



# An integrative approach to the taxonomy and systematics within the genus *Montenegrina* Boettger, 1877 (Mollusca, Gastropoda, Clausiliidae)

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## Abstract

The taxonomy and systematics of the door snail genus *Montenegrina* are revised based on an integrative approach including, for the first time, a comprehensive genital-anatomical investigation, which is combined with shell morphology and DNA sequence data. The reference molecular genetic data were published in Mason et al. (*Journal of Zoological Systematics and Evolutionary Research*, 58, 662–690, 2020). Besides, the well-visible external features of the genitalia, the inner sculpturing of their main anatomical parts is also carefully investigated. This represents an entirely new approach to the family. The genital morphology of 259 specimens of 88 taxa from 116 populations was investigated, and a new general description of the genital morphology of the genus is provided. The genus *Montenegrina* revealed an astonishing variability in genital morphology. The most variable parts of the genitalia are the inner sculpturing of the penis, the shape, and dimension of the penial papilla and the inner sculpturing of the distal vagina and atrium. Accordingly, out of 106 taxa accepted by the latest revision, 35 subspecific taxa were raised to the status of valid species (stat. nov.), 19 subspecific taxa were moved to a different species (comb. nov.), two new species and two new subspecies were described (*M. atanasiensis* n. sp., *M. globocica* n. sp., *M. radikae paparistoe* n. ssp., and *M. tenebrosa szekeresi* n. ssp.), and the status of 51 taxa remained unchanged. This study shows that the morphological characters (of both shell and genitalia) are essential for alpha-taxonomy. Nonetheless, several traits apparently appear randomly throughout the range of taxa, making their contribution to the phylogenetic reconstruction very limited.

## KEYWORDS

anatomy, Clausiliidae, *Montenegrina*, phylogeny, systematics, taxonomy

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## 1 | INTRODUCTION

### 1.1 | General statements on genital anatomy in clausiliids

Clausiliidae is a family of pulmonate land snails (Stylommatophora) with spindle-shaped and, in most cases, sinistrally coiled shells with interior folds and lamellae inside the ultimate whorl, which are developed as a closing apparatus. This is the so-called clausilial apparatus (Nordsieck, 2007). Clausiliidae are mainly distributed in Europe, East Asia, and South America. The presence of a clausilial apparatus is strong evidence for the monophyly of the Clausiliidae, which is confirmed by molecular genetic studies (Uit de Weerd & Gittenberger, 2013; Van Moorsel, 2001; Wade, Mordan, & Clarcke, 2001; Wade, Mordan, & Naggs, 2006). The family Clausiliidae is subdivided in nine subfamilies (Uit de Weerd & Gittenberger, 2013). In the Central and Eastern Mediterranean and adjacent fringes of Asia and Africa, the most speciose subfamily is Alopiinae (Nordsieck, 2007).

The systematics of species within Alopiinae clausiliids is almost exclusively based on shell features, even if certain differences in the genital apparatus have been used to define subfamilies, genera and partially also subgenera (Nordsieck, 1969b; Szekeres, 1969). Nonetheless, the intrageneric systematics in many genera are far from clear, despite comprehensive taxonomic literature.

Due to their morphological complexity, the clausiliids contain a large number of described species and subspecies (Páll-Gergely, Asami, & Sólymos, 2019). As clausiliid taxonomy is primarily based on shell characters, this should be tested by other approaches to arrive at a clearer picture. Molecular phylogeny reconstructions were done for some genera or groups of genera, and these studies produced some unexpected results and/or pointed at weak points of the shell-morphology-based system (Fehér, Németh, Nicoară, & Szekeres, 2013; Koch, Neiber, Walther, & Hausdorf, 2017; Kornilios, Stamatakis, & Giokas, 2015; Páll-Gergely, Fehér, Asami, & Harl, 2019; Uit de Weerd & Gittenberger, 2004, 2005). Hartmut Nordsieck devoted almost his entire scientific activity to Clausiliidae and unsurprisingly produced most of the Alopiinae taxonomic literature (among others: Nordsieck, 1963a, 1963b, 1969a, 1969b, 1970, 1972, 1974, 1997, 2002, 2007, 2008, 2011, 2012).

So far, the morphology of genitalia was considered of minor importance at specific/subspecific level. Moreover, the available genital investigations are limited to the external features of the genitalia and only rarely depict inner structures as the penial papilla. All the remaining structures (folds, pleats, diverticula, complex structures) were never considered for taxonomical purposes. The remarkable lack in the literature of genital data at the generic/specific level in Alopiinae (and Clausiliidae in general) opens the door for comparative genital morphology to play an important role as a complementary tool in morphology and in combination with molecular genetic analyses.

Importantly, genital morphology (external and inner features) is a taxonomic corner stone for most other western Palearctic

Stylommatophora families (e.g., Zonitidae, Hygromiidae, Vitrinidae, Limacidae, Milacidae, Agriolimacidae) and most Caenogastropoda (e.g., Hydrobiidae, Megalomastomatidae) (Bouchet et al., 2017). Note also that in another speciose pulmonate family, namely Pristilomatidae, the same situation is found as in Clausiliidae: exclusively shell-based taxonomy with hundreds of taxa whose validity remains to be assessed. Shell-character-based taxonomy has clearly showed clear limitations in land snail systematics, as abundantly illustrated by Giusti and Manganello (1992).

Alopiinae and clausiliids in general show great phenotypic variability in their shell dimensions and features. Differences in shell morphology might correlate with macro- or microgeographic and/or microclimatic variations of the habitat and thus show phenotypic variation. This extreme variability could also reflect the extremely low mobility and habitat specificity of rock-dwelling clausiliids. The result could be isolation and thus restricted gene flow between populations. This is one explanation for the tremendous richness of taxa. Among western Palearctic land snails, Clausiliidae currently present the highest number of taxa when considering subspecific ranking. Alopiinae, for example, consist of 22 genera, 31 subgenera, and 866 currently valid species/subspecies (Bank, 2013).

### 1.2 | Historical review of anatomical investigations on the genus *Montenegrina*

Information about the nomenclatural history and distribution of the genus *Montenegrina* is provided in Fehér and Szekeres (2016: 13 and following). To date, very few data and drawings concerning the genital anatomy have been published. Even if so, the morphology of the genitalia was depicted merely as "extra" information, considered as not essential for any (alpha)taxonomic purpose. Using genital morphological traits, Wagner (1924) was the first to unite all *Montenegrina* species known at that time within one subgenus, *Delima* (*Albanodelima*) Wagner, 1924. His first attempt to broadly describe the anatomy of *Delima* s.l. dates even earlier (1919: 131). He highlighted and summarized the main peculiarities of the genitalia as follows: "the penis at the transition into the epiphallus is swollen or thickened like an onion. It never possesses a (penial) diverticulum. The retractor muscle is strong. The diverticulum of the spermatheca (=bursa copulatrix) is longer but thinner than the duct itself, this latter connected with the general retractor muscle system". Later, in the same paper (1919: 184), he briefly focused on *Montenegrina cataroensis*, stating that this species differs from the others by virtue of a longer and thinner diverticulum of the bursa copulatrix.

The first drawing of the distal genitalia of a species belonging to the genus *Montenegrina* is found in Soós (1924: 182, fig. 3). Soós depicted the external distal genitalia of *Montenegrina skipetarica skipetarica* (Soós, 1924, fig. 1.1). The drawing is a simple sketch in which the genitalia are not properly displayed in order to depict all the external anatomical features. The whole length of the penial complex (PC) (=penis + epiphallus) is not visible, the junction of the retractor muscle and the penis is unclear, as is the penis-atrrium transition.

Moreover, the insertion of the free oviduct into the first duct of the complex of the bursa copulatrix and vagina is also unclear. The inner structure of the distal genitalia is not mentioned at all. Nonetheless, some interesting features are clearly visible, namely the very short free oviduct, the length of the vagina, and the diverticulum of the bursa copulatrix, the latter being shorter than the bursa itself.

Wagner (1925) depicted the external genitalia of two species of *Montenegrina*, namely *Montenegrina apfelbecki* (Sturany, 1907) and *Montenegrina subcristata* (Pfeiffer, 1848). The latter was depicted from two localities representing at that time the taxa *Delima* (*Albanodelima*) *subcristata* and *Delima* (*Albanodelima*) *kleciaki* (both currently = *Montenegrina subcristata*). The whole PC length and the vaginal retractor muscle are clearly visible (Figures 1.2 and 1.3).

Klemm (1962: 242–244) described *Montenegrina* (*Beieriella*) *irmengardis* (= *Montenegrina rugilabris irmengardis* Klemm, 1962) and provided a sketch of the distal genitalia. The drawing presents a few key errors because the epiphallus seems to directly merge into the distal penis and the vas deferens seems to merge into the middle part of the vagina. Moreover, the remarkable length of the first duct of the bursa copulatrix and the free oviduct seem to be artefacts (fig. 1.4). *Beieriella* Klemm, 1962 is now considered as a junior synonym of *Montenegrina* (Fehér & Szekeres, 2016: 12; Nordsieck, 1972).

Nordsieck (1969a: 259) provided a description of the genitalia of *Montenegrina* based on four dissections of four species, *M. cataroensis*, *M. umbilicata*, *M. subcristata*, and *M. stankovici*, but did not depict their genitalia. The comments and the description given by Nordsieck are as follows: "Canalis serosus relatively strong; Diverticulum as long or only a little bit longer than Bursa + Blasenhal; Blasenstiel shorter than Vagina, RRS (Retractor Receptaculi-seminis) muscular, connected to the distal vagina end by a high number of fibers; penial papilla short, shorter than half of the penis, more or less perforated, penis retractor with one arm". According to Nordsieck (1969a) *Montenegrina* differs from *Delima* by the short diverticulum and the long vagina, which connects with its distal end to the RRS. He considered *Beieriella* and *Strigilodelima* as next relatives to *Montenegrina*. According to Klemm's text and figures (1962), *Beieriella* was very similar to *Montenegrina*. Following the drawings provided by Wagner (1925), the group *Strigilodelima* shares with *Montenegrina* the length of the diverticulum but differs from it by its short vagina (Blasenstiel longer than vagina). More investigations are needed to check the generic separation of *Strigilodelima* and *Montenegrina*. These descriptions dealt mainly with the external features of the genitalia, whereby only the penial papilla was briefly considered. The anatomical differences between *Montenegrina* and *Strigilodelima* are discussed later in this paper.



Abb. 2. Genitalorgan von *Montenegrina* (*Beieriella*) *irmengardis* nov. spec. Platanusa im Epirus.

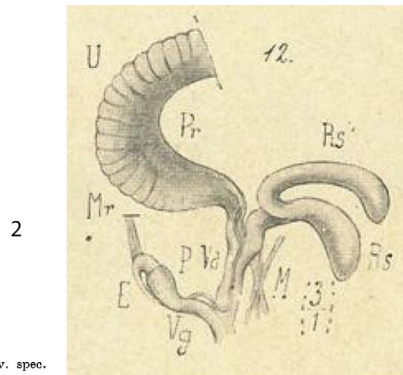


Fig. 23 [№ 366] *Delima* (*Albanodelima*) *subcristata* K. von Cetinje; Sexualorgane.

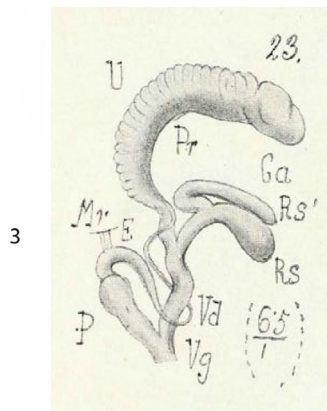


Fig. 12 [№ 377] *Delima* (*Albanodelima*) *apfelbecki* A. J. Wagner vom Mali Senjt (Mali-Sheit) bei Oroshi; Sexualorgane.

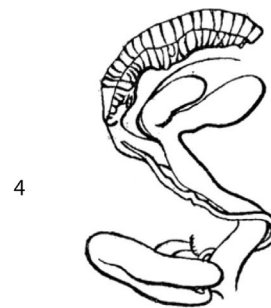


Fig. 3. Genital organs of *Cl.* (*Delima*) *skipetarica* n. sp.

**FIGURE 1** 1.1 External genitalia of *Montenegrina rugilabris irmengardis* Klemm, 1962 as depicted in Klemm (1962: 242–244). 1.2 External genitalia of *Montenegrina subcristata* (Pfeiffer, 1848) as depicted in Wagner (1925). 1.3 External genitalia of *Montenegrina apfelbecki* (Sturany, 1907). 1.4 External distal genitalia of *Montenegrina skipetarica skipetarica* (Soós, 1924) as depicted in Soós (1924: 182, fig. 3)

Nordsieck (1972: 26–27) described new *Montenegrina* taxa based exclusively on shell features, in particular the morphology of the clausiliar apparatus. Nevertheless, he focused on the general genital features of *Montenegrina* for the second time, providing a more detailed description for the genus: “The exact investigation of the genital system of several species confirmed Brandt’s idea and showed that *Montenegrina* is not closely related to *Delima*. The diagnosis from part VI (1969a: 259, additionally investigated: *rugilabris* Mousson [preparation 310]) can be improved as follows: albumen gland (AG) distally not surmounting the rectal loop; Canalis serosus strong, but becoming rapidly narrower distally; diverticulum longer than Bursa + Blasenhal, or of the same length; Blasenstiel much shorter than the long vagina; RRS muscular and inserting at the distal end of vagina; penis shorter than vagina, with a short,  $\pm$  perforated penial papilla (less than half length of the penis); epiphallus longer than penis, proximal section mostly as long as or longer than distal section, retractor penis simple”.

Recently, Nordsieck (2009) treated the whole genus with new notes on *Montenegrina*-specific systematics. He provided a third general description of the genitalia based on dissections of three additional taxa: *M. janinensis*, *M. rugilabris rugilabris*, and *M. irmengardis* (= *M. rugilabris irmengardis*) (2009: 73): “Diverticulum of bursa copulatrix longer than or equally long as bursa and proximal pedunculus; distal pedunculus shorter than the vagina, the latter long; vaginal retractor present, inserted on proximal vagina end or transition pedunculus-vagina, respectively; atrium and distal vagina end broadened; penis shorter than vagina; penial papilla short, pierced, to nearly missing; epiphallus longer than penis, proximal part mostly shorter than or equally long as distal part; penial retractor not divided”. He also stated that, “the genital organs of the different species are very similar; especially the length relations of the copulatory organs do not much differ”.

Páll-Gergely (2010) described a new subspecies, *M. dofleini sinosi*, from northwestern Greece. He briefly described the external genitalia (2010: 152) but without providing any iconography. His description fully matches those of Nordsieck (1969a, 1972, 2009), without adding any new data.

In summary, the genital morphology of the genus *Montenegrina* is known solely based on five drawings that exclusively depict the external features and on the descriptions mainly provided by Nordsieck (2009), in part by Wagner (1919, 1924, 1925) and Páll-Gergely (2010). These descriptions were based on dissections of eight specimens belonging to eight taxa. Currently, the genus *Montenegrina* has 106 valid taxa (Fehér & Szekeres, 2016). Accordingly, the published data on anatomical morphology must be considered as incomplete and probably not representative for the whole genus.

### 1.3 | Aims of the study

The present study analyzed the genital morphology in the genus *Montenegrina* Boettger, 1877 based on a comprehensive sample. This investigation includes not only the well-visible external features

of the genitalia (mainly shape and proportions among parts), but also the inner sculpturing of the main anatomical parts (atrium, PC, penial papilla, epiphallus, vagina, free oviduct, and complex of bursa copulatrix) known to be of fundamental importance in other groups (Giusti & Manganelli, 1992). This extensive study (by number of taxa, specimens, and populations) goes beyond the classic morphological approach by encompassing both “classic” genital morphological features (overall genitalia shape, ratio among the parts, shape of penial papilla) and new features never before taken into taxonomic consideration. This is a challenging step due to the time-consuming dissecting procedures.

As an integrative approach in clausiliid taxonomy, this comprehensive investigation of the genital morphology of *Montenegrina* is interpreted in the light of the current system based on shell morphology (Fehér & Szekeres, 2016) and a recent phylogenetic analysis (Mason et al., 2020). The latter study comprises almost all *Montenegrina* species and subspecies and was based mainly on mitochondrial (mt) marker sequences. The overall topology of the DNA-based tree was already introduced by Fehér et al. (2018). Mason et al. (2020) analyzed the clades and subclades in detail and, for most taxa, a representative sample was examined. That contribution, however, drew no taxonomic conclusions, leaving this task to the present study. Thus, we, here, combine the results of Mason et al. (2020) with anatomical and shell-morphological characters, yielding a revised taxonomy of the genus based on this integrative approach.

## 2 | MATERIALS AND METHODS

### 2.1 | Material

The study of *Montenegrina* was conducted with material available at the Hungarian Natural History Museum, Budapest (HNHM) and the Naturhistorisches Museum Wien, Vienna (NHMW), and partly using private collections.

According to the latest revision of Fehér and Szekeres (2016), *Montenegrina* comprises 29 species and, together with subspecies, 106 taxa are considered as valid. The present study investigates the genital morphology of 259 specimens from 116 populations belonging to 88 taxa (83%). Where possible, paratypes or topotypical specimens were dissected. The taxa had been identified based on their shell characters following the recent revision of Fehér and Szekeres (2016).

The anatomically investigated specimens are listed, for each taxon, in the section “Examined material” together with details of locality, inventory number of museum collections (e.g., HNHM 99520). Many, but not all of these specimens were also analyzed genetically. Such specimens are individually named by an acronym that includes the taxon’s initials, a number that identifies the locality, and a number that identifies the single specimen (e.g., Mjk-425-01). These same acronyms were also used in the phylogenetic investigation (and the trees) presented by Mason et al. (2020).

## 2.2 | Anatomical analysis

For each population at least two specimens were dissected in order to substantially reduce the possibility of being misled by abnormalities or single freak specimens (Nordsieck, 2007). The shells of all specimens dissected (except for a few taxa) were photographed in front and back view with a Canon EOS camera equipped with 60 mm macro lenses mounted on a Kaiser microslide frame for multi-image stacking. Maximum shell height (H) was measured with a digital caliper (accuracy  $\pm 0.05$  mm).

Dissections and anatomical examinations were performed under a Zeiss stereoscope with a ring LED illumination apparatus, connected to a digital, high-resolution camera and a camera lucida. The genitalia were separated from the rest of the body, usually after a controlled and careful crushing of the shell. Dissections were made using a pair of very fine and pointed microtweezers (Dumostar Biology 55) and a microscissor (FST 150000, Aesculap OC series) in a Petri dish with black paraffin on the bottom and filled with 70% ethanol. The genitalia were fixed with very fine steel micropins (commonly used for the preparation of microlepidopteran specimens in entomology). Inner features of the genitalia (based on cross and longitudinal sections) were examined after dissection with microtweezers or a pair of microscissors. Measurements were taken using a millimetric measurement scale. All genitalia were photographed in different positions (40–50 high-resolution images depicting all relevant anatomical features) to create an image database. Drawings were prepared by accurately tracing the most representative digital images after contrast enhancement with picture editing software. The drawings of the genitalia and other anatomical features (spermatophore) were preferred over digital photos (Figure 2) because photos usually suboptimally depict finer anatomical/morphological details of the soft tissues (small, fine pleats, striae, folds, papillae, sculpturing, and diverticula).

Whenever possible, specimens used for the molecular genetic investigations (Mason et al., 2020) were dissected. This yielded shell, genitalia, and phylogenetic information for a large number of

specimens. The molecular genetic analysis included 80% of the dissected specimens.

Measurements of anatomical features (e.g., length of penis, vagina, complex of the bursa copulatrix) were taken using image editing software directly on the high-resolution photographs. The anatomical nomenclature partially follows Nordsieck (1969a, 1972, 2009) and Giusti, Manganelli, and Schembri (1995). The anatomical partition and acronyms are depicted in Figure 3. Gonads, AGs, the first hermaphroditic duct and most of the spermoviduct are neither described and nor depicted in the drawings. The vaginal retractor muscle was found in the same position in all the investigated specimens: thus, in order to render the anatomical drawings clearer and focus on key taxonomic features, it is not depicted.

In order to provide a better impression of the relative dimensions of the genital apparatus, we calculated two metrics that compare the length of the PC and the vagina to the shell height, as follows:

$$\text{PCRL} = (P + E / H_s) 100$$

$$\text{VRL} = (V / H_s) 100$$

The measurements of different genital parts were converted into relative values (ratios). All the ratios are based on average measures of at least two specimens.

The lengths of the free oviduct (FO), the actual bursa copulatrix + second duct of the bursa (BC + SDBC = DB), and diverticulum of the bursa copulatrix (D) are compared to the length of the vagina (V). The length of first duct of the bursa copulatrix (DBC) is compared with the DB. The ratios values are categorized in Table 1.

## 2.3 | Anatomical nomenclature

The proximal/distal indications refer as seen from the gonads. The subdivision of the genital apparatus in anatomical parts follows Nordsieck (1969a: 249, fig. 1; 1972, and 2009). The nomenclature of

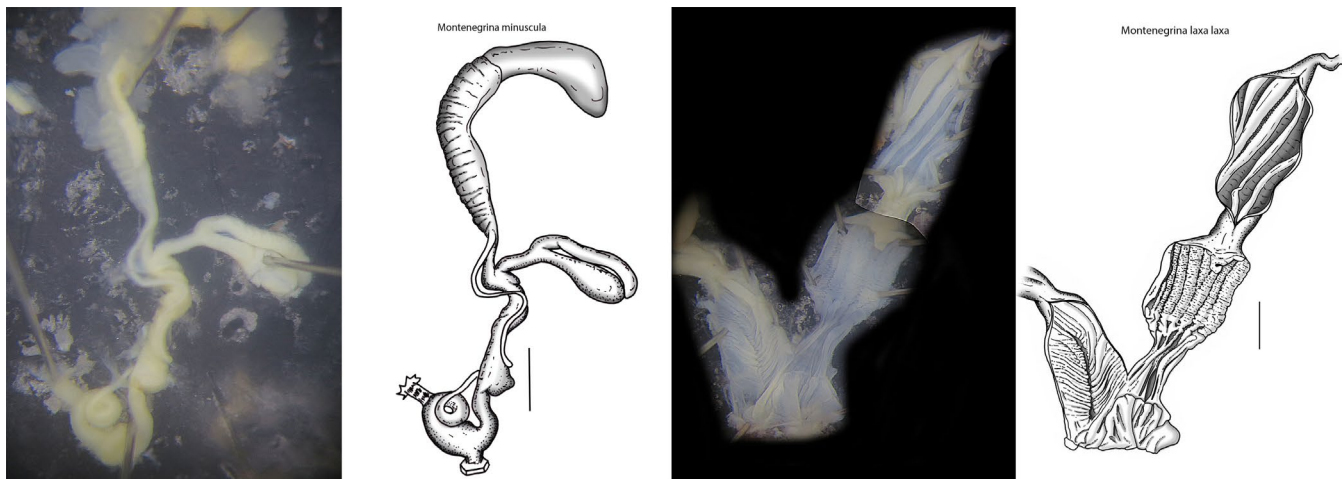
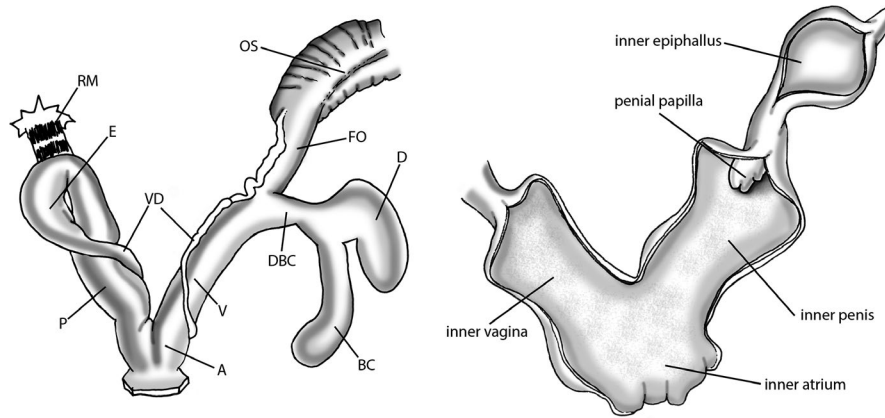


FIGURE 2 Direct comparison between the real sample and the iconography of both external and inner genitalia



**FIGURE 3** General scheme of the distal external and inner genitalia of the genus *Montenegrina*

**TABLE 1** Categorized ratios of genital parts

	Ratio	Small/short	Medium-sized	Large/long	Extremely large/long
Penial complex relative length	PCRL	$\leq 20$	$>20 < 30$	$\geq 30$	$\geq 45$
Free oviduct	FO/V	$\leq 0.4$	$>0.4 < 0.6$	$\geq 0.6$	$\geq 1.0$
Duct of bursa copulatrix	DBC/DB	$\leq 0.3$	$>0.3 < 0.5$	$\geq 0.5$	$\geq 0.6$
Bursa copulatrix	DB/V	$\leq 0.8$	$>0.8 < 1.0$	$\geq 1.0$	$\geq 1.2$
diverticulum	D/V	$\leq 1.0$	$>1.0 < 1.4$	$\geq 1.4$	$\geq 2.0$
Vagina relative length	VRL	$\leq 10$	$>10 < 20$	$\geq 20$	$\geq 30$

the different genital parts only partially follows the translation from German adopted by Nordsieck (1969a, 2007). Instead of Blasenhal (=proximal pedunculus), we use the common term (first) duct of the bursa copulatrix DBC, and for Blasenstiel (=distal pedunculus) we use the term second duct of the bursa copulatrix SDBC. The totality of the DBC, SDBC, BC (bursa copulatrix), and the D (diverticulum) is named complex of the bursa copulatrix. The spermoviduct OS is here considered as a whole. Nordsieck (1969a) subdivided and differently named it. CS is the canalis serosus and represents the allo-spermiduct, namely that part of the spermoviduct in which sperm of the mate is led to the fertilization pouch. CM is the canalis mucosus because of mucopolysaccharid-producing gland cells. The retractor vaginae Nordsieck (2007) is here named vaginal retractor VR because the receptaculum seminis (=seminal receptacle) is a part of the fertilization pouch-complex (=FPSC or carrefour), not the bursa copulatrix (H. Nordsieck, pers. comm. October 2017).

## 2.4 | Acronyms

A, atrium; BC (actual), bursa copulatrix; CSE, cross section of the (proximal) epiphallus; CSPP, cross section of the penial papilla; CSS, cross section of the spermatophore; D, diverticulum of the bursa copulatrix; DB, the actual bursa copulatrix + second duct of the bursa (BC + SDBC); DBC (first), duct of the complex of the bursa copulatrix; FDBC, as above; E, epiphallus; FO, free oviduct; FHD,

first hermaphroditic duct; FDBC, first duct of the bursa copulatrix;  $H_a$ , aperture height;  $H_s$ , shell height; IOP, inner sculpturing of penis; LSE, longitudinal section of the (proximal) epiphallus; LSPP, longitudinal section of the penial papilla; RM, retractor muscle; OS, spermoviduct (second hermaphroditic duct); P, penis; PC, penial complex (penis + epiphallus); PCRL, penial complex relative length; PG, prostatic gland; PP, penial papilla; S spermatophore; SDBC, second duct of the bursa copulatrix; SG, sperm groove; V, vagina; VD, vas deferens; VG, vaginal pilaster; VR, vaginal retractor; VRL, vaginal relative length;  $W_a$ , aperture width;  $W_s$ , shell width.

## 2.5 | Abbreviations of collectors

The names of the frequently mentioned collectors are abbreviated as follows: AH – András Hunyadi, AP – Anila Papparisto, AR – Alexander Reischütz, AS – Anna Szigethy, BV – Balázs Vági, CN – Csaba Németh, DA – Dorottya Angyal, DM – Dávid Murányi, DP – Dániel Pífkó, EH – Elisabeth Haring, EK – Éva Kiss, EM – Edvárd Mizsei, GP – Gellért Puskás, HS – Helmut Sattmann, ID – Ivailo Dedov, JU – János Ujszegi, JM – Jessica Macor, JG – Jozef Grego, JK – Jenő Kontschán, KJ – Katharina Mason, KK – Kornél Kovács, LD – László Dányi, LP – László Pintér, LT – Lilla Tamás, MD – Michael Duda, MS – Márton Szabolcs, NR – Nicole Reischütz, PJ – Péter Juhász, PR – Peter L. Reischütz, PS – Péter Subai, TD – Tamás Deli, TK – Tibor Kovács, TH – Tamás Huszár, TN – Tamás Németh, WDM – Willy De Mattia,

ZB – Zoltán Barina, ZE – Zoltán Erőss, ZF – Zoltán Fehér, ZU – Zsolt Ujvári.

In new taxon descriptions, where the number of the available type specimens is given, the following abbreviations are used: “a” adult specimen in ethanol, “ja” juvenile specimen in ethanol, “j” dry juvenile specimen, “fr” a fragment of a dry specimen. Numbers without such indication refer to dry adult specimens.

## 2.6 | Rationale and structure of the taxonomic part

The complexity of this huge genus, as evidenced by the many systematic changes in the past (and also revealed in the DNA analyses of Mason et al., 2020), the patchy distribution and the high variability found, hamper simple taxon delimitation strategies in *Montenegrina*. This is further demonstrated in Mason et al. (2020), where species delimitation tests failed to arrive at reasonable results. In principle, we prefer the Biological Species Concept, but its application in delineating species is often problematic, especially for allopatric taxa. Genetic data often only provide hints (and not proofs) regarding gene flow between populations and/or taxa. Additional criteria, such as monophyly (particularly stressed within the Phylogenetic Species Concept) or genetic distances, when considered alone, may be insufficient to delineate species. Pros and cons of the various species concepts have been debated in a plethora of publications (e.g., Gutiérrez & Garbino, 2018; Heller, Frandsen, Lorenzen, & Siegmund, 2014; Zachos, 2016), and the problem of species delimitation – which is often confused with species conceptualization – is still a matter of discussion (De Queiroz, 2007; Zachos, 2018). In the present contribution, we have therefore, for each taxon, attempted to compile all information available, considering as far as possible diagnosability, monophyly (in the mt tree), as well as population distribution in order to ultimately arrive at taxonomic decisions. Finally (as with all taxonomy), our decisions are to some extent arbitrary and await further testing.

We introduce many systematic and nomenclatural changes in the following pages. For this reason, each species header is followed by the “sensu Fehér & Szekeres, 2016”. Species are introduced alphabetically following this most recent revision. The present study raises many subspecific taxa to specific level (less frequently the other way round) or the subspecific status has changed species affiliation. Had we subsequently followed the new, revised checklist in alphabetical order, many specific taxa as found in Fehér and Szekeres (2016) would have been repeatedly discussed in the text, making it difficult to trace the systematic and nomenclatural changes they underwent over the course of this integrative analysis. The interpretation always considers the results of Mason et al. (2020) unless clearly stated otherwise.

In order to introduce the anatomical description of each taxon already with the revised systematic position and name, the section “Taxonomic and systematic remarks” is placed at the beginning, immediately following the species header. Accordingly, no new systematic position and name is introduced before any discussion

and full explanation of the underlying reasoning. At the end of the remarks section, a recapitulatory table compares the previous nomenclature (Fehér & Szekeres, 2016) with the new one. Additionally, we present a detailed list of examined material for each taxon. In these lists, we refer to the museum lots by their voucher numbers. In cases when DNA was isolated from the dissected specimen(s), the isolate's identifier is also listed together with the GenBank accession numbers in square brackets. Accession numbers are provided for sequences of the mitochondrial *cytochrome c oxidase subunit 1* gene (*COI*), the *12S rRNA* gene (*12S*), and the *16S rRNA* gene (*16S*). A full-comprehensive final table is presented at the end of the taxonomic part in order to present the full new *Montenegrina* checklist (Table 2).

## 3 | RESULTS

### 3.1 | General description of the *Montenegrina* genitalia

#### 3.1.1 | External genitalia

The relative dimensions of the genitalia (versus the shell size) substantially differ among the taxa, from very small (e.g., *M. skipetarica gurelurensis* PCRL = 13.9) to extremely large (e.g., *M. skipetarica* PCRL = 87.6). The overall appearance of the genitalia can be either extremely bulky and strong (as in *M. rugilabris irmengardis*) or extremely delicate and thin (as in *M. skipetarica skipetarica*). The general scheme of the genitalia is of the semidiaulic monotrematic type (Nordsieck, 1985). The hermaphroditic gland (ovotestis) is found along the two apical whorls of the animal's body. It has many, very densely consolidated acini where the gametes are produced. The ovotestis is closely adhered to the hepatopancreas and the upper digestive system. The FHD is very thin along its proximal portion but abruptly turns into a highly coiled, skein-like but irregular structure. The diameter of the FHD is much larger along the coiled part, and the number of whorls is approximately 7–10. The distal uncoiled part of the FHD is also very thin, straight, and ends directly into the ventral side of the AG. Despite the high number of dissected specimens, the talon has never been clearly identified in *Montenegrina*. Previously, this anatomical structure has been depicted for other Aloiinae genera such as *Lampedusa* (Giusti, Manganelli, & Schembr, 1995: 335). The general scheme of the FHD is stable among all the *Montenegrina* taxa. The AG varies in shape. It can be bean-like, roundish, usually subquadrangular, or bluntly irregular. The front and back surfaces are convex (“dorsal”) and concave (“ventral”), respectively. The FHD enters into the ventral side approximately in the central area. The AG is very variable in size compared to the spermatiduct (OS). It can be as long as the OS (i.e., as in *M. attemsi* [Wagner, 1914]) or half as long as the OS (i.e., in *M. stankovici* [Urbański, 1960]). It has never been found to be longer than the OS. The OS consists of a female and a male part including the seminal groove, which is not visible from outside. The female portion usually has a thick glandular wall. Externally, it can be either very

regularly spaced by smooth constrictions or, less frequently, randomly segmented into many irregular portions, giving the female OS part a rough appearance (as in *M. dofleini fagorum* Nordsieck, 1974). It is usually whitish to cream in color. The male, prostatic part consists of the visible prostatic gland (PG) and the sperm groove (SG). The PG is usually light to dark gray and clearly distinguishable from the lighter female part. It is randomly segmented into many irregular portions. The SG is usually visible when a section is performed across the OS. It is usually elliptic. The overall size of the OS is very variable among the *Montenegrina* taxa. It can be relatively short but extremely large and bulky (in *M. hiltrudae robusta* Nordsieck, 2009) or long and thin (in *M. janinensis* [Mousson, 1859]). Moreover, OS size is not related to any of the dimensions of other parts of the genitalia, such as the vagina or PC. Large and bulky OS are present in taxa where the distal genitalia are extremely delicate and elongated (in *M. skipetarica skipetarica* [Soós, 1924]). Be that as it may, the taxonomical value of the OS as a whole is low because the basic, general scheme is shared among all the taxa, and no taxon is precisely defined solely based on its OS shape and size.

The FO is usually large and short but can be remarkably variable in relation to the length of the vagina (V). The FO/V ratio ranges from 0.03 in *M. skipetarica* and *M. skipetarica ersekensis* Nordsieck, 1996 to 1.29 in *M. fuchsi muranyii* Fehér & Szekeres, 2006 and 1.31 in *M. prokletiana kovacsorum* Fehér & Szekeres, 2016. Thus, the FO can be either extremely shorter or longer than the V.

The vagina is simple, cylindrical, or irregular, without any appendix or cecum. It can be broadened along its proximal or, more often, along its distal part. Usually, it is broadened at both sides, assuming a barbell-like shape. The vagina starts from the branching of the FO with the bursa copulatrix complex (more precisely with the DBC) and runs as far as the atrium. The vaginal retractor is strong; it is always present and attached to the external vaginal walls at the level of the proximal vagina, next to the branching between the FO and DBC. Sometimes it exhibits a swelling (probably of glandular origin) along its distal portion and bordering with the genital atrium (as in *M. laxa disjuncta*). The vagina is very variable in length in relation both to shell height and penis length. The VRL ranges from 5.4 in *M. janinensis* and 5.8 in *M. cattaroensis umbilicata* to 49.2 in *M. skipetarica ersekensis* and 54.6 in *M. skipetarica skipetarica*. Thus, the interspecific difference in the relative size of the vagina can be almost an order of magnitude. The ratio between the length of the PC and the length of the vagina (PC/V) can also differ markedly. From a minimum of 0.75 in *M. minuscula* and 0.80 in *M. subcristata wohlberedti*, it can increase up to 4.47 in *M. laxa laxa* or 4.53 in *M. sporadica tropojensis*.

The bursa copulatrix complex consists of a first duct (DBC), a second duct (SDBC), a well-developed diverticulum (D) and the actual bursa copulatrix (BC). The overall dimensions of the complex and the ratios among its parts also vary considerably. The DDB/V ratio can differ by a factor of up to 60 times, from 0.02 in *M. perstriata ochridensis* to 1.15 in *M. prokletiana kovacsorum*. The diverticulum of the bursa copulatrix (D) can be either shorter or longer than the SDBC + BC. The ratio D/SDBC + BC ranges from 0.46 in *M. rugilabris golikutensis* to 3.0 in *M. rugilabris rugilabris*. The transitional

section between the actual bursa and the second duct of the bursa can be easily detected in some taxa (*M. fuchsi klemmi*) or missing in others (*M. rugilabris rugilabris* or *Montenegrina skipetarica konitsae*), and all degrees of transitional gradient are present among the taxa.

The PC comprises a penis (P) and an epiphallus (E). The flagellum is absent. The retractor muscle (RM) is single and undivided. It can be either short and stronger thin and long, or any transitional state in between. The RM usually originates along the tip of the folding part of the epiphallus, either more distally (as in *M. attemsi jakupicensis*) or more proximally (as in *M. helvola ornata*). The penis is usually uniformly cylindrical without any caecum or penial appendix. It can be swollen either only along its proximal or distal part or both, with a narrower central area. The position of the penial papilla (PP), if present, can be often detected based on the proximal swollen part of the penis. The penis can be either shorter or longer than the epiphallus. The E/P ratio ranges from 0.50 in *M. nana barinai* and 0.54 in *M. perstriata drimica* to 3.5 in *M. perstriata callistoma* and 4.0 in *M. dofleini kastoriae*. The epiphallus can be shorter or longer than the penis. It can be cylindrical and swollen or somewhat thinner and spindly. The transitional area between the epiphallus and the distal portion of the vas deferens can be either clearly recognizable or not at all. In some taxa the VD enters into a blunt proximal epiphallus (as in *Montenegrina laxa delii* or *Montenegrina perstriata drimica*), making the transition clearly visible. In other taxa, the transition is very progressive (in *M. drimmeri*) and thus the precise border between VD and E cannot be determined from outside. Regardless, this feature proved to be variable among specimens of a population (e.g., *M. dofleini pinteri*, Figure 10).

The atrium is usually large and short, but sometimes it can be quite long (as in *M. dofleini dofleini* and *M. grammica improvisa*).

### 3.1.2 | Inner genitalia

The inner sculpturing of the genitalia of *Montenegrina* revealed an astonishing variety of configurations in all the main parts (PC, atrium, vagina). The inner sculpturing was found to be stable (with only slight individual variability) among specimens of the same population and among con(sub) specific populations. The PC walls are always very thick and muscular. The PC showed the highest variability. This variability mainly involves the combination (or the absence) of pleats of different size and texture, arranged in a longitudinal, transversal or oblique direction or creating particular net-like patterns. The sculpturing also changes along the inner penis, from the base of the penial papilla towards the atrium. The background walls are also variable, ranging from perfectly smooth to finely sculptured. The epiphallus has a more stable inner arrangement with 9 or 10 different types. It always presents 1 up to five longitudinal pleats. These pleats and the background can be either smooth or more or less fringed and sculptured. Inside the genitalia, the transition area between the epiphallus and the vas deferens is very clear in all taxa. This is due to the clear change of the inner sculpturing, where the pleat(s) of the epiphallus suddenly fade into the smooth walls of the vas deferens.



The penial papilla is usually present, but can be absent. In that case, the transition between the penis and the epiphallus is detectable by a change of the wall sculpturing. We recorded around 20 different types of the penial papilla: with a smooth or irregular surface, globose to elongate with a sharp tip, small or large in size. The papilla has a central duct that usually opens laterally and, only in few taxa, apically. When it opens laterally the opening can be longitudinally or transversely oriented. Sometimes the penial papilla bears an “accessory” basal component (as in *M. dofleini pinteri* and *M. grammica improvisa*).

The atrium can exhibit around 20 different configurations, ranging from completely smooth to displaying variable pleats that are differently arranged. Often, a large fold originating directly from the aperture occupies the inner atrial volume. This fold can be uni- to polylobated. The background walls are also variable, either perfectly smooth or finely sculptured.

The inner vagina shows up to 18 different inner configurations. Similarly to the penis, its variability lies mainly in the combination (or absence) of pleats of different size and texture, arranged either in a longitudinal, transversal or oblique direction or creating particular net-like patterns. Most of the taxa have a vaginal pilaster. Only 14 out of the 88 investigated taxa lack such an anatomical structure. This is a strong, fleshy pleat that originates along the most distal part of the proximal tract of the first duct of the bursa copulatrix and longitudinally continues into the vagina. Sometimes the vaginal pilaster abruptly ends along the proximal vagina or it gradually fades out towards the distal vagina. Its surface is always smooth.

In general, the sculpturing of the internal wall of the genital parts is made of pletas that are arranged in various ways. The terms we used to describe these arrangements are defined as follows:

1. longitudinal: approximately parallel to the longitudinal axis of the organ,
2. transversal: perpendicular (~90°) to the longitudinal axis of the organ,
3. oblique: inclined (~45°) from the longitudinal axis of the organ,
4. chevron-like: pleats that diagonally branch off at both sides.

Combinations of these categories can result in complex patterns of the sculpturing, which are depicted and described in detail for each dissected taxon.

