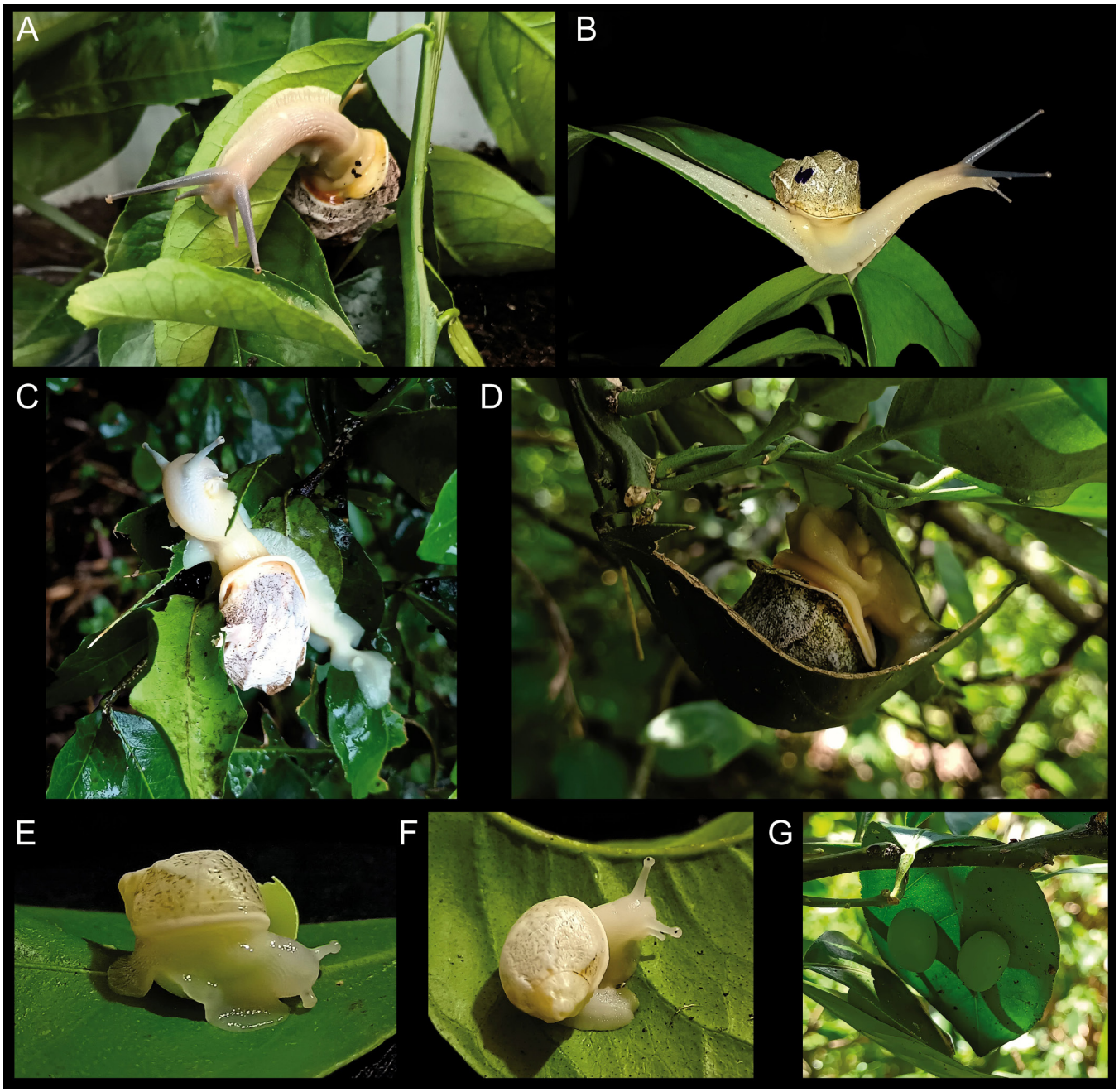

Figure 5. *Auris bilabiata*, live specimens. **A**, specimen (photographed in a terrarium in the lab) illustrating the extended head-foot. **B**, specimen with fully extended head-foot (shell is marked with a number 5). **C**, specimen moving along small tree branches and climbing over leaves, showing the extended spear-shaped tail and the "flaps" along the foot margin. **D**, specimen hiding inside folded leaves. **E**, hatchling freshly out of the eggshell (visible in the background). **F**, hatchling being the cutest little thing. **G**, a pair of green eggs affixed to the underside of a leaf.

Head-foot (Fig. 5A–C): whitish beige or yellowish beige, slightly darker (sometimes pinkish) on head and dorsal area ("back"), and lighter (sometimes near-white) on margins of foot. Tentacle stalks (of both tentacle pairs) grey, darker towards tip; tentacle tips of same base colour as head-foot. Eyespot black. Head-foot and tentacles completely white in young juveniles (Fig. 5E, F). Head-foot very elongated (can extend to approximately three times shell length, up to *c.* 12–14 cm in adults; Fig. 5B); tail-end progressively narrows towards tip, becoming spear-shaped (Fig. 5C); lateral margins of foot can extend in very thin "flaps" (Fig. 5C). Head-foot of rugose appearance; striae can be seen along foot

