



This work is licensed under a Creative Commons Attribution 3.0 License.

Research article

[urn:lsid:zoobank.org:pub:3C501DE6-AC85-4199-8CDC-D28E42753050](https://zoobank.org/pub:3C501DE6-AC85-4199-8CDC-D28E42753050)

Cochlostoma revised: the subgenus *Lovcenia* Zallot *et al.*, 2015 (Caenogastropoda, Cochlostomatidae)

Enrico ZALLOT^{1,*}, Zoltán FEHÉR², Sonja BAMBERGER³ & Edmund GITTENBERGER⁴

¹ Haagweg 29, NL-2681PA Monster, the Netherlands.

² Hungarian Natural History Museum, Baross 13, 1088 Budapest, Hungary.

^{2,3} Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria.

⁴ Naturalis Biodiversity Center, P.O. Box 9517, NL-2300RA Leiden, the Netherlands.

* Corresponding author: ezallot@gmail.com

² Email: feher.zoltan@nhmus.hu

³ Email: bambergeron@gmail.com

⁴ Email: egittenberger@yahoo.com

¹ [urn:lsid:zoobank.org:author:365E17AD-6938-4364-A526-F1BDA2663E10](https://zoobank.org/author:365E17AD-6938-4364-A526-F1BDA2663E10)

² [urn:lsid:zoobank.org:author:E801EC76-8B1E-450B-993E-BBBE57C00EA9](https://zoobank.org/author:E801EC76-8B1E-450B-993E-BBBE57C00EA9)

³ [urn:lsid:zoobank.org:author:2EC5303E-6D8A-4AAC-AD64-C74ED5BA6C45](https://zoobank.org/author:2EC5303E-6D8A-4AAC-AD64-C74ED5BA6C45)

⁴ [urn:lsid:zoobank.org:author:D786C279-FC92-4D08-AF16-F79A9705E0AE](https://zoobank.org/author:D786C279-FC92-4D08-AF16-F79A9705E0AE)

Abstract. Five species of the subgenus *Lovcenia* of *Cochlostoma* (Cochlostomatidae) are recognized, three of which are described as new to science: *C. (L.) tropojanum* sp. nov., *C. (L.) jakschae* sp. nov. and *C. (L.) lanatum* sp. nov. A lectotype is designated for *C. (L.) erika* (A.J. Wagner, 1906). The shell and the genital tracts are described for all species and the distributional data are summarized.

Keywords. Taxonomy, morphology, molecular phylogeny, the Balkans.

Zallot E., Fehér Z. Bamberger S. & Gittenberger E. 2018. *Cochlostoma* revised: the subgenus *Lovcenia* Zallot *et al.*, 2015 (Caenogastropoda, Cochlostomatidae). *European Journal of Taxonomy* 464: 1–25.
<https://doi.org/10.5852/ejt.2018.464>

Introduction

The most recent comprehensive revision of the genus *Cochlostoma* Jan, 1830 at the species level dates back to the end of the 19th century (Wagner 1897). Since then, only restricted taxonomical contributions or revisions concerning species of limited geographical ranges have been published (e.g., Schütt 1977; Bank 1988; Fehér *et al.* 2001; Fehér 2004).

In a revision of the generic taxonomy of the Cochlostomatidae, Zallot *et al.* (2015) showed the applicability of genital characters complementary to the traditional conchological data in taxon diagnoses within this family. This approach, combined with the use of molecular phylogenetic methods, has opened new prospects in the taxonomy of *Cochlostoma* and formed the basis for a revised system at the generic and subgeneric level (Zallot *et al.* 2015). Using the same methods, the various subgenera of *Cochlostoma* will be dealt with in a series of articles. Here, a start is made with the subgenus *Lovcenia* Zallot *et al.*, 2015.

Material and methods

The locality data, summarized in Table 1, are also indicated for each species in the taxonomic section of this paper. The location of the sampling localities is indicated in Fig. 1. Pre-GPS samples are represented as an approximate position.

High resolution images of the shell specimens were made with a Canon EOS 600D camera with an EF-S 60 mm 1:2.8 macro lens and an additional NL-5 close-up lens, mounted on a tripod with a micrometric slide. Using Helicon Focus stacking software, several photographs were combined into a single picture. With the GIMP 2.6.11–GNU software, potentially diagnostic distances and angles were established (see Fig. 2). The distances were measured in pixels and then translated into metric measurements on the basis of the number of pixels per millimetre. This ratio was determined by comparing the height in pixels on the picture and the height in millimetres that was measured directly.

The number of whorls was counted on the photographs in frontal view. The apical whorl, because it is variable in size, was counted in tenths of the height of the whorl before the apical whorl. For convenience, the whorls are numbered from the basal (body whorl) up. Therefore, the 1st whorl refers to the basal one.

Heights

The tip of the protoconch was aligned with the internal side of the columella visible in the left side of the aperture. The following heights were then measured on this main axis: total height (as above mentioned); height of the 1st, 2nd, 3rd, 4th whorls; height of the aperture between the highest point of the parietal lobe and the basis; height of the aperture along the main axis; height of the parietal lobe.

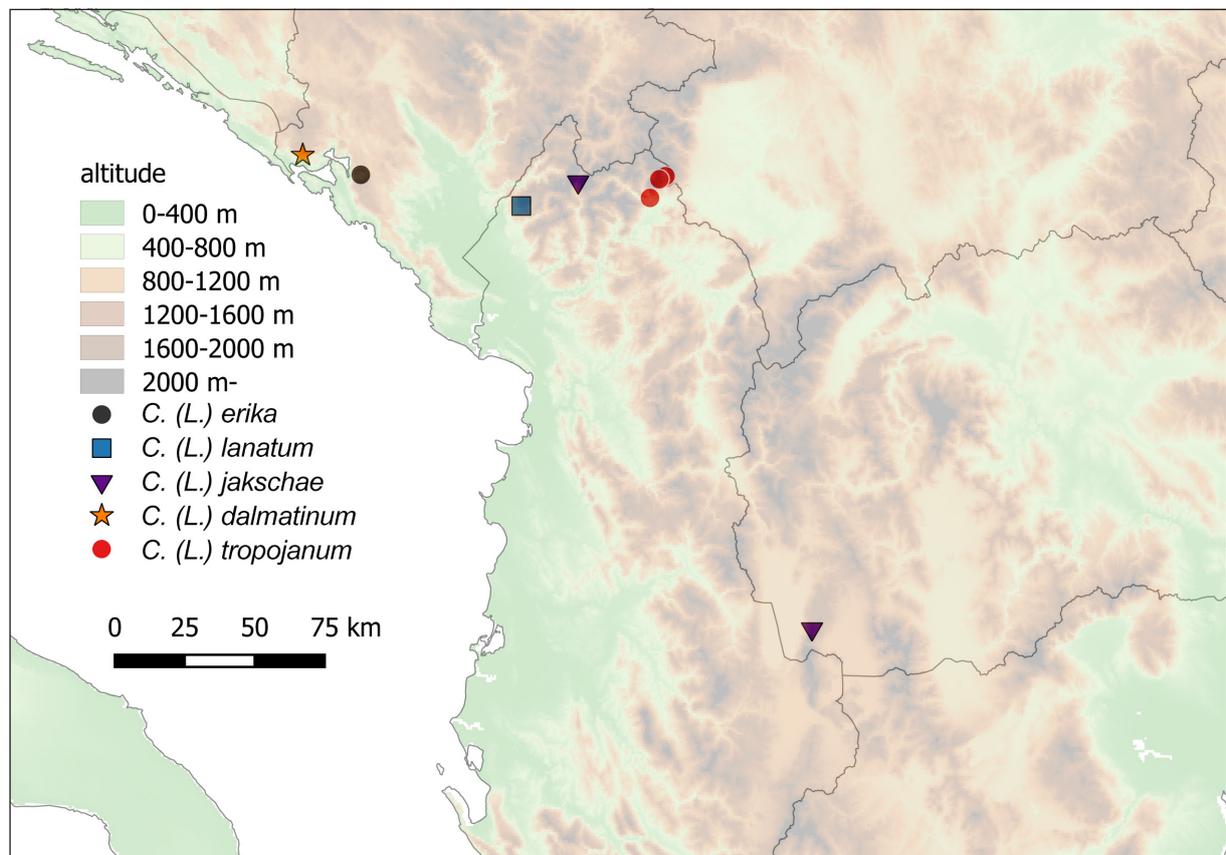


Fig. 1. Distribution of the species of *Cochlostoma (Lovcenia)* Zallot *et al.*, 2015 in the western part of the Balkan Peninsula.

Table 1 (continued on next page). List of sampling localities for species of *Cochlostoma* (*Lovcenia*) Zallot *et al.*, 2015, as well as for *C. (Turritus) arnautorum* (A.J. Wagner, 1906) and *C. (T.) mnelense* (A.J. Wagner, 1914). Countries: AL = Albania; KS = Kosovo; MAK = Macedonia; MONT = Montenegro.