### 3.2 | Anatomical diagnosis of the genus *Montenegrina*

The high number of specimens dissected during this study provided an accurate overall description of the genitalia of the genus *Montenegrina*. All the previous general descriptions (mainly Nordsieck, 1972: 26-27; 2007: 77; 2009: 73), although precise and accurate concerning the taxa investigated, have limitations due to the very few specimens considered. Following Nordsieck (2009: 73), a new diagnosis for the external genitalia of the genus *Montenegrina* can now be provided based on a much larger number of anatomical observations:

#### 3.2.1 | External genitalia

The diverticulum of the bursa copulatrix is shorter, longer than or equally as long as the BC + SDBC; the DBC is shorter, longer than or equally as long as that of the vagina; vagina with different shapes, shorter, longer than or equally as long as the penis; a vaginal retractor is present, inserted on the proximal vagina end or on the transition DBC-vagina, respectively; the PC without a flagellum, shorter, longer than or equally as long as the vagina without a penial appendix or cecum; the epiphallus is shorter, longer than or equally as long as the penis; the penial retractor is not divided.

#### 3.2.2 | Inner genitalia

The vaginal pilaster is mostly present; the vagina and penis with an inner sculpturing mainly comprising a combination (or also absence) of pleats of different size and texture, arranged in a longitudinal, transversal or oblique direction or creating particular net-like patterns; the atrium is simple or pleated, often with a more or less big fold directly originating from the aperture; the penial papilla is mostly present but sometimes missing, roundish to conical with blunt or pointed apex; the channel of the penial papilla opens on the tip or laterally; the epiphallus with 1 up to 5 longitudinal smooth or fringed pleats.

Except for very few examples (e.g., *Montenegrina minuscula*), the external shape of the genitalia is of relatively low taxonomic value because no particular configuration is correlated to one taxon or a well-defined group of taxa. In contrast, the inner sculpturing is stable at the population level.

### 3.3 | Spermatophore

During the dissections, five specimens were found with the spermatophore still intact and embedded into the diverticulum of the bursa copulatrix complex. The spermatophores of five taxa of the genus *Montenegrina* are described here for the first time. The taxa are *M. hiltrudae densicostulata* Nordsieck, 1974; *M. laxa miraka*; *M. perstriata callistoma* Fehér & Szekeres, 2006 *M. perstriata drimica* Nordsieck, 1972, and *M. subcristata* (Pfeiffer, 1848).

The spermatophores are slender and slightly longer than the diverticulum that houses them. The overall shape is always slightly or markedly bent. Usually, both the upper and the lower keels are present. The keels may or may not reach the tail or the head of the spermatophore. The head can be blunt, pointed, or bent downward in a hook-like manner. The tail is usually sharp and pointed. The cross section is usually irregularly roundish with two or more longitudinal excrescences. Our results show that every taxon has a unique and different spermatophore morphology as already known for other pulmonate families such as Milacidae (Wiktor, 1987).

## 4 | TAXONOMIC PART

***Montenegrina apfelbecki* (Sturany, 1907) sensu Fehér & Szekeres, 2016****Taxonomic and systematic remarks**

Since no alcohol-preserved specimens were available for anatomical investigations, no anatomical data were available. Following Mason et al. (2020), *M. apfelbecki* falls into a clearly distinct subclade within the main Clade E. Its separate position in the phylogenetic tree and its shell morphology (Fehér & Szekeres, 2016: 15) fully support it as a valid species.

Fehér &amp; Szekeres, 2016

*Montenegrina apfelbecki* (Sturany, 1907)De Mattia, Fehér,  
Mason & Haring, 2020*Montenegrina apfelbecki*  
(Sturany, 1907)***Montenegrina apfelbecki* (Sturany, 1907)**

*Clausilia apfelbecki* Sturany, 1907: 233. – Wohlberedt, 1909: 101.

*Delima (Delima) apfelbecki* – Sturany & Wagner, 1915: 74, plate 16, fig. 91.

*Delima (Albanodelima) apfelbecki* – Wagner, 1924: 120. – Wagner, 1925: 67, plate 1, fig. 12. (genital anatomy)

*Montenegrina apfelbecki* – Nordsieck, 1972: 28. – Zilch, 1981: 126, plate 14, fig. 30 – Nordsieck, 2009: 75 – Fehér & Szekeres, 2016: 15, fig. 11a, distribution map fig. 12.

No alcohol-preserved specimens were available for anatomical investigations.

***Montenegrina attemsi* (Wagner, 1914) sensu Fehér & Szekeres, 2016****Taxonomic and systematic remarks**

This species occupies two small areas that are 30 km apart with no populations in between and is very isolated from the other *Montenegrina* populations (Fehér & Szekeres, 2016: 19).

Following Mason et al. (2020), clade A is made up exclusively of this taxon and the two subspecies are monophyletic, falling into two separate subclades. *Montenegrina attemsi attemsi* and *M. attemsi jakupicensis* exhibit significant differences in genital morphology. *Montenegrina attemsi attemsi* has a completely smooth inner surface of the penis, vagina, and atrium, whereas the same genital parts of *M. attemsi jakupicensis* are strongly sculptured. Considering the significant differences in morphology, specifically of the genitalia, and the isolated distribution we here propose to consider the two taxa as valid species: *M. attemsi* and *M. jakupicensis* stat. nov.

Fehér &amp; Szekeres, 2016

*Montenegrina attemsi attemsi* (Wagner,  
1914)*Montenegrina attemsi jakupicensis*  
Fauer, 1993De Mattia, Fehér,  
Mason & Haring, 2020*Montenegrina attemsi*  
(Wagner, 1914)*Montenegrina*  
*jakupicensis*  
Fauer, 1993 stat. nov.***Montenegrina attemsi* (Wagner, 1914)**

Figures 4.1–4.6

*Delima (Delima) attemsi* Wagner, 1914 in Sturany & Wagner, 1915: 73–74, plate 16, fig. 92.

*Delima (Albanodelima) attemsi* – Wagner, 1924: 120.

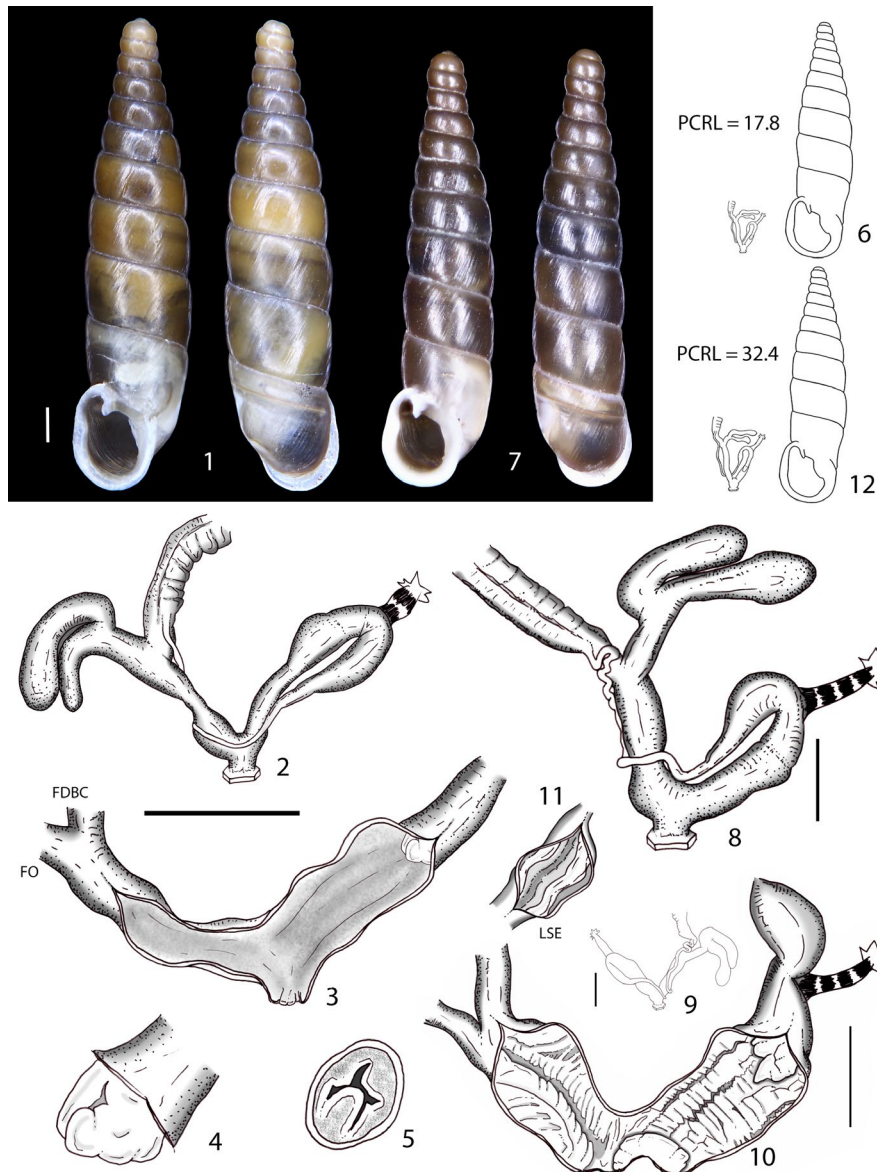
*Montenegrina janinensis attemsi* – Nordsieck, 1974: 151, plate 5, fig. 28 – Zilch, 1981: 129. – Nordsieck, 2009: 75.

*Montenegrina attemsi attemsi* – Fehér & Szekeres, 2016: 18, fig. 11B, distribution map fig. 12.

**Examined material:** two dissected specimens. North Macedonia, Skopje District, Matka Gorge near the Sv. Andreja Church, 300 m, 41.9610°N, 21.2943°E [type locality], leg. ZE, ZF, 10.iv.2004 (HNHM 94429, Mat-224-01 [CO: KU307592]; Mat-224-02 [KU307593, 16S: KU308055, 12S: KU307933]).

**External genitalia (Figure 4.2):** The whole genital complex is small (PCRL = 17.8). The FO is usually short (FO/V = 0.38). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is wide and medium-sized (DBC/DB = 0.38). The bursa copulatrix is cylindrical, short (DB/V = 1), with no distinction between the second duct and the bursa itself, slightly tapering towards the tip, but with a blunt apex. The diverticulum is long (D/V = 2.3) and longer than the bursa copulatrix (D/BC = 2.3), wider than the bursa copulatrix and cylindrical, gradually widening towards the end with a blunt rounded apex. The vagina is short (VRL = 5.9), usually slightly swollen at its proximal and distal ends. The atrium is short. The PC is longer than the vagina (PC/V = 3) and wider at the level of the penial papilla. The retractor muscle is short but strong. The epiphallus is slightly swollen and as long as the penis (E/P = 1), gradually tapering and merging the vas deferens. The actual transition area between epiphallus and vas deference is clearly visible only from inside.

**Inner genitalia (Figures 4.3–4.5):** The atrium is completely smooth. The fine structure of the walls exhibits a very subtle granulated pattern. Both vagina and penis are completely smooth, showing the same granulated pattern. The vaginal pilaster is missing. The penial papilla is medium-sized, globose, and irregular with a blunt apex. The aperture runs laterally and reaches the apical area. Its surface is smooth. The epiphallus has two or three smooth pleats that originate proximally at the distal end of the vas deferens. These pleats extend longitudinally and fade out before the origin of the penial papilla. The background wall surface is smooth.



**FIGURE 4** 4.1–4.6 *Montenegrogrina attemsi* (Wagner, 1914), I. Dedov coll. MK311. 4.1 shell 4.2 whole genitalia except gonads and proximal spermooviduct, 4.3 inner distal genitalia, 4.4 penial papilla, 4.5 cross section of the proximal epiphallus, 4.6 shell-genitalia ratio. 4.7–4.12 *Montenegrogrina jakupicensis* Fauer, 1993 stat. nov. HNHM 99520, 4.7 shell. 4.8–4.9 whole distal genitalia. 4.10 inner distal genitalia. 4.11 longitudinal section of proximal epiphallus. 4.12 shell-genitalia ratio

### *Montenegrogrina jakupicensis* Fauer, 1993 stat. nov.

Figures 4.7–4.12

*Montenegrogrina janinensis jakupicensis* Fauer, 1993: 56–57, plate 1, fig. 8. – Nordsieck, 2009: 75.

*Montenegrogrina attemsi jakupicensis* – Fehér & Szekeres, 2016: 18, fig. 11C, distribution map fig. 12.

**Examined material:** three dissected specimens. North Macedonia, Nežilovo, Babuna Spring NW of Nežilovo, 1,280 m, 41.6903°N, 21.4162°E, leg. DM, TK, 3.x.2013 (HNHM 99520, Mjk-425-01 [COI: KU307691, 16S: KU308118, 12S: KU307959]; Mjk-425-02 [COI: KU307692]; Mjk-425-04 [COI: MT251628]).

**External genitalia (Figures 4.8–4.9):** The whole genital complex is medium-sized (PCRL = 29.7). The FO is usually very short (FO/V = 0.23). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is wide and medium-sized (DBC/DB = 0.32). The bursa copulatrix is cylindrical, long (DB/V = 1.69) with weak distinction between the second duct and the bursa itself. It swells slightly towards the tip with a blunt apex. The diverticulum is medium-sized (D/V = 1.38), as wide as but shorter than the bursa copulatrix (D/BC = 0.82), and cylindrical with a blunt, rounded apex. The vagina is medium-sized (VRL = 10.2), usually slightly swollen at its proximal and distal end. The atrium is short. The PC is longer than the vagina (PC/V = 2.92) and wider at the level of the penial papilla. The retractor muscle is short but strong. The

epiphallus is slightly swollen and longer than the penis ( $E/P = 2.80$ ), gradually tapering into the vas deferens. The actual transition area between epiphallus and vas deference is clearly visible only from inside, where there is a sharp change in the inner sculpturing.

**Inner genitalia (Figures 4.10–4.11):** The atrium has a big, partially polylobated fold originating directly at the genital aperture. This fold occupies almost of the whole atrial volume. The proximal vagina has a lower main longitudinal cord that is polylobated. The background walls are smooth. The vaginal pilaster is present and remarkably fringed by a series of metameric small lobes. These lobes extend posteriorly, creating an irregular pattern. A portion of the smooth background wall is clearly visible between the cords. The two cords continue along the distal vagina but do not enter the atrium; they abruptly end by becoming a series of fine transversal pleats. The penis has four main fringed, metameric cords with large metamers that run longitudinally from the base of the penial papilla as far as the atrium. The cords can split or merge into one another, especially along the proximal part of the vagina. A smooth background is usually visible among the cords. The penial papilla is medium-sized, conical, with pointed but nonetheless broad apex and smooth surface. The aperture is lateral and does not reach the papilla's tip. The epiphallus has two or three smooth pleats originating proximally from the distal end of the vas deferens. These pleats run longitudinally and fade before reaching the origin of the penial papilla. The background surface is smooth.

### *Montenegrina cattaroensis* (Rossmässler, 1835) sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

*Montenegrina cattaroensis* (sensu Fehér & Szekeres, 2016) falls into a monophyletic subclade inside the main Clade F as the sister group of *M. subcristata*.

*Montenegrina cattaroensis umbilicata* and *M. cattaroensis antivari-costata* form a subclade and the single population of *M. cattaroensis antivari-costata* is well embedded (also geographically) within the *M. cattaroensis umbilicata* populations. *Montenegrina cattaroensis cattaroensis* forms the sister group of the previous two taxa (Fehér & Szekeres, 2016: 22), and it is geographically detached and isolated (ca. 30 km north) from their subclade.

One population of *M. cattaroensis cattaroensis* was dissected (topotype specimens from Kotor Fortress) and the arrangement of the genitalia was very different from that in *M. cattaroensis umbilicata* and *M. cattaroensis antivari-costata* (Figures 5–7). Although the phylogenetic analyses revealed that the taxa are closely related, based on the differences in shell morphology and genital anatomy, *M. umbilicata* comb. nov. should be considered as a valid species, independent from *M. cattaroensis*.

The genital morphology of *M. cattaroensis antivari-costata* and *M. umbilicata* is similar, with the inner walls of the penis exhibiting one or two longitudinal hollows separated by a few fringed pleats

(Figures 6.4 and 7.4). Although the shell of *M. cattaroensis antivari-costata* exhibits ribs, the whole shell is easily attributable to *M. umbilicata* and probably represents its local morphotype. Considering these results, we propose *M. cattaroensis antivari-costata* as a subspecies: *M. umbilicata antivari-costata* comb. nov., which is concordant with Nordsieck's (2009) opinion.

Fehér & Szekeres, 2016	De Mattia, Fehér, Mason, & Haring, 2020
<i>Montenegrina cattaroensis cattaroensis</i> (Rossmässler, 1835)	<i>Montenegrina cattaroensis</i> (Rossmässler, 1835)
<i>Montenegrina cattaroensis umbilicata</i> (Boettger, 1879)	<i>Montenegrina umbilicata umbilicata</i> (Boettger, 1879) stat. nov.
<i>Montenegrina cattaroensis antivari-costata</i> (Fehér & Szekeres, 2016)	<i>Montenegrina umbilicata antivari-costata</i> (Fehér & Szekeres, 2016) comb. nov.

### *Montenegrina cattaroensis* (Rossmässler, 1835)

Figures 5.1–5.5

*Clausilia cattaroensis* Rossmässler, 1835: Heft 2, pp. 8–9, plate 7, fig. 100. – Küster, 1844–1862: 40–41, plate 4, figs 14–17 – Pfeiffer, 1848: 437–438. – Schmidt, 1868: 68.

*Clausilia cattaroensis* var. *gracilior* Küster, 1850 in Küster, 1844–1862: 40.

*Clausilia cattaroensis* (partim) – Walderdorff, 1864: 509.

*Clausilia (Delima) cattaroensis* – Westerlund, 1884: 53–54. – Wohlberedt, 1907: 551. – Wohlberedt, 1909: 673–674, plate 14, figs 148–151.

*Clausilia (Delima) cattaroensis* f. *parvula* Westerlund, 1884: 54.

*Clausilia (Delima) catarvensis* (sic!) – Westerlund, 1884: 54.

*Clausilia (Delima) laevigata* Mhlf. – Westerlund, 1884: 54.

*Clausilia (Delima) lesinacensis* Parr. – Westerlund, 1884: 54.

*Clausilia (Delima) cattaroensis* var. *gracilior* – Westerlund, 1884: 54.

*Delima (Delima) cattaroensis* – Sturany & Wagner, 1915: 73–74, plate 16, fig. 92.

*Delima (Albanodelima) cattaroensis* – Wagner, 1924: 118.

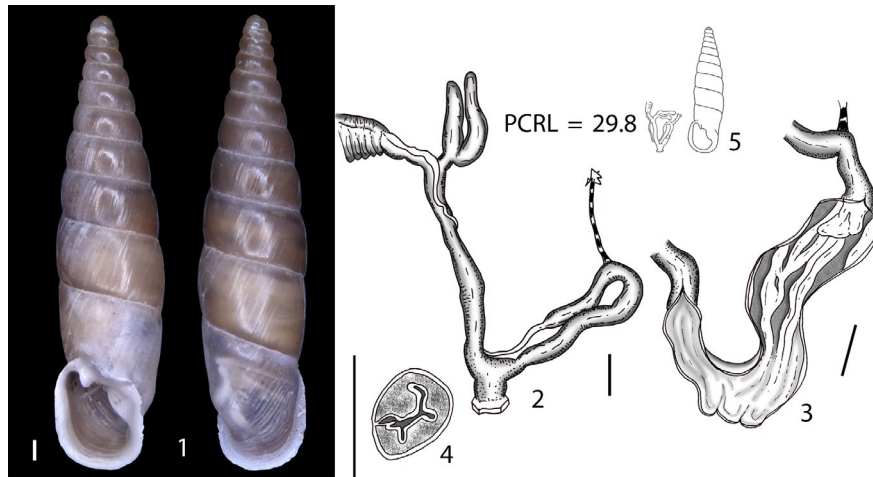
*Delima (Montenegrina) cattaroensis* – Zilch in Wenz, 1960: 429–430, fig. 1526.

*Montenegrina cattaroensis* – Nordsieck, 1969b: 259. (genital anatomy) – Zilch, 1981: 127, plate 12, fig. 16 – Nordsieck, 2009: 73.

*Montenegrina cattaroensis cattaroensis* – Fehér & Szekeres, 2016: 20, fig. 11D, distribution map fig. 13.

**Examined material: two dissected specimens.** Montenegro, Kotor fortress, 42.424°N, 18.774°E [type locality], leg. LP, PS, AS, 24.vii.1972 (HNHM 43127, Mct-568-02 [COI: KU307617]; Mct-568-03 [COI: KU307618]).

**External genitalia (Figure 5.2):** The whole genital complex is medium-sized (PCRL = 29.8). The FO is short (FO/V = 0.27). The



**FIGURE 5** *Montenegrina cattaroensis* (Rossmässler, 1835) HHNM 43127. 5.1 shell. 5.2 whole genitalia except gonads and proximal spermoviduct. 5.3 inner distal genitalia. 5.4 cross section of the proximal epiphallus. 5.5 shell-genitalia ratio

vas deferens is thin but slightly swollen proximally. The first duct of the bursa copulatrix complex is very short ( $DBC/DB = 0.15$ ). The bursa copulatrix is cylindrical, small ( $DB/V = 0.45$ ) with no distinction between the second duct and the actual bursa. It is not swollen towards the tip and has a blunt apex. The diverticulum is cylindrical, short ( $D/V = 0.52$ ), longer ( $D/BC = 1.15$ ) but as wide as the bursa copulatrix and with a blunt apex. The vagina is long ( $VRL = 21.2$ ), uniformly cylindrical or slightly swollen along its midportion. The atrium is short but large. The PC is longer than the vagina ( $PC/V = 1.41$ ) and is uniformly cylindrical. The retractor muscle is long and thin. The epiphallus is cylindrical and shorter than the penis ( $E/P = 0.88$ ), rather abruptly tapering into the vas deferens.

**Inner genitalia (Figures 5.3–5.4):** The atrium and the vagina are completely smooth. The vaginal pilaster is missing. The proximal penis has 4–6 main elevated, smooth pleats. Some of these pleats eventually split into two branches and distally merge again. The background walls are completely smooth. Along the distal penis the pleats gradually fade to disappear before the atrium. The penial papilla is medium-sized, conical, with a pointed but nonetheless broad apex and smooth surface. The aperture is lateral and does not reach the papilla's tip. The epiphallus has two or three smooth pleats originating proximally from the distal end of the vas deferens. These pleats run longitudinally and fade before the origin of the penial papilla. The background surface is smooth.

### *Montenegrina umbilicata umbilicata* (Boettger, 1879) **stat. nov.**

Figures 6.1–6.6

*Clausilia umbilicata* Boettger, 1879: 102, plate 2, fig. 3.

*Clausilia (Delima) umbilicata* – Westerlund, 1884: 53. – Wohlberedt, 1907: 551. – Wohlberedt, 1909: 674, plate 14, figs 152–155.

*Delima (Albanodelima) umbilicata* – Wagner, 1924: 118.

*Montenegrina umbilicata* – Nordsieck, 1969b: 259. (genital anatomy)

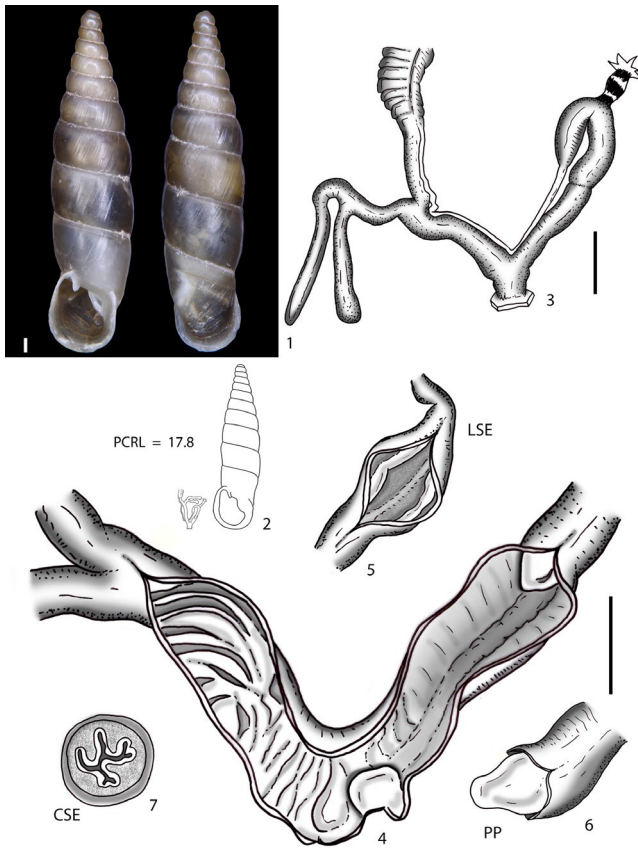
*Montenegrina umbilicata umbilicata* – Zilch, 1981: 132, plate 12, fig. 17 – Nordsieck, 2009: 73.

*Montenegrina cattaroensis umbilicata* – Fehér & Szekeres, 2016: 22, fig. 11F, distribution map fig. 13.

**Examined material: two dissected specimens.** Montenegro, Bar, Stari Bar near the spring, 198 m, 42.1002°N, 19.1412°E, leg. MD, EH, KJ, HS, 7.vii.2015 (NHMW 110430/MN/0152, Mum-634-01 [COI: MT251862]).

**External genitalia (Figure 6.3):** The whole genital complex is small ( $PCRL = 17.8$ ). The FO is very long ( $FO/V = 1.00$ ). The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is long ( $DBC/DB = 0.61$ ). The bursa copulatrix is club-like, large ( $DB/V = 1.29$ ), with no clear distinction between the second duct and the actual bursa. It is only slightly swollen towards the tip. The apex is blunt and rounded. The diverticulum is long ( $D/V = 1.93$ ), and longer ( $D/BC = 1.50$ ) but thinner than the bursa copulatrix; it is uniformly cylindrical with a pointed apex. The vagina is relatively short ( $VRL = 5.8$ ) and uniformly cylindrical. The atrium is short but large. The PC is cylindrical and much longer than the vagina ( $PC/V = 3.07$ ). The retractor muscle is short and strong. The epiphallus is cylindrical, proximally swollen, and longer than the penis ( $E/P = 1.39$ ). There is a clear transitional area between the epiphallus and the vas deferens.

**Inner genitalia (Figures 6.4–6.7):** The atrium has a big, unilobate fold originating directly at the genital aperture. The fold is smooth and spoon-like with a central depression. The distal vagina has 5–10 smooth transversal pleats that do not continue into the atrium. These pleats are minimally elevated and are variable in shape and length. The proximal vagina has many oblique, elevated pleats forming an irregular pattern. The vaginal pilaster is present but short. The background walls are smooth. The penis has a main large, not elevated longitudinal smooth pleat with jagged edges. It extends as far as the atrium. This pleat forms a “hollow” in the middle part of the penis. The side wall has a weak and well-spread transversal arrangement. The background



**FIGURE 6** *Montenegro umbilicata umbilicata* (Boettger, 1879) stat. nov. NHMW 110430/MN/0152. 6.1 shell. 6.2 shell-genitalia ratio. 6.3 whole genitalia except gonads and proximal spermoviduct. 6.4 inner distal genitalia. 6.5 longitudinal section of the proximal epiphallus. 6.6 penial papilla. 6.7 cross section of proximal epiphallus

walls are smooth. The penial papilla is medium-sized, globose, and irregular with a blunt apex. The aperture extends laterally and reaches the apical area. Its surface is smooth. The epiphallus has two or three smooth pleats originating proximally from the origin of the vas deferens. These pleats extend longitudinally and fade out before the origin of the penial papilla. The background surface is smooth.

### *Montenegro umbilicata antivariocostata* (Boettger, 1907) comb. nov.

Figures 7.1–7.6

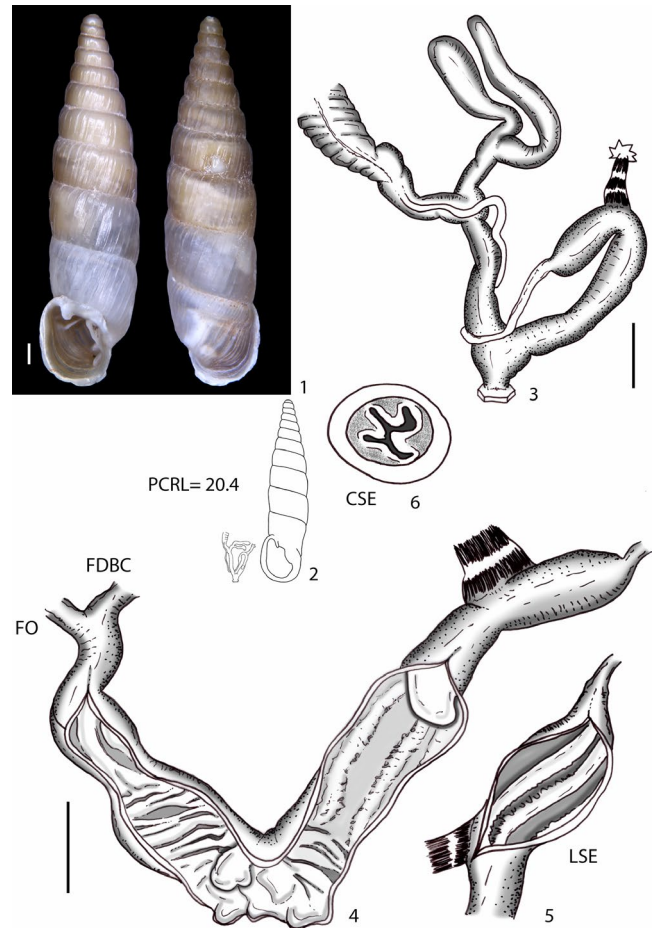
non *Clausilia costata* Pfeiffer, 1828: 42, plate 7, figs 17 and 18.

*Clausilia* (*Delima*) *umbilicata* var. *costata* Boettger, 1907 in Wohlberedt, 1907: 551. – Wohlberedt, 1909: 674, plate 14, figs 156–157.

*Delima* (*Albanodelima*) *umbilicata costata* – Wagner, 1924: 118.

*Montenegro umbilicata costata* – Zilch, 1981: 132, plate 12, fig. 18. – Nordsieck, 2009: 73.

*Montenegro cattaroensis antivariocostata* – Fehér & Szekeres, 2016: 21, fig. 11E, distribution map fig. 13.



**FIGURE 7** *Montenegro umbilicata antivariocostata* (Fehér & Szekeres, 2016) comb. nov. NHMW 110430/MN/0155. 7.1 shell. 7.2 shell-genitalia ratio. 7.3 whole genitalia except gonads and proximal spermoviduct. 7.4 inner distal genitalia. 7.5 longitudinal section of the proximal epiphallus. 7.6 cross section of the proximal epiphallus

**Examined material:** two dissected specimens. Montenegro, Rumija Mts, 3 km above Stari Bar, on the footpath to Veliki Mikulići, 340 m, 42.0973°N, 19.1458°E [type locality], leg. MD, EH, KJ, HS, 7.vii.2015 (NHMW 110430/MN/0155, Mco-637-01 [COI: MT251532]; Mco-637-02 [COI: MT251533]; Mco-637-03 [COI: MT251534]).

**External genitalia (Figure 7.3):** The whole genital complex is medium-sized (PCRL = 20.4). The FO is moderately long (FO/V = 0.59). The vas deferens is uniformly thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.41). The bursa copulatrix is cylindrical, medium-sized (DB/V = 1.00) with no clear distinction between the second duct and the actual bursa. It is slightly swollen towards the tip. The apex is blunt and rounded. The diverticulum is medium-sized (D/V = 1.53), longer (D/BC = 1.53), and thinner than the bursa copulatrix. It is uniformly cylindrical with a blunt apex. The vagina is relatively short (VRL = 9.1), uniformly cylindrical or only slightly swollen at its distal portion. The atrium is short but large. The PC is much longer than the vagina (PC/V = 2.24) and is usually uniformly cylindrical. The retractor muscle is short and strong. The epiphallus is cylindrical, proximally slightly swollen, and longer than the penis (E/P = 1.24). The vas deferens widens abruptly, with a clear transition area to the epiphallus.

**Inner genitalia (Figures 7.4–7.6):** The atrium has 3–5 big, pad-like, smooth, and fleshy calluses that are irregularly arranged. The distal vagina has 6–10 smooth transversal pleats that do not continue into the atrium. They randomly split and merge into one another at their ends. The proximal vagina has one or two large, smooth, elevated, longitudinal pleats. The background walls are smooth. The vaginal pilaster is completely smooth. The proximal penis has two main large but not elevated longitudinal pleats with jagged and irregular edges. A few minor folds can be also present. The distal penis has three or four large but not elevated, smooth, transversal pleats. These pleats are irregular. The background walls are very finely granulated. The penial papilla is medium-sized, globose, irregular with a blunt apex. The aperture extends laterally and reaches the apical area. Its surface is smooth. The epiphallus has 2 up to 3 smooth pleats with jagged edges, originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is finely granulated.

### ***Montenegrina chiasma* Nordsieck, 1972 sensu Fehér & Szekeres, 2016**

#### **Taxonomic and systematic remarks**

*Montenegrina chiasma* is known to inhabit the region of Mt. Dajti in Albania.

No alcohol-preserved specimens were available for the molecular genetic and anatomical investigations, thus its position in the phylogenetic tree and its anatomical features are currently unknown. Further field research is needed in order to find suitable samples, as stated in Fehér & Szekeres, 2016: 24.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina chiasma</i> Nordsieck, 1972	<i>Montenegrina chiasma</i> Nordsieck, 1972

### ***Montenegrina chiasma* Nordsieck, 1972**

*Montenegrina laxa chiasma* Nordsieck, 1972: 30, plate 5, fig. 42.

*Montenegrina chiasma* – Nordsieck, 2009: 73.

*Montenegrina chiasma* – Fehér & Szekeres, 2016: 23, fig. 11G.

No alcohol-preserved specimens were available for anatomical investigations.

### ***Montenegrina dofleini* (Wagner, 1928) sensu Fehér & Szekeres, 2016**

#### **Taxonomic and systematic remarks**

Most of the *M. dofleini* subspecies fall into the main Clade D2 (Mason et al., 2020). The specimens identified based on the shell

as *M. dofleini dofleini* proved to be distributed in distant positions in the tree. One population (Mdo-272) is the sister group of the big *M. dofleini prespaensis*-*M. dofleini sinosi* subclade, whereas the remaining *M. dofleini dofleini* samples form two separate lineages together with *M. dofleini fagorum*. *Montenegrina dofleini fagorum* itself is monophyletic. The overall situation is far from being resolved because only the topotypical population of *M. dofleini dofleini* was available for anatomical investigations. Nonetheless, we can compare the genital arrangement of *M. dofleini dofleini* (Mdo-537) with one *M. dofleini fagorum* population (Mfa-507) that was collected less than 5 km away, along the same mountain ridge (Galičica Mts). The genital morphology is very similar both concerning the external and inner features (Figures 8.5–8.8). Taking into account their distribution, their complex nomenclatural history (*M. dofleini fagorum* previously considered as *M. janinensis fagorum!*), the new anatomical data as well as the phylogeny, we provisionally retain *M. dofleini fagorum* as a subspecies of *M. dofleini* until new data becomes available.

The systematic position of other non-topotypical populations, provisionally ascribed to *M. dofleini dofleini* exclusively based on shell features, cannot be precisely determined until anatomical data are available.

According to shell morphology, *M. dofleini wagneri* was assigned to *M. dofleini* (Clade D2), but it falls very distant into Clade E, being the sister lineage of the taxa until now ascribed to *M. hiltrudae* (Mason et al., 2020). Unfortunately, no alcohol-preserved specimen was available for dissection. Despite this missing data, we consider it as a valid species *M. wagneri* stat. nov. because its position in the tree does not suggest inclusion into any other taxon.

*Montenegrina dofleini pinteri* is the sister group of *M. stankovici*. Its monophyly, different genital arrangements and shell morphology (Figure 10) lead us to consider *M. pinteri* stat. nov. as a valid species. The status of *M. stankovici* as a valid species is supported by the phylogenetic and the anatomical data (see below).

The *M. dofleini prespaensis*-*M. dofleini sinosi* clade (names attributed based on shell morphology) is phylogenetically distant from *M. dofleini dofleini* and thus it is not reasonable to consider these taxa as its subspecies. The genital morphology of *M. dofleini dofleini* (population Mdo-537) is very different from the topotypical *M. dofleini prespaensis* (Mpr-404) and from *M. dofleini sinosi* (Msi-553). We propose here to consider *M. prespaensis* stat. nov. as a valid species.

*Montenegrina dofleini sinosi* has a very restricted distribution and is known from a single site along the Lake Prespa shore, parapatric with *M. prespaensis*. It has been described due to its remarkably ribbed shell. Although it shows a different genital arrangement from *M. prespaensis* (Figure 12), it is not monophyletic in the phylogenetic tree, but intermingled within *M. prespaensis*. We, therefore, propose to consider the taxon *sinosi* as a subspecies of *M. prespaensis*: *M. prespaensis sinosi* comb. nov.

Although *M. dofleini kastoriae* and *M. hiltrudae robusta* have strikingly different shell features, these two taxa were found together within a distinct subclade within Clade D2, and were

separated by a remarkably small genetic distance (Mason et al., 2020). Due to this phylogenetic relationship, it remained an open question whether this affinity was due to introgression, incomplete lineage sorting or rapid change in shell morphology. Their identical genital anatomy supports their close phylogenetic relationship (Figure 9). We, therefore, suggest considering *M. kastoriae kastoriae* stat. nov. as a valid species and *M. kastoriae robusta* comb. nov. as its subspecies.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina dofleini dofleini</i> (Wagner, 1928)	<i>Montenegrina dofleini dofleini</i> (Wagner, 1928)
<i>Montenegrina dofleini fagorum</i> Nordsieck, 1974	<i>Montenegrina dofleini fagorum</i> Nordsieck, 1974
<i>Montenegrina dofleini kastoriae</i> Nordsieck, 1972	<i>Montenegrina kastroiae kastoriae</i> Nordsieck, 1972 stat. nov.
<i>Montenegrina dofleini pinteri</i> Nordsieck, 1974	<i>Montenegrina pinteri</i> Nordsieck, 1974 stat. nov.
<i>Montenegrina dofleini prespaensis</i> Nordsieck, 1988	<i>Montenegrina prespaensis prespaensis</i> Nordsieck, 1988 stat. nov.
<i>Montenegrina dofleini sinosi</i> Páll-Gergely, 2010	<i>Montenegrina prespaensis sinosi</i> Páll-Gergely, 2010 comb. nov.
<i>Montenegrina dofleini wagneri</i> Szekeres, 2006	<i>Montenegrina wagneri</i> Szekeres, 2006 stat. nov.
<i>Montenegrina hiltrudae robusta</i> Nordsieck, 2009	<i>Montenegrina kastoriae robusta</i> Nordsieck, 1972 comb. nov.

### *Montenegrina dofleini dofleini* (Wagner, 1928)

Figures 8.1–8.4

*Delima* (*Montenegrina*) *dofleini* Wagner, 1928 in Hesse, 1928: 19.

*Montenegrina dofleini dofleini* – Nordsieck, 1974: 153–154, plate 6, figs 31 and 32 – Zilch, 1981: 127. – Nordsieck, 2009: 74.

*Montenegrina* (*Montenegrina*) *kaiserii* Brandt, 1961: 4–5, plate 1, fig. 3.

*Montenegrina dofleini kaiserii* – Nordsieck, 1974: 154, plate 6, fig. 34. – Zilch, 1981: 127. – Nordsieck, 2009: 74.

*Montenegrina dofleini dofleini* – Fehér & Szekeres, 2016: 24, fig. 11H,J, distribution map fig. 14.

**Examined material: three dissected specimens.** Topotypes, North Macedonia, Ohrid District, Galičica Mts, ca. 500 m E of the Bugarska Chuka, 1,680 m, 41.0019°N, 20.8523°E [type locality of *kaiserii*], leg. ZF, EH, KJ, HS, 16.x.2014 (NHMW 110430/MN/0040, Mdo-537-01 [COI: KU307576, 16S: KU308047]).

**External genitalia (Figure 8.2):** The whole genital complex is medium-sized (PCRL = 23.5). The overall appearance of the genitalia is remarkably stocky. The FO is medium-sized (FO/V = 1.47) and wide in diameter. The vas deferens is uniformly thin. The first duct of the complex of the bursa copulatrix is short (DBC/DB = 0.18). The bursa copulatrix is club-like, very large, and wide (DB/V = 1.74), progressively swelling, without a distinct transition

zone between the second duct and the bursa itself. The apex is blunt and rounded. The diverticulum is medium-sized (D/V = 1.37), shorter than the bursa copulatrix (D/BC = 0.79), stocky, with a large base and rounded apex. The vagina is medium-sized (VRL = 10.4) and uniformly cylindrical. The atrium is long and large. The PC is longer than the vagina (PC/V = 2.26) and remarkably swollen and bulky. The retractor muscle is short and strong. The epiphallus is oval, swollen, and longer than the penis (E/P = 1.53). Proximally, it shrinks abruptly into the vas deferens.

**Inner genitalia (Figure 8.4):** The atrium has a big, polylobated fold originating directly at the genital aperture. The distal vagina has up to six smooth transversal pleats that do not continue into the atrium. These pleats merge into one another by means of small fleshy bridges forming a central small pleat. The proximal vagina has the vaginal pilaster surrounded by minor transversal pleats. The background walls are smooth. The penis has a variable number (4–7) of longitudinal metameric pleats. They are very irregularly arranged, proximally splitting, and distally merging into one another. The penial papilla is medium-sized, globose, irregular with a blunt apex. The aperture extends laterally and reaches the apical area. Its surface is smooth. The epiphallus has two or three smooth pleats originating proximally from the origin of the vas deferens. These pleats extend longitudinally and fade before the origin of the penial papilla. The background surface is smooth.