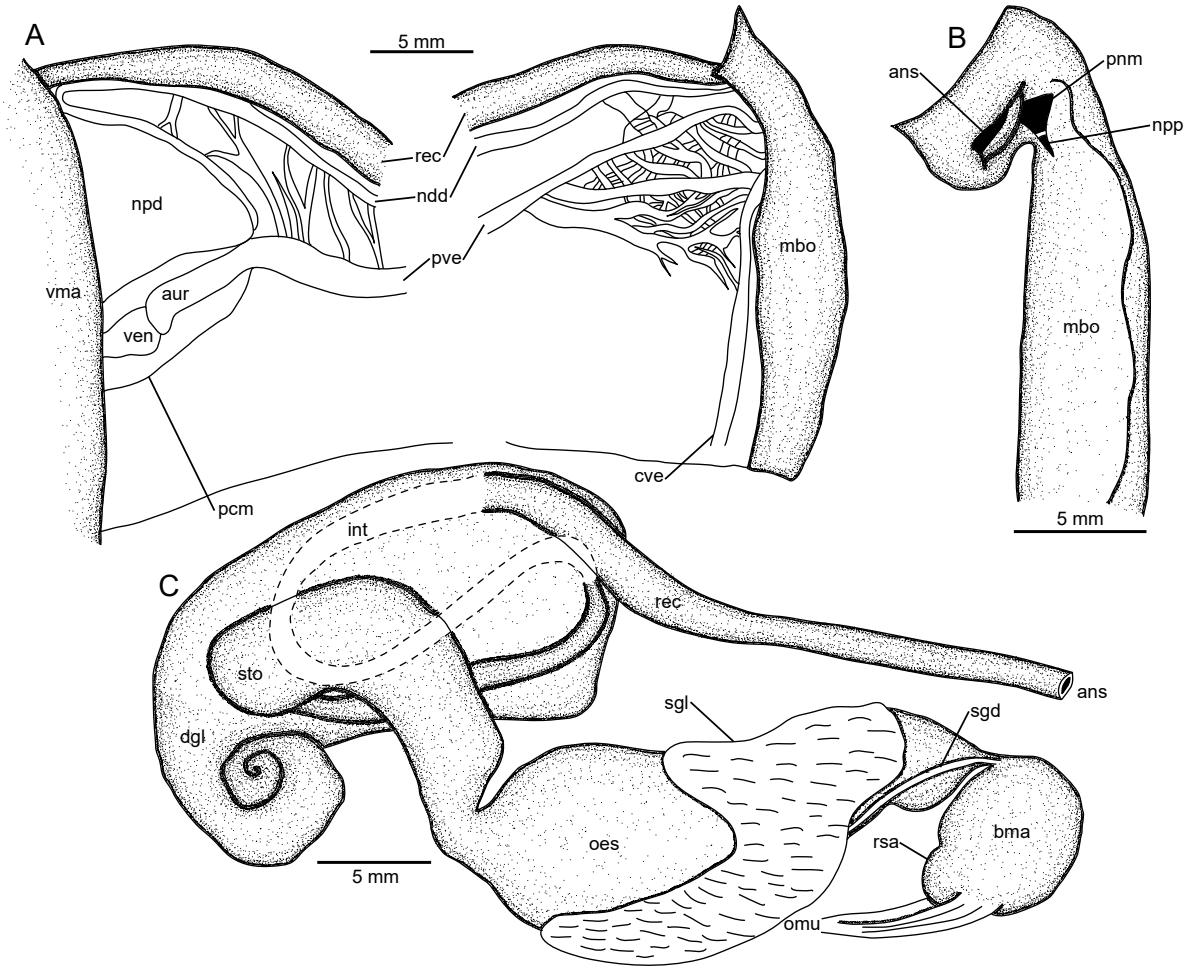

Figure 6. *Auris bilabiata* anatomy (MZSP162441). **A**, Pallial cavity. **B**, Details of pneumostome. **C**, Digestive system. Abbreviations: ans: anus; aur: auricle; bma: buccal mass; cve: collar vessel; dgl: digestive gland; int: intestine; mbo: mantle border; ndd: nephridioduct; npd: nephridium; npp: nephridiopore; oes: esophagus; omu: odontophore muscles; pcm: pericardium; pnm: pneumostome; pve: pulmonary vein; rec: rectum; rsa: radular sac; sgd: salivary gland duct; sgl: salivary gland; sto: stomach; ven: ventricle; vma: visceral mass.

margin when laterally extended (Fig. 5A,C).

Eggs (Fig. 5G): oval, bright green; surface smooth; egg *c.* 1.5 mm on its longest axis. Eggs change colour as they develop, shifting from green to milky white as they approach hatching.

Pallial cavity and associated organs (Fig. 6A, B): pallial cavity long and wide, occupying *c.* 1½ whorls. Mantle border thick, white. Pneumostome bearing an air entrance, a nephridiopore, and the anus as separate apertures. Rectum large, running parallel to nephridioduct. Imbricated veins on pallial surface, greater in abundance and width in anterior third of pallial cavity. Pulmonary vein *c.* ½ width of rectum, running to and inserting into pericardium. Collar vessel as wide as pulmonary vein, running perpendicular to it. Auricle occupies *c.* ¼ of pericardium space; ventricle almost same size as auricle. Heart and nephridium combined occupy *c.* ⅛ of pallial cavity. Nephridium deltoid, beige, about twice as wide as heart; primary nephridioduct *c.* ¼ width of rectum, originating close to heart and running near nephridium; secondary nephridioduct twice width of primary nephridioduct, running parallel to rectum. Nephridiopore opening next to pneumostome.

