Zoosyst. Evol. 98 (2) 2022, 365–375 | DOI 10.3897/zse.98.90797

PENSOFT.

MUSEUM FÜR NATURKUNDE BERLIN

Phylogenetic position of the relict South American genus *Idiopyrgus* Pilsbry, 1911 (Gastropoda, Truncatelloidea), with the description of two new cave species

Rodrigo B. Salvador[1], Fernanda S. Silva[2], Maria E. Bichuette[3]

1 *Museum of New Zealand Te Papa Tongarewa. 169 Tory Street, 6011 Wellington, New Zealand*
2 *Museu de Zoologia da Universidade de São Paulo, Avenida Nazaré 481, 04263-000, São Paulo, SP, Brazil*
3 *Laboratório de Estudos Subterrâneos, Universidade Federal de São Carlos. Rodovia Washington Luís km 235, CP 676, 13565-905, São Carlos, SP, Brazil*

https://zoobank.org/6CEC845A-7018-4DF3-ADE7-141B15FCBE05

Corresponding author: Rodrigo B. Salvador (salvador.rodrigo.b@gmail.com)

Academic editor: Thomas von Rintelen ♦ **Received** 25 July 2022 ♦ **Accepted** 24 August 2022 ♦ **Published** 14 September 2022

Abstract

Idiopyrgus is a relict genus of freshwater snails from Brazil traditionally classified in the family Pomatiopsidae. Herein, we use molecular data from newly acquired specimens to test that classification through Bayesian inference phylogenetic analysis. We conclude that *Idiopyrgus* belongs in the Gondwanan family Tomichiidae, together with the African genus *Tomichia* and the Australian genus *Coxiella*. Furthermore, we reassess currently synonymized genus- and species-level names in *Idiopyrgus*. The genera *Hydracme* and *Aquidauania* are considered synonymous with *Idiopyrgus*. The species *I. brasiliensis* and *I. pilsbryi* are restored as accepted species; *I. walkeri* is considered a taxon inquirendum. Two new species from caves in Bahia state are described herein: *Idiopyrgus adamanteus* **sp. nov.** and *Idiopyrgus minor* **sp. nov.**

Key Words

Caenogastropoda, Gondwana, molecular phylogenetics, Pomatiopsidae, Tomichiidae

Introduction

Idiopyrgus Pilsbry, 1911 is a relict genus of operculated freshwater snails from Brazil, which, as presently understood, includes only two species (Simone 2006). *Idiopyrgus* (Fig. 1) is the single South American representative of the family Pomatiopsidae, which is mostly an Asian family, albeit with representatives in North America (*Pomatiopsis* Tryon, 1862), southern Australia (*Coxiella* E. A. Smith, 1894) and South Africa (*Tomichia* Benson, 1851) (Wilke 2019). The other potential South American Pomatiopsidae genus, *Spiripockia* Simone, 2012, was recently transferred to Cochliopidae based on new anatomical data (Simone and Salvador 2021).

This disjunct distribution has been difficult to explain and competing biogeographic hypotheses have proved impossible to be fully untangled (Wilke 2019). Phylogenetic works involving the family have mostly been concerned with its Asian branch, which is by far the most diverse (e.g., Attwood et al. 2003; Guan et al. 2008; Kameda and Kato 2011; Liu et al. 2014). The only study to include both *Tomichia* and *Coxiella* was Wilke et al. (2013), which recovered both genera as sister taxa, separated from Pomatiopsidae and hence recognized as the family Tomichiidae. Nevertheless, this classification scheme has not yet gained widespread acceptance and is absent from later works (e.g., Wilke 2019).

As such, the inclusion of the South American *Idiopyrgus*, largely ignored so far, is the final piece of this puzzle. Herein we use newly collected material to include *Idiopyrgus* in a molecular phylogenetic framework of freshwater Truncatelloidea, in an attempt to resolve the matters of phylogeny and classification, and also shed light on the biogeographic history of the group. We also reassess synonymized genus and species level taxa within *Idiopyrgus* and describe two new species based on the newly collected material.

Material and methods

Taxonomic background

When first described, *Idiopyrgus* Pilsbry, 1911 contained only one species: *Idiopyrgus souleyetianus* Pilsbry, 1911 (type species by original designation), whose type locality is Rio Doce ("Doce River"), in Espírito Santo state, SE Brazil (Pilsbry 1911). Three further species were later described from other localities in Brazil, but are presently considered junior synonyms of *I. souleyetianus* according to Simone (2006): (1) *I. pilsbryi* Baker, 1914, type locality: Lago Papary, Rio Grande do Norte state; (2) *I. walkeri* Pilsbry, 1924, type locality: Rio das Velhas, Minas Gerais state; and (3) *Oncomelania brasiliensis* Rey, 1959, type locality: Campo Grande, Mato Grosso do Sul state. Likewise, two genera have been synonymized with *Idiopyrgus* (Simone 2006): *Aquidauania* Davies, 1979, whose only representative is *I. brasiliensis* (Rey, 1959) (Davis 1979); and *Hydracme* Haas 1938, which contained only *I. rudolphi* (Haas, 1938).

From the above, it follows that *I. souleyetianus* is currently considered a widespread species in Brazil, being reported from the states of Bahia, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, and Rio Grande do Norte (Birckolz et al. 2016). The only other currently accepted species in the genus is *I. rudolphi* (Haas, 1938) (Simone 2006), known only from its type locality in Jatobá, in Pernambuco state, NE Brazil (Haas 1938).

Material analyzed

The specimens (including types) analyzed for the present study are housed in the following collections: **ANSP**, Academy of Natural Sciences of Drexel University (Philadelphia, PA, USA); **LES**, Laboratório de Estudos Subterrâneos, Universidade Federal de São Carlos (São Carlos, SP, Brazil); **MZSP**, Museu de Zoologia da Universidade de São Paulo (São Paulo, SP, Brazil); **SMF**, Naturmuseum Senckenberg (Frankfurt am Main, Germany).

New specimens of *Idiopyrgus* spp. have been collected in Bahia state by the team at LES as part of cave surveys in the region. They come from the following localities (and caves): Central municipality (Gruta da Machadinha, Toca Bonita, Toca da Mulher, Toca de Candeias); Coribe municipality (Gruna Bem Bom); Feira da Mata municipality (Gruna da Pingueira II, Gruna do Engrunado). A paper is in preparation with a full account of the localities surveyed during those expeditions and the land and freshwater gastropods found.

The following abbreviations are used throughout the text: **BA**, Bahia state; **ES**, Espírito Santo state; **H**, shell height (measured parallel to columellar axis); **leg.**, collector(s); **MG**, Minas Gerais state; **MS**, Mato Grosso do Sul; **PE**, Pernambuco state; **RN**, Rio Grande do Norte state.