### *Montenegrina dofleini fagorum* Nordsieck, 1974

Figures 8.5–8.8

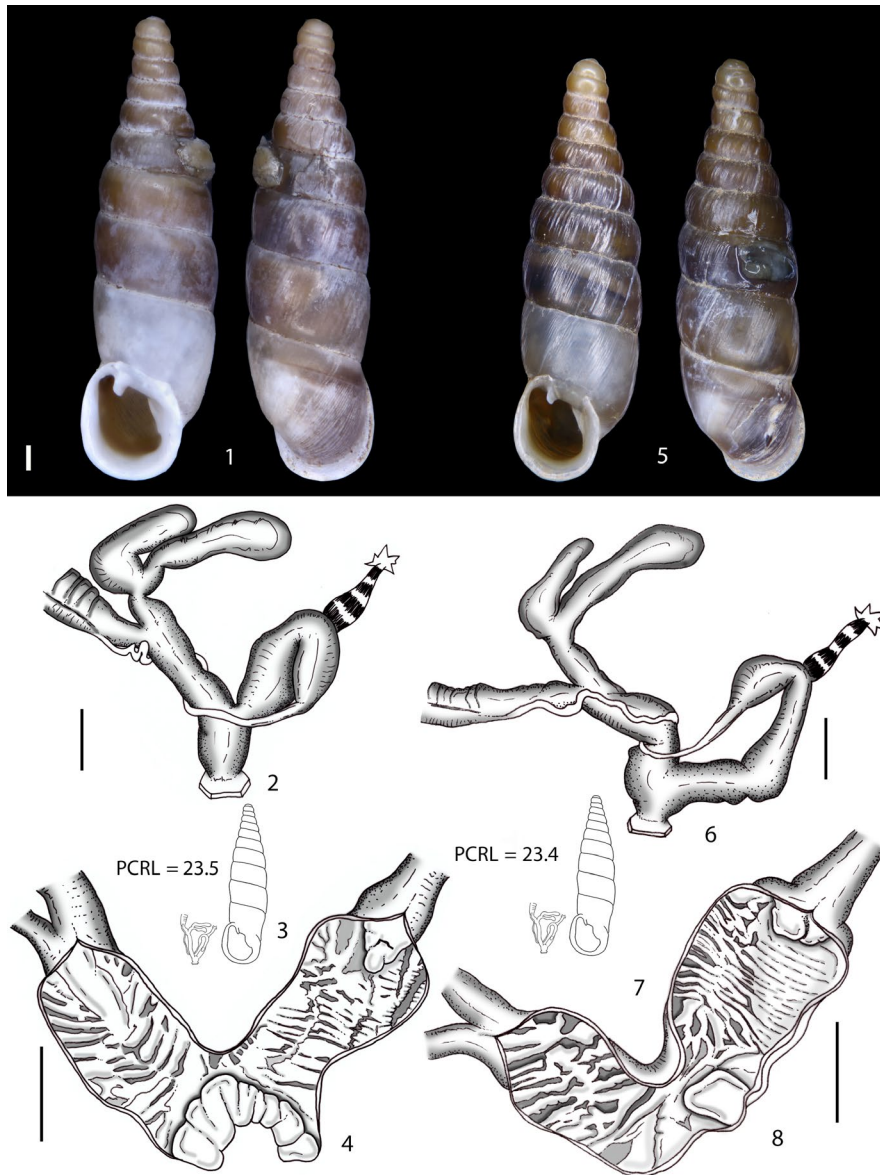
*Montenegrina janinensis fagorum* Nordsieck, 1974: 152, plate 5, fig. 30. – Zilch, 1981: 129, plate 13, fig. 27 – Nordsieck, 2009: 75.

*Montenegrina dofleini fagorum* – Fehér & Szekeres, 2016: 26, fig. 11I, distribution map fig. 14.

**Examined material: three dissected specimens.** North Macedonia, Galičica Mts, 12 km from the Sveti Naum to Ohrid road towards Carina, 1,540 m, 40.9627°N, 20.8171°E, leg. ZF, LT, 8.viii.2014 (NHMW 110430/MN/0052, Mfa-507-01 [COI: KU307668, 16S: KU308103]; Mfa-507-02 [COI: MT251596]).

**External genitalia (Figure 8.6):** The whole genital complex is medium-sized (PCRL = 23.5). The overall appearance of the genitalia is stocky. The FO is long (FO/V = 0.92) and wide in diameter. The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is very long (DBC/DB = 0.47). The bursa copulatrix is club-like, very large, and wide (DB/V = 1.46) with thinner base and progressively swelling, without a distinct transition zone between the second duct and the actual bursa. The apex is blunt and rounded. The diverticulum is short (D/V = 0.85), shorter than the bursa copulatrix (D/BC = 0.58), stocky, with a large base and rounded apex. The vagina is medium-sized (VRL = 10.2) and uniformly cylindrical. The atrium is long and large. The PC is longer than the vagina (PC/V = 2.31) and remarkably swollen and bulky. The retractor muscle is short and strong. The epiphallus is longer than the penis (E/P = 1.73). Its section from penial papilla to retractor muscle is





**FIGURE 8** 8.1–8.4 *Montenegrina dofleini dofleini* (Wagner, 1928) NHMW 110430/MN/0040. 8.1 shell, 8.2 shell-genitalia ratio, 8.3 whole genitalia except gonads and proximal spermoviduct, 8.4 inner distal genitalia. 8.5–8.8 *Montenegrina dofleini fagorum* Nordsieck, 1974 NHMW 110430/MN/0052. 8.5 shell, 8.6 whole genitalia except gonads and proximal spermoviduct, 8.7 shell-genitalia ratio, 8.8 inner distal genitalia

slim, whereas its proximal portion is oval, swollen, then abruptly tapering and turning into the vas deferens.

**Inner genitalia (Figure 8.8):** The atrium has a big, unilobate fold originating directly at the genital aperture. The fold is smooth and spoon-like. The distal vagina has a few smooth, irregularly arranged pleats. The proximal vagina has many elevated, oblique, and transversal pleats. These pleats are irregularly arranged, splitting, and merging into one another, with irregular fringed edges. The vaginal pilaster is absent or probably hard to detect, most likely becoming part of the irregular pleating. The penis has many small transversal pleats which split, forming spaces where the smooth background is visible. The pleats become irregular towards the distal penis, losing their regular transversal arrangement. The medium-sized, conical penial papilla has a pointed but nonetheless broad apex and a smooth surface. The aperture does not reach the papilla's tip

laterally. The epiphallus has three simple smooth pleats originating proximally from the distal end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina kastoriae kastoriae* Nordsieck, 1972 stat. nov.

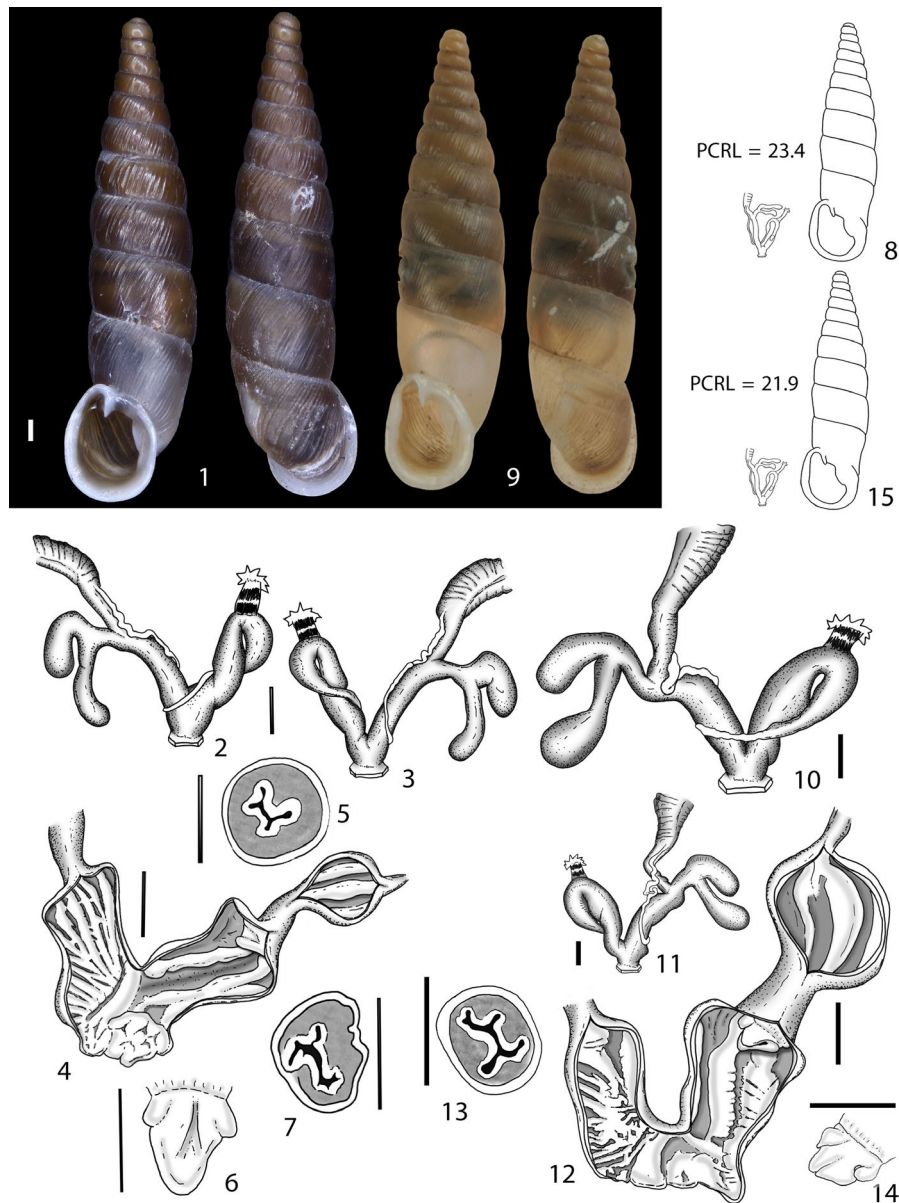
Figures 9.1–9.8

*Montenegrina kastoriae* Nordsieck, 1972: 34, plate 4, fig. 33.

*Montenegrina dofleini kastoriae* – Nordsieck, 1974: 153. – Zilch, 1981: 127, plate 14, fig. 35.

*Montenegrina kastoriae kastoriae* – Nordsieck, 2009: 74.

*Montenegrina dofleini kastoriae* – Fehér & Szekeres, 2016: 27, fig. 11K, distribution map fig. 14.



**FIGURE 9** *Montenegrina kastoriae kastoriae* Nordsieck, 1972 stat. nov. HNHM 99570. 9.1 shell. 9.2–9.3 whole genitalia except gonads and proximal spermoviduct. 9.4 inner distal genitalia. 9.5 cross section of epiphallus. 9.6 penial papilla. 9.7 cross section of penial papilla. 9.8 shell-genitalia ratio. 9.9–9.12 *Montenegrina kastoriae robusta* Nordsieck, 2009 comb. nov. NHMW 110430/MN/0118. 9.9 shell. 9.10–9.11 whole distal genitalia. 9.12 inner distal genitalia. 9.13 cross section of epiphallus. 9.14 penial papilla. 9.15 shell-genitalia ratio

**Examined material:** two dissected specimens. Greece, Western Macedonia, Kastoria, N side of the peninsula, behind Yacht Club, 640 m, 40.5233°N, 21.2747°E [type locality], leg. ZF, EH, KJ, HS, 17.x.2014 (HNHM 99570, Mks-401-01 [COI: KU307701, 16S: KU308126]; Mks-401-02 [COI: KU307702]).

**External genitalia (Figures 9.3–9.4):** The whole genital complex is medium-sized (PCRL = 23.9). The overall appearance of the genitalia is stocky. The FO is medium-sized (FO/V = 0.57) and wide in diameter. The vas deferens is uniformly thin, with only a slight swelling along its proximal part. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.27). The bursa copulatrix is club-like, short but wide (DB/V = 0.96); no distinct transition zone was detected between the second duct and the bursa itself. The apex is blunt and

rounded. The diverticulum is short ( $D/V = 0.96$ ), as long as the bursa copulatrix ( $D/BC = 1.0$ ), stocky, with a large base and rounded apex. The vagina is medium-sized ( $VRL = 12.2$ ) and uniformly cylindrical. The atrium is large. The PC is longer than the vagina ( $PC/V = 1.96$ ) and uniformly cylindrical. The retractor muscle is very short and strong. The epiphallus is longer than the penis ( $E/P = 1.53$ ), wide in diameter and without a visible transition area with the vas deferens.

**Inner genitalia (Figures 9.5–9.8):** The atrium has three or four big, pad-like, smooth, large, and irregular pleats. These pleats, at first glance, resemble an uninterrupted, continuous large fold. The distal vagina has a big, lone transversal pleat that is large, smooth, and well elevated. The proximal vagina has up to 10 elevated, longitudinal, or slightly oblique pleats that are more or less irregularly

arranged. The pleats are connected to each other with small fleshy bridges that are more or less thick. The vaginal pilaster is present, and the background walls are smooth. The penis has two main large and elevated longitudinal pleats, which often split proximally and distally without entering the atrium. The background walls are smooth. The penial papilla is medium-sized, pyramidal, and with a blunt apex. The aperture runs laterally, not reaching the apical area. The surface is smooth. The epiphallus has 2 up to 3 simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

***Montenegrina kastoriae robusta* Nordsieck, 2009  
comb. nov.**

Figures 9.9–9.12

*Montenegrina skipetarica robusta* – Nordsieck, 2009: 77–78, plate 2, fig. 8.

*Montenegrina hiltrudae robusta* – Fehér & Szekeres, 2016: 53, fig. 19I, distribution map fig. 20.

**Examined material: two dissected specimens.** Greece, Western Macedonia, 4 km from Gavros towards Kotas along the Kastoria to Florina road, 850 m, 40.6532°N, 21.1789°E [type locality], leg. ZF, EH, KJ, HS, 18.x.2014 (NHMW 110430/MN/0118, Mro-554-01 [COI: KU307778, 16S: KU308177, 12S: KU307978]; Mro-554-02 [COI: MT251759]).

**External genitalia (Figures 9.10–9.11):** The whole genital complex is medium-sized (PCRL = 21.9) and very strong. The FO is long (FO/V = 0.80). The vas deferens gradually swells towards the epiphallus. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.30). The bursa copulatrix is medium-sized (DB/V = 0.80), wide and club-like. The second duct is cylindrical, and a transition into the bursa is distinguishable. The bursa is wide and rounded. The diverticulum is short (D/V = 0.52), wide, uniformly cylindrical, and shorter than the bursa copulatrix (D/BC = 0.65). The apex is wide and rounded. The vagina is medium-sized (VRL = 11.2), wide, and uniformly cylindrical. The atrium is short but very large. The PC is much longer than the vagina (PC/V = 1.96). The penis is wide and swollen at the level of the penial papilla. The epiphallus is slightly longer than the penis (E/P = 1.72) and swollen along both its distal and proximal sections. A clear transitional area is visible between the epiphallus and vas deferens. The retractor muscle is very short and strong.

**Inner genitalia (Figures 9.12–9.14):** The atrium shows three or four big, pad-like, irregular smooth folds. The distal vagina has many smooth, scattered, irregularly arranged pleats, eventually splitting and merging into one another. The proximal vagina exhibits many smooth pleats that slant and are irregularly arranged. The background walls are smooth. The vaginal pilaster is present. The penis has two or three main pleats originating from the proximal section close to the penial papilla and extending as far the atrium. These pleats are irregularly fringed. The background walls are finely granulated. The medium-sized penial papilla is pyramidal and pointed. The aperture extends

laterally and does not reach the apical area. The surface is smooth and two small, roundish basal lobes are present, yielding an overall tricuspid-like shape. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

***Montenegrina pinteri* Nordsieck, 1974 stat. nov.**

Figures: 10.1–10.11

*Montenegrina janinensis pinteri* Nordsieck, 1974: 154, plate 6, fig. 33.

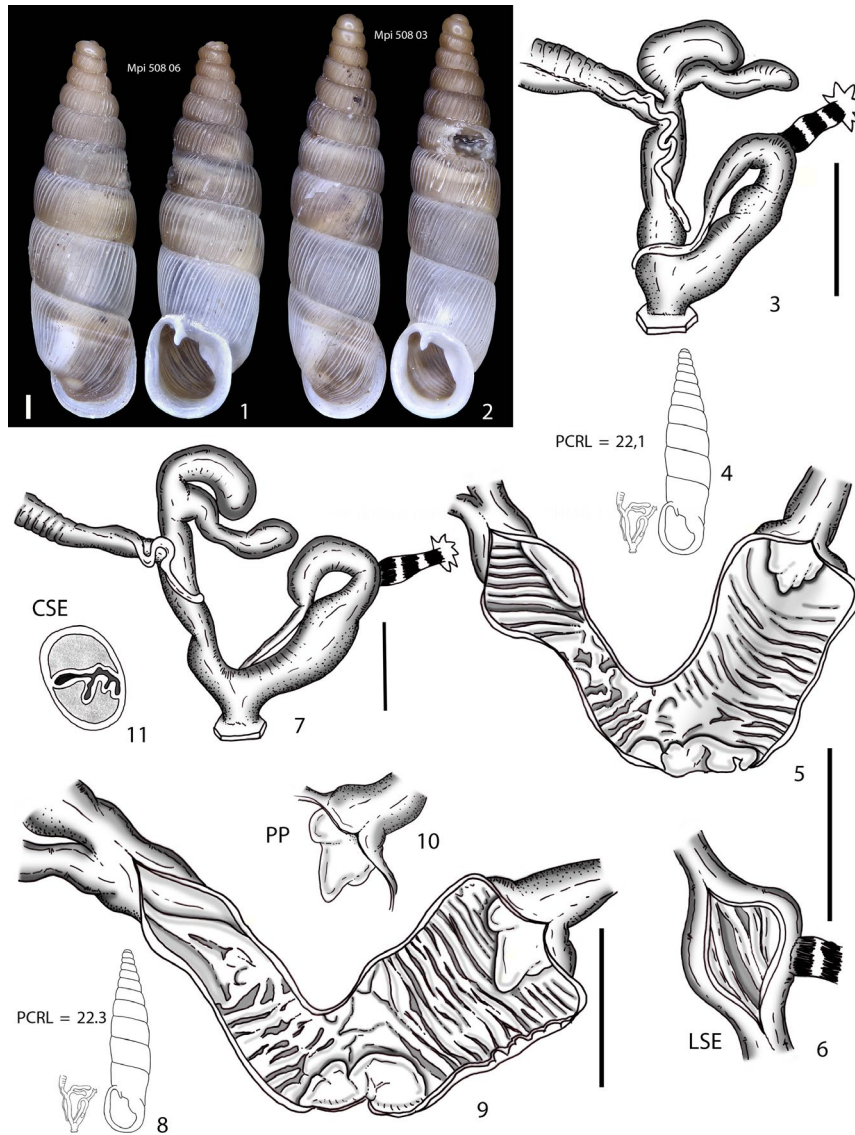
*Montenegrina dofleini pinteri* – Zilch, 1981: 127, plate 15, fig. 39.  
– Nordsieck, 2009: 74.

*Montenegrina dofleini pinteri* – Fehér & Szekeres, 2016: 28, fig. 11L, distribution map fig 14.

**Examined material: two dissected specimens.** North Macedonia, Ohrid District, N of Trpejca, shore of Lake Ohrid, 700 m, 40.9656°N, 20.7858°E [type locality], leg. ZF, LT, 9.viii.2014 (NHMW 110430/MN/0051, Mpi-508-02 [COI: KU307745]; Mpi-508-03 [COI: KU307746]).

**External genitalia (Figures 10.3 and 10.7):** The whole genital complex is medium-sized (PCRL = 22.1). The FO is medium-sized (FO/V = 0.44). The vas deferens is uniformly thin, only slightly swollen along its proximal part. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.18). The bursa copulatrix is club-like, large (DB/V = 1.06) and no distinct transition zone between the second duct and the actual bursa is detectable. The apex is blunt. The diverticulum is medium-sized (D/V = 1.06) and as long as the bursa copulatrix (D/BC = 1.0), stocky, with a large base and rounded apex. The vagina is short (VRL = 9.8) and narrows along its midportion. The atrium is large. The PC is longer than the vagina (PC/V = 2.25) with a swelling at the level of the penial papilla. The retractor muscle is short and strong. The epiphallus is longer than the penis (E/P = 1.12). Its section extending from the penial papilla to the retractor muscle is large and cylindrical, whereas the proximal part gradually tapers and becomes the vas deferens without a clear transitional area.

**Inner genitalia (Figures 10.5 and 10.9):** The atrium has a big and polylobated fold originating directly at the genital aperture. The distal vagina has 5–10 transversal and irregular pleats that do not continue into the atrium. The proximal vagina has many elevated, oblique, or transversal pleats that converge towards the vaginal pilaster. The background walls are smooth. The whole penis has many small transversal pleats. These pleats split from each other, forming visible spaces between them, especially along the upper, proximal part of the penis. They become irregular towards the distal penis. The medium-sized penial papilla is pyramidal and has a pointed apex. The aperture extends laterally but does not reach the apical area. The surface is smooth, and small, roundish basal lobes are present, yielding an overall “tricuspid” shape. The epiphallus has up to five simple, smooth pleats originating proximally from the end of the vas deferens and fading



**FIGURE 10** *Montenegrina pinteri* Nordsieck, 1974 stat. nov. NHMW 110430/MN/0051. 10.1–10.2 shells. 10.3 whole genitalia except gonads and proximal spermoviduct specimen Mpi-508-6. 10.4 shell-genitalia ratio specimen Mpi-508-6. 10.5 inner distal genitalia specimen Mpi-508-6. 10.6 longitudinal section of epiphallus specimen Mpi-508-6. 10.7 whole genitalia except gonads and proximal spermoviduct specimen Mpi-508-3. 10.8 shell-genitalia ratio specimen Mpi-508-3. 10.9 inner distal genitalia specimen Mpi-508-3. 10.10 penial papilla specimen Mpi-508-3. 10.11 cross section of epiphallus specimen Mpi-508-3

before the origin of the penial papilla. The background is smooth, only slightly granulated.

***Montenegrina prespaensis prespaensis* Nordsieck, 1988 stat. nov.**

Figures 11.1–11.11

*Montenegrina dofleini prespaensis* Nordsieck, 1988: 199–200, fig. 4.

*Montenegrina dofleini* ssp. – Nordsieck, 1974: 153.

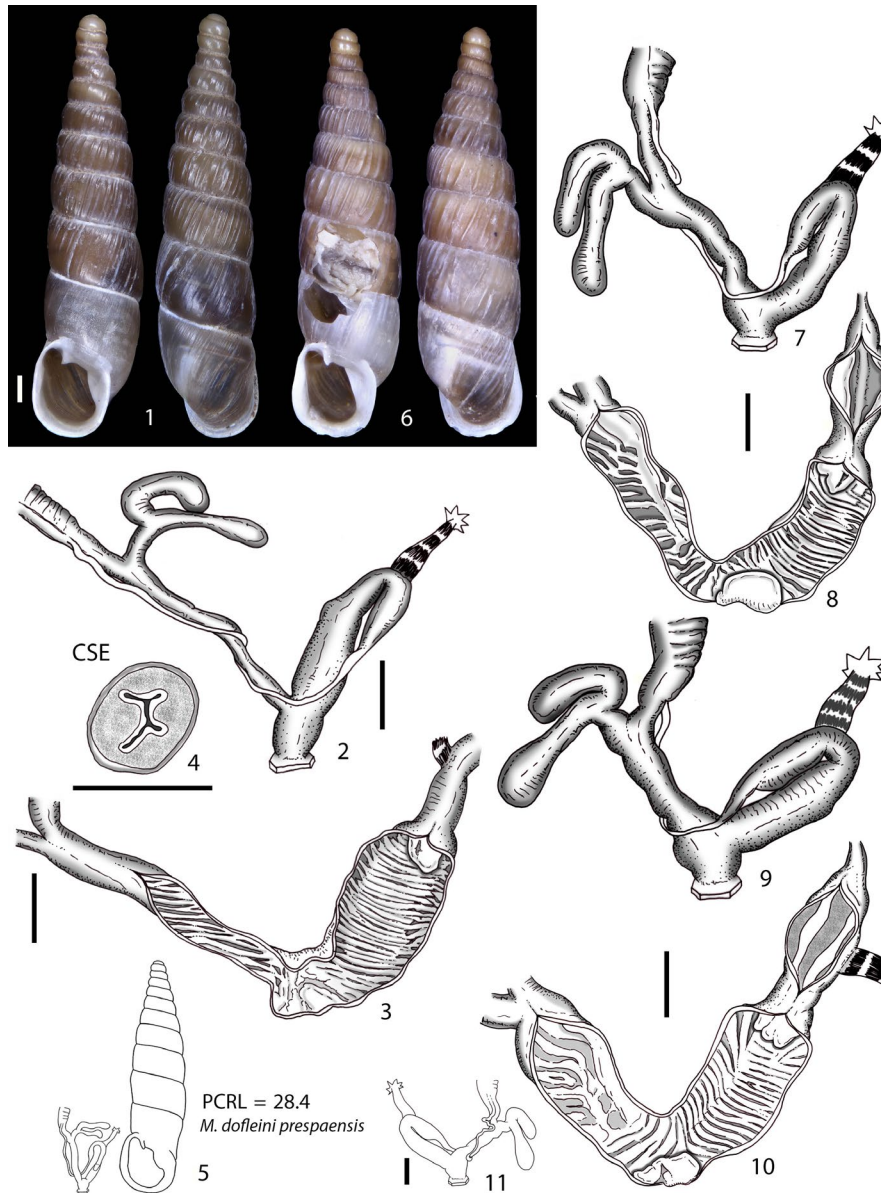
*Montenegrina kastoriae prespaensis* – Nordsieck, 2009: 74.

*Montenegrina dofleini prespaensis* – Fehér & Szekeres, 2016: 29, fig. 11M, distribution map fig. 14.

**Examined material:** nine dissected specimens. Greece, Psarades, N of the village, E side of the bay, 870 m, 40.8316°N, 21.0287°E [type locality], leg. PS, 10.v.1995 (HNHM 12040, Mpr-110 [COI: KU307753, 16S: KU308169, 12S: KU307974]); same locality, leg. ZE, ZF, JG, 28.vi.2013 (HNHM 99573, Mpr-404-01 [COI: KU307754, 12S: KU307975]; Mpr-404-03 [COI: KU307755]);

Albania, Korçë district, Sv. Marena cave temple, ca. 4 km E of Kallamas, at Liqeni i Prespës, 850 m, 40.8872°N, 20.9729°E, leg. ZE, ZF, JG, 29.vi.2015 (NHMW 110430 MN0134, Mpr-616-02 [COI: MT251568, 12S: MT249805]).

**External genitalia (Figures 11.2, 11.7, and 11.9):** The whole genital complex is medium-sized (PCRL = 28.2). The FO is short (FO/V = 0.24). The vas deferens is uniformly thin. The first duct



**FIGURE 11** *Montenegrina prespaensis prespaensis* Nordsieck, 1988 stat. nov. HNHM 99573. 11.1 shell. 11.2 whole distal genitalia. 11.3 inner distal genitalia. 11.4 cross section of the epiphallus. 11.5 shell-genitalia ratio. NHMW 110430/MN/0134 Mrp-616\_04. 11.6 shell. 11.7 whole distal genitalia. 11.8 inner distal genitalia NHMW 110430/MN/0134 Mrp-616\_01. 11.9 whole distal genitalia. 11.10 inner distal genitalia. 11.11 whole distal genitalia

of the bursa copulatrix complex is medium-sized ( $DBC/DB = 0.39$ ). The bursa copulatrix is short ( $DB/V = 0.58$ ). Its proximal and distal portions are swollen, the midportion thinner. A transition zone between the second duct and the bursa itself is detectable at the level of the thinner portion. The apex is blunt. The diverticulum is short ( $D/V = 0.4$ ), and shorter ( $D/BC = 0.70$ ) but slightly wider than the bursa. It is cylindrical or only slightly distally swollen and with a rounded apex. The vagina is long ( $VRL = 24.5$ ), considerably thinner than the penis and uniformly cylindrical. The atrium is large and long. The PC is slightly longer than the vagina ( $PC/V = 1.15$ ) with a wide and large penial portion and a thinner epiphallus. The retractor muscle is moderately long and strong. The epiphallus is longer than

the penis ( $E/P = 1.88$ ), narrows progressively, and merges into the vas deferens without a clearly visible transitional area.

**Inner genitalia (Figures 11.3, 11.8, and 11.10):** The atrium has few irregular smooth and fleshy large pleats. The distal vagina has 5–8 oblique, smooth pleats that are irregular, splitting, and merging into one another. The proximal vagina has many oblique, elevated, transversal pleats that split and merge and that directly continue into the distal vaginal portion. The background walls are smooth. The vaginal pilaster is present but short and limited to the first portion of proximal vagina. The penis has many small transversal and fine pleats. These pleats branch off each other, especially along the proximal portion of the penis. They become progressively more

irregular along the distal penis. The penial papilla is medium-sized, globose, irregular, and with blunt apex. The aperture extends laterally, reaching the apical area. The surface is smooth. The epiphallus has up to five simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

***Montenegrina prespaensis sinosi* Páll-Gergely, 2010  
comb. nov.**

Figures 12.1–12.5

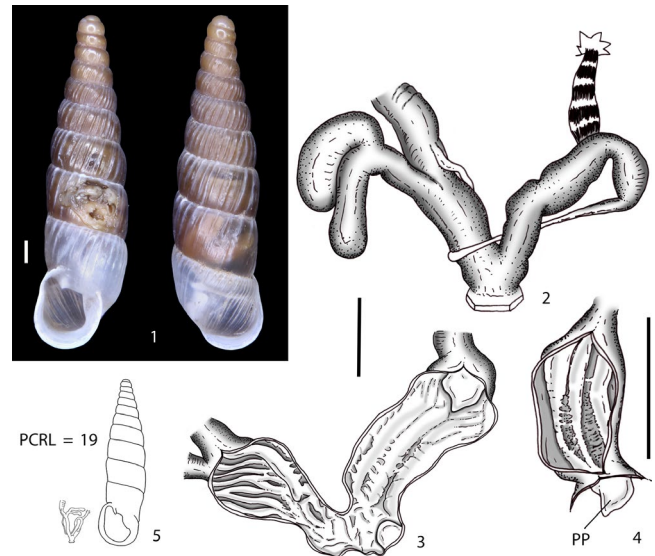
*Montenegrina dofleini sinosi* Páll-Gergely, 2010: 150–152, figs 1 and 2 (genital anatomy, clausilium plate).

*Montenegrina dofleini sinosi* – Fehér & Szekeres, 2016: 30, fig. 11N, distribution map fig. 14.

**Examined material: three dissected specimens.** Greece, Western Macedonia, southern shore of Lake Prespa, Agios Achillios, near the junction to Psarades, 850 m, 40.8105°N, 21.0702°E [type locality], leg. ZF, EH, KJ, HS, 18.x.2014 (NHMW 110430/MN/0058, Msi-553-02 [COI: KU307795]; Msi-553-03 [COI: KU307796]; Msi-553-05 [COI: MT251769]).

**External genitalia (Figure 12.2):** The whole genital complex is short (PCRL = 19.0). The overall appearance of the genitalia is stocky. The FO is medium-sized (FO/V = 0.42) and wide in diameter. The vas deferens is distally thinner. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.40). The bursa copulatrix is long (DB/V = 1.25). It is uniformly cylindrical with no distinct transition zone between the second duct and the bursa itself. The apex is blunt and well rounded. The diverticulum is uniformly cylindrical, long (D/V = 1.42), and longer (D/BC = 1.13) and slightly wider than the bursa copulatrix. The vagina is very short (VRL = 7.8) but very wide in diameter. The atrium is large. The PC is much longer than the vagina (PC/V = 2.42) with a wide and large penial portion and a swollen proximal epiphallus. The retractor muscle is moderately long and strong. The epiphallus is longer than the penis (E/P = 1.64). Its proximal portion narrows and merges into the vas deferens with a clearly visible transitional area.

**Inner genitalia (Figures 12.3–12.4):** The atrium has one small, smooth, spoon-like fold. The background of the atrium shows a variety of smooth and irregularly arranged large fleshy pleats. The distal vagina has a number of smooth, scattered, irregularly arranged fleshy pleats. The proximal vagina has many elevated, oblique, or transversal pleats that converge towards the vaginal pilaster. The background walls are smooth. The proximal penis has 6–10 smooth fleshy folds, all abruptly merging into one another, forming three main smooth, large longitudinal pleats. These pleats are connected distally with many fleshy smooth bridges. This pattern abruptly stops at the atrium level. The background is smooth. The medium-sized, conical penial papilla has a pointed but nonetheless broad apex and a smooth surface. The aperture is lateral and does not reach the papilla's tip. The epiphallus has three fringed pleats with jagged edges, originating proximally from



**FIGURE 12** *Montenegrina prespaensis sinosi* Páll-Gergely, 2010 comb. nov. NHMW 110430/MN/0058. 12.1 shells. 12.2 whole distal genitalia. 12.3 inner distal genitalia. 12.4 longitudinal section of the epiphallus. 12.5 shell-genitalia ratio

the end of the vas deferens and fading before the origin of the penial papilla. The background has a fine, irregular pattern.

***Montenegrina wagneri* Szekeres, 2006 stat. nov.**

*Montenegrina apfelbecki wagneri* Szekeres, 2006 in Eröss, Fehér, & Szekeres, 2006: 186–188, fig. 6.

*Montenegrina dofleini wagneri* – Fehér & Szekeres, 2016: 30, fig. 11O, distribution map fig. 14.

No alcohol-preserved specimen was available for anatomical investigations.

***Montenegrina drimmeri* Fehér & Szekeres, 2006 sensu Fehér & Szekeres, 2016**

**Taxonomic and systematic remarks**

In the phylogenetic tree, one specimen, Mde-204-01, was positioned in the *M. drimica* subclade H2 within Clade H, while all the others formed a subclade in Clade L, rendering *M. laxa* paraphyletic. This finding suggested (any lab mistake could be excluded) introgression between quite distant taxa. The genital anatomy of the single specimen of *M. drimmeri* of Clade H (Mde-204-01) proved to be identical with one from Clade L (Mde-204-02), supporting the assumption of introgression (regarding specimen Mde-204-01). The distinct position of *M. drimmeri* within Clade L and the fact that its genital anatomy differs from *M. laxa* (Figure 10), together with its peculiar shell features (Fehér & Szekeres, 2016: 31), supports the validity of this species.

Fehér &amp; Szekeres, 2016

De Mattia et al., 2020

*Montenegrina drimmeri* Fehér & Szekeres, 2006*Montenegrina drimmeri* Fehér & Szekeres, 2006***Montenegrina drimmeri* Fehér & Szekeres, 2006**

Figures 13.1–13.5

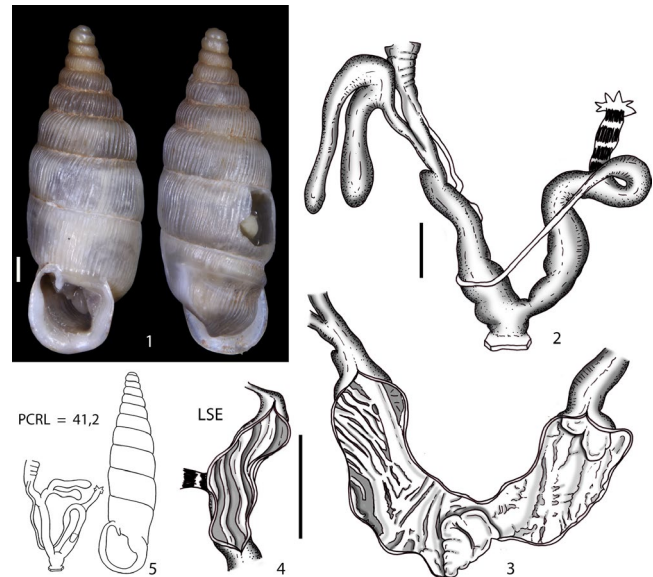
*Montenegrina drimmeri* Fehér & Szekeres, 2006 in Eröss et al., 2006: 182–184, fig. 1.

– Nordsieck, 2009: 73 – Fehér & Szekeres, 2016: 31, fig. 15N, distribution map fig. 16.

**Examined material:** two dissected specimens (paratypes). Albania, Dibrë District, Lunarë, at the bridge of the Lumi i Murrës (22 km W of Fushë-Muhurr along the Peshkopi to Burrel road) 730 m, 41.6256°N, 20.2498°E [type locality], leg. ZE, ZF, JK, DM, 26.vi.2003, (HNHM 94830, Mde-204-01 [COI: MT251546, 16S: MT160791]; Mde-204-02 [COI: KU307629, 16S: KU308076]).

**External genitalia (Figure 13.2):** The whole genital complex is long (PCRL = 41.2). The FO is medium-sized (FO/V = 0.45) and thin in diameter. The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is very long (DBC/DB = 0.68) and very thin. The bursa copulatrix is short (DB/V = 0.39). It is club-like and no distinct transition zone between the second duct and the bursa itself is visible. The apex is blunt. The diverticulum is medium-sized (D/V = 1.15), longer (D/BC = 1.58) but thinner than the bursa copulatrix and more or less uniformly cylindrical. The vagina is long (VRL = 24.3), very thin proximally and not continuing directly into the wider portion of the distal vagina, but inserting into it laterally, forming a kind of proximal sac. The atrium is large with a lateral lobe of likely glandular origin. The PC is longer than the vagina (PC/V = 1.70) and slightly swollen at the level of the penial papilla. The retractor muscle is short and strong. The epiphallus is much longer than the penis (E/P = 3.0), merging into the vas deferens with a clearly visible transitional area.

**Inner genitalia (Figures 13.3–13.4):** The atrium has a big, polylobated fold originating directly at the genital aperture. The distal vagina has 6–10 smooth transversal pleats that are very irregular in shape, often splitting, and merging into one another. The proximal vagina has many oblique, transversal, elevated pleats that irregularly converge towards the vaginal pilaster. The vaginal background is smooth. The penis has a set of 5–8 longitudinal or slightly oblique, smooth pleats. These pleats are very irregular, broadly fringed, randomly splitting, or merging at proximal and distal level. The background is visible and smooth. The papilla is medium-sized, globose with blunt apex. The aperture runs laterally, reaching the apical area. The surface is smooth. The epiphallus has up to five simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.



**FIGURE 13** *Montenegrina drimmeri* Fehér & Szekeres, 2006 HNHM 94830. 13.1 shells. 13.2 whole distal genitalia. 13.3 inner distal genitalia. 13.4 longitudinal section of the epiphallus. 13.5 shell-genitalia ratio

***Montenegrina fuchsi* Brandt, 1961 and *Montenegrina rugilabris* (Mousson, 1859) sensu Fehér & Szekeres, 2016**

**Taxonomic and systematic remarks**

Most of the subspecific taxa (including the nominal one) of *M. fuchsi* are positioned in Clade D1, with the only exception being *M. fuchsi muranyii*, which is in Clade K and will be discussed together with *M. tomorosi*. All the *M. rugilabris* taxa fall into Clade D1.

The Clade D1 taxa inhabit an area that extends from southern Albania to the Epirus, along an axis of ca. 130 km in NW–SE direction. The sympatry of *M. fuchsi*, *M. rugilabris*, and *M. janinensis* (sensu Fehér & Szekeres, 2016) over this territory (Fehér & Szekeres, 2016: 59 and 92) supports the phylogenetic situation of this group.

*Montenegrina rugilabris gregoi* splits from the most basal node within Clade D1. *Montenegrina fuchsi fuchsi* is the sister group of *M. rugilabris golikutensis*. *Montenegrina fuchsi pallida* is the sister group of the clade containing *M. rugilabris lambdaformis* and *M. rugilabris welterschultesi*. *Montenegrina fuchsi klemmi* is the sister group of *M. rugilabris rugilabris* and *M. rugilabris irmengardis*. Finally, *M. rugilabris edmundi* is the sister group of *M. janinensis*. Thus, both *M. fuchsi* and *M. rugilabris* (in the sense of Fehér & Szekeres, 2016) are paraphyletic (Mason et al., 2020).

The subspecies of *M. fuchsi* and *M. rugilabris* have been grouped together based on shell morphology and the lunella complex in particular (Fehér & Szekeres, 2016).

The genital morphology proved to be different in most of the subspecific taxa of both *M. fuchsi* and *M. rugilabris*, supporting the molecular genetic evidence that most of the taxa grouped within

these two species by Fehér and Szekeres (2016) are not conspecific; we therefore treat *M. edmundi* stat. nov., *M. klemmi* stat. nov., *M. rugilabris*, *M. fuchsi*, *M. golikutensis* stat. nov., *M. pallida* stat. nov., *M. lambdaformis* stat. nov., and *M. gregoi* stat. nov. as valid species.

The typical *M. rugilabris irmengardis* and *M. rugilabris rugilabris* show a similar genital morphology, differing only slightly in the inner sculpturing of the penis (weak transversal pattern and a central hollow versus a chevron-like pattern with central groove, see Figures 16 and 18). Therefore, we prefer to keep *M. rugilabris irmengardis* as a subspecies of *M. rugilabris*.

Having no anatomical data for *M. lambdaformis*, and based on its close phylogenetic relationship with *M. rugilabris welterschultesi* (the latter revealing a peculiar genital arrangement), we treat them as conspecific. Since *M. lambdaformis* has the priority, we consider *M. lambdaformis lambdaformis* stat. nov. as a valid species and *M. lambdaformis welterschultesi* comb. nov. as its subspecies.

*Montenegrina gregoi* stat. nov. appears in a distinct monophyletic subclade. Nevertheless, its genital anatomy is remarkably similar to *M. golikutensis*, with very elongated and thin genitalia and the inner walls of both male and female parts totally smooth.

