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3D X-ray microscopy (Micro-CT) and SEM reveal *Zospeum troglobalcanicum* Absolon, 1916 and allied species from the Western Balkans (Ellobioidea: Carychiidae)

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[6]urn:lsid:zoobank.org:author:00C5A26B-6E4A-41D9-BC9B-F36A2799E1AF
[7]urn:lsid:zoobank.org:author:683D0AB7-CDD8-4FAA-94B6-436F3BFB8873
[8]urn:lsid:zoobank.org:author:9A8A56B0-19FA-42AB-A85E-4FCA98BF4A6F

Abstract. Though recent investigations have contributed substantially to our understanding of the Alpine-Dinaric radiation of the genus *Zospeum* Bourguignat, 1856, its southernmost member, *Zospeum troglobalcanicum* Absolon, 1916, has remained a taxonomic ghost. The assumed absence of type material, the insufficient original description, and the lack of new samples from its Western Balkan type locality have stymied further clarification. The recent discovery of a single syntype shell housed at the Natural History Museum Vienna now enables the first morphological assessment via 3D X-ray and SEM imaging. Based on this image data, different characters for assessing the southernmost members of the genus are determined and a lectotype is designated. Eleven allied species from 15 Western Balkan populations are described from museum material and recent sampling efforts: *Z. amplioscutum* Jochum & Ruthensteiner sp. nov., *Z. biokovoense* Jochum & Ruthensteiner sp. nov., *Z. constrictum* Jochum & Ruthensteiner sp. nov., *Z. dubokidoense* Jochum & Ruthensteiner sp. nov., *Z. intermedium* Jochum & Ruthensteiner sp. nov., *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov., *Z. neuberti* Jochum & Ruthensteiner sp. nov., *Z. njegusiense* Jochum & Ruthensteiner sp. nov., *Z. njunjicae* Jochum, Schilthuizen & Ruthensteiner sp. nov., *Z. tortuosum* Jochum & Ruthensteiner sp. nov. and *Z. tumidum* Jochum, Schilthuizen & Ruthensteiner sp. nov. One species, *Z. kolbae*, is described using DNA sequence data and one species, *Z. simplex* Inäbnit, Jochum & Neubert, 2021 for which DNA sequence data is already available, is supported by morphological data presented in this study. The DNA sequence dataset (COI, 16S and H3) is included here and implemented in the most recent phylogenetic reconstruction of the genus. A translation of Karel Absolon's notes from the Balkan scientific expeditions is provided.

Keywords. Dinarides, lectotype, shell morphology, subterranean ecology, troglobitic microsnails.

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Introduction

Recent phylogenetic and morphological investigations of the subterranean snails of the genus *Zospeum* Bourguignat, 1856 have covered much ground in clarifying their ancestry, distribution, and anatomical systems (Weigand *et al*. 2013; Jochum *et al*. 2015; Inäbnit *et al*. 2019, 2021; Kneubühler *et al*. 2021). While Inäbnit *et al*. (2019, 2021) raised the number of the Eastern Alpine-Dinaride species to 26, Kneubühler *et al*. (2021) described the northern Spanish radiation, *Iberozospeum* Jochum, Kneubühler, Prieto & Neubert, 2021, now comprising nine taxa.

Much of this coverage stems from recent decades of speleobiological sampling and accessibility into caves using state of the art contemporary kit to collect live material. For *Zospeum*, this includes cave systems from northeastern Italy, Austria, Slovenia, Croatia, Bosnia and Herzegovina and Montenegro (Inäbnit *et al*. 2019, 2021). Historically, caves of *Zospeum*'s Eastern Alpine and Dinaride range have been unevenly sampled such that the northern half of the distribution is richly represented by shells in several European museum collections, while *Zospeum* diversity of the southernmost, Croatian and Western Balkan extension is hardly known.

Before Inäbnit *et al*. (2019, 2021), only one southern species, *Zospeum troglobalcanicum* Absolon, 1916 was known, which was imaged initially as a pile of 13 shells from Benetina pećina (Bosnia and Herzegovina) and published together with other organisms from different Balkan caves in a speleological report. Detective work and recent translations of two of Absolon's original works in Czech give us an idea with whom he discussed his finds and exchanged material. Up to now, no *Z. troglobalcanicum*

type material is known and, as is the case for many older European collections, it likely disappeared in the ravages of two World Wars. Subsequently, when rare, southern *Zospeum* finds were documented by others, they automatically were considered *Z. troglobalcanicum* (Gittenberger 1975; Maier 1982) or *Z. amoenum* (Frauenfeld, 1856) because these shells fitted within the spectrum of *Z. amoenum* shell variability and similarly lacked apertural dentition (Absolon 1916b; Bole 1974).

Due to technological advances, finer image resolution is achieved using Micro-CT and SEM imagery. Characters such as low, discrete lamellae, can now be seen on the columella of shells, distinguishing them morphologically further from those of earlier classifications. As part of an ongoing effort to clarify carychiid diversity, *Zospeum* shells housed at the Natural History Museum Vienna (NHMW), including a newly discovered syntype of *Z. troglobalcanicum*, shells from the France Velkovrh collection housed at the Slovenian Museum of Natural History (MCSMNH), a shell from the Naturalis Biodiversity Center mollusk collection (RMNH) plus shells from three populations deriving from recent collecting trips in Bosnia and Herzegovina and Montenegro (Fig. 1 Map), are treated herein using Micro-CT and SEM imaging data. The NHMW syntype is consequently designated lectotype in this work. One population (Njeguši, NMBE 571122–571123) could be assessed by DNA sequencing, whereby sequences from this population are added to the existing DNA sequence dataset. These new data are integrated into Inäbnit *et al.*'s (2021) most recent phylogenetic reconstruction and presented here in context with its zospeid and iberozospeid congeners. One species, *Z. simplex* Inäbnit, Jochum & Neubert, 2021, assessed by DNA sequencing in Inäbnit *et al.* (2021), but morphologically insufficently described in that work, receives enhanced morphological assessment and description in this present paper. In

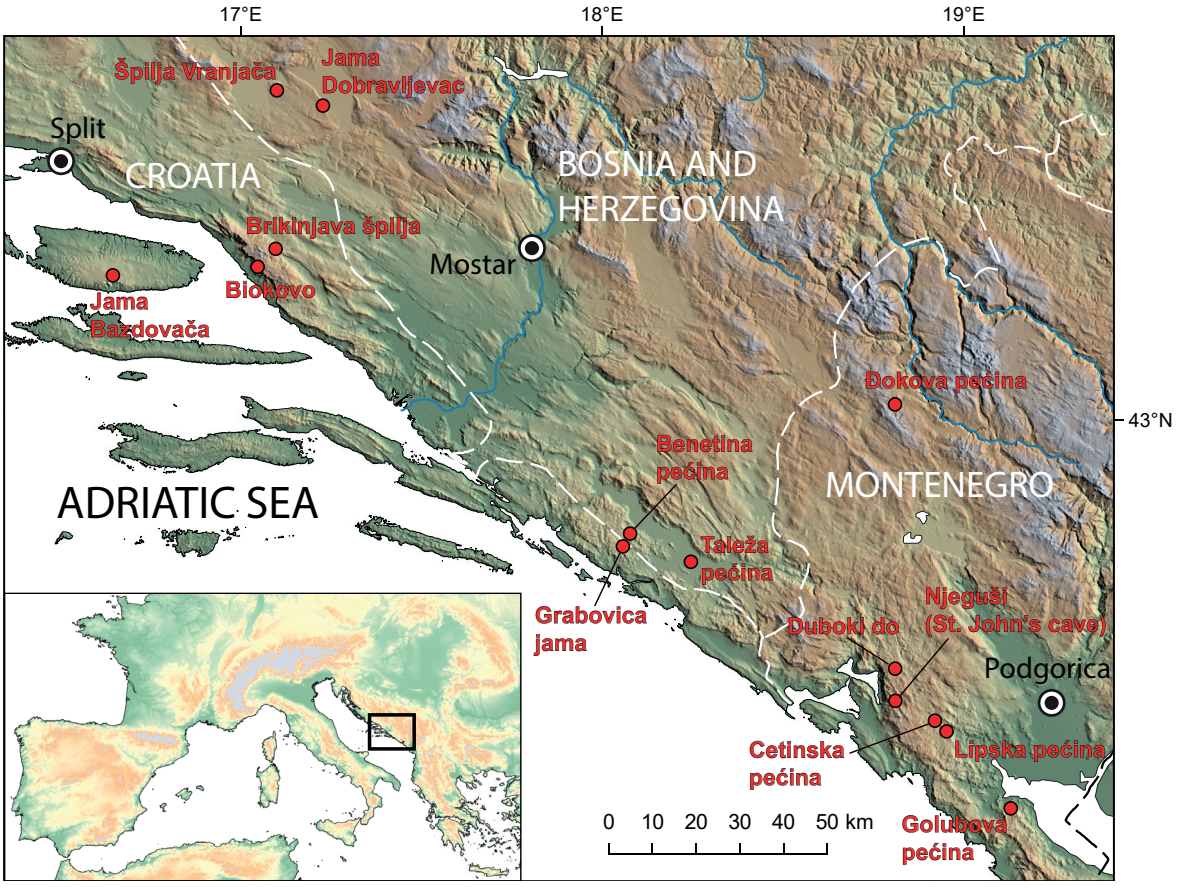

Fig. 1. Map showing Western Balkan cave localities of populations of *Zospeum* Bourguignat, 1856. Cave localities are indicated in red.

addition, based on the proposed lectotype of *Z. troglobalcanicum*, the single shell (NMBE 553414/1) attributed to *Z. troglobalcanicum* in Inäbnit *et al*. (2019: fig. 7u) is reassessed to the affinity status of *Z*. cf. *neuberti* sp. nov. while the shell (RMNH.MOL. 234132) illustrated in Gittenberger (1975) and considered *Z. troglobalcanicum* therein is re-evaluated and assigned to *Z. intermedium* Jochum & Ruthensteiner sp. nov. in this work. In addition, a translation from the original Czech (by M. Leinfelder 2019) documenting *Z. troglobalcanicum* in Karel Absolon's (1916a) two paragraphs ("Ku Kap VI") in the "Results of the Balkan expeditions" is presented here in English.

One cannot assess this rare, Western Balkan material without considering the intense geodynamic processes influencing its terrain and subterranean systems as well as the geopolitical history that has largely impacted the Western Balkan region. This region constitutes a geologically complex and highly seismically active zone comprising different stratigraphic units from the Paleozoic to the Quaternary (Baselt *et al*. 2023). Due to its lithologic composition, the region is subject to erosion, landslides, and floods while situated geographically at the intersection of multiple tectonic plates (Baselt *et al*. 2023). Though exploration of the complex cave systems in the Western Balkans has remained hazardous for several reasons, most of the shells in this study were collected prior to two World Wars and the hostilities of the 1991–1995 Western Balkan conflict. Since this time, and judging from the most recent landmine maps, quantities of landmines and explosive remnants of war (ERWs) remain in forested mountain slopes and fields atop of the cave systems that harbored the shells of this study. It is known that ordnance from the hostilities of the 1990's in Bosnia and Herzegovina are reported to have become mobilized and displaced by rainfall events (i.e. flooding caused by Cyclone Tamara, May 2014) causing them to migrate several kilometers from known and unknown cluster sites, contaminating previously uncontaminated areas (Baselt *et al*. 2023). Western Balkan subterranean cave systems, including those in this study, are frequently subjected to flooding events and enhanced river flows. These caves are not only geologically hazardous, but they constitute probable, undetected localities of potential ordnance displacement and mobilization events as well. Though 25 years have passed, and landmine sites are largely documented, Bosnia and Herzegovina is currently the most landmine-contaminated European country shown on minefield maps (see Baselt *et al*. 2023). Contrary to other cave systems harboring zospeid snails in Spain, France, Italy, Austria and even Slovenia, several caves in this study, including those in southern Croatia, BiH and parts of Montenegro, still lie in a highly concentrated landmine and ERW zone. Under these conditions, we emphasize that acquisition of fresh *Zospeum* in this study is remarkable and that additional material will probably remain, for the longer term, rare.

Material and methods

The studied material derived primarily from specimens housed in museum collections. The shells are devoid of any residual soft tissue precluding eventual molecular study via mummified remains.

Thirty-one adult individuals from 15 populations are housed in the following institutions and listed with locality data in Table 1. Specimens from recent exploration in Montenegro (Bajovo polje, Gornja Seoca and Njeguši) are deposited as vouchers in the NMBE, SMF and TxEx collections. All Micro-CT data are documented and stored at the Zoologische Staatssammlung München (ZSM). The Micro-CT data from the shell RMNH.MOL. 234132 from the Naturalis Biodiversity Center (Leiden, NL) is documented and stored at both institutions.

Although we endeavor to acquire DNA sequence data whenever possible, the rareness of comparative material from Southern Balkan caves and the fact that shells may express variation within the few known conchological characters (i.e., lamella formation, columella configuration, parietal shield form and umbilical notch configuration in conjunction with the coiling of the last whorl) (Jochum *et al*. 2015a), we opt to take a "conchology first" assessment strategy to describe these rare individuals for those cases that we can differentiate without DNA sequence data. The species are presented alphabetically in Table 1,

with the exception of *Z. troglobalcanicum* (NHMW Mol.Coll.Edlauer 32.749) due to its lectotype status in this work. All material that was determined *Z. troglobalcanicum* by previous authors (i.e., Gittenberger 1975; Maier 1982; Inäbnit *et al*. 2019, and notes in vials) is addressed first and presented in figures as near to the lectotype as possible for easy comparison irrespective of the alphabetical order of their assigned names in this study.

Cave GPS coordinates in Table 1 and in individual population descriptions have been provided by Roman Ozimec (Croatian Biospeleological Society) and were derived in part from the recent literature.

Institutional abbreviations

AJC	=	Adrienne Jochum Collection, Kelkheim, Germany
MCSMNH	=	Malacological Collection, Slovenian Museum of Natural History (former CSR SASA, MZBI & SMNH) Ljubljana, Slovenia
NHMW	=	Naturhistorisches Museum Wien, Vienna, Austria
NMBE	=	Naturhistorisches Museum der Burgergemeinde Bern, Bern, Switzerland
RMNH	=	Naturalis Biodiversity Center (former RijksMuseum van Natuurlijke Historie), Leiden, The Netherlands
RSC	=	Rajko Slapnik Collection, Kamnik, Slovenia
SMF	=	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt/M, Germany
TxEx	=	Taxon Expeditions Collection, Leiden, The Netherlands
ZSM	=	Zoologische Staatssammlung München, Germany

Abbreviations of shell characters

ah = aperture height
aw = aperture width
co = columella
hlw = height of last whorl
la = lamella
pe = peristome
pr = protoconch
ps = parietal shield
pw = penultimate whorl
SA = spire angle
sh = shell height
sw = shell width
te = teleoconch
um = umbilicus
wh = whorl

Terminology (from Slovenian and Croatian languages)

jama = cave or pit (‘horizontal’ or ‘vertical’ in Slovenian and ‘vertical cave’ in Croatian)
pećina = špilja = ‘horizontal cave’ (in Croatian)

Taxon naming

The new species’ designations are attributed to the listed authors in Table 1. For example, when a new species described in this work is cited, the complete citation of the new species is i.e., *Zospeum amplioscutum* Jochum & Ruthensteiner, 2023 in Jochum *et al*. 2023.

Table 1 (continued on the next page). Collation of species data, including species classifications, museum or population catalog numbers, figure designations in this work, cave localities and GPS data.

species	taxonomic classification	museum cat. nr.	figure(s) in this work	cave, locality, and text on label (in German or Slovenian)	lat.	long.
Zospeum troglobalcanicum Absolon, 1916	Absolon 1916a, 1916b	NHMW Mol.Coll.Edlauer 32.749	Fig. 2, 3A, 4A–F	Benetina pećina ober Slano Südostherzegovina lg Absolon [SE Herzegovina]	42.8105° N	17.9142° E
Z. amplioscutum Jochum & Ruthensteiner sp. nov.	this work	NHMW Mol.Coll.Edlauer 19.069	Fig. 9	Adria, Insel Brać (Brazza) Bazgova jama, com. Kuščer [Croatia, Island of Brać, Jama Bazdovača]	43.2918° N	16.6469° E
Z. biokovoense Jochum & Ruthensteiner sp. nov.	this work	NHMW Mol.Coll.Edlauer 16.390	Fig. 15A–B, 15B: C–H	Dalmatien, kl. Grotte beim Alpenvereinshaus, Biokovogebirge, kleine Grotte am Weg vom Alpenvereins zum Hegerhaus. [Croatia, estimated location: Biokovo – vrh Vosac]	43.3091° N	17.0473° E
Z. constrictum Jochum & Ruthensteiner sp. nov.	this work	NHMW Mol.Coll.Edlauer 16.693	Figs 13A–D, 14A–L	Dalmatien, Ostfuss des Biokovogebirge, Grotte bei Turija com. Kuščer [Croatia, Brikinjava špilja]	43.3452°N	17.0971° E
Z. dubokidoense Jochum & Ruthensteiner sp. nov.	this work	MCSMNH-PMSL-Moll.-FVelkovrh 30360[a] (holotype)	Figs 7D, 8G–L	Duboki do; potoček v dvorani [a stream in the cave chamber], -60m, Mtg. 8.1975 [Montenegro]	42.4949° N	18.8106° E
Z. dubokidoense Jochum & Ruthensteiner sp. nov.	this work	MCSMNH-PMSL-Moll.-FVelkovrh 30360[spm1]	Fig. 7E–F	Duboki do; potoček v dvorani [a stream in the cave chamber], -60m, Mtg. 8.1975 [Montenegro]	42.4949° N	18.8106° E
Z. intermedium Jochum & Ruthensteiner sp. nov.	*Z. troglobalcanicum*: Maier, in Gittenberger 1975: fig. 3	RMNH 234132	Fig. 6	Cetinjska pećina [= Cetinska pećina] near Cetinje, Crna Gora (=Montenegro) behind monastery, 15 May 1974	42.3886° N	18.9208° E
Z. kolbae Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov.	this work	NMBE 571122, NMBE 571123,	Figs 16A–B, 24	Montenegro, Njeguši, St John's cave, leg. László Dányi & Nikolett Ujhegyi	42,4307° N	18,8115° E
Zospeum sp. 1	this work	NMBE 577052, NMBE 577053/2	Fig. 16C–E	Montenegro, Njeguši, St John's cave, leg. László Dányi & Nikolett Ujhegyi	42,4307° N	18,8115° E
Z. njegusiense Jochum &Ruthensteiner sp. nov.	this work	NMBE 572639 (holotype); NMBE 578378 (paratype) (ex. AJC 2483) (SEM)	Figs 17A–E, 24	Montenegro, Njeguši, St John's cave, leg. László Dányi and Nikolett Ujhegyi	42,4307° N	18,8115° E
Z. njunjicae Jochum, Schilthuizen & Ruthensteiner sp. nov.	this work	NMBE 572617 (holotype); NMBE 572616 (2 paratypes); SMF 349426 (2 paratypes); TxEx-DU0018 (3 paratypes); NHMW-MO-113651 (2 paratypes)	Fig. 11	Montenegro, Virpazar, Gornja Seoca, Golubova pećina, 26 Jun. 2018, leg. M. Schilthuizen c.s. and I. Njunjić	42.2093°N	19.1306° E
Z. neuberti Jochum & Ruthensteiner sp. nov.	this work	NHMW Mol.Coll.Edlauer 32006	Fig. 12	Grabovica-Höhle bei Trebinje com. Kuščer [Croatia]	42.7438° N	18.0578° E
Zospeum sp. 2	*Z. troglobalcanicum:* Inäbnit *et al*. 2019: fig. 7u1–u4)	NMBE 553414/1 (ex RS 1981)	Fig. 20	Bosnia and Herzegovina, Taleža pećina, bei Trebinje, 9 Aug. 2010, leg. R. Slapnik	42.7097 ° N	18.2430° E
Z. simplex Inäbnit, Jochum & Neubert 2021	*Z. simplex* Inäbnit, Jochum & Neubert 2021	NHMW-MO-113642 (ex RS 3760)	Fig. 18	Jama Dobravljevac, Gornji Brišnik, Bosnia	43.6347° N	17.2328° E
Z. simplex Inäbnit, Jochum & Neubert 2021	*Z. simplex* Inäbnit, Jochum & Neubert 2021	SMF 349425 (ex RS 3760), SEM	Fig 19	Jama Dobravljevac, Gornji Brišnik, Bosnia	43.6347° N	17.2328° E

Table 1 (continued).

species	taxonomic classification	museum cat. nr.	figure(s) in this work	cave, locality, and text on label (in German or Slovenian)	lat.	long.
Z. tortuosum Jochum & Ruthensteiner sp. nov.	*Z. troglobalcanicum*: Maier, in Gittenberger 1975: fig. 3	MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm1]	Figs 3B–D, 4G–L	Cetinska pećina, Cetinje, vhod [cave entrance]; Mtg. 9.1976 [Mtg = Montenegro]	42.3886° N	18.9208° E
Deformed shell	this work	MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm2]	Figs 3E, 5A–F	Cetinska pećina, Cetinje, vhod [cave entrance]; Mtg. 9.1976 [Mtg = Montenegro]	42.3886° N	18.9208° E
Z. troglobalcanicum Absolon, 1916	Maier, in Gittenberger (1975)	MCSMNH-PMSL-Moll.-FVelkovrh 29603	Figs 7A–C, 8A–F	Lipska pećina, Lipa, Cetinje, Mtg; 7.1975 [Mtg = Montenegro]	42.3668° N	18.9531° E
Z. tumidum Jochum, Schilthuizen & Ruthensteiner sp. nov.	this work	NMBE 572615 (holotype) (ex. TxEx-DU0025	Fig. 10A–G	Montenegro, Piva Region, Bajovo Polje, Đokova pećina, 1 Jul. 2018, at cave entrance, leg. M. Schilthuizen c.s. and I. Njunjić	43.0315° N	18.8104° E

Imaging acquisition

Light microscopy (LM)

Images were taken with a Nikon 1 V1 camera mounted on a Leica Z16 APO microscope. Each specimen was captured by a series (ca 5–15) of images in z-direction (re. 3D Cartesian coordinate system) which were subsequently stacked using the software Helicon Focus ver. 7.6.1. (Helicon Soft, Kharkiv, Ukraine).

Images of the shell (RMNH.MOL.234132) illustrated in Gittenberger (1975: fig. 3) from Cetinjska pećina (= Cetinska pećina) were taken with a Canon EOS 500D mounted via a Leica beam splitter module on a Leica MZ7.5 stereo microscope and stacked using the software Helicon Focus ver. 7.7.5 (Helicon Soft, Kharkiv, Ukraine).

For specimens of *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov. (NMBE 571122–571123) subjected to DNA extraction, both specimens were imaged under sterile conditions from frontal and lateral view using the Leica DFC425 microscope camera implementing the image-processing program (IMS Client V15Q4, Imagic, Switzerland). We additionally included three, full-bodied individuals not described in this study (*Zospeum* sp. 1) from St John's cave (NMBE 577052–577053), which were imaged using a Leica MC190 HD digital camera attached to a Leica M205 C stereo microscope (Leica Microsystems GmbH, Wetzlar, Germany). The multifocal images were processed using the software Leica Application Suite X (LAS X) ver. 5.1.0.25593 (Leica Microsystems).

X-ray microscopy (Micro-CT)

The X-ray micro-computed tomography system, Phoenix Nanotom m (mostly 1600 projection images, 360° rotation for ca 80 min, voxel size ca 1 µm, voltage 80 kV, current 325 µA) (GE Measurement & Control, Wunstorf, Germany), an XRadia MicroXCT-200 imaging system (mostly 1600 projection images, 360° rotation for ca 90 min, voxel size ca 2 µm, voltage 40 kV, current 200 µA), and an XRadia 520 Versa (both XRadia: Carl Zeiss Microscopy GmbH, Pleasanton, CA, United States) were used for the Micro-CT acquisition. Scanning parameters are given in Table 2. The shell of *Zospeum intermedium* Jochum & Ruthensteiner sp. nov. (RMNH.MOL.234132) (Gittenberger 1975) was scanned separately at the Naturalis Biodiversity Center, Leiden, NL using an XRadia 520 Versa imaging system (mostly 1600 projection images, 360° rotation for 120 min, voxel size 1.8 µm, voltage 80 kV, current 88 µA). The tomographic reconstruction was performed using the phoenix datos|x ver. 2.2 software or XMReconstructor software respectively. The 16 bit data sets generated by reconstruction were cropped, histogram adjusted and converted to 8 bit using VGStudio MAX ver. 2.2 software (Volume Graphics, Heidelberg, Germany). Further 3D graphical procedures were conducted with Amira ver. 6.4 software (Thermo Fischer Scientific, Electron Microscopy Solutions, Hillsboro, Oregon, USA) applying manual segmentation for discrimination of external and internal shell structures. Final visualization was conducted using the Volume Rendering module.

Scanning electron microscopy (SEM)

Scanning electron microscopy (SEM) was performed at the Senckenberg Forschungsinstitut und Naturmuseum (SMF). Shells selected for SEM were mounted on aluminum stubs covered with double-sided carbon tabs and viewed unsputtered at a voltage of 20 kV (probe current 25 Pa) using the JEOL JSM-6490 LV Scanning Electron Microscope (JEOL Ltd., Japan). Due to the fragility of the empty subfossil shells, SEM was used to image *Zospeum njegusiense* Jochum & Ruthensteiner sp. nov. (NMBE 572639 and NMBE 578378 (ex. AJC 2483)).

Measurements

Shell measurements were made on Micro-CT images as shown in Fig. 2 using dimension tools of the software Corel Draw 2017 (Corel Corporation, Ottawa, Ontario, Canada). Shell whorl number was counted to the nearest quarter whorl according to Kerney & Cameron (1979).