Digestive system (Fig. 6C): buccal mass subcircular. Odontophore retractor muscle large, running from columellar muscle, parallel to it, to the ventral surface of the odontophore, and attaching postero-dorsally to buccal mass after branching twice: the first in two almost symmetrical muscles, and the second in three closely attached packs of fibres. Radular sac posterior, *c.* ⅑ volume of buccal mass. One fused pair of white salivary glands, partially overlay-

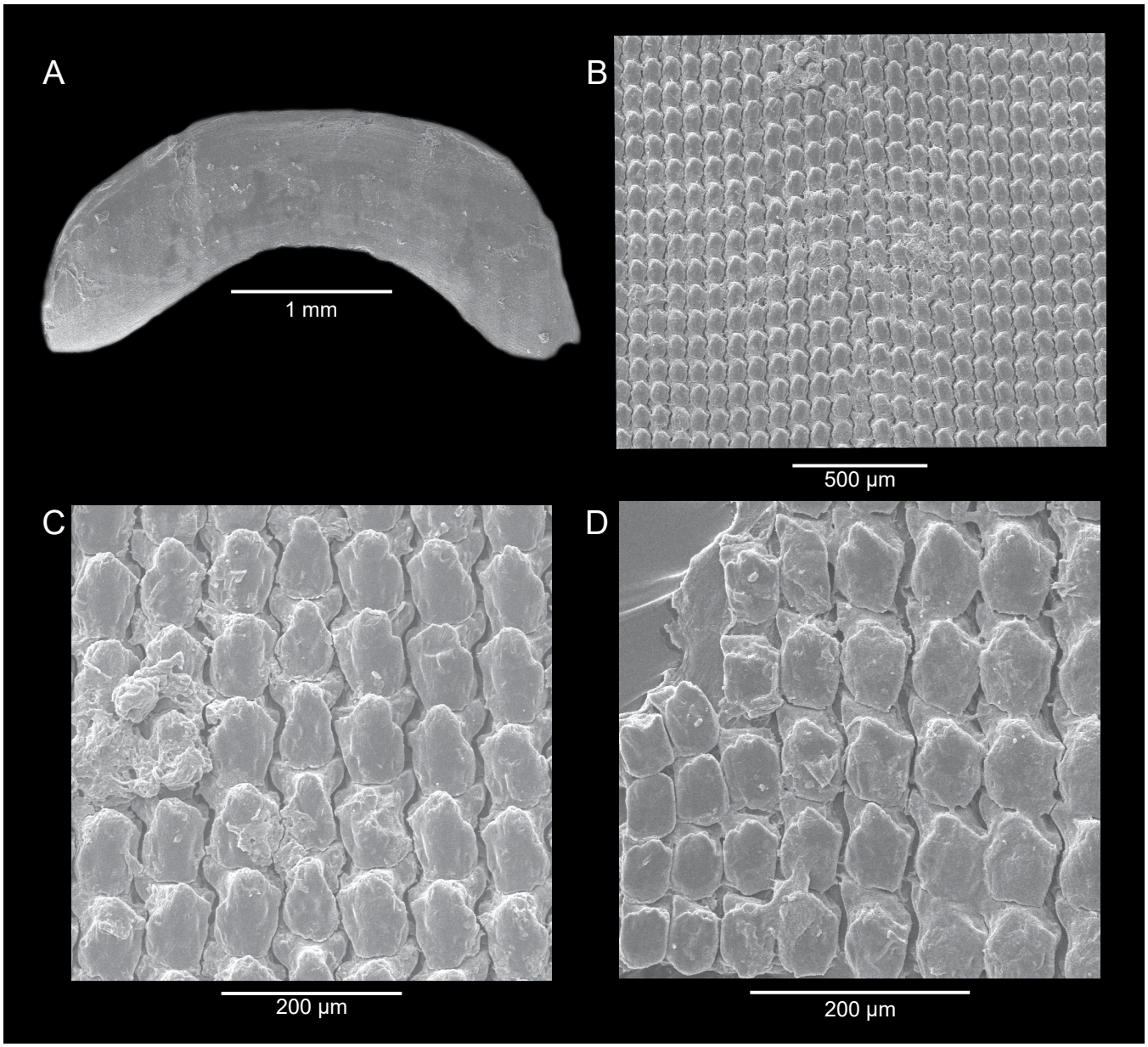

Figure 7. *Auris bilabiata*, SEM micrographs of jaw and radula (MZSP162441). **A**, jaw. **B**, radula, general view. **C**, radula, details of rachidian and lateral teeth. **D**, radula, details of marginal teeth.

ing around oesophagus in its anterior third; salivary ducts opening into buccal mass close to insertion of oesophagus. Oesophagus postero-dorsally inserted in buccal mass. Oesophageal walls thin. Stomach muscularised, partially embedded in digestive gland. Intestine long, *c.* ⅛ width of oesophagus, with thin and almost translucent walls. Intestinal loop on anterior lobe of digestive gland. Digestive gland brown, granulose, with thin walls, occupying *c.* 3 whorls. Rectum thick-walled, *c.* ¼ width of oesophagus. Anus opening close to pneumostome.

Radula and jaw (Fig. 7): Radula *c.* 2 mm in width, with 39 teeth per row (19–1–19). Rachidian tooth symmetrical, tricuspid: mesocone larger, blunt, ovate; ectocones *c.* ¼ the width of the mesocone, blunt, elongate-truncate. Lateromarginal teeth asymmetrical, bicuspid: mesocone weakly arched towards radular margin, larger, blunt, elongate; ectocone blunt, elongate-truncate, *c.* ¼ width of mesocone. Jaw thin, smooth, dark orange, crescent-shaped, with completely indistinguishable fused plates.