The two taxa inhabit the two extremes of the known distribution area of Clade D1, around 120 km apart. Assuming that isolation soon leads to a change in the morphology of the genitalia, it is likely that even phylogenetically distant taxa show similarities merely by chance. The similarity in the genital anatomy between *M. gregoi* stat. nov. and *M. golikutensis* stat. nov. (extremely thin and elongated genitalia) could be due to plesiomorphy or homoplasy.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina fuchsi fuchsi</i> Brandt, 1961	<i>Montenegrina fuchsi</i> Brandt, 1961
<i>Montenegrina fuchsi klemmi</i> Brandt, 1962	<i>Montenegrina klemmi</i> Brandt, 1962 stat. nov.
<i>Montenegrina fuchsi pallida</i> Fauer, 1993	<i>Montenegrina pallida</i> Fauer, 1993 stat. nov.
<i>Montenegrina rugilabris rugilabris</i> (Mousson, 1859)	<i>Montenegrina rugilabris rugilabris</i> (Mousson, 1859)
<i>Montenegrina rugilabris edmundi</i> Szekeres, 2006	<i>Montenegrina edmundi</i> Szekeres, 2006 stat. nov.
<i>Montenegrina rugilabris golikutensis</i> Fehér and Szekeres, 2016	<i>Montenegrina golikutensis</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina rugilabris gregoi</i> Fehér and Szekeres, 2016	<i>Montenegrina gregoi</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina rugilabris irmengardis</i> Klemm, 1962	<i>Montenegrina rugilabris irmengardis</i> Klemm, 1962
<i>Montenegrina rugilabris welterschultesi</i> Fehér and Szekeres, 1999	<i>Montenegrina lambdaformis welterschultesi</i> Fehér & Szekeres, 1999 comb. nov.
<i>Montenegrina rugilabris lambdaformis</i> Reischütz and Sattmann, 1990	<i>Montenegrina lambdaformis lambdaformis</i> Reischütz and Sattmann, 1990 stat. nov.

## Montenegrina fuchsi Brandt, 1961

Figures 14.1–14.7

*Montenegrina (Heteroptycha) fuchsi* Brandt, 1961: 2–3, plate 1, fig. 1.

*Montenegrina fuchsi fuchsi* – Zilch, 1981: 128, plate 13, fig. 25 – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 32, fig. 15b, distribution map fig. 16.

**Examined material: three dissected specimens.** Albania, Tepelenë District, 7 km W of Këlcyre, near the bridge at the Peshtan junction, 170 m, 40.2961°N, 20.1076°E [type locality], leg. DA, ZE, ZF, JG, 29.vi.2014 (NHMW 110430/MN/0036, Mfu-474-01 [COI: KU307675, 16S: KU308108]).

**External genitalia (Figures 14.2, 14.5):** The whole genital complex is medium-sized (PCRL = 22.8). The FO is very short (FO/V = 0.23). The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is long (DBC/DB = 0.56) and thin. The bursa copulatrix is short (DB/V = 0.6). It is uniformly cylindrical, thin and lacks a visible transition zone between the second duct and the bursa proper. The apex is blunt. The diverticulum is very short (D/V = 0.47), and shorter (D/BC = 0.78) and as wide as the bursa copulatrix. It is more or less uniformly cylindrical. The vagina is long (VRL = 22.1), thin proximally, but gradually swelling slightly distally. The atrium is large. The PC is as long as the vagina (PC/V = 1.03), slightly swollen at the level of the penial papilla. The epiphallus abruptly merges into the vas deferens with a clearly visible transitional area. The retractor muscle is long and slim. The epiphallus is shorter than the penis (E/P = 0.82).

**Inner genitalia (Figures 14.3–14.4, 14.6):** The atrium has a set of 4–7 fleshy, overlapping, irregular large folds. The surface of the folds is smooth. The distal vagina has many smooth, scattered, and irregularly arranged fleshy pleats that do not form any organized pattern. The proximal vagina has 5–10 elevated longitudinal pleats, which can be connected with small fleshy bridges of variable thickness. Along the distal vagina the pleats suddenly become irregular and merge into one another, forming one irregular pattern. The vaginal pilaster is present. The penis is smooth but with trace of flat, minimally elevated longitudinal pleats. The proximal pleats merge into one another midway to distal penis. The penial papilla is medium-sized and clearly bilobed with the aperture in the middle of the two lobes. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

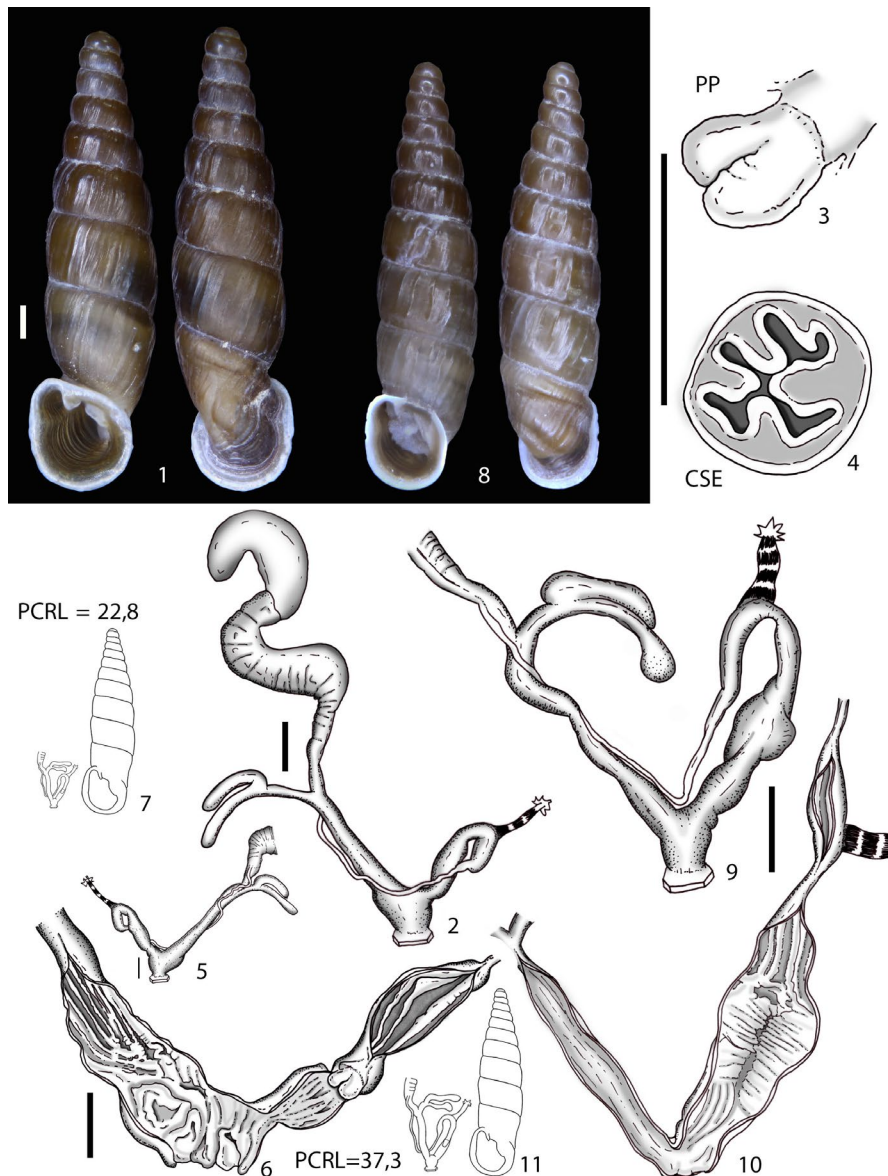
## Montenegrina klemmi Brandt, 1962 stat. nov.

Figures 14.8–14.11

*Montenegrina (Heteroptycha) fuchsi klemmi* Brandt, 1962: 143, plate 5, fig. 13.

*Montenegrina fuchsi klemmi* – Zilch, 1981: 128, plate 13, fig. 26 – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 34, fig. 15C, distribution map fig. 16.





**FIGURE 14** 14.1–14.7 *Montenegrina fuchsi* Brandt, 1961 NHMW 110430/MN/0036. 14.1 shells. 14.2 whole distal genitalia. 14.3 penial papilla. 14.4 cross section of epiphallus. 14.5 whole distal genitalia. 14.6 inner distal genitalia. 14.7 shell-genitalia ratio. 14.8–14.11 *Montenegrina klemmi* Brandt, 1962 stat. nov. HNHM 99272. 14.8 shell, 14.9 whole distal genitalia, 14.10 inner distal genitalia, 14.11 shell-genitalia ratio

**Examined material:** two dissected specimens. Albania, Gjirokastër District, 3 km NE of Suhë, along the Libohovë to Sheper road, 430 m, 40.0882°N, 20.2716°E [type locality], leg. DA, ZE, ZF, JG, 27.vi.2014 (HNHM 99272, Mkl-472-02 [COI: MT251632, 16S: MT160793]).

**External genitalia (Figure 14.9):** The whole genital complex is large (PCRL = 37.3). The FO is very short (FO/V = 0.20). The vas deferens is uniformly thin. The first duct of the complex of the bursa copulatrix is long (DBC/DB = 0.53). The bursa copulatrix is short (DB/V = 0.5). The second duct is cylindrical and thin, with a clearly visible transition zone between the second duct and the bursa itself. The diverticulum is short (D/V = 0.57), yet longer (D/BC = 1.13) and somewhat wider than the bursa copulatrix. It is more or less uniformly cylindrical. The vagina is long (VRL = 23.8), larger both at its

proximal and distal part and slightly thinner in the middle. The atrium is large and long. The PC is longer than the vagina (PC/V = 1.57), remarkably swollen at the level of the penial papilla, and with a cylindrical epiphallus that gradually merges into the vas deferens without a clearly visible transitional area. The retractor muscle is short and strong. The epiphallus is longer than the penis (E/P = 1.24).

**Inner genitalia (Figure 14.10):** The atrium is smooth, with trace of 5 or 6, flat, minimally elevated, longitudinal, smooth pleats that are the faded continuation of the penial longitudinal pleats. The distal vagina is completely smooth and slightly swollen at its distal end. The proximal vagina is also completely smooth and the vaginal pilaster is missing. The proximal penis has two main large, smooth and polylobated, fleshy, pad-like pleats. The pleats are clearly divided by a smooth section of the wall surface. Distally, these pleats abruptly

become a series of smooth, fine pleats that reach the atrium. The penial papilla is missing. The epiphallus has up to five simple, smooth pleats originating proximally from the end of the vas deferens and extending towards the penis, where the pleats gradually fade out. The background is smooth.

### *Montenegrina pallida* Fauer, 1993 stat. nov.

Figures 15.1–15.5

*Montenegrina fuchsi pallida* Fauer, 1993: 54–55, plate 1, fig. 6. – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 36, fig. 15e, distribution map fig. 16.

**Examined material:** two dissected specimens. Greece, Epirus, Ioannina district, Molivdokepastos SW 2 km, at the Pogonisko junction, 515 m asl., 40.0468°N, 20.5648°E [type locality], leg. ZE, ZF, JG, 26.vi.2013 (HNHM 99566, Mpa-392-01 [COI: KU307735, 16S: KU308159, 12S: KU307972]; Mpa-392-02 [COI: KU307736]).

**External genitalia (Figure 15.2):** The whole genital complex is large (PCRL = 30.6). The FO is very short (FO/V = 0.18). The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.21). The bursa copulatrix is short (DB/V = 0.82). The second duct is wide, progressively swollen towards the bursa, with no clearly distinguishable transition. The diverticulum is short (D/V = 0.82), as long as the bursa copulatrix (D/BC = 1) but somewhat thinner. It is progressively swollen towards the tip. The vagina is medium-sized (VRL = 14.0), larger at its proximal and distal part and slightly thinner in the middle. The atrium is medium-sized. The PC is much longer than the vagina (PC/V = 2.18), swollen at the level of the penial papilla and with a cylindrical epiphallus that gradually merges into the vas deferens without a clearly visible transitional area. The retractor muscle is short and strong. The epiphallus is longer than the penis (E/P = 1.64).

**Inner genitalia (Figures 15.3 and 15.4):** The atrium has a big, polylobed fold originating directly at the genital aperture. The distal vagina is mainly smooth with only one evident smooth pleat transversely running along the transitional area with the atrium. This pleat is the direct continuation of the vaginal pilaster. The vaginal pilaster represents the smooth longitudinal pleat that extends from the FO as far as the atrium. The vaginal background walls are smooth. The proximal penis has 2–3 smooth and minimally elevated pleats. The pleats are transversely and irregularly fringed and are divided by a portion of the wall surface. In addition, the wall surface is transversely fringed and finely granulated. These pleats abruptly stop when they reach the atrium. The penial papilla is medium-sized, globose, irregular with blunt apex. The aperture runs laterally, reaching the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina rugilabris rugilabris* (Mousson, 1859)

Figures 16.1–16.6

*Clausilia rugilabris* Mousson, 1859: 275–276.

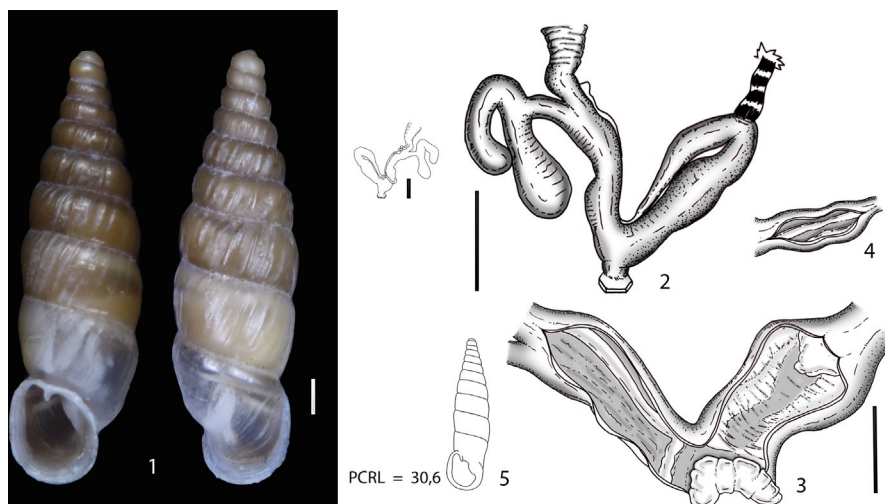
*Clausilia (Delima) rugilabris* – Westerlund, 1884: 53.

*Delima (Albanodelima) rugilabris* – Wagner, 1924: 120.

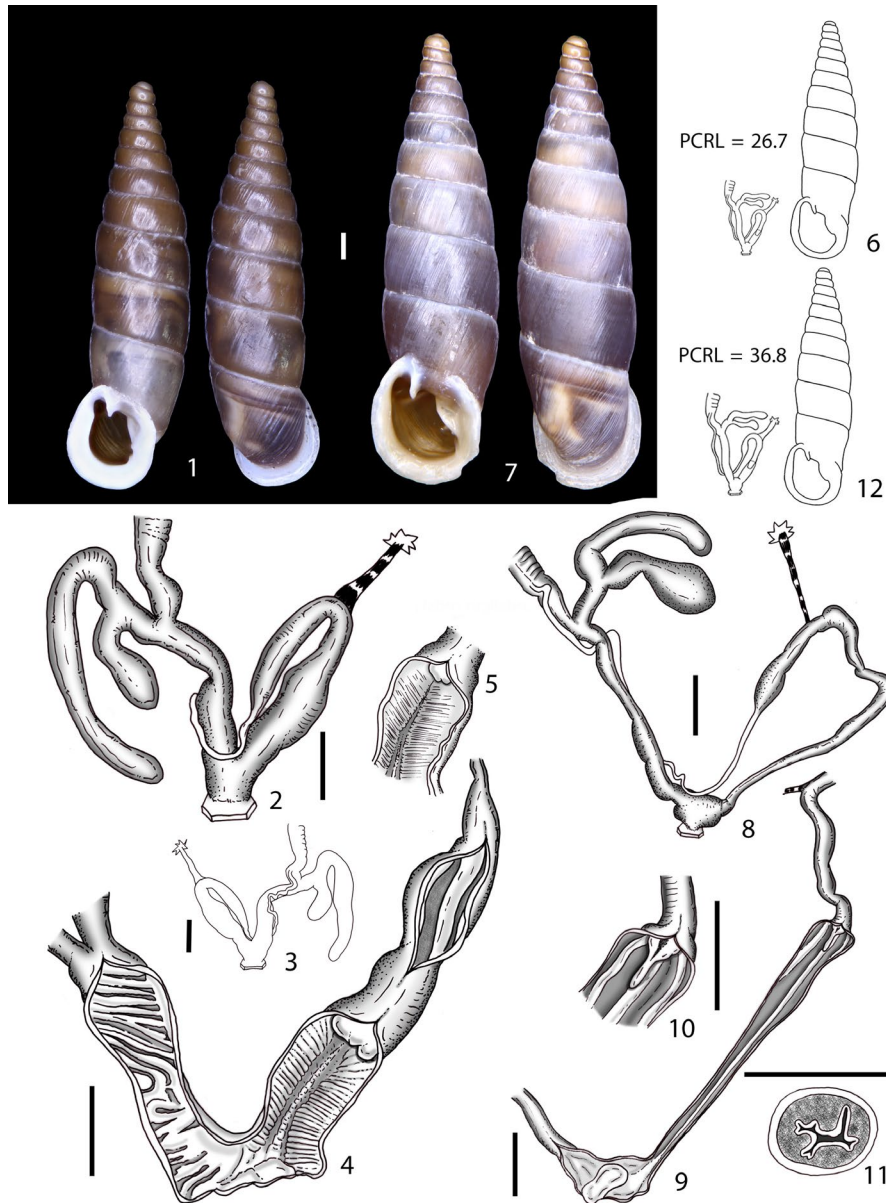
*Montenegrina rugilabris* – Zilch, 1981: 130, plate 14, fig. 34. – Nordsieck, 2009: 74.

*Montenegrina rugilabris rugilabris* – Fehér & Szekeres, 2016: 88, fig. 28A, distribution map fig. 29.

**Examined material:** two dissected specimens. Greece, Epirus, Amfithea to Spothi road N of the Lake Pamvotis, 0.5 km E of the Ligkiades junction, 600 m, 39.6828°N, 20.8887°E, leg. ZE, ZF, JG, 24.vi.2014 (HNHM 99547, Mrl-381-01 [COI: KU307777, 16S: KU308176]).



**FIGURE 15** *Montenegrina pallida* Fauer, 1993 stat. nov. HNHM 99566. 15.1 shell. 15.2 whole distal genitalia. 15.3 inner distal genitalia. 15.4 longitudinal section of epiphallus. 15.5 shell-genitalia ratio



**FIGURE 16** 16.1–16.6 *Montenegrogrina rugilabris rugilabris* (Mousson, 1859) HHNM 99547. 16.1 shell. 16.2–16.3 whole distal genitalia. 16.4 inner distal genitalia. 16.5 penial papilla and inner proximal penis. 16.6 shell-genitalia ratio. 16.7–16.12 *Montenegrogrina edmundi* Szekeres, 2006 stat. nov. HHNM 99697. 16.7 shell. 16.8 whole distal genitalia. 16.9 inner distal genitalia. 16.10 penial papilla and inner proximal penis. 16.11 cross section of epiphallus. 16.12 shell-genitalia ratio

**External genitalia (Figures 16.2 and 16.3):** The whole genital complex is medium-sized (PCRL = 26.7). The FO is extremely short (FO/V = 0.17). The vas deferens is thinner distally. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.25). The bursa copulatrix is short (DB/V = 0.67), almost uniformly cylindrical with a blunt apex. There is no clearly visible transitional area. The diverticulum is very long (D/V = 2.0), uniformly cylindrical, as wide as the bursa copulatrix and much longer (D/BC = 3.00). The apex is blunt. The vagina is medium-sized (VRL = 12.8) and uniformly cylindrical. The atrium is large. The PC is longer than the vagina (PC/V = 2.08). The penis is swollen distally and also at the level of the penial papilla. The epiphallus is much longer than the penis (E/P = 2.33), almost uniformly cylindrical and not swollen. It merges into the vas deferens

with a more or less clear transitional area. The retractor muscle is long and strong.

**Inner genitalia (Figures 16.4 and 16.5):** The atrium has few irregular, smooth and fleshy, small, pad-like pleats. The distal vagina bears 6–10 smooth, irregular transversal pleats merged into one another at their ends. The proximal vagina shows many oblique, transversal pleats converging towards the vaginal pilaster. The background walls are smooth. The whole penis has two main, large longitudinal cords composed of many smooth, fine transversal pleats regularly arranged in a chevron-like pattern. The two main cords are clearly separated and the smooth background is visible. A central, thin metameric cord is also present. The wide but short penial papilla has a central opening. The surface is smooth with some moderate

swelling. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina edmundi* Szekeres, 2006 stat. nov.**

Figures 16.7–16.12

*Montenegrina irmengardis edmundi* Szekeres, 2006 in Eröss et al., 2006: 190–192, fig. 11.

*Montenegrina skipetarica edmundi* – Nordsieck, 2009: 73.

*Montenegrina rugilabris edmundi* – Fehér & Szekeres, 2016: 88, fig. 28D, distribution map fig. 29.

**Examined material: two dissected specimens.** Greece, Epirus, 6 km from Lia towards Lista, NE of Filiates, 460 m, 39.7358°N, 20.4537°E [type locality], leg. ZE, ZF, JG, 25.vi.2013 (HNHM 99697, Mem-387-02 [COI: KU307662]).

**External genitalia (Figure 16.8):** The whole genital complex is very long (PCRL = 36.8) with a remarkably slender appearance. The FO is short (FO/V = 0.31). The vas deferens is thin distally but swollen proximally. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.41). The bursa copulatrix is short (DB/V = 0.61), very wide, compressed, club-like with a huge bursa. No clearly visible transitional area is present. The diverticulum is also generally short (D/V = 0.92), uniformly cylindrical, thinner but usually longer (D/BC = 1.5) than the bursa copulatrix. The apex is blunt. The vagina is medium-sized (VRL = 16.1), uniformly cylindrical and thin. The atrium is large and swollen. The PC is considerably longer than the vagina (PC/V = 2.28). The penis is very thin, slender with a very weak swelling at the level of the penial papilla. The epiphallus is shorter than the penis (E/P = 0.74), moderately swollen along its proximal part and distally cylindrical. It merges into the vas deferens with a more or less clear transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 16.9–16.11):** The atrium has one small, oblique, and smooth fold. The background is completely smooth. The whole vagina is also completely smooth. The proximal penis shows three smooth longitudinal pleats. Only the central one continues as far as the atrium, whereas the other two suddenly fade into the smooth background of the distal penis. The small penial papilla is elongated and slim with a smooth surface. The aperture is longitudinal and does not reach the tip. The epiphallus exhibits five simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina golikutensis* Fehér & Szekeres, 2016 stat. nov.**

Figures 17.1–17.5

*Montenegrina rugilabris golikutensis* – Fehér & Szekeres, 2016: 89, fig. 28b, distribution map fig. 29.

### **Examined material: two dissected specimens (paratypes).**

Albania, Tepelenë District, Kendrevicë Mts, N slope of the Maja e Golikut, 1,350 m, 40.2758°N, 20.0947°E [type locality], leg. DA, ZF, JG, 28.vi.2014 (NHMW 111215, Mgo-473-01 [COI: KU307569, 16S: KU308040]).

**External genitalia (Figure 17.2):** The whole genital complex is medium-sized (PCRL = 20.9) with a very slender appearance. The FO is extremely short (FO/V = 0.07). The vas deferens is very thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.38). The bursa copulatrix is short (DB/V = 0.32), thin, and cylindrical. There is no distinctly visible transition area and the apex is blunt. The diverticulum is short (D/V = 0.68), cylindrical, wider than the bursa copulatrix and usually much longer (D/BC = 0.46). The apex is slightly rounded. The vagina is medium-sized (VRL = 23.8), slender, and uniformly cylindrical, only slightly swollen distally. The atrium is small. The PC is shorter than the vagina (PC/V = 0.88). The penis is thin and almost completely cylindrical. The epiphallus is longer than the penis (E/P = 1.12) and thin. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 17.3 and 17.4):** The atrium is smooth. The whole vagina is completely smooth and the vaginal pilaster is missing. The penis is also completely smooth without any sculpturing or pleat. The very small penial papilla is of spongy texture, with no detectable penial channel or aperture. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina gregoi* Fehér & Szekeres, 2016 stat. nov.**

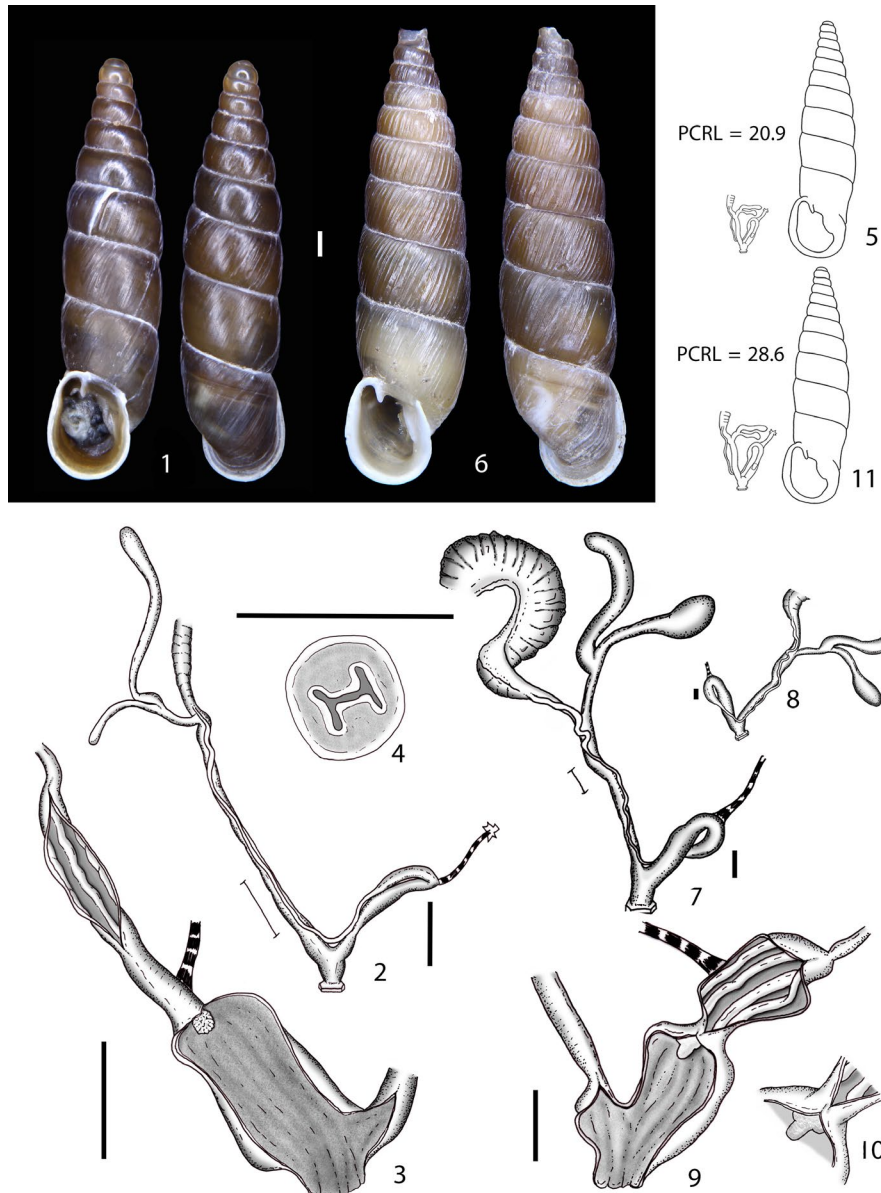
Figures 17.6–17.11

*Montenegrina rugilabris gregoi* – Fehér & Szekeres, 2016: 91, fig. 28C, distribution map fig. 29.

### **Examined material: two dissected specimens (paratypes).**

Greece, Epirus, Ioannina District, 3 km NE of Prosilio, along the road to Syrrako, 1,130 m, 39.5768°N, 21.0969°E [type locality], leg. ZE, ZF, JG, 23.vi.2013 (HNHM 99475, Mgr-375-01 [COI: KU307552, 16S: KU308026, 12S: KU307927]; Mgr-375-03 [COI: KU307554, 16S: KU308028]).

**External genitalia (Figure 17.8):** The whole genital complex is medium-sized (PCRL = 28.6) with a slender appearance. The FO is short (FO/V = 0.34). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.20). The bursa copulatrix is medium-sized (DB/V = 0.92), club-like with a wide actual bursa. The transitional area is more or less clearly visible. The diverticulum is short (D/V = 0.85), uniformly cylindrical, wider than the second duct of the bursa copulatrix and usually shorter (D/BC = 0.93). The apex is blunt. The vagina is very long (VRL = 32.3) and uniformly



**FIGURE 17** 17.1–17.5 *Montenegrina golikutensis* Fehér & Szekeres, 2016 stat. nov. NHMW 111215. 17.1 shell. 17.2 whole distal genitalia. 17.3 inner distal genitalia. 17.4 cross section of epiphallus. 17.5 shell-genitalia ratio. 17.6–17.11 *Montenegrina gregoi* Fehér & Szekeres, 2016 stat. nov. HHNM 99475. 17.6 shell. 17.7–17.8 whole distal genitalia. 17.9 inner distal genitalia. 17.10 penial papilla and inner proximal penis. 17.11 shell-genitalia ratio

cylindrical. The atrium is relatively large. The PC is shorter than the vagina ( $PC/V = 0.89$ ). The penis is swollen along its distal course and at the level of the penial papilla. The epiphallus is longer than the penis ( $E/P = 2.0$ ) and uniformly cylindrical. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 17.9–17.10):** The atrium is smooth. The whole vagina is completely smooth and the vaginal pilaster is absent. The penis is completely smooth without any sculpturing. The very small-sized penial papilla is smooth with the aperture opening almost at its base. The epiphallus exhibits five simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina rugilabris irmengardis* Klemm, 1962

Figures: 18.1–18.6

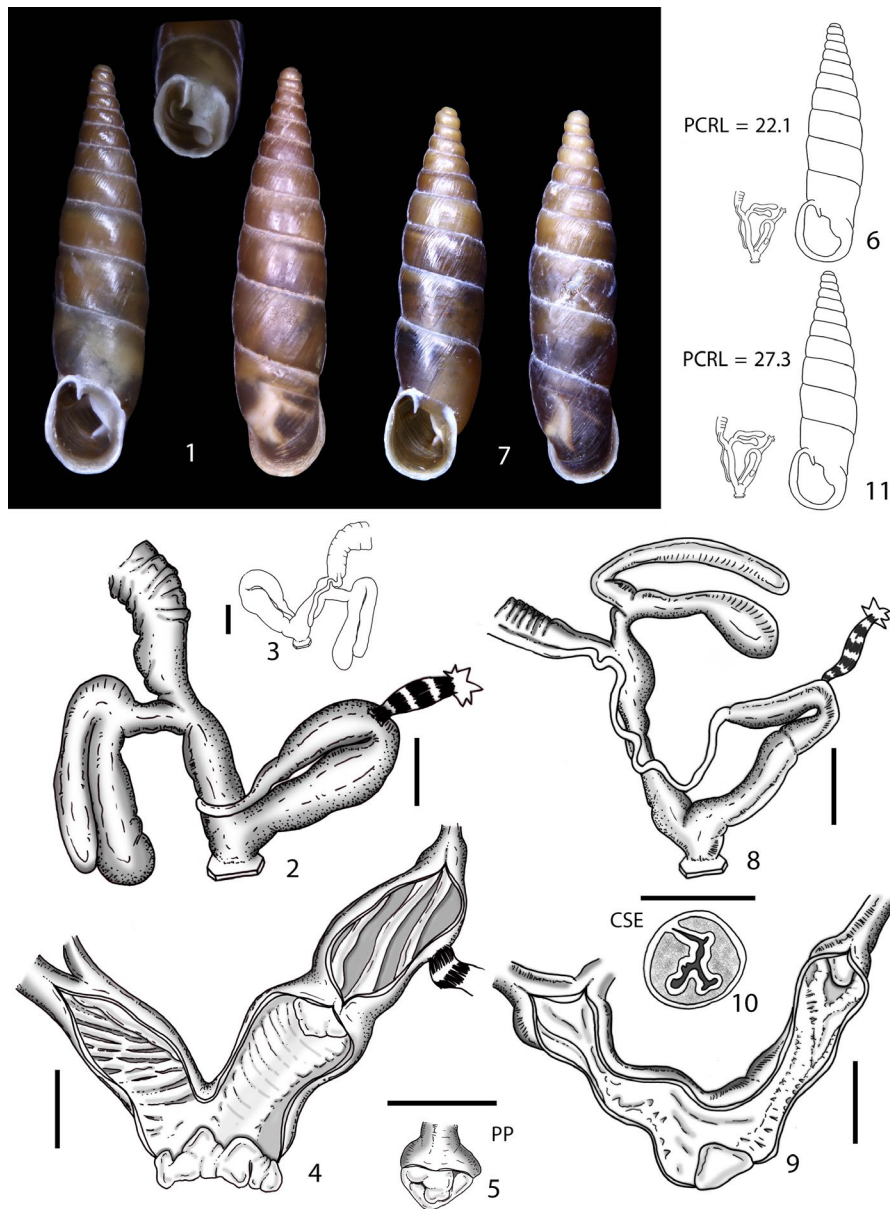
*Montenegrina (Beieriella) irmengardis* – Klemm, 1962: 242–244, plate 3, fig. 2 (genital anatomy), 8 (shell).

*Montenegrina irmengardis irmengardis* – Nordsieck, 1972: 35, plate 4, fig. 34 – Zilch, 1981: 128, plate 15, fig. 40.

*Montenegrina skipetarica irmengardis* – Nordsieck, 2009: 73.

*Montenegrina rugilabris irmengardis* – Fehér & Szekeres, 2016: 93, fig. 28f, distribution map fig. 29.

**Examined material:** two dissected specimens. Greece, Epirus, W of Kedros, 2 km towards Charakopi, 730 m, 39.5728°N, 20.9861°E,



**FIGURE 18** 18.1–18.6 *Montenegrina rugilabris irmengardis* Klemm, 1962 HNHM 99552. 18.1 shell. 18.2–18.3 whole distal genitalia. 18.4 inner distal genitalia. 18.5 penial papilla. 18.6 shell-genitalia ratio. 18.7–18.11 *Montenegrina lambdaformis welterschultesi* Fehér & Szekeres, 1999 NHMW 110430/MN/0316. 18.7 shell. 18.8 whole distal genitalia. 18.9 inner distal genitalia. 18.10 cross section of epiphallus. 18.11 shell-genitalia ratio

leg. ZE, ZF, JG, 24.vi.2013 (HNHM 99552, Mir-376-01 [COI: KU307687]; Mir-376-02 [COI: KU307688]).

**External genitalia (Figures 18.2–18.3):** The whole genital complex is medium-sized (PCRL = 21.7). The FO is short (FO/V = 0.33). The vas deferens is moderately wide along its whole course and swollen proximally. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.32). The bursa copulatrix is extremely long (DB/V = 1.67), very wide, club-like with a well-rounded apex. There is no clearly visible transitional area. The diverticulum is also generally very long (D/V = 2.13), uniformly cylindrical, slightly thinner, and usually longer (D/BC = 1.28) than the bursa copulatrix. The apex is slightly pointed. The vagina is extremely short (VRL = 6.8),

wide, and uniformly cylindrical. The atrium is large. The PC is considerably longer than the vagina (PC/V = 3.2). The penis is swollen at the level of the penial papilla. The epiphallus is longer than the penis (E/P = 1.67) and moderately swollen along its proximal part. It merges into the vas deferens without a distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 18.4–18.5):** The atrium presents a big, polylobated fold originating directly at the genital aperture. The distal vagina has 5–10 smooth transversal or slightly oblique pleats that do not continue into the atrium. The pleats merge into one another at their ends. The background is smooth. The proximal vagina has many oblique, transversal pleats converging towards the vaginal

pilaster. The background walls are smooth. The whole penis shows a medial longitudinal "hollow". This depression is marked by many transversal metameric segments and it ends up before the atrium. The medium-sized, conical penial papilla has a pointed but nonetheless broad apex and a smooth surface. The aperture is lateral, not reaching the papilla's tip. The epiphallus has three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina lambdaformis welterschultesi* Fehér & Szekeres, 1999 comb. nov.

Figures 18.7–18.11

*Montenegrina irmengardis welterschultesi* Fehér & Szekeres, 1999 in Erőss, Fehér, & Szekeres, 1999: 450, fig. 6.

*Montenegrina skipetarica welterschultesi* – Nordsieck, 2009: 73.

*Montenegrina rugilabris welterschultesi* – Fehér & Szekeres, 2016: 94, fig. 28g, distribution map fig. 29.

**Examined material: two dissected specimens.** Albania, Permet district, Petran, 263 m, 40.124°N 20.249°E [type locality], leg. MD, EH, HS, 28.iv.2017 (NHMW 110430/MN/0316, Mwe-350-01 [COI: KU307869,16S: KU308221, 12SKU307993]).

**External genitalia (Figure 18.8):** The whole genital complex is medium-sized (PCRL = 27.3). The FO is also medium-sized (FO/V = 0.41). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.26). The bursa copulatrix is medium-sized (DB/V = 0.85). The bursa proper is large, club-like with a big rounded apex. The transition area is more or less visible. The diverticulum is long (D/V = 1.37), uniformly cylindrical, thinner than the bursa copulatrix and generally longer (D/BC = 1.61). The apex is blunt. The vagina is medium-sized (VRL = 15.5) and uniformly cylindrical. The atrium is moderately large and long. The PC is longer than the vagina (PC/V = 1.63). The penis is almost uniformly cylindrical. The epiphallus is shorter than the penis (E/P = 0.76), only slightly swollen along its proximal part and as wide as the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 18.9–18.10):** The atrium is mainly smooth with traces of very weak, irregular, large pleats. A big unilobate, smooth fold originates from the aperture and occupies part of the atrial volume. The whole vagina is mainly smooth but bears the vaginal pilaster. Only few, scattered, small pleats, and wrinkles are present. The proximal penis shows two or three principal, fringed, longitudinal pleats that abruptly merge into one another, forming a single large but only slightly elevated pleat that extends as far as the atrium. The penial papilla is small with a rounded apex, and the aperture is lateral and longitudinally oriented. The epiphallus has three fringed pleats with jagged edges, originating proximally from the end of the vas deferens and fading before the base of the penial papilla. The background is transversely irregular.

### *Montenegrina lambdaformis lambdaformis* Reischütz & Sattmann, 1990 stat. nov.

*Montenegrina irmengardis lambdaformis* Reischütz & Sattmann, 1990: 260, plate 3, fig. 7.

*Montenegrina skipetarica lambdaformis* – Nordsieck, 2009: 73.

*Montenegrina rugilabris lambdaformis* – Fehér & Szekeres, 2016: 93, fig. 28E, distribution map fig. 29.

No alcohol-preserved specimens were available for anatomical investigations.

### *Montenegrina janinensis* (Mousson, 1859) sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

The specific name *janinensis* has been used in the past to name or identify many populations currently belonging to many different (sub)species (e.g., *M. attemsi*, *M. jakupicensis*, *M. dofleini fagorum*, *M. pinteri*, and *M. grammica*). Populations currently referred to this taxon are restricted to a small area near Joannina (Epirus, Greece), as stated in Fehér and Szekeres (2016: 56). Their haplotypes form a subclade inside Clade D1. The genital anatomy supports the genetic results, being different from all the remaining taxa within this clade and from the taxa formerly attributed to this species.

Two of the dissected specimens came from a population (Mcl-384) described as "*crassilabris*" by Fauer (1993). The genital morphology showed very little differences from the typical form (Mjn-383) (Figures 19.9–19.11), supporting the opinion of Fehér and Szekeres (2016), namely that "*crassilabris*" is a junior synonym of *M. janinensis*.

#### Fehér & Szekeres, 2016

*Montenegrina janinensis* (Mousson, 1859)

#### De Mattia et al., 2020

*Montenegrina janinensis* (Mousson, 1859)

### *Montenegrina janinensis* (Mousson, 1859)

Figures 19.1–19.12

*Clausilia janinensis* Mousson, 1859: 276.

*Clausilia (Delima) janinensis* – Westerlund, 1884: 54–55.

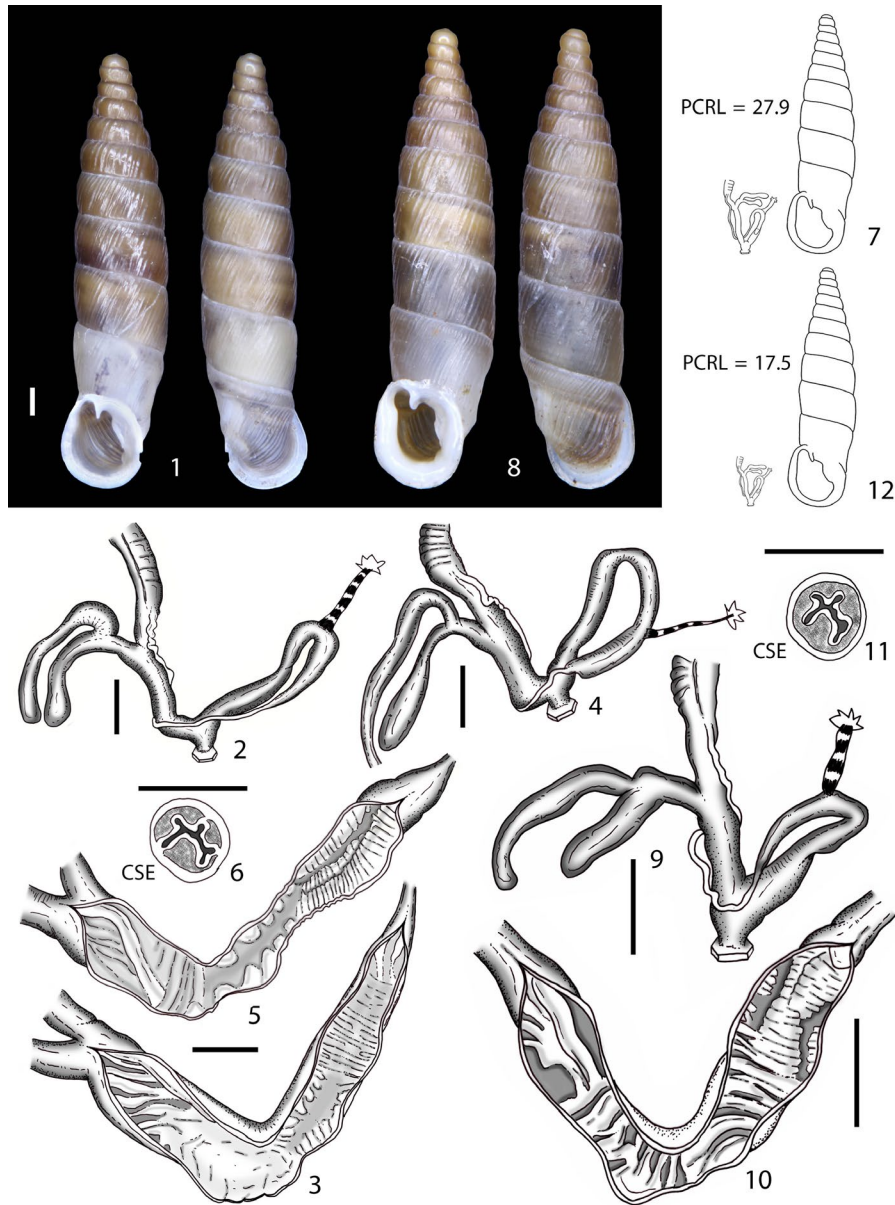
*Delima (Albanodelima) janinensis* – Wagner, 1924: 120.