Table 2. Micro-CT parameters.

species designation	CT system	Voxel size	kV	µA	duration	projections
Zospeum troglobalcanicum Absolon, 1916	Phoenix Nanotom m	1.088.83	80	325	82 min	1600
Zospeum amplioscutum Jochum & Ruthensteiner sp. nov.	Phoenix Nanotom m	1.010.92	80	325	88 min	1600
Zospeum biokovoense Jochum & Ruthensteiner sp. nov.	Phoenix Nanotom m	1.088.83	80	325	82 min	1600
Zospeum constrictum Jochum & Ruthensteiner sp. nov.	Phoenix Nanotom m	0.999.81	80	325	82 min	1600
Zospeum dubokidoense Jochum & Ruthensteiner sp. nov.	XRadia MicroXCT-200	2.195.50	40	200	ca 90 min	1600
Zospeum njunjicae Jochum, Schilthuizen & Ruthensteiner sp. nov.	Phoenix Nanotom m	1.033.14	80	325	89 min	1520
Zospeum neuberti sp. nov. Jochum & Ruthensteiner	Phoenix Nanotom m	0.924.81	80	325	144 min (2 z-acquis; merged)	1440
Zospeum simplex Inäbnit, Jochum & Neubert 2021	XRadia MicroXCT-200	1.908.20	40	200	ca 90 min	1600
Zospeum tortuosum Jochum & Ruthensteiner sp. nov.	XRadia MicroXCT-200	1.926.00	40	200	ca 90 min	1600
Deformed shell	XRadia MicroXCT-200	1.926.00	40	200	ca 90 min	1600
Zospeum intermedium Jochum & Ruthensteiner sp. nov.	XRadia 520 Versa	1.8048	80	88	121 min	1601
Zospeum sp. 2	Phoenix Nanotom m	0.980.17	80	325	144 min 2 z-acquis; merged)	1440
Zospeum troglobalcanicum Absolon, 1916	XRadia MicroXCT-200	2.195.50	40	200	ca 90 min	1600
Zospeum tumidum Jochum, Schilthuizen & Ruthensteiner sp. nov.	Phoenix Nanotom m	0.924.81	80	325	144 min (2 z-acquis; merged)	1440

DNA sequence analysis

DNA extraction and PCR amplification

Live specimens of *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov. (NMBE 571122–571123) were preserved in 80% ethanol and imaged before DNA extraction as described above. For total DNA extraction, the Qiagen Blood and Tissue Kit (Qiagen; Hilden, Germany) was used. Each specimen was placed in a mix of 180 µl ATL buffer and 20 µl Proteinase K and incubated for ca 2 h at 56°C in a thermo shaker (Labnet, Vortemp 56, witec AG, Littau, Switzerland). For subsequent DNA extraction the QIAcube extraction robot with the Protocol 430 (DNeasy Blood Tissue and Rodent tails Standard) was used.

Two mitochondrial markers (COI and 16S) and one nuclear marker (H3) were investigated. PCR mixtures consisted of 12.5 µl GoTaq G2 HotStart Green Master Mix (Promega M7423), 4.5 µl ddH_2O, 2 µl forward and reverse primer each and 4 µl DNA template. In Table 3 the primer pairs for the PCR are recorded. The PCR cycles were used as follows: for COI the admixture was heated 2 min at 94°C, followed by 35 cycles of 1 min at 95°C, 1 min at 40°C and 1 min at 72°C and, finally, 5 min at 72°C; for 16S the admixture was heated 5 min at 95°C, followed by 45 cycles of 30 s at 95°C, 30 s at 48°C and 45 s at 72°C and, finally, 5 min at 72°C; for H3 the admixture was heated 3 min at 95°C, followed 40 cycles of 1 min at 95°C, 1 min at 42°C and 1 min at 72°C and, finally, 10 min at 72°C (SensoQuest Tabcyclet and

Table 3. Primer pairs used for the PCR.

marker	primer	sequence	sequence length (bp)	reference
COI	LCO1490	5'-GGTCAACAAATCATAAAGATATTGG-3'	680	Folmer *et al*. 1994
	HCO2198	5'-TAAACTTCAGGGTGACCAAAAAATCA-3'		
16S	16S ar	5'-CGC CTG TTT ATC AAA AAC AT-3'	440	Simon *et al*. 1994
	16S br	5'- CCG GTC TGA ACT CTG ATC AT -3'		
H3	H3AD	5'-ATGGCTCGTACCAAGCAGACVGC-3'	380	Colgan *et al*. 1998
	H3BD	5'-ATATCCTTRGGCATRATRGTGAC-3'		

Techne TC-512, witec AG, Littau, Switzerland). The purification and sequencing of the PCR products were performed by LGC (LGC Genomics Berlin, Germany). The nucleotide sequences reported in this study have been deposited in GenBank with the accession numbers: ON037484–ON037485 for COI, ON041449–ON041450 for 16S and ON088652–ON088653 for H3. All those of the other congeners from previous works and represented in the current tree reconstruction are listed in Inäbnit *et al*. (2021).

Alignment optimization and phylogenetic tree reconstruction

Sequences for every marker were aligned using MAFFT ver. 7.450 (Katoh *et al*. 2002; Katoh & Standley 2013) for Windows with the FFT-NS-2 algorithm. We additionally implemented sequences previously used in Inäbnit *et al*. (2021) (Table 4). For the newly sequenced specimens, the markers ITS2 and 28S were not included (Table 4).

Tree topologies were estimated using two different phylogenetic methods: Maximum Likelihood (ML) and Bayesian Inference (BI). The five markers were set as partitions in both methods, using a distinct model for the third codon in protein-coding genes (COI, H3). The Maximum Likelihood tree was calculated using IQTree ver. 2.1.2 (Chernomor *et al*. 2016; Nguyen *et al*. 2015) for Linux, including the ModelFinder function (Kalyaanamoorthy *et al*. 2017) and an ultrafast Bootstrap with 1000 replicates (Hoang *et al*. 2018).

The Bayesian tree was reconstructed with MrBayes 3.2.7 (Ronquist *et al*. 2012) using the mixed substitution model (which incorporates model testing into the MCMC), invgamma rate variation and a Markov Chain Monte Carlo (MCMC) chain length of 10 000 000 generations and a subsampling frequency of every 4000 generations with the first 100 000 generations being discarded as burn-in, four heated chains and a chain temperature parameter of 0.2.

An Automatic Barcode Gap Discovery (ABGD; Puillandre et al. 2012; https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) analysis was performed on the COI alignments of the *Z. pretneri* group using the default settings (Pmin = 0.001, Pmax = 0.1, Steps = 10, X = 1.5, Nb bins = 20, distance = Jukes-Cantor).

Morphological assessment

A diagnostic table was constructed to compare significant morphological features (i.e. character states) recognized in each of the 3D-scanned perspectives, starting with the aperture frontal view and the long axis vertical (Table 5). From this position, each shell was then studied with aperture facing right, apical view, dorsal, aperture facing left and the ventral side. The respective cave populations are recorded in alphabetical order. Aspects such as apertural shape and parietal shield definition (frontal view), columellar configuration (aperture facing right), peristome and whorl configuration (ventral view), upper lamella and its position relative to the penultimate whorl (aperture facing right), the upper peristome rim alignment to the penultimate whorl (aperture facing left), the presence and degree of formation of a

Table 4 (continued on the next 4 pages). Specimens used for calculating the tree. Accession numbers written in italic type derive from BOLD (Biodiversity of Life Database). Accession numbers in roman type derive from GenBank.

species	source	collection number	locality	coordinates [° North, East]	COI	16S	H3	28S	ITS2
Carychium tridentatum (Risso, 1826)	Inäbnit *et al.* 2019	NMBE 549936	Taunus, Eppstein, Germany	50.1601, 8.3846	MH383001	MH382969	MH383018	MH382989	MH383038
Iberozospeum vasconicum (Prieto, de Winter, Weigand, Gómez & Jochum, 2015)	Weigand *et al.* 2013	AJC 1875a	Cueva del Cráneo, Dima, Bizkaia, Spain	43.1287, -2.7348	*BARCA206-12*	KC206116	KC206249	—	—
	Weigand *et al.* 2013	AJC 1847c	Cueva de Ermita de Sandaili, Valle de Araotz, Bizkaia, Spain	42.9994, -2.4381	KM281092	KC206119	KC206247	—	—
I. schaufussi (Frauenfeld, 1862)	Kneubühler *et al.* 2021	NMBE 559630	Cueva del Buho, Cantabria, Spain	43.29427, -4.0028	*MW626880*	MW621967	MW622241	—	MW621334
I. costulatum Prieto & Jochum, 2021	Kneubühler *et al.* 2021	NMBE 559626	Cueva del Cesáreo, Cantabria, Spain	43.32034, -3.72279	MW626878	MW621965	MW622239	—	MW621332
I. bellesi (Gittenberger, 1973)	Kneubühler *et al.* 2021	NMBE 557236	Lezea, Navarra, Spain	43.26853, -1.57164	*MW626867*	MW621953	MW622225	—	MW621320
I. praetermissum (Jochum, Prieto & de Winter, 2019)	Weigand *et al.* 2013; Romero *et al.* 2017	AJC 1842a	Cueva del Bosque, Inguanzo, Asturias, Spain	43.3123, -4.8724	KM281091	KC206121	KC206245	KM281051	—
I. zaldivarae (Prieto, de Winter, Weigand, Gómez & Jochum, 2015)	Weigand *et al.* 2013	AJC 1876c	Cueva de Las Paúles, Monte Santiago, Castilla y León, Spain	43.1282, -2.7362	*BARCA209-12*	KC206114	KC206251	—	—
	Weigand *et al.* 2013	AJC 1876b	Cueva de Las Paúles, Monte Santiago, Castilla y León, Spain	43.1282, -2.7362	*BARCA208-12*	KC206115	KC206250	—	—
Zospeum costatum (Freyer, 1855)	Weigand *et al.* 2013	NMBE 553383	Jama 2 pri Jabljah, Loka pri Mengšu, Slovenia	46.1426, 14.5533	HQ171599	KC206158	KC206208	—	—
	Weigand *et al.* 2013	NMBE 553383	Jama 2 pri Jabljah, Loka pri Mengšu, Slovenia	46.1426, 14.5533	HQ171601	KC206159	KC206207	—	—

Table 4 (continued). Specimens used for calculating the tree. Accession numbers written in italic type derive from BOLD (Biodiversity of Life Database). Accession numbers in roman type derive from GenBank.

species	source	collection number	locality	coordinates [° North, East]	COI	16S	H3	28S	ITS2
Z. spelaeum (Rossmässler, 1839)	Weigand *et al*. 2013	NMBE 553316	Grotte Bac, Trieste Municipality, Trieste Prov., Italy	45.6361, 13.8717	*BARCA182-12*	KC206110	KC206255	—	—
	Weigand *et al*. 2013	AJC 1898a	Grotte Bac, Trieste Municipality, Trieste Prov., Italy	45.6361, 13.8717	*BARCA184-12*	KC206108	KC206257	—	—
	Weigand *et al*. 2013	NMBE 553316	Grotte Bac, Trieste Municipality, Trieste Prov., Italy	45.6361, 13.8717	—	KC206109	KC206256	—	—
	Weigand *et al*. 2013	NMBE 553314	Grotte d'Ercole, near Gabrovizza, Trieste Prov., Italy	45.731, 13.7261	*BARCA181-12*	KC206111	KC206254	—	—
	Weigand *et al*. 2013	NMBE 553311	Velika Pasica, Gornji Ig, Slovenia	45.9189, 14.4934	*BARCA179-12*	KC206135	KC206231	—	—
	Inäbnit *et al*. 2019	NMBE 554396	Hotiške Ponikve, Hotičina, Slovenia	45.5735, 14.0309	MH382992	MH382954	MH383022	MH382974	MH383024
Z. isselianum Pollonera, 1887	Weigand *et al*. 2013	NMBE 553389	Turjeva jama, Robič, Kobarid, Slovenia	46.2435, 13.5046	HQ171594	KC206097	KC206268	—	—
Z. amoenum (Frauenfeld, 1856)	Inäbnit *et al*. 2019	RS 2037	Ihanščica, Ihan, Ljubljana, Slovenia	46.1216, 14.6476	MH383003	MH382971	MH383020	—	—
	Weigand *et al*. 2013	NMBE 553378	Konečka zijalka, Šmihel nad Mozirjem, Mozirje, Slovenia	46.4024, 14.9393	*BARCA123-10*	KC206179	KC206187	—	—
	Weigand *et al*. 2013	NMBE 553378	Konečka zijalka, Šmihel nad Mozirjem, Mozirje, Slovenia	46.4024, 14.9393	*BARCA124-10*	KC206178	KC206188	—	—
	Jochum *et al*. 2015	MCSMNH 40600a	Potočka zijalka, Olševa, Slovenia	46.4493, 14.6693	*BARCA211-13*	—	—	—	—
	Jochum *et al*. 2015	MCSMNH 40600a-2	Potočka zijalka, Olševa, Slovenia	46.4493, 14.6693	*BARCA212-13*	—	—	—	—
Zospeum sp.	Kruckenhauser *et al*. 2019	NHMW109000/ AL/01821/8139	Steiner Lehmhöhle, Austria	46.42228, 14.53462	*AMOL570-19*	—	—	—	—
	Kruckenhauser *et al*. 2019	NHMW109000/ AL/01821/8140	Steiner Lehmhöhle, Austria	46.42228, 14.53462	*AMOL571-19*	—	—	—	—
	Kruckenhauser *et al*. 2019	NHMW109000/ AL/01822/8141	Hafnerhöhle, Austria	46.51200, 14.21623	*AMOL572-19*	—	—	—	—
	Kruckenhauser *et al*. 2019	NHMW109000/ AL/01822/8142	Hafnerhöhle, Austria	46.51200, 14.21623	*AMOL573-19*	—	—	—	—

Table 4 (continued). Specimens used for calculating the tree. Accession numbers written in italic type derive from BOLD (Biodiversity of Life Database). Accession numbers in roman type derive from GenBank.

species	source	collection number	locality	coordinates [° North, East]	COI	16S	H3	28S	ITS2
Z. alpestre (Freyer, 1855)	Weigand *et al*. 2013	NMBE 553391	Jama pod Mokrico, Kamniška Bistrica, Slovenia	46.3093, 14.5832	HQ171593	KC206099	KC206266	—	—
	Inäbnit *et al*. 2019	MCSMNH 40651a	Jelenska zijalka, Raduha, Slovenia	46.3656, 14.7567	MH383002	MH382970	MH383019	MH382990	MH383039
Z. kupitzense A. Stummer, 1984	Weigand *et al*. 2013; Romero et al. 2017	NMBE 553393	Ložekarjeva zijalka, Solčava, Slovenia	46.4268, 14.624	*BARCA125-10*	KC206150	KC206216	KM281049	—
Z. exiguum Kuščer, 1932	Inäbnit *et al*. 2019	NMBE 548774	Jama Borušnjak 3, Lupoglav, Ćićarija, Istra	45.3702, 14.1841	MH382994	MH382959	MH383009	MH382979	MH383030
	Weigand *et al*. 2013	NMBE 553384	Križna jama, Lož, Cerknica, Slovenia	45.7452, 14.4673	HQ171582	KC206162	KC206204	—	—
	Weigand *et al*. 2013	NMBE 553384	Križna jama, Lož, Cerknica, Slovenia	45.7452, 14.4673	HQ171585	KC206163	KC206203	—	—
Z. obesum (Frauenfeld, 1854)	Weigand *et al*. 2013	NMBE 553409	Krška jama, Krška vas, Slovenia	45.8899, 14.7711	*BARCA177-12*	KC206136	KC206230	—	—
	Weigand *et al*. 2013	NMBE 553409	Krška jama, Krška vas, Slovenia	45.8899, 14.7711	*BARCA175-12*	KC206137	KC206229	—	—
Z. pretneri Bole, 1960	Weigand *et al*. 2013	AJC 1370	Donja Cerovačka špilja, Kesići, Gračac, Croatia	44.2701, 15.8855	HQ171595	KC206151	KC206215	—	—
Z. tholussum Weigand, 2013	Weigand 2013	SMF 341633	Lukina jama – Trojama, Krasno, Croatia	44.7621, 15.0296	*BARCA120-10*	—	—	—	—
Z. manitaense Inäbnit, Jochum & Neubert, 2019	Inäbnit *et al*. 2019	NMBE 548800	Manita peć, Starigrad, Croatia	44.311, 15.4792	—	MH382963	MH383012	MH382983	—
	Inäbnit *et al*. 2019	NMBE 548811	Manita peć, Starigrad, Croatia	44.311, 15.4792	MH383000	MH382968	MH383017	MH382988	MH383037
Z. kolbae sp. nov.	this work	NMBE 571122	Montenegro, Njeguši, Szt Janos Cave	42.4307, 18.8115	ON037484	ON041449	ON088652		
	this work	NMBE 571123	Montenegro, Njeguši, Szt Janos Cave		ON037485	ON041450	ON088653		
Z. aff. *troglobalcanicum* Absolon, 1916	Inäbnit *et al*. 2021	NMBE 568052	Špilja Jezero, Cavtat, Konavle, Croatia	42.5858, 18.2569	MW786768	—	MW796484	MW784525	MW784537
	Inäbnit *et al*. 2021	NMBE 568053	Špilja Jezero, Cavtat, Konavle, Croatia	42.5858, 18.2569	MW786767	—	MW796485	MW784524	MW784536

Table 4 (continued). Specimens used for calculating the tree. Accession numbers written in italic type derive from BOLD (Biodiversity of Life Database). Accession numbers in roman type derive from GenBank.

species	source	collection number	locality	coordinates [° North, East]	COI	16S	H3	28S	ITS2
Z. simplex Inäbnit, Jochum & Neubert, 2021	Inäbnit *et al.* 2021	NMBE 568055	Jama u kamenolomu, Cebara, Bosnia and Herzegovina	43.6517, 17.2133	MW786764	MW784509	MW796481	MW784526	MW784530
	Inäbnit *et al.* 2021	NMBE 568056	Jama u kamenolomu, Cebara, Bosnia and Herzegovina	43.6517, 17.2133	MW786765	MW784510	MW796478	MW784521	MW784532
	Inäbnit *et al.* 2021	NMBE 568057	Jama u kamenolomu, Cebara, Bosnia and Herzegovina	43.6517, 17.2133	MW786766	MW784511	MW796476	MW784520	MW784531
	Inäbnit *et al.* 2021	NMBE 568058	Jama u kamenolomu, Cebara, Bosnia and Herzegovina	43.6517, 17.2133	MW786763	MW784512	MW796477	—	MW784529
	Inäbnit *et al.* 2021	NMBE 568059	Vranjača, Grabovica, Bosnia and Herzegovina	43.6625, 17.1039	MW786762	MW784513	MW796486	MW784522	—
	Inäbnit *et al.* 2021	NMBE 568060	Jama Dobravljevac, Gornji Brišnik, Bosnia and Herzegovina	43.6347, 17.2328	MW786761	MW784515	MW796482	MW784527	MW784535
	Inäbnit *et al.* 2021	NMBE 568061	Jama Dobravljevac, Gornji Brišnik, Bosnia and Herzegovina	43.6347, 17.2328	MW786760	MW784516	MW796479	MW784523	MW784533
	Inäbnit *et al.* 2021	NMBE 568062	Jama Dobravljevac, Gornji Brišnik, Bosnia and Herzegovina	43.6347, 17.2328	MW786759	MW784514	MW796483	—	MW784534
	Inäbnit *et al.* 2021	NMBE 568063	Jama Dobravljevac, Gornji Brišnik, Bosnia and Herzegovina	43.6347, 17.2328	MW786758	MW784517	MW796480	MW784519	MW784528
Z. subobesum Bole, 1974	Weigand *et al.* 2013	NMBE 553326	Tounjčica, Tounj, Ogulin, Croatia	45.2439, 15.3253	HQ171602	KC206152	KC206214	—	—
	Weigand *et al.* 2013	NMBE 553326	Tounjčica, Tounj, Ogulin, Croatia	45.2439, 15.3253	HQ171604	KC206153	KC206213	—	—
	Weigand *et al.* 2013	NMBE 553328	Jopićeva špilja, Brebovnica, Krnjak, Karlovac, Croatia	45.2951, 15.5939	*BARCA172-12*	KC206125	KC206241	—	—
Z. frauenfeldii (Freyer, 1855)	Weigand *et al.* 2013	NMBE 553388	Podpeška jama, Podpeč, Dobrepolje, Slovenia	45.8393, 14.6863	HQ171587	KC206160	KC206206	—	—
	Weigand *et al.* 2013	NMBE 553388	Podpeška jama, Podpeč, Dobrepolje, Slovenia	45.8393, 14.6863	HQ171589	KC206161	KC206205	—	—
	Inäbnit *et al.* 2019	NMBE 548771	Hrustovača špilja, Hrustovo, Sanski Most, Bosnia and Herzegovina	44.6607, 16.7285	—	—	MH383006	MH382976	MH383027

Table 4 (continued). Specimens used for calculating the tree. Accession numbers written in italic type derive from BOLD (Biodiversity of Life Database). Accession numbers in roman type derive from GenBank.

species	source	collection number	locality	coordinates [° North, East]	COI	16S	H3	28S	ITS2
Z. bucculentum Inäbnit, Jochum & Neubert, 2019	Inäbnit *et al.* 2019	NMBE 548801	Jama na Škrilama, Netretić, Croatia	45.5277, 15.3476	MH382997	MH382964	MH383013	MH382984	MH383033
	Inäbnit *et al.* 2019	NMBE 548772	Pivnica špilja, Žakanje, Croatia	45.6108, 15.3617	—	MH382957	MH383007	MH382977	MH383028
	Inäbnit *et al.* 2019	NMBE 548806	Vrelić špilja, Donje Dubrave, Ogulin, Croatia	45.3114, 15.352	—	MH382966	MH383015	MH382986	MH383035
Z. pagodulum Inäbnit, Jochum & Neubert, 2019	Inäbnit *et al.* 2019	NMBE 548805	Kučka jama, Lovran, Učka, Istra, Croatia	45.2985, 14.2135	MH382998	MH382965	MH383014	MH382985	MH383034
	Inäbnit *et al.* 2019	NMBE 548807	Grnjača špilja, Lovran, Učka, Istra, Croatia	45.2835, 14.2381	MH382999	MH382967	MH383016	MH382987	MH383036
Z. robustum Inäbnit, Jochum & Neubert, 2019	Inäbnit *et al.* 2019	NMBE 554397	Tonkovića špilja, Ogulin, Croatia	45.3359, 15.2541	—	MH382953	MH383004	MH382973	MH383023
	Inäbnit *et al.* 2019	NMBE 548773	Budina špilja, Studenci, Croatia	44.7121, 15.3639	MH382993	MH382958	MH383008	MH382978	MH383029
	Inäbnit *et al.* 2019	NMBE 548777	Markov ponor, Lipovo polje, Croatia	44.7606, 15.1797	MH382995	MH382961	MH383010	MH382981	MH383032
	Inäbnit *et al.* 2019	NMBE 548787	Markov ponor, Lipovo polje, Croatia	44.7606, 15.1797	MH382996	MH382962	MH383011	MH382982	—
	Inäbnit *et al.* 2019	NMBE 548776	Vrlovka, Kamanje, Croatia	45.6319, 15.3934	—	MH382960	—	MH382980	MH383031
	Inäbnit *et al.* 2019	RS 2210a	Vrlovka, Kamanje, Croatia	45.6319, 15.3934	—	MH382972	MH383021	MH382991	MH383040
	Inäbnit *et al.* 2019	NMBE 554399	Židovske kuće, Cerovica, Žumberak, Croatia	45.8, 15.48	—	MH382955	—	MH382975	MH383025
	Inäbnit *et al.* 2019	NMBE 554400	Pušina jama, Jezemice, Žumberak, Croatia	45.7369, 15.3606	—	MH382956	MH383005	—	MH383026

peristome notch at the upper junction with the parietal shield (frontal and apical views), the configuration and placement of the basal peristome in relation to the umbilicus (ventral view), teleoconch sculpture and a description of the umbilical region. To estimate the upper peristome rim alignment to the penultimate whorl (aperture facing left), the distance from the left side of the penultimate whorl to the point of junction of the uppermost, right side of the parietal shield with the uppermost part of the peristome rim (forming the upper peristome notch) was measured manually. Hereby, the derived segment of distance was then measured in the same increment across the entire width of the body whorl along the suture line and presented in fraction form as distance of apertural rim alignment relative to the extension of the penultimate whorl in profile view (aperture facing left).

Species assignments based on these criteria are presented in Table 5. Shell measurements were taken for each specimen and recorded for each cave locality including shell height (sh), shell width (sw), aperture height (ah), aperture width (aw), height of last whorl (hlw) and spire angle (SA) (Table 6). We remark that the measurements in Table 6 are grouped first by cave names with the chronological presentation of populations in this work according to their previous occurrence in the literature with respect to *Z. troglobalcanicum*. More recent acquisitions are listed last.

Taxonomic inferences in this study are based on fully grown specimens.

Major characters investigated

Aperture shape and orientation on the columellar side

Aperture shape is reniform, ovate reniform or elliptical ovate with the basal columellar side showing either an oblique and angular or straight and angular or expanded and angular form. Sometimes the entrance into the columellar side of the shell is thickly callused, forming a wall deep into the shell. The degree of contortion of the columella and its impact on the shell axis (aperture facing frontal view) can be species specific.

Ventral view considering umbilicus, peristome and whorl configuration

The last ¼ coiling of the final whorl affects the position of the left side of the peristome (often callused) and its relation to the umbilical notch (depression). The peristome (left side) may arch high above the notch and twist outward to the right of it (*Z. troglobalcanicum*), or it does not arch high over it but is positioned oblique to the umbilical notch (*Z. simplex*) or it is positioned directly on top of the notch, blocking it completely with callus (*Z. tortuosum* sp. nov. (Cetinska pecina)). On the ventral side of the shell, the last ¼ section of the final whorl (encompassing the aperture) shows either a compact or non-compact form.

Columellar configuration (aperture facing right view)

The columella is either centrally aligned or askew in relation to the shell axis. The thickness of the columella is either moderately thick (*Z. troglobalcanicum*), slender (*Z. simplex*) or fat (*Z. biokovoense* sp. nov.).

Lamellar configuration (aperture facing right view)

The lamella is either tightly positioned under the penultimate whorl as in *Z. troglobalcanicum* or forms a bulge on the columella as in *Z. njunjicae* sp. nov. In all shells of this study, it is a weak structure in contrast to the well-defined lamellae known in the congeners from the northern Dinarides.

Table 5 (continued on the next 3 pages). Major differential diagnostic characters revealed by Micro-CT or SEM.

cave population	aperture shape (frontal view)	peristome & whorl configuration (ventral view)	columellar configuration (aperture facing right)	upper internal lamella & position to penultimate whorl (pw) (aperture facing right)	upper peristome rim alignment to penultimate whorl (pw) (aperture facing left)	parietal shield	peristome notch at upper junction with parietal shield	apical view	teleoconch structure	umbilicus	proposed assignment
Bazgova jama, Brać, HR (NHMW Mol. Coll.Edlauer 19.069)	reniform, columellar side oblique, not angular	left side of peristome thickly callused; arches high above & positioned high & to right of umbilical notch; last ¼ whorl not compact	cylindrical, centrally aligned; slender	present, weak and incomplete; tightly positioned under pw	aperture rim $^{1}/_{8}$ < width of pw	well defined, curved at max. whorl convexity, long, angular; thickly callused; extends high to periphery of shell (ventral view)	present, prominent	peristome reflected; notch visible	tendency towards costate; irreg. low ribbing behind peristome	hint of shallow depression, callused	*Zospeum amplioscutum* Jochum & Ruthensteiner sp. nov.
Benetina pećina, Slano, BiH (NHMW Mol. Coll.Edlauer 32.749)	reniform, columellar side oblique, angular	arches over and oblique to umbilical notch; positioned to right side, last ¼ whorl compact	cylindrical, centrally aligned; not slender	present, weak and incomplete; tightly positioned under pw	aperture rim $^{1}/_{5}$ < width of pw	well defined, straight, long, angular	present, prominent	peristome slightly reflected; apertural notch visible	irregularly costate; irreg. low ribbing behind peristome	depression	lectotype *Z. troglobalcanicum* Absolon, 1916
Biokovo, Dalmatia, HR, kl. Grotte bei Vereinshaus (NHMW Mol. Coll.Edlauer 16.390)	reniform, columellar side oblique, not angular	left side of peristome thickly callused; arches above & positioned to right of umbilical notch; last ¼ whorl not compact	cylindrical, centrally aligned; Fat, slightly less than ⅓ width of body whorl	lamellar bulge; lamella visible on dorsal & aperture left views	aperture rim ca $^{1}/_{7}$ < width of pw	well defined, straight, angular	present	peristome slightly reflected; apertural notch visible	irregularly costate; Body whorl coiling uniform with rest of spire; irreg. low ribbing behind peristome; weak radial banding	depression, callused, puckered	*Z. biokovoense* Jochum & Ruthensteiner sp. nov.
Brikinjava špilja, Biokovo, Dalmatian, HR (NHMW Mol. Coll.Edlauer 16.693)	ovate reniform, columellar side expanded, roundish, not angular	p. simple, left side of peristome callused, arches high above and oblique to umbilical notch; last ¼ whorl not compact	cylindrical, centrally aligned; not slender	not present in shell of Fig. 13A–B, D–E; partially present in shell of Fig. 13G–H, J	Fig. 13E: aperture rim $^{1}/_{7}$ < width of pw; Fig 13K: aperture rim $^{1}/_{10}$ < width of pw	well defined, straight, angular	present, prominent	peristome widely reflected; apertural notch prominent	irregularly costate; body whorl (upper right side) tucked under spire; irreg. low ribbing behind peristome; weak radial banding	shallow depression, puckered	*Z. constrictum* Jochum & Ruthensteiner sp. nov.