Reproductive system (Fig. 8): Ovotestis beige, arborescent, embedded in digestive gland along second whorl, with two lobes; numerous digitiform ramifications leading each

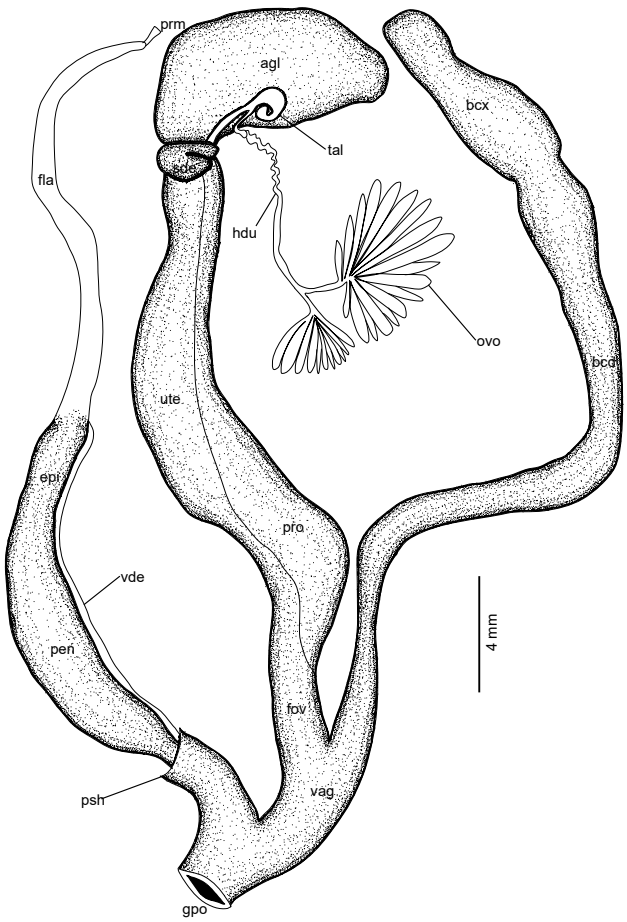

Figure 8. *Auris bilabiata*, reproductive system (MZSP162441). Abbreviations: agl: albumen gland; bcd: bursa copulatrix duct; bcx: bursa copulatrix; epi: epiphallus; fla: flagellum; fov: free oviduct; gpo: genital pore; hdu: hermaphrodite duct; ovo: ovotestis; pen: penis; prm: penis retractor muscle; pro: prostate; psh: penis sheath; sde: spermoviduct distal end; tal: talon; ute: uterus; vag: vagina; vde: vas deferens.

lobe to an arborescent shape. Hermaphroditic duct beige, slightly convoluted anteriorly, with *c.* ⅓ length of spermoviduct; hermaphroditic duct connected to talon by a slender duct thinner than talon. Talon thin, blind-ended, almost as long as albumen gland and partially immersed in it. Spermoviduct connected to talon by a short elongation, thinner than talon, completely embedded by albumen gland. Albumen gland white, slender, *c.* ¼ length of spermoviduct. Spermoviduct *c.* 2½ whorls long. Prostate compressed, white, running alongside uterus, occupying *c.* ½ volume of spermoviduct. Uterus translucent, without lobes, external walls thin. Bursa copulatrix duct slender, slightly longer than spermoviduct; bursa copulatrix white, large, elongate, *c.* ½ width of albumen gland. Vagina long. Vas deferens narrow and long. Penis long, cylindrical, muscular, oval in transverse section. Epiphallus white, short, slightly compressed, *c.* ½ length of penis. Flagellum three times length of epiphallus. Penial retractor muscle short and thin, apically attached to flagellum. Penis and vagina insert, alongside each other, into a wide genital atrium. Genital pore round, simple.

Nervous system (Fig. 9): One pair of buccal ganglia (bgl) connected through a short lateral connective (bgc); five paired nerves emerge from each buccal ganglion, running to posterior region of buccal mass (bcn1–4) and salivary glands (sgn). Nervous ring almost symmetrical. Cerebral ganglia (cgl) partially fused, connected to buccal ganglia by a pair of long cerebro-buccal connectives (cbc). Cerebral ganglia also connected to pleural and pedal ganglia by cerebro-pleural (cpl) and cerebro-pedal (cpc) connectives, respectively. Five paired nerves run from each cerebral ganglion: two pairs connect to ocular tentacles (ten1–2, connected to tip and base of tentacle, respectively); three pairs connect to buccal mass (bcn5–7). One paired nerve (omn) emerges from anterior section of cpl, inserting in odontophore muscles. Left parietal (pag) and unpaired visceral (vig) ganglia completely fused, forming a homogeneous mass, partially fused with right parietal and both pleural (plg) ganglia. Seven nerves run from right parietal ganglion: three run to anterior reproductive system (rpn1–3); four run to visceral mass (vin1–4). Seven nerves emerge from left parietal ganglion: three run to anterior digestive system (dgn1–3); two run to columellar muscle (cmn1–2); two run to tentacle retractor muscles, close to their columellar muscle insertion (otn1–2). Five nerves emerge from visceral ganglion: four run to visceral mass (vin5–8); one ventrally attaches to odontophore (one). Pedal ganglia (pdg) partially fused. Twelve paired nerves emerge from each pedal ganglion: three pairs run anteriorly (apn2–4) to pedal sole, two run medially (mpn1–2) to it, and six run posteriorly (ppn1–6); one pair of nerves emerges close to the statocyst and run to pedal sole medially (syn). One unpaired nerve emerges between both pedal ganglia, running to pedal sole anteriorly (apn1). One paired, small, oval statocyst (syt) inserted ventro-laterally inside each pedal ganglion.