Isolate	Species	collCODE	Country	Locality	°N	°E	Date	Leg.	Type	Voucher	H3	COI	I6S
CO-3029	<i>dalmatinum</i>	2015/057	MONT	Orjen Mts, Kameno 6 km to Crkvice, 890 m a.s.l. (limestone rocks)	42.4877	18.5603	29 May 2015	Deli, Eröss, Fehér	–	NHMW 110430/ MN/0162	MG991787	MG991770	MG991805
CO-3030	<i>dalmatinum</i>	2015/057	MONT	Orjen Mts, Kameno 6 km to Crkvice, 890 m a.s.l. (limestone rocks)	42.4877	18.5603	29 May 2015	Deli, Eröss, Fehér	–	NHMW 110430/ MN/0162	MG991788	MG991771	MG991806
CO-3031	<i>dalmatinum</i>	2015/057	MONT	Orjen Mts, Kameno 6 km to Crkvice, 890 m a.s.l. (limestone rocks)	42.4877	18.5603	29 May 2015	Deli, Eröss, Fehér	–	NHMW 110430/ MN/0162	MG991789	MG991772	–
EZ1284	<i>dalmatinum</i>	2015/057	MONT	Orjen Mts, Kameno 6 km to Crkvice, 890 m a.s.l. (limestone rocks)	42.4877	18.5603	29 May 2015	Deli, Eröss, Fehér	–	NHMW EZ1284	KX120883	–	KX120822
EZ0093	<i>erika</i>	–	MONT	Njegus Plateau, Popova Cave	42.434	18.8189	17 May 1975	Gittenberger	–	RMNH, MOL.117451	KP408303	–	KP408385
EZ9004	<i>erika</i>	–	MONT	Njegus Plateau, Popova Cave	42.434	18.8189	4 Apr. 2006	Deli, Domokos, Nacsá, PGB	–	HNHM 097109	–	KX120970	–
CO-3003	<i>jakschae</i>	2014/159	MAK	Prov. Ohrid, Galičica Mts, Bugarska Cuka peak E side, 1795 m a.s.l. (rocks, rocky grassland)	41.0037	20.847	16 Oct. 2014	Fehér, Haring, Jaksch, Sattmann	paratype	NHMW 111.651	MG991775	MG991758	MG991794
CO-3009	<i>jakschae</i>	2003/084	AL	Petiferi Shkoder, Qafa e Pejës, N of Okol, 1700 m a.s.l.	42.4438	19.77	16 Jul. 2003	Eröss, Fehér, Kontischán, Murányi	–	HNHM 097221	MG991781	MG991764	MG991799
CO-3010	<i>jakschae</i>	2003/084	AL	Petiferi Shkoder, Qafa e Pejës, N of Okol, 1700 m a.s.l.	42.4438	19.771	6 Jul. 2003	Eröss, Fehér, Kontischán, Murányi	–	HNHM 097221	MG991782	MG991765	MG991800
CO-3032	<i>jakschae</i>	2014/161	MAK	Prov. Ohrid, Galičica Mts, ca. 200 m N of Bugarska Cuka peak, 1795 m a.s.l. (rocks, rocky grassland)	41.0051	20.8462	16 Oct. 2014	Fehér, Haring, Jaksch, Sattmann	paratype	NHMW 111249	MG991790	–	–
CO-3033	<i>jakschae</i>	2014/161	MAK	Prov. Ohrid, Galičica Mts, ca. 200 m N of Bugarska Cuka peak, 1795 m a.s.l. (rocks, rocky grassland)	41.0051	20.8462	16 Oct. 2014	Fehér, Haring, Jaksch, Sattmann	paratype	NHMW 111249	MG991791	–	–
EZ0180	<i>jakschae</i>	2003/084	AL	Petiferi Shkoder, Qafa e Pejës, N of Okol, 1700 m a.s.l.	42.4438	19.771	6 Jul. 2003	Eröss, Fehér, Kontischán, Murányi	–	HNHM 097221	KX120833	–	–
EZ1260	<i>jakschae</i>	2014/161	MAK	Prov. Ohrid, Galičica Mts, ca. 200 m N of Bugarska Cuka peak, 1795 m a.s.l. (rocks, rocky grassland)	41.0051	20.8462	16 Oct. 2014	Fehér, Haring, Jaksch, Sattmann	paratype	NHMW 111249	KX120881	–	KX120820

Table 1 (continued).

Isolate	Species	colCODE	Country	Locality	°N	°E	Date	Leg.	Type	Voucher	H3	COI	I6S
CO-3004	<i>lanatum</i>	2016/031	AL	Malësia District, Mali e Veleçikut SW slope, Shpellë e Deleve, NW of Razëm, 1300 m a.s.l. (limestone rock in and around the cave)	42.5576	19.5269	28 Jun. 2016	Eröss, Fehér, Szekeres, Grego	paratype	NHMW 111.652	MG991776	MG991759	–
CO-3005	<i>lanatum</i>	2016/031	AL	Malësia District, Mali e Veleçikut SW slope, Shpellë e Deleve, NW of Razëm, 1300 m a.s.l. (limestone rock in and around the cave)	42.5576	19.5269	28 Jun. 2016	Eröss, Fehér, Szekeres, Grego	paratype	NHMW 111.652	MG991777	MG991760	MG991795
EZ1100	<i>lanatum</i>	–	AL	Malësia District, Mali e Veleçikut SW slope, Shpellë e Deleve, NW of Razëm, 1300 m a.s.l. (limestone rock in and around the cave)	42.5576	19.5269	16 Oct. 2011	Gittenberger	–	RMNH. MOL.282897	KP408304	–	KP408386
CO-3006	<i>tropojanum</i>	2016/51	AL	Tropojë District, gorge of Lumi i Gashit SW of Dretovë 390 m a.s.l. (limestone rocks, forest)	42.4009	20.0879	1 Jul. 2016	Eröss, Fehér, Szekeres, Grego	–	NHMW 111.654	MG991778	MG991761	MG991796
CO-3025	<i>tropojanum</i>	2014/094	AL	Tropojë District, Pr. i Tropojës Gorge ca 13 km N of Tropojë, 925 m a.s.l. (rocky forest)	42.4692	20.1554	26 Jun. 2014	Angyal, Fehér, Grego	–	NHMW 111.247	MG991783	MG991766	MG991801
CO-3026	<i>tropojanum</i>	2014/094	AL	Tropojë District, Pr. i Tropojës Gorge ca 13 km N of Tropojë, 925 m a.s.l. (rocky forest)	42.4692	20.1554	26 Jun. 2014	Angyal, Fehér, Grego	–	NHMW 111.247	MG991784	MG991767	MG991802
CO-3027	<i>tropojanum</i>	2014/095	AL	Tropojë District, Pr. i Tropojës Gorge ca 14 km N of Tropojë, 965 m a.s.l. (rocky forest)	42.474	20.152	26 Jun. 2014	Angyal, Fehér, Grego	–	NHMW 111.248	MG991785	MG991768	MG991803
CO-3028	<i>tropojanum</i>	2014/095	AL	Tropojë District, Pr. i Tropojës Gorge ca 14 km N of Tropojë, 965 m a.s.l. (rocky forest)	42.474	20.152	26 Jun. 2014	Angyal, Fehér, Grego	–	NHMW 111.248	MG991786	MG991769	MG991804
EZ1190	<i>tropojanum</i>	2014/095	AL	Tropojë District, Pr. i Tropojës Gorge ca 14 km N of Tropojë, 965 m a.s.l. (rocky forest)	42.474	20.152	26 Jun. 2014	Angyal, Fehér, Grego	–	NHMW 111.248	KX120875	–	KX120808
CO-3001	<i>arnautorum</i>	2016/70	KS	Pejë District, Rugovo Gorge upper part, at the Qokorrit border crossing point, 1200 m a.s.l. (limestone rocks)	42.6849	20.0545	4 Jul. 2016	Eröss, Fehér, Szekeres, Grego	–	NHMW 111.653	MG991773	MG991756	MG991792
CO-3002	<i>arnautorum</i>	2016/70	KS	Pejë District, Rugovo Gorge upper part, at the Qokorrit border crossing point, 1200 m a.s.l. (limestone rocks)	42.6849	20.0545	4 Jul. 2016	Eröss, Fehér, Szekeres, Grego	–	NHMW 111.653	MG991774	MG991757	MG991793
CO-3007	<i>mnelense</i>	2016/46	AL	Mirditë District, Mali i Munellës E slope, 1510 m a.s.l. (rocky forest, limestone rocks)	41.9697	20.1131	30 Jun. 2016	Eröss, Fehér, Szekeres, Grego	–	NHMW 111.655	MG991779	MG991762	MG991797
CO-3008	<i>mnelense</i>	2016/46	AL	Mirditë District, Mali i Munellës E slope, 1510 m a.s.l. (rocky forest, limestone rocks)	41.9697	20.1131	30 Jun. 2016	Eröss, Fehér, Szekeres, Grego	–	NHMW 111.655	MG991780	MG991763	MG991798

Widths

On a plane orthogonal to the main axis the following widths were measured: width of the basal whorl; width of the 2nd whorl; width of the lower and upper suture of the 2nd whorl; width of the basal protoconch whorl; width of the aperture; maximum width of the lips on the columellar side.