Material analyzed

Idiopyrgus adamanteus **sp. nov.:** BRAZIL • holotype; BA, Central, Toca Bonita; 13 Mar. 2017; M.E. Bichuette, J. E. Gallão leg.; MZSP 158237. 14 paratypes; BA, Central, Toca Bonita; 13 Mar. 2017; M.E. Bichuette, J. E. Gallão leg.; LES 0027975. 3 paratypes; BA, Central, Toca Bonita; 13 Mar. 2017; M.E. Bichuette, J. E. Gallão leg.; LES 0027975. 2 shells; BA, Central, Toca da Mulher; 03 Jul. 2018; M.E. Bichuette, J. E. Gallão leg.; LES 0027976. 3 shells; BA, Central, Toca de Candeias; 03 Jul. 2018; M.E. Bichuette, J. E. Gallão leg.; LES 0027977. 4 shells; BA, Central, Toca de Candeias; 03 Jul. 2018; M.E. Bichuette, J. E. Gallão leg.; LES 0027978. 13 shells; BA, Central, Gruta da Machadinha; 15 Mar. 2017; M.E. Bichuette, J. E. Gallão leg.; LES 0027979. ***Idiopyrgus pilsbryi*****:** BRAZIL • lectotype; RN, Lago Papary; F. Baker leg.; ANSP 130700. ***Idiopyrgus rudolphi*****:** BRAZIL • holotype; PE, Jatobá, Rio São Francisco; SMF 24365. ***Idiopyrgus minor*** **sp. nov.:** BRAZIL • holotype; BA, Feira da Mata, Gruna da Pingueira II; 14 Oct. 2020; M.E. Bichuette, J. E. Gallão, J. S. Gallo, D. F. Torres leg.; MZSP 158238. 2 paratypes; BA, Feira da Mata, Gruna do Engrunado; 8 Jul. 2021; M.E. Bichuette, J. E. Gallão, J. S. Gallo leg.; LES 0027980. ***Idiopyrgus souleyetianus*****:** BRAZIL • holotype; ES, Rio Doce; 1910; H. v. Ihering leg.; ANSP 100534. 1 shell; ES, Rio Doce; H. v. Ihering leg.; ANSP 275181. 15 shells; BA, São Desidério, Gruta do Catão; 03 Nov. 2012; M.E. Bichuette, J. E. Gallão leg.; MZSP 122772–122775. ***Idiopyrgus*** **cf.** ***souleyetianus*****:** BRAZIL • 1 shell; MG, Parque Nacional Cavernas do Peruaçu; 06 May 2014; M.E. Bichuette et al. leg.; MZSP 138998. 1 shell; MG, Parque Nacional Cavernas do Peruaçu, Lapa do Branco I; 09 May 2015; M.E. Bichuette et al. leg.; MZSP 139003. ***Idiopyrgus*** **cf.** ***walkeri*****:** BRAZIL • 3 shells; BA, Coribe, Gruna Bem Bom; 07 Jul. 2021; M.E. Bichuette, J. E. Gallão et al. leg.; LES 0027981.

The holotype of *Idiopyrgus brasiliensis* (MZSP 14598; MS, Campo Grande) could not be found in the MZSP collection and is therefore considered lost. Pilsbry (1924) did not indicate the type material of *I. walkeri*, which is a very unusual situation for that author; the specimen(s) could not be located in the ANSP collection, where most of his types are housed.

Molecular data

One juvenile and one adult specimen (paratypes of each of the new *Idiopyrgus* species) preserved in ethanol 98% were used for DNA extraction. With the exception of the holotypes and other paratypes of these species, all other available specimens of *Idiopyrgus* spp. are dry shells only.

DNA extraction followed the standard protocol of the QIAGEN DNEasy® Blood & Tissue Kit, with the addition of a repetition of the final step in order to increase yield. The following markers were target herein: (1) the barcoding fragment of the mitochondrial COI gene (c. 650 bp; primers LCO/HCO of Folmer et al. 1994); (2) the mitochondrial 16S rRNA gene (c. 450 bp; primers 16SarL/16SbrH of Simon et al. 1994); (3) the ITS2 region and the 5′ end of the 28S rRNA gene (c. 1,400 bp; primers LSU-1/LSU-3 and LSU-2/LSU-5 of Wade et al. 2006). The protocol for PCR were as follows. COI and 16S: initial denaturation at 96 °C (3 min); 35 cycles of denaturation at 95 °C (30 s), annealing at 48 °C (1 min), and extension at 72 °C (2 min); final extension at 72 °C (5 min). ITS2+28S: initial denaturation at 95 °C (3 min); 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 (5 min for ITS2 section; 2 min for 28S section); final extension at 72 °C (4 min).

The PCR products were assessed via agarose gel electrophoresis, cleaned (following the manufacturer's protocol) with ExoSAP-IT™ (Affymetrix Inc.), and sent to Massey Genome Service (Massey University, Palmerston North, New Zealand) for Sanger sequencing. Sequences were quality-proofed and assembled in Geneious Prime (v.2020.2.2, Biomatters Ltd.). The consensus sequence of each marker was uploaded to GenBank (registration numbers are listed under each species entry below).

The DNA sequences for the phylogenetic analysis were extracted from GenBank (Table 1), with a focus on Pomatiopsidae and Tomichiidae. Representatives of other closely-related families were also selected, including those families and genera in which *Idiopyrgus* has been historically classified or been considered related to, such as Amnicolidae, Assimineidae and Tateidae (e.g., Pilsbry 1924; Morretes 1949; Rey 1959). A Littorinidae species was chosen as outgroup (Table 1).

Sequence alignment was conducted in Geneious Prime via the MAFFT plugin (v.7.450; Katoh et al. 2002; Katoh and Standley 2013) with default settings. The resulting alignment of each marker (COI, 16S, and ITS+28S) was visually proofed for inconsistencies and then run through Gblocks (Castresana 2000; Talavera and Castresana 2007) with the least restrictive settings to eliminate poorly-aligned or data-deficient positions that could hamper the analysis. The resulting post-Gblocks alignments were concatenated (2,610 bp in total) for a single Bayesian inference phylogenetic analysis, conducted with MrBayes (v.3.2.7, Ronquist et al. 2012) via the CIPRES Science Gateway (v. 3.3, Miller et al. 2015). Two concurrent analyses were run, each with 4 Markov chains of 40 million generations (the first 20% discarded as 'burn-in'), the default priors, nst = 6, rates = invgamma, temperature parameter = 0.1, sampling every 1,000 generations, and with substitution model parameters unlinked across the markers (COI, 16S, ITS+28S). MCMC convergence was assessed by examining the standard deviation of split frequencies (<0.01) and the potential scale reduction factor (PSRF ~1.0), as well as trace plots in Geneious (Ronquist et al. 2009).

Results and discussion

The specimens used herein for DNA analysis were identified as two new species of *Idiopyrgus*, described below: *Idiopyrgus adamanteus* sp. nov. and *Idiopyrgus minor* sp. nov.

Genus *Idiopyrgus* Pilsbry, 1911

***Idiopyrgus adamanteus* sp. nov.**
https://zoobank.org/277BBC82-4F6F-4810-A0E0-7E23B7301D18
Fig. 2A–H

Type material. MZSP 158237 (holotype), LES 0027974 (14 paratypes, from type locality), LES 0027975 (3 paratypes, from type locality).

Type locality. Brazil, Bahia state, Central municipality, Toca Bonita cave.

Distribution. Known from four caves in Central municipality.

Etymology. From Latin, meaning 'of diamond'; an allusion to the region in Bahia known as Chapada Diamantina, where all the caves in the species' known distribution are located.

Diagnosis. Elongated shell spire; narrow body whorl; more circular aperture when compared to congeners.

Description. Shell small, truncatelloid, of translucent beige to whitish color. Protoconch bulbous and translucent, of fragile appearance (it is broken off in many specimens). Spire narrow. Shell smooth except for fine growth lines; growth lines can be more marked in some specimens, forming a light axial ribbing pattern (Fig. 2E, G). Suture deep; subsutural cord observed in one specimen (Fig. 2E). Whorl profile markedly convex, rounded. Whorls initially increasing regularly in size with growth, but final whorls are typically similar in size (Fig. 2A, D–G). Aperture small in proportion to body whorl; oval to circular, with a more acuminate end towards the upper lip insertion. Peristome complete; reflexed but not thickened. Shell rimate. Operculum translucent, of same color as the shell. Soft body white.