Distribution. Brazil: Sergipe, Bahia, Minas Gerais, Espírito Santo, and Rio de Janeiro states (Birckolz *et al.* 2016).

Habitat and biology data. *Auris bilabiata* is predominantly an arboreal species, frequently found on branches and among foliage (Fig. 5D), a behaviour we suspect is made easier by its remarkably long foot that can extend up to three times the shell length (Fig. 5B, C). In the studied area, it was commonly found on citrus trees, especially orange and lemon, as well as acerola trees. Field observations also show

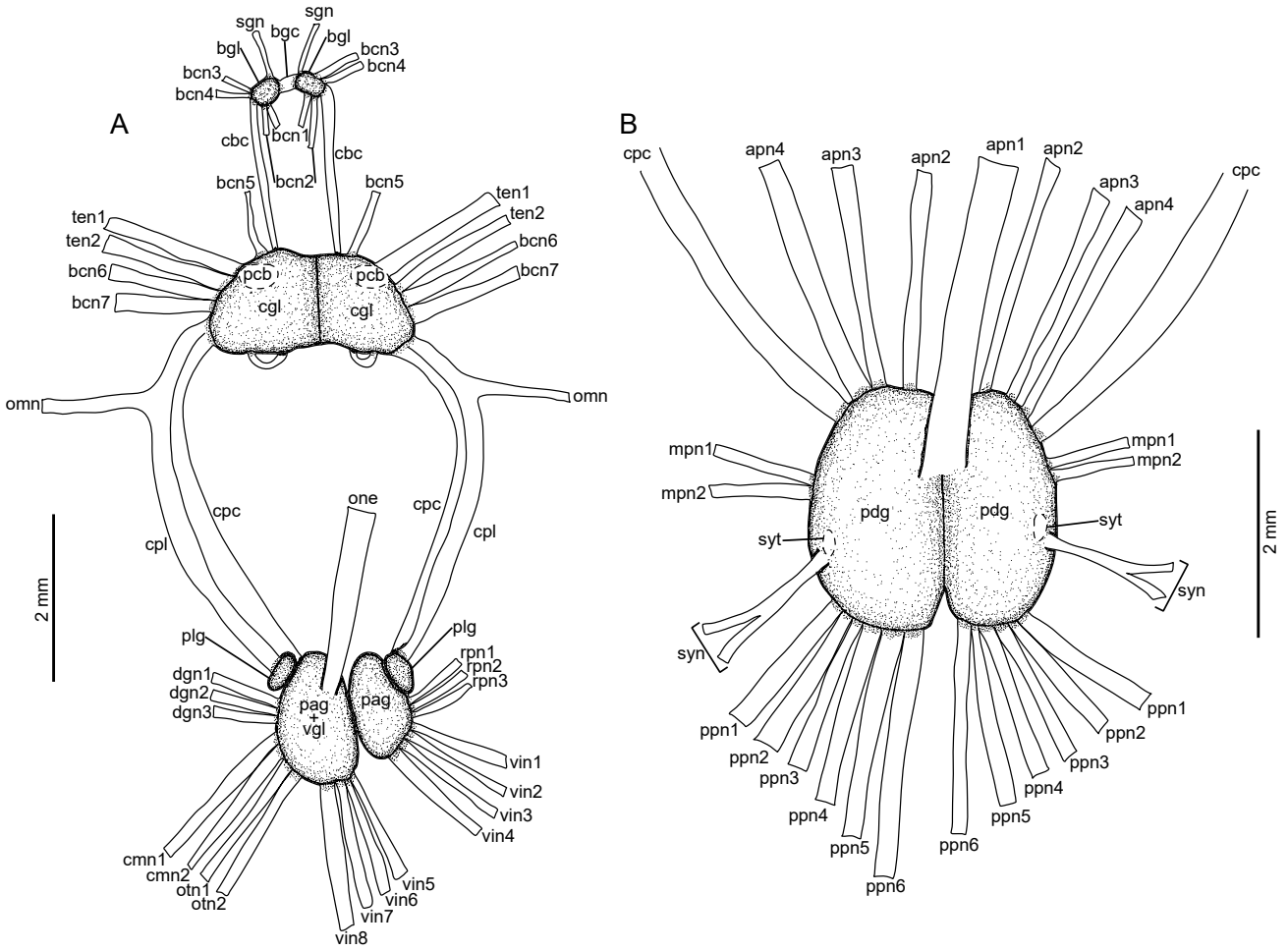

Figure 9. *Auris bilabiata*, nervous system (MZSP162441). **A**, dorsal view; ventral nerves removed for clarity. **B**, pedal ganglia, ventral view; dorsal nerves removed for clarity. Abbreviations: apn1–4 = anterior pedal nerves; bcn1–7 = buccal nerves; bgc = buccal ganglia connective; bgl = buccal ganglion; cbc = cerebro-buccal connective; cgl = cerebral ganglion; cmn1–2 = columellar muscle nerves; cpc = cerebro-pedal connective; cpl = cerebro-pleural connective; mpn1–2 = medial pedal nerves; omn = odontophore muscle nerve; one = odontophore nerve; otn1–2 = ocular tentacle retractor muscle nerves; pag = parietal ganglion; pcb = procerebrum; pdg = pedal ganglion; plg = pleural ganglion; ppn1–6 = posterior pedal nerves; sgn = salivary gland nerve; syn = statocyst nerve; syt = statocyst; ten1–2 = tentacle nerve; vgl = visceral ganglion; vin1–8 = visceral nerves.

that these snails also quite often move along the ground. The snails lay large eggs under or on leaves, affixed to the leaf's surface (Fig. 5G) and sometimes on fruit. Egg-laying was observed in December in specimens brought to the laboratory and eclosion took place two months later, in February. Hatchlings measured *c.* 14 mm in shell length. A full report on the species' natural history is in preparation, including observations in laboratory settings (Macabeu *et al.* in prep.).