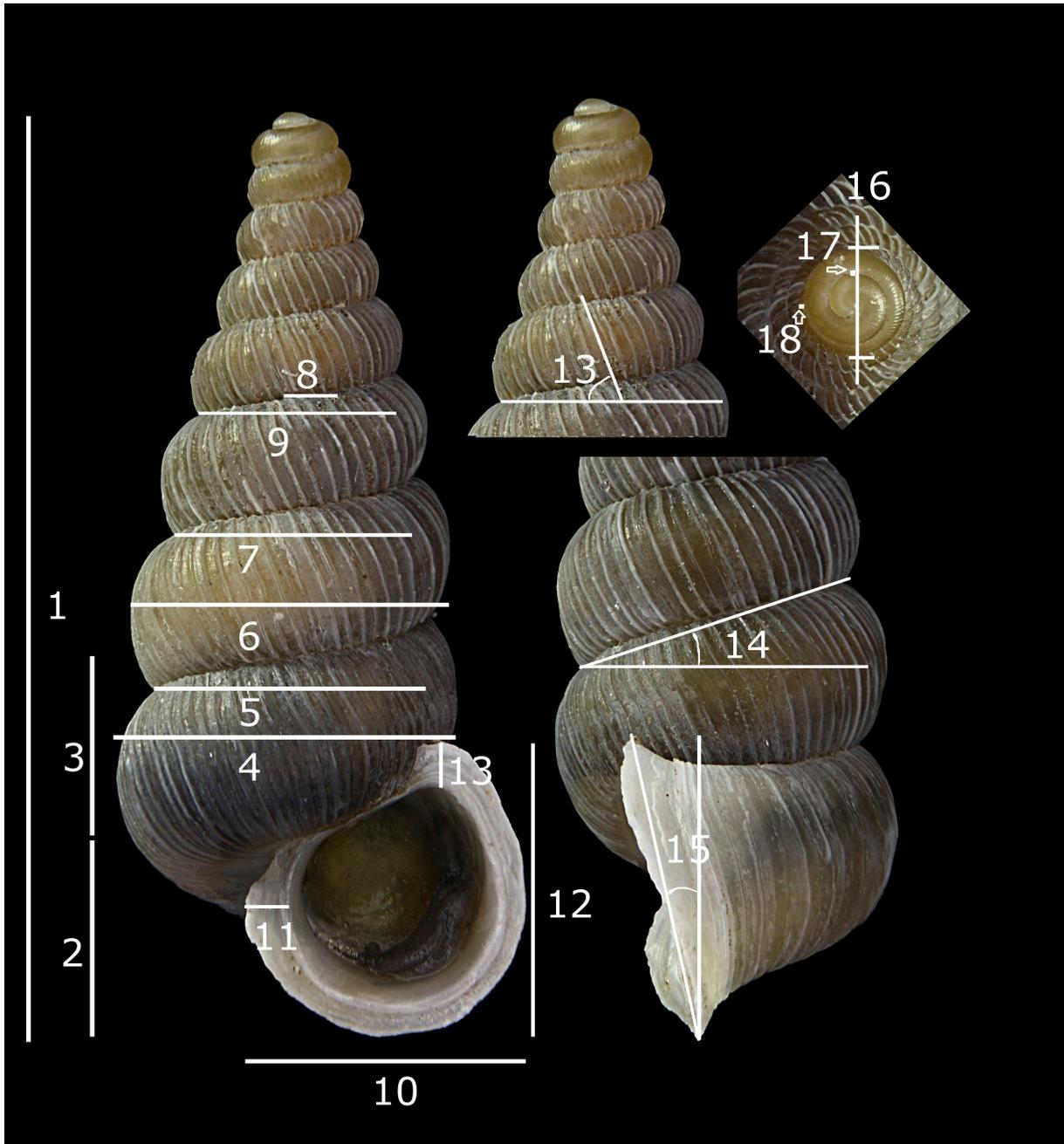


Fig. 2. Potentially diagnostic distances and angles. 1 = shell height (H). 2 = height of aperture at the columellar side. 3 = height of the first whorl. 4 = width of body whorl (Wbw). 5 = width of the suture above the body whorl. 6 = width of the penultimate whorl. 7 = width of the suture above the penultimate whorl. 8 = distance between the 5 most central ribs on the 4th whorl up. 9 = diameter of the 4th whorl up. 10 = aperture width (Wa). 11 = width of the lip at the columellar side. 12 = aperture height (Ha). 13 = rib inclination. 14 = suture inclination. 15 = aperture inclination. 16 = protoconch diameter in upper view (Dp). 17 = end of the smooth part of the protoconch. 18 = end of the protoconch.

The ratio between the width of the 2nd whorl and the average width of the upper and lower sutures of the 2nd whorl gives an index of the roundness of the whorl, a feature frequently mentioned in the description of the taxa within *Cochlostoma*. The ratio between the width of the 1st and the 4th whorl is an index of the slenderness of the shell.

Ribs per mm and rib features

The number of ribs per mm was calculated by measuring the distance between the first and the last of the most central 5 ribs of a whorl in frontal view. Because the ribbing is normally different in the apical rather than in the basal whorls, the measurement was repeated on the 1st (taking the distance on the upper suture of the whorl) and on the 4th whorl (taking the distance on the lower suture). Because the roundness of the 4th whorl can distort the distances measured on the photograph, this distance (equal to the chord of the circumference) was translated to the distance along the arc.

The observed rib features (on the ribs of the 4th whorl) were the following: type of ribbing (regular, irregular, double ribbing); shape of the ribs (sharp, rounded; straight or sinuous); height.

Inclination of the ribs

This was calculated taking the average of the inclination of the 3 most central ribs of the 4th whorl and the most central rib of the 3rd whorl with respect to the main axis. The angle between the main axis and the lower suture of the 4th whorl was also recorded. In this way, the inclination of the ribs can be related either to the main axis or the suture itself.

Inclination of the aperture

In lateral view, the shell was moved into a standard position in order to have the basal point of the aperture aligned with the tip of the protoconch. Then, the angle between the lip of the aperture and the resulting main axis was measured. The inclination of the suture between the 1st and the 2nd whorl was also measured, allowing us to relate the inclination of the aperture to it.

To investigate the genital morphology, the lower whorls of the shells of male animals were removed in order to expose the right side of the foot. Shells of females were entirely removed. The body was then fixed in absolute ethanol. Females were positioned in such a way that the ventral side was visible at the level of the bursa copulatrix, between the 2nd and the 3rd whorls. In males, the mantle was cut vertically from the front up to the anus and, behind it, the tip of the prostatic gland. The anatomical details of individual specimens were figured with the help of a camera lucida and a stereo microscope. The description of the genitalia (see Fig. 3 for the terminology) begins with the structures that are located in the apical part of the body (i.e., the ovary or the testis). For more details, see Zallot (2002: 95–96) and Zallot *et al.* (2015).

List of abbreviations for material and shell characters:

- a = alcohol stored individual
- ja = alcohol-stored juvenile individual
- fr = broken or juvenile shell
- D4th = diameter of the 4th whorl
- Dp = diameter of the protoconch
- H = shell height
- Ha = aperture height
- Rr = roundedness of the 2nd whorl
- W = shell width
- Wa = aperture width
- Wbw = width of the body whorl

Institutional abbreviations used:

- GR = Private collection of J. Grego, Banska Bystrica, Slovakia
 HNHM = Hungarian Natural History Museum, Budapest, Hungary
 NHMW = Naturhistorisches Museum, Vienna, Austria
 NHMW-E = Edlauer collection in NHMW
 NHMW-K = Klemm collection in NHMW
 RMNH = Naturalis Biodiversity Center, Leiden, the Netherlands
 SMF = Naturmuseum Senckenberg, Frankfurt am Main, Germany

In the 'Material examined' sections, the number of specimens is only provided for type material lots.

When Zallot *et al.* (2015) presented the first phylogenetic reconstruction for the genus *Cochlostoma*, only two species of *Lovcenia* were included, i.e., *C. (L.) erika* (A.J. Wagner, 1906) and the species described here as *C. (L.) lanatum* sp. nov. That study was based on only two markers, the nuclear Histone *H3* gene (*H3*) and the mitochondrial *16S rRNA* gene (*16S*). Due to the incomplete overlap of the available samples, the trees based on these two markers were calculated separately. In the present study, more taxa and more populations per taxon are included, and an additional marker, the mitochondrial cytochrome oxidase subunit I (*COI*) was used. The molecular analysis was performed on the basis of material from 13 different locations. Additionally, we used two populations of two different species belonging to the subgenus *Turritus* Westerlund, 1883.

The analysed specimens had either been kept in ethanol 70% or were dried animals, i.e., shells containing mummified bodies (Table 1). From specimens in ethanol, DNA was extracted with the DNeasy Blood

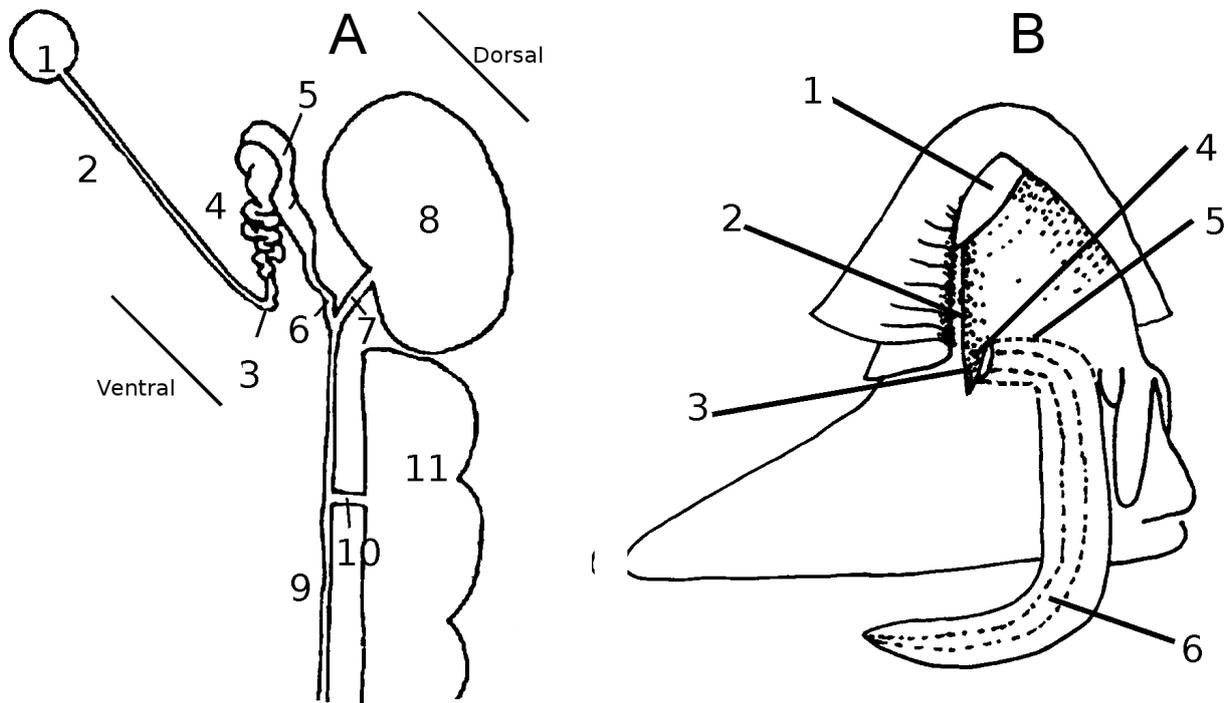


Fig. 3. Genitals of *Cochlostoma* Jan, 1830. **A.** Female genitalia. 1 = ovary; 2 = visceral oviduct; 3 = proximal loop; 4 = loops of the visceral oviduct; 5 = seminal receptacle; 6 = distal oviduct; 7 = pedunculus of the bursa copulatrix; 8 = bursa copulatrix; 9 = copulatory duct; 10 = channel of the uterine gland; 11 = uterine gland. **B.** Male genitalia. 1 = anus; 2 = groove fold; 3 = sperm pocket; 4 = penial funnel; 5 = body spermiduct; 6 = penis with the penial spermiduct.

and Tissue Kit (QIAGEN, Hilden, Germany) following the manufacturer's protocol. Extraction and purification of DNA from mummified samples were done according to the method of Thomsen *et al.* (2009) modified for gastropods by Páll-Gergely *et al.* (2015). Fragments of the *COI* (658 bp), *16S* (499–509 bp) and *H3* (309 bp) genes were amplified by polymerase chain reaction (PCR) using the following primers: *16SarF* (Palumbi 1996) plus *16SLOrc_rev* (Harl *et al.* 2014) for the *16S*, HCO2198 (Folmer *et al.* 1994) plus COI_schneckrev (Duda *et al.* 2011) for the *COI* and H3ColF (Colgan *et al.* 2000) plus H3PulR (Uit de Weerd & Gittenberger 2013) for the *H3*. PCR protocols followed Harl *et al.* (2014) for *COI* and Páll-Gergely *et al.* (2015) for *16S* and *H3*. Successfully amplified products were sequenced at LGC Genomics (Berlin, Germany). Sequences were assembled and edited using BioEdit ver. 7.0.1 (Hall 1999) and deposited in GenBank (Table 1).