Measurements. holotype: 6½ whorls, H = 5.3 mm, D = 2.3 mm; mean (n = 7), 6½ whorls (min 6, max 7), H = 5.6 ± 0.39 mm, D = 2.5 ± 0.12 mm.

Genetic data. GenBank reg. nrs: COI, ON323464; 16S, ON359913; ITS2+28S, ON324828.

Remarks. *Idiopyrgus adamanteus* sp. nov. is most similar in shell shape to *I. souleyetianus* and *I. brasiliensis*, but it can be diagnosed from them by the fewer number of whorls and the much narrower body whorl, as well as a more circular aperture (Fig. 1). It can be distinguished from *I. rudolphi* by the deeper suture, more convex whorl profile and more circular aperture. It differs from the remaining congeners by its narrower shell, more elongated spire and smaller aperture (in proportion to body whorl).

Idiopyrgus adamanteus sp. nov. displays a fair amount of morphological variation in the shell, even in specimens

Table 1. Species used in the phylogenetic analysis, with GenBank registration number of each marker, locality data, and reference. The taxa are arranged alphabetically for ease of use; type species of the genera are indicated by an asterisk after their name.

Taxon	COI	16S	28S	Locality	Reference
Amnicolidae					
Akiyoshia kobayashii Kuroda & Habe, 1958	AB611823	AB611822	AB611821	Japan, Shiga, Taga	Kameda and Kato 2011
Amnicola limosus (Say, 1817)	AF213348	AF212903	—	USA, Michigan, Blind Lake	Wilke et al. 2001
Assimineidae					
Angustassiminea satumana (Habe, 1942)	AB611803	AB611802	AB611801	Japan, Kagoshima, Kikai Is.	Kameda and Kato 2011
Assiminea grayana Fleming, 1828*	HQ623170	HQ623153	—	Germany, Lower Saxony, Varel	Wilke et al. 2013
Assiminea hiradoensis Habe, 1942	AB611807	AB611806	AB611805	Japan, Nagasaki, Urakami	Kameda and Kato 2011
Assiminea ovata (Krauss, 1848)	—	KC109939	KC109991	South Africa, Western Cape, Knysna Lagoon	Criscione and Ponder 2013
Paludinellassiminea japonica (Pilsbry, 1901)*	AB611811	AB611810	AB611809	Japan, Ehime, Hiburi Is.	Kameda and Kato 2011
Pseudomphala miyazakii (Habe, 1943)	AB61815	AB611814	AB611813	Japan, Saga, Ashikari	Kameda and Kato 2011
Falsicingulidae					
Falsicingula athera Bartsch in Golikov & Scarlato, 1967	HQ623172	HQ623155	—	Japan, Hokkaido, Etorofu Is.	Wilke et al. 2013
Falsicingula mundana (Yokoyama, 1926)	AB930492	AB930424	AB930366	Japan, Kyoto, Kotobikihama	Takano and Kano 2014
Littorinidae					
Littoraria pallescens (Philippi, 1846)	AB611831	AB611830	AB611829	Japan, Okinawa, Nago	Kameda and Kato 2011
Pomatiopsidae					
Blanfordia bensoni (Adams, 1861)	AB611711	AB611710	AB611709	Japan, Hokkaido, Nigorikawa	Kameda and Kato 2011
Blanfordia integra Pilsbry, 1924	AB611719	AB611718	AB611717	Japan, Shizuoka, Mt. Mikuni	Kameda and Kato 2011
Blanfordia japonica (Adams, 1861)*	AB611727	AB611726	AB611725	Japan, Niigata, Sado	Kameda and Kato 2011
Blanfordia simplex Pilsbry, 1902	AB611731	AB611730	AB611729	Japan, Yamagata, Yunohama	Kameda and Kato 2011
Cecina manchurica Adams, 1861*	AB611743	AB611742	AB611741	Japan, Ishikawa, Nanao	Kameda and Kato 2011
Delavaya dianchiensis Davis & Guo, 1986	KC832692	KC832713	—	China, Yunnan, Dianchi Lake	Liu et al. 2014
Fukuia kurodai Abbott & Hunter, 1949*	AB611767	AB611766	AB611765	Japan, Fukui, Takeda	Kameda and Kato 2011
Fukuia multistriata Abbott & Hunter, 1949	AB611779	AB611778	AB611777	Japan, Fukui, Umeura	Kameda and Kato 2011
Fukuia ooyagii Minato, 1982	AB611783	AB611782	AB611781	Japan, Aomori, Iwaya	Kameda and Kato 2011
Gammatricula shini (Habe, 1961)	AB611799	AB611798	AB611797	Japan, Okinawa, Yonaguni Is.	Kameda and Kato 2011
Gammatricula songi Davis, Chen & Yu, 1994	EF394902	EF394867	EF394879	China, Zhejiang, Zhongcun	Guan et al. 2008
Hubendickia schuetti (Brandt, 1968)	KC832688	KC832709	—	Laos, Ban Xieng-Wang	Liu et al. 2014
Jinghongia jinghongensis (Guo & Gu, 1985)*	KC832707	KC832728	—	China, Yunnan, Xishuangbanna	Liu et al. 2014
Manningiella polita Brandt, 1970*	KC832694	KC832715	—	Thailand, Phibun Mangsahan	Liu et al. 2014
Neoprososthenia levayi (Bavay, 1896)	KC832687	KC832708	—	Laos, Ban Hat-Xai-Kuhn	Liu et al. 2014
Neotricula aperta (Temcharoen, 1971)*	AF531541	AF531556	AY207034	Mekong River (28S Thailand, 16S/COI Laos)	Attwood et al. 2003
Neotricula burchi (Davis, 1968)	AF531544	AF531542	AY207035	Thailand, Chiang-Mai	Attwood et al. 2003
Oncomelania hupensis Gredler, 1881*	AB611787	AB611786	AB611785	Japan, Yamanashi, Nirasaki	Kameda and Kato 2011
Oncomelania minima (Bartsch, 1936)	AB611791	AB611790	AB611789	Japan, Ishikawa, Wajima	Kameda and Kato 2011
Pachydrobia munensis Brandt, 1968	KC832700	KC832721	—	Thailand, Phibun Mangsahan	Liu et al. 2014
Pomatiopsis lapidaria (Say, 1817)*	AF367636	AY676118	—	USA, Michigan, Bridgewater	Wilke et al. 2001
Robertsiella silvicola Attwoodet al., 2005	AF531550	AF531548	—	Malaysia, Kedah, Baling	Attwood et al. 2003
Tricula bambooensis Davis & Zheng, 1986	KC832699	KC832720	—	China, Yunnan, Dianchi Lake	Liu et al. 2014
Tricula bollingi Davis, 1968	AF531553	AF531551	AY207039	Thailand, Chiang-Mai	Attwood et al. 2003
Tricula fujianensis (Liu et al., 1983)	EF394893	EF394873	EF394885	China, Fujian, Sanming	Guan et al. 2008
Tricula hongshanensis Tang et al., 1986	EF394896	EF394876	EF394888	China, Hubei, Kedian	Guan et al. 2008
Tricula hortensis Attwood & Brown, 2003	EF394900	EF394871	EF394883	China, Sichuan, Han-Wang	Guan et al. 2008
Tricula hsiangi Kang, 1984	EF394897	EF394877	EF394889	China, Hubei, Shenjiabao	Guan et al. 2008
Stenothyridae					
Stenothyra australis Hedley, 1901	KC439692	KC439814	KC439915	Australia, Queensland, Magazine Cr.	Golding 2014
Stenothyra paludicola van Benthem Jutting, 1963	KC439733	KC439855	KC439923	Timor-Leste, Manufahi	Golding 2014
Tateidae					
Potamolithus ribeirensis Pilsbry, 1911	JX970618	JX970549	—	Brazil, São Paulo, Iporanga	Wilke et al. 2013
Potamopyrgus antipodarum (Gray, 1843)	AY631102	AY314009	AY014159	Undetermined	Guan et al. 2008
Potamopyrgus estuarinus Winterbourn, 1970	AB930485	—	AB930357	New Zealand, Auckland, Orewa	Takano and Kano 2014
Tatea huonensis (Tenison Woods, 1876)*	JX970619	JX970550	—	Australia, New South Wales, Manly Lagoon	Wilke et al. 2013
Tomichiidae					
Coxiella striatula (Menke, 1843)*	KC439800	KC109948	KC110000	Australia, Victoria, Nelson	Criscione and Ponder 2013
Tomichia ventricosa (Reeve, 1842)*	—	JX970552	—	South Africa, Agulhas Plain	Wilke et al. 2013
Truncatellidae					
Truncatella pfeifferi Martens, 1860	AB611819	AB611818	AB611817	Japan, Ishikawa, Nanao	Kameda and Kato 2011
Truncatella subcylindrica (Linnaeus, 1767)*	—	KC110035	KC109982	Italy, Sicily, Trapani	Criscione and Ponder 2013