Table 5 (continued). Major differential diagnostic characters revealed by Micro-CT or SEM.

cave population	aperture shape (frontal view)	peristome & whorl configuration (ventral view)	columellar configuration (aperture facing right)	upper internal lamella & position to penultimate whorl (pw) (aperture facing right)	upper peristome rim alignment to penultimate whorl (pw) (aperture facing left)	parietal shield	peristome notch at upper junction with parietal shield	apical view	teleoconch structure	umbilicus	proposed assignment
Cetinska pećina, Cetinje, MNE (PMSL-Moll.-FVelkovrh 34099[spm1])	reniform, columellar side straight, angular	left side of peristome thickly callused, positioned leftwards above umbilicus; palatal side not expanded	slanted cylindric, not centrally aligned; not slender, abapically attenuate	not present	aperture rim almost flush with penultimate whorl, curves back	well defined, straight	no peristome notch	last whorl tightly coiled, almost disappearing under spire; peristome slightly reflected	tendency towards costate; ribbing behind peristome, weak radial banding	no depression, thickly callused, puckered	*Z. tortuosum* Jochum & Ruthensteiner sp. nov.
Cetinska pećina, Cetinje, MNE (PMSL-Moll.-FVelkovrh 34099[spm4])	elliptical ovate, columellar side straight, angular	peristome positioned above umbilicus; straight	slanted cylindric, not centrally aligned; not slender, abapically attenuate	present but incomplete; not tightly positioned under pw	aperture rim 1/5 < width of pw	well defined, roundish,	no peristome notch	last whorl tightly coiled, almost disappearing under spire; peristome truncated, not reflected	irregularly costate; ribbing behind peristome, weak radial banding	slight depression, callused, puckered	Deformed shell
Cetinska pećina, Cetinje, MNE (RMNH. MOL.234132)	reniform, columellar side straight, angular	left side of peristome thickly callused, positioned above umbilicus; palatal side not expanded	cylindric, centrally aligned; not slender, equally thick	not present in this view, but present in aperture facing left, deep set lamella forms a parietalis	aperture rim 1/5 < width of pw	well defined, straight, angular	present; slight	last whorl evenly coiled, not disappearing under spire; peristome slightly reflected	irregular growth lines on smooth shell; ribbing behind peristome; weak radial banding on body whorl	slight depression, callused, puckered	*Z. intermedium* Jochum & Ruthensteiner sp. nov.
Dobravljevac jama, BiH (SMF 349425 (paratype) (SEM)	small callus, angular	not visible/ accessible in this shell	not visible/ accessible in this shell	not visible/ accessible in this shell	not visible/ accessible in this shell	well defined	present; slight	not visible/ accessible in this shell	tendency towards costate; ribbing behind peristome & around body whorl; weak radial bands	not visible/ accessible in this shell	*Z. simplex* Inäbnit, Jochum & Neubert, 2021
Dobravljevac jama, BiH (RS 3760)	reniform, columellar side slightly oblique, small callus, angular	arches over and oblique to umbilical notch, last ¼ whorl compact	cylindrical and slender, centrally aligned	slight lamella under pw	aperture rim 1/5 < width of pw	well defined, curved at max. whorl convexity, long, angular	present; slight	peristome slightly reflected; apertural notch barely visible	tendency towards costate; ribbing behind peristome	depression	*Z. simplex* Inäbnit, Jochum & Neubert, 2021

Table 5 (continued). Major differential diagnostic characters revealed by Micro-CT or SEM.

cave population	aperture shape (frontal view)	peristome & whorl configuration (ventral view)	columellar configuration (aperture facing right)	upper internal lamella & position to penultimate whorl (pw) (aperture facing right)	upper peristome rim alignment to penultimate whorl (pw) (aperture facing left)	parietal shield	peristome notch at upper junction with parietal shield	apical view	teleoconch structure	umbilicus	proposed assignment
Đokova pećina, Bajovo polje, MNE (ex TxEx-DU0025)	reniform, columellar side oblique, angular	arches high over and oblique to umbilical notch	cylindrical, centrally aligned; not slender, apically tapered	lamellar bulge rather than lamella	aperture rim ⅛ < width of pw, almost shear with pw	well defined, straight, long, angular	present; slight	peristome slightly reflected; apertural notch barely visible	tendency towards costate	depression, deep	*Z. tumidum* Jochum, Schilthuizen & Ruthensteiner sp. nov.
Duboki do, MNE (PMSL-Moll.-FVelkovrh 30360 [a-cspm1-3])	ovate, columellar side roundish, not angular; callus on basal-columellar side	peristome callus of left side positioned straight at center with leftward tendency	cylindrical, centrally aligned; moderately slender; attenuate	present, loosely positioned under pw	aperture rim 1/6 < width of pw	short with low straightish edge	present	peristome slightly reflected	irregularly costate	no depression, callused, puckered	*Z. dubokidoense* Jochum & Ruthensteiner sp. nov.
Golubova pećina, Gornja Seoca, MNE (TxEx-DU0018)	reniform, columellar side slightly oblique, angular; low conpicuous denticle present	peristome thickly callused; arches high above & positioned right of umbilical notch	cylindrical, centrally aligned; not slender	present; not tightly positioned under pw	aperture rim 1/6 < width of pw	well defined, straight, long, angular	present, prominent	last whorl tightly coiled, almost disappearing under spire; peristome slightly reflected	tendency towards costate; ribbing behind peristome	depression, puckered	*Z. njunjicae* Jochum, Schilthuizen & Ruthensteiner sp. nov.
Grabovica-Höhle bei Trebinje (NHMW Mol. Coll.Edlauer 32006)	reniform, columellar side straight, roundish	positioned directly above and leans to right of umbilical notch	cylindric, centrally aligned; not slender, totally smooth	not present, smooth columella	aperture rim 1/6 < width of pw, peristome thin halfway down palatal side, then curves back.	well defined, straight, angular	present, slightly flipped back in apical view	peristome slightly reflected	tendency towards costate; irreg. low ribbing behind peristome	depression, slightly puckered	*Z. neuberti* Jochum & Ruthensteiner sp. nov.
Lipska pećina, Lipa, Cetinje, MNE (PMSL-Moll.-FVelkovrh 29603)	reniform, columellar side slightly oblique, angular	peristome callus thick on left side, arches over and oblique to umbl.; peristome grows thinner	cylindrical, centrally aligned; not slender	present; tightly positioned under pw	aperture rim 1/5 < width of pw	well defined, straight, long, angular	present; slight	slightly reflected	irregularly costate; ribbing behind peristome, weak radial banding	slight depression, callused, puckered	*Z. troglobalcanicum* Absolon, 1916
Njeguši, St. John's cave, MNE (AJC 2483 (SEM))	reniform, columellar side slightly oblique, angular	not visible/ accessible in this shell	not visible/ accessible in this shell	present; prominent and loosely coiled obliquely below pw	not visible/ accessible in this shell	well defined, curved at max. whorl convexity, thick, long, angular	present, eroded	not visible/ accessible in this shell	smooth; impressed irregular ribbing behind peristome	not visible/ accessible in this shell	*Z. njegusiense* Jochum & Ruthensteiner sp. nov.

Table 5 (continued). Major differential diagnostic characters revealed by Micro-CT or SEM.

cave population	aperture shape (frontal view)	peristome & whorl configuration (ventral view)	columellar configuration (aperture facing right)	upper internal lamella & position to penultimate whorl (pw) (aperture facing right)	upper peristome rim alignment to penultimate whorl (pw) (aperture facing left)	parietal shield	peristome notch at upper junction with parietal shield	apical view	teleoconch structure	umbilicus	proposed assignment
Njeguši, St. John's cave, MNE (NMBE 571122)	elliptical-ovate, columellar side slightly oblique, long and angular	not visible/ accessible in this shell	not visible/ accessible in this shell	not visible/ accessible in this shell	aperture rim flush with penultimate whorl	well defined, positioned high up on teleoconch, thick, long, angular	present, prominent	not visible/ accessible in this shell	smooth; impressed irregular striations	not visible/ accessible in this shell	*Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov.
Taleža pećina, BiH (NMBE 553414 (ex. RS 1981))	reniform, columellar side slightly oblique, angular, palatal side with thick callus	peristome thickly callused; positioned directly parallel to umbilical notch	cylindrical, centrally aligned; not slender; totally smooth	not present	aperture rim $^{1}/_{5}$ < width of pw	well defined, straight, long, angular; thickly callused	present, slightly flipped back in apical view	peristome slightly reflected; apertural notch visible	only a few low ribs behind peristome	depression, slightly puckered	*Zospeum* sp. 2

Table 6. List of shell measurements denoted by cave locality, museum or collection catalog number, and individual specimens assessed per population. Measurements include shell height (sh), shell width (sw), aperture height (ah), aperture width (aw), height of last whorl (hlw) (in mm) and Spire Angle (SA) (in degrees). Abbreviations: BiH = Bosnia and Herzegovina; MNE = Montenegro; HR = Croatia (Republika Hrvatska).

locality	specimen	sh	sw	ah	aw	hlw	SA
Benetina pećina, BiH	NHMW-32.749	1.398	1.007	0.605	0.640	0.886	67.50
Cetinska pećina, BiH	MCSMNH-PMSL-34099-spm1	1.435	0.944	0.515	0.511	0.841	57.93
Cetinska pećina, BiH	MCSMNH-PMSL-34099-spm2	1.430	0.951	0.548	0.609	0.844	61.20
Cetinska pećina, BiH	MCSMNH-PMSL-34099-spm3	1.349	0.972	0.559	0.575	0.827	65.16
Cetinska pećina, BiH	MCSMNH-PMSL-34099-spm4	1.396	0.922	0.566	0.590	0.836	60.01
Cetinska pećina, BiH	RMNH.MOL.234132	1.57	1.08	0.58	0.66	0.95	66.35
Lipska pećina, MNE	MCSMNH-PMSL-29603-spm1	1.356	0.960	0.543	0.571	0.794	60.30
Lipska pećina, MNE	MCSMNH-PMSL-29603-spm2	1.320	1.071	0.590	0.619	0.854	73.45
Lipska pećina, MNE	MCSMNH-PMSL-29603-spm3	1.428	1.053	0.630	0.666	0.879	63.83
Duboki do, MNE	MCSMNH-PMSL-30360-spm1	1.514	1.088	0.622	0.642	0.921	63.64
Duboki do, MNE	MCSMNH-PMSL-30360-spm2	1.546	1.085	0.663	0.611	0.982	65.73
Duboki do, MNE	MCSMNH-PMSL-30360-spm3	1.512	1.103	0.639	0.645	0.961	68.83
Jama Bazdovača, Brać, HR	NHMW-19.069-spm1	1.304	0.940	0.608	0.609	0.804	63.53
Jama Bazdovača, Brać, HR	NHMW-19.069-spm2	1.362	0.966	0.631	0.574	0.808	63.28
Đokova pećina, MNE	TxEx-Du0025	1.537	1.177	0.731	0.712	1.028	74.75
Golubova pećina, MNE	TxEx-DU0018-spm1	1.214	0.944	0.588	0.507	0.764	71.38
Golubova pećina, MNE	TxEx-DU0018-spm2	1.248	0.947	0.578	0.524	0.790	71.83
Golubova pećina, MNE	TxEx-DU0018-spm3	1.271	0.914	0.560	0.578	0.811	69.69
Grabovica, BiH	NHMW-32006-spm1	1.308	0.915	0.555	0.562	0.794	61.88
Grabovica, BiH	NHMW-32006-spm2	1.305	0.932	0.532	0.551	0.786	67.49
Grabovica, BiH	NHMW-32006-spm3	1.205	0.854	0.517	0.539	0.737	66.77
Brikinjava špilja, HR	NHMW-16.693-spm1	1.331	1.055	0.620	0.689	0.912	76.14
Brikinjava špilja, HR	NHMW-16.693-spm3	1.537	0.985	0.647	0.540	0.855	57.56
Brikinjava špilja, HR	NHMW-16.693-spm2	1.308	1.051	0.702	0.623	0.938	59.24
Brikinjava špilja, HR	NHMW-16.693-spm4	1.305	0.966	0.680	0.596	0.769	66.39
Biokovogebirge, HR	NHMW-16390-spm1	1.370	0.966	0.620	0.559	0.833	62.99
Biokovogebirge, HR	NHMW-16390-spm2	–	–	–	–	–	–
St John's cave, Njeguši, MNE	NMBE 571122 (DNA extraction)	1.38	1.00	0.66	0.59	0.96	75.69
St John's cave, Njeguši, MNE	NMBE 571123 (DNA extraction)	1.59	0.95	0.73	0.62	0.73	62.88
St John's cave, Njeguši, MNE	NMBE 577052-spm1	1.29	0.93	0.49	0.57	–	–
St John's cave, Njeguši, MNE	NMBE 577053-spm2	1.30	0.97	0.50	0.62	–	–
St John's cave, Njeguši, MNE	NMBE 577053-spm3 (subadult)	1.27	0.90	0.48	0.47	–	–
St John's cave, Njeguši, MNE	NMBE 572639 (SEM)	1.37	0.96	0.61	0.63	0.88	68.04
Jama Dobravljevac, BiH	NMHW-MO-113642-spm1	1.41	0.93	0.57	0.61	0.84	56.46
Jama Dobravljevac, BiH	NMHW-MO-113642-spm2	1.40	0.96	0.57	0.62	0.83	59.45
Taleza pećina, BiH	NMBE 553414/1 (ex RS 1981)	1.30	1.00	0.58	0.60	0.83	71.60

Results

Taxonomy

Class Gastropoda Cuvier, 1795
Subclass Heterobranchia Burmeister, 1837
Superorder Eupulmonata Haszprunar & Huber, 1990
Superfamily Ellobioidea L. Pfeiffer, 1854 (1822)
Family Carychiidae Jeffreys, 1830

Genus ***Zospeum*** Bourguignat, 1856

Zospeidae – Brusina 1886: 48.

Speozoum – Hamann, 1896: 49.

Zospeum troglobalcanicum Absolon, 1916
Figs 2, 3A, 4A–F, 7A–C, 8A–F

Zospeum troglobalcanicum – Absolon 1916a: 15: 242–309. — Absolon 1916b: 33 (48): 586 [Benetina Pećina, a cave above Zatokou Slanskou = Zatoka Slanska?? by Grebci].

Zospeum troglobalcanicum – Maier in Gittenberger 1975: 27.

Zospeum troglobalcanicum – Inäbnit *et al*. 2019: 160, fig. 7u.

Diagnosis

Shell ca 1.4 mm with conical form, 5¼ regularly coiled irregularly formed whorls, no aperture dentition; peristome with notch at upper parietal and palatal junction, basal columellar side thickly callused entering into shell; columella centrally aligned, moderately thick, swollen at base; internal lamella weak and tightly positioned on the columella directly under penultimate whorl.

Lectotype designation and rationale

We conclude that this shell, bearing the label notation "...lg Absolon" (Fig. 3A), is the only known syntype of *Z. troglobalcanicum* and thus, designate it here as the lectotype. The purpose of this lectotype designation is the fixation of a taxon name to a specific morphology and to stabilize nomenclature.

Type material

Lectotype (here designated)
BOSNIA AND HERZEGOVINA • "Benetina pećina ober Slano Südostherzegovina lg Absolon" [Benetina pećina above Slano SE Herzegovina leg. Absolon]; [42.8105° N, 17.9142° E]; Absolon leg.; NHMW Mol.Coll.Edlauer 32.749.

Other material examined

MONTENEGRO • 3 specs; Cetinje [Dobrsko Selo], Lipa, Lipska pećina; [42.3668° N, 18.9531° E]; Jul. 1975; F. Velkovrh leg.; MCSMNH-PMSL-Moll.-FVelkovrh 29603 (CT imaged) • 37 specs; same collection data as for preceding; MCSMNH-PMSL-Moll.-FVelkovrh 29603.

Description

Measurements. MCSMNH-PMSL-Moll.-FVelkovrh 29603 (N = 3): sh: 1.320–1.428 mm, sw: 0.960–1.071 mm; ah: 0.543–0.630 mm; aw: 0.571–0.666 mm; hlw: 0.794–0.879 mm; SA: 60.30–73.45 deg.

Lectotype: sh: 1.398 mm; sw: 1.007 mm; ah: 0.605 mm; aw: 0.640 mm; hlw: 0.886 mm; SA: 67.50 deg.; number of whorls: 5¼.

Shell with average height ca 1.38 mm, conical, with 5¼ convex whorls, regularly coiled, more or less irregularly shouldered, irregularly formed at the junction of the suture and the next whorl; teleoconch sculpture of thick irregular and blunt growth lines, sometimes crossed by weak radial banding (seen in fresh individuals), some distinct axial ribbing present for a short distance immediately behind palatal lip; height of last whorl slightly less than half of shell height; aperture reniform, peristome somewhat wider than high, columellar side oblique and angular with a thickened, long, straight parietal callus (shield), palatal rim unevenly thickened; basal columellar side of peristome slightly oblique and callused, callus extends deep into shell, basal columellar side forms a wall inside shell; degree of notch indentation at upper parietal and palatal junction variable; no aperture dentition; columellar and palatal-basal lip narrowly reflected; with aperture facing left, upper rim of peristome is indented 1/5 the width of the penultimate whorl; pronounced umbilical depression; in ventral perspective, the columellar side of the peristome arches over and is positioned to the right of and oblique to the umbilical depression, extending well beyond it, some puckering is present around the depression, alignment of last ¼ whorl not compact; columella centrally aligned, moderately thick, swollen at the base; internal lamella is a weak fold tightly positioned on the columella directly under penultimate whorl.

Distribution

This species is known from two caves within ca 80 km from each other in southern Bosnia and Herzegovina and western Montenegro.

Remarks

The shell of the lectotype bears an angular crack at the suture junction of the penultimate whorl and the body whorl (frontal view), extending almost midway onto the body whorl (Figs 2, 4A). On the dorsal side, a short crack begins at the junction of the suture of the fourth whorl and the penultimate whorl, descending ⅓ the height of the penultimate whorl (Fig. 4D).

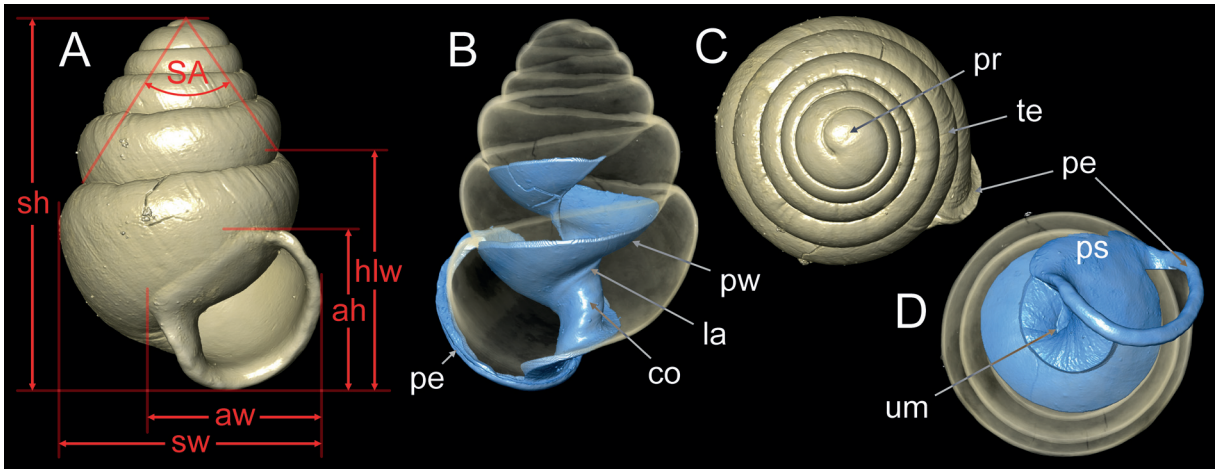

Fig. 2. 3D visualizations of Micro-CT data of the lectotype of *Zospeum troglobalcanicum* Absolon, 1916 (NHMW Moll.Coll.Edlauer 32.749) with shell parts and terms indicated. **A**. Measurements include shell height (sh), shell width (sw), aperture height (ah), aperture width (aw), height of last whorl (hlw) and spire angle (SA). **B**. Internal view showing columella (co), lamella (la), peristome (pe) and penultimate whorl (pw). **C**. Apical view showing protoconch (pr), teleoconch (te) and peristome (pe). **D**. Ventral view showing peristome configuration (pe) parietal shield (ps) and umbilicus (um).

Absolon (1916a) wrote in his Balkan expedition notes about finding *Z. troglobalcanicum* and considerations he had in naming this species. These two paragraphs are the only record of a shell description originally written in Czech (translated by M. Leinfelder into German 2019 and by AJ into English). A single photograph of the 13 syntype shells with a short caption of the locality, "Benetina pećina" was provided in a second publication (Absolon 1916b).

Original (translated) description of *Zospeum troglobalcanicum* (Absolon 1916a):

"My most interesting find during 1914, was the discovery of the first Balkan Zospeum "troglobalcanicum" n. sp., which I found in the cave "Benetina Pecina" over the bay of "Slanka" (loc. ca 122 [on Absolon's map by Grebci], still in Herzegovina). According to Clessin's keys and Kobelt's iconography, it would be easy for me to identify my Zospeum, like the other Zospeum, that has absolutely no dentition in its shell, to be ancestral to Z. amoenum. To be sure, I sent a cotype to Herrn Dr. F. Baborov for review and [who] confirmed my find as I expected Zospea to exist in the western Balkan. The fauna in Herzegovina generally has many special characteristics in common with the Croatian-Kranj [Slovenian] region, albeit specifically modified, for example, certain Myriapoda, Stalita, Titanethes, Monolistra, Troglocaris; the border seems to be the Valley of the Neretva.

The collection activity of other colleagues has contributed considerably to this collection (Aspasita Hauffeni, kranj-istrien-croatian Zospea, Auritus erika etc.) and through exchanges, I have received many valuable and unique morphs, some of which I received on loan (Museum Wien, Stuttgart = Clessin type (Vitrelly 4), Croatian Zoological Museum Zagreb, L. Kuščer (Triest), Dr. R. Schröder (Munich) and others. An extensive investigation of all the known material up to now has hereby been undertaken, including Eastern European troglobitic malacofauna. With much help from my wife, I have processed 95 morphs (in literature) using new methods from the microphotographic atlas consisting of about 500 images. This requires a separate and comprehensive report."

In sync with Absolon's identification quandary above, H.C. Maier tucked his handwritten considerations into vials of shells at the NHMW via specimen assessment notes, stamped "revid Maier, 1977" (Figs 3, 9, 12–13, 15). We remark that the author of these notes is Heinz Christian Maier, whose unpublished doctoral thesis on *Zospeum* was realized in 1982 and accessed for this work.

Zospeum tortuosum Jochum & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:BDD1308E-7D4C-447C-8009-E60D76AB38D2
Figs 3B–D, 4G–L

Diagnosis

Shell ca 1.4 mm, conical or elongate-conical with ca 5¼ regularly coiled, slightly shouldered whorls; last coiling of shell twists a fraction beyond the frontal plane ca ⅛ the width of body whorl; columella slanted and not centrally aligned; no lamella; ventral side swollen with columellar side of peristome heavily callused on top of and plugging umbilicus.

Etymology

This species is named after the characteristic ⅛ additional turn of the last whorl. Due to the twisted off-center alignment of the columella, the last whorl and the aperture are slightly turned to the left.

Type material

Holotype

MONTENEGRO • "Cetinska pećina, Cetinje, vhod; Mtg." [Cetinska cave, Cetinje, entrance; Montenegro]; [42.3886°N, 18.9208°E]; Sep. 1976; F. Velkovrh leg.; MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm1].

Paratypes

MONTENEGRO • 2 specs; same collection data as for holotype; MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm2-3].

Description

Measurements. Holotype: sh: 1.435 mm; sw: 0.944 mm; ah: 0.515 mm; aw: 0.511 mm; hlw: 0.841 mm; SA: 57.93 deg. Paratypes (N = 2): sh: 1.349–1.43 mm; sw: 0.951–0.972 mm; ah: 0.548–0.559 mm; aw: 0.575–0.609 mm; hlw: 0.827–0.844 mm; SA: 61.20–65.16 deg.