Some previously published *H3* and *16S* sequences (Zallot *et al.* 2015, Table 1) were also used in the reconstruction of the phylogeny. *COI* and *H3* sequences could be unambiguously aligned manually. *16S* sequences were aligned with the online version of MAFFT (Katoh & Standley 2013, <http://mafft.cbrc.jp/alignment/software/>) with the following settings: G-INS-i iterative refinement algorithm, gap opening penalty=1.53, offset value=0.123 and 'leave gappy regions'. This resulted in a 511 bp long *16S* alignment. Thereafter, the three alignments were concatenated and divided initially into seven partitions. The ModelFinder function of IQ-Tree (Kalyaanamoorthy *et al.* 2017) selected the following partitioning scheme and best-fit models of sequence evolution according to the Bayesian Information Criterion (BIC): *H3* 1st, 2nd and 3rd codon positions: JC; *COI* 1st codon position: TN+I; *COI* 2nd codon position: F81+I; *COI* 3rd codon position: TVM+I; *16S*: HKY+I. Phylogenetic relationships were estimated by employing a Maximum Likelihood-based (ML) method of tree reconstruction, as well as Bayesian Inference. ML tree reconstruction was done using IQ-TREE ver. 1.6.1 (Nguyen *et al.* 2015). Nodal supports were estimated by performing 1000 ultra-fast bootstrap repeats (Hoang *et al.* 2017), as well as employing the SH-aLRT test (Anisimova *et al.* 2011). All analyses, including model test, tree reconstruction and bootstrapping, were run on the W-IQ-TREE webserver (Trifinopoulos *et al.* 2016, <http://iqtree.cibiv.univie.ac.at>). An unconstrained Bayesian tree was inferred by MrBayes ver. 3.2.1 (Ronquist *et al.* 2012) using the following parameters: a four-chain (one cold, three heated; T=0.2) Metropolis-coupled Markov chain Monte Carlo (MCMC) analysis, run for 5×10⁶ generations; trees were sampled every 1000 generations and the first 10% of them was discarded as burn-in. Convergence of the Bayesian runs was checked with Tracer ver. 1.6 (Rambaut *et al.* 2014).

Genetic distances were calculated using MEGA ver. 6 (Tamura *et al.* 2013).

Results

We accept five species in *Cochlostoma* (*Lovcenia*), three of which are new to science. The molecular phylogenetic reconstruction, based on three markers (*H3*, *16S*, *COI*), supports the monophyly of the subgenus *Lovcenia* as well as that of each species of *Lovcenia*.

At the same time, two different tree reconstruction methods resulted in partly incongruent topologies concerning relationships within the *Lovcenia* clade. *Cochlostoma* (*L.*) *jakschae* sp. nov. and *C.* (*L.*) *tropojanum* sp. nov. are sister taxa with high branch support in both of the trees. However, the relationships among the other three species are unclear: in the Bayesian tree *C.* (*L.*) *dalmatinum* (L. Pfeiffer, 1863) is in a basal position, in the ML tree *C.* (*L.*) *erika* is in that position (Fig. 4).

For the most widely used marker (*COI*), the uncorrected p-distances among conspecific populations vary from 0.015 (*C.* (*L.*) *tropojanum* sp. nov.) to 0.021 (*C.* (*L.*) *jakschae* sp. nov.), whereas it varies between species from 0.034 (*C.* (*L.*) *jakschae* sp. nov. and *C.* (*L.*) *lanatum* sp. nov.) to 0.087 for *C.* (*L.*) *erika* and *C.* (*L.*) *dalmatinum*) (Table 2). The subgenus is known from a relatively small range that includes W Montenegro, N Albania and W Macedonia.

Taxonomy

Subclass Orthogastropoda Ponder & Lindberg, 1996
 Superorder Caenogastropoda Cox, 1960
 Order Architaenioglossa Haller, 1890
 Superfamily Cyclophoroidea J.E. Gray, 1847
 Family Cochlostomatidae Kobelt, 1902
 Genus *Cochlostoma* Jan, 1830

Subgenus *Lovcenia* Zallot, Groenenberg, De Mattia, Fehér & Gittenberger, 2015

Lovcenia Zallot, Groenenberg, De Mattia, Fehér & Gittenberger, 2015: 80.

Type species

Auritus (Auritus) erika A.J. Wagner, 1906, by original designation.

Diagnosis

Shell slender conical, with more or less regularly spaced riblets, which may vary in prominence. Unlike the species of most subgenera of *Cochlostoma*, those belonging to *Lovcenia* can be distinguished conchologically, i.e., by the early ribbing of the protoconch, with fine riblets appearing already after

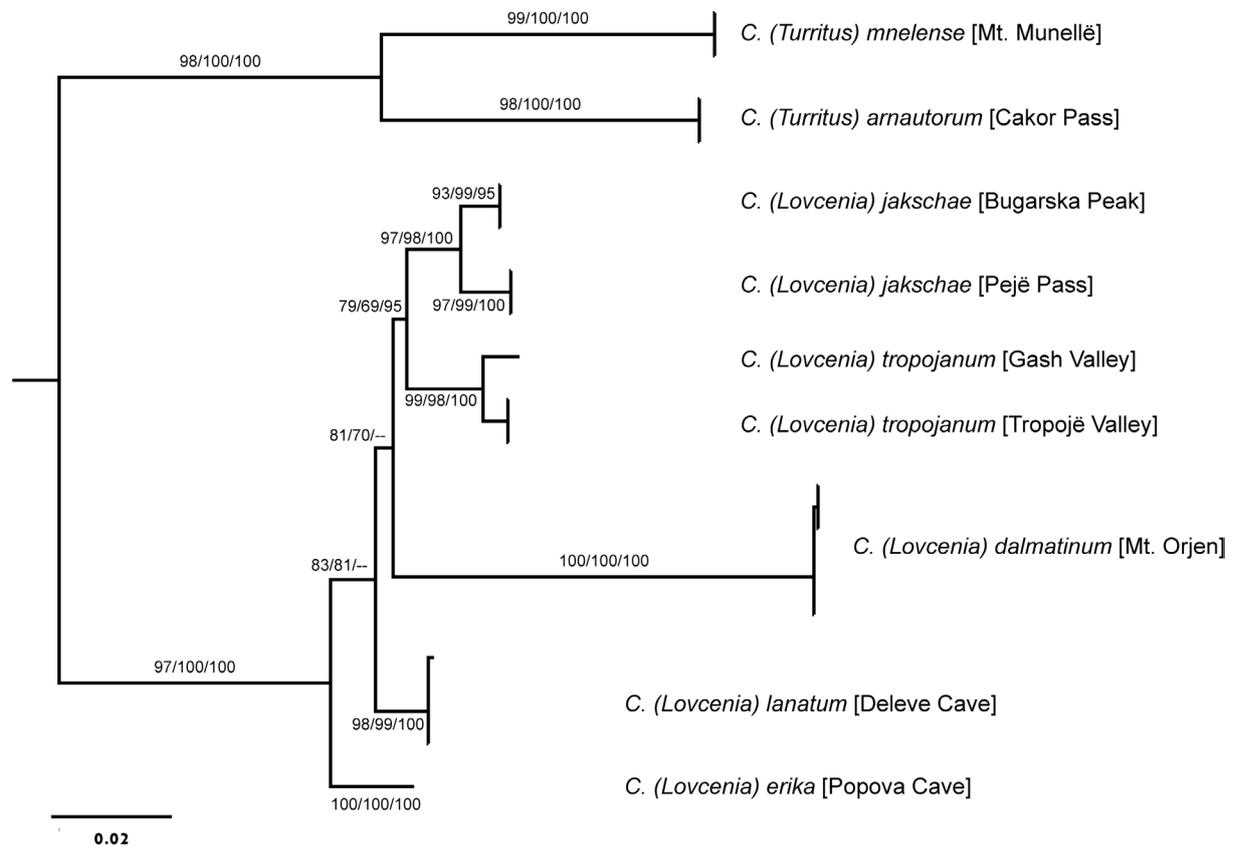


Fig. 4. Maximum Likelihood consensus tree of *Cochlostoma (Lovcenia)* Zallot *et al.*, 2015 inferred from *COI*, *16S* rRNA and nuclear histone *H3* genes. Branch support values are: SH-aLRT support/ML ultrafast bootstrap support/Bayesian posterior probability percentage estimates. Note that two species of *C. (Turritus)* Westerlund, 1883 were used to define the root of the *C. (Lovcenia)* clade.

Table 2. Estimates of evolution divergence between populations and species in *Cochlostoma (Lovcenia)* Zallot *et al.*, 2015. Mean uncorrected *COI* p-distances are shown between species (in the lower half of the matrix) and between conspecific population (in the matrix axis).

	<i>C. (L.) jakschae</i>	<i>C. (L.) deleve</i>	<i>C. (L.) tropojanum</i>	<i>C. (L.) dalmatinum</i>	<i>C. (L.) erika</i>
<i>C. (L.) jakschae</i>	[0.021]				
<i>C. (L.) deleve</i>	0.034	[–]			
<i>C. (L.) tropojanum</i>	0.036	0.035	[0.015]		
<i>C. (L.) dalmatinum</i>	0.084	0.081	0.078	[–]	
<i>C. (L.) erika</i>	0.04	0.036	0.049	0.087	[–]

its initial 0.3–0.5 whorl. In other taxa of *Cochlostoma* the protoconch is smooth for at least the initial 1.0–1.2 whorls. The female genitalia are characterized by the relatively large bursa copulatrix.

Cochlostoma (Lovcenia) erika (A.J. Wagner, 1906)

Figs 5A, 6A, 7–8

Auritus (Auritus) erika A.J. Wagner, 1906: 132, pl. 4, fig. 15a–b.

Auritus (Auritus) erika – Kobelt 1907: 40, pl. 350, fig. 2178.