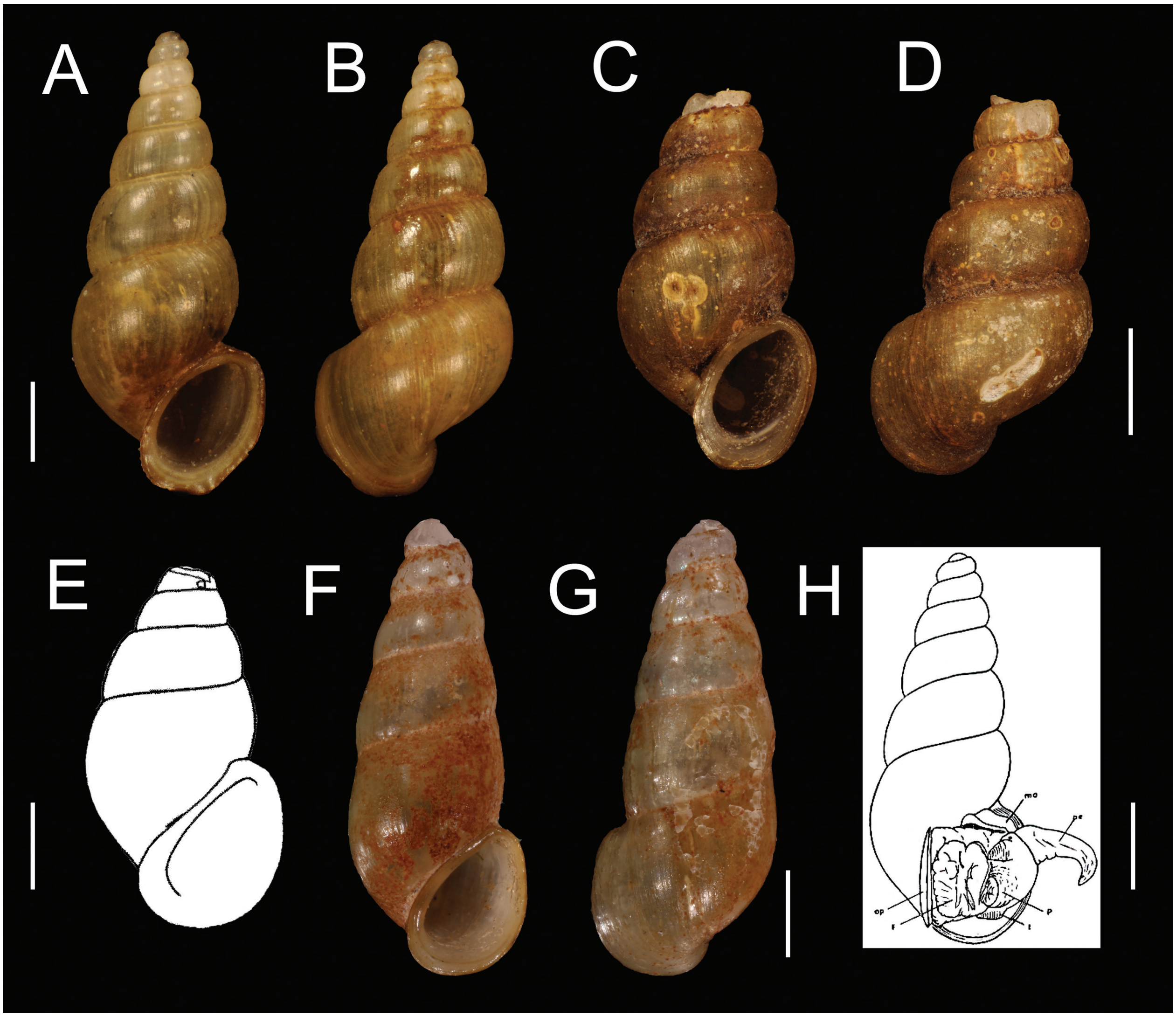

Figure 1. Shells of *Idiopyrgus* spp. **A, B.** *I. souleyetianus* Pilsbry, 1911, holotype ANSP 100534; **C, D.** *I. pilsbryi* Baker, 1914, lectotype ANSP 130700; **E.** *I. walkeri* Pilsbry, 1924, reproduced from Pilsbry (1924: p. 6, fig. 9); **F, G.** *I. rudolphi* (Hass, 1938), holotype SMF 24365; **H.** *I. brasiliensis* (Rey, 1959), reproduced from Rey (1959: p. 145, fig. 2). Scale bars: 1 mm.

from the same cave (Fig. 2A–D, F–H), like what is observed in many other freshwater truncatelloids. The shell and the spire of some specimens can be shorter (Fig. 2C) or taller and more elongated (Fig. 2D), the body whorl can be slighter wider (Fig. 2C, H), the shell sculpture can be more prominent (Fig. 2E, G), and a subsutural cord can be present (Fig. 2E).

Given its occurrence in four distinct caves of Central region (Bahia state), *Idiopyrgus adamanteus* sp. nov. is considered a troglophilic species rather than a strict troglobitic one. The region of Central is characterized by a dry vegetation type (Caatinga) and the caves represent good shelters for these animals, given their high-humidity microhabitats. Few collections were conducted outside the caves and, as such, this species occurrence outside subterranean habitats was not tested. Nevertheless, the lack of body pigmentation and the translucent shell of some specimens (Fig. 2A–H) are possible troglomorphisms, i.e., morphological traits typically observed in cave-dwelling gastropods (Christiansen 2012; Trontelj et al. 2012; Salvador et al. 2022).

The caves of Central municipality and their surroundings are impacted by deforestation caused by subsistence agriculture, mining activities, and wind energy installations in the karst landscapes (Bichuette, pers. obs.).

Idiopyrgus minor sp. nov.

https://zoobank.org/5472AFA6-F079-4FE7-B05F-801ADC23B749

Fig. 2I–K

Type material. MZSP 158238 (holotype), LES 0027980 (2 paratypes, from Gruna do Engrunado).

Type locality. Brazil, Bahia state, Feira da Mata municipality, Gruna da Pingueira II cave.

Distribution. Known only from two caves in Feira da Mata municipality.

Etymology. From Latin, meaning 'little'.