Shell conical, height 1.35–1.44 mm with 5¼ convex whorls. Whorls unevenly formed and slightly shouldered; protoconch bulbous; spire angle narrow; last whorl coils beyond the frontal plane ca ⅛width of body whorl, right side sometimes almost disappears under spire in apical view; aperture reniform, somewhat narrower than high, no aperture dentition, columellar side straight, not oblique, thickly and irregularly callused; peristome notch at upper parietal and palatal junction; parietal callus (shield) thick, long and straight; palatal rim uniformly thickened to halfway the height of peristome, palatal-basal lip thins to a ridgelike edge, reflected; suture moderately deep; teleoconch generally smooth with occasional surface irregularity; last whorl shows occasional, irregular blunt growth lines at suture with penultimate whorl, extending downwards to ca ⅓ the height of the last whorl; weak radial banding on last whorl

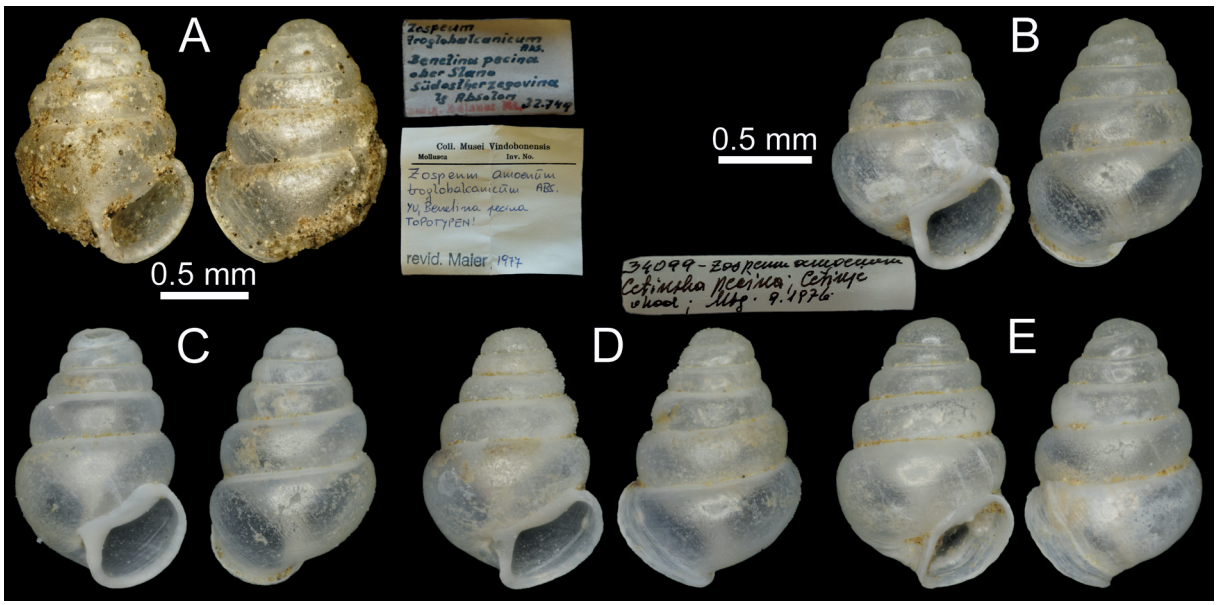

Fig. 3. Light microscopic images of shells from the caves Benetina pećina (SE Bosnia and Herzegovina) and Cetinska pećina (Montenegro) with specimen labels. **A**. *Zospeum troglobalcanicum* Absolon, 1916, lectotype (NHMW Moll.Coll.Edlauer 32.749) from Benetina pećina. **B–C**. *Zospeum tortuosum* Jochum & Ruthensteiner sp. nov., paratypes (MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm2-3]) from Cetinska pećina. **D**. *Zospeum tortuosum* Jochum & Ruthensteiner sp. nov., holotype (MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm1]) from Cetinska pećina. **E**. Deformed shell (MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm4]) from Cetinska pećina.

(seen in fresh individuals); some ribbing and irregular growth lines immediately behind palatal lip; light irregular ribbing on last whorl; height of last whorl greater than half of shell height; upper peristome rim almost flush with left side of penultimate whorl (in aperture facing left view); columella unevenly formed, moderately thick, not centrally aligned, tightly twisted, abapically attenuated, swollen at base;

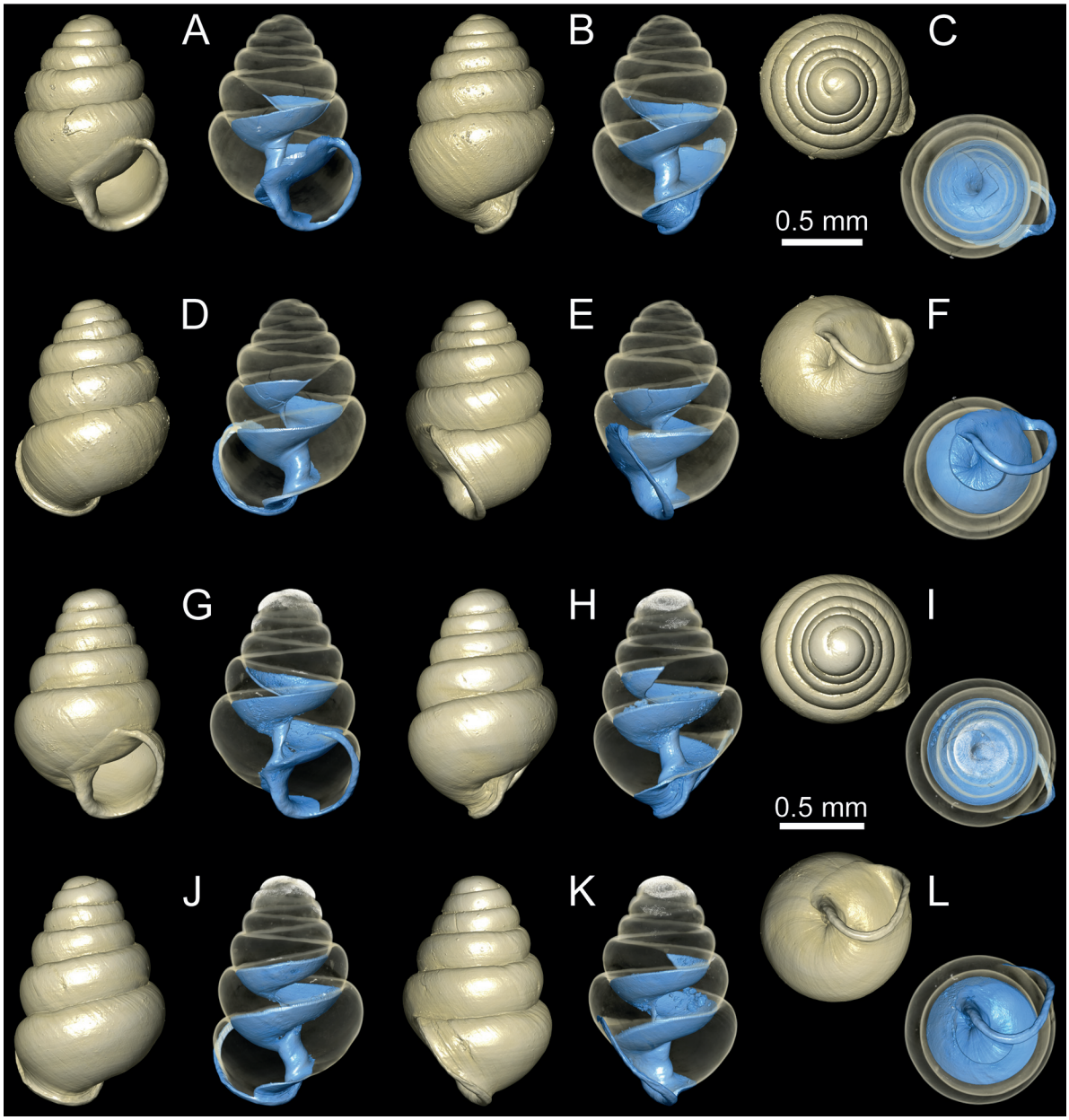

Fig. 4. 3D visualizations using Micro-CT data of shells from the caves Benetina pećina (SE Bosnia and Herzegovina) and Cetinska pećina (Montenegro). **A–F**. *Zospeum troglobalcanicum* Absolon, 1916, lectotype (NHMW Moll.Coll.Edlauer 32.749). **A**. Aperture view. **B**. Aperture facing right view. **C**. Apical view. **D**. Dorsal view. **E**. Aperture facing left view. **F**. Ventral view showing umbilical depression. **G–L**. *Zospeum tortuosum* Jochum & Ruthensteiner sp. nov., holotype (MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm1]). **G**. Aperture view. **H**. Aperture facing right view. **I**. Apical view. **J**. Dorsal view. **K**. Aperture facing left view. **L**. Ventral view showing callused peristome positioned mostly on top of umbilicus.

no umbilical depression is present; umbilicus thickly callused at junction of peristome and base of columella, columellar side of peristome positioned on top of callused umbilicus, base swollen with some puckering; alignment of last ¼ whorl compact.

Distribution

This species is only known from its type locality, Cetinska pećina, Cetinje in western Montenegro.

Remarks

The species is most similar in shell form and dimensions to *Z. troglobalcanicum*. It differs mostly by the extra turning of the final whorl and the associated sideways twisting of the columella. It differs from *Z. troglobalcanicum* in that it does not bear a conspicuous threadlike lamella on its twisted columella.

Deformed shell (Figs 3E, 5)

A deformed second shell, (MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm4]), similar to that of *Zospeum tortuosum* Jochum & Ruthensteiner sp. nov. and found in the same lot from Cetinska pećina, is additionally described and considered in chronological context with the image figures of *Zospeum tortuosum*.

Data of the deformed shell

The species data are: "Cetinska pećina, Cetinje, vhod; Mtg." [Cetinska cave, Cetinje, entrance; Montenegro]; [42.3886° N, 18.9208° E]; Sept. 1976; F. Velkovrh leg. MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm4].

Measurements of the deformed shell

Shell: sh: 1.396 mm; sw: 0.922 mm; ah: 0.566 mm; aw: 0.590 mm; hlw: 0.836 mm; SA: 60.01 deg.

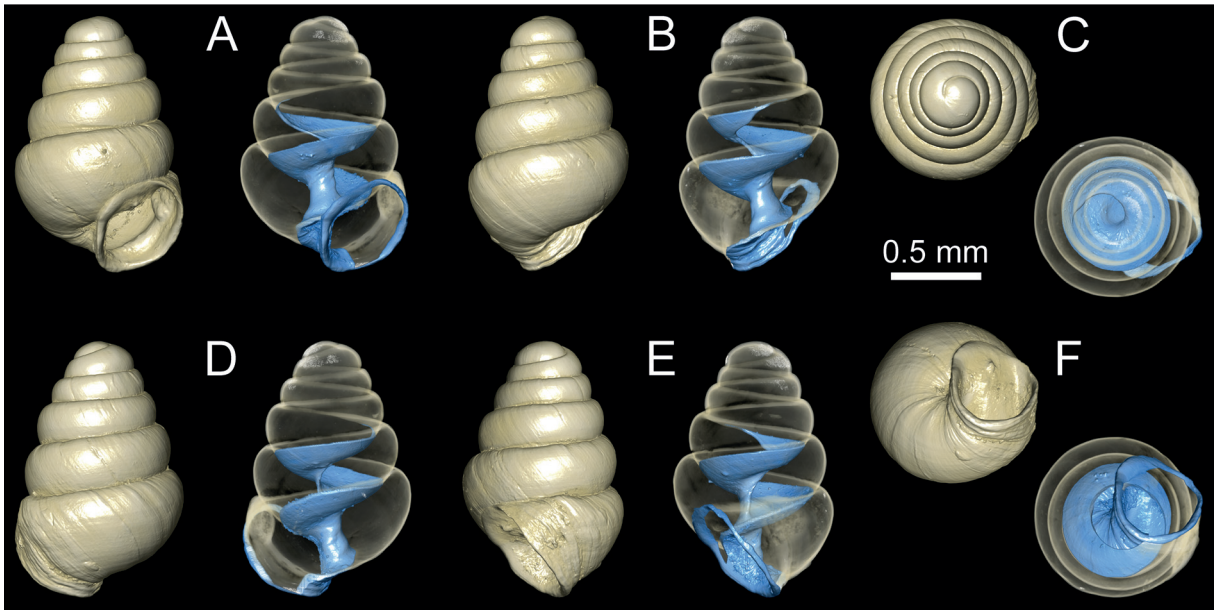

Fig. 5. 3D visualizations of Micro-CT data of the deformed shell, (MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm4]) from Cetinska pećina. **A**. Aperture view. **B**. Aperture facing right view. **C**. Apical view. **D**. Dorsal view. **E**. Aperture facing left view. **F**. Ventral view with umbilicus covered by last quarter of shell whorl.

Description of the deformed shell

Shell conical, height 1.4 mm with 5¼ whorls; transparent. Whorls convex, and slightly shouldered, spire regularly coiled; suture moderately deep; aperture oriform, elliptical ovate, wider than high, interior of aperture heavily callused with wartlike growths on palatal side and in mid parietal region, giving the impression of a wart-like tooth; columellar side of peristome straight and angular; no notch at upper parietal and palatal junction; parietal callus (shield) well defined, narrow, roundish; palatal rim unevenly thin, thickening only at basal-columellar zone; palatal-basal lip thins to a ridgelike edge, narrowly reflected; teleoconch with course irregular growth lines; weak radial banding on penultimate and body whorl; course irregular growth lines present immediately behind palatal-basal lip and extending some distance from peristome rim; height of last whorl greater than half of shell height; upper peristome rim recedes $^{1}/_{5}$ width of penultimate whorl (in aperture facing left view); columella oblique, moderately thick, not centrally aligned, swollen at base; incomplete callused lamella under penultimate whorl; no umbilical depression; umbilicus thickly callused at junction of peristome and base of columella, columellar side of peristome positioned on top of callused umbilicus, base swollen with some puckering; upper palatal rim not reflected (as seen from umbilical view), alignment of last ¼ whorl compact.

Remarks on the deformed shell

Although this shell has wart-like deformation in the aperture, the elliptical ovate aperture shape and the columella configuration, which is unaffected by the deformation, largely corresponds to that of *Z. tortuosum* Jochum & Ruthensteiner sp. nov. (MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm1]) from the same cave. Though the aperture shape also resembles that of *Z. dubokidoense* Jochum & Ruthensteiner sp. nov. (Fig. 7D, 8G), the deformed shell shows narrower and smaller dimensions. Due to the compactness of the last quarter whorl, the straight alignment of the left side of the peristome on top of the umbilical depression and the narrowness of the parietal shield, this shell cannot be unequivocally determined as *Z. tortuosum* sp. nov.

Zospeum intermedium Jochum & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:5F135CC4-5DCF-4CD0-9EDF-D694561E37D8
Fig. 6

Zospeum troglobalcanicum – Maier in Gittenberger 1975: 26: fig. 3.

Diagnosis

A tall shell ca 1.6 mm, conical or elongate-conical with ca 5½ regularly coiled, slightly shouldered whorls; columella bears a well-formed lamella forming a conspicuous and short parietalis visible in umbilical view (Fig. 6H); ventral side swollen with small umbilical depression.

Etymology

This species is named after its mixture of significant shell characteristics in four species of *Zospeum* from nearby caves described in this study, making for a composite, intermediary form of these species.

Type material

Holotype

MONTENEGRO • Cetinjska pećina [= Cetinska pećina] near Cetinje, Crna Gora [= Montenegro] behind monastery; 15 May 1974; E. Gittenberger leg.; RMNH.MOL.234132.

Description

Measurements. Holotype: sh: 1.57 mm; sw: 1.08 mm; ah: 0.58 mm; aw: 0.66; hlw: 0.95 mm; SA: 66.35 deg.

Shell conical or elongate conical, height ca 1.6 mm with 5½ whorls; transparent. Whorls convex, and slightly shouldered, spire regularly and tightly coiled; suture moderately deep; aperture reniform, almost elliptical ovate; aperture wider than high, columellar side slightly rounded; slight notch at upper parietal and palatal junction; parietal callus (shield) well defined, straight, long and angular; palatal rim thin; palatal-basal lip narrowly reflected; teleoconch smooth with irregular growth lines; weak radial banding on body whorl; course irregular growth lines present immediately behind palatal-basal lip; height of last whorl less than half of shell height; apertural rim thin and receding $^{1}/_{5}$ width of penultimate whorl (in aperture facing left view), exposing deeply set parietalis (Fig. 6G); columella centrally aligned, moderately thick, not swollen at base; low lamella under penultimate whorl forming a conspicuous, short parietalis reaching up as high as the umbilical depression in umbilical view; umbilical depression small; umbilicus callused at junction of peristome and base of columella, columellar side of peristome positioned above and to the right of the umbilicus, base swollen with little puckering; upper palatal rim not reflected (as seen from umbilical view); alignment of last ¼ whorl compact with a slightly rightward tendency (seen in umbilical view).

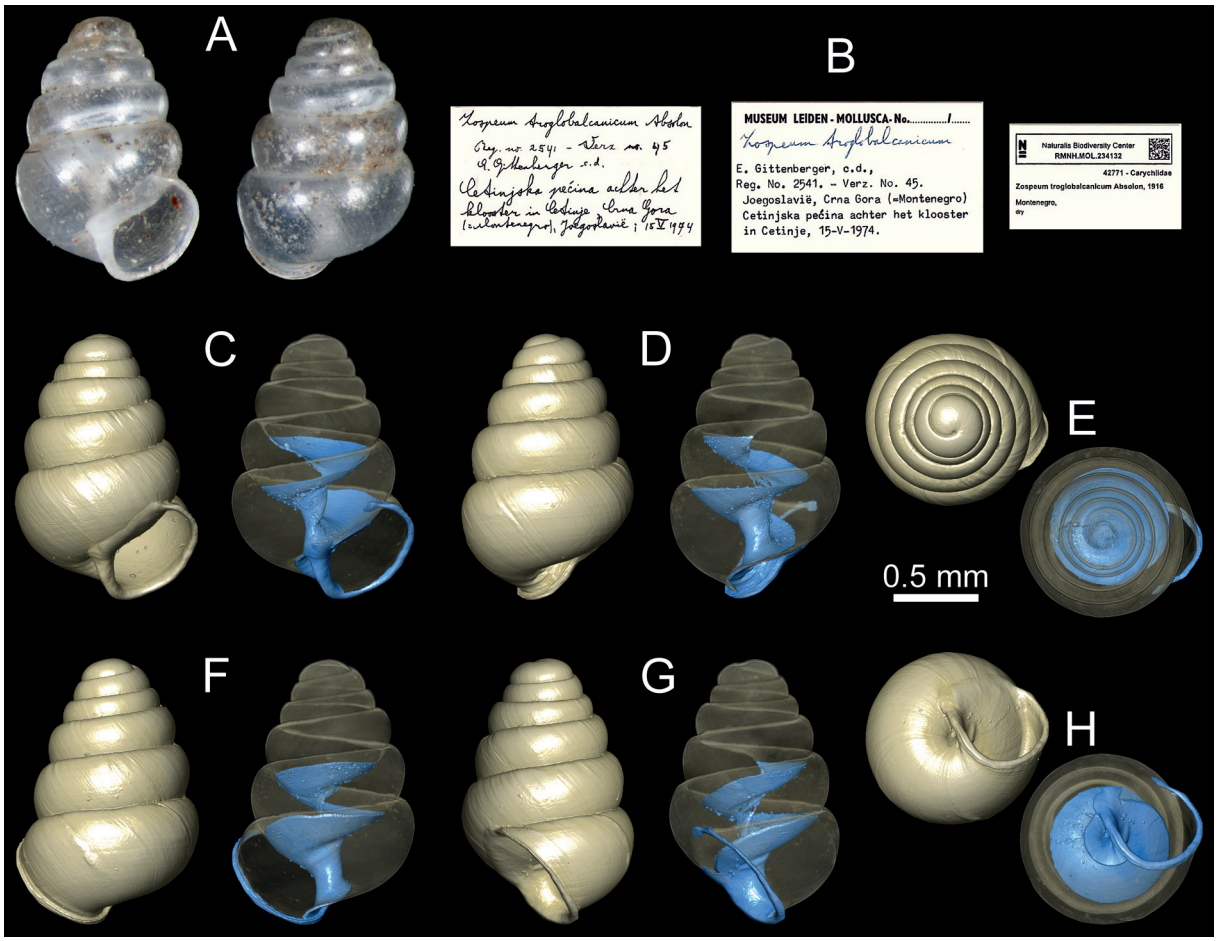

Fig. 6. *Zospeum intermedium* Jochum & Ruthensteiner sp. nov. (RMNH.MOL.234132) from Gittenberger (1975). **A**. Light microscopic images of apertural and dorsal views. **B**. Sample labels. **C–H**. 3D visualizations of X-ray Micro-CT data. **C**. Aperture view. **D**. Aperture facing right view. **E**. Apical view. **F**. Dorsal view. **G**. Aperture facing right view. **H**. Umbilical view showing slight umbilical depression and lamella projecting from the columellar side.

Remarks

It is not known from which section of the cave this shell derived except that it was amidst a larger sample (RMNH.MOL.234134) comprising 64 shells from a part of the cave "with absolute darkness" (Gittenberger 1975). The species represents an intermediary form between *Z. troglobalcanicum*, *Z. tortuosum* Jochum & Ruthensteiner sp. nov., *Z. dubokidoense* Jochum & Ruthensteiner sp. nov. and *Z. simplex*. It is significantly larger than these species in shell height, shell width, aperture height, aperture width, height of the last whorl and narrower in spire angle. The columella shows similarity with that of Z. *dubokidoense* in turning angle, its slightly off-centered alignment, and superficial irregularities. In dorsal and aperture facing left views, the columella is similar to that of *Z. troglobalcanicum* and *Z. dubokidoense*. However, *Z. intermedium* Jochum & Ruthensteiner sp. nov. differs from these species in that the umbilical depression grades from a pronounced umbilical depression in *Z. troglobalcnicum* and *Z. simplex* to that of a slight umbilical depression in *Z. intermedium* to that of no umbilical depression in *Z. dubokidoense*, which is largely covered by the columellar side of the peristome directly above it. *Z. intermedium* differs from the rest of the Southern Balkan species in this study in that it bears a pronounced lamella forming a deeply set, conspicuous parietalis. Only *Z. dubokidoense* shows a very slight but visible parietalis (Fig. 8L). *Z. troglobalcanicum* bears a threadlike partial lamella that does not form a visible parietalis.

Zospeum dubokidoense Jochum & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:118E4771-C551-49E8-AAC1-371E5E279FFB
Figs 7D–F, 8G–L

Diagnosis

Shell ca 1.5 mm, conical, with 5–5¼ slightly shouldered whorls, punctuated by deep, irregular growth lines; aperture elliptical-ovate to subquadrate; parietal shield compact, positioned low on the body whorl; columella centrally aligned, moderately slender, attenuate; lamella loosely positioned under penultimate whorl succeeded by an incomplete middle lamella and a basal bulge above the umbilicus, forming a thick basal lamella; basal lamella extends out of the aperture as a low ridge on the columellar side of the parietal shield.

Etymology

This species is named after the type locality cave, Duboki do in western Montenegro.

Type material

Holotype

MONTENEGRO • Duboki do; "potoček v dvorani, Mtg." [a stream in the cave chamber, Montenegro]; depth -60 m; [42.4949°N, 18.8106°E]; Aug. 1975; F. Velkovrh leg.; MCSMNH-PMSL-Moll.-FVelkovrh 30360[spm1].

Paratypes

MONTENEGRO • 2 specs; same collection data as for holotype; MCSMNH-PMSL-Moll.-30360[spm2-3].

Description

Measurements. Holotype: sh: 1.514 mm; sw: 1.088 mm; ah: 0.622 mm; aw: 0.642 mm; hlw: 0.921 mm; SA: 63.64 deg. Paratypes (N = 2): sh: 1.512–1.546 mm; sw: 1.085–1.103 mm; ah: 0.639–0.663 mm; aw: 0.611–0.645 mm; hlw: 0.961–0.982 mm; SA: 65.73–68.83 deg.

Shell conical, height ca 1.5 mm with 5 convex shouldered whorls, punctuated by deep irregular growth lines; last half of final whorl coils tightly under penultimate whorl such that right side almost disappears under spire (apical view); aperture elliptical-ovate to subquadrate; peristome narrow on upper palatal side, pronounced notch present at upper junction with parietal shield, columellar side of peristome roundish-angular, callused, rim slightly reflected; rim recedes less than $^{1}/_{6}$ width of penultimate whorl (aperture facing left view); parietal shield compact, thickly callused with a low straightish edge; columella centrally aligned, slender, attenuate; lamella loosely positioned under penultimate whorl followed by an incomplete weak middle lamella and a lamellar bulge above the umbilicus forming a blunt basal lamella; basal lamella extends out of the aperture as a low ridge on the columellar side of the parietal shield (umbilical view); umbilicus closed, no depression, region callused and puckered; columellar side of peristome callused and positioned straight at center with leftward tendency in relation to the umbilicus; alignment of last ¼ whorl compact.

Distribution

This species is only known from its type locality.

Remarks

This species is the closest to *Z. intermedium* Jochum & Ruthensteiner sp. nov. in that it has a lamella set deep in the shell, which is positioned high up on the columella, but differs in forming a short, very weak parietalis that runs out to less than half of the extension of the parietal shield (umbilical view). The base of the shell (umbilical view) is heavily puckered in *Z. dubokidoense* Jochum & Ruthensteiner sp. nov. and smooth in *Z. intermedium*. The shell dimensions are comparable except that the aperture height and the height of the last whorl is greater in *Z. dubokidoense*. The only other shell to show an elliptical ovate

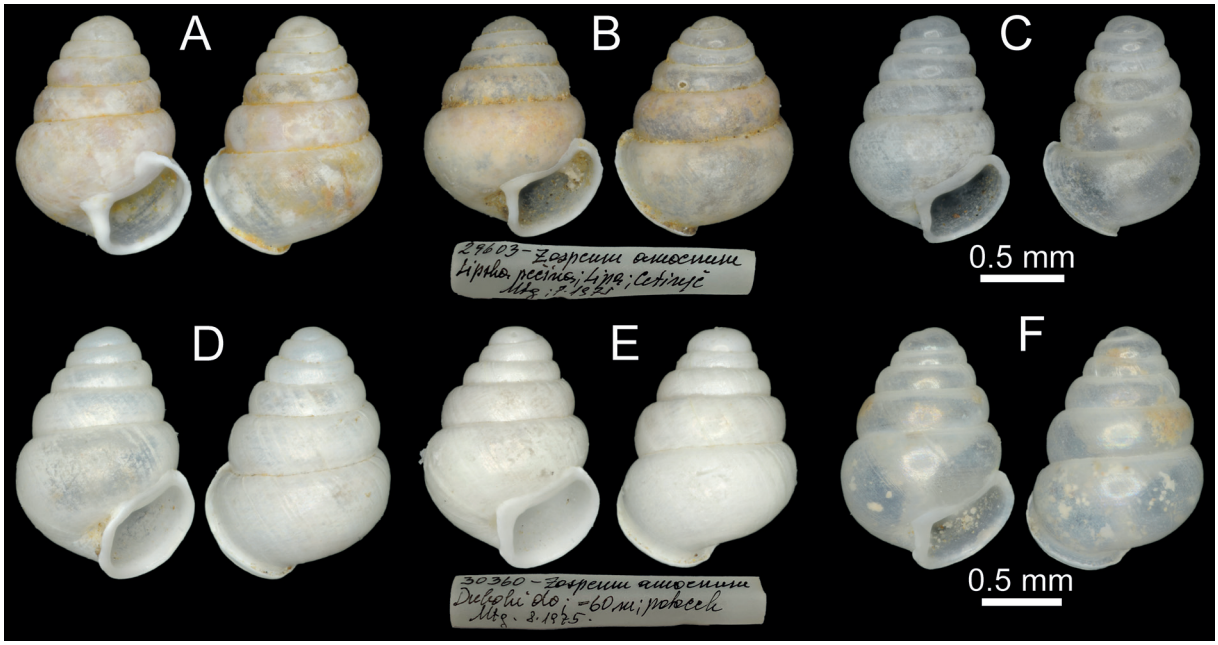

Fig. 7. Light microscopic images of shells from the caves Lipska pećina and Duboki do (Montenegro) with specimen labels. **A–C**. *Zospeum troglobalcanicum* Absolon, 1916 (MCSMNH-PMSL-Moll.-FVelkovrh 29603). **D–F**. *Zospeum dubokidoense* Jochum & Ruthensteiner sp. nov. **D**. Holotype (MCSMNH-PMSL-Moll.-FVelkovrh 30360[spm1]). **E–F**. Paratypes, Duboki do, Montenegro (MCSMNH-PMSL-Moll.-FVelkovrh 30360[spm2-3]).

aperture and a reduced parietal shield is the deformed shell from Cetinska pećina, Cetinje, MCSMNH-PMSL-Moll.-FVelkovrh 34099[spm4] (Fig. 5).