In agricultural settings, the species has been listed as an economically important pest for coffee, citrus, and miscellaneous vegetables due to damage to leaves (Teodoro *et al.* 2014). That study, however, did not provide numbers or even estimates to assess the extent (or significance) of damage. Labelling a native species, and one that seems to be a K-strategist, as a pest and without any type of systematic study to back the claims is an unwarranted and dangerous move, which can have serious implications for the native malacofauna.

Remarks. The anatomical data presented by Jurberg (1964) as *Auris bilabiata melanostoma* actually refers to *Auris melastoma* (Swainson, 1820).

Family Megaspiridae Pilsbry, 1904

Included genera. *Callionepion* Pilsbry & Vanatta, 1899; *Megaspira* Lea, 1836 [= *Pyrgelix* H. Beck, 1837].

Diagnosis. Shell elongated (more bulimoid in *Callionepion* to subuliform in *Megaspira*), multiwhorled (from *c.* 9 whorls

in *Callionepion* to over 20 in some *Megaspira*). Protoconch smooth. Teleoconch with densely packed axial ribs, weaker in *Callionepion* and stronger in *Megaspira*. Peristome lightly reflected. Aperture without barriers in *Callionepion* or with columellar and palatal lamellae in *Megaspira* (columellar lamella can be seen inside the shell along the columella).

Discussion. The family Megaspiridae, previously recognised as a non-monophyletic assemblage of convenience (Salvador *et al.* 2023), is here split into distinct lineages so that classification better reflects the phylogenetic arrangement discovered. Thus, the "actual" Megaspiridae is herein restricted to only the type genus and *Callionepion*.

Remarks. Anatomical information can be found in Daniel *et al.* (2022).

Family Koridae Salvador, Cavallari & Breure fam. nov.

ZooBank identifier. urn:lsid:zoobank.org:act:F063D34D-1349-4B8D-8DC9-57B6C24A1F15

Type genus. *Kora* Simone, 2012.

Included genera. *Kora* Simone, 2012 [= *Koltrora* Simone, 2024].

Diagnosis. Shell fusiform to obese-fusiform, robust; aperture slightly displaced from shell axis; umbilicus usually wide; epiphragm calcified; protoconch smooth except for terminal axial riblets. Odontophore lacking M11 muscle; jaw muscle MJ forming a ventral muscular platform. Radula composed of very narrow, hook-shaped teeth with little distinction among rachidian, lateral, and marginal series.

Discussion. Considering present knowledge, Koridae fam. nov. is monotypic and restricted in its distribution to an area that stretches along both sides of the São Francisco river basin in the states of Bahia and Minas Gerais, eastern Brazil (Simone 2024).

Genus *Kora* Simone, 2012

Kora Simone, 2012: 432.
Koltrora Simone, 2024: 74.

Type species. *Kora corallina* Simone, 2012

Common name. English: crowned snail. Portuguese: caracol-coroado.

Included species. *K. aetheria* Simone, 2024; *K. corallina* Simone, 2012; *K. curumim* Simone, 2024; *K. kremerorum* Simone, 2024; *K. nigra* Simone, 2015 [= *K. ajar* Simone, 2024; *K. itacarambi* Simone, 2024 nomen nudum; *K. tupan* Simone, 2024]; *K. pyrostoma* (Simone, 2024) **comb. nov.**; *K. rupestris* Salvador & Simone, 2016 [= *K. arnaldoi* Pena, 2024; *K. jimenezi* Simone, 2024]; *K. uhlei* Simone, 2024; *K. vania* Simone, 2024.

Distribution. Currently restricted to the São Francisco river basin in eastern Brazil, ranging from western-southwestern Bahia to northern Minas Gerais (Simone 2024: fig. 60).

Biomes. These species occur across areas assigned to the Caatinga and Cerrado domains, as well as transitional zones and rupestrian habitats, but all records are restricted to the São Francisco Basin. Most species are associated with seasonally dry, rocky landscapes, particularly limestone and karst outcrops, although the genus is not restricted to a single vegetation type.

Discussion. The genus and its species were discovered and described over the past 15 years. The first five species were known only from shells (Simone 2012, 2015; Salvador & Simone 2016); two of them were later shown to be synonymous with the bulimulid *Drymaeus coarctatus* (Pfeiffer, 1845) (Salvador *et al.* 2021). In recent years, the genus saw an explosion of new species descriptions, with nine new species described in 2024, all from a geographically small area (Pena 2024; Simone 2024). A new, related, and monotypic genus, *Koltrora*, was also described from the same area (Simone 2024).