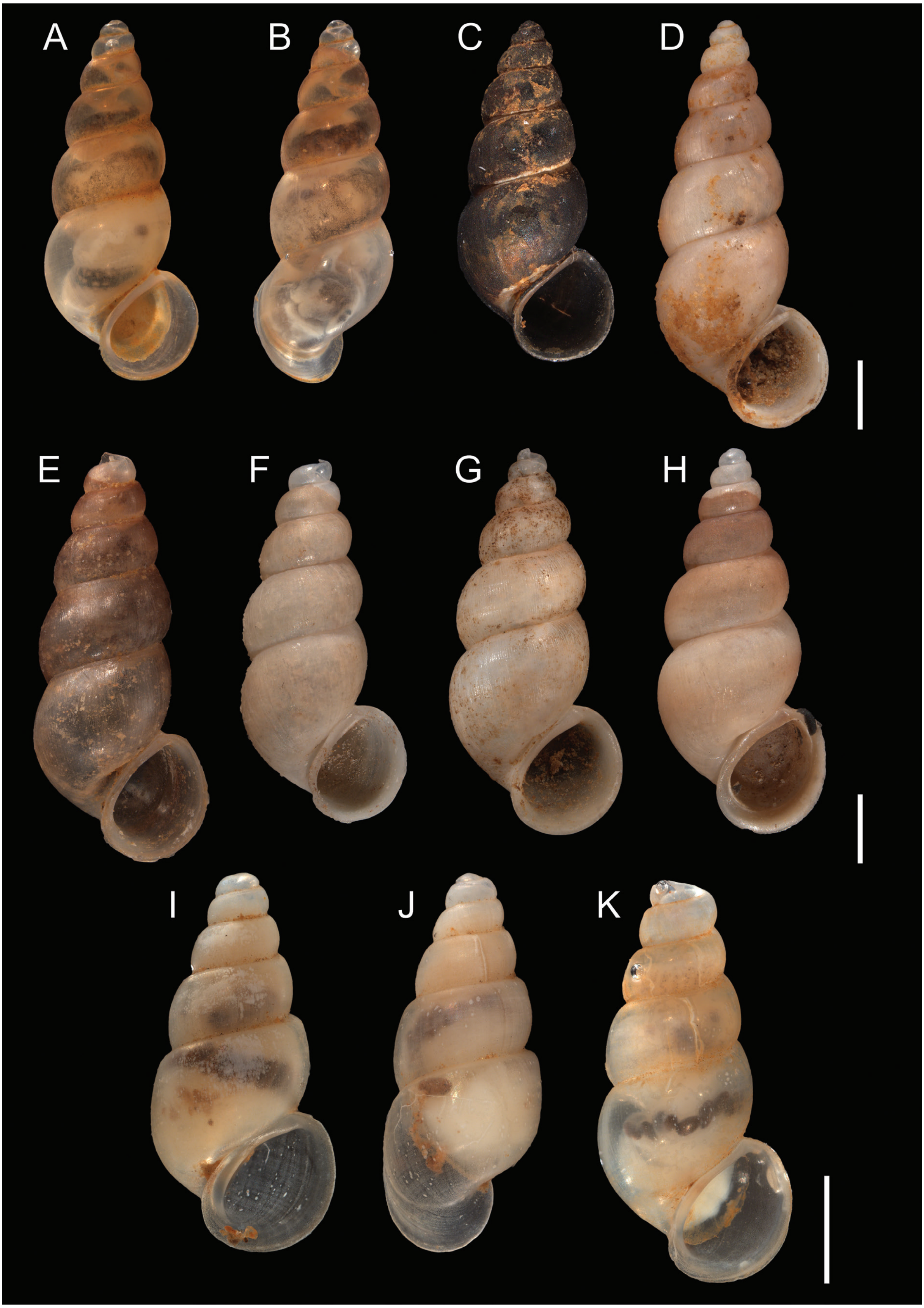

Figure 2. Shells of the two new species of *Idiopyrgus*. **A–H.** *Idiopyrgus adamanteus* sp. nov.; **A, B.** Holotype MZSP 158237; **C.** Paratype LES 0027975; **D.** Paratype LES 0027975; **E.** LES 0027975 (from Gruta da Machadinha); **F.** LES 0027978 (from Toca de Candeias); **G.** LES 0027977 (from Toca de Candeias); **H.** LES 0027978 (from Toca de Candeias); **I–K.** *Idiopyrgus minor* sp. nov.; **I, J.** Holotype MZSP 158238; **K.** Paratype LES 0027980 (from Gruna do Engrunado). Scale bars: 1 mm

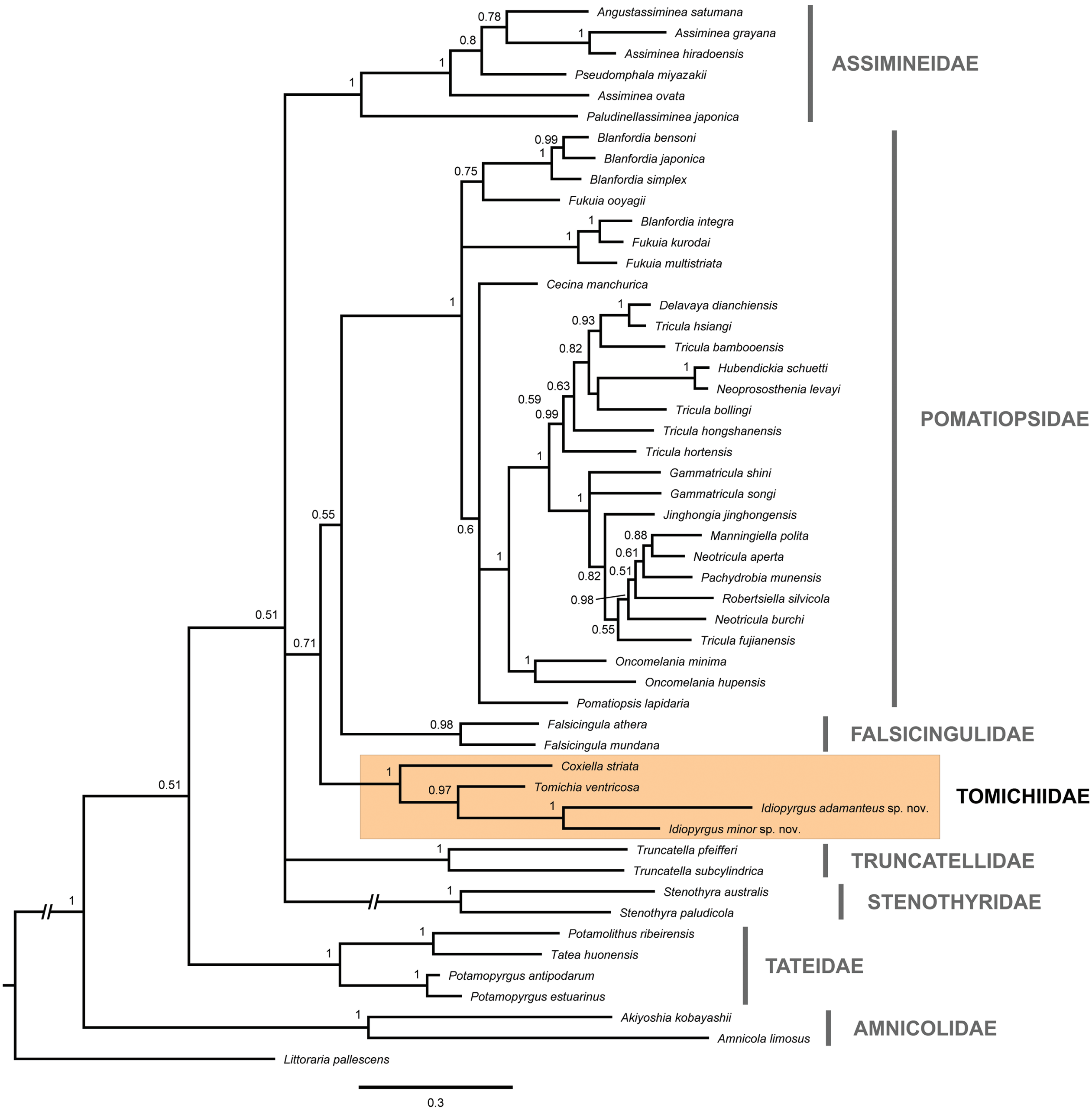

Figure 3. Bayesian inference phylogenetic tree based on CO1, 16S, ITS2 and 28S, highlighting the family Tomichiidae and the position of *Idiopyrgus*. The posterior probabilities are shown on the nodes; scale bar is substitutions per site.