According to the speleologist, László Dányi (pers. comm. May 2022), Duboki do cave is longer than 4.2 km and more than -530 m deep. "It has many chambers and very different parts."

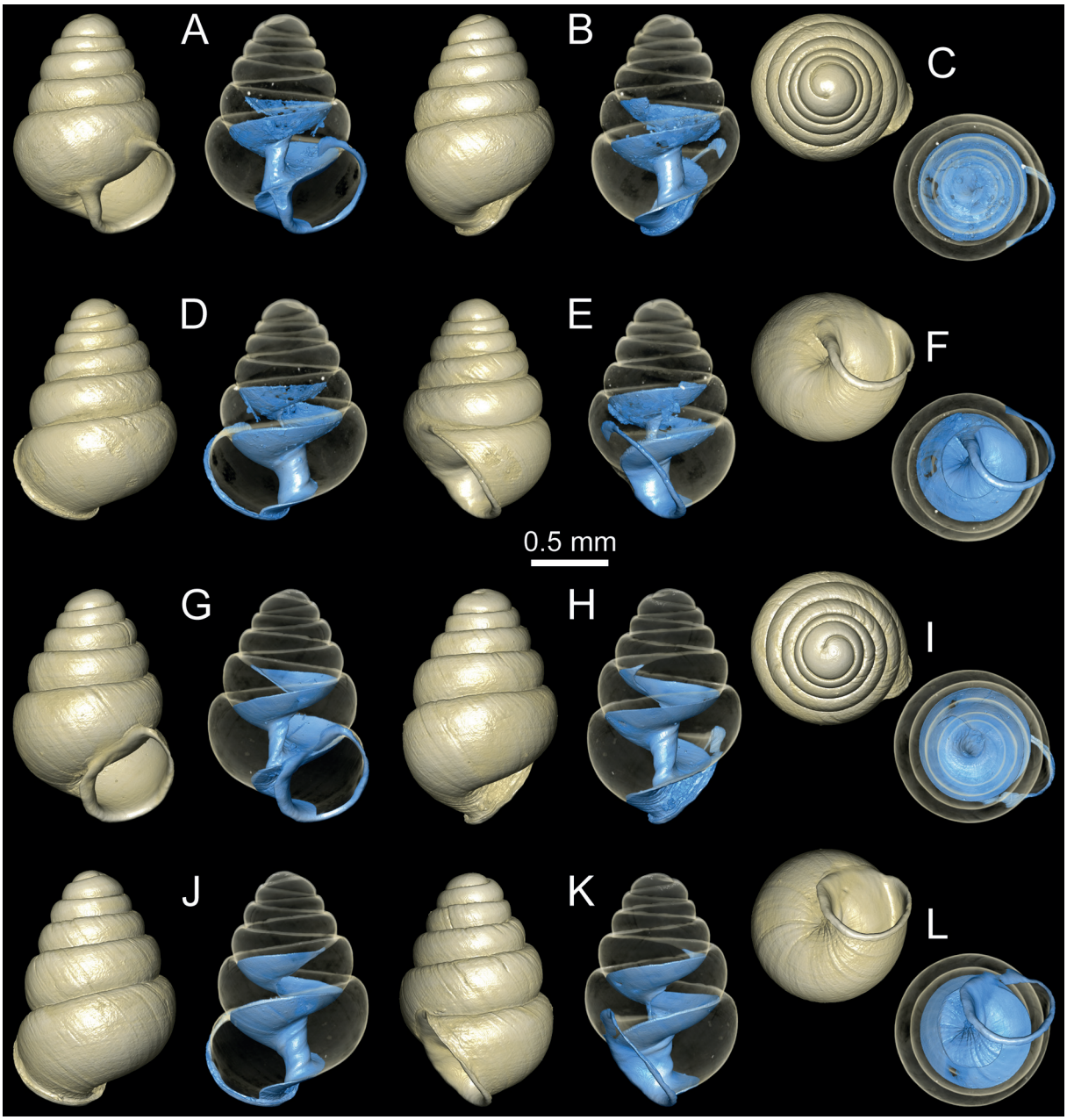

Fig. 8. 3D visualizations of Micro-CT data of shells from the caves Lipska pećina and Duboki do (Montenegro). **A–F**. *Zospeum troglobalcanicum* Absolon, 1916 (MCSMNH-PMSL-Moll.-FVelkovrh 29603) (Fig. 7A). **A**. Aperture view. **B**. Aperture facing right view. **C**. Apical view. **D**. Dorsal view. **E**. Aperture facing left view. **F**. Ventral view showing reduced umbilical depression. **G–L**. *Zospeum dubokidoense* Jochum & Ruthensteiner sp. nov., holotype (MCSMNH-PMSL-Moll.-FVelkovrh 30360[spm1]). **G**. Aperture view. **H**. Aperture facing right view. **I**. Apical view. **J**. Dorsal view. **K**. Aperture facing left view. **L**. Ventral view showing no umbilical depression.

Zospeum amplioscutum Jochum & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:870FA5D2-6A9A-43AA-A533-B25CFC89A96D
Fig. 9

Diagnosis

Shell ca 1.30–1.36 mm, conical with 5½ irregularly convex whorls; peristome thickly callused on columellar side causing it to project beyond plane of shell (ventral side view); parietal shield well defined, positioned conspicuously high on body whorl and heavily callused; columella slender (aperture facing right) (Fig. 9D) with two weak, incomplete lamellae. Last ¼ of body whorl elongate on ventral side.

Etymology

This species is named after the characteristic, large and heavily callused parietal shield.

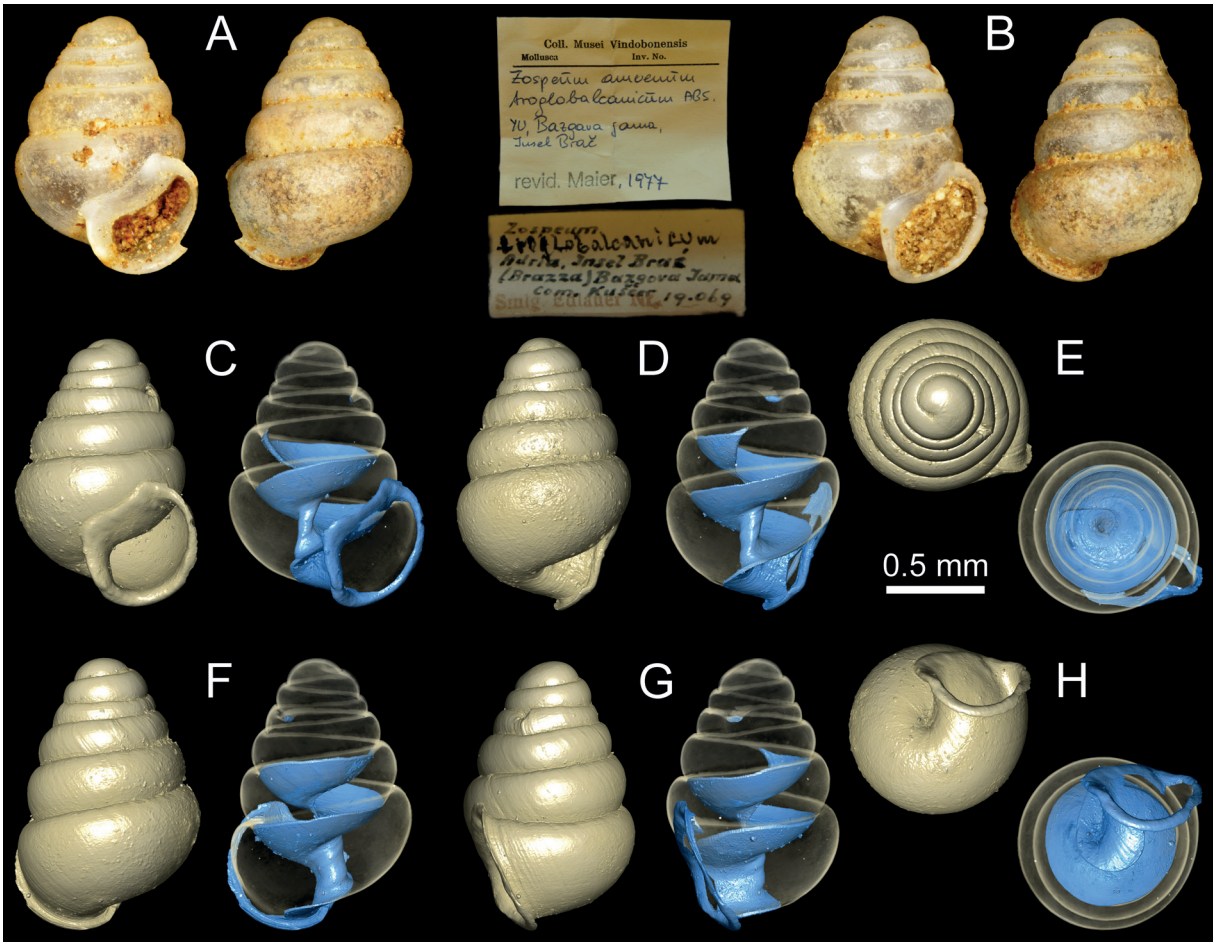

Fig. 9. *Zospeum amplioscutum* Jochum & Ruthensteiner sp. nov., (NHMW Mol.Coll.Edlauer 19.069) with sample labels. **A**. Light microscopic images of paratype (NHMW Mol.Coll.Edlauer 19.069), apertural and dorsal views. **B**. Light microscopic images of holotype (NHMW Mol.Coll.Edlauer 19.069), aperture and dorsal views. **C–H**. 3D visualizations of X-ray Micro-CT data of holotype (NHMW Mol. Coll.Edlauer 19.069). **C**. Aperture view. **D**. Aperture facing right view. **E**. Apical view. **F**. Dorsal view. **G**. Aperture facing left view. **H**. Ventral view showing coiling projecting high up on shell and peristome oblique to umbilicus.

Type material

Holotype

CROATIA • (Fig. 9B); "Adria, Insel Brać (Brazza) Bazgova jama, com. Kuščer" [Adriatic, Island of Brać, Jama Bazdovača, communication with Kuščer]; [43.2918° N, 16.6469° E]; NHMW Mol.Coll. Edlauer 19.069.

Paratype

CROATIA • 1 spec. (Fig. 9A); same collection data as for holotype; NHMW Mol.Coll.Edlauer 19.069.

Description

Measurements. Holotype: sh: 1.362 mm; sw: 0.966 mm; ah: 0.631 mm; aw: 0.574 mm; hlw: 0.808 mm; SA: 63.28 deg. Paratype (N = 1): sh: 1.304 mm; sw: 0.940 mm; ah: 0.608 mm; aw: 0.609 mm; hlw: 0.804 mm; SA: 63.53 deg.

Shell conical, height 1.30–1.36 mm with 5½ irregularly convex whorls bearing numerous, course irregular growth lines; aperture lunate-reniform; peristome narrow on upper palatal side, pronounced notch present at upper junction with parietal shield, lower columellar side of peristome rounded and thickly callused, causing it to project beyond plane of shell (aperture facing left), rim narrowly reflected with some low, irregular ribbing behind basal-palatal part; rim recedes ca ⅛ width of penultimate whorl; parietal shield long, angular, thickly callused, extending ⅓ to ½ the height of the body whorl, with a curved edge at point of maximum whorl convexity; columella centrally aligned, slender with hint of two weak incomplete lamellae, the first tightly positioned under the penultimate whorl, the second, a wider band loosely positioned below it, and a slight bulge at base; umbilical region callused with a shallow depression; (ventral view) columellar side of peristome positioned high, arching above and to the right of umbilical depression, alignment of last ¼ whorl elongate, not compact.

Distribution

This species is only known from its type locality, Jama Bazdovača on the Croatian Island of Brać.

Remarks

Though *Z. amplioscutum* Jochum & Ruthensteiner sp. nov. resembles *Z. simplex*, the heavily callused parietal shield and the degree of its extension onto the body whorl differs from that of this species. It is smaller, has a wider spire angle and a substantially more textured teleoconch due to the numerous, course irregular growth lines in comparison to that of *Z. simplex*. *Zospeum simplex* does not have a second lamella on the columella (aperture facing right) (Fig. 18B) but weak ripples of a potential double one (Fig. 18D) or a stronger, incomplete single one in dorsal view (Fig. 18J). The narrow columella (Fig. 9C–D) and the elongation of the last whorl further beyond the umbilical depression (ventral side) additionally differentiate *Z. amplioscutum* from *Z. simplex*.

Zospeum tumidum Jochum, Schilthuizen & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:1F6F1AB3-137B-4AA9-ABB8-46E0AF777F8C
Fig. 10

Diagnosis

Shell ca 1.5 mm, turbinate-conical with 5–5¼ regularly coiled, irregularly formed convex whorls; last coiling of shell twists a fraction beyond the frontal plane ca ⅛ the width of penultimate whorl; columella centrally aligned and moderately fat bearing a lamellar bulge rather than a fine lamella; umbilical depression deep.

Etymology

The species is named after the squat and wide, turbinate form of the shell.

Type material

Holotype

MONTENEGRO • Piva Region, Bajovo Polje, Đokova pećina, at cave entrance; 43.0315° N, 18.8104° E; 1 Jul. 2018; M. Schilthuizen and I. Njunjić leg; at cave entrance; NMBE 572615 (ex TxEx-DU0025).

Description

Measurements. Holotype: sh: 1.537 mm; sw: 1.177 mm; ah: 0.731 mm; aw: 0.712 mm; hlw: 1.028 mm; SA: 74.75 deg.

Shell ca 1.5 mm, turbinate-conical with 5–5¼ irregular, flatly convex whorls; shell comparatively large; milky translucent; suture shallow with irregular indentations at the junction of the suture and the succeeding whorl growing into course growth lines; teleoconch sculpture of blunt irregular growth

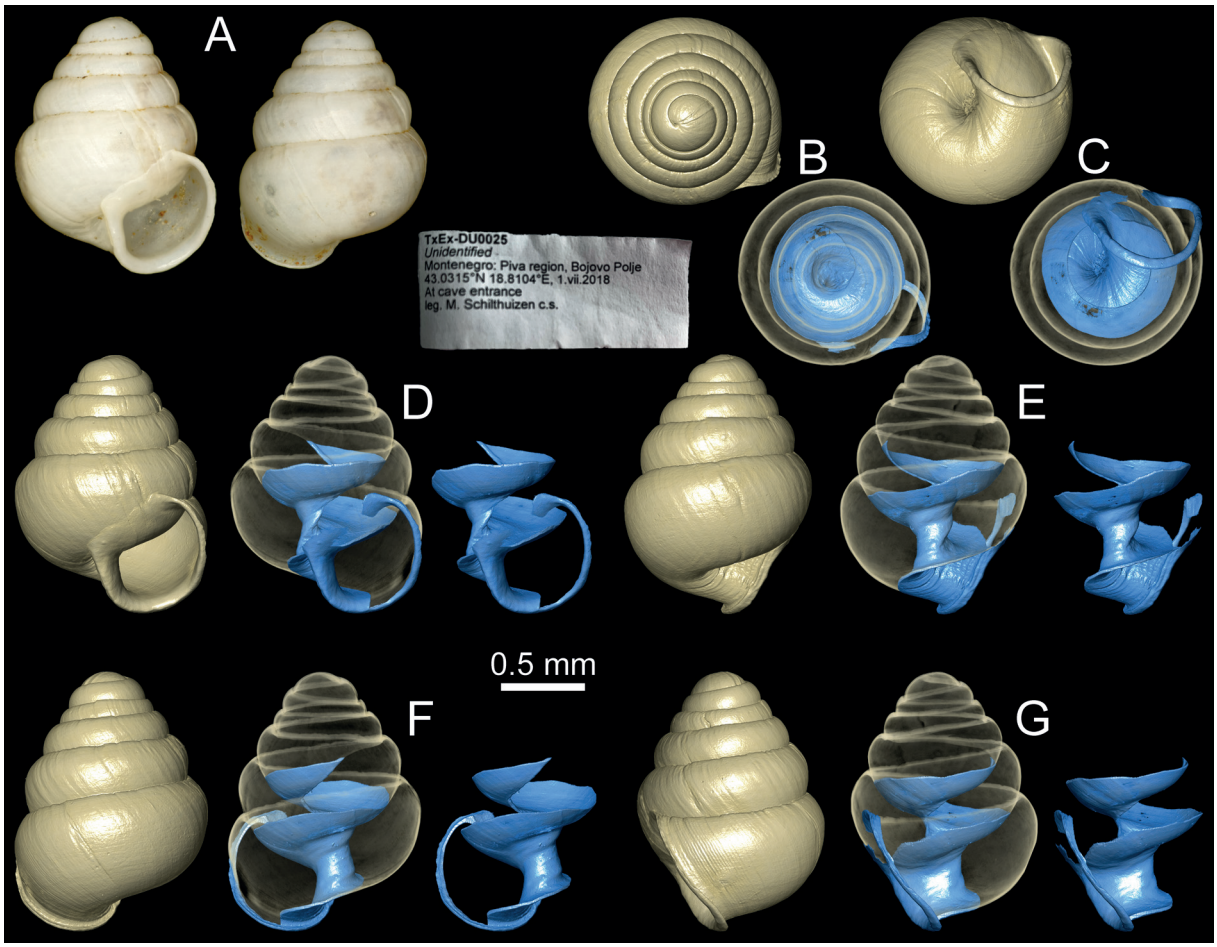

Fig. 10. *Zospeum tumidum* Jochum, Schilthuizen & Ruthensteiner sp. nov., holotype (NMBE 572615). **A**. Light microscopic images, showing aperture and dorsal views and TxEx Collection label. **B**. 3D visualizations of Micro-CT data, apical view. **C**. Ventral view showing deep umbilical depression. **D**. Aperture view. **E**. Aperture facing right view showing tapered columella and lamellar bulge. **F**. Dorsal view. **G**. Aperture facing left view.

lines interspersed with fine, weak thread-like striations; distinct, fine, thread-like axial ribbing extends for a distance immediately behind palatal-basal lip; last whorl large and tumid, encompassing ca ⅔ of shell height; last coiling twists a fraction beyond the frontal plane ca ⅛ the width of body whorl; suture shallow; aperture reniform, somewhat higher than wide; peristome generally thin especially at upper palatal side, slightly expanded; weak notch present at upper junction with parietal shield, columellar side oblique and thickly callused, columellar and palatal-basal lip narrowly reflected; parietal shield well defined, straight, long, angular with course growth lines crossing into it; columella thick and centrally aligned, apically tapered (aperture facing right) with a lamellar bulge and no defined lamella; umbilical depression deep, callused and puckered; columellar side of peristome arches high over and oblique to umbilical depression, alignment of last ¼ whorl not compact.

Distribution

This species is only known from its type locality cave, Đokova pećina in the Bajovo Polje of Montenegro.

Remarks

The species is the only Southern Balkan species to possess a thick lamellar bulge. It has the widest shell with the greatest aperture height and aperture width as well as the highest last whorl and greatest spire angle of all 13 species (and one morphospecies *Zospeum* sp. 2) (encompassing 31 shells) measured in this study.

Zospeum njunjicae Jochum, Schilthuizen & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:F762D981-D8FB-4EE7-BB0F-489E3D596A04
Fig. 11, 22A–B

Diagnosis

The smallest species of southern Balkan *Zospeum*, ca 1.2 mm, conical with 5 regularly coiled irregularly formed whorls; protoconch askew; peristome heavily callused on basal columellar side with a low, blunt, more or less conspicuous denticle some distance inside; columella centrally aligned, moderately thick, swollen at base; low lamella; well-defined umbilical depression.

Etymology

This species is dedicated to the biospeleologist and collector, Iva Njunjić.

Type material

Holotype

MONTENEGRO • (Fig. 11C–I); Virpazar, Gornja Seoca, Golubova pećina; 42.2093° N, 19.1306° E; 26 Jun. 2018; M. Schilthuizen and I. Njunjić leg.; in cave entrance; NMBE 572617.

Paratypes

MONTENEGRO • 2 specs; same collection data as for holotype; NMBE 572616 • 2 specs; same collection data as for holotype; SMF 349426 • 2 specs; same collection data as for holotype; NHMW-MO-113651 • 3 specs; same collection data as for holotype; TxEx-DU0018.

Description

Measurements. Holotype: sh: 1.271 mm; sw: 0.914 mm; ah: 0.560 mm; aw: 0.578 mm; hlw: 0.811 mm; SA: 69.69 deg. Paratypes (N = 2): sh: 1.214–1.248 mm; sw: 0.944–0.947 mm; ah: 0.578–0.588 mm; aw: 0.507–0.524 mm; hlw: 0.764–0.790 mm; SA: 71.38–71.83 deg.; NMBE 572616.

Shell minute, ca 1.2 mm, conical, with 5 regularly coiled convex whorls; transparent when fresh, opaque when older; protoconch leans slightly left (frontal view); aperture reniform; teleoconch sculpture with few irregular and occasional course growth lines, last whorl weakly crossed by radial banding; some weak axial ribbing present immediately behind palatal lip; palatal rim narrowly reflected; peristome thickly callused, notch indentation at upper parietal and palatal junction pronounced, upper palatal side thin and expanded, columellar side oblique and angular with a low, blunt, more or less conspicuous denticle inside; parietal shield thickly callused, long and straight, extending beyond half of height of last whorl; last whorl height about half of shell height (Fig. 11E), last whorl tightly coiled and almost disappearing under spire at last ⅓ of coiling (apical view); upper rim of peristome recedes ca 1/6 the width of the penultimate whorl (aperture facing left); columella centrally aligned, moderately thick (Fig. 11E), lamella loosely coiled on columella under penultimate whorl; umbilical depression callused, puckered; columellar side of peristome arches high over with curvature of whorl on top of umbilical depression, alignment of last 1/4 whorl is not compact.

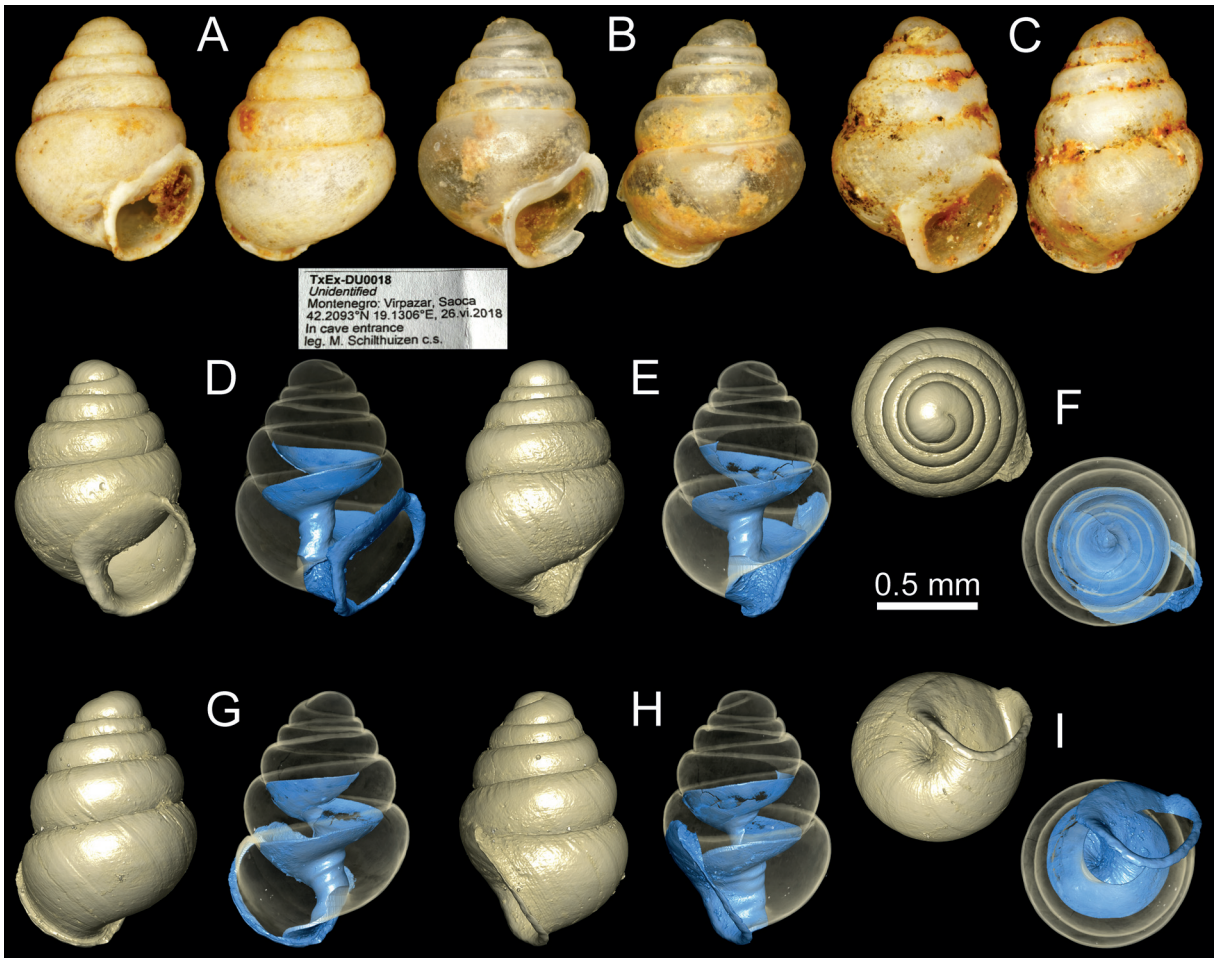

Fig. 11. *Zospeum njunjicae* Jochum, Schilthuizen & Ruthensteiner sp. nov. **A–B**. Light microscopic images of paratypes (NMBE 572616) showing aperture and dorsal views. **C**. Light microscopic images of holotype (NMBE 572617) showing aperture and dorsal views. **D–I**. 3D visualizations of X-ray micro-CT data of holotype (NMBE 572617). **D**. Aperture view. **E**. Aperture facing right view showing well defined lamella. **F**. Apical view. **G**. Dorsal view. **H**. Aperture facing left view. **I**. Ventral view.

Distribution

This species is only known from its type locality cave, Golubova pećina in southwestern Montenegro.

Remarks

This species differs from all others in that it demonstrates the smallest shells of the Southern Balkan region so far. The columella is more robust than that of *Z. troglobalcanicum* and the lamella comprises a low bulge rather than an incomplete thread atop of the columella directly under the penultimate whorl as in *Z. troglobalcanicum*. The columella of this species is also unevenly contoured with a few low humps due to the tight twisting of the inner coiling.