Here we could analyse five of the new *Kora* spp. described in 2024 and show that four of them (*K. ajar*, *K. arnaldoi*, *K. tupan*, and *K. jimenezi*) are synonymous with two of the first three species described (*K. nigra* and *K. rupestris*). The new genus *Koltrora* also proved to be synonymous with *Kora*, although its single species is demonstrably different from the rest, both genetically (this study) and morphologically (Simone 2024); thus, it is herein transferred to *Kora* under the new combination *Kora pyrostoma* (Simone, 2024) **comb. nov.** This synonymization is also congruent with the biogeographic pattern observed in the genus, as *K. pyrostoma* occurs in the middle São Francisco basin of western Bahia, within the same general distributional area occupied by all other known species of *Kora*. Rather than representing a geographically isolated lineage, it further reinforces the apparent restriction of the genus to the São Francisco drainage (Simone 2024). Moreover, such a high rate of synonymy observed here raises the question of whether the other four new species described in 2024 would stand closer scrutiny. Despite being a relatively new genus, *Kora* is thus paradoxically already in need of further revision.

Remarks. Anatomical details are described in Pena (2024) and Simone (2024).

Family Orphaicidae Salvador, Rosa, Cavallari & Breure fam. nov.

ZooBank identifier. urn:lsid:zoobank.org:act:5736035C-8108-4162-A93E-4D256618EB0D

Type and only genus. *Orphaicus* Schaufuss, 1869.

Diagnosis. Shell oval-elongated, bulimoid, thick-walled; ground colour cream to brown, with varying degrees of dark axial bands; spire tall, longer than ½ of total shell height; apex truncated; rounded whorls; suture well marked, shallow; protoconch sculptured by oblique striae; teleoconch sculptured by well-marked growth lines; aperture oval; peristome thickened and slightly reflected in adults.

Discussion. As explained above, the Brazilian "*Thaumastus*" form a distinct family-level branch within crown Orthalicoidea, widely separated from the Andean *Thaumastus* (see Paeniscutalidae Breure & Salvador fam. nov. below). The genus *Orphaicus* Schaufuss, 1869 was thus recovered from the literature to house these species and a new family bearing its name is necessary considering our results (Fig. 3).

Genus *Orphaicus* Schaufuss, 1869

Bulimus (*Orphnus*) Albers, 1850: 146. [Non *Orphnus* McLeay, 1819: Coleoptera]
Bulimus (*Orphaicus*) Schaufuss, 1869: 14.
Thaumastus of authors, when referring to Brazilian species.

Type species. *Helix* (*Cochlostyla*) *taunaisii* Férussac, 1822.

Common name. English: orphic tree snail. Portuguese: caracol-órfico.

Included species. All Brazilian species formerly assigned to *Thaumastus* (as listed by Salvador *et al.* 2024) are herein transferred to *Orphaicus*, resulting in the following new combinations: *O. ascendens* (Pfeiffer, 1853) **comb. nov.**; *O. baixoguanduensis* (Pena, Coelho & Salgado, 1996) **comb. nov.**; *O. caetensis* (Pena, Salgado & Coelho, 2011) **comb. nov.**; *O. contortuplicatus* (Reeve, 1850) **comb. nov.**; *O. dukinfieldi* (Melvill, 1900) **comb. nov.** [nomen inquirendum]; *O. hebes* (Strebel, 1910) **comb. nov.**; *O. largillierti* (Philippi, 1845) **comb. nov.** [= *Bulimus consimilis* Reeve, 1848]; *O. lundi* (Pena, Salgado & Coelho, 2005) **comb. nov.**; *O. magnificus* (Grateloup, 1840) **comb. nov.**; *O. nehringi* (Martens, 1889) **comb. nov.**; *O. parvus* (Pena, Salgado & Coelho, 2011) **comb. nov.**; *O. requieni* (Pfeiffer, 1853) **comb. nov.**; *O. spixii* (Wagner, 1827) **comb. nov.** [= *Bulimus fragilis* Spix, 1827; *Bulimus hyalinus* Wagner, 1827; *Columna bulimea* Spix, 1827]; *O. straubei* (Colley, 2012) **comb. nov.**; *O. taunaisii* (Férussac, 1822) **comb. nov.** [= *Bulimus monozonalis* Deshayes, 1851; *Bulimus achilles* Pfeiffer, 1853]; *O. tiradentensis* (Pena, Coelho & Salgado, 1996) **comb. nov.**

Distribution. Southwestern Brazil, with species distributed across the states of Minas Gerais, Espírito Santo, São Paulo, Rio de Janeiro and Paraná. Some of the lesser-known species have been only vaguely reported to occur in "Brazil", without precise localities (Simone 2006).

Biome. Atlantic Forest.

Discussion. As explained above, the type species of *Thaumastus*, *T. hartwegi* (Pfeiffer, 1846), is an Ecuadorian species. That Andean lineage is represented in our phylogenetic tree by two Peruvian *Thaumastus* spp. (Fig. 1; Table 1). The Brazilian species that have historically been referred to as *Thaumastus* form their own, completely separate lineage, within Orthalicoidea. Hence, they must have their own genus. Luckily, there is already one name available in the literature, *Orphaicus*, whose type species is represented in our phylogenetic tree (Fig. 3; Table 2). The resurrection of *Orphaicus* and reclassification of Brazilian "*Thaumastus*" species result in several new combinations.

Remarks. Anatomical studies on some Brazilian "*Thaumastus*" species can be found mostly in unpublished dissertations in Brazil, though some of that data has been published (e.g. Jurberg 1988; Pena *et al.* 1996, 2005, 2011; Colley 2012). Conchological features seem widely variable in a few species (e.g. *O. taunaisii* comb. nov.), while some other species (e.g. *O. parvus* comb. nov.) do not seem to have enough diagnostic characters to be sustained as distinct taxa. Thus, species in this genus need urgent revision.