Diagnosis. Smaller shell than congeners; spire not as elongated and wider than most congeners; aperture proportionately larger in relation to preceding whorl.

Description. Shell minute, truncatelloid, of translucent white color. Protoconch not too prominent. Shell smooth except for fine growth lines. Suture deep, rendering whorls lightly shouldered in holotype (Fig. 2I, J). Whorl profile convex. Whorls increasing regularly in size with growth. Aperture large in proportion to body whorl; oval to circular, with a more acuminate end towards the upper lip insertion. Peristome complete; reflexed but not thickened. Shell rimate. Operculum translucent, of same color as the shell. Soft body white.

Measurements. holotype: 5 whorls, H = 3.5 mm, D = 1.7 mm; paratype: H = 3.7 mm, D = 1.7 mm.

Genetic data. GenBank reg. nrs: COI, ON720330; 16S, ON720564; ITS2+28S, ON720562.

Remarks. *Idiopyrgus minor* sp. nov. can be distinguished from its congeners by its small size. It also has a less elongated and wider spire than most of its congeners, the exceptions being *I. pilsbryi* and *I. walkeri* (Fig. 1). Nevertheless, it can also be easily diagnosed from them: *I. minor* sp. nov. is much smaller and has a narrower shell than *I. walkeri*, and has a larger and wider aperture than *I. pilsbryi*. Finally, there is a reasonably large genetic distance separating *I. minor* sp. nov. from *I. adamanteus* sp. nov. (Fig. 3), comparable to the distance between the species of Truncatellidae and Stenothyridae present on the tree and larger than the distances between species of Pomatiopsidae.

This species is considered troglobitic, given its occurrence in a single cave of the Serra do Ramalho karst area. The specimens were collected in pools resulting from infiltration water and seem to be restricted to this habitat. Besides the translucent shell and lack of body pigmentation, the smaller body size of *I. minor* sp. nov. can also be interpreted as a possible troglomorphism, given that miniaturization is common in cave organisms, including snails (Christiansen 2012; Salvador et al. 2022).

The Serra do Ramalho region has been historically exploited for agriculture, charcoal production, and mining, from small to large scales (Gallão and Bichuette 2018).

Phylogenetics and biogeography

The phylogenetic analysis included a total of 51 species (counting the outgroup) and all family level taxa were well-supported (posterior probability, PP = 1 in all cases except Falsicingulidae, for which PP = 0.98). As such, even though there is an unsolved polytomy in the tree (Fig. 3; in all likelihood a result of the exclusion of northern hemisphere families not immediately related to our question), the membership of each species to a particular family can be readily and reliably assessed.

In that regard, it can be seen that *Idiopyrgus* does not belong to Pomatiopsidae; rather, it is grouped together with *Tomichia* and *Coxiella*. These three genera together form the family Tomichiidae, which recovers the results of Wilke et al. (2013) and fully establishes this family as a Gondwanan clade. The most basal branch in Tomichiidae appears to be the Australian *Coxiella*, with the South African *Tomichia* and the South American *Idiopyrgus* spp. forming a well-supported monophyletic clade (PP = 0.97; Fig. 3). This represents a typical Gondwanan scenario, with the Australian branch being the most basal one. Furthermore, it can be surmised that all three genera are relicts in their respective continents, given their present low diversity and restricted distributions (Wilke 2019).

Nevertheless, the diversity of the Brazilian branch of this family might be underestimated. Specimens of *I. souleyetianus* have been reported from several localities in Brazil, including the aphotic zones of caves (e.g., Thiengo et al. 2005; Salvador et al. 2017; Salvador and Simone 2021). Shell morphology and the apparent isolation of some populations in cave systems indicate, however, that "*I. souleyetianus*" from the literature is likely a species complex (see also the discussion below). The two new species described herein from caves also point towards this conclusion. Future morphological and molecular studies might thus shed light on the real diversity of this group in Brazil.

It is also noteworthy that Tomichiidae is absent from Zealandia, especially considering that the family Tateidae is likewise a Gondwanan clade and has representatives in South America, Australia and New Zealand (Fig. 3; Zielske et al. 2016; Ponder 2019). Given the more basal position of Tateidae in relation to Tomichiidae, it can be hypothesized that it represents an earlier branch of Truncatelloidea and that Tomichiidae therefore arose after Zealandia had split from Gondwana (circa 80 Ma).

Taxonomy

Based on the study of type material and further specimens available to us, it was possible to reassess those species of *Idiopyrgus* that are presently considered synonyms (as per Simone 2006) of *I. souleyetianus*. This assessment was done based on conchological characters of the type specimens, topotypes, and additional voucher specimens, as no additional DNA-grade material could be acquired. Therefore, we are aware that our proposed arrangement may change in the future when more material becomes available.

I. souleyetianus (Fig. 1A, B) is here restricted to populations from Espírito Santo state (Southeast Atlantic hydrographic region), which includes the type locality, and Bahia state (São Francisco hydrographic region; specimens reported by Salvador et al. 2017) (Fig. 4). The specimens from northern Minas Gerais (São Francisco hydrographic region; Fig. 4) assigned by Salvador and Simone (2021) to *I. souleyetianus* display much smaller shells, with fewer whorls and a weak axial teleoconch sculpture. As such, they might represent a still unrecognized species. Likewise, the records from Goiás state assigned to *I. souleyetianus* by Thiengo et al. (2005: not illustrated) stem from an area belonging to yet another hydrographic region (Tocantins-Araguaia; Fig. 4) and should be reassessed; they are treated here as *Idiopyrgus* sp.

Idiopyrgus pilsbryi (Fig. 1C, D) has a much smaller shell than *I. souleyetianus*, having circa 2/3 of the latter's shell length. The whorls of *I. souleyetianus* are taller than those of *I. pilsbryi*, and it has a taller spire with more whorls. *I. pilsbryi* inhabits Rio Grande do Norte state, ca. 1,500 km north of the type locality of *I. souleyetianus*, in a completely different climate and biome. It is geographically isolated from *I. souleyetianus*, whose northernmost occurrence is in central Bahia state (Fig. 4), and in a different hydrographic region (Eastern Northeast Atlantic region). As such, we reinstate *I. pilsbryi* as an accepted species.