*Montenegrina janinensis janinensis* – Zilch, 1981: 129. – Nordsieck, 2009: 75.

*Montenegrina janinensis crassilabris* Fauer, 1993: 55–56, plate 1, fig. 7. – Nordsieck, 2009: 75.

*Montenegrina janinensis* – Fehér & Szekeres, 2016: 55, fig. 21J,K, distribution map fig. 22.

**Examined material: two dissected specimens.** Greece, Epirus, Perama, near entrance of the cave, 500 m, 39.6947°N, 20.8463°E, leg.



**FIGURE 19** 19.1–19.7 *Montenegrina janinensis* (Mousson, 1859) HNHM 99560. 19.1 shell. 19.2 whole distal genitalia. 19.3 inner distal genitalia. 19.6 cross section of epiphallus. 19.7 shell–genitalia ratio. 19.8–19.12 HNHM 99561 *M. janinensis crassilabris* morphotype. 19.8 shell. 19.9 whole distal genitalia. 19.10 inner distal genitalia. 19.11 cross section of epiphallus. 19.12 shell–genitalia ratio

ZE, ZF, JG, 24.vi.2013 (HNHM 99560, Mjn-383-01 [COI: KU307695, 16S: KU308120, 12S: KU307960]; Mjn-383-02 [COI: MT251631]).

**External genitalia (Figures 19.2 and 19.4):** The whole genital complex is medium-sized (PCRL = 27.9). The FO is short (FO/V = 0.33) and wide. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.29). The bursa copulatrix is very long (DB/V = 1.13), almost completely cylindrical and only the bursa itself slightly swollen. The second duct is cylindrical, with no clearly distinguishable transition into the bursa. The diverticulum is long (D/V = 1.87), somewhat thinner than the bursa but longer (D/BC = 1.65). The apex is blunt. The vagina is extremely short (VRL = 9.7), uniformly cylindrical but wide. The atrium is short and moderately thin. The PC is much longer than the vagina (PC/V = 2.87). The penis is slightly swollen, gradually tapering

proximally. The epiphallus is shorter than the penis ( $E/P = 0.79$ ), slender, and thinner than the penis. It merges into the vas deferens without a distinct transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 19.3, 19.5–19.6):** The atrium has few irregular, smooth, and fleshy large pleats, almost forming a single irregular, fleshy, pad-like large pleat. The distal vagina shows an irregular, fleshy surface similar to the atrium. The proximal vagina has only the vaginal pilaster and one or two minor small pleats originating from it. The background is smooth. The proximal penis has two or three main large metameric cords. A central, shorter, and smaller metameric cord is sometimes also present. The cords abruptly end at penis midlength. The smooth background becomes fully visible, but two lateral, irregular roundish, fleshy sets of “lumps” extend as far as the atrium. The dimension of the lumps gradually decreases



towards the atrium. There is no penial papilla, and the border between the epiphallus and penis is clearly distinguishable where the pleats of the epiphallus distally end. The epiphallus has up to five simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

**Examined material: two dissected specimens – *M. janinensis* “*crassilabris*”.** Greece, Epirus, Perama, near the exit of the stalactite cave, 520 m, 39.6971°N, 20.8433°E, leg. ZE, ZF, JG, 24.vi.2013 (HNHM 99561, Mcl-384-01 [COI: KU307604, 16S: KU308064, 12S: KU307937\*]; Mcl-384-02 [COI: MT251530]).

**External genitalia (Figure 19.9):** The whole genital complex is short (PCRL = 17.5). The FO is long (FO/V = 0.89) and wide. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is long (DBC/DB = 0.50). The bursa copulatrix is long (DB/V = 1.33), almost completely cylindrical. The second duct is cylindrical, with no distinguishable transitional area into the bursa. The diverticulum is very long (D/V = 2.44), thinner than the bursa but longer (D/BC = 1.83). The apex is blunt. The vagina is extremely short (VRL = 5.4) and uniformly cylindrical. The atrium is long and moderately large. The PC is much longer than the vagina (PC/V = 3.22). The penis is slightly swollen, gradually tapering proximally. The epiphallus is longer than the penis (E/P = 1.23), slender, and thinner than the penis. It merges into the vas deferens without a distinct transitional area. The retractor muscle is short and thin.

**Inner genitalia (Figures 19.10–19.11):** The atrium shows many irregular smooth and fleshy pleats. The distal vagina has 5–10 smooth, irregular transversal pleats that continue directly into the atrium. The pleats split and merge at their ends. The background walls are smooth. The proximal vagina shows three or four oblique, elevated, transversal pleats. The vaginal pilaster is present. The proximal penis has three main, large, slightly obliquemetameric cords, with portions of the smooth background visible. These cords merge along the midpenial length, forming a pattern of irregular transversal cords randomly splitting and merging. This arrangement is present as far as the atrium. The penial papilla is medium-sized, pyramidal, pointed but with a blunt apex. The aperture extends laterally and does not reach the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina grammica* Nordsieck, 1988 sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

*Montenegrina grammica* forms a subclade in Clade K. The nominal subspecies *M. grammica grammica* inhabits Epirus, Gramos Mts (Greece), whereas the other two subspecies (*M. grammica improvisa* and *M. grammica erosszoltani*) are located more than 160 km away at Mat district in central Albania (Fehér & Szekeres, 2016: 39).

Despite this large geographic distance, *M. grammica grammica* and *M. grammica erosszoltani* show very little genetic distance (populations Mez-303, Mez-322 and Mgm-395) and highly similar shells.

*Montenegrina grammica improvisa* (pop. Mgi-457, one sample only Mgi-457-01) seems to be more distant, both by shell morphology and genetically, from the other two taxa.

Unfortunately, only one sample of *M. grammica improvisa* was available for anatomical research (Figure 20) and, therefore, no comparison with the other two taxa was possible. Nevertheless, concerning *M. grammica improvisa*, a considerable phylogenetic distance (the same range as the distance to the next related species *M. tomorosi*) and its peculiar shell morphology lead us to consider *M. improvisa* stat. nov. as a valid species.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina grammica grammica</i> Nordsieck, 1988	<i>Montenegrina grammica grammica</i> Nordsieck, 1988
<i>Montenegrina grammica erosszoltani</i> Fehér & Szekeres, 2016	<i>Montenegrina grammica erosszoltani</i> Fehér & Szekeres, 2016
<i>Montenegrina grammica improvisa</i> Fehér & Szekeres, 2016	<i>Montenegrina improvisa</i> Fehér & Szekeres, 2016 stat. nov.

### *Montenegrina grammica grammica* Nordsieck, 1988

*Montenegrina janinensis grammica* Nordsieck, 1988: 198–199, fig 2. – Nordsieck, 2009: 75.

*Montenegrina grammica grammica* – Fehér & Szekeres, 2016: 37, fig. 15f, distribution map fig. 17.

No alcohol-preserved specimens were available for anatomical investigations.

### *Montenegrina grammica erosszoltani* Fehér & Szekeres, 2016

*Montenegrina grammica grammica* – Fehér & Szekeres, 2016: 37, fig. 15G, distribution map fig. 17.

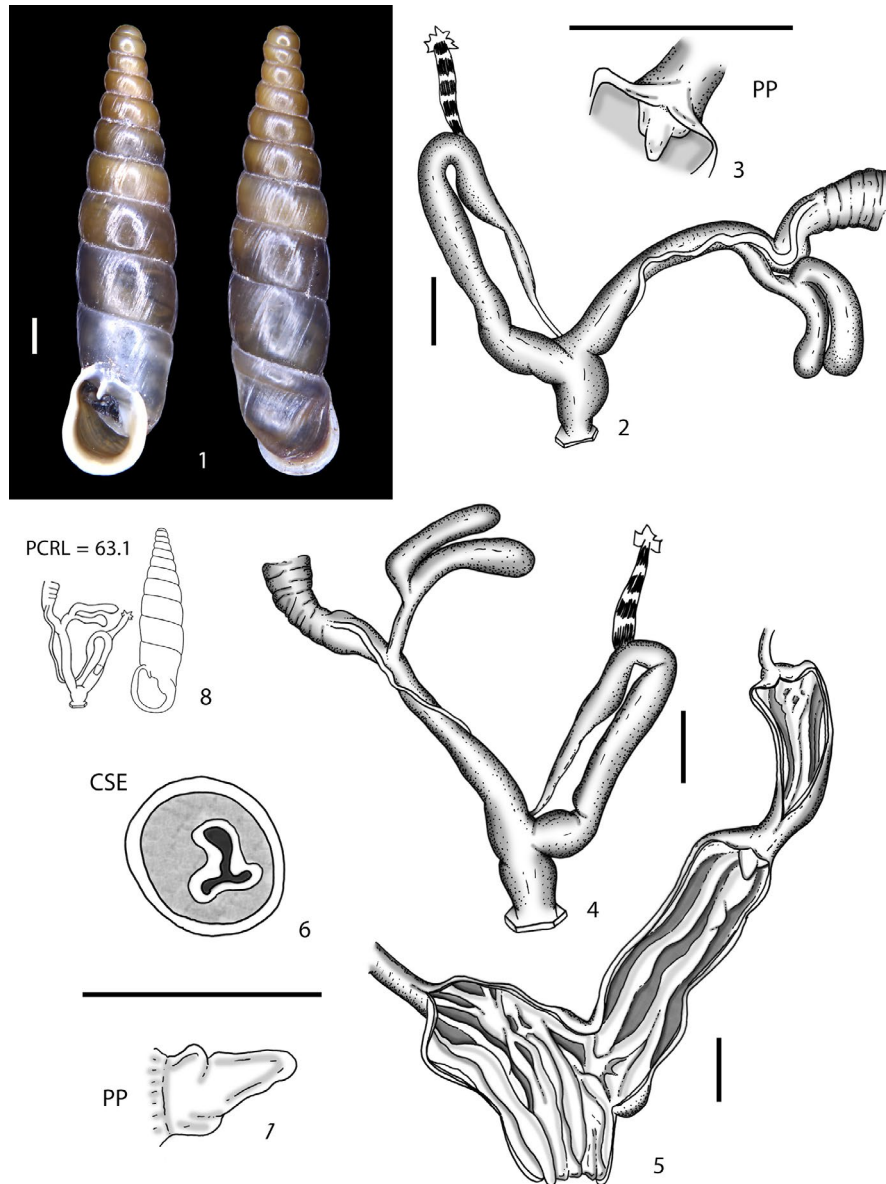
No alcohol-preserved specimens were available for anatomical investigations.

### *Montenegrina improvisa* Fehér & Szekeres, 2016 stat. nov.

Figures 20.1–20.8

*Montenegrina grammica improvisa* – Fehér & Szekeres, 2016: 38, fig. 15H, distribution map fig. 17.

**Examined material: two dissected specimens (paratypes).** Albania, Mat District, Gropa Mts, 3.5 km W of Gurri i Bardhë, N slope of the Maja e Bastarit, 1,160 m, 41.4361°N, 20.0485°E [type locality], leg. ZF, TN, EM, 15.iv.2014 (HNHM 99019, Mgi-457-02 [COI: KU307568, 16S: KU308039]).



**FIGURE 20** *Montenegrina improvisa* Fehér & Szekeres, 2016 stat. nov. HHNM 99019. 20.1 shell. 20.2 whole distal genitalia. 20.3 penial papilla. 20.4 whole distal genitalia. 20.5 inner distal genitalia. 20.6 cross section of epiphallus. 20.7 penial papilla. 20.8 shell-genitalia ratio

**External genitalia (Figure 20.2, 20.4):** The whole genital complex is extremely long (PCRL = 63.1) – the longest recorded for *Montenegrina*. The FO is short (FO/V = 0.34). The vas deferens is uniformly thin, except for its distal portion, where it is slightly swollen. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.42). The bursa copulatrix is short (DB/V = 0.59). The second duct is wide, cylindrical, only slightly swollen towards the bursa; no transition area is distinguishable. The apex is rounded and blunt. The diverticulum is short (D/V = 0.73) and only slightly longer (D/BC = 1.25) and wider than the bursa copulatrix. It is almost uniformly cylindrical. The apex is blunt. The vagina is long (VRL = 29.1), larger proximally and distally but slightly thinner in the middle. The atrium is large and long. The PC is much longer than the vagina (PC/V = 2.17), only slightly swollen at the level of the penial papilla and with a cylindrical epiphallus that gradually merges into the vas deferens without a visible transitional area. The epiphallus is longer than the penis

(E/P = 1.97) and its proximal half is swollen. The retractor muscle is long and strong.

**Inner genitalia (Figures 20.3, 20.5–20.7):** The atrium has 5–8 overlapping longitudinal folds that directly continue into the distal vagina. The surface of the folds is smooth. The distal vagina has 6–10 smooth transversal pleats that are the direct continuation of the atrial pleats. These pleats eventually split and/or merge into each other. The background walls are smooth. The proximal vagina has 5–10 elevated longitudinal pleats. The pleats can be connected with small fleshy bridges and can be more or less thick. The vaginal pilaster is present. The penis has two main, large, and elevated longitudinal pleats. These pleats often split both proximally and distally. The background walls are smooth and thick with a fine granulation. The penial papilla is medium-sized, pyramidal, pointed but with a blunt apex. The aperture extends laterally and does not reach the apical area. The surface is smooth and small; roundish basal lobes are present, giving an overall

tricuspid shape. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina haringae* Fehér & Szekeres, 2016 sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

In the tree of Mason et al. (2020), *M. haringae* falls into Clade F, forming the sister group to the rest of the clade. The range of this species is restricted to a very small area on Mt. Zezë in northern Albania (Fehér & Szekeres, 2016: 39). The closest population of *M. subcristata* is known to occur only 4 km eastward.

*Montenegrina haringae* presents a genital morphology remarkably different from the other taxa of the clade, confirming the shell-based distinction as a valid species.

Fehér & Szekeres, 2016

De Mattia et al., 2020

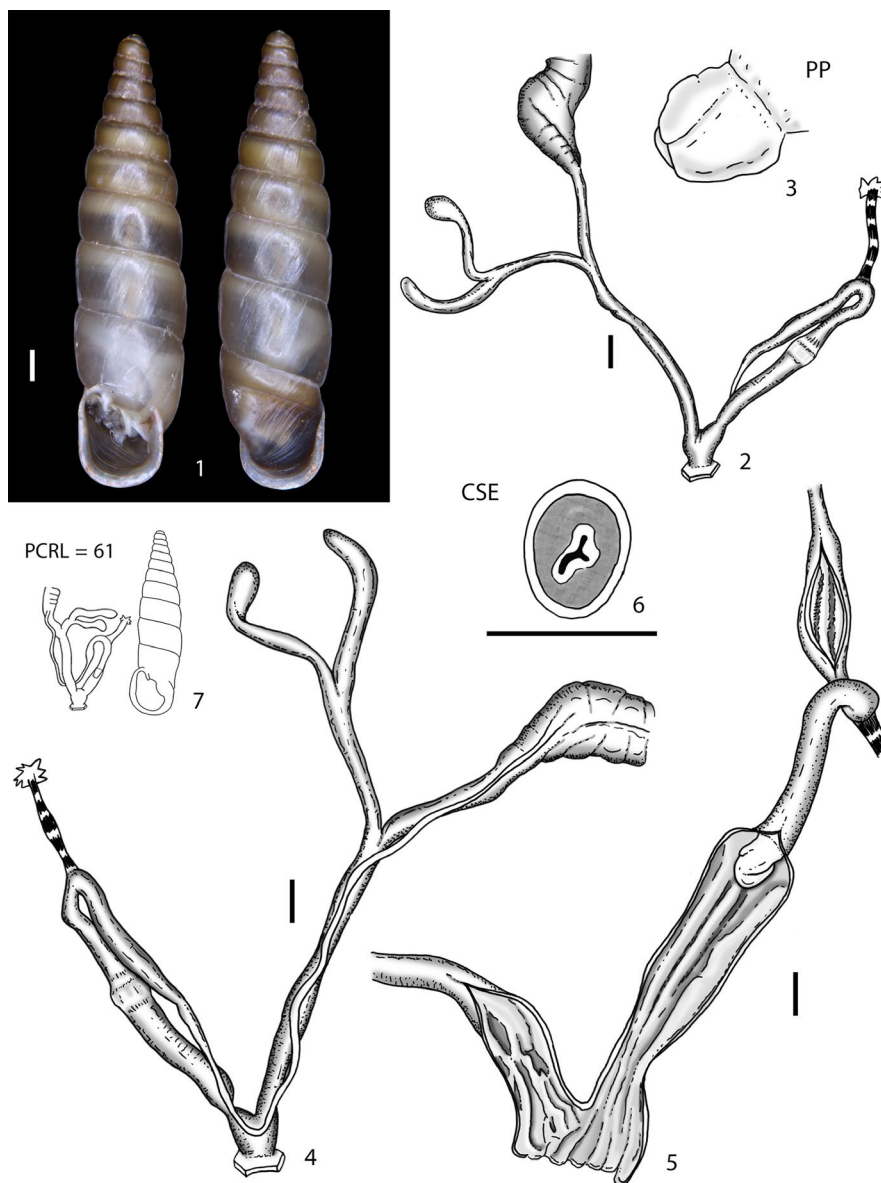
*Montenegrina haringae* Fehér & Szekeres, 2016

*Montenegrina haringae* Fehér & Szekeres, 2016

### *Montenegrina haringae* Fehér & Szekeres, 2016

Figures 21.1–21.7

*Montenegrina haringae* – Fehér & Szekeres, 2016: 39, fig. 15A, distribution map fig. 17.



**FIGURE 21** *Montenegrina haringae* Fehér & Szekeres, 2016 NHMW 111220. 21.1. shell. 21.2 whole distal genitalia. 21.3 penial papilla. 21.4 whole distal genitalia. 21.5 inner distal genitalia. 21.6 cross section of epiphallus. 21.7 shell-genitalia ratio

**Examined material: two dissected specimens (paratypes).** Albania, Shkodër District, Mt. Renc, dry gorge S of Baks-Rjollë, (SW of the Maja e Zezë), 30 m, 41.8577°N, 19.4923°E [type locality], leg. TD, ZE, ZF, 27.v.2015 (NHMW 111220, Mha-602-01 [COI: KU307583]; Mha-602-02 [COI: MT251622]).

**External genitalia (Figures 21.2, 21.4):** The whole genital complex is extremely long (PCRL = 61.0). The FO is long (FO/V = 0.77). The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is extremely long (DBC/DB = 1.37). The bursa copulatrix is short (DB/V = 0.37). The second duct is thin, cylindrical, only slightly swollen towards the bursa, with no distinguishable transition. The apex is rounded and blunt. The diverticulum is short (D/V = 0.38) and only slightly longer than the bursa copulatrix (D/BC = 1.05). It is almost uniformly cylindrical and as wide as the bursa copulatrix. The apex is pointed. The vagina is extremely long (VRL = 35.6), thin, and uniformly cylindrical – the longest recorded for *Montenegrina* until now. The atrium is short and small. The PC is longer than the vagina (PC/V = 1.71), clearly swollen at the level of penial papilla. The epiphallus is cylindrical and gradually merges into the vas deferens without a clearly visible transitional area. The proximal half of the epiphallus is slightly swollen. The retractor muscle is long and thin. The epiphallus is longer than the penis (E/P = 1.07).

**Inner genitalia (Figures 21.3, 21.5–21.6):** The atrium is smooth, with a trace of five or six slightly elevated longitudinal pleats that are the faded continuation of the penial longitudinal pleats. The surface of the folds is smooth. The distal vagina has 5–10 smooth longitudinal pleats that continue into the atrium. The background walls are smooth. The proximal vagina has two or three large, smooth, elevated longitudinal pleats that are irregular in shape. The vaginal pilaster is present. The penis has four or five elevated, smooth longitudinal pleats that directly continue into the atrium, splitting, and distally becoming thinner. The background walls are smooth and thick. The penial papilla is medium-sized, globose, irregular, with a blunt apex. The aperture extends longitudinally, reaching the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats with jagged edges, originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background walls are transversely irregular.

### *Montenegrina helvola* (Küster, 1860) sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

*Montenegrina helvola* s.l. is distributed in central Albania and is clearly distinguished by its shell morphology from all other *Montenegrina* species (Fehér & Szekeres, 2016: 43).

Its subspecies are positioned within a subclade of Clade I. *Montenegrina helvola helvola* has been reported only along a small isolated area near Krujë, whereas *M. helvola magna* is known from

three scattered localities; both taxa inhabit the northern part of the species range. They are monophyletic sister groups presenting relatively distant mt lineages from the remaining taxa. *Montenegrina helvola ornata*, *M. helvola pageti*, and *M. helvola carinata*, occurring in the southern part of the species range, fall into another subclade and show a similar but distinguishable morphology of the genitalia. They are more closely related to each other than to *M. helvola magna*. The latter shows differences especially as regards the inner sculpturing of the penial wall (Figure 22.4).

No suitable specimen of the nominal *M. helvola helvola* was available for the genital-anatomical research. As long as no additional morphological data are available, we prefer not to change the current system, thus keeping the systematic arrangement of Fehér and Szekeres (2016: 40 and following).

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina helvola helvola</i> (Küster, 1860)	<i>Montenegrina helvola helvola</i> (Küster, 1860)
<i>Montenegrina helvola carinata</i> Eröss and Szekeres, 1999	<i>Montenegrina helvola carinata</i> Eröss and Szekeres, 1999
<i>Montenegrina helvola helvola magna</i> Fehér & Szekeres, 2006	<i>Montenegrina helvola helvola magna</i> Fehér & Szekeres, 2006
<i>Montenegrina helvola ornata</i> Eröss and Szekeres, 1999	<i>Montenegrina helvola ornata</i> Eröss and Szekeres, 1999
<i>Montenegrina helvola pageti</i> Brandt, 1962	<i>Montenegrina helvola pageti</i> Brandt, 1962

### *Montenegrina helvola helvola* (Küster, 1860)

*Clausilia helvola* Küster, 1860 – Küster, 1844–1862: 176, plate 19, figs 15–18 – Schmidt, 1868: 70–71.

*Clausilia (Heteroptycha) helvola* – Westerlund, 1884: 40.

*Delima (Alpidelima) helvola* – Wagner, 1924: 120.

*Delima (Heteroptycha) helvola* – Zilch in Wenz, 1960: 429–430, fig. 1527.

*Montenegrina helvola helvola* – Zilch, 1981: 128. – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 41, fig. 151, distribution map fig. 18.

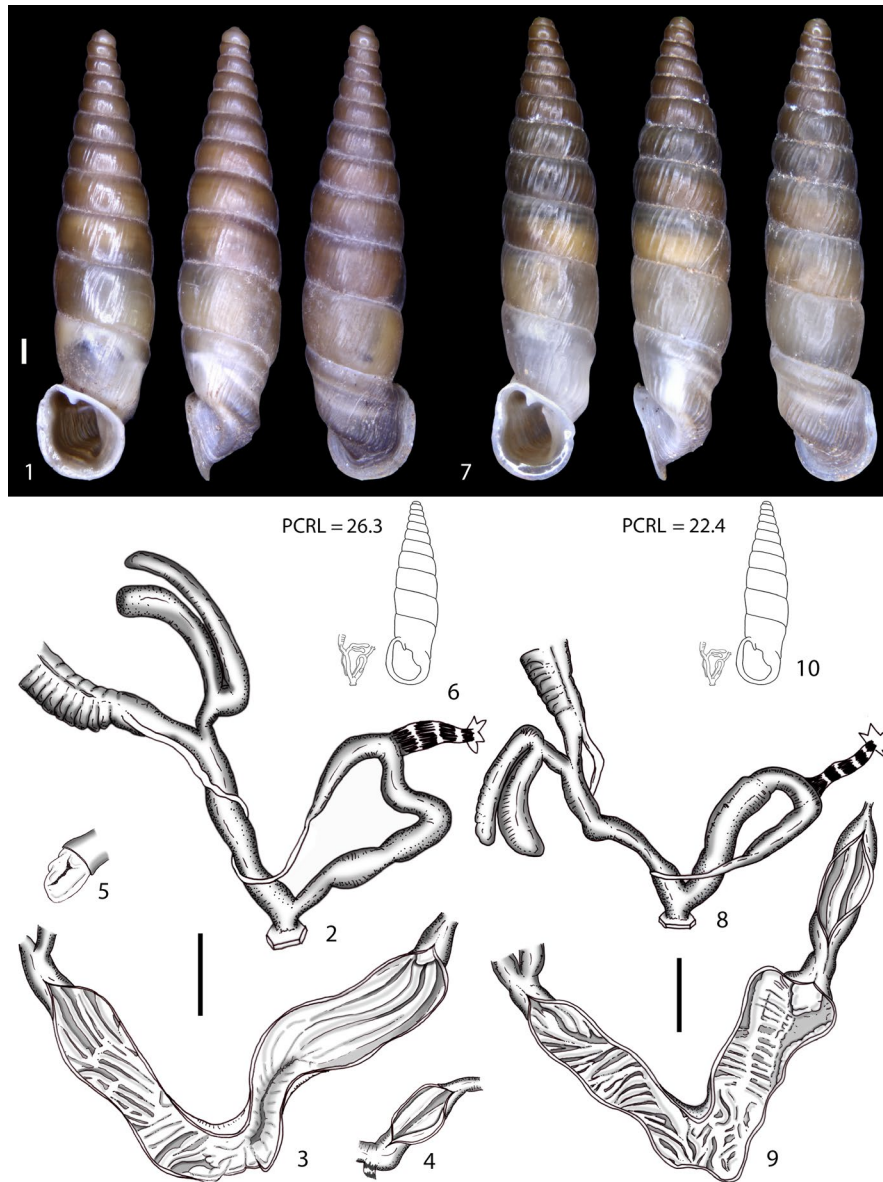
No alcohol-preserved specimens were available for anatomical investigations.

### *Montenegrina helvola carinata* Eröss and Szekeres, 1999

Figures 22.1–22.6

*Montenegrina helvola carinata* Eröss and Szekeres, 1999 in Eröss et al., 1999: 449–450, fig. 4. – Fehér & Szekeres, 2016: 42, fig. 15J, distribution map fig. 18.

**Examined material: three dissected specimens.** Albania, Mallakastër District, Poçem, bank of the Vjosë, 50 m, 40.4926°N,



**FIGURE 22** 22.1–22.6 *Montenegrina helvola carinata* Erőss and Szekeres, 1999 HNHM 99618. 22.1 shell. 22.2 whole distal genitalia. 22.3 inner distal genitalia. 22.4 longitudinal section of epiphallus. 22.5 penial papilla. 22.6 shell-genitalia ratio. 22.7–22.10 *Montenegrina helvola magna* Fehér & Szekeres, 2006 HNHM 98962. 22.7 shell. 22.8 whole distal genitalia. 22.9 inner distal genitalia. 22.10 shell-genitalia ratio

19.7261°E, leg. ZB, DP, GP, 11.v.2014 (HNHM 99618, Mci-466-01 [COI: KU307598, 16S: KU308060]).

**External genitalia (Figure 22.2):** The whole genital complex is medium-sized (PCRL = 26.3). The FO is medium-sized (FO/V = 0.45) and wide in diameter. The vas deferens is uniformly thin along its whole length. The first duct of the bursa copulatrix complex is extremely short (DBC/DB = 0.16). The bursa copulatrix is medium-sized (DB/V = 0.86) and club-shaped. The second duct is wide, cylindrical, only slightly swollen towards the bursa, with no distinguishable transition to the actual bursa. The apex is rounded and blunt. The diverticulum is medium-sized (D/V = 1.23) and longer than the bursa copulatrix (D/BC = 1.42). It is almost uniformly cylindrical and thinner than the bursa copulatrix. The apex is blunt. The vagina is medium-sized (VRL = 12.3)

and uniformly cylindrical. The atrium is short. The PC is much longer than the vagina (PC/V = 2.14), only slightly swollen at the level of penial papilla and with a cylindrical epiphallus that gradually merges into the vas deferens without a visible transitional area. The epiphallus is much longer than penis (E/P = 2.36) and its proximal half is not swollen. The retractor muscle is short and strong.

**Inner genitalia (Figures 22.3–22.5):** The atrium has some irregular, smooth and fleshy, large pleats. The distal vagina has 6–10 smooth transversal pleats that are the continuation of the atrial pleats. These pleats are irregular, splitting, and merging into each other. The background walls are smooth. The proximal vagina has 5–10 longitudinal, elevated, more or less thick pleats that are connected with random, small fleshy bridges. The vaginal pilaster is present.

The proximal penis has four or five smooth, elevated longitudinal pleats. They are, along the proximal section, well separated and the smooth background walls are visible. Distally, the pleats merge and turn into two main, separate, cord-like longitudinal thickenings that extend as far as the genital atrium. The two thickenings are transversely segmented. The penial papilla is small, globose, and rounded. The aperture extends laterally, reaching the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina helvola magna* Fehér & Szekeres, 2006.

Figures 22.7–22.10

*Montenegrina helvola magna* Fehér & Szekeres, 2006 in Erőss et al., 2006: 190, fig. 10. – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 42, fig. 15K, distribution map fig. 18.

**Examined material: two dissected specimens.** Albania, Mat District, 6 km S of Gurri i Bardhë along the Klos to Elbasan road, gorge of the Lumi i Guisës, 1,030 m, 41.4306°N, 20.0920°E, leg. LD, ZE, ZF, AH, DM, 30.vi.2007 (HNHM 98962, Mmg-435-01 [COI: KU307711, 16S: KU308133]; Mmg-435-02 [COI: MT251647]).

**External genitalia (Figure 22.8):** The whole genital complex is medium-sized (PCRL = 22.4). The FO is short (FO/V = 0.21) but wide in diameter. The vas deferens is uniformly thin along its whole length. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.25). The bursa copulatrix is short (DB/V = 0.67), wide in diameter, and club-shaped. The second duct is wide, cylindrical, gradually swelling towards the bursa, with no distinguishable transition into the bursa. The apex is wide and rounded. The diverticulum is short (D/V = 0.71) and slightly longer than the bursa copulatrix (D/BC = 1.06). It is uniformly cylindrical and thinner than the bursa copulatrix. The apex is blunt. The vagina is medium-sized (VRL = 13.1), cylindrical, and only slightly swollen at its proximal portion. The atrium is short. The PC is longer than the vagina (PC/V = 1.71). The penis is wider than the epiphallus. The epiphallus is cylindrical and gradually merges into the vas deferens without a clearly visible transitional area. The epiphallus is longer than the penis (E/P = 1.28). The retractor muscle is short and strong.

**Inner genitalia (Figure 22.9):** The atrium has many irregular, smooth pleats that branch and form a net-like pattern. The distal vagina has 6–10 smooth, obliquetransversal pleats that converge and merge towards a lateral, longitudinal, main pleat. The proximal vagina has up to 10 oblique, elevated pleats that distally merge together. The background walls are smooth. The vaginal pilaster is present. The proximal penis has one big main pleat. This pleat is smooth with a large reticulated pattern inside that eventually turns into a set of 6–9 transversely oriented minor pleats that merge at the center by a fleshy bridge forming a central, longitudinal main pleat. Towards the atrium these pleats become irregular and blurred. The small penial papilla is globose and rounded with a smooth surface. The aperture

extends laterally and reaches the apical area. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina helvola ornata* Erőss and Szekeres, 1999

Figures 23.1–23.5

*Montenegrina helvola ornata* Erőss and Szekeres, 1999 in Erőss et al., 1999: 450–451, fig. 5. – Nordsieck, 2009: 73.

*Montenegrina* n. sp. – Dhora & Welter-Schultes, 1999: 17.

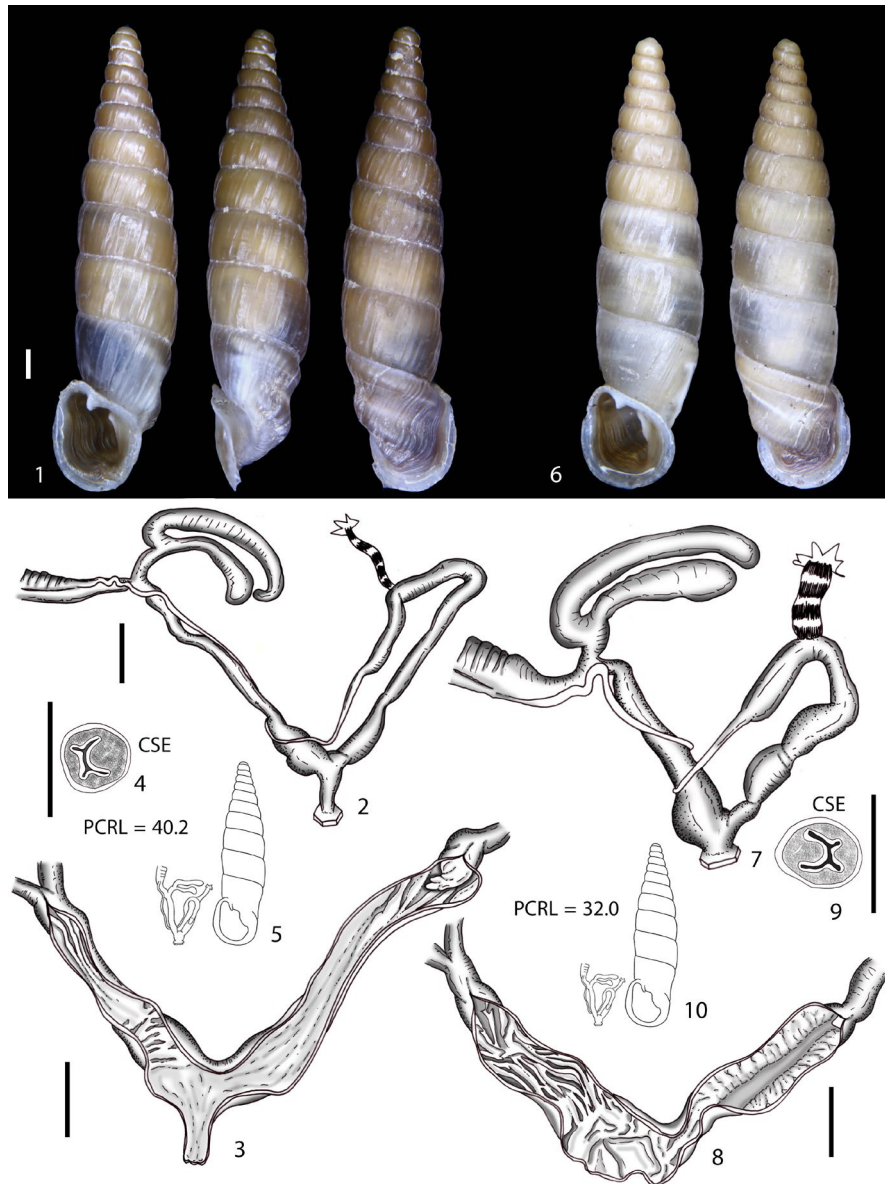
*Montenegrina helvola carinata* – Nordsieck, 2009: 77, plate 2, figs 6–7.

*Montenegrina helvola ornata* – Fehér & Szekeres, 2016: 44, fig. 15L, distribution map fig. 18.

**Examined material: two dissected specimens.** Albania, Elbasan District, Petresh (=5 km SSE of Graçen), along the Tiranë to Elbasan road, S of the village, 440 m, 41.1030°N, 20.0064°E [type locality], leg. ZF, TK, DM, 22.vi.2012 (HNHM 99617, Mor-318-01 [COI: KU307733, 16S: KU308157, 12S: KU307971]; Mor-318-02 [COI: MT251684]).

**External genitalia (Figure 23.2):** The whole genital complex is medium-sized (PCRL = 40.2). The FO is short (FO/V = 0.15) but wide in diameter. The vas deferens is uniformly thin along its whole length. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.37). The bursa copulatrix is short (DB/V = 0.40), wide in diameter and club-shaped. The second duct is wide, cylindrical, gradually swelling towards the bursa, with no distinct transition into the bursa. The apex is wide and rounded. The diverticulum is short (D/V = 0.77) and slightly longer than the bursa copulatrix (D/BC = 1.89). It is uniformly cylindrical and thinner than the bursa copulatrix. The apex is blunt. The vagina is medium-sized (VRL = 27.0), cylindrical, and only slightly swollen proximally. The atrium is short. The PC is longer than the vagina (PC/V = 1.49). The penis is wider than the epiphallus. The epiphallus is cylindrical and gradually merges into the vas deferens without a clearly visible transitional area. The epiphallus is longer than the penis (E/P = 1.0). The retractor muscle is short and strong.

**Inner genitalia (Figures 23.4–23.5):** The atrium is completely smooth. The distal vagina is mainly smooth with only a few little, smooth, transversely arranged pleats. The proximal vagina has four or five longitudinal, elevated pleats (vaginal pilaster included). The background is smooth. The proximal penis has 4–6 smooth longitudinal pleats that immediately merge, forming a completely smooth penis as far as the atrium. The penial papilla is medium-sized, hand-shaped, with many pointed “fingers”. The aperture is very short and extends laterally, not reaching the apical area. The surface is irregular. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.



**FIGURE 23** 23.1–23.5 *Montenegro helvola ornata* Eröss and Szekeres, 1999 HNHM 99617. 23.1. shell 23.2 whole distal genitalia. 23.3 inner distal genitalia. 23.4 cross section of epiphallus. 23.5 shell-genitalia ratio. 23.6–23.10 *Montenegro helvola pageti* Brandt, 1962 NHMW 110430/MN/0077. 23.6 shell. 23.7 whole distal genitalia. 23.8 inner distal genitalia. 23.9 cross section of epiphallus. 23.10 shell-genitalia ratio

### *Montenegro helvola pageti* Brandt, 1962

Figures 23.6–23.10

*Montenegro (Heteroptycha) pageti* Brandt, 1962: 143–144, plate 5, fig. 14.

*Montenegro helvola pageti* – Zilch, 1981: 128, plate 13, fig. 24. – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 44, fig. 15M, distribution map fig. 18.

**Examined material:** two dissected specimens. Albania, Berat, SW side of the castle hill, 70 m, 40.7041°N, 19.9479°E [type locality], leg. DA, ZE, ZF, JG, 27.vi.2014 (NHMW 110430/MN/0077, Mpg-471-01 [COI: KU307742, 16S: KU308163]).

**External genitalia (Figure 23.7):** The whole genital complex is large (PCRL = 32.0). The FO is medium-sized (FO/V = 0.58) and wide in diameter. The vas deferens is slightly swollen at its proximal portion, but uniformly thin along the remaining part. The first duct of the bursa copulatrix complex is extremely short (DBC/DB = 0.16). The bursa copulatrix is medium-sized (DB/V = 0.81), wide in diameter, with an irregular shape. The second duct is wide, cylindrical, irregularly swelling towards the bursa, with no distinguishable transition into the bursa. The apex is wide and rounded. The diverticulum is long (D/V = 1.35) and longer than the bursa copulatrix (D/BC = 1.68). It is uniformly cylindrical and more or less as wide as the bursa copulatrix. The apex is blunt. The vagina is medium-sized (VRL = 18.3), cylindrical, thinner proximally

but gradually increasing in diameter distally. The atrium is short. The PC is longer than the vagina ( $PC/V = 1.74$ ). The penis shows two swellings. The epiphallus is cylindrical, thinner along its distal portion (between retractor muscle and penial papilla) and merges into the vas deferens with a clearly visible transitional area. The epiphallus is as long as the penis ( $E/P = 1.0$ ) and its proximal half is only slightly swollen. The retractor muscle is short and very strong.

**Inner genitalia (Figures 23.8–23.9):** The atrium has three or four big, pad-like, large, and smooth pleats that are irregularly arranged. The distal vagina has up to 10 smooth, fine longitudinal and irregular pleats that do not continue into the atrium. The pleats merge at their distal ends. The proximal vagina has many irregularly arranged pleats, randomly splitting, and merging into each another. The vaginal pilaster is missing. The proximal penis shows two main large, longitudinal, and smooth metameric pleats. These pleats are longitudinally separated by a smooth section of the wall's surface. These pleats extend as far as the atrium. The penial papilla is small, globose, and rounded. The aperture extends laterally, reaching the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

## *Montenegrina hiltrudae* Nordsieck, 1972 sensu Fehér & Szekeres, 2016

### Taxonomic and systematic remarks

*Montenegrina hiltrudae* subspecific taxa are distributed over three main areas. The first is located in the surroundings (southern and western) of Lake Prespa in Albania and Greece with *M. hiltrudae fusca*, *M. hiltrudae sattmanni*, *M. hiltrudae selcensis*, *M. hiltrudae desaretica*, and *M. hiltrudae costulata*. About 40 km southeast of Lake Prespa, only *M. hiltrudae hiltrudae* and *M. hiltrudae densicostulata* are present. The remaining taxa – *M. hiltrudae protruda* (more isolated), *M. hiltrudae maasseni*, and *M. hiltrudae dennisi* (in close proximity) – inhabit isolated spots about 70–80 km south of Lake Prespa in Greece (Fehér & Szekeres, 2016: 47). In the phylogenetic tree of Mason et al. (2020), most *M. hiltrudae* taxa are positioned in clade E. The exceptions in clade D2 are discussed below.