Cochlostoma erika – Jaeckel *et al.* 1957: 171. — Welter-Schultes 2012: 94.

Cochlostoma (Turritus) erika – Zilch 1958: 64. — Gittenberger 1976: 281, fig. 9.

Cochlostoma (Lovcenia) erika – Zallot *et al.* 2015: 80, figs 7–8, 13, 14.

Diagnosis

Cochlostoma (Lovcenia) erika differs from *C. (L.) dalmatinum* by the more regularly spaced and uniform ribs, which are larger and more variable in prominence in the latter species. It differs from *C. (L.) jakschae* sp. nov. and *C. (L.) tropojanum* sp. nov. by the indented, acutely curved columellar lobe, which is not gently curved inward, and from *C. (L.) lanatum* sp. nov. by the larger and more tumid shell with less prominent ribs.

Material examined

Lectotype

MONTENEGRO: “Popovo Höhle bei Njeguš” [Popovo cave near Njeguš], 43.5291° N, 19.2074° E, 30 May 1903, Sturany leg. (NHMW 38260a). Here designated.

Paralectotypes

MONTENEGRO: 24 spec., same collection data as for lectotype (NHMW 38260b/10, NHMW 38469/6, NHMW-K 15368/4, NHMW 71640/O/8548/2, SMF 160854/2).

Other material

MONTENEGRO: same locality as lectotype but 1120 m a.s.l., Eröss and Fehér leg., 21 April 2000 (HNHM 86387); same locality as lectotype, Deli, Domokos, Nacsá and Páll-Gergely leg., 4 April 2006 (HNHM 97109); same locality as lectotype, Fuchs leg. (NHMW-K 47075); same locality as lectotype, Dabović leg. (NHMW-E 49343, NHMW-E 18270, NHMW-K 4447, NHMW-K 51886, NHMW-K 47074); Njeguš, karstic doline near a cave entrance, 900 m a.s.l., Jul. 1977, Maassen leg. (NHMW 81027); same locality as preceding, 17 May 1975, Gittenberger leg. (RMNH 117451); Duboki Do Cave near Krstac, Fuchs leg. (NHMW-E 28673, NHMW-K 15369, NHMW-K 8173).

Measurements

Lectotype: H 9.5 mm, W 4.5 mm, Wbw 3.8 mm, Ha 3.6 mm, Wa 3.6 mm.

NHMW 38260b (N=6) and NHMW-K 47075 (N=6): H 8.9–10.1 mm, W 4.4–4.9 mm, Wbw 3.7–4.0 mm, Ha 2.9–3.6 mm, Wa 3.1–3.7 mm.

Description

SHELL. Large, with $8\frac{1}{2}$ –10 whorls, H/W ratio 2.55. The apical 2.4 whorls form the protoconch, which is smooth on only the initial 0.5 whorl; further on the whorls have fine, rather widely spaced riblets.



Fig. 5. Female specimens of *Cochlostoma* (*Lovcenia*) Zallot *et al.*, 2015 used for anatomy (shells were destroyed before dissection). **A.** *C. (Lovcenia) erika* (A.J. Wagner, 1906) (HNHM 86387). **B.** *C. (Lovcenia) dalmatinum* (L. Pfeiffer, 1863) (NHMW 110430/MN/0162). **C.** *C. (Lovcenia) tropojanum* sp. nov. (NHMW 111248). **D.** *C. (Lovcenia) jakschae* sp. nov. (NHMW 111249). **E.** *C. (Lovcenia) lanatum* sp. nov. (HNHM 99861).

The protoconch is relatively small, $Dp/D4^{th}$ 0.55. The shell is more or less light horn-brown, without spots. The teleoconch whorls are sculptured with whitish, rounded but thin ribs, which are uniform in height, spacing and shape; on the body whorl the ribs become more narrowly spaced and weaker while approaching the aperture. The aperture has a well-developed lip, which broadens at the columellar side before curving abruptly back, forming an acute angle and covering the umbilicus. The body whorl widens near the aperture.

FEMALE GENITALIA. Bursa copulatrix large, with a pedunculus connected proximally; its proximal lobe smaller than the distal one. Short seminal receptacle, without distal oviduct, confined to the ventral side of the body. Visceral oviduct nearly linear while running over the apex of the seminal receptacle. The junction of the uterine gland and the copulatory duct is far from the connection between the distal oviduct and the pedunculus of the bursa.

Distribution

This species lives on the Njeguši Plateau in Montenegro, where only two locations are known.

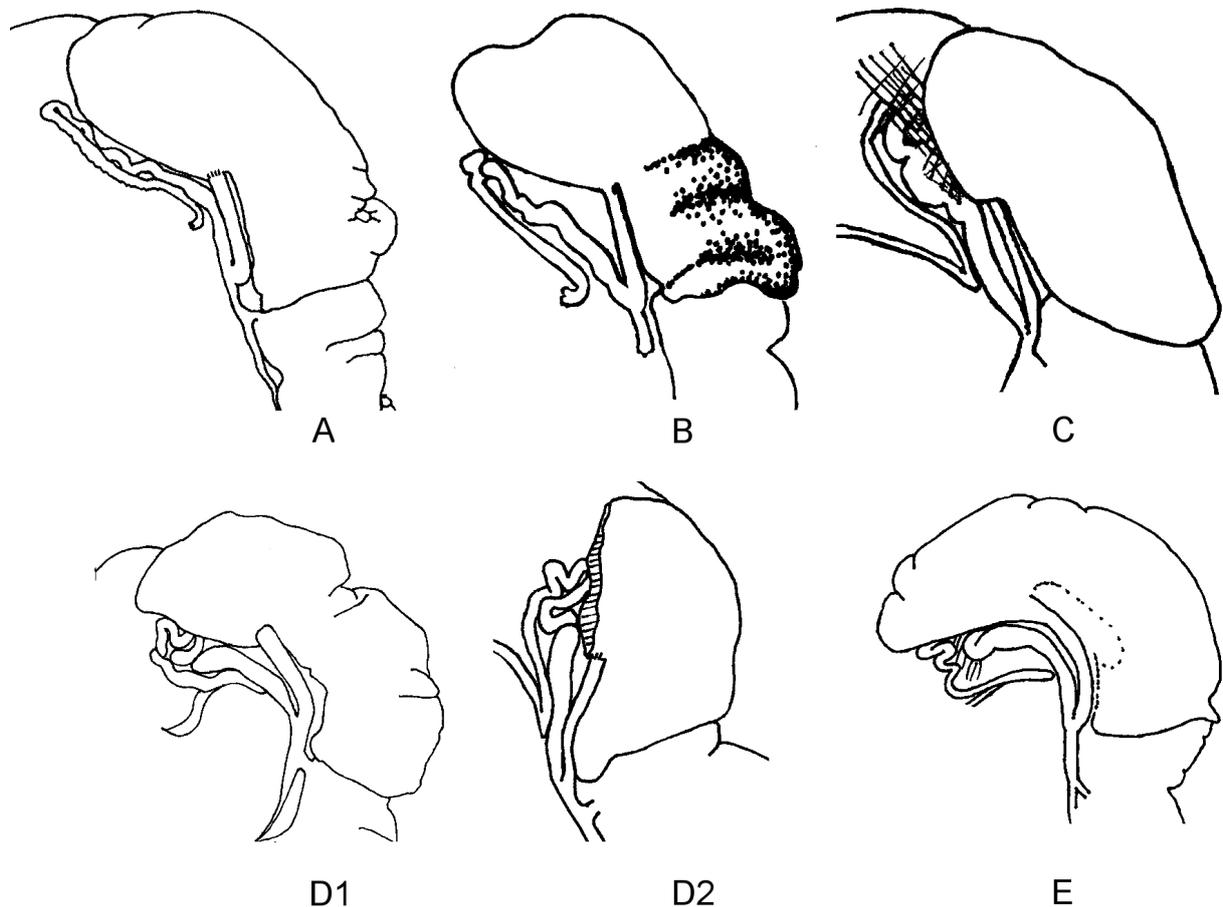


Fig. 6. Female genital morphology. See Table 1 for localities and Table 3 for measurements. **A.** *Cochlostoma (Lovcenia) erika* (A.J. Wagner, 1906) (HNHM 86387). **B.** *Cochlostoma (Lovcenia) dalmatinum* (L. Pfeiffer, 1863) (NHMW 110430/MN/0162). **C.** *Cochlostoma (Lovcenia) trojanum* sp. nov. (NHMW 111248). **D1.** *Cochlostoma (Lovcenia) jakschae* sp. nov., Bugarska Peak population (NHMW 111249). **D2.** *Cochlostoma (Lovcenia) jakschae* sp. nov., Pejë Pass population (HNHM 97221). **E.** *Cochlostoma (Lovcenia) lanatum* sp. nov. (HNHM 99861).

Table 3. Shell features of the analysed specimens of the 5 species of *Cochlostoma* (*Lovcenia*) Zallot *et al.*, 2015.