Idiopyrgus walkeri was described from Minas Gerais state and its type specimen could not be located in the ANSP collection during the present study. By its description and published illustrations (Pilsbry 1924, reproduced here as Fig. 1E), it has a more conical shell and wider and more convex whorls than *I. souleyetianus* (being of similar size to it), alongside a shorter spire with fewer whorls. It inhabits the São Francisco hydrographic region (Fig. 4), but on a different area from where *I. souleyetanus* is known. In absence of type material, *I. walkeri* is here considered potentially distinct from *I. souleyetanus*, but it is regarded as a taxon inquirendum until the types come to light or topotypes are collected. Three specimens collected from caves in Coribe municipality, southern Bahia state (Fig. 4), have wider shells and could represent specimens of *I. walkeri.*

Idiopyrgus rudolphi (Fig. 1F, G) is the most immediately diagnosable species, as its shell has a straighter spire

Figure 4. Map of Brazil showing state borders, hydrographic regions, and occurrence of *Idiopyrgus* spp. Black squares represent the known records of each species, while the red circles represent specimens of uncertain identification (potentially representing new species) here labeled *Idiopyrgus* sp.; the red square indicates the area where the specimen used in the phylogeny was collected.

profile, almost subulinid-like, with whorls only slightly convex in profile. This feature was deemed sufficient by Haas (1938) to describe the genus *Hydracme* to house this species. Considering the morphological variation known in the shell shape of truncatelloids, we prefer to follow the most conservative approach for now and to maintain *Hydracme* as a synonym of *Idiopyrgus* until molecular studies on *I. rudolphi* can be conducted and its position in the group's phylogeny assessed. *I. rudolphi* is known only from its type locality in Pernambuco state (São Francisco hydrographic region), seemingly isolated from *I. souleyetianus* to the south and *I. pilsbryi* to the north (Fig. 4).

The type material of *Idiopyrgus brasiliensis*, despite being databased in the MZSP collection, could not be located during the present study. According to the species description and published illustrations (Rey 1959, reproduced here as Fig. 1H), this species is very similar in shell shape and size to *I. souleyetianus*, but it has a taller body whorl, a more vertically positioned aperture, and a less reflected lip. It is also geographically isolated from other *Idiopyrgus* spp. (Fig. 3). Therefore, we reinstate it as an accepted species. It inhabits Mato Grosso do Sul state (Paraguay hydrographic region) and, given its occurrence in Corumbá municipality (Rey 1959) close to the border, it should likely be found in Bolivia and perhaps Paraguay as well. The record from Mato Grosso state (Simone 2006; Birckolz et al. 2016) is in all likelihood a misinterpretation of the records of Rey (1959), since back then the state of Mato Grosso still contained the area that later became Mato Grosso do Sul state. The genus *Aquidauania*, which was erected to house *I. brasiliensis* (erroneously described as belonging to *Oncomelania* Gredler, 1881, an Asian genus; Rey 1959), is therefore a synonym of *Idiopyrgus*, as already indicated by Simone (2006).

The two new species described herein, *I. adamanteus* sp. nov. and *I. minor* sp. nov., are from Bahia state, belonging to the Middle São Francisco hydrographic region (Fig. 4). *Idiopyrgus adamanteus* sp. nov. is apparently isolated from *I. souleyetianus* in the south and *I. rudolphi* in the north (Fig. 4). The distribution of *I. minor* sp. nov., however, overlaps with *I. souleyetianus* and potentially with *I. walkeri* as well (Fig. 4). It is thus tempting to consider *I. souleyetianus* and/or *I. walkeri* as widespread species whose isolated populations in caves might have given rise to new species such as *I. minor* sp. nov.

Conclusion

Based on our results, we transfer *Idiopyrgus* (and *Coxiella*) from Pomatiopsidae to Tomichiidae, and reinstate previously synonymized species-level taxa. Hence, we propose the following arrangement for family Tomichiidae and, in particular, the genus *Idiopyrgus*.

Superfamily Truncatelloidea Gray, 1840
Family Tomichiidae Wenz, 1938 [=Coxiellidae Iredale, 1943]
Genus *Tomichia* Benson, 1851
Genus *Coxiella* E. A. Smith, 1894
Genus *Idiopyrgus* Pilsbry, 1911 [=*Hydracme* Haas, 1938; *Aquidauania* Davies, 1979]
Idiopyrgus souleyetianus Pilsbry, 1911 [type species]
Idiopyrgus adamanteus sp. nov.
Idiopyrgus brasiliensis (Rey, 1959)
Idiopyrgus minor sp. nov.
Idiopyrgus pilsbryi Baker, 1914
Idiopyrgus rudolphi (Haas, 1938)
Idiopyrgus walkeri Pilsbry, 1924 [taxon inquirendum]

Acknowledgements

We are very grateful to Paul Callomon (ANSP), Sigrid Hof (SMF), and Jean-Claude Stahl (NMNZ), for information and/or photos of the specimens used in the present study; to J.E. Gallão, J.S. Gallo and D.F. Torres for help in the field trips and organization of LES collection; to GBPE and Grupo Pierre Martin de Espeleologia (GPME) for sharing speleological information, respectively, of Serra do Ramalho karst area and of Central region with MEB; to SISBIO (Sistema de Autorização e Informação em Biodiversidade) for the collection permit to MEB (#28992); and to Frank Köhler and Thomas von Rintelen for the comments and suggestions. MEB thanks FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo, Brazil, regular Project number 2010/08459-4, Central collections), CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil, productivity fellowship 310378/2017–6), and ICMBio/CECAV (Instituto Chico Mendes para Conservação da Biodiversidade/ Centro Nacional de Pesquisa e Conservação de Cavernas, Brazil) for financial support to the project "Estudos para definição de áreas prioritárias para a Conservação de Proteção Espeleológico na Serra do Ramalho – BA", under execution by the GBPE (Grupo Bambuí de Pesquisas Espeleológicas), coordinated by Ezio Rubbioli.

References

Attwood SW, Ambu S, Meng XH, Upatham ES, Xu FS, Southgate VR (2003) The phylogenetics of triculine snails (Rissooidea: Pomatiopsidae) from south-east Asia and southern China: historical biogeography and the transmission of human schistosomiasis. The Journal of Molluscan Studies 69(3): 263–271. https://doi.org/10.1093/mollus/69.3.263

Benson WH (1851) Characters of Tomichia, a new palustrine testaceous mollusk from Southern Africa, heretofore referred to the genus *Truncatella*. Annals & Magazine of Natural History 7(2): 377–380.

Birckolz CJ, Salvador RB, Cavallari DC, Simone LRL (2016) Illustrated checklist of newly described (2006–2016) land and freshwater Gastropoda from Brazil. Archiv für Molluskenkunde 145(2): 133–150. https://doi.org/10.1127/arch.moll/145/133-150

Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17(4): 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Christiansen K (2012) Morphological adaptations. In: Culver DC, White WB (Eds) Encyclopedia of Caves, Elsevier Academic Press, Asmterdam, 2nd edn., 517–528. https://doi.org/10.1016/B978-0-12-383832-2.00075-X

Criscione F, Ponder WF (2013) A phylogenetic analysis of rissooidean and cingulopsoidean families (Gastropoda: Caenogastropoda). Molecular Phylogenetics and Evolution 66(3): 1075–1082. https://doi.org/10.1016/j.ympev.2012.11.026

Davis GM (1979) The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. Academy of Natural Sciences, Philadelphia, 120 pp.

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

Gallão JE, Bichuette ME (2018) Brazilian obligatory subterranean fauna and threats to the hypogean environment. ZooKeys 746: 1–23. https://doi.org/10.3897/zookeys.746.15140

Golding RE (2014) Molecular phylogeny and systematics of Australian and East Timorese Stenothyridae (Caenogastropoda: Truncatelloidea). Molluscan Research 34(2): 102–126. https://doi.org/10.1080/13235818.2014.888969

Guan F, Niu AO, Attwood SW, Li YL, Zhang B, Zhu YH (2008) Molecular phylogenetics of triculine snails (Gastropoda: Pomatiopsidae) from southern China. Molecular Phylogenetics and Evolution 48(2): 702–707. https://doi.org/10.1016/j.ympev.2008.04.021

Haas F (1938) Neue Binnen-Mollusken aus Nordost-Brasilien. Archiv für Molluskenkunde 70(1): 46–51.