*Montenegrina hiltrudae hiltrudae*, *M. hiltrudae protruda*, and *M. hiltrudae densicostulata* are located in the same subclade within clade E and not well separated. Despite their phylogenetic close affinities, *M. hiltrudae densicostulata*, and *M. hiltrudae protruda* showed a very different genital arrangement (Figures 25 and 29), with the first taxon showing an almost smooth inner genitalia and a well-developed penial papilla, and the latter with a sculptured inner genitalia and no penial papilla but only a fleshy callous that marks the transition zone between the penis and epiphallus. Unfortunately, no suitable specimens of *M. hiltrudae hiltrudae* were available for dissecting. Due to the striking differences in the genital apparatus and shell morphology (and despite close relationships to the other two taxa

in the mt tree), we consider *M. protruda* stat. nov. as a valid species. Taking into account the considerable distance between the respective collecting localities and their phylogenetic affinity, one could assume a relative recent jump dispersal in which either a rapid morphological change or even hybridization with a local population of another (as yet undetected) taxon could have taken place. Because we have no anatomical data for the nominal subspecies, we leave *M. hiltrudae densicostulata* as a subspecies of *M. hiltrudae*.

*Montenegrina hiltrudae dennisi* and *M. hiltrudae maasseni* are intermingled within the same distinct subclade and showed an anatomy very different from all the other known taxa of Clade E. Considering the distinct mitochondrial lineage as well as anatomical and shell-morphological differences, we consider these two taxa to be an independent species.

These two taxa, despite of their phylogenetic affinity, present a different genital arrangement, whereby the first taxon lacks a penial papilla and the latter has a well-developed one; they also differ in the inner wall sculpturing of both penis and vagina (Figures 24.8 and 28.10). Because of their close phylogenetic relationship in the MT tree, we suggest keeping the two taxa at the subspecific level until new data become available. We propose *M. dennisi dennisi* stat. nov. as a valid species and *M. dennisi maasseni* comb. nov.

*Montenegrina hiltrudae sattmanni* is widely distributed along the southern side of Lake Prespa, and it is not monophyletic because it is located within the same subclade as the parapatric, ribbed *M. hiltrudae costulata*, where the specimens of both taxa are intermingled. They differ in genital anatomy from each other and from all the other known taxa of Clade E; moreover, they are phylogenetically very distant from the nominal subspecies. Thus, they should not be considered conspecific with *M. hiltrudae hiltrudae*. Furthermore, *Montenegrina hiltrudae sattmanni* and *Montenegrina hiltrudae costulata* differ from each other considerably both in their shells and in the inner structure of the male and female genitalia (Figures 24.3 and 30.3). Although lineage sorting is not complete, the two taxa may have been isolated from each other long enough to develop their own shell and genital morphology. Considering these differences as significant, we propose *M. sattmanni sattmanni* Nordsieck, 1988 stat. nov. as a valid species and *M. sattmanni costulata* Eröss and Szekeres, 2006 comb. nov. as its subspecies.

Among the populations identified as *M. hiltrudae desaretica* (Fehér & Szekeres, 2016: 50), those from Liqenas (Sveti Atanas i Veliki Antoni Church, Mds-408) and Ishull i Vogël island (Mds-563), Albania, were reported to differ slightly in shell morphology from *M. hiltrudae desaretica*. Furthermore, the genital anatomy of the Sveti Atanas and Ishull i Vogël island populations proved to be considerably different from the topotypical population of *M. hiltrudae desaretica* (Korçë District, 4 km S of Glloboçeni, Mds-618) (Figure 27). This differentiation was confirmed by the phylogenetic analysis: they form a distinct lineage widely separated from the *M. hiltrudae hiltrudae* lineage. Following these results, we consider *M. desaretica* stat. nov. as a valid species and the Sveti Atanas and Ishull i Vogël island populations as *Montenegrina atanasiensis* n. sp., which will be described in a subsequent section.



Note that specimens of the Sv. Marina population Mds-616 harbored two different mitochondrial haplotypes, one closely related to the *M. dofleini prespaens*-*M. dofleini sinosi* clade D2, the other one located within *M. deseratica* (Mason et al., 2020). This population inhabits the Lake Prespa lake shoreline near typical *M. dofleini prespaensis* and typical *M. deseratica* populations. The shell morphology of these specimens is intermediate between *M. deseratica* and *M. dofleini prespaensis*. Specimens of both haplotypes were dissected. In genital morphology they are clearly *M. dofleini prespaensis*. This finding can be explained most plausibly by interspecific hybridization within this contact area.

*Montenegrina hiltrudae fusca* is known only from Mt. Thatë, Albania. This taxon forms a subclade next to *M. deseratica* stat. nov. Its genital anatomy shows a unique arrangement among the former *M. hiltrudae* group of taxa. Moreover, both the shell and genital anatomy of *M. hiltrudae fusca* differ substantially from *M. deseratica*, in particular concerning the inner structure of the penis and vagina (Figure 28.4). Taking into account these differences and its phylogenetic distance from the nominal subspecies, we consider *M. fusca* stat. nov. as a valid species.

*Montenegrina hiltrudae selcensis* is known from a very narrow, isolated area, and distant from the other “*hiltrudae*” taxa (Fehér & Szekeres, 2016: 47). This taxon forms a distinct clade and its genital anatomy is clearly distinguishable from all the other related taxa (Figure 30). Following these new results, we consider *M. selcensis* stat. nov. as a valid species.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina hiltrudae hiltrudae</i> Nordsieck, 1972	<i>Montenegrina hiltrudae hiltrudae</i> Nordsieck, 1972
<i>Montenegrina hiltrudae costulata</i> Eröss and Szekeres, 2006	<i>Montenegrina sattmanni costulata</i> Eröss and Szekeres, 2006 comb. nov.
<i>Montenegrina hiltrudae deseratica</i> Fehér & Szekeres, 2016	<i>Montenegrina deseratica</i> Fehér & Szekeres, 2016 stat. nov.
	<i>Montenegrina atanasiensis</i> n. sp. De Mattia, Fehér, Mason & Haring, 2020
<i>Montenegrina hiltrudae densicostulata</i> Nordsieck, 1974	<i>Montenegrina hiltrudae densicostulata</i> Nordsieck, 1974
<i>Montenegrina hiltrudae dennisi</i> Gittenberger, 2002	<i>Montenegrina dennisi dennisi</i> Gittenberger, 2002 stat. nov.
<i>Montenegrina hiltrudae fusca</i> Fehér & Szekeres, 2006	<i>Montenegrina fusca</i> Fehér & Szekeres, 2006 stat. nov.
<i>Montenegrina hiltrudae maasseni</i> Gittenberger, 2002	<i>Montenegrina dennisi maasseni</i> Gittenberger, 2002 comb. nov.
<i>Montenegrina hiltrudae protruda</i> Gittenberger, 2002	<i>Montenegrina protruda</i> Gittenberger, 2002 stat. nov.
<i>Montenegrina hiltrudae sattmanni</i> Nordsieck, 1988	<i>Montenegrina sattmanni sattmanni</i> Nordsieck, 1988 stat. nov.
<i>Montenegrina hiltrudae selcensis</i> Fehér & Szekeres, 2016	<i>Montenegrina selcensis</i> Fehér & Szekeres, 2016 stat. nov.

## *Montenegrina hiltrudae hiltrudae* Nordsieck, 1972

*Montenegrina hiltrudae* Nordsieck, 1972: 33–34, plate 4, fig. 32.

*Montenegrina hiltrudae hiltrudae* – Zilch, 1981: 128, plate 14, fig. 35. – Nordsieck, 2009: 74. – Fehér & Szekeres, 2016: 45, fig. 19A, distribution map fig. 20.

No alcohol-preserved specimens were available for anatomical investigations.

## *Montenegrina sattmanni costulata* Eröss and Szekeres, 2006 comb. nov.

Figures 24.1–24.5

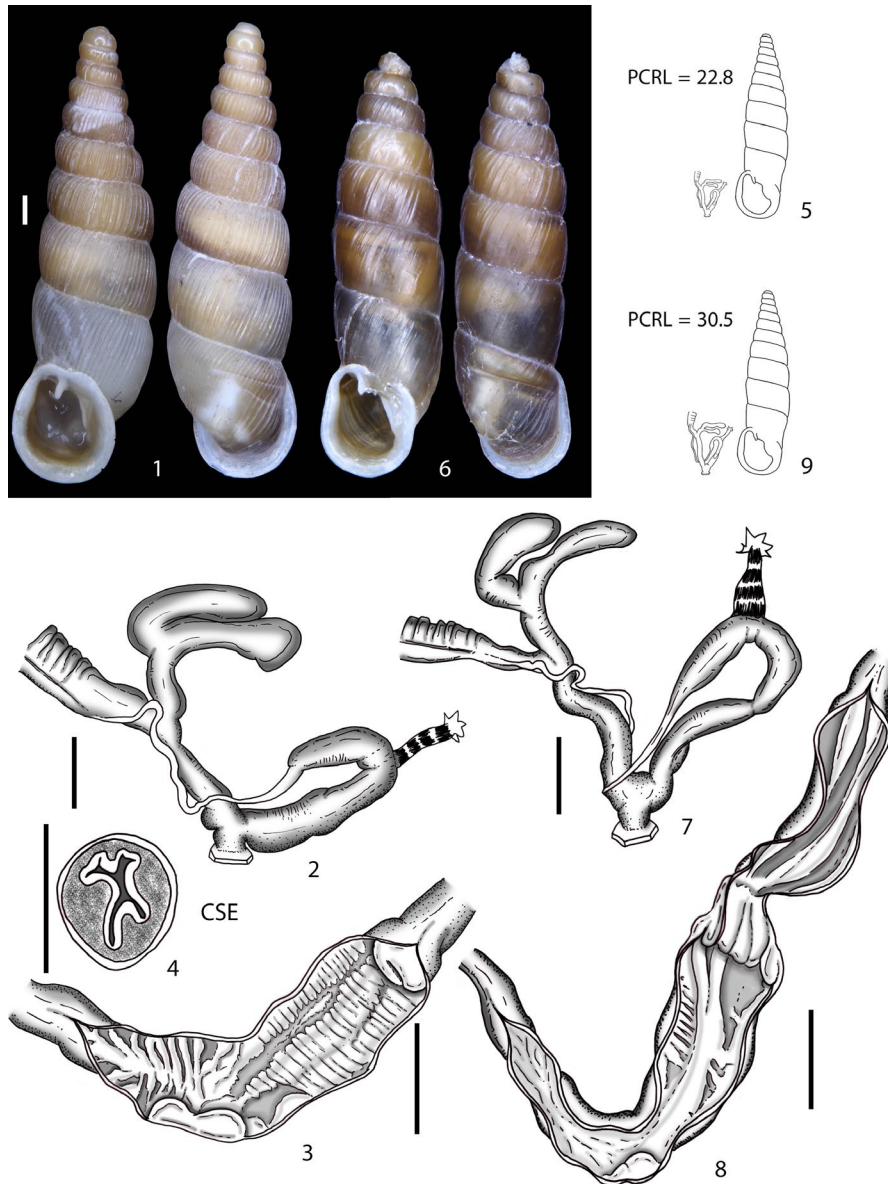
*Montenegrina sattmanni costulata* Eröss and Szekeres, 2006 in Eröss et al., 2006: 204, fig. 27. Nordsieck, 2009: 73.

*Montenegrina hiltrudae costulata* – Fehér & Szekeres, 2016: 47, fig. 19b, distribution map fig. 20.

**Examined material: two dissected specimens.** Albania, Korçë District, Qafa e Zvezdës, 4 km from Zvezdë along the road to the Prespa Lake, 1,030 m, 40.7330°N, 20.8729°E [type locality], leg. ZE, ZF, JG, 29.vi.2013 (HNHM 99590, Mcu-407-01 [COI: KU307626, 16S: KU308073, 12S: KU307940]; Mcu-407-02 [COI: MT251542]).

**External genitalia (Figure 24.2).** The whole genital complex is medium-sized (PCRL = 22.8). The FO is medium-sized (FO/V = 0.53) and very wide in diameter. The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is long (DBC/DB = 0.51). The bursa copulatrix is large (DB/V = 1.33) and very wide in diameter. The second duct of the bursa is wide, cylindrical, and lacks a distinct transition into the bursa. The apex is wide and rounded. The diverticulum is medium-sized (D/V = 1.33) and as long as the bursa copulatrix (D/BC = 1.0). It is uniformly cylindrical and more or less as wide as the bursa copulatrix. The apex is rounded. The vagina is short (VRL = 9.5), uniformly cylindrical, only slightly thinner along its proximal portion. The atrium is short but large. The PC is much longer than the vagina (PC/V = 2.40). The penis is cylindrical, with only a slight swelling at the level of the penial papilla and wider than the epiphallus. The epiphallus is cylindrical, thinner along its distal portion (between retractor muscle and penial papilla) and proximally merges into the vas deferens with a clearly visible transitional area. The epiphallus is longer than the penis (E/P = 1.25). The retractor muscle is short and strong.

**Inner genitalia (Figures 24.3–24.4):** The atrium has one small, smooth fold. The background of the atrium shows a variety of smooth and irregularly arranged plates. The distal vagina shows 5–7 big, smooth transversal pleats, all of them merging into a medial main longitudinal pleat. The proximal vagina has few oblique, elevated, transversal pleats. The background walls are smooth. The vaginal pilaster is present. The penis exhibits three or four main, fringed, metameric cords that extend from the penial papilla base as far as the atrium but abruptly stop before entering it. The cords can merge, especially both at the very proximal or distal level. The



**FIGURE 24** 24.1–24.5 *Montenegrina hiltrudae costulata* Erőss and Szekeres, 2006 comb. nov. HNHM 99590. 24.1 shell. 24.2 whole distal genitalia. 24.3 inner distal genitalia. 24.4 cross section of epiphallus. 24.5 shell-genitalia ratio. 24.6–24.9 *Montenegrina dennisi dennisi* Gittenberger, 2002 stat. nov. HNHM 99591. 24.6 shell. 24.7 whole distal genitalia. 24.8 inner distal genitalia. 24.9 shell-genitalia ratio

background walls also show a fringed transversal sculpture. The medium-sized penial papilla is globose, irregular, with a blunt apex. The aperture extends laterally, reaching the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina dennisi dennisi* Gittenberger, 2002 stat. nov.

Figures 24.6–24.9

*Montenegrina dennisi dennisi* Gittenberger, 2002: 134, figs 7 and 8. – Nordsieck, 2009: 73, plate 2, fig. 10. – Fehér & Szekeres, 2016: 48, fig. 19C, distribution map fig. 20.

**Examined material:** two dissected specimens. Greece, 0.5 km N of Spileo, towards Zakas, 930 m, 40.0080°N, 21.2847°E, leg. ZE, ZF, JG, 22.vi.2013 (HNHM 99591, Mdn-369-01 [COI: KU307637]; Mdn-369-02 [COI: MT251558]).

**External genitalia (Figure 24.7):** The whole genital complex is large (PCRL = 30.5). The FO is medium-sized (FO/V = 0.53). The vas deferens is uniformly thin along the remaining part. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.45). The bursa copulatrix is large (DB/V = 1.16) and wide in diameter. The second duct is wide, cylindrical, with no distinguishable transitional area into the bursa. The apex is rounded. The diverticulum is short (D/V = 0.95), shorter than the bursa copulatrix (D/BC = 0.82). It is swollen and slightly wider than the bursa copulatrix. The apex is big and rounded. The vagina is medium-sized (VRL = 12.16), uniformly cylindrical, and only slightly thinner proximally. The

atrium is moderately long. The PC is much longer than the vagina (PC/V = 2.42). The penis is cylindrical, slightly swollen, and with a marked constriction the level of the penial papilla. The epiphallus is cylindrical, thinner along its distal portion (between retractor muscle and penial papilla) and merges into the vas deferens without a clearly visible transitional area. The epiphallus is longer than the penis (E/P = 1.56), and its proximal half is only slightly swollen. The retractor muscle is short and strong.

**Inner genitalia (Figure 24.8):** The atrium show one very small and smooth fold originating from the genital aperture. The background walls are smooth. The whole vagina is completely smooth, with no vaginal pilaster. The proximal penis bears two or three smooth, main longitudinal pleats that merge into one another approximately along the penis midlength. Other minor and transversely arranged small pleats are also present in the central section of the penis. These main pleats form a main single, smooth, and wide surface along the distal penis. The penial papilla is absent, but a clearly visible, finely pleated invagination of the penial walls marks the transition between the penis and the epiphallus. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina hiltrudae densicostulata* Nordsieck, 1974

Figures 25.1–25.10

*Montenegrina hiltrudae densicostulata* Nordsieck, 1974: 155, plate 6, fig. 37. – Zilch, 1981: 128, plate 14, fig. 36 – Nordsieck, 2009: 74.

*Montenegrina hiltrudae* (partim) – Nordsieck, 1972: 33–34.

*Montenegrina hiltrudae densicostulata* – Fehér & Szekeres, 2016: 49, fig. 19D, distribution map fig. 20.

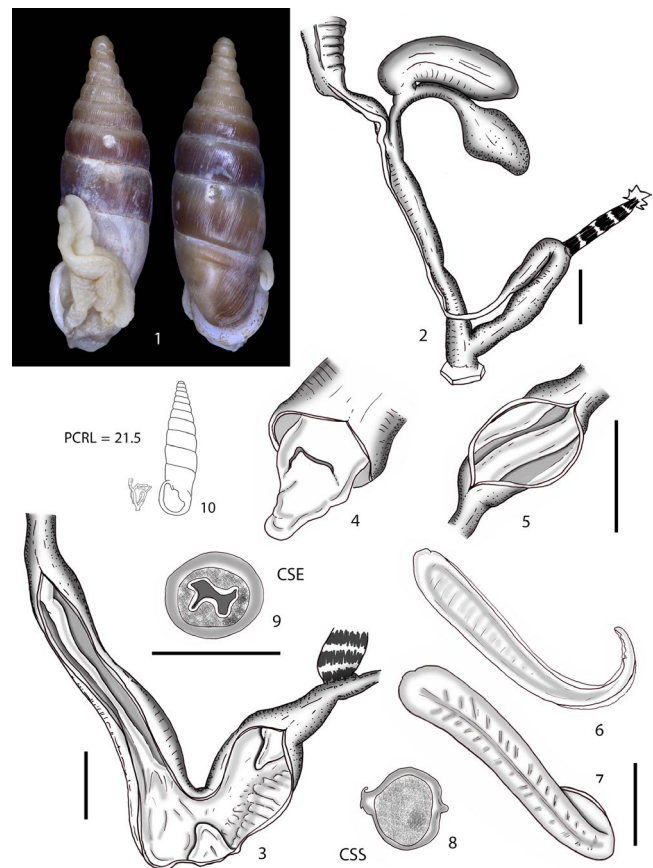
**Examined material:** two dissected specimens. Greece, Kastoria District, 1 km W of Germas, dry gorge, 840–880 m, 40.4430°N, 21.4111°E, leg. ZE, ZF, JG, 28.vi.2013 (HNHM 99583, Mdc-398-01 [COI: KU307555, 16S: KU308029, 12S: KU307928]).

**External genitalia (Figure 25.2):** The whole genital complex is medium-sized (PCRL = 21.5). The FO is medium-sized (FO/V = 0.49). The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.32). The bursa copulatrix is short (DB/V = 0.64) and wide in diameter. The second duct is thin, cylindrical, with a clearly distinguishable transition into the bursa. The apex is big and rounded. The diverticulum is short (D/V = 0.67), uniformly cylindrical and more or less as long as the bursa copulatrix (D/BC = 1.04). The apex is rounded. The vagina is medium-sized (VRL = 10.2) and uniformly cylindrical. The atrium is moderately long and large. The PC is more or less as long as the vagina (PC/V = 1.03). The penis is cylindrical, slightly swollen at the level of the penial papilla and slightly wider than the epiphallus. The epiphallus is cylindrical, thinner along its proximal portion, and merges into the vas deferens without a clearly visible transitional area. The epiphallus is shorter than the penis

(E/P = 0.90). The retractor muscle is long and strong. The overall genital scheme gives the impression of representing a “long vagina” type, but this is merely due to the unusual shortness of the PC. Nevertheless, the small shell yields a medium-sized genitalia type.

**Inner genitalia (Figures 25.3–25.5, 25.9):** The atrium shows a unilobate fold originating directly at the genital aperture. This fold occupies only a small part of the atrium. The distal vagina is smooth but with weak traces of flat, slightly elevated longitudinal pleats. The proximal vagina has one elevated longitudinal pleat that corresponds to the vaginal pilaster. The background walls are smooth. The penis shows two flat and poorly visible smooth pleats arranged in a chevron-like pattern. The inferior pleat is visible, whereas the upper one is usually barely evident. The penial papilla is medium-sized, conical, with a pointed apex and smooth surface. The aperture is lateral but transversely oriented. The apical, apertureless part is smaller in diameter. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

**Spermatophore (Figures 25.6–25.8):** The spermatophore is bent and has a large head that gradually narrows towards the tail. The head



**FIGURE 25** *Montenegrina hiltrudae densicostulata* Nordsieck, 1974 HNHM 99583. 25.1 shell. 25.2 whole distal genitalia. 25.3 inner distal genitalia. 25.4 penial papilla. 25.5 longitudinal section of epiphallus. 25.6–25.7 spermatophore. 25.8 cross section of spermatophore. 25.9 cross section of epiphallus. 25.10 shell-genitalia ratio

is blunt. The tail is pointed, sharp, and blade-shaped. The lower carina begins immediately behind the head and extends as far as the tip of the tail. The upper carina starts approximately where the body of the spermatophore begins to bend and extends as far as the tip of the tail. The dorsal surface presents a fishbone-like sculpturing. The cross section is roundish with two lateral, blunt keels. The largest one, which is roughly "T"-shaped, runs dorsally and eventually becomes the upper carina. The smaller one represents the longitudinal base of the lower, thin carina. The spermatophore is 3.2 mm long and 0.4 mm wide.

### *Montenegrina atansiensis* n. sp.

urn:lsid:zoobank.org:act:83CA4A42-EA2A-472F-990B-C595D-58F17AF.

Figures 26.1–26.6

**Type locality:** Albania, Korçë District, 1 km NE of Liqenas, Sveti Atanas i Veliki Antoni Church, 850 m, 40.7919°N, 20.9152°E.

**Type material:** Type locality: Albania, Korçë District, 1 km NE of Liqenas, Sveti Atanas.

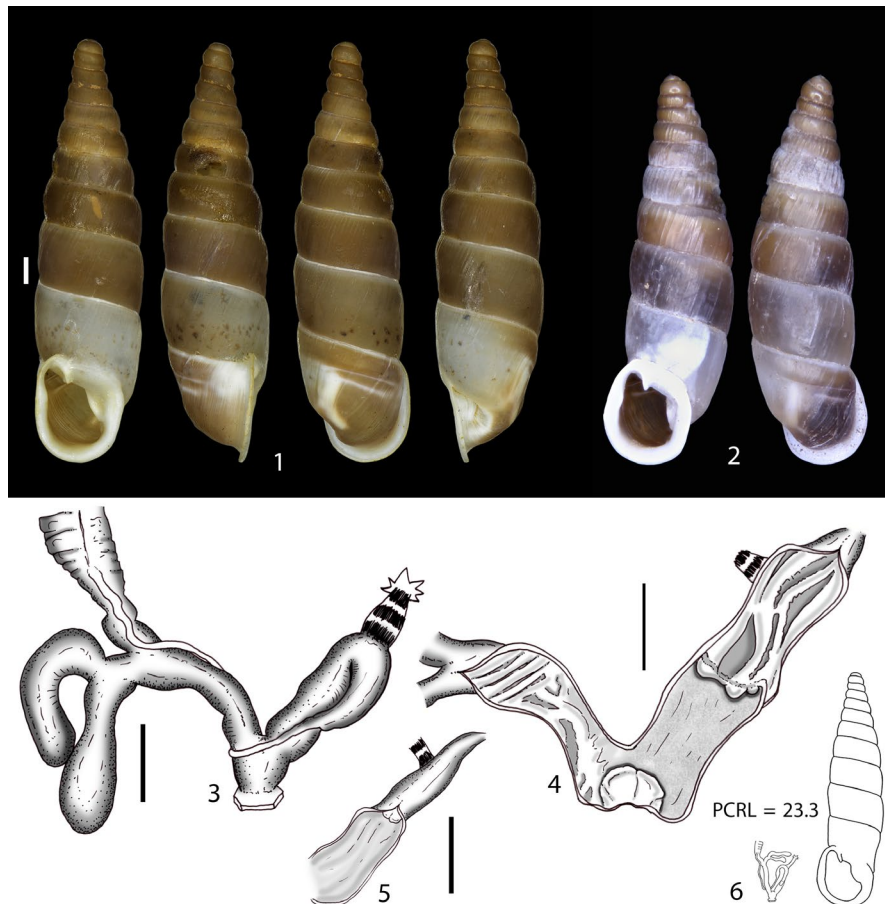
i Veliki Antoni Church, 850 m, 40.7919°N, 20.9152°E.

**Type material:** type locality, leg. ZE, ZF, JG, 28.vi.2013, holotype (HNHM 104159 = Mds-408-07 [COI: MT251566]), paratypes (HNHM 99587/7 + 2fr+6a (=Mds-408-01 [COI: KU307787, 16S: KU308182, 12S: KU307981] to Mds-408-06); coll. Grego/11; coll. Eröss/11 specimens); same locality, leg. ZE, ZF, JK, DM, 2.vii.2003 (HNHM 94901/34 + 6fr; coll. Eross, 37 specimens).

**Other material:** Liqenas, 860 m, 40.7891°N, 20.9072°E, leg. ZE, ZF, JK, DM, 2.vii.2003 (HNHM 94898); Ishull i Vogël, E of Liqenas, 860 m, 40.7915°N, 20.9324°E, leg. ZF, LT, 17.viii.2007 (HNHM 99572).

**Distribution:** *Montenegrina atansiensis* n. sp. is known from only two localities along the SW branch of Lake Prespa between Pustec and Diellas and the small island of Ishull i Vogël (in Fehér & Szekeres, 2016: 50).

**Shell differential diagnosis:** The new species is heterogeneous, with many of its shell characters ranging between those of the nearby occurring, typical *M. dofleini prespaensis*, *M. sattmanni*, and *M. hiltrudae desaretica* populations. It can be distinguished from *M. hiltrudae desaretica* by the weaker shell sculpture and from *M. dofleini prespaensis* by the presence of the basal.



**FIGURE 26** *Montenegrina atansiensis* n. sp. HNHM 99587 Mds-408-07. 26.1 shell of the Holotype. 26.2 shell of the dissected specimen HNHM 99587 Msa-408-01. 26.3 whole distal genitalia and inner distal genitalia. 26.4 inner distal genitalia. 26.5 penial papilla and proximal inner penis. 26.6 shell-genitalia ratio

**Diagnosis:** Medium-size subspecies with costate shell, attached peristome, and non-overlapping lamellae superior and spiralis. The genitalia exhibit a big, polylobated atrial fold, the inner walls of the penis are completely smooth, and the penial papilla is broad but very short. The vaginal pilaster is absent.

**Dimensions** (in mm): Holotype Hs: 18.5,  $W_s$ : 4.9,  $H_a$ : 4.8,  $W_a$ : 4.0; paratypes Hs: 15.0–20.0;  $W_s$ : 4.0–5.5,  $H_a$ : 3.5–5.0;  $W_a$ : 3.0–4.0.

**Shell description (Figures 26.1–26.2):** The tumid, horn-brown shell consists of  $9\frac{1}{2}$  to  $10\frac{1}{2}$  whorls. The upper whorls are finely striate to bluntly costate, the sculpture becomes weaker on the lower whorls. The neck is not or only very weakly inflexed, usually striate. The basal crest is weak, the peripheral one is not recognizable. The aperture is angular, its broadly attached margin is somewhat swollen and deflexed. Depending on the varying length of lamella superior, it does or does not overlap with the spiralis. In front view, the lamella inferior is moderately emerged, and the end of the broadly bent subcolumellaris is visible. The basalis is long to short and missing. When long, it is visible in front view. It is mostly connected to the dorsal–dorsolateral lunella. The subclaustralis is short or missing, the sulcalis is usually well developed. The plica superior is long to missing, when longer it tends to fuse with the lunella.

**External genitalia (Figure 26.3):** The whole genital complex is medium-sized (PCRL = 23.3). The FO is medium-sized (FO/V = 0.48) and wide in diameter. The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.21). The bursa copulatrix is long (DB/V = 1.14) and wide in diameter. The second duct is cylindrical, with no distinguishable transition into the bursa. The apex is big and rounded. The diverticulum is short (D/V = 1.0), uniformly cylindrical, and shorter than the bursa copulatrix (D/BC = 0.88). The apex is rounded. The vagina is medium-sized (VRL = 12.2) and uniformly cylindrical, only slightly swollen along its proximal part. The atrium is long and large. The PC is longer than the vagina (PC/V = 1.90). The penis is cylindrical, uniformly slightly swollen, and slightly wider than the epiphallus. The epiphallus is longer than the penis (E/P = 1.67), cylindrical, thinner along its proximal portion, and merges into the vas deferens without a clearly visible transitional area. The proximal half of the epiphallus is not swollen. The retractor muscle is short and very strong.

**Inner genitalia (Figure 26.4–26):** The atrium has a big, polylobated fold originating directly at the genital aperture. The background is smooth. The distal vagina is mainly smooth, only with weak traces of a few irregular, smooth, transversal/oblique pleats; a single longitudinal and irregular pleat connects with the distal vagina. The proximal vagina has 5–7 smooth, oblique pleats and the vaginal pilaster is missing. The penis is completely smooth without any sculpturing. The walls are very finely granulated. The very small penial papilla is bilobated. The aperture reaches the apical area. The surface is smooth. The epiphallus has up to five simple smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

**Etymology:** The new taxon was named after Sveti Atanas, the namesake of the church at the type locality.

## *Montenegrina desaretica* Fehér & Szekeres, 2016 stat. nov.

Figures 27.1–27.6

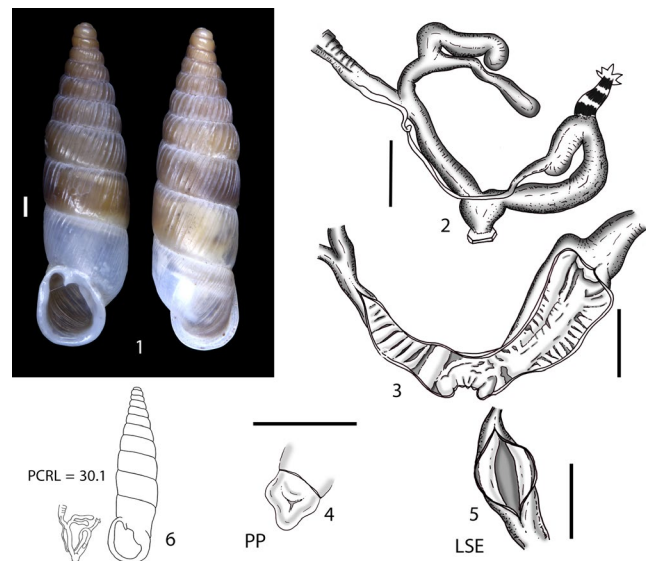
*Montenegrina sattmanni sattmanni* – Erőss et al., 2006: 206.

*Montenegrina hiltrudae desaretica* – Fehér & Szekeres, 2016: 50, fig. 19e, distribution map fig. 20.

**Examined material: two dissected specimens (paratypes).** Albania, Korçë District, cave temple ca. 4 km S of Gllboçeni, at the Prespa Lake, 850 m, 40.8422°N, 20.9616°E [type locality], leg. ZE, ZF, JG, 30.vi.2015 (NHMW 111251, Mds-618-01 [COI: KU307585]; Mds-618-02 [COI: MT251586]).

**External genitalia (Figure 27.2):** The whole genital complex is large (PCRL = 30.1). The FO is medium-sized (FO/V = 0.46) and moderately wide in diameter. The vas deferens is thin and slightly swollen at its distal and proximal ends. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.31) and wide in diameter. The bursa copulatrix is long (DB/V = 1.04). The second duct is cylindrical, thin, with no clear transition into the bursa. The apex is thin and rounded. The diverticulum is short (D/V = 0.86), wide, uniformly cylindrical and shorter than the bursa copulatrix (D/BC = 0.83). The apex is big and rounded. The vagina is medium-sized (VRL = 16.2) and uniformly cylindrical. The atrium is long and very large. The PC is longer than the vagina (PC/V = 1.86). The penis is wide and uniformly cylindrical. The epiphallus is longer than the penis (E/P = 1.36), cylindrical, thinner along its distal portion and merges into the vas deferens with a well-visible transitional area. The proximal half of the epiphallus is swollen. The retractor muscle is short and very strong.

**Inner genitalia (Figures 27.3–27.3):** The atrium has three or four big, pad-like, smooth folds. The distal vagina has a single transversal,



**FIGURE 27** *Montenegrina desaretica* Fehér & Szekeres, 2016 stat. nov. NHMW 111251. 27.1 shell. 27.2 whole distal genitalia. 27.3 inner distal genitalia. 27.4 longitudinal section of epiphallus. 27.5 penial papilla. 27.6 shell-genitalia ratio

smooth, and large pleat. This pleat is not very elevated. The proximal vagina shows 8–10 large transversal pleats that all merge at their ends. The vaginal pilaster is missing. The proximal penis has four or five smooth, large, oblique longitudinal pleats that merge distally, forming a single large longitudinal pleat with many fleshy transversal bridges, yielding a comb-like shape. The very small-sized penial papilla is bilobated. The aperture reaches the apical area. The surface is smooth. The epiphallus has up to five simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina fusca* Fehér & Szekeres, 2006 stat. nov.

Figures 28.1–28.7

*Montenegrina sattmanni fusca* Fehér & Szekeres, 2006 in Eröss et al., 2006: 204–206, fig. 28.

*Montenegrina skipetarica fusca* – Nordsieck, 2009: 73.

*Montenegrina hiltrudae fusca* – Fehér & Szekeres, 2016: 51, fig. 19F, distribution map fig. 20.

**Examined material: two dissected specimens.** Albania, Korçë District, Korit e Bregas, 6 km S of Podgorje along the Pogradec to Zvezdë road, 900 m, 40.7688°N, 20.8275°E [type locality], leg. ZE, ZF, JG, 29.vi.2013 (HNHM 99596, Mfc-409-01 [COI: KU307671, 16S: KU308104, 12S: KU307952]; Mfc-409-01 [COI: MT251598]).

**External genitalia (Figures 28.2–28.3):** The whole genital complex is large (PCRL = 36.6). The FO is extremely short (FO/V = 0.28) but wide in diameter. The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is extremely short (DBC/DB = 0.06). The bursa copulatrix is short (DB/V = 0.79) and club-like. The second duct is cylindrical, wide, with no distinguishable transition into the bursa. The apex is rounded. The diverticulum is short (D/V = 0.87), wide, uniformly cylindrical, and slightly longer than the bursa copulatrix (D/BC = 1.10). The apex is rounded. The vagina is medium-sized (VRL = 19.4) and uniformly cylindrical. The atrium is short but large. The PC is longer than the vagina (PC/V = 1.87). The penis is wide and swollen. The epiphallus is much longer than the penis (E/P = 2.84), cylindrical, thinner along its proximal portion and merges into the vas deferens without a clearly visible transitional area. The retractor muscle is short and very strong.

**Inner genitalia (Figures 28.4–28.6):** The atrium is divided in two sections. The left-central section is smooth, whereas the right side shows the continuation of the two main longitudinal penial pleats that continue as far as genital aperture. The distal vagina is smooth with many scattered, irregularly arranged pleats. The proximal vagina shows many smooth, elevated pleats arranged in an irregular chevron-like pattern. The background walls are smooth. The vaginal pilaster is present. The penis has two main longitudinal pleats originating from the proximal section close to penial papilla and extending as far as the genital aperture. The pleats are fringed, with a quite large interspace. Some minor, fringed longitudinal pleats are visible in the

proximal section of the penis. The background walls are finely granulated. The medium-sized conical penial papilla has a pointed but nonetheless broad apex and a smooth surface. The aperture is lateral and does not reach the papilla's tip. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina dennis maasseni* Gittenberger, 2002 comb. nov.

Figures 28.8–28.12

*Montenegrina janinensis maasseni* Gittenberger, 2002: 131–134, figs 5 and 6 – Nordsieck, 2009: 75.

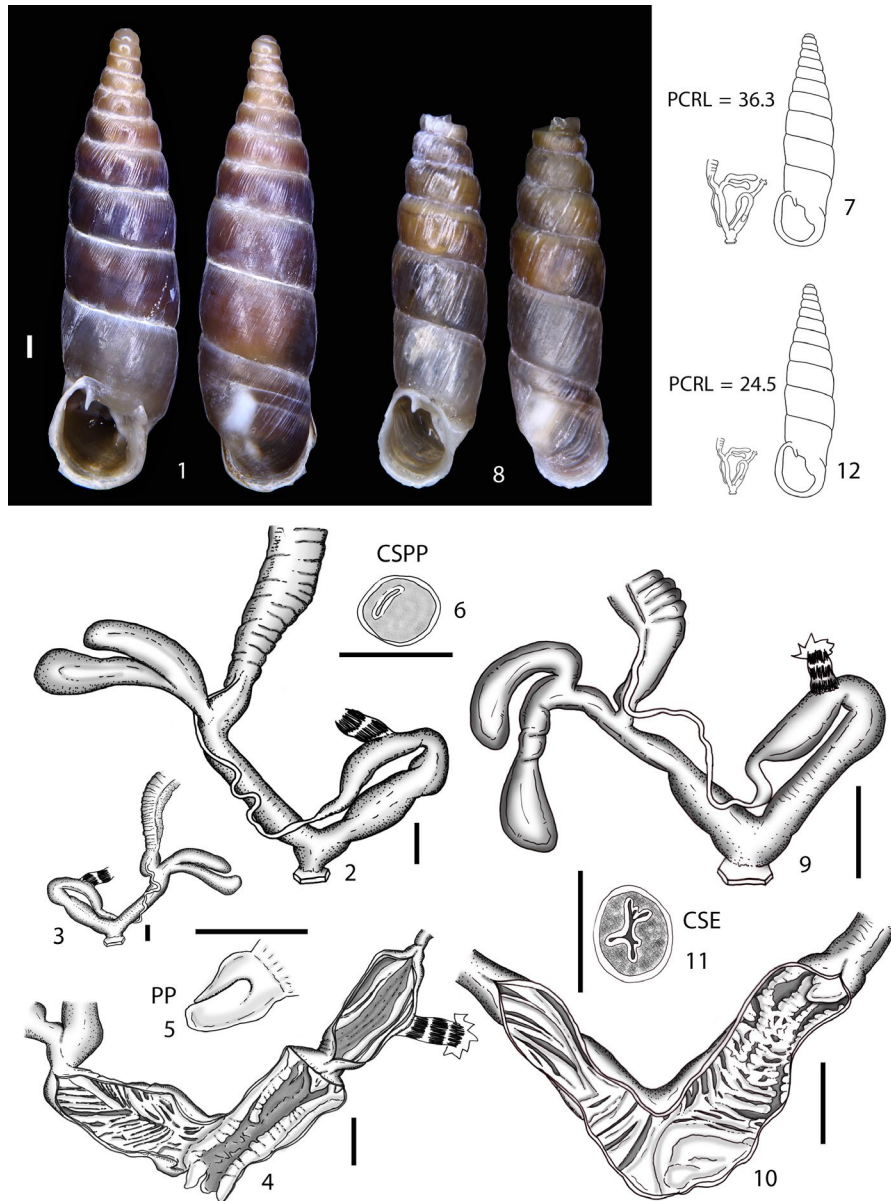
*Montenegrina janinensis maasii* (sic! typographic error) – Uit de Weerd & Gittenberger, 2004: 307, fig. 1D.

*Montenegrina hiltrudae maasseni* – Fehér & Szekeres, 2016: 51, fig. 19G, distribution map fig. 20.

**Examined material: three dissected specimens.** Greece, Portitsa Farangi, near Spileo, 39.9965°N, 21.2855°E [type locality], leg. ZE, ZF, JG, 22.vi.2013 (HNHM 99595, Mma-367-02 [COI: KU307708, 16S: KU308130]).

**External genitalia (Figure 28.9):** The whole genital complex is medium-sized (PCRL = 24.5). The FO is medium-sized (FO/V = 0.56) and wide in diameter. The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.30). The bursa copulatrix is long (DB/V = 1.11), wide, and club-like. The second duct is cylindrical, wide, and irregular. A transition into the bursa is distinguishable. The apex is wide and rounded. The diverticulum is short (D/V = 0.89), wide, uniformly cylindrical, and shorter than the bursa copulatrix (D/BC = 0.80). The apex is wide and rounded. The vagina is medium-sized (VRL = 12.6), cylindrical, and slightly swollen distally. The atrium is short but very large. The PC is longer than the vagina (PC/V = 1.94). The penis is wide and usually uniformly cylindrical. The epiphallus is slightly shorter than the penis (E/P = 0.94), swollen along both its distal and proximal sections, and merges into the vas deferens with a visible transitional area. The retractor muscle is very short and strong.

**Inner genitalia (Figures 28.10–28.11):** The atrium has few irregular, smooth and fleshy large pleats. The distal vagina bears 5–10 smooth, irregular transversal pleats. These pleats merge into each other at their distal ends. The background is smooth. The proximal vagina has a few oblique, elevated transversal pleats. The background walls are smooth. The vaginal pilaster is present. The proximal penis has 5–7 irregular, “pearl-necklace”-like longitudinal pleats with few irregular, obliqueminor folds. Additional small, irregular transversal pleats run through the distal penis, continuing into the atrium. The medium-sized, conical penial papilla has a pointed but nonetheless broad apex and a smooth surface. The lateral aperture does not reach the papilla's tip. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.