Pop #	Population	Species	Number of whorls	H = height (mm)	W = width (mm)	H/W	Average height increase per whorl	Ha/H	w roundness	Ha = aperture height (mm)	lip expansion (mm)	Parietal lobe expansion (mm)	Rib inclination	Aperture inclination	Ribs/mm 1 st whorl	Ribs/mm 4 th whorl	Protoconch	Protoconch smooth	Protoconch size	Protoconch/4 th whorl diameter
NHMW110430/ MN/0162	Kameno	<i>dalmatinum</i>	10.1	12.7	4.90	2.59	1.37	0.20	1.21	2.53	0.11	0.09	64.4	20.3	2	3	2.4	0.6	0.94	0.46
NHMW110430/ MN/0162	Kameno	<i>dalmatinum</i>	10.3	14.0	5.24	2.67	1.35	0.20	1.21	2.77	0.15	0.12	62.1	26.6	6	4	2.3	0.7	0.83	0.36
NHMW 110430/ MN/0162	Orjen	<i>dalmatinum</i>	10.1	13.0	4.85	2.68	1.37	0.20	1.21	2.58	0.15	0.15	60.4	15.5	2	4	2.5	0.6	0.99	0.46
RMNH. MOL.117451	Crna Gora	<i>erika</i>	9.0	10.8	4.20	2.57	1.38	0.22	1.18	2.36	0.22	0.21	63.5	21.0	5	5	2.4	0.5	1.00	0.56
HNHM86387	Popova pecina	<i>erika</i>	9.0	10.6	4.21	2.52	1.35	0.23	1.23	2.40	0.20	0.19	64.6	16.0	12	7	2.4	0.5	0.96	0.55
NHMW111249	Bukarsa Cuka	<i>jakschae</i>	7.8	7.9	3.26	2.42	1.36	0.22	1.23	1.73	0.13	0.10	66.2	17.2	9	10	2.4	0.7	0.91	0.73
NHMW111249	Bukarsa Cuka	<i>jakschae</i>	7.5	8.1	3.15	2.57	1.34	0.22	1.25	1.76	0.22	0.11	64.9	17.0	10	9	2.4	0.5	0.98	0.73
HNHM97221	Qafa e Pejës	<i>jakschae</i>	8.3	9.2	3.37	2.73	1.31	0.21	1.24	1.92	0.15	0.14	70.0	13.0	9	8	2.2	0.5	1.02	0.68
HNHM99861	Shellë e Deleve	<i>lanatum</i>	8.9	10.5	3.69	2.84	1.33	0.19	1.25	2.01	0.19	0.15	66.5	22.0	7	6	2.2	0.2	0.97	0.54
NHMW111248	Lumi I Tropojës	<i>tropoianum</i>	8.6	10.0	3.38	2.96	1.31	0.19	1.25	1.94	0.20	0.08	65.0	21.2	7	8	2.4	0.5	0.97	0.61
NHMW111248	Lumi I Tropojës	<i>tropoianum</i>	8.2	9.1	3.21	2.83	1.30	0.20	1.23	1.83	0.14	0.07	64.8	14.6	9	7	2.4	0.3	0.97	0.65
NHMW111248	Lumi I Tropojës	<i>tropoianum</i>	8.6	9.4	3.35	2.80	1.31	0.20	1.25	1.91	0.14	0.08	68.3	16.5	11	9	2.5	0.5	0.89	0.58
HNHM99865	Lumi I Gashit	<i>tropoianum</i>	8.5	9.2	3.30	2.79	1.31	0.21	1.25	1.93	0.13	0.10	67.0	16.0	8	5	2.1	0.3	0.92	0.60
HNHM99871	Tropojë	<i>tropoianum</i>	7.9	8.1	3.17	2.56	1.38	0.21	1.28	1.68	0.13	0.08	64.9	16.2	11	10	2.1	0.5	0.93	0.72

Habitat preference

Like the majority of known *Cochlostoma*, this is an obligate rock-dwelling species. Although it can be found at Popovo Cave together with its congener *Cochlostoma* (*Auritus*) *auritum* (Rossmässler, 1837), this is not syntopy in the strict sense, because there is a difference in their niches. *Cochlostoma* (*A.*) *auritum* lives on the exposed rock surface around the cave entrance, whereas *C. (L.) erika* is found in the twilight zone inside the cave. Though little is known about its ecological requirements, *C. (L.) erika* is supposedly bound partly to the epigeal environment (i.e., subtroglophile in the sense of Sket 2008).

Remarks

In order to promote nomenclatural stability, a female specimen, which was illustrated in the original description by Wagner (1906: fig. 15a–b), is herein designated as the lectotype.

Cochlostoma (*Lovcenia*) *dalmatinum* (L. Pfeiffer, 1863) Figs 5B, 6B, 9

Pomatias dalmatinum L. Pfeiffer, 1863: 136–137.

Pomatias turritus Walderdorff, 1864: 508, 511.

Pomatias (Auritus) dalmatinus – A.J. Wagner 1897: 620, pl. 9, fig. 95a–b.

Cochlostoma (Auritus) dalmatinum – Kobelt 1902: 518.

Auritus dalmatinus – A.J. Wagner 1906: 133.

Cochlostoma dalmatinum – Jaeckel *et al.* 1957: 171. — Zallot *et al.* 2015: 85.

Cochlostoma (Turritus) dalmatinum – Zilch 1958: 63, pl. 4, fig. 12.

Diagnosis

The irregular sculpture and its large shell height distinguish *C. (L.) dalmatinum* from other species of *Cochlostoma (Lovcenia)*.



Fig. 7. *Cochlostoma (Lovcenia) erika* (A.J. Wagner, 1906), lectotype, “Popovo Höhle bei Njegus”, Montenegro (NHMW 38260a).

Type material

The type series from “Castel Nuovo Dalmatiae” (= Montenegro, Herceg-Novi) (L. Pfeiffer 1863: 136) was not available for study, but specimens from the type locality were compared (see below) as well as a photograph of a syntype (SMF 160850, ex coll. Parreys) published by Zilch (1958: fig. 12).

Material examined

MONTENEGRO: Orjen Mts, Kameno, 6 km to Crkvice, 890 m a.s.l., 42.4877° N, 18.5603° E, 29 May 2015, Deli, Eröss and Fehér leg. (NHMW 110430/MN/0162, HNHM 100133); 2 spec., Hercegnovi, Berg Radoštak, Mar. 1928, Käufel leg. (NHMW-K 15367); 5 spec., Radoštak at the source, Mar. 1928, Käufel leg. (NHMW-E 28682/1, NHMW-E 32879/2, NHMW-K 47084/2).

Measurements

HNHM 100133 (N=12): H 11.6–13.3 mm, W 5.3–5.8 mm, Wbw 4.4–4.8 mm, Ha 3.5–4.2 mm, Wa 3.6–4.1 mm.

Description

SHELL. Large, with many (10–11) whorls, H/W ratio 2.63. The apical 2.3–2.4 whorls form the protoconch, which is smooth only on the initial 0.6–0.7 whorl and finely ribbed with closely spaced riblets further on. The protoconch is relatively small, i.e., $Dp/D4^{th}=0.36-0.46$. The shell is more or less dark horn-brown, without spots. The teleoconch whorls are ribbed with whitish ribs that are irregular in height, spacing and shape. Between these main ribs, there are fine riblets, which have the same colour as the shell. There is no difference in rib distances between the upper whorls and the body whorl. The sculpture fades on the last part of the body whorl behind the aperture. The aperture is relatively small ($Ha/H=0.20$), with an irregular lip. The lip enlarges on the columellar side before curving abruptly back and covering the umbilicus. The body whorl abruptly enlarges near the aperture, forming a moderately large external lobes.



Fig. 8. *Cochlostoma (Lovcenia) erika* (A.J. Wagner, 1906), Popova Cave near Njeguš, Pljevlja, Montenegro (HNHM 86387).

FEMALE GENITALIA. Large bursa copulatrix, with a pedunculus connected proximally; its proximal lobe smaller than the distal one. Short seminal receptacle, without distal oviduct and confined to the ventral side of the body. Loops of the visceral oviduct situated over the apex of the seminal receptacle. The junction of the uterine gland and the copulatory duct is situated far from the connection between the distal oviduct and the pedunculus of the bursa.



Fig. 9. *Cochlostoma (Lovcenia) dalmatinum* (L. Pfeiffer, 1863), Kameno, 6 km from Crkvice, Montenegro (NHMW 110430/MN/0162).

Distribution

Northwest of the bay of Kotor in Montenegro. Wagner (1897) reported this species from ‘Mont Falcone’ (= Mt Radoštak), not far from the site where we have recently collected it. As this area is poorly explored and because it is difficult to access, the species may be more widely distributed than believed earlier (see Gittenberger 1976).

Habitat preference

Unlike *C. (L.) erika*, this species is not bound to cave environments. We have found it on large limestone cliffs, mostly hidden in shady fissures.

Remarks

Due to the lack of material, Zallot *et al.* (2015) did not assign this species to any of the subgenera of *Cochlostoma*. The available anatomical and molecular data now unequivocally support its classification in *Lovcenia*.

Cochlostoma (Lovcenia) tropojanum Zallot, Fehér & Gittenberger sp. nov.

[urn:lsid:zoobank.org:act:F986C8B8-F64C-41FE-9422-5B0FF2D749FB](https://zoobank.org/urn:lsid:zoobank.org:act:F986C8B8-F64C-41FE-9422-5B0FF2D749FB)

Figs 5C, 6C, 10

Diagnosis

Rather small, with a very slender, spotless and regularly ribbed shell, which has a poorly developed lip, inclined towards the front and broadening at the columellar side, before curving back and covering the umbilicus. In *C. (L.) erika* and *C. (L.) dalmatinum*, which are both larger, the columellar lobe differs; the latter species may also be distinguished by its prominent, irregular ribs, which are more uniform in *C. (L.) tropojanum* sp. nov. *Cochlostoma (L.) lanatum* sp. nov. differs by its regularly spaced, prominent, sharp ribs on the upper whorls. The geographically separate *C. (L.) jakschae* sp. nov. is conchologically similar but less slender, with an even narrower lip. It also differs in the female genitalia, i.e., by the less convoluted visceral oviduct. Moreover, *C. (L.) jakschae* sp. nov. has, relative to its shell size, a smaller protoconch.

Material examined**Holotype**

ALBANIA: ♀ (in ethanol), Tropojë District, gorge of Lumi i Tropojës, ca 14 km N of Tropojë, 965 m a.s.l., 42.4740° N, 20.1520° E, 26 Jun. 2014, Angyal, Fehér and Grego leg. (NHMW 111638).

Paratypes

ALBANIA: 28 spec., same collection data as for holotype (NHMW 111248/8a+2ja, HNHM 99243/10a+3ja; GR/5a); 4 spec., ca 13 km N of Tropojë, 925 m a.s.l., 42.4692° N, 20.1554° E, 26 Jun. 2014, Angyal, Fehér and Grego leg. (NHMW 111247/2ja, HNHM 99241/1a+1ja).

Other material

ALBANIA: Tropojë District, gorge of Lumi i Gashit, SW of Dretovë, 390 m a.s.l., 42.4009° N, 20.0879° E, 1 Jul. 2016, Eróss, Fehér, Szekeres and Grego leg. (NHMW 111654, HNHM 99865); Tropojë District, above Tropojë, at N foot of Mt Shkëlzen, in rocky grassland, 2020 m a.s.l., 42.4632° N, 20.1258° E, 6 Jun. 2006, Barina leg. (HNHM 99871).

Measurements

Holotype: H 9.3 mm, W 3.8 mm, Wbw 3.3 mm, Ha 2.7 mm, Wa 2.7 mm.