Iredale T (1943) A basic list of the fresh water Mollusca of Australia. Australian Zoologist 10(2): 188–230.

Kameda Y, Kato M (2011) Terrestrial invasion of pomatiopsid gastropods in the heavy-snow region of the Japanese Archipelago. BMC Evolutionary Biology 11(1): e118. https://doi.org/10.1186/1471-2148-11-118

Katoh K, Standley DM (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in performance and usability.

Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Katoh K, Misawa K, Kuma K, Miyata T (2002) MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30(14): 3059–3066. https://doi.org/10.1093/nar/gkf436

Liu L, Huo GN, He HB, Zhou B, Attwood SW (2014) A phylogeny for the Pomatiopsidae (Gastropoda: Rissooidea): a resource for taxonomic, parasitological and biodiversity studies. BMC Evolutionary Biology 14(1): e29. https://doi.org/10.1186/1471-2148-14-29

Miller MA, Schwartz T, Pickett BE, He S, Klem EB, Scheuermann RH, Passarotti M, Kaufman S, O'Leary MA (2015) A RESTful API for access to phylogenetic tools via the CIPRES Science Gateway. Evolutionary Bioinformatics Online 11: 43–48. https://doi.org/10.4137/EBO.S21501

Morretes FL (1949) Ensaio de catálogo dos moluscos do Brasil. Arquivos do Museu Paranaense 7: 5–216.

Pilsbry HA (1911) Non-marine Mollusca of Patagonia. In: Scott WB (Ed.) Reports of the Princeton University Expeditions to Patagonia, 1896–1899. Volume III, 2. Zoology. Princeton University, Princeton, N.J, Schweizerbart'sche Verlagshandlung, Stuttgart, 513–633. https://doi.org/10.5962/bhl.title.10337

Pilsbry HA (1924) South American land and fresh-water mollusks: Notes and descriptions. Proceedings. Academy of Natural Sciences of Philadelphia 76: 49–66.

Ponder W (2019) Tateidae Thiele, 1925. In: Lydeard C, Cummings KS (Eds) Freshwater Mollusks of the World. A Distribution Atlas. John Hopkins University Press, Baltimore, 134–138.

Rey L (1959) Molluscs of the genus *Oncomelania*, in Brazil, and their possible epidemiological significance. Revista do Instituto de Medicina Tropical de São Paulo 1(2): 144–149.

Ronquist F, van der Mark P, Huelsenbeck JP (2009) Bayesian phylogenetic analysis using MrBayes. In: Lemey P, Salemi M, Vandamme A-M (Eds) The Phylogenetic Handbook: a Practical Approach to Phylogenetic Analysis and Hypothesis Testing. Cambridge University Press, Cambridge, 210–266. https://doi.org/10.1017/CBO9780511819049.009

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Salvador RB, Simone LRL (2021) New records of Orthalicoidea land snail species for the state of Minas Gerais, southeastern Brazil (Gastropoda, Stylommatophora). Check List 17(2): 395–399. https://doi.org/10.15560/17.2.395

Salvador RB, Cavallari DC, Simone LRL (2017) Taxonomical study on a sample of land and freshwater snails from caves in central Brazil, with description of a new species. Zoosystematics and Evolution 93(1): 135–141. https://doi.org/10.3897/zse.93.10995

Salvador RB, Silva FS, Cavallari DC, Cunha CM, Bichuette ME (2022) Cave-dwelling gastropods (Mollusca: Gastropoda) of Brazil: state of the art and conservation. Zoologia 39: e21033. https://doi.org/10.1590/s1984-4689.v39.e21033

Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and compilation of Conserved Polymerase Chain Reaction primers. Annals of the Entomological Society of America 87(6): 651–701. https://doi.org/10.1093/aesa/87.6.651

Simone LRL (2006) Land and Freshwater Molluscs from Brazil. EGB/Fapesp, São Paulo, 390 pp.

Simone LRL (2012) A new genus and species of cavernicolous Pomatiopsidae (Mollusca, Caenogastropoda) in Bahia, Brazil. Papéis Avulsos de Zoologia 52(40): 515–524. https://doi.org/10.1590/S0031-10492012022000001

Simone LRL, Salvador RB (2021) A new species of *Spiripockia* from eastern Brazil and reassignment to Cochliopidae (Gastropoda, Truncatelloidea). Journal of Natural History 54(47–48): 3121–3130. https://doi.org/10.1080/00222933.2021.1890850

Smith EA (1894) On the land-shells of Western Australia. Proceedings of the Malacological Society of London 1(3): 84–99.

Takano T, Kano Y (2014) Molecular phylogenetic investigations of the relationships of the echinoderm-parasite family Eulimidae within Hypsogastropoda (Mollusca). Molecular Phylogenetics and Evolution 79: 258–269. https://doi.org/10.1016/j.ympev.2014.06.021

Talavera G, Castresana J (2007) Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Systematic Biology 56(4): 564–577. https://doi.org/10.1080/10635150701472164

Thiengo SC, Santos SB, Fernandez MF (2005) Malacofauna límnica da área de influência do lago da usina hidrelétrica de Serra da Mesa, Goiás, Brasil. I. Estudo qualitativo. Revista Brasileira de Zoologia 22(4): 867–874. https://doi.org/10.1590/S0101-81752005000400010

Trontelj P, Blejec A, Fišer C (2012) Ecomorphological convergence of cave communities. Evolution 66(12): 3852–3865. https://doi.org/10.1111/j.1558-5646.2012.01734.x

Wade CM, Mordan PB, Naggs F (2006) Evolutionary relationships among the Pulmonate land snails and slugs (Pulmonata, Stylommatophora). Biological Journal of the Linnean Society. Linnean Society of London 87(4): 593–610. https://doi.org/10.1111/j.1095-8312.2006.00596.x

Wenz W (1938–1944) Teil 1: Allgemeiner Teil und Prosobranchia. In: Schindewolf OH (Ed.) Handbuch der Paläozoologie, Band 6, Gastropoda. Borntraeger, Berlin, 1639 pp.

Wilke T (2019) Pomatiopsidae Stimpson, 1865. In: Lydeard C, Cummings KS (Eds) Freshwater Mollusks of the World. A Distribution Atlas. John Hopkins University Press, Baltimore, 126–130.

Wilke T, Davis GM, Falniowski A, Giusti F, Bodon M, Szarowska M (2001) Molecular systematics of Hydrobiidae (Mollusca: Gastropoda: Rissooidea): testing monophyly and phylogenetic relationships. Proceedings. Academy of Natural Sciences of Philadelphia 151(1): 1–21. https://doi.org/10.1635/0097-3157(2001)151[0001:MSOHMG]2.0.CO;2

Wilke T, Haase M, Hershler R, Liu H-P, Misof B, Ponder W (2013) Pushing short DNA fragments to the limit: phylogenetic relationships of 'hydrobioid' gastropods (Caenogastropoda: Rissooidea). Molecular Phylogenetics and Evolution 66(3): 715–736. https://doi.org/10.1016/j.ympev.2012.10.025

Zielske S, Ponder WF, Haase M (2016) The enigmatic pattern of long-distance dispersal of minute freshwater gastropods (Caenogastropoda, Truncatelloidea, Tateidae) across the South Pacific. Journal of Biogeography 44(1): 195–206. https://doi.org/10.1111/jbi.12800