**FIGURE 28** 28.1–28.7 *Montenegrogrina fusca* Fehér & Szekeres, 2006 stat. nov. HNHM 99596. 28.1 shell. 28.2–28.3 whole distal genitalia. 28.4 inner distal genitalia. 28.5 penial papilla. 28.6 cross section of penial papilla. 28.7 shell-genitalia ratio. 28.8–28.12 *Montenegrogrina dennis maasseni* Gittenberger, 2002 comb. nov. HNHM 99595. 28.8 shell, 28.9 whole distal genitalia, 28.10 inner distal genitalia, 28.11 cross section of epiphallus, 28.12 shell-genitalia ratio

### *Montenegrogrina hiltrudae protruda* Gittenberger, 2002

Figures 29.1–29.5

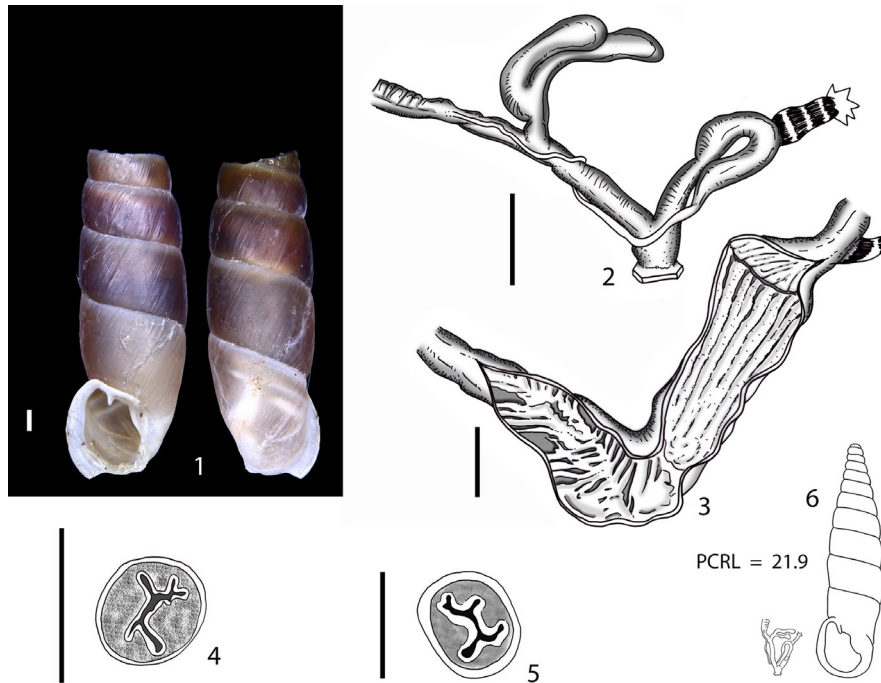
*Montenegrogrina dennis protruda* Gittenberger, 2002: 135, figs 9–10 (clausilium plate), 17–19 (clausilium plate microarmature). – Nordsieck, 2009: 73.

*Montenegrogrina hiltrudae protruda* – Fehér & Szekeres, 2016: 52, fig. 19H, distribution map fig. 20.

**Examined material:** three dissected specimens. Greece, Western Macedonia, 2.3 km before Aetia along the Aetia to Anavrita road, along the path to the Nymphoon Cave, W slope, 990 m, 40.0741°N,

21.2017°E [type locality], leg. ZE, ZF, JG, 22.vi.2013 (HNHM 99593, Mpo-370-03 [COI: KU307752, 16S: KU308168]).

**External genitalia (Figure 29.2):** The whole genital complex is medium-sized (PCRL = 20.7). The FO is long (FO/V = 0.70). The vas deferens is thin proximally and is gradually swollen towards the epiphallus. The first duct of the bursa copulatrix complex is very short (DBC/DB = 0.13). The bursa copulatrix is long (DB/V = 1.20), wide, and club-like. The second duct is cylindrical, wide, and irregular. A transition into the bursa is not distinguishable. The apex is wide and rounded. The diverticulum is medium-sized (D/V = 1.05), wide, uniformly cylindrical and shorter than the bursa copulatrix (D/BC = 0.88). The apex is wide and rounded. The vagina is medium-sized (VRL = 10.4)



**FIGURE 29** 29.1–29.5 *Montenegrina hiltrudae protruda* Gittenberger, 2002 HNHM 99593. 29.1 shell, 29.2 whole distal genitalia, 29.3 inner distal genitalia, 29.4 cross section of epiphallus. 29.5 shell-genitalia ratio

and uniformly cylindrical. The atrium is short but very large. The PC is much longer than the vagina ( $PC/V = 2.00$ ). The penis is not very wide and usually uniformly cylindrical. The epiphallus is slightly longer than the penis ( $E/P = 1.5$ ), swollen along both its distal and proximal sections, and merges into the vas deferens with a visible transitional area. The retractor muscle is very short and strong.

**Inner genitalia (Figures 29.3–29.4):** The atrium shows many irregular, smooth and fleshy pleats. The distal vagina has 5–10 smooth transversal pleats that do not continue into the atrium. The pleats are arranged in a chevron-like pattern and merge in the middle, forming a longitudinal central pleat. The pleats split and merge into one another at their ends. The background is smooth. The proximal vagina shows a few oblique, elevated, irregular transversal pleats. The vaginal pilaster is present. The whole penis has 9 or 10 longitudinal, fleshy metameric pleats that tend to merge together towards the atrium, forming a fleshy platform that does not enter the atrium. The penial papilla is absent, but a visible, finely pleated invagination of the penial walls clearly marks the transition between the penis and epiphallus. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina sattmanni sattmanni* Nordsieck, 1988 stat. nov.

Figures 30.1–30.6

*Montenegrina sattmanni* Nordsieck, 1988: 200–201, fig. 5.

*Montenegrina sattmanni sattmanni* – Nordsieck, 2009: 73, plate 2, fig. 9.

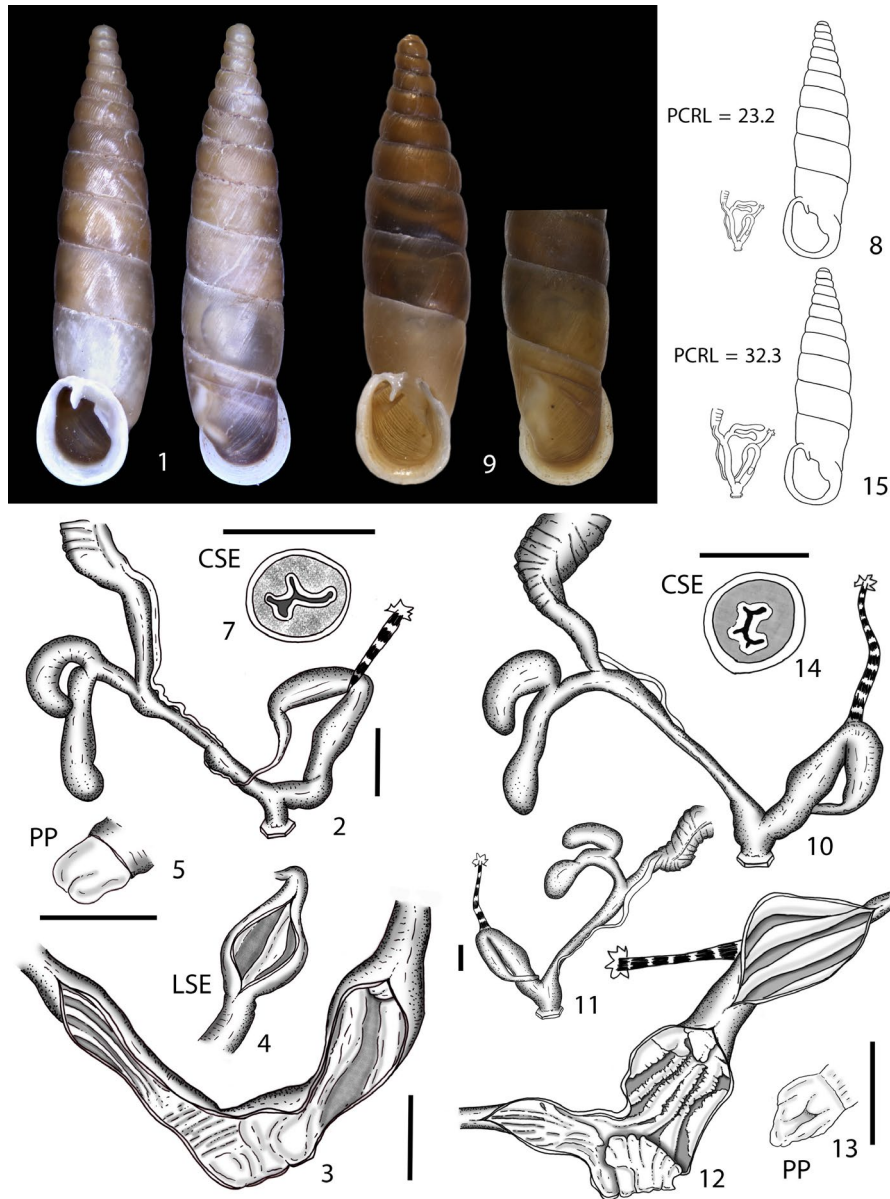
*Montenegrina hiltrudae sattmanni* – Fehér & Szekeres, 2016: 53, fig. 19J, distribution map fig. 20.

**Examined material: two dissected specimens.** Greece, Western Macedonia, Mikrolimni, near the Biological Station, 40.7429°N, 21.1102°E [type locality], leg. ZE, ZF, JG, 28.vi.2013 (HNHM 99585, Msa-402-01 [COI: KU307786, 16S: KU308181]; Msa-402-01 [COI: MT251761]).

**External genitalia (Figure 30.2):** The whole genital complex is medium-sized ( $PCRL = 23.2$ ). The FO is long ( $FO/V = 0.75$ ). The vas deferens is thin but is gradually swollen towards its proximal end. The first duct of the bursa copulatrix complex is medium-sized ( $DBC/DB = 0.38$ ). The bursa copulatrix is medium-sized ( $DB/V = 0.86$ ), almost completely cylindrical, only slightly swollen towards the tip. The second duct is cylindrical, with no distinguishable transition into the bursa. The diverticulum is short ( $D/V = 0.79$ ), wide, uniformly cylindrical and shorter than the bursa copulatrix ( $D/BC = 0.92$ ). The apex is rounded. The vagina is medium-sized ( $VRL = 13.8$ ) with a swelling proximally part and another swelling midway towards its distal end. The atrium is long and thin. The PC is longer than the vagina ( $PC/V = 1.68$ ). The penis is slender and slightly swollen at the level of the penial papilla. The epiphallus is slightly longer than the penis ( $E/P = 1.24$ ), slender, and slightly swollen along its proximal part. It merges into the vas deferens without a clear transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 30.3–30.6):** The atrium has a few irregular, smooth and fleshy large pleats. The distal vagina is almost smooth with very fine transversal wrinkles. The proximal vagina shows four or five elevated longitudinal pleats (vaginal pilaster included). The background is smooth. The penis shows two smooth, large longitudinal pleats that extend as far as the atrium. The background walls are





**FIGURE 30** 30.1–30.6 *Montenegrogrina sattmanni sattmanni* Nordsieck, 1988 stat. nov. HHNM 99585, 30.1 shell, 30.2 whole distal genitalia, 30.3 inner distal genitalia, 30.4 longitudinal section of epiphallus, 30.5 penial papilla, 30.6 cross section of epiphallus. 30.7 shell-genitalia ratio. 30.7–30.14 *Montenegrogrina selcensis* Fehér & Szekeres, 2016 stat. nov. NHMW 111218. 30.8 shell. 30.9–30.10 whole distal genitalia. 30.11 inner distal genitalia. 30.12 penial papilla. 30.13 cross section of epiphallus. 30.14 shell-genitalia ratio

smooth. The medium-sized penial papilla is globose, with blunt apex. The aperture extends laterally and reaches the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrogrina selcensis* Fehér & Szekeres, 2016 stat. nov.

Figures 30.6–30.14

*Montenegrogrina hiltrudae selcensis* – Fehér & Szekeres, 2016: 54, fig. 29K, distribution map fig. 20.

**Examined material: two dissected specimens (paratypes).** Albania, Korçë District, NE of Strelcë, in the limestone gorge of the Lumi i Verbës at the foot of the Shkëmb i Selcës, 990 m, 40.7480°N, 20.5219°E [type locality], leg. ZF, JG, 30.vi.2014 (NHMW 111218, Mse-479-01 [COI: KU307571,16S: KU308041]).

**External genitalia (Figures 30.9–30.10):** The whole genital complex is medium-sized (PCRL = 32.3) and very slender. The FO is short (FO/V = 0.32) and thin. The vas deferens is thin but gradually swollen towards its proximal end. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.40). The bursa copulatrix is short (DB/V = 0.47), almost completely cylindrical, only slightly swollen towards the tip. The second duct is cylindrical, without a distinguishable transition into the bursa. The diverticulum is short

(D/V = 0.62), wider but shorter than the bursa (D/BC = 1.32) and uniform. The apex is blunt. The vagina is long (VRL = 27.6) and very slender. The atrium is short and large. The PC is only slightly longer than the vagina (PC/V = 1.17). The penis is slender and slightly swollen at the level of the penial papilla. The epiphallus is longer than the penis (E/P = 1.82), slender and slightly swollen proximally portion. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 30.11–30.13):** The atrium shows a big, polylobated fold originating directly at the genital aperture. The distal vagina has a few smooth, scattered, and irregularly arranged loose pleats. The proximal vagina has 5–10 smooth longitudinal pleats. The pleats can be connected with small fleshy bridges of varying thickness. The vaginal pilaster is present. The proximal penis has six or seven main elevated, fringed, and irregular longitudinal pleats. The background walls are very finely granulated. The medium-sized penial papilla is pyramidal, pointed but with a blunt apex. The aperture extends laterally and does not reach the apical area. The surface is smooth. Two small, roundish basal lobes are present. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

## *Montenegrina laxa* (Küster, 1861) sensu Fehér & Szekeres, 2016

### Taxonomic and systematic remarks

*Montenegrina laxa* s.l. is distributed over a wide area in central Albania (Fehér & Szekeres, 2016: 58). All the *M. laxa* s.l. subspecific taxa fall inside the main Clade L, but *M. laxa* is not monophyletic due to the presence of *M. drimmeri* within this clade (its systematics was already discussed above). *Montenegrina laxa* has two main clades, one containing the nominal *M. laxa laxa* (Mlx) and *M. laxa iba* (Mib) and the other containing all the other *M. laxa* ssp.

The phylogeny of *M. laxa laxa* and *M. laxa iba* is further complicated by the fact that the populations of *M. laxa laxa* show two separate mitochondrial lineages, but material for anatomical dissection was available for only one of them (Mlx-461-01). The genital anatomy of *M. laxa laxa* (Mlx-461-01) and of *M. laxa iba* (Mib-463-01) differ substantially (Figures 24 and 26) both in external and inner features. Nonetheless, one similarity is the common shape of the inner vagina. Based on the above differences and their different shell morphology, they should be considered as valid species, namely *M. laxa* and *M. iba*. stat. nov.

All the remaining taxa of former *M. laxa* fall together into one clade, separate from the nominal *M. laxa* and *M. iba*, and therefore should not be considered as subspecies of *M. laxa*. All these subspecies are differentiated in their anatomical features, whereby those of *M. laxa miraka*, *M. laxa errans*, *M. laxa dedovi* and *M. laxa disjuncta* show more similarities with each other. The most differentiated

anatomies were found in *M. laxa kotschani* and *M. laxa delii*. In the phylogenetic tree, these taxa are not well differentiated and they all are not monophyletic. The only exception is *M. laxa lakmosensis*, which is the sister group of all the other taxa.

All these taxa have been recently described based solely on shell features, that is, on minor morphological details (position of lunella, buccal apparatus with its plicae and lamellae, overall shell shape). The anatomical analyses confirmed these taxa, although some of the subspecies are quite similar. Combining these findings together and considering the close phylogenetic relationships, we propose that they should remain at subspecific rank as subspecies of *M. miraka miraka* stat. nov., which is the oldest available name. Consequently, its subspecies are: *M. miraka errans* comb. nov., *M. miraka disjuncta* comb. nov., *M. miraka delii* comb. nov., *M. miraka kotschani* comb. nov., and *M. miraka dedovi* comb. nov. The phylogenetic position of “*lakmosensis*” indicates that it could be considered a separate species. Nonetheless, based on the lack of anatomical information on this taxon, we prefer to keep it within *M. miraka*: *M. miraka lakmosensis* comb. nov.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina laxa laxa</i> (Küster, 1861)	<i>Montenegrina laxa</i> (Küster, 1861)
<i>Montenegrina laxa dedovi</i> Nordsieck, 2009	<i>Montenegrina miraka dedovi</i> Nordsieck, 2009 comb. nov.
<i>Montenegrina laxa delii</i> Fehér & Szekeres, 2016	<i>Montenegrina miraka delii</i> Fehér & Szekeres, 2016 comb. nov.
<i>Montenegrina laxa disjuncta</i> Fehér & Szekeres 2006	<i>Montenegrina miraka disjuncta</i> Fehér & Szekeres 2006 comb. nov.
<i>Montenegrina laxa iba</i> Nordsieck, 1972	<i>Montenegrina iba</i> Nordsieck, 1972 stat. nov.
<i>Montenegrina laxa kotschani</i> Eröss and Szekeres, 2006	<i>Montenegrina miraka kotschani</i> Eröss and Szekeres, 2006 comb. nov.
<i>Montenegrina laxa errans</i> Eröss and Szekeres, 2006	<i>Montenegrina miraka errans</i> Eröss and Szekeres, 2006 comb. nov.
<i>Montenegrina laxa lakmosensis</i> Nordsieck, 2009	<i>Montenegrina miraka lakmosensis</i> Nordsieck, 2009 comb. nov.
<i>Montenegrina laxa miraka</i> Nordsieck, 1996	<i>Montenegrina miraka miraka</i> Nordsieck, 1996 stat. nov.

## *Montenegrina laxa* (Küster, 1861)

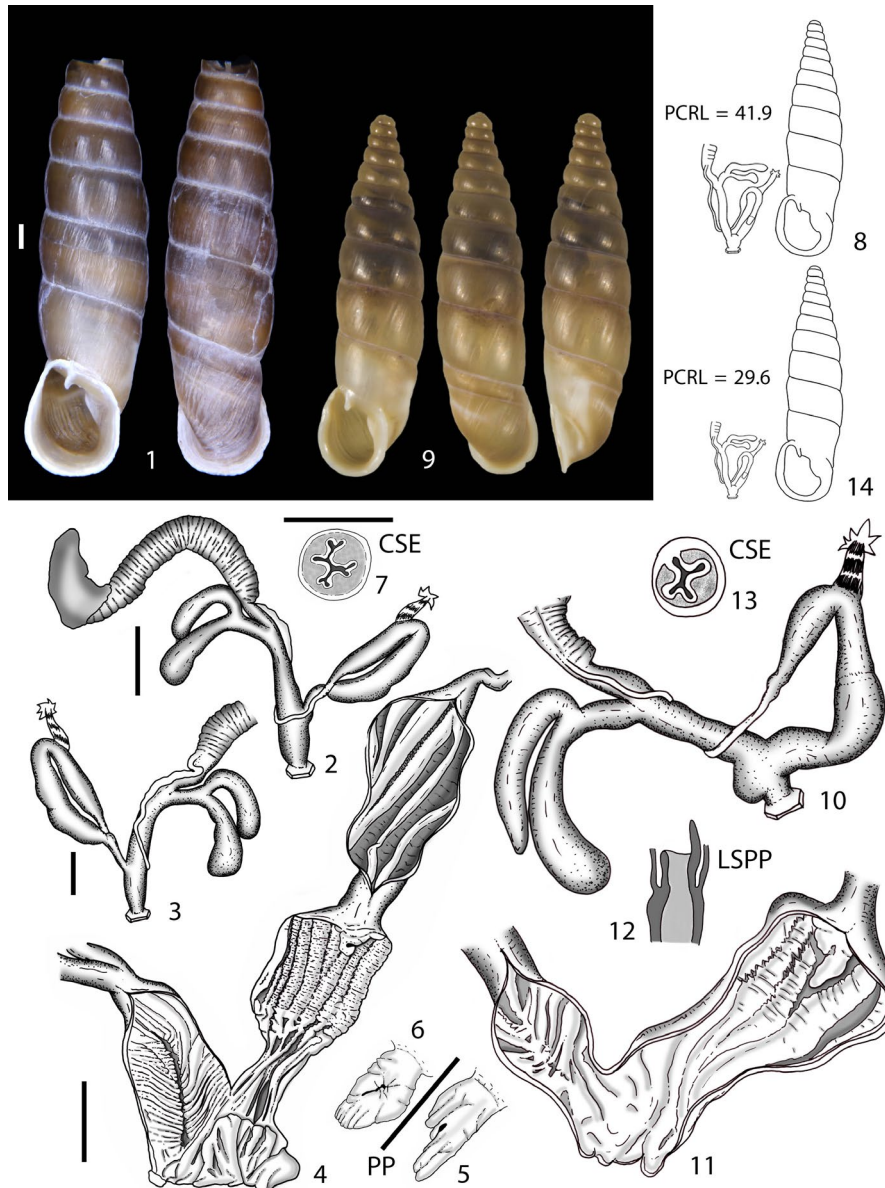
Figures 31.1.–31.8

*Clausilia laxa* Küster, 1861 in Küster, 1844–1862: 276, plate 31, figs 14–16 – Schmidt, 1868: 68–69.

*Delima* (*Albanodelima*) *weigneri* Poliński, 1924: 143–145, plate 4, figs 7–8 – Wagner, 1924: 119.

*Clausilia* (*Delima*) *laxa* – Westerlund, 1884: 54.

*Montenegrina laxa laxa* – Nordsieck, 1972: 29–30, plate 5, fig. 40. – Zilch, 1981: 130. – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 57, fig. 21A, distribution map fig. 23.



**FIGURE 31** 31.1–31.8 *Montenegrina laxa* (Küster, 1861) HNHM 99033. 31.1 shell. 31.2–31.3 whole distal genitalia. 31.4 inner distal genitalia. 31.5–31.6 penial papilla. 31.7 cross section of epiphallus. 31.8 shell-genitalia ratio. 31.9–31.14 *Montenegrina miraka dedovi* Nordsieck, 2009 comb. nov. DED-580, 31.9 shell, 31.10 whole distal genitalia, 31.11 inner distal genitalia, 31.12 longitudinal section of penial papilla, 31.13 cross section of epiphallus, 31.14 shell-genitalia ratio

**Examined material:** three dissected specimens. Albania, Tirana, gorge of the Lumi i Tërkuzës 0.5 km beneath the dam, 240 m, 41.4412°N, 19.8636°E [type locality], leg. ZF, TN, EM, 16.iv.2014 (HNHM 99033, Mlx-461-04 [COI: MT251643]).

**External genitalia (Figures 31.2–31.3):** The whole genital complex is long (PCRL = 41.9). The FO is medium-sized (FO/V = 0.53) and slender. The vas deferens is thin along its whole course, only slightly swollen towards its proximal end. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.36). The bursa copulatrix is long (DB/V = 1.47), club-like, wide, and without a visible transition area between the second duct and the actual

bursa. The bursa is elongated, and the apex is rounded. The diverticulum is long ( $D/V = 1.42$ ), but slightly shorter ( $D/BC = 0.96$ ) than the bursa. The apex is rounded. The vagina is short ( $VRL = 9.4$ ), slightly swollen at its distal end. The atrium is very long – the longest found in *Montenegrina*. The PC is much longer than the vagina ( $PC/V = 4.47$ ). The penis is cylindrical but its distal part is very thin and narrow, resembling a pedunculus emerging from the atrium. The epiphallus is longer than the penis ( $E/P = 1.13$ ), slightly thinner than the penis and almost uniformly cylindrical. It merges into the vas deferens with no distinct transitional area. The retractor muscle is short and thin.

**Inner genitalia (Figures 31.4–31.7):** The atrium has a big, irregular, polylobated fold originating directly at the genital aperture. The fold occupies the whole atrial volume. The whole distal vagina exhibits many smooth, fine pleats that are regularly arranged in a chevron-like pattern. The proximal vagina has 5–10 elevated, smooth longitudinal pleats. These pleats can be connected to each other with small fleshy bridges of varying thickness. The vaginal pilaster is present. The proximal penis has 6–8 main, elevated, fringed longitudinal pleats. These pleats are very close to one another. At the level of the distal penis, they abruptly become smooth, very fine, irregular longitudinal pleats. The background wall is smooth but poorly visible. The medium-sized penial papilla is hand-shaped with many pointed “fingers”. The aperture is very short and extends laterally, not reaching the apical area. The surface is smooth but irregular. The epiphallus bears up to five simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background walls are irregular and finely granulated.

### ***Montenegrina miraka dedovi* Nordsieck, 2009 comb. nov.**

Figures 31.9–31.14

*Montenegrina dedovi dedovi* Nordsieck, 2009: 75–77, plate 2, fig. 4. – Dedov & Neubert, 2009: 92, plate 1, fig. 5.

*Montenegrina laxa dedovi* – Fehér & Szekeres, 2016: 60, fig. 21B, distribution map fig. 23.

**Examined material: two dissected specimens.** North Macedonia, Jablanica Mts, up to Gorna Belitsa, alpine limestone meadow, ca. 1,600–1,700 m, 41.22°N, 20.54°E, leg. ID, 10.vii.2009 (DED-580, Mdd-360-01 [COI: KU307628, 16S: KU308075]).

**External genitalia (Figure 31.10):** The whole genital complex is medium-sized (PCRL = 29.6). The FO is long (FO/V = 1.08) and wide. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.27). The bursa copulatrix is very long (DB/V = 1.69), club-like, becoming gradually swollen towards the rounded apex. Np transitional area from the second duct into the bursa is distinguishable. The diverticulum is long (D/V = 1.77), thinner but longer (D/BC = 1.28) than the bursa. The apex is pointed. The vagina is extremely short (VRL = 8.0), uniformly cylindrical but wide. The atrium is short but very wide, with a lateral swelling that is likely of glandular origin. The PC is much longer than the vagina (PC/V = 3.69). The penis is slightly swollen at the level of the penial papilla. The epiphallus is shorter than the penis (E/P = 0.92), slender, and thinner than the penis, only slightly swollen along its proximal section. It merges into the vas deferens without a clear transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 31.11–31.13):** The atrium has few irregular, smooth and fleshy large pleats, almost forming a single, irregular, fleshy, pad-like large pleat. The proximal vagina shows many smooth, elevated, and irregular pleats arranged in a rough chevron-like pattern. The background walls are smooth. The vaginal pilaster is

present. The proximal penis has five or six main, elevated, fringed longitudinal pleats that merge along the distal penis and become smooth. The single pleats remain recognizable as far as the genital atrium. The medium-sized, conical penial papilla has a pointed apex and smooth surface. The aperture is lateral but transversely oriented. The apical, apertureless part is thinner in diameter. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina miraka delii* Fehér & Szekeres, 2016 comb. nov.**

Figures 32.1–32.4

*Montenegrina laxa delii* – Fehér & Szekeres, 2016: 60, fig. 21C, distribution map fig. 23.

**Examined material: two dissected specimens (paratypes).** Albania, Kukës District, S of Draj-Reç, entrance of the Vilë Gorge, 430 m, 41.8830°N, 20.3370°E [type locality], leg. ZF, JG, 2.vii.2005 (NHMW 111235, Mel-633-01 [COI: KU307581]; Mel-633-02 [COI: MT251590]).

**External genitalia (Figure 32.2):** The whole genital complex is small (PCRL = 19.3). The FO is very long (FO/V = 0.83) and moderately wide. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.43). The bursa copulatrix is very long (DB/V = 1.28) and club-like. The transition area from the second duct into the bursa is not clearly distinguishable. The diverticulum is medium-sized (D/V = 1.33), as wide as the bursa but longer (D/BC = 1.04). The apex is rounded. The vagina is medium-sized (VRL = 10.8), gradually tapering towards its distal part but abruptly widening at the atrium. The atrium is short but very wide. The PC is longer than the vagina (PC/V = 1.78). The penis is short and uniformly wide up until the level of the penial papilla, where it is constricted around the base of the papilla. The epiphallus is longer than the penis (E/P = 1.46), wide, but slightly thinner than the penis, uniformly cylindrical. It merges into the vas deferens with a clear transitional area. The proximal part of the epiphallus is blunt. The retractor muscle is long and strong.

**Inner genitalia (Figure 32.3):** The atrium shows a big, polylobated fold originating directly at the genital aperture. The distal vagina is very short with one smooth, pad-like cushion that originates from the atrium. Minor upper transversal pleats are sometimes present. The proximal vagina has many oblique elevated transversal, pleats, which are irregular and randomly merge as they approach the vaginal pilaster. The background walls are smooth. The penis exhibits flat and poorly visible, smooth, large pleats arranged in a chevron-like pattern. The inferior pleats are slightly more visible. The medium-sized, conical penial papilla has a pointed but nonetheless broad apex and a smooth surface. The aperture is lateral. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

***Montenegrina miraka disjuncta* Fehér & Szekeres, 2006  
comb. nov.**

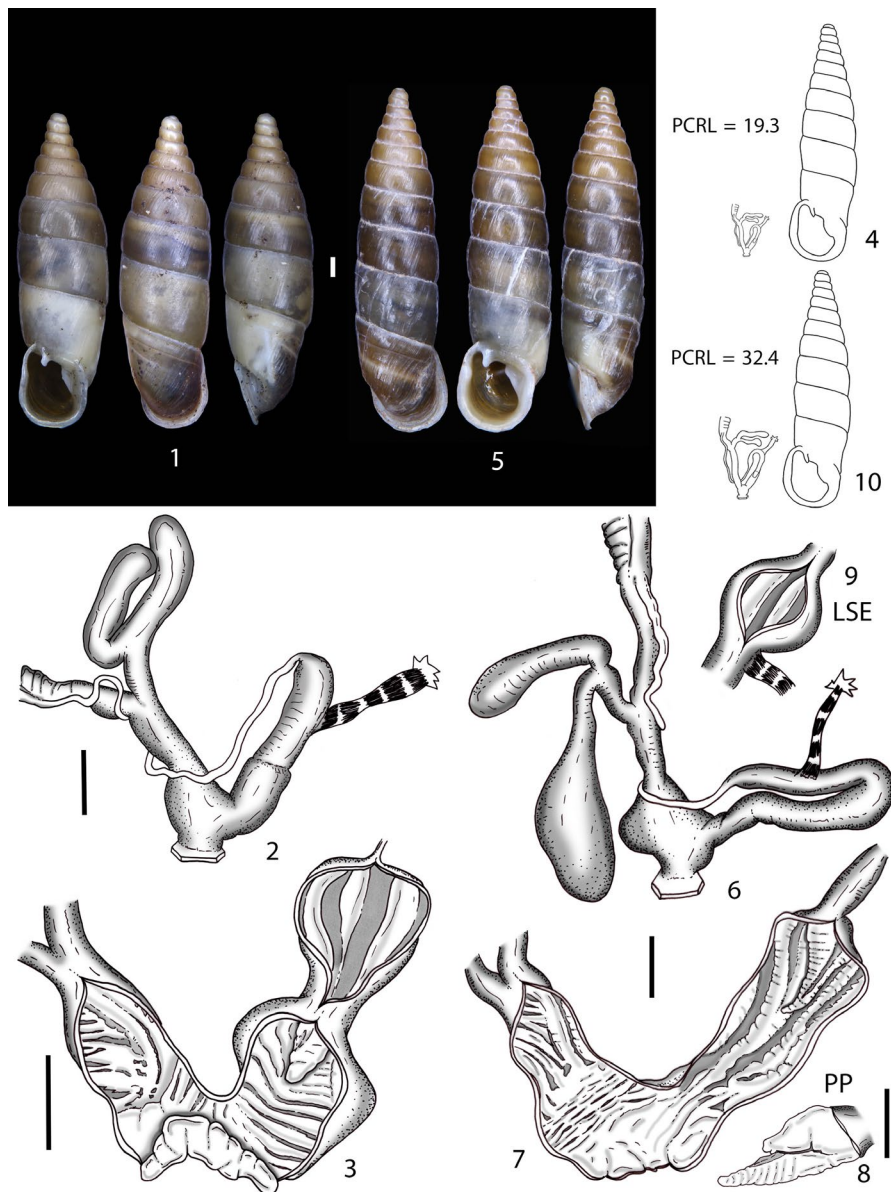
Figures 32.5–32.10

*Montenegrina laxa disjuncta* Fehér & Szekeres, 2006 in Eröss et al., 2006: 197–198, fig. 19 – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 62, fig. 21D, distribution map fig. 23.

**Examined material:** two dissected specimens. Albania, Dibrë District, 2 km E of Selishtë, 760 m, 41.6228°N, 20.2886°E, leg. ZF, TN, EM, 14.iv.2014 (HNHM 99000, Mdj-451-01 [COI: MT251555]).

**External genitalia (Figure 32.6):** The whole genital complex is large (PCRL = 32.4). The FO is long (FO/V = 0.95) and slender. The vas deferens is thin along its whole course. The first duct of the bursa

copulatrix complex is short (DBC/DB = 0.20). The bursa copulatrix is extremely long (DB/V = 2.05), club-like, with a rounded apex. The transitional area from the second duct to the bursa is not clearly distinguishable. The diverticulum is medium-sized (D/V = 1.25), almost completely cylindrical, thinner than the bursa and much shorter (D/BC = 0.61). The apex is rounded. The vagina is medium-sized (VRL = 11.4), gradually becoming swollen towards its distal part and rather abruptly widening into the atrium. The atrium is short but very wide. The PC is much longer than the vagina (PC/V = 2.85). The penis is uniformly cylindrical. The epiphallus is longer than the penis (E/P = 1.48), slightly wider than the penis and uniformly cylindrical. It merges into the vas deferens with a clear transitional area. The proximal part of the epiphallus is blunt. The retractor muscle is long and thin.



**FIGURE 32** 32.1–32.4 *Montenegrina miraka delii* Fehér & Szekeres, 2016 comb. nov. NHMW 111235. 32.1 shell, 32.2 whole distal genitalia, 32.3 inner distal genitalia, 32.4 shell-genitalia ratio. 32.5–32.10 *Montenegrina miraka disjuncta* Fehér & Szekeres, 2006 comb. nov. HNHM 99000. 32.5 shell, 32.6 whole distal genitalia, 32.7 inner distal genitalia, 32.8 penial papilla, 32.9 longitudinal section of epiphallus, 32.10 shell-genitalia ratio

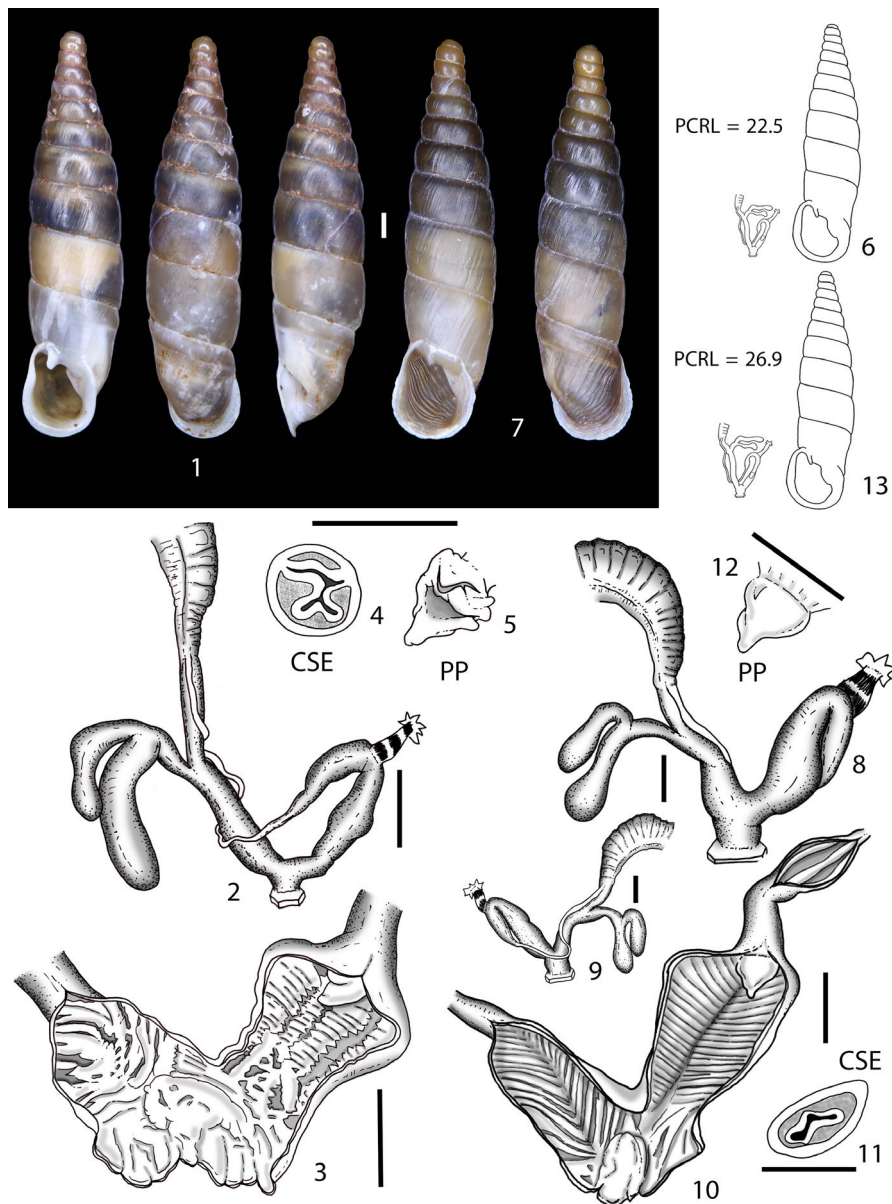
**Inner genitalia (Figures 32.7–32.9):** The atrium has three or four big, pad-like, smooth, and flat large pleats. The distal vagina shows 5–10 smooth transversal pleats that do not continue into the atrium. These pleats randomly merge into one another along their course. The proximal vagina has many oblique, elevated transversal pleats all heading towards the vaginal pilaster and merging into it. The background walls are smooth. The penis has three or four main, fringed metameric cords that extend from the penial papilla's origin as far as the atrium. These cords merge together distally, at the level of the distal penis, and become rather abruptly smooth. The background walls are smooth. The medium-sized, conical penial papilla has a pointed apex and pleated surface. The aperture is lateral, not reaching the papilla's tip. The apical, apertureless part is

smaller in diameter. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

***Montenegrina miraka errans* Erőss and Szekeres, 2006 comb. nov.**

Figures 33.1–33.6

*Montenegrina laxa errans* Erőss and Szekeres, 2006 in Erőss et al., 2006: 198, fig. 20 – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 63, fig. 21E, distribution map fig. 23.



**FIGURE 33** 33.1–33.6 *Montenegrina miraka errans* Erőss and Szekeres, 2006 comb. nov. HNHM 98950. 33.1 shell, 33.2 whole distal genitalia, 33.3 inner distal genitalia. 33.4 cross section of epiphallus, 33.5 penial papilla, 33.6 shell-genitalia ratio. 33.7–33.13 *Montenegrina iba* Nordsieck, 1972 stat. nov. HNHM 99036, 33.7 shell. 33.8–33.9 whole distal genitalia, 33.10 inner distal genitalia, 33.11 cross section of epiphallus, 33.12 penial papilla, 33.13 shell-genitalia ratio

**Examined material: two dissected specimens.** Albania, Pogradec District, 4 km SW of Bishnicë, Shkemb i Qytetit, 1140 m, 40.9210°N, 20.4491°E, leg. ZF, TN, EM, 12.iv.2014 (HNHM 98950, Mer-431-01 [COI: KU307665, 16S: KU308100]).

**External genitalia (Figure 33.2):** The whole genital complex is medium-sized (PCRL = 22.5). The FO is long (FO/V = 0.76) but slender. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.25). The bursa copulatrix is medium-sized (DB/V = 0.95), almost uniformly cylindrical, very wide with no transitional area visible between the second duct and the bursa itself. The diverticulum is small (D/V = 0.86), much thinner and shorter (D/BC = 0.62) than the bursa. The apex is blunt. The vagina is medium-sized (VRL = 12.4) and uniformly cylindrical. The atrium is small. The PC is longer than the vagina (PC/V = 1.81). The penis is slightly swollen at the level of the penial papilla. The epiphallus is longer than the penis (E/P = 1.24) and slightly swollen along its proximal section. It merges into the vas deferens without a clear transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 33.3–33.5):** The atrium shows many pad-like, smooth, irregular pleats. The distal vagina has many smooth, scattered, irregularly arranged pleats. The proximal vagina shows many smooth, elevated, and irregular pleats arranged in a rough chevron-like pattern. The background walls are smooth. The vaginal pilaster is present. The proximal penis has four main, elevated, fringed longitudinal pleats. The pleats are recognizable as far as the genital atrium even if they become blurred as they approach the atrium. The medium-sized, conical penial papilla has a pointed apex and a smooth surface. The aperture is lateral but transversely oriented. The apical, apertureless part is smaller in diameter. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina iba* Nordsieck, 1972 stat. nov.**

Figures 33.7–33.13

*Montenegrina laxa iba* Nordsieck, 1972: 30, plate 5, fig. 41 – Zilch, 1981: 130, plate 13, fig. 23. – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 63, fig 21F, distribution map fig. 23.

**Examined material: two dissected specimens.** Albania, gorge of the Lumi i Erzenit, 290 m, 41.2598°N, 19.9676°E [type locality], leg. ZF, TN, EM, 17.iv.2014 (HNHM 99036, Mib-463-01 [COI: KU307684, 16S: KU308115]).