Paratypes (N=12): H 7.7–9.3 mm, W 3.4–4.0 mm, Wbw 2.8–3.2 mm, Ha 2.2–2.8 mm, Wa 2.1–2.9 mm.

Description

SHELL. Small, with $8\frac{1}{2}$ whorls, H/W ratio 2.8. The initial 2.4–2.5 whorls form the protoconch, which is smooth for only the initial 0.3–0.5 whorl and finely ribbed with narrowly spaced riblets further on. The spotless shell is light yellowish. The teleoconch whorls are convex ($Rr=1.24$) with whitish, rounded, moderately developed ribs. The ribs are regularly spaced, without any variation between the upper whorls and the body whorl. The ribbing is still present on the final part of the body whorl, approaching the aperture. The aperture is relatively small ($Ha/H=0.19$ – 0.20), with a poorly developed lip, inclined towards the front. The lip is broadened at the columellar side before curving back and covering the umbilicus. The body whorl has a small external lobe.

FEMALE GENITALIA. Bursa copulatrix large, with a pedunculus connected proximally; its proximal lobe clearly smaller than the distal one. Short seminal receptacle, confined to the ventral side of the body and connected with the pedunculus without a distal oviduct. The 3–4 wide and small loops of the visceral oviduct are situated over the apex of the seminal receptacle. The junction of the uterine gland and the copulatory duct is moderately far from the connection between the seminal receptacle and the pedunculus of the bursa.

MALE GENITALIA. The penis is longer than the body and thin, with a tapering tip. The spermiduct is narrowly twisted. The body spermiduct is straight. There is a sharp and long groove, ending in a well-formed sperm pocket, delimited on the frontal side by an ascending sperm funnel.

Etymology

This species is named after the Tropojë Valley, its type locality.



Fig. 10. *Cochlostoma (Lovcenia) tropojanum* Zallot, Fehér & Gittenberger sp. nov., holotype, Tropojë Valley, Albania (NHMW 111638).

Distribution

Mount Shkëlzen in the eastern part of the Prokletije Mts in NE Albania. Known from four nearby locations.

Habitat preference

Like most species of *Cochlostoma*, these are obligate rock-dwelling snails that can be found on the surface of limestone cliffs or under boulders on rocky alpine grasslands.

Cochlostoma (Lovcenia) jakschae Zallot, Fehér & Gittenberger sp. nov.

[urn:lsid:zoobank.org:act:BBA8F11F-4FAD-4049-A685-1C2CBF95B5E2](https://zoobank.org/act:BBA8F11F-4FAD-4049-A685-1C2CBF95B5E2)

Figs 5D, 6D1–D2, 11

Diagnosis

The smallest species of *Cochlostoma (Lovcenia)*, differing from both *C. (L.) dalmatinum* and *C. (L.) lanatum* sp. nov. by the more regular, narrowly spaced, rather prominent ribs. The apertural lip is narrower and less conspicuously curved at the columellar side than in the consubgeneric species. The conchologically most similar species, *C. (L.) tropojanum* sp. nov., differs by its relatively larger protoconch and, in the female genitalia, by the less conspicuously convoluted visceral oviduct.

Material examined

Holotype

MACEDONIA: ♀ (in ethanol), Ohrid District, Galičica Mts., Bugarska Peak, E side, 1795 m a.s.l., 41.0037° N, 20.8470° E, 16 Oct. 2014, Fehér, Haring, Jaksch and Sattmann leg. (NHMW 111649).

Paratypes

MACEDONIA: 9 spec., same collection data as for holotype (NHMW 111651/4+4a+1ja); 4 spec., ca 200 m N of Bugarska Peak, 1795 m a.s.l., 41.0051° N, 20.8462° E, 16 Oct. 2014, Fehér, Haring, Jaksch and Sattmann leg. (NHMW 111249/2a+2ja); 1 spec., ca 300 m W of Bugarska Peak, 1735 m a.s.l., 41.0046° N, 20.8432° E, 16 Oct. 2014, Fehér, Haring, Jaksch and Sattmann leg. (NHMW 111650).

Other material

ALBANIA: Shkodër District, Qafa e Pejës, N of Okol, 1700 m, 42.4332° N, 19.7671° E, 6 Jul. 2003, Eröss, Fehér, Kontschán and Murányi leg. (HNHM 97221); path from Qafa e Pejës to Maja e Harapit, 1800 m a.s.l., 42.4431° N, 19.7637° E, 1 Jun. 2005, Barina, Murányi, Pifkó leg. (HNHM 94927).

Measurements

Holotype: H 7.3 mm, W 3.4 mm, Wbw 2.8 mm, Ha 2.4 mm, Wa 2.3 mm.

Paratypes (N=10): H 6.7–7.7 mm, W 3.2–3.6 mm, Wbw 2.7–3.0 mm, Ha 2.1–2.6 mm, Wa 1.9–2.5 mm.

Description

SHELL. Small, with 7½–8½ whorls (H/W ratio 2.42–2.57). The initial 2.4 whorls form the protoconch, which is smooth for the first 0.5–0.7 whorl and then finely costulate with closely spaced riblets. The protoconch is relatively large ($Dp/D4^{th}=0.73$). The shell is more or less dark horn-brown, without spots. The teleoconch whorls are costate, with whitish, slightly irregular in height, rounded ribs. The ribs are quite regularly and narrowly spaced, with 9–10 ribs per mm both on the 4th whorl and on most of the body whorl. The ribbing is less prominent and denser on the last part of the body whorl approaching the aperture. The peristome is moderately developed; the lip broadens at the columellar side before curving

increasingly back and covering the umbilicus. While approaching the aperture, the body whorl enlarges, while forming a moderately developed external lobe.

FEMALE GENITALIA. Bursa copulatrix very large, with a more or less posterior connection of the pedunculus. The short seminal receptacle is confined to the ventral side of the body. The tortuous loops of the visceral oviduct are situated over the apex of the seminal receptacle. The junction of the uterine gland and the copulatory duct is moderately far from the connection between the distal oviduct and the pedunculus.

Etymology

This species is named after Ms Katharina Jaksch-Mason (NHMW) who found the first individual of this species at Bugarska Peak.

Distribution

This species is known from two mountain ranges that are nearly 200 km apart, i.e., the Galičica Mts in southwestern Macedonia, Ohrid District, and the Prokletije (= Bjeshkët e Nemuna) Mts in northern Albania. It occurs at altitudes above 1700 m. The former area is the southernmost occurrence known for the subgenus *Lovcenia*.

Habitat preference

Like most species of *Cochlostoma*, this is an obligate rock-dwelling snail that can be found on limestone cliffs or under boulders on rocky alpine grasslands.

Remarks

The molecular analyses confirm that the morphologically similar but geographically distant populations of the Bugarska Peak and the Pejë Pass are indeed conspecific.



Fig. 11. *Cochlostoma (Lovcenia) jakschae* Zallot, Fehér & Gittenberger sp. nov., holotype, Bugarska Peak, Macedonia (NHMW 111649).

Cochlostoma (Lovcenia) lanatum Zallot, Fehér & Gittenberger sp. nov.
[urn:lsid:zoobank.org:act:E615F65C-B3DC-4978-883C-4D10A06606E6](https://zoobank.org/urn:lsid:zoobank.org:act:E615F65C-B3DC-4978-883C-4D10A06606E6)

Figs 5E, 6E, 12

Cochlostoma (Lovcenia) sp. – Zallot *et al.* 2015: 80.

Diagnosis

Shell without spots or color bands, relatively large and slender, with sharp, regularly spaced ribs on the upper whorls; ribs less sharp and more narrowly spaced on the lower whorls.

Material examined

Holotype

ALBANIA: ♀, Malësia District, SW slope of Mali e Veleçikut, Shpellë e Deleve, NW of Razëm, 1300 m a.s.l., limestone rock within cave, 42.3576° N, 19.5269° E, 28 Jun. 2016, Eröss, Fehér, Szekeres and Grego leg. (HNHM 102806).

Paratypes

ALBANIA: 129 spec., same collection data as for holotype (NHMW 111652/7+ 12fr.+19a+ 6 ja; GR/38+2fr; HNHM 99861/6+13fr.+ 26a); 1 ♂, same locality as holotype, 16 Oct. 2011, Gittenberger leg.

Measurements

Holotype: H 10.5 mm, W 4.6 mm, Wbw 3.8 mm, Ha 3.4 mm, Wa 3.1 mm.

Paratypes (N=12): H 8.4–9.5 mm, W 3.9–4.4 mm, Wbw 3.2–3.5 mm, Ha 2.7–3.1 mm, Wa 2.5–3.2 mm.



Fig. 12. *Cochlostoma (Lovcenia) lanatum* Zallot, Fehér & Gittenberger sp. nov., holotype, Deleve Cave, Albania (HNHM 102806).

Description

SHELL. Rather large and slender, with $8\frac{1}{2}$ – $9\frac{1}{4}$ whorls (H/W ratio 2.84). The apical 2.2 whorls form the protoconch, which is smooth for only the initial 0.2 whorl and finely ribbed with close riblets further on. The shell is more or less light horn-brown, without spots. The teleoconch is sculptured with rather prominent, sharp ribs, which are widely spaced on the upper whorls and increasingly more narrowly spaced and less sharp towards the aperture. The aperture has a moderately developed lip, enlarged at the columellar lobe, which is abruptly bent inwards to cover the umbilicus. While approaching the aperture, the body whorl abruptly enlarges, forming a rather prominent external lobe.

FEMALE GENITALIA. Bursa copulatrix large, with a pedunculus connected proximally; its proximal lobe smaller than the distal one. The short seminal receptacle is confined to the ventral side of the body, under (ventrally) the bursa copulatrix. The loops of the visceral oviduct are situated over the apex of the seminal receptacle. The junction of the uterine gland and the copulatory duct is far away from the connection between the pedunculus of the bursa and the distal oviduct.

Distribution

This species is only known from its type locality, the Deleve Cave on the southwestern slope of Mount Veleçik in northern Albania.

Habitat preference

Like the majority of known species of *Cochlostoma*, this is an obligate rock-dwelling snail. It was found in the twilight zone inside the Deleve Cave. Though little is known about its ecological requirements, it may be restricted to the epigeal environment, like *C. (L.) erika* (i.e., subtroglophile in the sense of Sket 2008). At the Deleve Cave, its niche partitioning with *Cochlostoma (Auritus) roseoli* (A.J. Wagner, 1901) is similar to that of *C. (L.) erika* and *C. (A.) auritum* at the Popovo Cave in Montenegro.