Family Paeniscutalidae Breure & Salvador fam. nov.

ZooBank identifier. urn:lsid:zoobank.org:act:CC9D9EC5-12F5-41B7-8B15-3E7D1B725504

Type genus. *Paeniscutalus* Wurtz, 1947.

Included genera. *Paeniscutalus* Wurtz, 1947, *Thaumastus* Martens, 1860 [= *Atahualpa* Strebel, 1910; *Pachytholus* Strebel, 1910; *Tatutor* Jousseaume, 1887].

Diagnosis. Shells medium-sized to large, (elongate-)ovate, solid, rimate to imperforate. Protoconch with axial wrinkles, which may, on second whorl, be broken into oblong granules. Surface of teleoconch with incrassate growth striae. Whorls hardly to slightly convex; suture hardly to well impressed, usually crenulate. Aperture subovate. Peristome (slightly) thickened and not or narrowly expanded.Radula with tricuspid central teeth, usually with rather acute, ovate mesocones and elongate, truncate ectocones. Lateromarginal teeth bicuspid, with rather blunt to acute, elongate mesocones and elongate-truncate to ovate ectocones; rudi-

mentary endocones may be present in some species. No supporting denticles in outermost teeth. Half-row formula: C/3 + LM x/2 (x = 32–43).

Genitalia with a rather thick penis, with a sheath, more or less subcylindrical, passing without external differentiation into epiphallus; flagellum subcylindrical to tapering, up to half as long as phallus. Vagina relatively short, spermathecal duct subcylindrical, with an elongate-globose spermatheca at end.

Distribution. Ecuador, Peru, Bolivia.

Discussion. This lineage is one of the earliest to branch off in the superfamily (Fig. 1) and its relationship to other branches suggests it should be recognised as a family-level taxon.

These genera were classified on conchological grounds by Pilsbry (1901 [1901–1902]) as *Thaumastus* (together with taxa now placed in Orphaicidae fam. nov.), respectively considered as a *Strophocheilus* species (*Paeniscutalus crenellus*). Thiele (1931 [1929–1931]) either considered them as a section within *Thaumastus* in Bulimulidae, or as *Tholus* (*Pachytholus*) in Orthalicidae. Zilch (1960 [1959–1960]) did the same but considered them as subgenera. Breure (1979) classified all taxa, including *Paeniscutalus*, as subgenera of *Thaumastus*. We have excluded here the subgenera *Kara* Strebel, 1910, *Quechua* Strebel, 1910, *Scholvienia* Strebel, 1910, and *Thaumastiella* Weyrauch, 1956, as these differ notably by conchological and anatomical characteristics (Breure 1978, 1979). As explained above, we hypothesise that *Thaumastus* belongs to this family, though we would need genetic data for the type species *T. hartwegi* from Ecuador to prove that.

Conclusion

According to the new results obtained in our phylogenetic analysis, family Megaspiridae, as previously understood, comprises five separate lineages "scattered" throughout the Orthalicoidea tree. As such, Megaspiridae was here restricted to two genera, and four new families were described: Auriidae Salvador, La Pasta, Silva & Breure fam. nov.; Koridae Salvador, Cavallari & Breure fam. nov.; Orphaicidae Salvador, Rosa, Cavallari & Breure fam. nov.; Paeniscutalidae Breure & Salvador fam. nov. Thus, the superfamily Orthalicoidea now contains 12 families, in a classification scheme that better reflects its diversity. In addition, the family Liguidae, previously considered synonymous with Orthalicidae, is here reestablished as subfamily Liguinae, sister to Orthalicinae.

Furthermore, some changes in the taxonomy of genus and species-level taxa were warranted: (1) *Quechua* is considered a junior synonym of *Corona*, resulting in new combinations of its four species (see Discussion); (2) *Sultana labeo* and *Sultana liae* are transferred to the genus *Kara*, resulting in the new combinations *Kara labeo* comb. nov. and *Kara liae* comb. nov.; (3) *Koltrora* is considered a junior synonym of *Kora*, resulting in the new combination of its single species as *Kora pyrostoma* comb. nov.; (4) *Kora ajar* and *Kora tupan* are junior synonyms of *Kora nigra*; (5) *Kora arnaldoi* and *Kora jimenezi* are junior synonyms of *Kora rupestris*; (6) the genus *Orphaicus* was "resurrected" to include the Brazilian species formerly assigned to *Thaumastus*, resulting in multiple new combinations (see Systematics section).

Beyond the taxonomic changes proposed herein, our results illustrate how much of the evolutionary relationships of Orthalicoidea remains obscured by traditional classifications. Lineages previously grouped on conchological grounds (e.g. *Thaumastus*/*Orphaicus*) were shown to represent deeply divergent entities, while others thought to be distinct based on morphoanatomical data (e.g. *Kora*/*Koltrora*) proved to be artificial divisions unsupported by molecular evidence. Still, cases of morphoanatomical uniqueness (e.g. *Auris* and *Megaspira*) are supported by molecular evidence in their status as distinct lineages. The recognition of new families, the redefinition of existing ones, and the synonymization of recently proposed taxa collectively demonstrate that the higher-level classification of Orthalicoidea is still far from stable. As broader molecular sampling becomes available, particularly for poorly known South American lineages, additional diversity and further taxonomic rearrangements are likely to emerge, gradually revealing a clearer picture of the evolutionary relationships within Orthalicoidea.

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