Zospeum neuberti Jochum & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:9BABF583-23ED-4ACF-92DE-1A52D8F7D0E0
Fig. 12

Diagnosis

Shell ca 1.3 mm, conical with 5¼ regularly coiled whorls, with blunt irregular growth lines; parietal shield thickly callused; columella centrally aligned, completely smooth; no lamella; ventral side swollen with well-defined umbilical depression; columellar side of peristome is positioned directly above umbilical depression with last coiling of whorl leaning to right of it.

Etymology

This species honors the German malacologist, mentor, and curator of molluscs, Dr Eike Neubert at the Naturhistorisches Museum der Burgergemeinde Bern (NMBE), Bern, Switzerland in recognition of his support, dedicated mentorship, and contributions to malacology and specifically, to carychiid research.

Type material

Holotype

CROATIA • (Fig. 12C–I); "Grabovica-Höhle bei Trebinje com. Kuščer" [Grabovica cave by Trebinje communicated with Kuščer]; [42.7438° N, 18.0578° E]; NHMW Mol.Coll.Edlauer 32006.

Paratypes

CROATIA • 1 spec. (Fig. 12A); same collection data as for holotype; NHMW Mol.Coll.Edlauer 32006 • 1 spec. (Fig. 12B); same collection data as for holotype; NHMW Mol.Coll.Edlauer 32006.

Description

Measurements. Holotype: sh: 1.308 mm; sw: 0.915 mm; ah: 0.555 mm; aw: 0.562 mm; hlw: 0.794 mm; SA: 61.88 deg. Paratypes (N = 2): sh: 1.205–1.305 mm; sw: 0.854–0.932 mm; ah: 0.517–0.532 mm; aw: 0.539–0.551 mm; hlw: 0.737–0.786 mm; SA: 66.77–67.49 deg.

Shell ca 1.3 mm, conical, with 5–5¼ regularly coiled convex whorls; transparent when fresh, opaque when older; aperture reniform; teleoconch sculpture with few irregular and occasional course growth lines; some weak axial ribbing present immediately behind palatal lip; palatal-basal lip narrowly reflected; aperture wider than high; peristome thickly callused on parietal shield and on basal columellar side, upper palatal side thin and slightly expanded, columellar side more straight than oblique, roundish not angular; parietal shield long and straight with narrow notch indentation at upper parietal and palatal junction; height of last whorl greater than half of shell height; upper rim of peristome recedes ca $^1/_6$ the width of the penultimate whorl (aperture facing left); columella centrally aligned, moderately thick,

smooth; umbilical depression callused; columellar side of peristome positioned directly above with last coiling of whorl leaning to right of umbilical depression, alignment of last ¼ whorl is not compact.

Distribution

This species is only known from its type locality cave, Grabovica jama in southwestern Croatia.

Remarks

Zospeum neuberti Jochum & Ruthensteiner sp. nov. is the only species to possess a totally smooth columella. Although the narrow shell spire and the straight parietal shield resembles that of *Z. simplex*, it differs from this species in that *Z. neuberti* is smaller in shell height, aperture height, aperture width, height of the last whorl and it bears a much broader spire than that of *Z. simplex*.

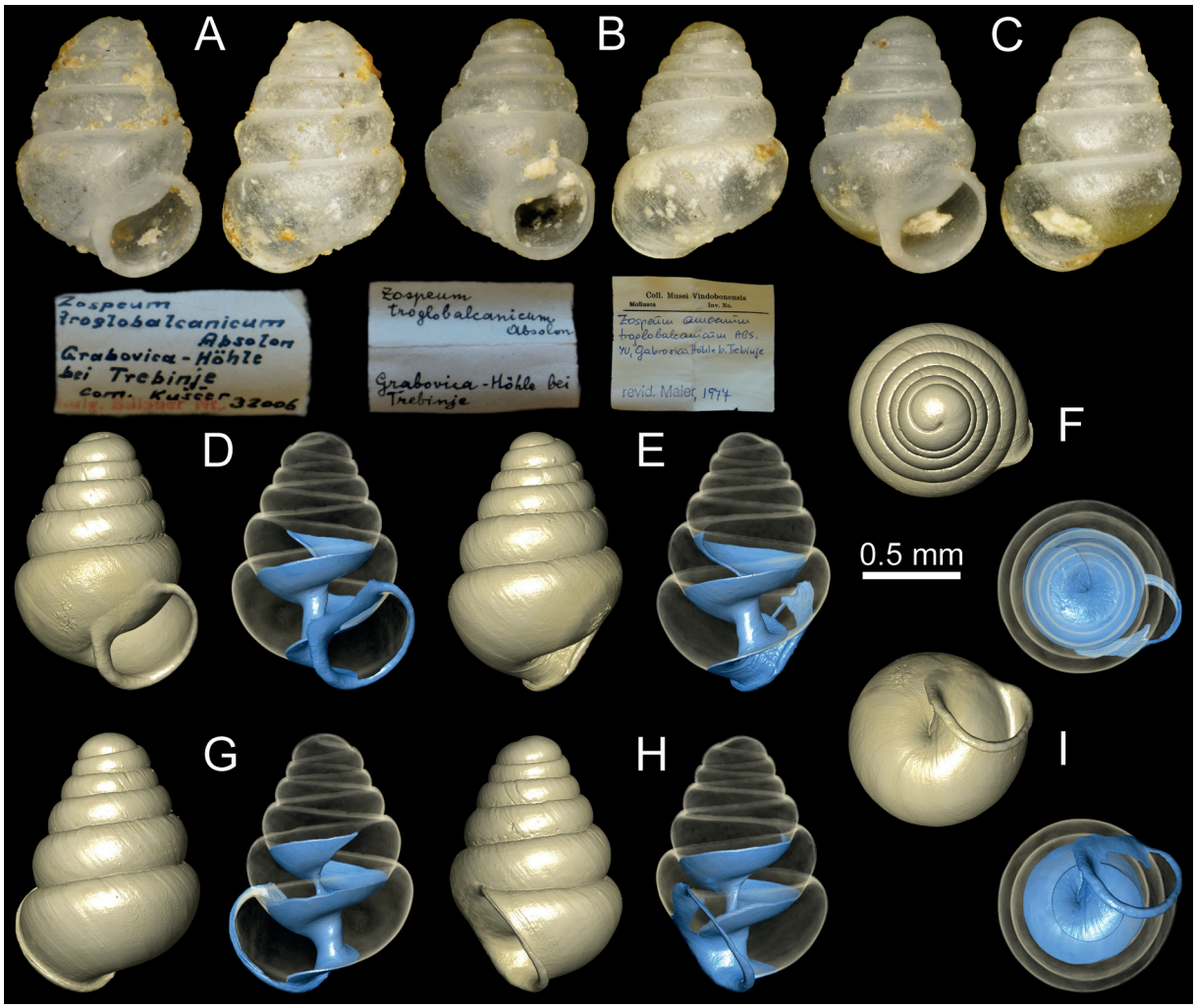

Fig. 12. *Zospeum neuberti* Jochum & Ruthensteiner sp. nov. (NHMW Mol.Coll.Edlauer 32006). **A–B**. Light microscopic images of paratypes showing aperture and dorsal views and collection labels. **C**. Light microscopic images of holotype showing aperture and dorsal views. **D–I**. 3D visualizations of Micro-CT data of holotype. **D**. Aperture view. **E**. Aperture facing right view showing smooth columella. **F**. Apical view. **G**. Dorsal view showing smooth columella. **H**. Aperture facing left view. **I**. Ventral view.

Zospeum constrictum Jochum & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:350FE557-2298-40E7-A194-737D62B4303E
Figs 13–14

Diagnosis

Shell ca 1.4 mm, conical with 5½ irregularly coiled and partially flattened whorls, with ca ⅔ of the last whorl compressed under the penultimate whorl and expanding again at last quarter as it approaches the aperture; entire peristome widely reflected; peristome notch pronounced; columella centrally aligned, smooth with irregularities; no lamella; last ¼ whorl coils high up shell on ventral side with basal palatal lip almost horizontally aligned.

Etymology

This species is named for the tightly compressed coiling and tightening (constricting) of the last whorl placing it partially underneath the penultimate whorl (seen best from apical perspective).

Type material

Holotype

CROATIA • (Figs 13A, 14A–F); "Dalmatien Ostfuss des Biokovogebirge, Grotte bei Turija com. Kuščer" [Dalmatia, eastern foot of the Biokovo mountains, cave by Turija communicated by Kuščer]; [Brikinjava špilja]; [43.3452° N, 17.0971° E]; NHMW Mol.Coll.Edlauer 16.693.

Paratypes

CROATIA • 3 specs (Figs 13B–D, 14G–L); same collection data as for holotype; NHMW Mol.Coll. Edlauer 16.693.

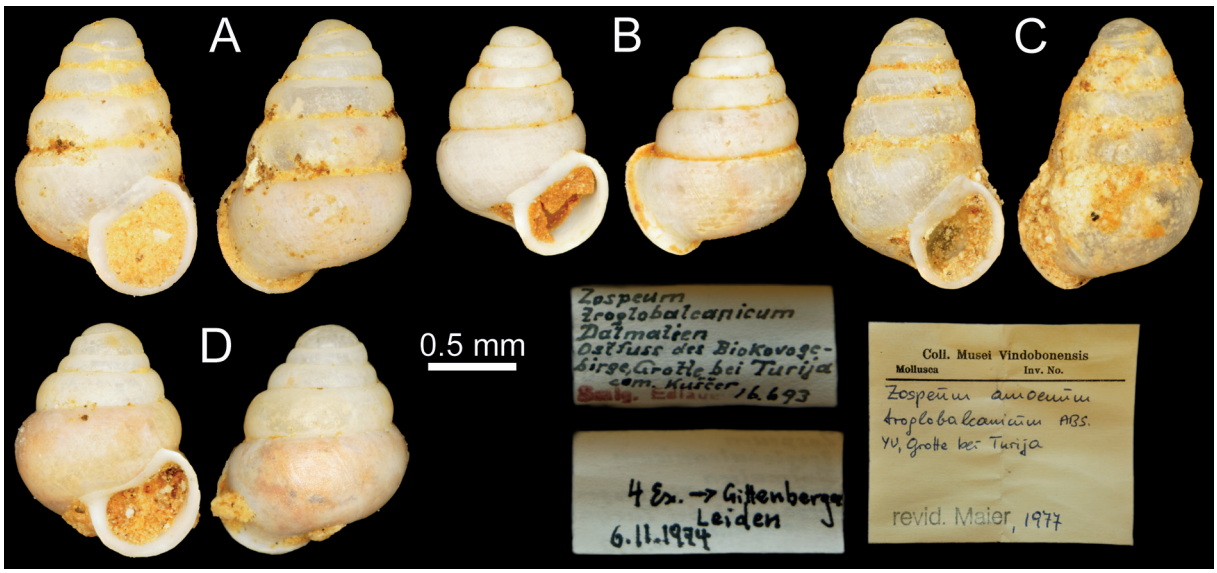

Fig. 13. Light microscopic images of *Zospeum constrictum* Jochum & Ruthensteiner sp. nov. (NHMW Mol.Coll.Edlauer 16.693) and collection labels. **A**. Holotype, aperture, and dorsal views. **B–D**. Paratypes, aperture and dorsal views.

Description

Measurements. Holotype: sh: 1.308 mm; sw: 1.051 mm; ah: 0.702 mm; aw: 0.623 mm; hlw: 0.938 mm; SA: 59.24 deg. Paratypes (N = 3): sh: 1.305–1.537 mm; sw: 0.966–1.055 mm; ah: 0.620–0.680 mm; aw: 0.540–0.689 mm; hlw: 0.769–0.912 mm; SA: 57.56–76.14 deg.

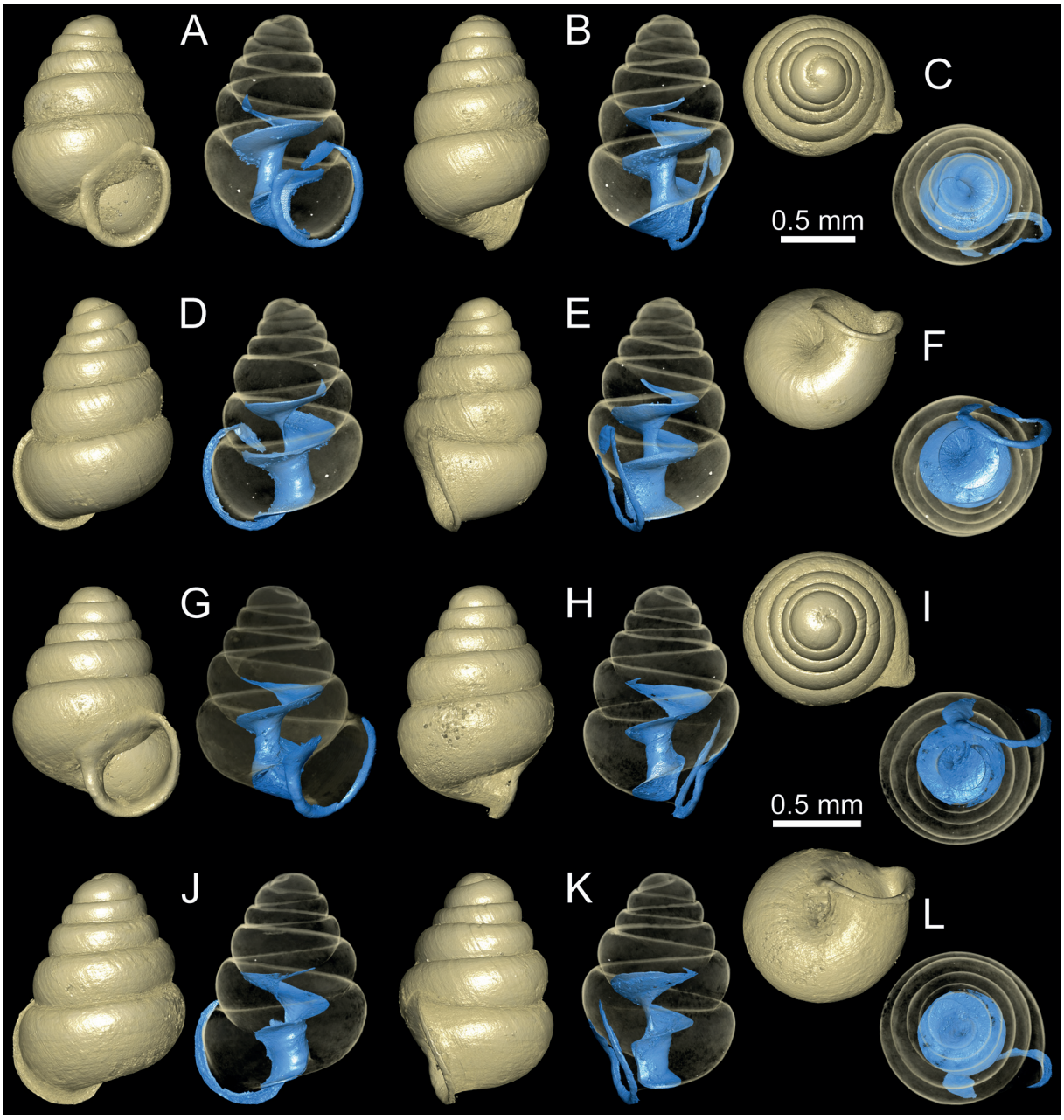

Fig. 14. 3D visualizations of Micro-CT data of *Zospeum constrictum* Jochum & Ruthensteiner sp. nov. (NHMW Mol.Coll.Edlauer 16.693). **A–F**. Holotype. **A**. Aperture and dorsal views. **B**. Aperture facing right view. **C**. Apical view showing upper right side of final whorl tucked underneath spire. **D**. Dorsal view. **E**. Aperture facing left view. **F**. Ventral view. **G–L**. Paratype (Fig. 13B). **G**. Aperture view. **H**. Aperture facing right view. **I**. Apical view showing upper right side of final whorl tucked underneath spire. **J**. Dorsal view. **K**. Aperture facing left view. **L**. Ventral view.

Shell ca 1.4 mm, conical, with 5½ irregularly coiled convex and partially flattened whorls; opaque; aperture ovate; teleoconch sculpture with intervals of irregular blunt growth lines and weak radial banding; ⅔ of the last whorl compressed under the penultimate whorl and expanding again at last quarter as it approaches the aperture; peristome entirely reflected; aperture higher than wide; peristome thickly callused on parietal shield and on basal columellar side, columellar side roundish and slightly expanded; parietal shield straight with pronounced notch at upper parietal and palatal junction; height of last whorl greater than half of shell height; upper rim of peristome recedes ca $^{1}/_{7}$ the width of the penultimate whorl (aperture facing left); last part of body whorl widens towards the aperture (aperture facing left) such that the spire appears to be sinking into the body whorl; columella centrally aligned, moderately thick, either smooth with bumpy irregularities and/or with a partial lamella positioned above mid-section of columella; ventral side swollen with shallow umbilical depression; columellar side of peristome positioned directly above umbilical depression with final coiling of last whorl high up shell on ventral side with peristome base almost horizontally aligned due to minimal basal reflection (Fig. 14F, L); alignment of last $^{1}/_{5}$ whorl is not compact.

Distribution

This species is only known from its type locality cave, Brikinjava špilja in the Biokovo mountains of Croatia.

Remarks

This species is most similar to *Z. tortuosum* Jochum & Ruthensteiner sp. nov., *Z. dubokidoense* Jochum & Ruthensteiner sp. nov., *Z. njunjicae* Jochum, Schilthuizen & Ruthensteiner sp. nov. and *Z. simplex* in that the towering spire projects above the body whorl, causing the body whorl to almost disappear underneath the right side of the penultimate whorl before the aperture when studied in apical view (Fig. 14C, I). It differs from these species in that the penultimate whorl extends beyond the upper righthand side of the body whorl such that it disappears under the spire while the last part of coiling extends beyond the shell spire causing the peristome to conspicuously flare out from beneath it. In *Z. tortuosum*, *Z. dubokidoense* and *Z. simplex*, the body whorl and peristome tightly conform to the contour of the shell spire.

Zospeum biokovoense Jochum & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:A976D460-68C4-460E-9023-E32539BE2C5B
Fig. 15

Diagnosis

Shell ca 1.4 mm, conical with 5¼ whorls; suture zone of penultimate and final whorl with irregular indentations succeeding into course growth lines with some crossing over parietal shield into the aperture; columella fat and short, almost 1/3 width of final whorl with lamellar bulge and an incomplete lamella; umbilical depression deep, callused with much puckering.

Etymology

This species is named after the Biokovo mountain range where it was found.

Type material

Holotype

CROATIA • (Fig. 15B–H); "Dalmatien, kl. Grotte beim Alpenvereinshaus, Biokovogebirge, kleine Grotte am Weg vom Alpenvereins zum Hegerhaus" [Dalmatia, small cave by Alpine Club house, (today

probably Biokovo Alpine Club Vosac), Biokovo Mountains, small cave on the way from the Alpine Club house to Heger house]; [43.3091° N, 17.0473° E]; NHMW Mol.Coll.Edlauer 16.390.

Other material examined

CROATIA • 1 spec.; juvenile with damaged shell (Fig. 15A); same collection data as for holotype; NHMW Mol.Coll.Edlauer 16.390.

Description

Measurements. Holotype: sh: 1.37 mm; sw: 0.966 mm; ah: 0.680 mm; aw: 0.596 mm; hlw: 0.769 mm; SA: 66.39 deg. Other material: (N = 1): juvenile with damaged shell, not Micro-CT scanned or measured.

Shell ca 1.4 mm, conical, with 5¼ regularly coiled, convex whorls with penultimate and last whorl being irregularly formed and somewhat lopsided; height of last whorl greater than half of shell height; opaque; aperture reniform, slightly higher than wide; teleoconch sculpture with some irregular blunt growth lines and weak radial banding; suture zone of penultimate and final whorl with dense, deep indentations of

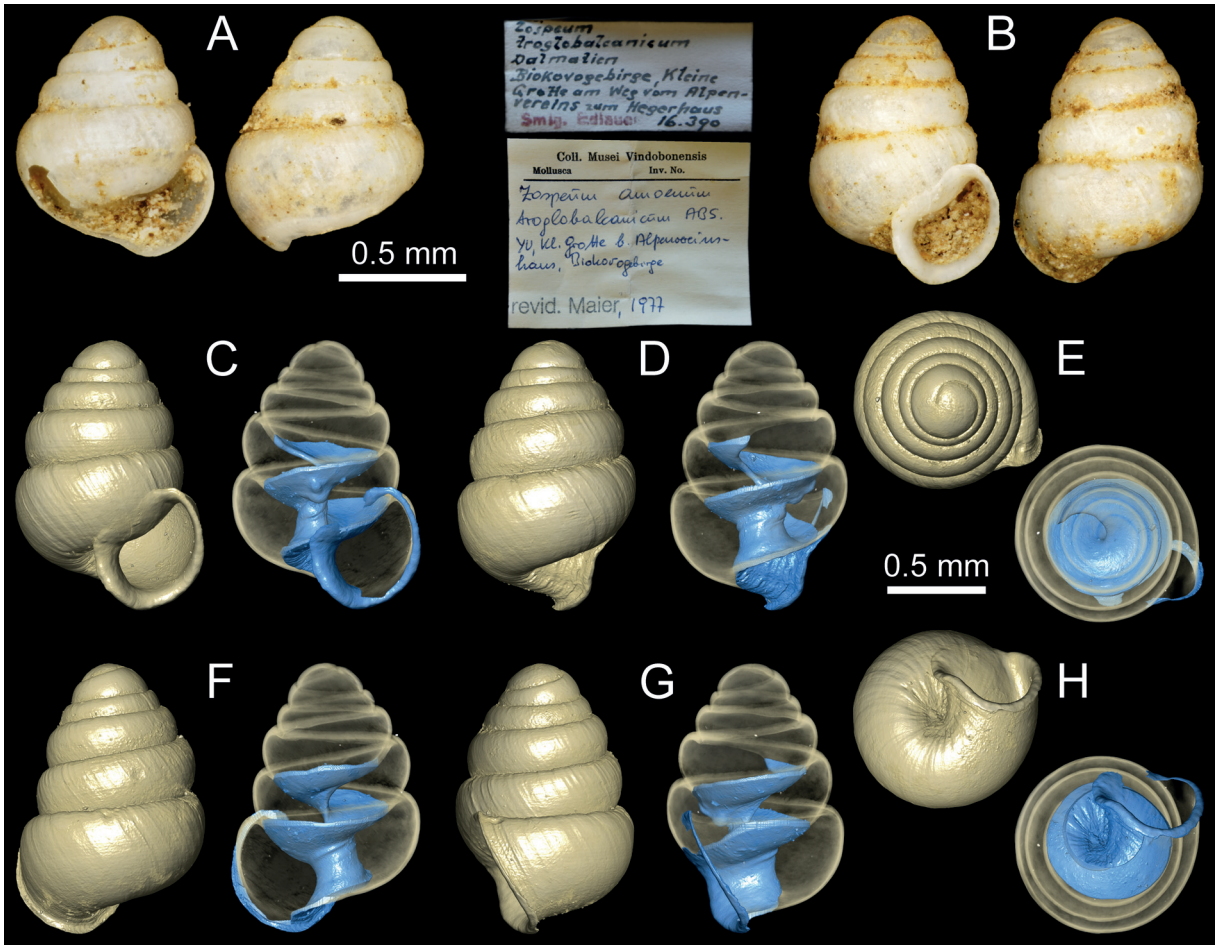

Fig. 15. *Zospeum biokovoense* Jochum & Ruthensteiner sp. nov. (NHMW Mol.Coll.Edlauer 16.390). **A–B**. Light microscopic images showing aperture and dorsal views and collection labels. **A**. Juvenile shell. **B**. Holotype. **C–H**. 3D visualizations of Micro-CT data of holotype. **C**. Aperture view showing gnarled deformation of the columella. **D**. Aperture facing right view showing fat columella and lamella. **E**. Apical view. **F**. Dorsal view showing lopsided spire and incomplete lamella on top of fat columella. **G**. Aperture facing left view. **H**. Ventral view showing puckered umbilical depression.

course growth lines extending at irregular intervals showing tendency towards costateness; peristome thin at upper palatal side, columellar side thickly callused roundish in form and slightly expanded, callosity extends beyond plane of shell (aperture facing left), basal palatal side narrowly reflected with some low ribbing behind palatal side; parietal shield thins at mid-section with some irregular growth lines bisecting it and entering into the aperture on the columellar side; notch at upper parietal and palatal junction; upper rim of peristome recedes ca $^{1}/_{7}$ the width of the penultimate whorl (aperture facing left); columella fat and short, almost ⅓ width of final whorl, centrally aligned and bulging at top with a thin, incomplete lamella; ventral side with deep, callused umbilical depression with much puckering and wrinkles; columellar side of peristome positioned directly above umbilical depression; alignment of last $^{1}/_{5}$ whorl is not compact.

Distribution

This species is only known from its type locality cave located in the Biokovo region of the central Dinarides between the Cetina and the Neretva Rivers of Croatia.

Remarks

Absolon (1916a) noted that the Neretva River was a distinctive geographical barrier reflected in different morphological features in species of subterranean fauna between the central Dinarides and the southern Balkans. The species *Z. biokovoense* Jochum & Ruthensteiner sp. nov. differs from all other so far internally viewed (via Micro-CT) species by its remarkably fat columella. Though the lower side of the penultimate whorl shows some shell deformation directly above the columella, the columella itself bulges and demonstrates a threadlike lamella like that of *Z. troglobalcanicum.* The teleoconch however, differs in the lopsided formation of the penultimate whorl, the radial banding on the body whorl and the more numerous irregular growth lines extending in part across the parietal shield into the aperture of the species. The shell diameter is narrower, the aperture is taller and narrower, the height of the last whorl is shorter, and the spire is narrower in *Z. biokovoense* than in *Z. troglobalcanicum*. Ventrally, the last whorl is less swollen and the final coiling towards the aperture extends high above the umbilical depression such that is not compact versus that in *Z. troglobalcanicum*, which does not extend as far beyond the depression and is compact in relation to it. The umbilical depression is callused, puckered, and wrinkled in *Z. biokovoense* and differs significantly from the smooth and relatively uniform umbilical formation in *Z. troglobalcanicum.* Coiling of the final whorl (ventral side) is similar to that of *Z. amplioscutum* Jochum & Ruthensteiner sp. nov. but it does not extend as far up the shell as in that species. Though growth lines extend into the parietal shield and into the aperture also in Z. *tumidum* Jochum, Schilthuizen & Ruthensteiner sp. nov., the two species differ in aperture shape, whorl alignment, teleoconch structure, columellar configuration and size dimensions.

Zospeum kolbae Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:02B1232B-1BC5-404A-8F6D-FD189619B3AA
Figs 16, 22C

Diagnosis

Shell 1.38–1.52 mm, conical with 4.5–5 flatly convex, regular, tightly coiled whorls; aperture elliptical-ovate to subquadrate-oblique; columellar side of peristome thickly callused; teleoconch sculpture with conspicuous irregular scratch-like growth lines and milky, horizontal banding on the penultimate and body whorls.

Etymology

This species is named in honour of Prof. Dr. Annette Klussmann-Kolb for providing valuable mentorship and introducing AJ to the Ellobioidea.