Remarks

Zallot *et al.* (2015) assigned this species to *Cochlostoma (Lovcenia)*, but with only one male specimen available, its systematic status remained difficult to judge. The shell morphology, in particular the protoconch sculpture, showed affinity to that of *C. erika*, whereas the molecular data suggested a status as a separate species. Since then, we have been able to collect and dissect female specimens. The structure of the female genitalia supports regarding it as a species on its own.

Discussion

As far as is known, the range of the subgenus *Lovcenia* extends from the Orjen Mts and the Njeguš Plateau (Montenegro) in the northwest to the Galičica Mts (Macedonia) in the south, with the central area of distribution in the Prokletije Mts.

Cochlostoma (Lovcenia) erika and *C. (L.) lanatum* sp. nov. are the only subtroglophile species known in the Cochlostomatidae. According to the trees based on concatenated *COI*, *16S* and *H3* sequences, these two taxa are not sister species, but relatively low supports of some branches indicate that relationships among the taxa of *Lovcenia* are not clarified beyond any doubt. Therefore, it seems feasible that the subtroglophile lifestyle evolved only once in this subgenus and was lost secondarily, but it is difficult to say whether the ancestral form of *Lovcenia* was already a subtroglophile species or not. *Cochlostoma (L.) erika* and *C. (L.) lanatum* sp. nov. occur syntopically with other large cochlostomatid species, namely *C. (A.) auritus* and *C. (A.) roseoli*. Snails of small species of *Cochlostoma* (e.g., of the subgenera *Wagneriola* Zallot *et al.*, 2015 or *Turritus* Westerlund, 1883) and snails of large congeneric species often co-occur, but only very rarely are two large-sized species found syntopically.

Acknowledgements

The authors are grateful to Dorottya Angyal, Tamás Deli, Michael Duda, Zoltán Eröss, Jozef and Maroš Grego, Elisabeth Haring, Katharina Jaksch-Mason, Dávid Murányi, Jenő Kontschán, Helmut Sattmann and Miklós Szekeres, who assisted during multiple field trips to the Balkans, and to Christoph Leeb for his help with the laboratory work.

This study was partly supported by the Austrian Research Fund (grant no. FWF P 26581- B25).

References

- Anisimova M., Gil M., Dufayard J.-F., Dessimoz C. & Gascuel O. 2011. Survey of branch support methods demonstrates accuracy, power, and robustness of fast likelihood-based approximation schemes. *Systematic Biology* 60: 685–699. <https://doi.org/10.1093/sysbio/syr041>
- Bank R.A. 1988. Revision der nordostitalienischen Arten und Unterarten der Gattung *Cochlostoma* Jan, 1830 (Gastropoda Prosobranchia: Cyclophoridae). *Basteria* 52 (4/6): 151–170.
- Colgan D.J., Ponder W.F. & Egglar P.E. 2000. Gastropod evolutionary rates and phylogenetic relationships assessed using partial 28S rRNA and histone H3 sequences. *Zoologica Scripta* 29: 29–63. <https://doi.org/10.1046/j.1463-6409.2000.00021.x>
- Duda M., Sattmann H., Haring E., Bartel D., Winkler H., Harl J. & Kruckenhauser L. 2011. Genetic differentiation and shell morphology of *Trochulus oreinos* (Wagner, 1915) and *Trochulus hispidus* (Linnaeus, 1758) (Pulmonata: Hygromiidae) in the northeastern Alps. *Journal of Molluscan Studies* 77: 30–40. <https://doi.org/10.1093/mollus/eyq037>
- Fehér Z. 2004. A revision of the genus *Cochlostoma*, subgenus *Titanopoma* (Gastropoda, Caenogastropoda, Cochlostomatidae), in particular the forms occurring in Albania. *Basteria* 68: 25–44.
- Fehér Z., Eröss Z. & Varga A. 2001. Contributions to the knowledge of the Albanian *Cochlostoma* fauna (Gastropoda: Cyclophoridae). *Schriften zur Malakozoologie* 17: 71–78.
- Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- Gittenberger E. 1976. Vier wenig bekannte troglophile Schneckenarten aus Montenegro. *Zoologische Mededelingen* 49 (21): 273–283.
- Hall T.A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Harl J., Páll-Gergely B., Kirchner S., Sattmann H., Duda M., Kruckenhauser L. & Haring E. 2014. Phylogeography of the land snail genus *Orcula* (Orculidae, Stylommatophora) with emphasis on the Eastern Alpine taxa: speciation, hybridization and morphological variation. *BMC Evolutionary Biology* 14: e223. <https://doi.org/10.1186/s12862-014-0223-y>
- Hoang D.T., Chernomor O., Haeseler A. von, Minh B.Q. & Vinh L.S. 2017. UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35: 518–522. <https://doi.org/10.1093/molbev/msx281>
- Jaekel S.G., Klemm W. & Meise W. 1957. Die Land- und Süßwasser-Mollusken der nördlichen Balkanhalbinsel. *Abhandlungen und Berichte aus dem Staatlichen Museum für Tierkunde in Dresden* 23: 141–205.

- Kalyaanamoorthy S., Quang Minh B., Wong T.K.F., Haeseler A. von & Jermiin L.S. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589. <https://doi.org/10.1038/nmeth.4285>
- Katoh K. & Standley D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kobelt W. 1902. Mollusca. Cyclophoridae. *Das Tierreich* 16: 1–663.
- Kobelt W. 1907. *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten von E. A. Rossmässler; Neue Folge* 13 (1–2): 1–68. Kreidel, Wiesbaden. Available from <https://biodiversitylibrary.org/page/16302427> [accessed 8 Aug. 2018].
- Nguyen L.-T., Schmidt H.A., Haeseler A. von & Minh B.Q. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. <https://doi.org/10.1093/molbev/msu300>
- Páll-Gergely B., Fehér Z., Hunyadi A. & Asami T. 2015. Revision of the genus *Pseudopomatias* and its relatives (Gastropoda: Cyclophoroidea: Pupinidae). *Zootaxa* 3937 (1): 1–49. <https://doi.org/10.11646/zootaxa.3937.1.1>
- Palumbi S.R. 1996. PCR and molecular systematics. In: Hillis D., Moritz C. & Mable B. (eds) *Molecular Systematics*: 205–248. 2nd edition. Sinauer Press, Sunderland.
- Pfeiffer L. 1863. Beschreibung eines neuen *Pomatias*. *Malakozoologische Blätter* 10: 136–137.
- Rambaut A., Suchard M.A., Xie D. & Drummond A.J. 2014. Tracer ver. 1.6. Available from <http://beast.bio.ed.ac.uk/Tracer> [accessed 8 Aug. 2018].
- Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. 2012. MRBAYES 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Sket B. 2008. Can we agree on an ecological classification of subterranean animals? *Journal of Natural History* 42 (21–22): 1549–1563. <https://doi.org/10.1080/00222930801995762>
- Schütt H. 1977. Revision der griechischen *Cochlostoma*. *Archiv für Molluskenkunde* 108 (1–3): 17–35.
- Tamura K., Stecher G., Peterson D., Filipowski A. & Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. <https://doi.org/10.1093/molbev/mst197>
- Thomsen P.F., Elias S., Gilbert M.T.P., Haile J., Munch K., Kuzmina S., Froese D.G., Sher A., Holdaway R.N. & Willerslev E. 2009. Non-destructive sampling of ancient insect DNA. *PLoS ONE* 4 (4): e5048. <https://doi.org/10.1371/journal.pone.0005048>
- Trifinopoulos J., Nguyen L.T., Haeseler A. von & Minh B.Q. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44 (W1): W232–W235. <https://doi.org/10.1093/nar/gkw256>
- Uit de Weerd D.R. & Gittenberger E. 2013. Phylogeny of the land snail family Clausiliidae (Gastropoda: Pulmonata). *Molecular Phylogenetics and Evolution* 67: 201–216. <https://doi.org/10.1016/j.ympev.2013.01.011>
- Wagner A.J. 1897. Monographie der Gattung *Pomatias* Studer. *Denkschriften der kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe* 64: 565–632.

Wagner A.J. 1906. Neue Formen und Fundorte der Genera *Pomatias* Studer und *Auritus* Westerlund. *Nachrichtsblatt der deutschen malakozoologischen Gesellschaft* 38 (2–3): 92–101, 121–140. Available from <https://biodiversitylibrary.org/page/15599307> [accessed 8 Aug. 2018].

Walderdorff R. 1864. Systematisches Verzeichniss der im Kreise Cattaro (Süd-Dalmatien) mit Ausnahme der Biela-Gora und in einigen angrenzenden Theilen von Montenegro und türkisch Albanien vorkommenden Land- und Süsswasser-Mollusken. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien* 14: 503–514.

Welter-Schultes F.W. 2012. *European Non-Marine Molluscs, a Guide for Species Identification: A1–A3, 1–679, Q1–Q78*. Planet Poster Editions, Göttingen, Germany.

Zallot E. 2002. Alcune note sul genere *Cochlostoma* Jan, 1830 (Gastropoda, Prosobranchia) in Friuli (Italia nord-orientale). *Gortania* 24: 93–113.

Zallot E., Groenenberg D.S.J., De Mattia W., Fehér Z. & Gittenberger E. 2015. Genera, subgenera and species of the Cochlostomatidae (Gastropoda, Caenogastropoda, Cochlostomatidae). *Basteria* 78 (4–6): 63–88.

Zilch A. 1958. Die Typen und Typoide des Natur-Museums Senckenberg, 21: Mollusca, Cyclophoridae, Craspedopominae-Cochlostominae. *Archiv für Molluskenkunde* 87 (1/3): 53–76.

Manuscript received: 28 March 2018

Manuscript accepted: 16 July 2018

Published on: 2 October 2018

Topic editor: Rudy Jocqué

Section editor: Kurt Jordaens

Desk editor: Danny Eibye-Jacobsen

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum national d’Histoire naturelle, Paris, France; Botanic Garden Meise, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Natural History Museum, London, United Kingdom; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Real Jardín Botánico de Madrid CSIC, Spain; Zoological Research Museum Alexander Koenig, Bonn, Germany.