Type material

Holotype

MONTENEGRO • [holotype and body destroyed for DNA extraction, photograph and DNA are the only remnants of the holotype]; Njeguši, St John's cave; 42.4307° N, 18.8115° E, 915 m a.s.l.; ca -85 m vertical depth below the cave entrance; 5 Aug. 2021; László Dányi & Nikolett Ujhegyi leg.; GenBank CO1 gene: ON037484; GenBank 16S gene: ON041449; GenBank H3 gene: ON088652; imaged shell of aliquot NMBE 571122.

Paratype

MONTENEGRO • 1 spec. [paratype and body destroyed for DNA extraction, photograph and DNA are the only remnants of the paratype]; same collection data as for holotype; GenBank CO1 gene: ON037485; GenBank 16S gene: ON041450; GenBank H3 gene: ON088653; imaged shell of aliquot NMBE 571123.

Description

Measurements. Snails processed for DNA sequence data and thus, the type series has been destroyed. Holotype: sh: 1.38 mm; sw: 1.00 mm; ah: 0.66 mm; aw: 0.59 mm; hlw: 0.96 mm; SA: 75.69 deg.; NMBE 571122 (Fig. 16A). Paratype: (N = 1): sh: 1.59 mm; sw: 0.95 mm; ah: 0.73 mm; aw: 0.62 mm; hlw: 0.73mm; SA: 62.88 deg.; NMBE 571123 (Fig. 16B).

Shell 1.38–1.59 mm, conical; transparent; with 4.5–5 flatly convex, regular, tightly coiled whorls; penultimate whorl equal or slightly over ½ height of body whorl (in lateral view); aperture elliptical-ovate to subquadrate; columellar side long; suture shallow; teleoconch sculpture with conspicuous irregular scratch-like growth lines and milky, horizontal banding on the penultimate and body whorls; some weak axial ribbing present immediately behind palatal lip; palatal lip narrowly reflected, palatal-basal side reflected; peristome thickly callused on basal columellar side; parietal shield long and straight with conspicuous narrow notch indentation at upper parietal and palatal junction.

Distribution

This species is only known from the type locality, St John's cave, in Njeguši, Montenegro.

Remarks

The two shells demonstrate a significant range in shell height (1.39–1.59 mm), constituting what might be the ends of the size spectrum for *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov. or that shell B is a potential hybrid with *Z. dubokidoense* Jochum & Ruthensteiner sp. nov. or a potential freak. Of all the shells in this study, shell B is by far the largest with that of one shell from *Z. dubokidoense* measuring a close second in shell height (1.546 mm). With its molecularly closest congener, *Z. simplex*, (1.41–1.40 mm) it is comparable at the lower end of the size range but demonstrates a much broader spire angle than that of the narrower *Z. simplex* and a markedly larger aperture (ah) compared to that of *Z. simplex*. The elliptical-ovate to subquadrate shape of the aperture, the height of the penultimate whorl equaling or extending slightly over ½ the height of the body whorl (lateral view) are reminiscent of *Z. dubokidoense* from Duboki do cave (Figs 6D, 7G) (MCSMNH-PMSL-Moll.-FVelkovrh 30360[spm1]). Their affinity in conjunction with the recent discovery of a connection between St John's cave and Duboki do cave (Csepreghy & Lenkei 2021) may be clarified by future sampling opportunities and DNA sequence analysis. Imaged with *Z. kolbae*, is an undescribed species (*Zospeum* sp. 1) (Fig. 16C–E) (NMBE 577052–577053) found in the same cave chamber with two adults showing a substantially smaller size (1.29–130 mm) than that of *Z. kolbae*. A third, subfossil species, found in the dry part of the same cave, *Z. njegusiense* Jochum & Ruthensteiner sp. nov. (Fig. 17) measures within the same size range as the two shells of *Z. kolbae* but shows no other affinity with it.

Type locality

According to the collector, László Dányi, "The small chamber, where all the snails were collected, is really a rather dry part of the cave, a so called 'fossil' part which doesn't have any active water-flow – even temporarily – since ages. However, on the rocks there is a thin layer of clay which is wet around micro fissures because of percolating water." (Fig. 22B). Maximum depth of St John's cave is -537 m (László Dányi pers. comm May 2022). Recent exploration by the Hungarian Speleo Camp detected a connection between St John's cave and Duboki do cave (Csepreghy & Lenkei 2021).

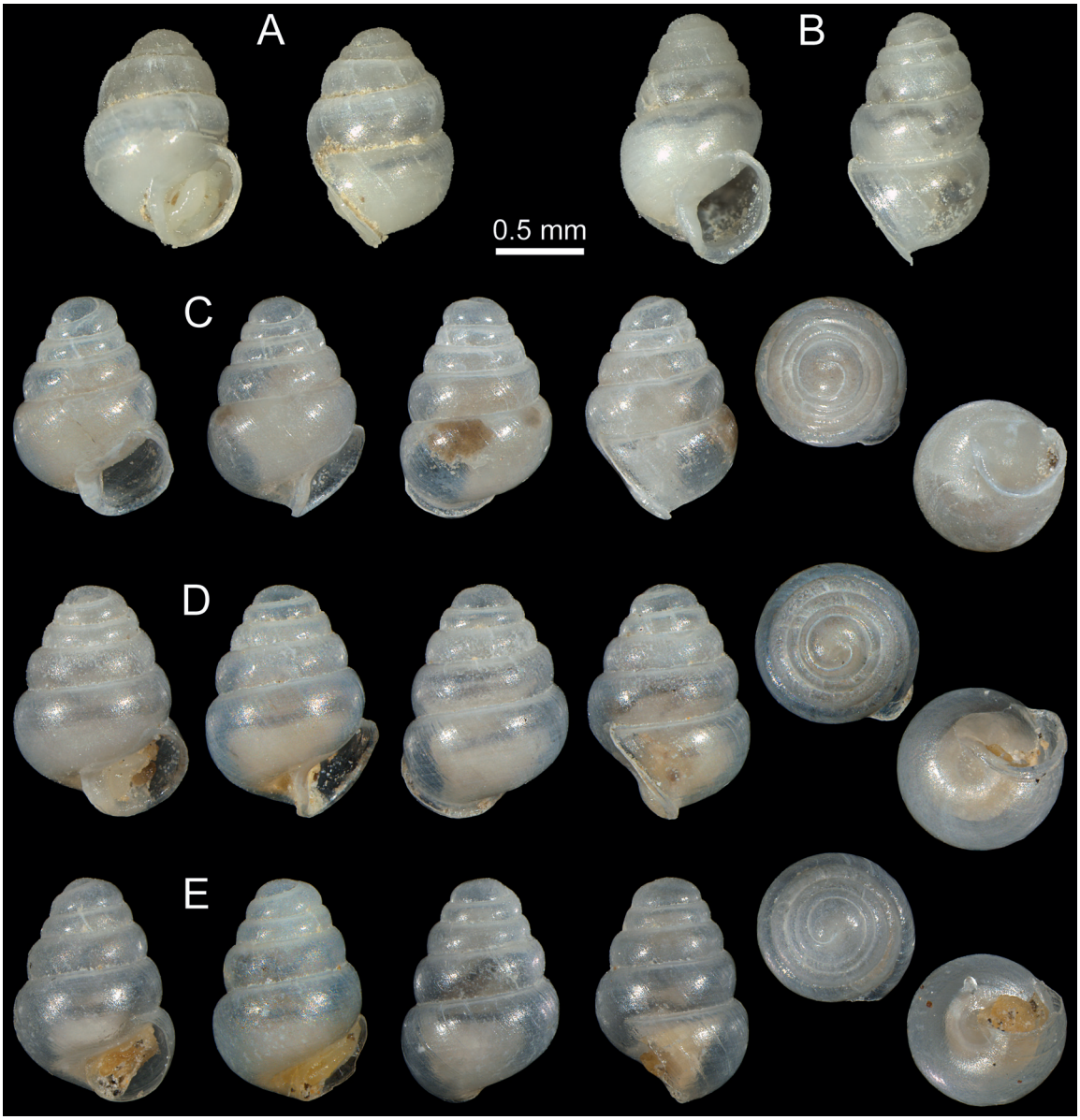

Fig. 16. Light microscopic images of full-bodied *Zospeum* Bourguignat, 1856 from Njeguši, St John's cave. **A–B**. *Zospeum kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov. (NMBE 571122–571123), individuals assessed by DNA sequencing with sigmoid intestine showing through shells (shells were destroyed post imaging for tissue extraction). **A**. Holotype (NMBE 571122), shell of aliquot, aperture, and aperture facing left view. **B**. Paratype (NMBE 571123), shell of aliquot, aperture, and aperture facing left view. **C**. Undescribed *Zospeum* sp. 1 (NMBE 577052) showing all perspectives. **D–E**. Undescribed *Zospeum* sp. 1 (NMBE 577053/2) showing all perspectives.

Zospeum njegusiense Jochum & Ruthensteiner sp. nov.
urn:lsid:zoobank.org:act:882B9D99-6028-4DC7-B9A0-82033E474B39
Fig. 17

Diagnosis

Shell conical with 5¼ flatly convex whorls; aperture reniform; penultimate whorl over ½ height of body whorl; columella slender with a distinctly sculpted and broad lamellar band obliquely projecting ca ⅓ beyond the width of the slender columella; a second, barely visible low lamella is present at mid-section of the columella. Suture deep.

Etymology

This species is named after its type locality Njeguši, Montenegro.

Type material

Holotype (SEM sample)
MONTENEGRO • (Fig. 17A, D); Njeguši, St John's cave; 42.4307° N, 18.8115° E, 915 m a.s.l.; ca -85 m vertical depth below the cave entrance; 5 Aug. 2021; László Dányi & Nikolett Ujhegyi leg.; NMBE 572639 (ex AJC 2483).

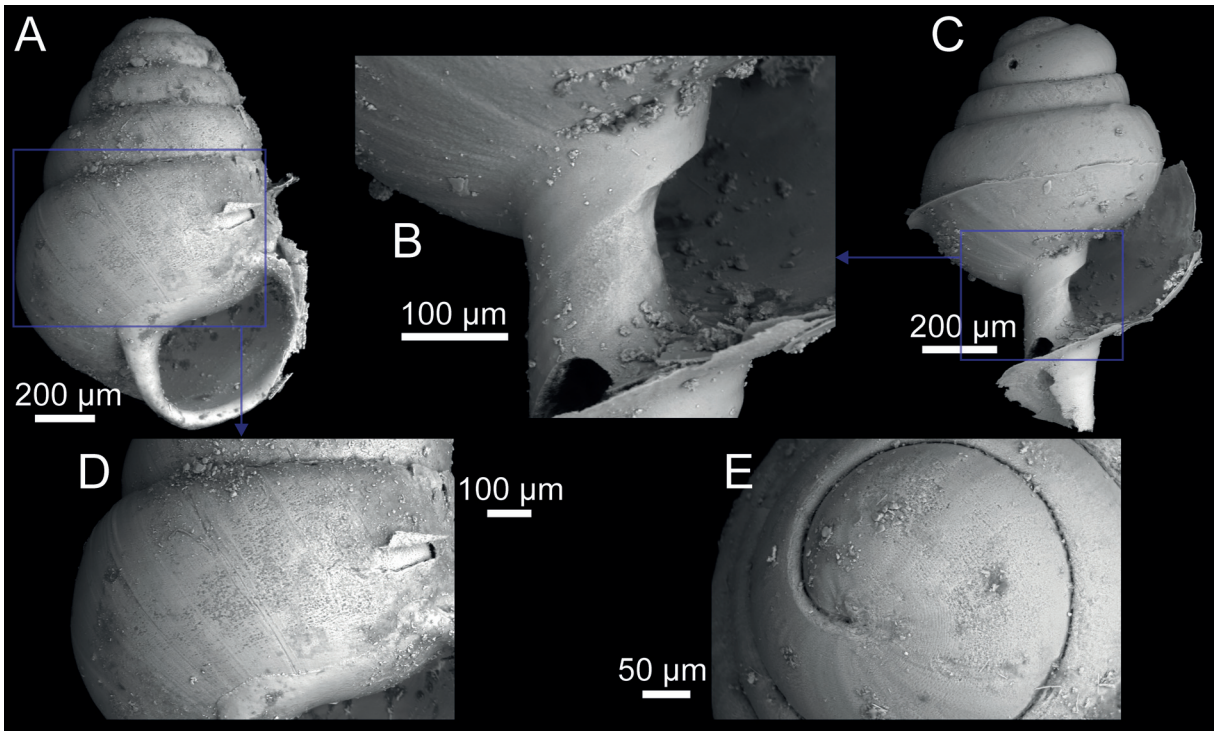

Fig. 17. *Z. njegusiense* Jochum & Ruthensteiner sp. nov., Scanning Electron Microscopy images. **A**. Holotype (NMBE 572639), aperture view showing subfossil shell with superficial erosion of shell layer. **B**. Paratype (NMBE 578378), aperture view showing close up of lamellar band on columella (Fig. C). **C**. Paratype (NMBE 578378), aperture view showing damaged shell and columella. **D**. Close up view of holotype (NMBE 572639), showing body whorl with low, irregular growth lines. **E**. Paratype (NMBE 578378), protoconch.

Paratypes (SEM sample)
MONTENEGRO • (Fig. 17B–C, E); 2 specs (broken shells); same collection data as for holotype; NMBE 578378 (ex AJC 2483).

Description

Measurements. Holotype: sh: 1.37 mm; sw: 0.96 mm; ah: 0.61 mm; aw: 0.61 mm; 0.63; hlw: 0.88 mm; SA: 68.04 deg.

Shell subfossil, eroded; conical with 5¼ flatly convex whorls; aperture reniform; penultimate whorl over ½ height of body whorl; teleoconch smooth with intermittent impressed striations on the body whorl; suture deep; parietal shield well defined, thick, long, and angular, curved at max. whorl convexity; peristome notch prominent at upper junction with parietal shield; smooth, impressed irregular ribbing behind peristome; columella slender with a distinctly sculpted and broad lamellar band obliquely projecting ca ⅓ beyond the width of the slender columella; a second, barely visible low ripple is present at mid-section of the columella.

Distribution

This species is only known from the type locality, St John's cave in Njeguši, Montenegro.

Remarks

The species differs from *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov. in its uniformly conical shell form and its narrow, reniform apertural shape. Though the straight and robust columella is reminiscent of that in *Z. njunjicae* Jochum, Schilthuizen & Ruthensteiner sp. nov., the pronounced configuration of the lamella differentiates significantly from the weak low lamella of that species (as seen in all its Micro-CT perspectives) except perhaps the dorsal view, which is different altogether in bearing a distinctive lamellar bulge and a secondary low lamella above the tortional formation at the base of the columella. Though the shell is eroded, it shares no whorl size dimensions nor body whorl or penultimate whorl shape with the unidentified and unassessed morphospecies, *Zospeum* sp. 1 (NMBE 577052–577053) (Fig. 16C–E) also found in St John's cave.

Zospeum simplex Inäbnit, Jochum & Neubert, 2021
Figs 18–19

Original diagnosis

Shell usually ca 1.3 mm in height, transparent, conical, peristome thickened, roundish, with a differentiated parietal shield, lamellae not present.

Type material

Holotype
BOSNIA AND HERZEGOVINA • municipality of Tomislavgrad, Gornji Brišnik, Jama Dobravljevac; 43.6347° N, 17.2328° E; 25 Aug. 2019; R. Slapnik and J. Valentinčič leg.; NMBE 568060 (ex RSC 3760).

Other material examined (via Micro-CT and SEM)

BOSNIA AND HERZEGOVINA • 2 specs (Fig. 18, MicroCT); same collection data as for holotype; NHMW-MO-113642 (ex RSC 3760) • 2 specs (Fig. 19, SEM); same collection data as for holotype; SMF 349425 (ex RSC 3760).

Emended diagnosis considering Micro-CT and SEM Data

Shell ca 1.4 mm and 5½–6 whorls; conical with narrow spire; peristome bears slight indentation at upper junction of parietal and palatal sides; low, hump-like callus on the inner columellar side of peristome; teleoconch with dense rows of microscopic, radially aligned, elongated pits; medium-sized columella with either two weak, loosely coiled low incomplete lamellae or a single incomplete lamella.

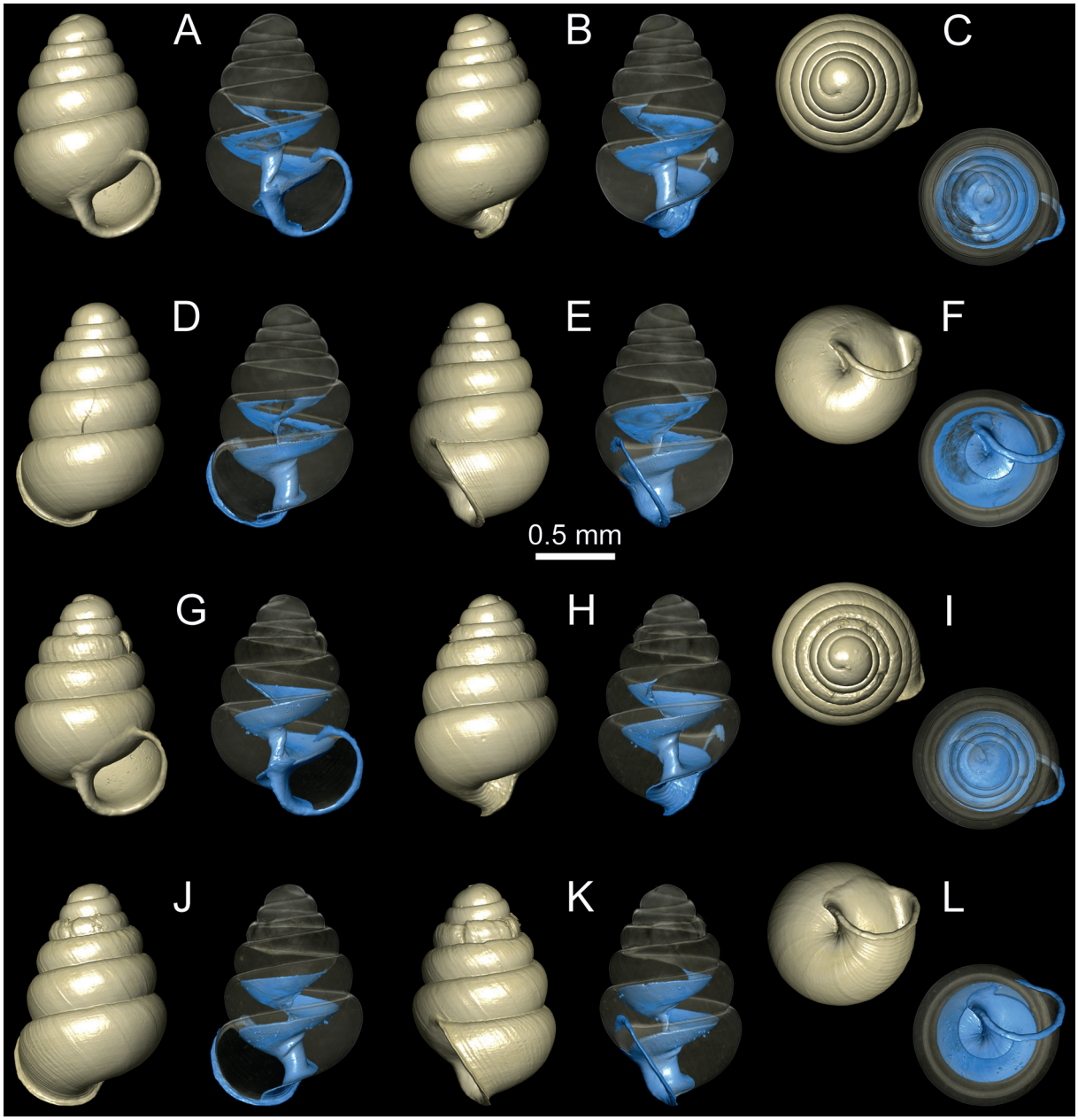

Fig. 18. 3D visualizations of Micro-CT data of *Zospeum simplex* Inäbnit, Jochum & Neubert, 2021, (NMHW-MO-113642 ex RSC 3760) from Dobravljevac jama, Gornji Brišnik, Bosnia and Herzegovina. **A–F**. Specimen 1 (spm1). **A**. Aperture view. **B**. Aperture facing right view. **C**. Apical view. **D**. Dorsal view. **E**. Aperture facing left view. **F**. Ventral view. **G–L**. Specimen 2 (spm2). Same perspectives as Specimen 1.

Enhanced description with Micro-CT and SEM Data

Measurements (N = 2). sh: 1.40–1.41 mm; sw: 0.93–0.96 mm; ah: 0.57 mm; aw: 0.61–0.62 mm; hlw: 0.83–0.84 mm; SA: 56.46–59.45 deg., NHMW-MO-113642 (ex RSC 3760).

Shell ca 1.4 mm, conical, with 5½–6 regularly coiled, convex whorls with height of last whorl slightly greater than half of shell height; spire angle narrow; protoconch bulbous with microstructure of dense pitting and some irregular raised bands extending to the suture; the second and third whorls bear rows of interrupted dashes of radial pitting; teleoconch sculpture includes blunt irregular growth lines and weak radial banding on all whorls; density of blunt striations varies, showing a tendency towards costateness at the suture zones; high magnification of shell surface (5 µm) shows tiny pinpoint perforations; aperture reniform, wider than high; peristome slightly oblique on columellar side with a low, hump-like thickening on the inner columellar side (Fig. 18A), palatal side narrowly reflected with low ribbing extending some distance beyond the lip; parietal shield well defined, long and angular, with a slight indentation at upper parietal and palatal junction; upper rim of peristome recedes ca $^{1}/_{5}$ the width of the penultimate whorl (aperture facing left) (Fig. 18E); columella centrally aligned and slender; a low lamella is present under penultimate whorl (aperture facing right) (Fig. 18B) which then turns into either two incomplete loosely coiled low lamellae (dorsal view) (Fig. 18D) or constitutes one well pronounced one (Fig. 18J); ventral side with small, umbilical depression with no puckering; columellar side of peristome arches slightly over and oblique to umbilical depression, alignment of last 1/4 whorl somewhat compact (Fig. 18F).

Remarks

Differs from *Z. troglobalcanicum* in that it bears at least one additional or ½ whorl; the upper parietal and palatal junction has a slight indentation in contrast to a well-defined notch; protoconch is more bulbous and somewhat elevated; the shell spire angle is narrower than that of *Z. troglobalcanicum* but within the spectrum of the narrowest spire measurements of two shells of *Z. constrictum* Jochum & Ruthensteiner sp. nov. (57.5–59.2 deg.); width of the shell is narrower than that of *Z. troglobalcanicum*;

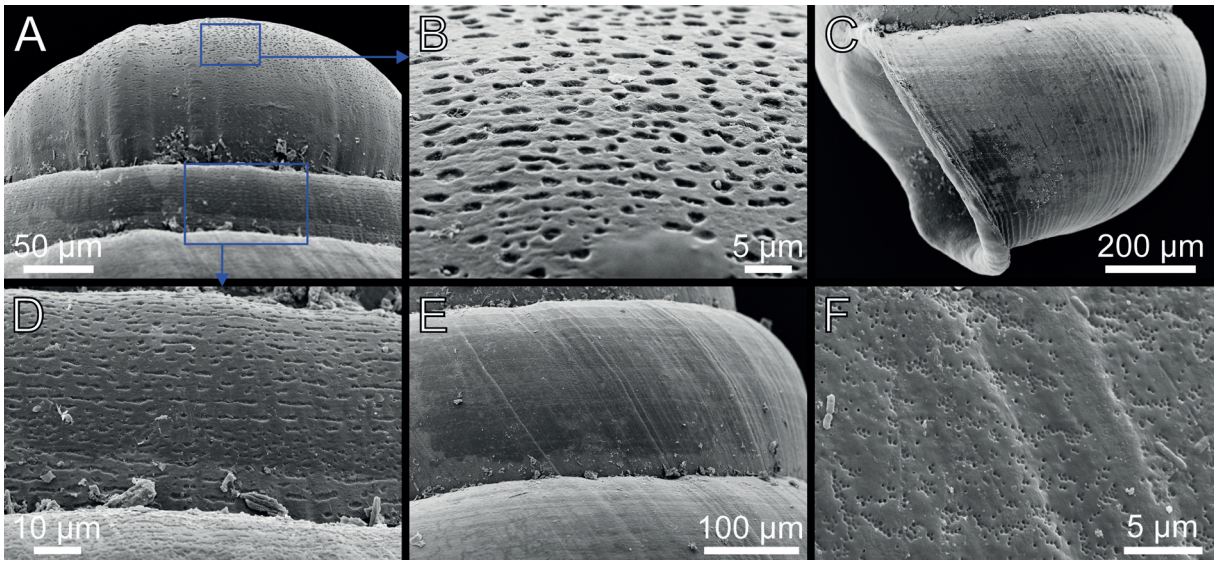

Fig. 19. *Zospeum simplex* Inäbnit, Jochum & Neubert, 2021, (SMF 349425) Scanning Electron Microscopy images. **A**. Protoconch and upper teleoconch showing microstructure of superficial pitting. **B**. Close up view of pitting microstructure. **C**. Last whorl with axial ribbing extending beyond peristome lip. **D**. Close up view of second whorl showing rows of interrupted dashes of radial pitting. **E**. Growth lines and radial banding on teleoconch. **F**. Close up view of growth lines and shell microstructure.

the low, hump-like thickening of callus (not a denticle) a short distance inside the columellar side of the peristome is so far distinctive for this species.

When compared to its molecularly closest congener, *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov., *Z. simplex* Inäbnit, Jochum & Neubert, 2021 shows a significantly lower apertural height of an almost equal width with that of *Z. kolbae* as well as a narrower spire angle than that of *Z. kolbae*. Shell height shows more range in *Z. kolbae* than in *Z. simplex*.

Though *Z. simplex* Inäbnit, Jochum & Neubert, 2021 resembles *Z. amplioscutum* Jochum & Ruthensteiner sp. nov., it differs by its reduced extension onto the body whorl and less heavily callused parietal shield. *Z. simplex* is larger, has a narrower spire angle and a markedly less textured teleoconch in comparison to that of *Z. amplioscutum*. *Zospeum simplex* does not have a second lamella on the columella (aperture facing right) (Fig. 18B) but rather, weak ripples of a potential double one (Fig. 18D) or a stronger, incomplete single one in dorsal view (Fig. 18J). The narrow columella (Fig. 9C–D) and the elongation of the last whorl further beyond the umbilical depression (ventral side) additionally differentiate *Z. amplioscutum* from *Z. simplex*.

The incidence of the one solid lamella versus the two incomplete low lamellae occurred in one of the two shells scanned. In sync with Inäbnit *et al*. (2021), the shell height:shell width ratio is the most effective way to differentiate *Z. simplex* Inäbnit, Jochum & Neubert, 2021 from morphs of *Z. troglobalcanicum*. The low, hump-like callus on the inner columellar side of the peristome is consistent in the three shells from the type locality.

Zospeum sp. 2
Fig. 20

Zospeum troglobalcanicum – Inäbnit *et al.* 2019: 19, fig. 7u.

Diagnosis (from Inäbnit *et al.* 2019)

Shell ca 1.3 mm, transparent, with a globose conical form, peristome with well-defined parietal shield, totally smooth columella, lamellae missing completely.

Material examined

BOSNIA AND HERZEGOVINA • Trebinje, Taleža, "Trebinjska šuma" [Trebinje Forest], Taleža pećina; 42.7097° N, 18.2430° E; 9 Aug. 2010; M. Lukić leg.; NMBE 553414/1 (ex RSC 1981).

Description (using Micro-CT image data)

Measurements (Micro-CT). sh: 1.30 mm; sw: 1.00 mm; ah: 0.58 mm; aw: 0.60 mm; hlw: 0.83 mm; SA: 71.60 deg.

Shell ca 1.3 mm, conical, with 5¼ regularly coiled, flatly convex whorls; transparent when fresh; suture uneven and shallow; height of last whorl greater than half of shell height; aperture reniform, narrow, slightly wider than high; teleoconch sculpture with some irregular blunt growth lines; suture zone of penultimate and final whorl with indentations from which growth lines extend irregularly; peristome thin and flattened at upper palatal side, with thickened callused zone starting after ca ⅓ the length of the palatal side; columellar side of peristome slightly oblique and callused, palatal and basal palatal edge narrowly reflected; parietal shield well-defined, thickly callused, long and straight with notch at upper parietal and palatal junction; upper rim of peristome recedes ca 1/5 the width of the penultimate whorl (aperture facing left); columella centrally aligned and totally smooth, lower part of internal penultimate

whorl shows a low ridge-like fold independent of and above the formation of the columella but not leading onto it; ventral side with a shallow umbilical depression with some puckering of blunt ridges leading into it behind the columellar side of the peristome; columellar side of peristome positioned directly above umbilical depression; alignment of last $^{1}/_{5}$ whorl somewhat compact.

Distribution

Taleža pećina is located in the Trebinjska šuma region, a 23 km long karst rocky plateau of eastern Bosnia and Herzegovina.

Remarks

Inäbnit *et al.* (2019) compared this shell to the Western Balkan congeners in their molecular study of the radiation of Dinaride *Zospeum*, concluding that it mostly shared an overall resemblance to the photograph of *Z. troglobalcanicum* supplied by Absolon (1916b). This conclusion was based on the globose conical form of the shell, the peristome with a well-defined parietal shield and that lamellae were lacking completely. Though Inäbnit *et al.* (2019) considered this morph *Z. troglobalcanicum*, it differs from the lectotype by the smooth columella and the configuration of the umbilical zone, including the shallow umbilical depression and the relatively tight alignment of the columellar side of the peristome in relation to it. It is also much smaller than *Z. troglobalcanicum*, constituting one of the smallest morphs in this study, except for *Z. njunjicae* Jochum, Schilthuizen & Ruthensteiner sp. nov., which on the average, bears the smallest shell.

This shell is very similar to *Z. neuberti* Jochum & Ruthensteiner sp. nov. in that the columella is smooth, albeit somewhat attenuate, with the umbilical zone bearing similar morphology. The spire is wider, the aperture width is broader and there are fewer low ribs behind the peristome compared to the three

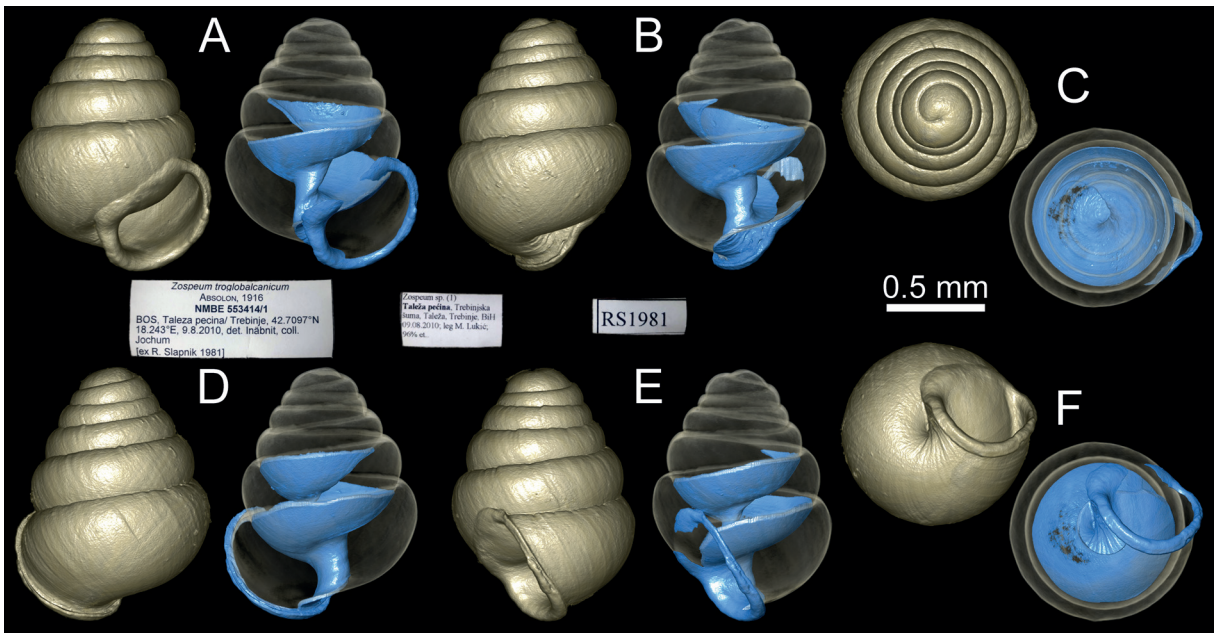

Fig. 20. 3D visualizations of Micro-CT data of *Zospeum* sp. 2, Taleža pećina, bei Trebinje, BiH, presented as *Z. troglobalcanicum* in Inäbnit *et al.* 2021 (NMBE 553414/1 (ex RSC 1981). **A**. Aperture view showing low, ridge-like fold on inner penultimate whorl. **B**. Aperture facing right view showing smooth columella. **C**. Apical view. **D**. Dorsal view. **E**. Aperture facing right view. **F**. Ventral view showing peristome edge directly parallel to umbilical depression.

individuals of *Z. neuberti* from the type locality, Grabovica cave. Due to the lack of comparative material from Taleža pećina, no conclusive conchological determination can be made based on this one shell.

Molecular analysis

Zospeum troglobalcanicum is revealed based on a single syntype shell discovered in the NHMW collection and morphologically assessed along with shells deriving from 15 populations of southern Balkan *Zospeum* from both museum collections and recent sampling efforts (Figs 2–19). Two recently collected individuals from one population from Njeguši, Montenegro were additionally assessed by DNA sequencing in accordance with the most recent integrative study by Inäbnit *et al*. (2021). The phylogeny is updated in this work (Fig. 21).

Tree topologies in both the ML and the BI tree were identical to each other and largely congruent to the ones published in Inäbnit *et al*. (2021). The two new specimens from Njeguši, Montenegro (*Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov. NMBE 571122–571123), were recovered as the sister group of *Z.* aff. *troglobalcanicum* from Špilja Jezero in southernmost Croatia.

The ABGD analysis for the *Z. pretneri*-group yielded two different topologies, one with six clades (Prior Maximal Distance P = $3.59e^{-02}$; barcode gap distance: 0.042) and one with eight clades (Prior Maximal Distance P = $4.64e^{-03}$; barcode gap distance: 0.004). Both topologies regard the species from Njeguši, Montenegro, as a distinct species. The topology with six clades corresponds to the one that was ultimately used for species delimitation in Inäbnit *et al.* (2021) and which accepts all currently accepted species within the group as independent lineages, while the topology with eight clades subdivides *Z. simplex* and *Z.* aff. *troglobalcanicum* into two lineages each (with the two lineages in the latter co-occurring in the same cave). We will use the topology with six clades from now on.

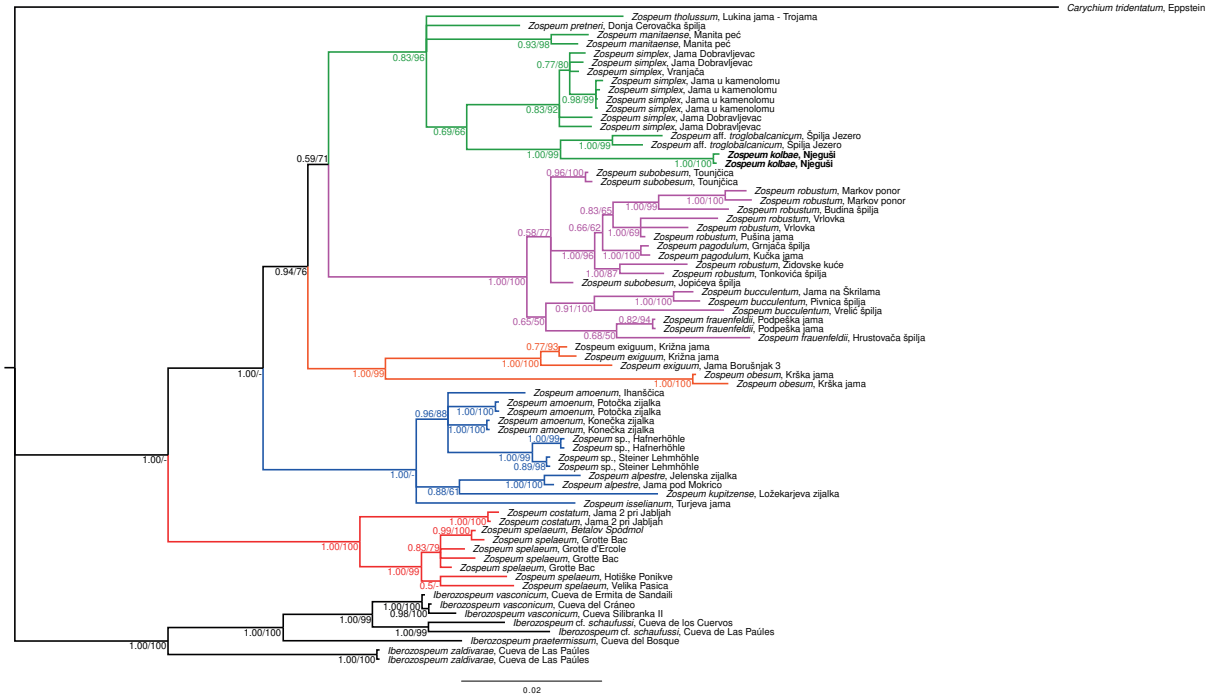

Fig. 21. Bayesian tree of the genus *Zospeum* Bourguignat, 1856. Node support values of both the Bayesian Inference (left) and the Maximum Likelihood analysis (right) are given. Branches are coloured to denote the informal species groups within the eastern radiation of *Zospeum* following Inäbnit *et al.* (2019). Emboldened specimen names indicate samples sequenced for this study.

Discussion

Our study integrated both internal and external shell data, providing taxonomic support for the inadequately described species, *Z. troglobalcanicum* and *Z. simplex* as well as significant morphological (conchological) evidence for 11 undescribed species and one potential new species, treated inconclusively as *Zospeum* sp. 2. Our species hypotheses are based largely on the configuration of the columella and the presence and formation of a lamella in relationship to it as well as columellar alignment and degree of torsion and its influence in forming the umbilical depression. These considerations in conjunction with DNA sequence analyses (if available) and shell measurement data provide a foundation for interpretation of zospeid diversity in the geologically complex Southern Balkan region. The diversification of *Zospeum* is characterized by long-distance colonization events with radiations into multiple lineages inhabiting isolated cave systems (Weigand *et al*. 2013). Our conchological assessment suggests multiple lineages with cave populations bearing some characters or variations of characters similar to those but not congruent with the lectotype of *Z. troglobalcanicum*. Mostly, the internal coiling configuration of the columella and the respective formation of the final coiling reflected in the umbilical zone provide more information about these species than the largely nondescript outer aspects of the teleoconch. Overall, we found that Micro-CT and SEM significantly aided the determination of characters and their interpretation in our morphological analyses. Moreover, since the tiny shells are mostly filled with sediment and mixed with or devoid of recognizable soft tissue (i.e., mummies) for DNA sequence analysis, Micro-CT is the most effective means for accessing morphological data in this microgastropod material. The one new DNA sequence analysis in this study showed that *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov. is a well-supported species in the inferred phylogeny but could not be morphologically fully assessed due to the destruction of the type series during the DNA extraction. The only morphological characters that could be diagnostically attributed to this species are the elliptical-ovate to subquadrate-oblique aperture form, the scratch-like microstructure on the teleoconch, and the milky, radial banding on the penultimate and body whorls of both shells.

Our investigation addressed the taxonomic uncertainty of shells in museum collections that had been identified as *Z. troglobalcanicum* or attributed to *Z. amoenum* by earlier researchers. The notes in specimen vials (i.e., "revid Maier, 1977") and the unpublished doctoral thesis of H.C. Maier (1982) were considered in this work. Although his findings are now superseded by current works incorporating DNA and Micro-CT and SEM studies (Jochum *et al*. 2015; Inäbnit *et al*. 2019, 2021; Kneubühler *et al*. 2021), H.C. Maier's (1982) unpublished contribution to the knowledge of *Z. troglobalcanicum* provided a valuable resource in locating material for this study and in our consideration of earlier interpretations of *Zospeum*'s southernmost member (Bole 1974; Gittenberger 1975).

This study provides an updated description of *Z. troglobalcanicum* and proposes a lectotype from the single syntype shell (NHMW 32.749). The only descriptive information in Absolon's (1916a) original description of Z. *troglobalcanicum* is limited to the seven words "has absolutely no dentition in its shell" plus a photograph of the 13 syntype shells (Absolon 1916b). According to Art. 12.2.7 of the ICZN (ICZN 1999), Absolon's brief account and photograph suffice in documenting the date of description. Our investigation revealed distinct characters for this species, such as the centrally aligned, moderately thick columella, the distinct upper position of the reduced, thread like lamella and the degree and size of the umbilical depression in conjunction with the coiling of the last whorl and the columellar side of the peristome in relationship to it. With these significant characters now visually accessible, we were able to compare individuals sampled from 12 other caves. During our study, we discovered ten characters upon which we could compare population to population irrespective of their geographical context (Table 5). By assembling these characters in a diagnostic table (Table 5), we could interpret differences as well as determine tendencies in shell morphology such as a tendency towards costateness, expressed by the density and coarseness of indentations and blunt or coarse growth lines emanating at the suture and the beginning of the new whorl. In addition, we discovered that the coiling of the body whorl (ventral

perspective) advances / extends differently in respect to its alignment with the umbilical depression such that it is either "to the right and oblique of", "directly parallel to" or "on top of the umbilicus". In turn, the last quarter of the body whorl (ventral perspective) presents a compact or non-compact coiling dynamic, whereby the aperture ends up positioned either lower or higher up on the ventral side of the shell.

Zospeum's southernmost relatives show a different internal morphology than their northern congeners, including lack of apertural dentition and a very reduced to partially present or non-existent lamella on a differentiated, species specific and variably aligned columella. Specifically, *Z. troglobalcanicum* shows a distinctly weak, low lamella aligned directly below the penultimate whorl, tightly coiling atop the columella. This signatory feature, in conjunction with the integrative studies by Inäbnit *et al*. (2019, 2021), further distinguishes *Z. troglobalcanicum* from the only known syntype of its northern congener *Z. amoenum* (NHMW 71976) (Grotte Juhanča = Ihanščica, Ihan). Moreover, this Alpine-Dinaride species typically bears a well-formed and diagonally aligned lamella (see Inäbnit *et al*. 2019: 151, figs 6l, o) on a moderately thick columella, which is not at all seen in any of the southern congeners in this study. We remark that all but one northern species of *Zospeum* so far investigated via Micro-CT and SEM (Jochum *et al*. 2015; Inäbnit *et al*. 2019), bear a well-formed, internal columellar lamella irrespective of the presence of apertural dentition. The exception, is the specimen (RS0059) from Potočka zijalka from the Kamnik-Savinja Alps, imaged in Jochum *et al*. (2015: 58–59, figs 10j–k, 11i–m) and which was considered *Z. amoenum* by these authors before the image of the broken *Z. amoenum* syntype (NHMW 71976 from Ihanščica) was published in Inäbnit *et al*. (2019: 151, fig. l). Since the columella of the shell from Potočka zijalka is smooth, Inäbnit *et al*. (2021) later questioned the species assignment of this atypical *Z. amoenum* shell. Although this shell bears some superficial affinity to its southern congener, *Z. neuberti* Jochum & Ruthensteiner sp. nov., the geographical distance (ca 735 km), size differences, the more robust columella in the Potočka zijalka shell and the very compact alignment of the peristome in relationship to the highly callused umbilical depression, rule out any closer affinity.

In addition to *Z. troglobalcanicum*, 11 species of *Zospeum* from 15 populations are recognized and described in this study. These include *Z. amplioscutum* Jochum & Ruthensteiner sp. nov., *Z. biokovoense* Jochum & Ruthensteiner sp. nov., *Z. constrictum* Jochum & Ruthensteiner sp. nov., *Z. dubokidoense* Jochum & Ruthensteiner sp. nov., *Z. intermedium* Jochum & Ruthensteiner sp. nov., *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov., *Z. neuberti* Jochum & Ruthensteiner sp. nov., *Z. njegusiense* Jochum & Ruthensteiner sp. nov., *Z. njunjicae* Jochum, Schilthuizen & Ruthensteiner sp. nov., *Z. tortuosum* Jochum & Ruthensteiner sp. nov., *Z. tumidum* Jochum, Schilthuizen & Ruthensteiner sp. nov. An inconclusive assignment of *Zospeum* sp. 2 from Taleža pećina, Trebinje is included. We corroborated the assignment of the Montenegrin population of *Z. troglobalcanicum* (MCSMNH-PMSL-Moll.-FVelkovrh 29603) (Figs 7A–C, 8A–F) from Lipska pećina (Cetinje) (also in Gittenberger 1975). Four Shells (one deformed in the aperture) from the nearby cave, Cetinska pećina (Cetinje), are assessed whereby three were assigned to the species, *Z. tortuosum* sp. nov. The deformed shell is presented here but not assigned species status. Moreover, the shell (RMNH.MOL.234132) illustrated in Gittenberger (1975: fig. 3) and identified as *Z. troglobalcanicum* therein, was re-assessed using Micro-CT in this work (Fig. 6). Based on this new image data and considering that the shell (RMNH. MOL.234132) derived from another part of the same cave (Cetinska pećina) and likely not far from one or many potential "entrances" and does not bear the additional characteristic coiling of the last whorl preceding the aperture, but rather, a conspicuous parietalis not seen in any of the other species except in much weaker form in *Z. dubokidoense* sp. nov., we reassign the shell to *Z. intermedium*. The shell of *Z. intermedium* is also significantly larger in all size dimensions compared to the others. Moreover, assuming this shell most probably was not found in the same part of the cave as the other morphs, it may have inhabited a nearby wall or washed in from another chamber connected to the same subterranean river drainage system as Lipska pećina and Duboki do caves. Cetinje pećina (= Cetinjska pećina) and

Lipska pećina are located less than 5 km from each other. Lipska pećina consists of 2.5 km of passages and part of it contains an underground river. We remark that when *Z. intermedium* was collected in 1974, it appears to have belonged to a cohort of a thriving population or populations. The sample lot (RMNH.MOL.234134) from which RMNH.MOL.234132 was separated for illustration in Gittenberger (1975), consists of 64 "air-dried shells" of which only 19 are opaque white, an indication of shell senescence and maybe older, earlier deposited specimens from elsewhere in the cave. The remaining 45 shells show a fresh condition of translucence and waxy texture. Future study of the remaining 64 shells of the cohort lot RMNH.MOL.234134 and DNA analyses would ultimately further clarify this species' status.

Fig. 22. Sites of localities and collections. **A**. Site of type locality of Zospeum *njunjicae* Jochum, Schilthuizen & Ruthensteiner sp. nov., Golubova pećina, Gornja Seoca, Montenegro. Credit: I. Njunjić. **B**. Collection site within St John's cave, type locality of *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov. and *Z. njegusiense* Jochum & Ruthensteiner sp. nov., Njeguši, Montenegro (42.4307° N, 18.8115° E) with speleologist, P. Kunisch. Credit: Péter Lenkei. **C**. Entrance to Golubova pećina (42.2093° N, 19.1306° E), Gornja Seoca, Montenegro. Credit: I. Njunjić.

Although *Z. neuberti* Jochum & Ruthensteiner sp. nov. (NHMW Mol.Coll.Edlauer 32006) derives from a cave geographically close (ca 3–4 km) to Benetina pećina, the internal shell morphology and size ranges differ significantly (i.e., columella is completely smooth and character sizes all smaller) from that of *Z. troglobalcanicum*. We emphasize in this case, that although caves may be relatively close to each other geographically, they are often geologically, completely isolated from each other such that DNA sequence divergence of cave populations occurs even in instances where no morphological differences of the fauna are apparent (Dányi *et al*. 2019). Considering the complex geology of this region, these caves are probably not contiguous such that it is unlikely that the two *Zospeum* populations share the same subterranean system. It is also plausible that these species inhabit opposite sides of different subterranean drainage boundaries (Grego & Pešic 2021). On the other hand, in the case of *Z. dubokidoense* Jochum & Ruthensteiner sp. nov. and *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov., recent exploration (Csepreghy & Lenkei 2021) has discovered a connection between the two caves Duboki do and St John's cave such that speculation regarding species affinity implied by the elliptical-ovate to oblique-subquadrate apertural shape of these two species is conceivable.

The occurrence of a second and third species in a single chamber, such as the situation represented by the subfossil shell, *Z. njegusiense* Jochum & Ruthensteiner sp. nov. from St John's cave, is not surprising considering the collector, László Dányi's (pers. comm. May 2022) comments about this cave's ecology: "The small chamber, where all the snails were collected, is really a rather dry part of the cave, a so called 'fossil' part, which doesn't have any active waterflow – even temporarily – since ages. However, on the rocks there is a thin layer of clay which is wet around micro fissures because of percolating water." The dual presence of live *Z. kolbae* Jochum, Inäbnit, Kneubühler & Ruthensteiner sp. nov. and another unidentified morphospecies in the same small cavity in St John's cave (*Zospeum* sp. 1) is most probably a recent colonization event due to hydrogeological changes opening new fissures for water to seep in and allow mud to accumulate in the otherwise, old, and dry chamber. In effect, this process likely allowed *Z. kolbae* and the second, herein unassessed morphospecies *Zospeum* sp. 1 (NMBE 577052–577053), (Fig. 16C–E) to "percolate" in from another chamber in the cave, enabling new habitation in a formerly moist cavity, previously occupied by the third species *Z. njegusiense*. Taxonomic treatment of the second, conchologically different morphospecies found in St John's cave was not undertaken due to immaturity of some of the individuals and lack of empty adult shell material for a more thorough morphological investigation. It is, however, imaged and mentioned here in case future exploration recovers more individuals for further investigation.

During our study, we found that cave systems of the Dinarides often have similar names with different spellings, causing confusion in interpretation of older labels regarding their geographical context. For example, the locality of *Z. neuberti* Jochum & Ruthensteiner sp. nov., Grabovica pećina, is also known as Grabrovica pećina in Croatian (R. Ozimec & I. Njunjić pers. comm. April 2022). According to these biospeleologists and, in records of four other animal taxa for which this cave is the type locality, it is located near Slivnica Bobani, BiH (northwest of Grebci) with a beeline distance of ca 20 km west of Trebinje. In the literature (Absolon 1927; Beier 1938b, 1939b; Noesske 1914), this cave is frequently mentioned in conjunction with "near Trebinje" (R. Ozimec pers. comm. April 2022). Grabovica cave is located ca 3–4 km away from Grebci, the region where Absolon collected *Z. troglobalcanicum* in Benetina pećina. On the other hand, *Z. simplex* in Inäbnit *et al*. (2021) was found in Vranjača cave near the town of Grabovica in northwestern Bosnia and Herzegovina, ca 230 km away (see Fig. 1).

Although the shell of the inconclusively determined species, *Zospeum* sp. 2 was presented in Inäbnit *et al*. (2019: fig. 7u1–u4) as *Z. troglobalcanicum* (NMBE 553414/1), the new image data provided by the lectotype (NHMW 32.749), shows that the shell in Inäbnit *et al*. (2019) constitutes rather, a different entity closer to *Z. neuberti* Jochum & Ruthensteiner sp. nov. (i.e., smooth columella and similar umbilical configuration). Considering that both these shells derive from caves in the region of Trebinje, regarded

as a subterranean biodiversity "hotspot" in Bosnia and Herzegovina (Lewarne 2018), it is not surprising that these two populations show closer affinity than to other shells in this study. Future speleological exploration, sampling efforts and investigations incorporating DNA sequence data will hopefully clarify this issue.

We conclude that the 15 populations investigated in this study encompass mostly single-site or narrow range endemics, subjected to low colonization rates and reduced gene flow between isolated populations. Our results are in sync with studies of other subterranean Western Balkan taxa showing that DNA sequence and morphological diversity reflect the highly differentiated geology and subterranean drainage boundaries associated with the Dinaric karst (Previšić *et al*. 2014; Hlaváč *et al*. 2019; Proćków *et al*. 2019; Grego & Pešic 2021; Ozimec *et al*. 2021) whereby locally isolated island-like landscapes, characteristic of this terrain, provide spatial fragmentation, limited area and low connectivity between subterranean systems (Itescu, 2018). For continental molluscs, the Balkan region is one of the richest reservoirs of endemism in Europe (Cuttelod *et al.* 2011). Moreover, the Dinarides harbor subterranean species that thrive in specific abiotic environmental conditions characteristic of each cave habitat such that species can only inhabit a single cave (Ozimec *et al*. 2021). Considering that the Dinaride mountain chain encompasses an estimated 100 000 caves of which 30 000 have been explored (Ozimec *et al*. 2021), we have only just begun to scratch the surface in accessing and understanding this region's rich zospeid diversity.

Lastly, to understand the extent of this diversity in the Western Balkans, we strongly encourage increased exploration and sampling of *Zospeum*'s southernmost range. In this crucial time of relentless environmental modification and rapid climate change, the microclimatic conditions of subterranean systems in conjunction with low dispersal ability and reduced thermal tolerance of subterranean biota will become increasingly impacted (e.g., Sánchez-Fernández *et al*. 2021). Finding live individuals is imperative in determining if *Z. troglobalcanicum* and the 11 new species described herein alone from museum collections, which were mostly collected in the early decades of the 20th century, have survived. Their existence would provide valuable natural history and ecological data as well as additional DNA sequence data for phylogenetic investigations. Moreover, as new populations are found in the future, and because the conchological differences between many species are subtle and their interiors not always accessible via expensive technological means, it remains critical to study them using DNA sequence data particularly to determine whether they are distinct species, species lineage complexes or divergent populations of known species. For now, and at the risk of revision and potential synonymization down the road, it is crucial to describe sensitive subterranean, morphologically recognizable species now before they disappear and not to wait for DNA sequence analyses (or other methods) to describe them (Pall-Gergely *et al*. 2023).

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