**External genitalia (Figures 33.8–33.9):** The whole genital complex is medium-sized (PCRL = 26.9). The FO is long (FO/V = 0.61) but slender. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is very long (DBC/DB = 0.70). The bursa copulatrix is long (DB/V = 1.11), club-like, wide, and without a distinct transition area between the second duct and the actual bursa. The apex is rounded. The diverticulum

is small (D/V = 0.94) and shorter (D/BC = 0.85) than the bursa. The apex is blunt. The vagina is medium-sized (VRL = 10.5), gradually becoming swollen towards distal end. The atrium is very large. The PC is much longer than the vagina (PC/V = 2.56). The penis is very swollen, with thick walls. The epiphallus is longer than the penis (E/P = 1.56), slightly swollen along its distal section and thinner along its proximal part. It merges into the vas deferens without a clear transitional area. The retractor muscle is very short and strong.

**Inner genitalia (Figures 33.10–33.12):** The atrium shows a big, irregular, unilobate fold originating directly at the genital aperture. The whole vagina bears many smooth, fine pleats that are regularly arranged in a chevron-like pattern. The vaginal pilaster is absent. The background walls are smooth. The whole penis shows many smooth, fine pleats regularly arranged in a chevron-like pattern. The medium-sized penial papilla is pyramidal, pointed. The aperture extends laterally but does not reach the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina miraka kotschani* Eröss and Szekeres, 2006 comb. nov.**

Figures 34.1–34.5

*Montenegrina laxa kotschani* Eröss and Szekeres, 2006 in Eröss et al., 2006: 199–200, fig. 21 – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 64, fig. 21G, distribution map fig. 23.

**Examined material: two dissected specimens.** Albania, Tiranë District, ca. 3.5 km E of the Shën Mëri junction, 1,400 m, 41.3507°N, 20.0583°E [type locality], leg. ZF, TK, DM, 20.vi.2012 (HNHM 99634, Mko-314-01 [COI: KU307700, 16S: KU308125, 12S: KU307962]).

**External genitalia (Figure 34.2):** The whole genital complex is long (PCRL = 37.4). The FO is long (FO/V = 0.61) but slender. The vas deferens is thin along its whole course, only slightly swollen towards its proximal and distal ends. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.44). The bursa copulatrix is long (DB/V = 1.17), club-like, wide, and without a distinct transition area between the second duct and the actual bursa. The bursa is elongated and the apex is rounded. The diverticulum is long (D/V = 1.57) and longer (D/BC = 1.33) than the bursa. The apex is rounded. The vagina is medium-sized (VRL = 13.5) and slightly swollen at its proximal end. The atrium is small but with a swelling bordering the distal vagina. The PC is much longer than the vagina (PC/V = 2.78). The penis is cylindrical, and the origin of the penial papilla is clearly visible also from outside. The epiphallus is longer than the penis (E/P = 1.21), thinner than the penis and almost uniformly cylindrical. It merges into the vas deferens without a distinct transitional area. The retractor muscle is long and thin.

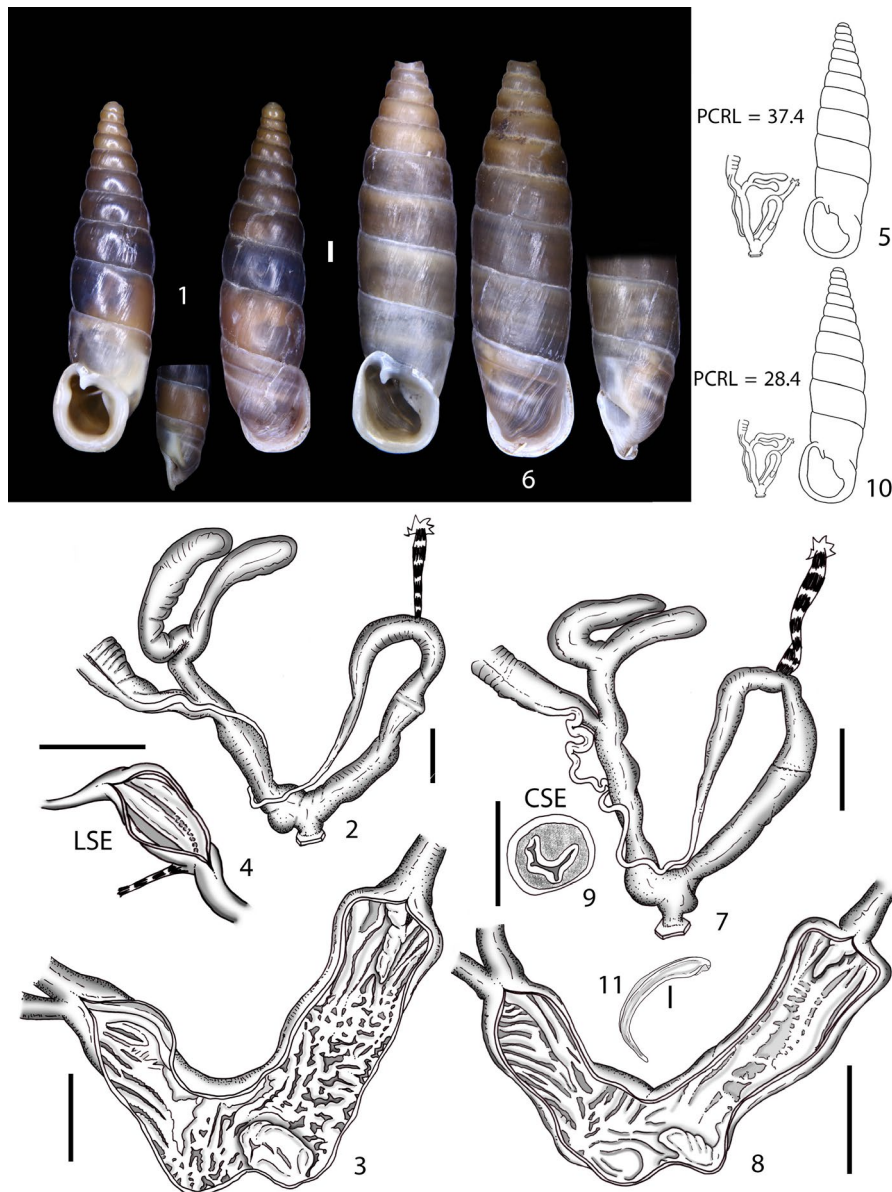
**Inner genitalia (Figures 34.3–34.4):** The atrium shows a big, polylobated, and irregular fold originating directly at the genital aperture. The background atrial walls exhibit an irregular net of small, smooth pleats that continue in both directions inside the penis and the vagina. The distal vagina has many smooth, fine pleats that are irregularly arranged. The proximal vagina shows many oblique, elevated, irregular transversal pleats. The background walls are smooth. The vaginal pilaster is present. The proximal penis shows 6–9 small, smooth but blurred longitudinal pleats that abruptly turn into an irregular, reticulated pattern that continues as far as the atrium. The background walls are smooth. The medium-sized, conical penial papilla has a pointed apex and a pleated, irregular surface. The aperture is lateral and does

not reach the papilla's tip. The apical, aperture less part is smaller in diameter. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

***Montenegrina miraka miraka* Nordsieck, 1996 stat. nov.**

Figures 34.6–34.10

*Montenegrina laxa miraka* Nordsieck, 1996: 8–9, plate 2, fig. 2 – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 65, fig. 21H, distribution map fig. 23.



**FIGURE 34** 34.1–34.5 *Montenegrina miraka kotschani* Eröss and Szekeres, 2006 comb. nov. HNHM 99634. 34.1 shell, 34.2 whole distal genitalia, 34.3 inner distal genitalia, 34.4 longitudinal section of epiphallus, 34.5 shell-genitalia ratio. 34.6–34.10 *Montenegrina miraka miraka* Nordsieck, 1996 stat. nov. HNHM 94905. 34.6 shell, 34.7 whole distal genitalia, 34.8 inner distal genitalia, 34.9 cross section of epiphallus, 34.10 shell-genitalia ratio, 34.11 spermatophore



**Examined material: four dissected specimens.** Albania, Librazhd district, 1 km S of Lunik, along the Librazhd–Peshkopi road, 690 m asl., [limestone rocks], 41.2661°N 20.3176°E, leg. ZF, LN, DM, 13.iv.2014 (HNHM 98964, Mmr-436-01 [16S: KU308138\*]).

Albania, Librazhd district, Mali i Polisit, canyon of creek Mali Plak above Gafer, 1480 m, 41.059°N, 20.353°E, leg. ZB, GP, 27.viii.2015 (HNHM 99721, M54-650-01 [COI: MT251496]).

**External genitalia (Figure 34.7):** The whole genital complex is long (PCRL = 28.4). The FO is medium-sized (FO/V = 0.33) and slender. The vas deferens is thin along its whole course, only slightly swollen proximally. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.57). The bursa copulatrix is long (DB/V = 0.58), club-like, wide, and without a visible transitional area between the second duct and the actual bursa. The bursa is elongated, and the apex is rounded. The diverticulum is long (D/V = 0.83) but slightly shorter (D/BC = 1.43) than the bursa. The apex is rounded. The vagina is short (VRL = 11.5), slightly swollen at its distal end. The atrium very long – the longest in *Montenegrina*. The PC is much longer than the vagina (PC/V = 2.46). The penis is cylindrical but its distal origin is very thin and narrow, resembling a pedunculus emerging from the atrium. The epiphallus is longer than the penis (E/P = 1.27), slightly thinner than the penis and almost uniformly cylindrical. It merges into the vas deferens without a distinct transitional area. The retractor muscle is short and thin.

**Inner genitalia (Figures 34.8–34.9):** The atrium exhibits one small and irregular fold. The background atrium wall shows a variety of smooth and irregularly arranged pleats. The distal vagina has many smooth, fine pleats that are irregularly arranged. The proximal vagina has many oblique, elevated, fine transversal pleats that often connect to each other at their ends. The background walls are smooth. The vaginal pilaster is present. The proximal penis has 6–8 small, smooth, irregular longitudinal pleats that abruptly merge into two or three main, smooth, and flat pleats that extend as far as the atrium. These pleats connect via small fleshy bridges. The background is smooth. The medium-sized, conical penial papilla has a pointed apex and a smooth surface. The aperture is lateral but transversely oriented. The apical, apertureless part is smaller in diameter. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

**Spermatophore (Figures 34.11):** The spermatophore is moderately bent along the caudal part and has a large, slightly swollen head that gradually narrows towards the tail. The head is hook-like with a pointed apex. A membrane connects the tip of the head with the body. The tail is pointed, sharp, and blade-shaped. The lower carina is absent. The upper carina starts immediately behind the head and extends as far as 3/4 of the total length towards the tail. The cross section is roundish with two lateral blunt keels. Both of the keels are large and simple. The spermatophore is 5.3 mm long and 0.8 mm wide.

## *Montenegrina miraka lakmosensis* Nordsieck, 2009 comb. nov.

*Montenegrina janinensis* – Sattmann & Reischütz, 1994: 46.

*Montenegrina dedovi lakmosensis* – Nordsieck, 2009: 77, plate 2, fig. 5

*Montenegrina laxa lakmosensis* – Fehér & Szekeres, 2016: 65, fig. 21H, distribution map fig. 23.

No alcohol-preserved specimens were available for anatomical investigations.

## *Montenegrina lillae* Fehér & Szekeres, 2016, *Montenegrina okolensis* Szekeres, 2006, *Montenegrina prokletiana* Fehér & Szekeres, 2016, and *Montenegrina sporadica* Nordsieck, 1974 sensu Fehér & Szekeres, 2016

### Taxonomic and systematic remarks

Following Mason et al. (2020), Clade G includes *M. lillae*, *M. prokletiana* s.l., *M. okolensis* s.l., and *M. sporadica tropojana*. This clade is divided into four subclades representing *M. sporadica tropojana*, *M. okolensis* s.l., *M. lillae*, and *M. prokletiana* s.l. All these taxa are known to occur in northern Albania.

*Montenegrina lillae* is restricted to a very small area east of the town Koman. Its genitalia are extremely elongated and, based on external shape, strictly resemble the genital arrangement of the monophyletic *M. sporadica tropojana*, which is known from a few sites about 60 km NE (gorge of the Përroi i Tropojës). These two taxa mainly differ in the length of the vagina (longer in the former, shorter in the latter), the sculpturing of the atrium and the absence of the penial papilla in the latter (Figures 34.5 and 37.3). The status of a valid species is also confirmed by this integrative approach in which phylogeny and genital anatomy both support this view. Despite the similarities in genital anatomy, *M. tropojana* stat. nov. deserves the status of a valid species for the following reasons. First, it displays specific shell-morphological features distinguishing it from *M. lillae*. Second, it forms a distinct lineage quite distant from *M. okolensis* and *M. lillae*. Moreover, it has a completely different phylogenetic position than the nominal form *M. sporadica sporadica*, which is the sister group of clades B + C (see Mason et al., 2020). Although the genital anatomy of *M. sporadica sporadica* is unknown, its distinct position corroborates that it should remain as a separate species.

*Montenegrina okolensis* is monophyletic and its genital anatomy is clearly distinguishable from *M. tropojana*, *M. sporadica*, and *M. lillae*. Conversely to these taxa, *M. okolensis* shows a bulky shape of the genitalia. Its subspecies *M. okolensis okolensis* and *M. okolensis caesia* are clearly distinguishable in their shell features and, furthermore, both phylogeny and genital anatomy confirmed their

conspecific status. Both subspecies lack the penial papilla, and the transition between the epiphallus and the penis is marked by a narrow section. They differ in the sculpturing of the inner penial walls and partly the atrium (Figure 38). For these reasons we leave the systematics of the two taxa unchanged, as stated by Fehér and Szekeres (2016: 71). We remark that Nordsieck (2009) synonymized *M. apfelbecki okolenensis* and *M. janinensis caesia* and, as a first reviewer, gave priority to *M. janinensis caesia*. However, in the review of Fehér & Szekeres, 2016, this synonymy was not accepted, and those authors argued that *M. okolenensis* and *M. caesia* were distinct taxa.

*Montenegrina prokletiana* s.l. is monophyletic, and its two subspecies are also monophyletic. Samples from two populations of *M. prokletiana prokletiana* were dissected (Mpp-651-01 and Mpp-652-01). The genital anatomy proved to be identical. In particular, both populations lack a penial papilla and a narrower transition area between epiphallus and penis (as in *M. okolenensis* s.l.). The genital anatomy of *M. prokletiana kovacsorum* (Mpk-311-01) is similar to that of *M. prokletiana prokletiana*, differing only by a very well-developed penial papilla. This confirms their differentiation at sub-specific level.

## Fehér &amp; Szekeres, 2016

*Montenegrina lillae* Fehér & Szekeres, 2016

*Montenegrina sporadica sporadica* Nordsieck, 1974

## De Mattia et al., 2020

*Montenegrina lillae* Fehér & Szekeres, 2016

*Montenegrina sporadica* Nordsieck, 1974

## Fehér &amp; Szekeres, 2016

*Montenegrina sporadica tropojana* Fehér & Szekeres, 2016

*Montenegrina okolenensis okolenensis* Szekeres, 2006

*Montenegrina okolenensis caesia* Fehér & Szekeres, 2006

*Montenegrina prokletiana prokletiana* Fehér & Szekeres, 2016

*Montenegrina prokletiana kovacsorum* Fehér & Szekeres, 2016

## De Mattia et al., 2020

*Montenegrina tropojana* Fehér & Szekeres, 2016 stat. nov.

*Montenegrina okolenensis okolenensis* Szekeres, 2006

*Montenegrina okolenensis caesia* Fehér & Szekeres, 2006

*Montenegrina prokletiana prokletiana* Fehér & Szekeres, 2016

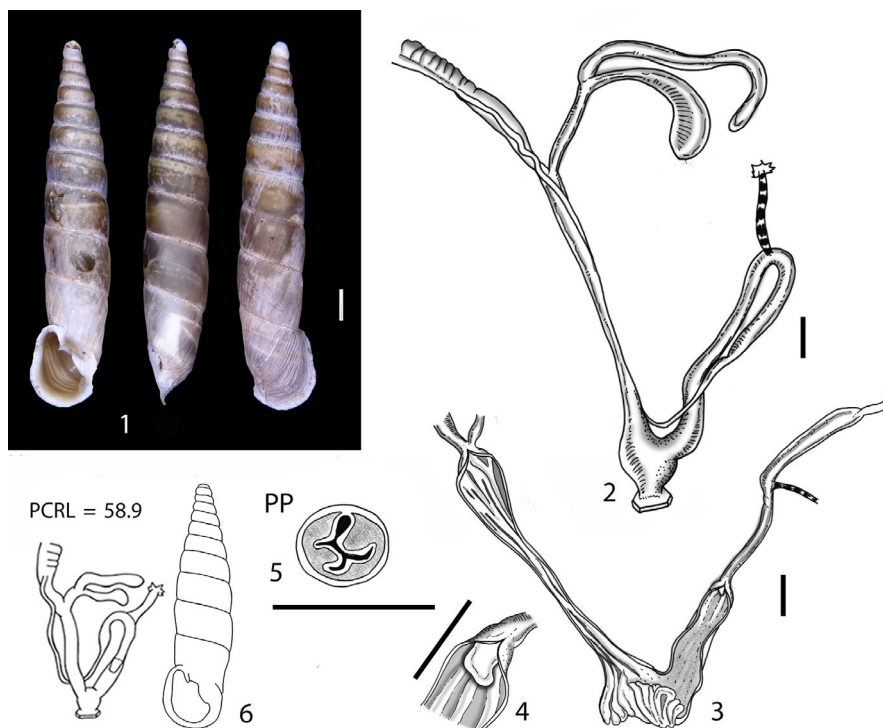
*Montenegrina prokletiana kovacsorum* Fehér & Szekeres, 2016

**Montenegrina lillae** Fehér & Szekeres, 2016

Figures 35.1–35.6

*Montenegrina lillae* – Fehér & Szekeres, 2016: 66, fig. 21L, distribution map fig. 22.

**Examined material:** two dissected specimens. Albania, Shkodër district, Koman, limestone walls at the ferry harbor of Lake Koman, 180 m asl, 42.1085°N 19.8261°E [type locality], leg. ZF, LT, 22.vii.2017 (NHMW 11043/MN/0594, Mli-312-01 [COI: KU307529, 16S: KU308012, 12S: KU307924]; Mli-312-02 [COI: KU307530]).



**FIGURE 35** *Montenegrina lillae* Fehér & Szekeres, 2016 NHMW 11043/MN/0594. 35.1 shell. 35.2 whole distal genitalia. 35.3 inner distal genitalia. 35.4 penial papilla and proximal inner penis. 35.5 cross section of epiphallus. 35.6 shell-genitalia ratio

**External genitalia (Figure 35.2):** The whole genital complex is very long (PCRL = 58.9). The FO is medium-sized (FO/V = 0.41) and slender. The vas deferens is extremely thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.49). The bursa copulatrix is short (DB/V = 0.52), club-like, without a visible transition area between the second duct and the actual bursa. The bursa has a rounded apex. The diverticulum is short (D/V = 0.86), cylindrical, thinner but longer than the bursa copulatrix (D/BC = 1.65). Its apex is pointed. The vagina is very long (VRL = 42.0) but extremely thin. The atrium is long and large. The PC is longer than the vagina (PC/V = 1.4). The penis is extremely long and very thin. The epiphallus is much longer (E/P = 2.07) and thinner than the penis. It merges into the vas deferens without a distinct transitional area. The retractor muscle is long and very fragile.

**Inner genitalia (Figures 35.3–35.5):** The atrium exhibits a set of smooth longitudinal pleats. These pleats are swollen and well visible. They continue inside the vagina but abruptly stop on the side of the penis. The whole vagina has a few irregular longitudinal pleats that run throughout its length. The penis is mainly smooth; nevertheless, weak longitudinal pleats are often visible, usually stronger along the proximal area. The very small penial papilla is pointed and has a smooth surface. The aperture is lateral and very small. The epiphallus has only one simple smooth pleat originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina prokletiana prokletiana* Fehér & Szekeres, 2016**

Figures 36.1–36.7

*Montenegrina prokletiana prokletiana* – Fehér & Szekeres, 2016: 85, fig. 24F, distribution map fig. 26.

**Examined material: four dissected specimens.** Albania, Tropojë district, gorge of Lumi i Gashit, footpath between Dretovë and Bradoshnicë 580 m, 42.4058°N, 20.0855°E, leg. ZF, JG, 1.vii.2016 (NHMW 110430/MN/0184, Mpp-651-01 [COI: MT251707, 16S:MT160800, 12S: MT249810]).

Albania, Tropojë district, Çerem, right side of Çerem Valley, 1,300 m, 42.4829°N, 19.9568°E, leg. ZE, ZF, MS, JG, 2.vii.2016 (NHMW 110430/MN/0185, Mpp-652-01 [COI: MT251710, 16S: MT160801, 12S: MT249813]).

**External genitalia (Figures 36.2 and 36.5):** The whole genital complex is very long (PCRL = 44.2) and slender. The FO is very short (FO/V = 0.19). The vas deferens is thin distally but swollen proximally. The first duct of the bursa copulatrix complex is very long (DBC/DB = 0.61). The bursa copulatrix is very long (DB/V = 1.69), cylindrical, or slightly club-like. There is no clearly visible transitional area. The diverticulum is generally long (D/V = 1.63), uniformly cylindrical, slightly wider but shorter (D/BC = 0.96) than the bursa copulatrix. Its apex is slightly pointed. The vagina is medium-sized (VRL = 15.4), uniformly cylindrical and wide in diameter. The atrium is moderately large, swollen at the penial side. The PC is much longer than the

vagina (PC/V = 2.88). The penis is moderately wide with a distinct transitional area with the epiphallus. The epiphallus is considerably longer than the penis (E/P = 2.54), moderately swollen proximally and thin distally. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 36.3–36.4, 36.6):** The atrium is uniformly smooth. The distal vagina is completely smooth and slightly swollen at its distal end. The proximal vagina is also completely smooth without the vaginal pilaster. The penis is mainly smooth with weak traces of three or four flat longitudinal pleats. The penial papilla is absent, but the transition area between epiphallus and proximal penis is nevertheless well visible due to a distinct narrowing where the penial walls invaginate in a distal direction. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina prokletiana kovacsorum* Fehér & Szekeres, 2016**

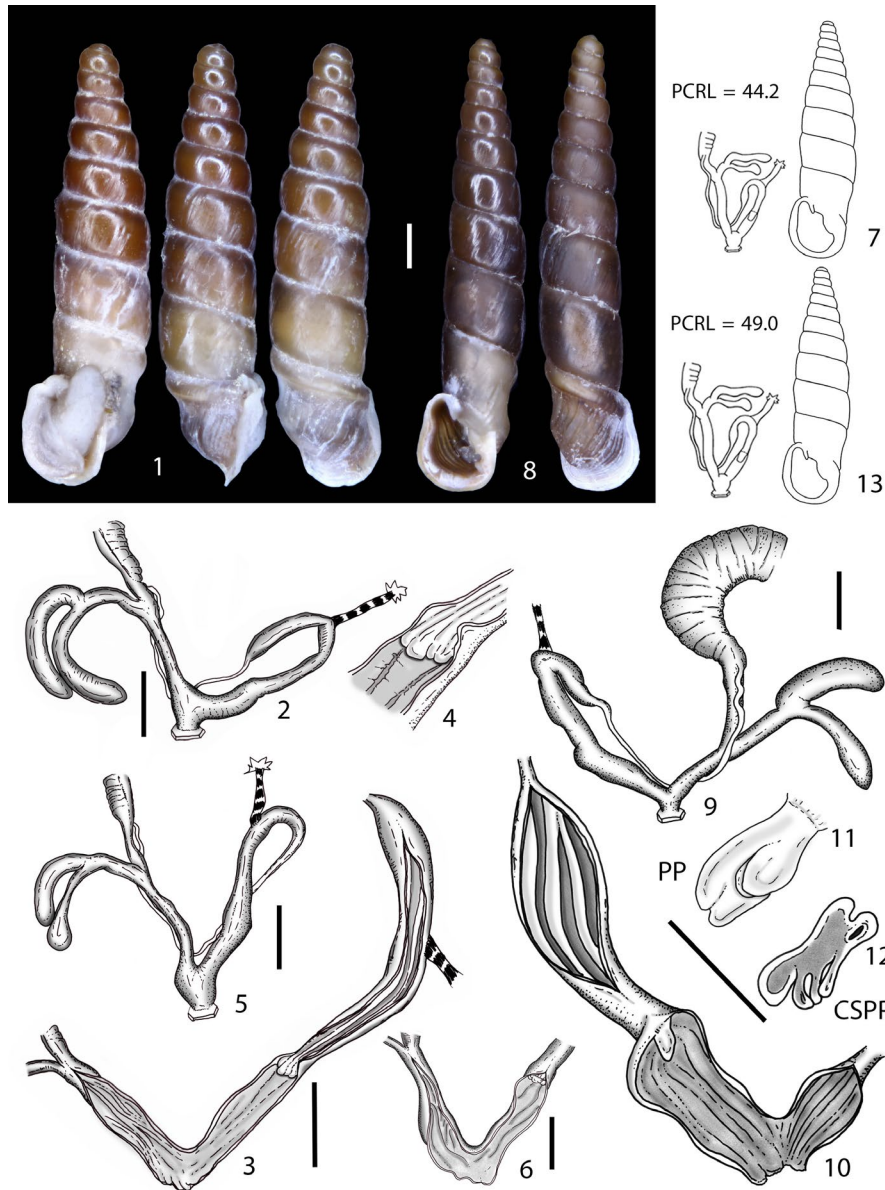
Figures 36.8–36.13

*Montenegrina prokletiana kovacsorum* – Fehér & Szekeres, 2016: 86, fig. 24G, distribution map fig. 26.

**Examined material: two dissected specimens (paratypes).** Albania, Shkodër District, Toplanë, Drin Valley 20.5 km upstream of the Koman Dam, limestone gorge and a cave on the right bank of Lake Koman, 180 m, 42.2339°N, 19.8741°E [type locality], leg. ZF, TK, DM, 18.vi.2012 (HNHM 99486, Mpk-311-02 [COI: KU307527, 16S: KU308011, 12S: KU307923]).

**External genitalia (Figure 36.9):** The whole genital complex is very long (PCRL = 49.0) with a slender appearance. The FO is extremely long (FO/V = 1.31). The vas deferens is thin distally but swollen proximally. The first duct of the bursa copulatrix complex is long (DBC/DB = 0.75). The bursa copulatrix is long (DB/V = 1.54), cylindrical, or slightly club-like. There is no distinct transition area. The diverticulum is also generally long (D/V = 1.46), uniformly cylindrical, wider but usually shorter (D/BC = 0.95) than the bursa copulatrix. The apex is slightly rounded. The vagina is medium-sized (VRL = 12.5) and uniformly cylindrical. The atrium is small. The PC is considerably longer than the vagina (PC/V = 3.92). This represents the highest ratio documented in *Montenegrina*. The penis is irregular and swollen along its distal course and at the level of the penial papilla. The epiphallus is longer than the penis (E/P = 1.55), moderately swollen along its proximal and distal parts. It merges into the vas deferens with a more or less clear transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 36.10–36.12):** The atrium is uniformly smooth. The distal vagina is completely smooth and slightly swollen distally. The proximal vagina is also completely smooth, and the vaginal pilaster is absent. The penis is mainly smooth with weak traces of three or four flat longitudinal pleats. The penial papilla is small and



**FIGURE 36** 36.1–36.7 *Montenegrina prokletiana prokletiana* Fehér & Szekeres, 2016 NHMW 110430/MN/0184. 36.1 shell, 36.2 whole distal genitalia, 36.3 inner distal genitalia, 36.4 transition zone between proximal penis and epiphallus. NHMW 110430/MN/0185. 36.5 whole distal genitalia, 36.6 inner distal genitalia, 36.7 shell-genitalia ratio. 36.8–36.13 *Montenegrina prokletiana kovacsorum* Fehér & Szekeres, 2016 HNHM 99486. 36.8 shell, 36.9 whole distal genitalia, 36.10 inner distal genitalia, 36.11 penial papilla, 36.12 cross section of penial papilla, 36.13 shell-genitalia ratio

bilobated at the tip. The aperture is transversely oriented and stops halfway to the apical area. The fine surface is smooth but entirely pleated. The epiphallus has two or three simple smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina sporadica* Nordsieck, 1974

*Montenegrina janinensis sporadica* Nordsieck, 1974: 151–152, plate 5, fig. 29.

*Montenegrina janinensis sporadica* Zilch, 1981: 129, plate 13, fig. 28.

*Montenegrina janinensis sporadica* Nordsieck, 2009: 75.

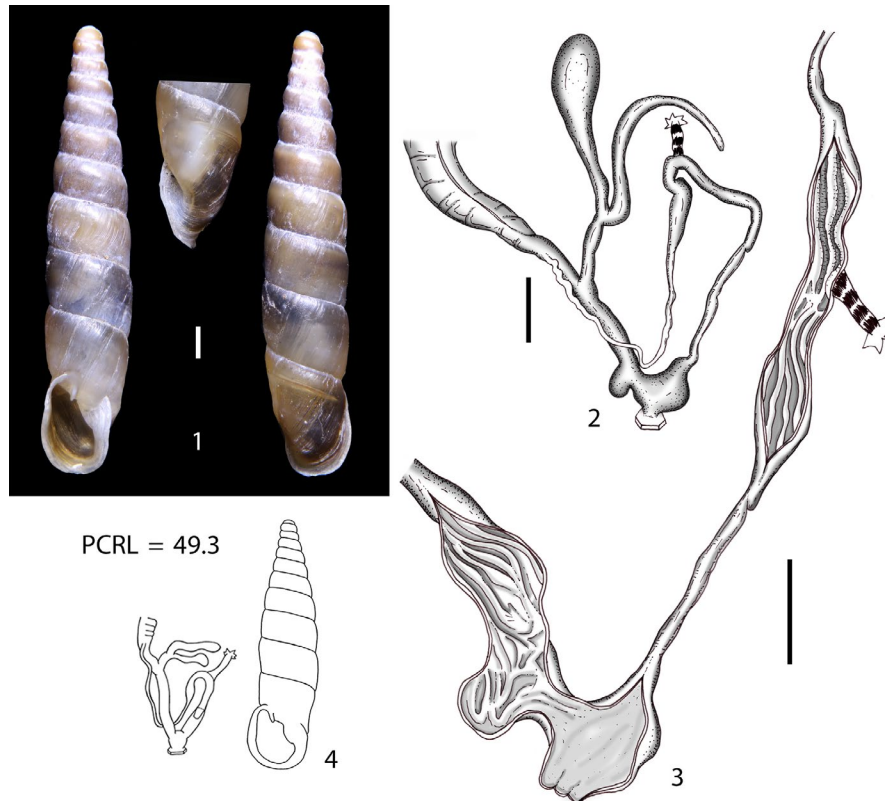
*Montenegrina sporadica sporadica* Fehér & Szekeres, 2016: 110, fig. 28J, distribution map fig. 32.

No suitable specimen was available for anatomical investigations.

### *Montenegrina tropojana* Fehér & Szekeres, 2016 stat. nov.

Figures 37.1–37.4

*Montenegrina sporadica tropojana* – Fehér & Szekeres, 2016: 111, fig. 28K, distribution map fig. 32.



**FIGURE 37** *Montenegro tropojana* Fehér & Szekeres, 2016 stat. nov. NHMW 111225. 37.1 shell. 37.2 whole distal genitalia. 37.3 inner distal genitalia. 37.4 shell-genitalia ratio

**Examined material: two dissected specimens (paratypes).**

Albania, Tropojë District, gorge of the Përroi i Tropojës, ca. 14 km N of Tropojë, 970 m, 42.4740°N, 20.1520°E [type locality], leg. DA, ZF, JG, 26.vi.2014 (NHMW 111225, Mtj-469-01 [COI: MT251836]).

**External genitalia (Figure 37.2):** The whole genital complex is extremely long (PCRL = 49.3) with a very slender appearance. The FO is medium-sized (FO/V = 0.40). The vas deferens is thin along its whole course and becomes moderately wider towards the epiphallus. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.32). The bursa copulatrix is extremely long (DB/V = 2.27), markedly club-like with a big and rounded apex. The transitional area between the second duct and the actual bursa is more or less clearly visible. The diverticulum is long (D/V = 1.93), uniformly cylindrical, much thinner than the bursa copulatrix and generally shorter (D/BC = 0.85). The apex is pointed. The vagina is medium-sized or short (VRL = 10.9) and wider than the penis. The atrium is very large with a huge swelling along the vaginal side. The PC is much longer than the vagina (PC/V = 4.53). This represents the highest ratio PC/V in the whole genus *Montenegro*. The penis is much thinner than the vagina, with a small swelling at the level of transition zone between the penis and epiphallus. The epiphallus is approximately as long as the penis (E/P = 1.0), slightly swollen proximally and thinner distally. It is wider than the penis throughout. It merges into the vas deferens without a distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figure 37.3):**

The atrium is completely smooth. The distal vagina exhibits many smooth and scattered, irregularly arranged pleats. The proximal vagina has 5 up to 10 elevated longitudinal pleats that are connected by small fleshy bridges of varying thickness. The vaginal pilaster is present. The whole penis is completely smooth without any sculpturing. The penial papilla is absent. The transition zone between the penis and the epiphallus is marked by the beginning of the four or five pleats of the distal epiphallus. Along the proximal epiphallus, these pleats turn into four or five fringed pleats with jagged edges, originating proximally from the end of the vas and continuing as the distal epiphallus pleats. The background is transversely irregular.

***Montenegro okolensis okolensis* Szekeres, 2006**

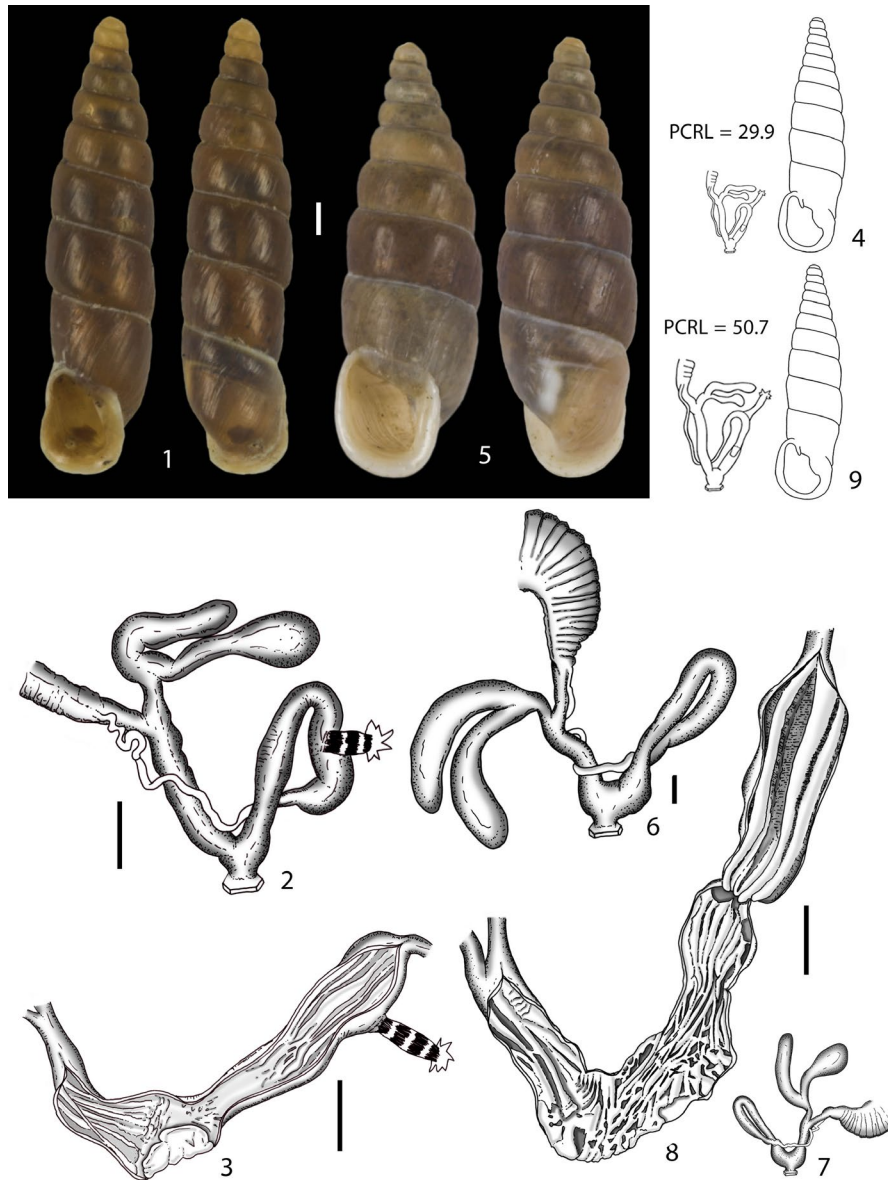
Figures 38.1–38.4

*Montenegro apfelbecki okolensis* Szekeres, 2006 in Eröss et al., 2006: 186, fig. 5.

*Montenegro janinensis caesia* (partim) – Nordsieck, 2009: 75.

*Montenegro okolensis okolensis* – Fehér & Szekeres, 2016: 71, fig. 24D, distribution map fig. 26.

**Examined material: two dissected specimens.** Albania, Malësia District, above the N side of the Qafa e Valbonës, along the footpath



**FIGURE 38** 38.1–38.4 *Montenegrina okolenis okolenis* Szekeres, 2006 HNHM 99614. 38.1 shell, 38.2 whole distal genitalia, 38.3 inner distal genitalia, 38.4 shell-genitalia ratio. 38.5–38.9 *Montenegrina okolenis caesia* Fehér & Szekeres, 2006 HNHM 94836. 38.5 shell, 38.6–38.7 whole distal genitalia, 38.8 inner distal genitalia, 38.9 shell-genitalia ratio

between Rragam and Theth, 1,850 m, 42.4068°N, 19.8122°E, leg. GP, 5.ix.2005 (HNHM 99614, Mok-486-02 [COI: KU307731, 16S: KU308155]).

**External genitalia (Figure 38.2):** The whole genital complex is medium-sized (PCRL = 29.9). The FO is also medium-sized (FO/V = 0.48) but wide. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.37). The bursa copulatrix is extremely long (DB/V = 1.29), wide, club-like, and with a more or less clearly visible transition area between the second duct and the bursa itself. The apex is rounded. The diverticulum is short (D/V = 1), uniformly cylindrical, slightly wider and shorter than the bursa copulatrix (D/BC = 0.78). The apex is blunt. The vagina is medium-sized (VRL = 13.6) wide and uniformly cylindrical. The atrium is large. The PC is much longer than the vagina

(PC/V = 2.19). The penis is wide, long and swollen at the level of the penial papilla. The epiphallus is longer than the penis (E/P = 1.88), wider than the penis and slightly swollen proximally. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and very strong.

**Inner genitalia (Figure 38.3):** The atrium shows a big, irregular, polylobated fold originating directly at the genital aperture. The fold occupies most of the atrial volume. The distal vagina has 5–8 smooth longitudinal pleats that are the direct continuation of the proximal vagina's pleats. These pleats abruptly stop before entering the atrium. The proximal vagina has 5–10 elevated longitudinal pleats. The pleats can be connected with small fleshy bridges of varying thickness. The vaginal pilaster is present. The proximal penis shows 4–6 smooth, irregular longitudinal pleats that all merge

together, forming a completely smooth penis, as far as the atrium. There is no penial papilla. The epiphallus bears up to five simple, smooth pleats originating proximally from the end of the vas deferens and fading before the penis. The background walls are irregular and finely granulated.

### *Montenegrina okolensis caesia* Fehér & Szekeres, 2006

Figures 38.5–38.9

*Montenegrina apfelbecki caesia* Fehér & Szekeres, 2006 in Eröss et al., 2006: 185, fig. 3.

*Montenegrina janinensis caesia* (partim) – Nordsieck, 2009: 75.

*Montenegrina okolensis caesia* – Fehér & Szekeres, 2016: 72, fig. 24E, distribution map fig. 26.

#### **Examined material: two dissected specimens (paratypes).**

Albania, Prokletije Mts, N side of the Qafa e Tërthorës, 11 km from Bogë towards Theth, 1,800 m, 42.392°N, 19.730°E [type locality], leg. ZE, ZF, JK, DM, 20.x.2002 (HNHM 94836, Mca-495-02 [COI: KU307594]).

**External genitalia (Figures 38.6–38.7):** The whole genital complex is extremely long (PCRL = 50.7) and very strong. The FO is long (FO/V = 0.62) but slender. The vas deferens is moderately thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.28). The bursa copulatrix is extremely long (DB/V = 1.71), very wide, markedly club-like and with a more or less clearly visible transition area between the second duct and the bursa itself. The apex is swollen and rounded. The diverticulum is also very long (D/V = 1.43), uniformly cylindrical, slightly thinner than the bursa copulatrix and slightly shorter (D/BC = 0.83). The apex is blunt. The vagina is medium-sized (VRL = 14.8), wide, cylindrical and slightly swollen at its distal end. The atrium is very large. The PC is much longer than the vagina (PC/V = 3.43). The penis is thin and long, lacking a swelling at the level of the penial papilla. The epiphallus is longer (E/P = 1.67) and only slightly wider than the penis and slightly swollen proximally. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and very strong.

**Inner genitalia (Figure 38.8):** The atrium shows an irregular set of many fleshy, irregularly arranged, fine pleats. Also the distal vagina presents many smooth scattered, irregularly arranged pleats. The proximal vagina shows one or two large, smooth, elevated longitudinal pleats. The background walls are smooth. The vaginal pilaster is present. The proximal penis has 9–12 smooth, irregular longitudinal pleats. The distal penis bears a high number of irregularly arranged, fine, smooth pleats that frequently connect to each other with fine, fleshy bridges. A true penial papilla is missing, but the transition area between epiphallus and proximal penis is well visible due to a constriction. The epiphallus has three simple, smooth pleats that originate proximally from the end of the vas deferens, fading towards the proximal penis. The background has a fine, chevron-like, jagged pattern.

### *Montenegrina minuscula* Eröss and Szekeres, 2006 sensu Fehér & Szekeres, 2016

#### **Taxonomic and systematic remarks**

*Montenegrina minuscula* is known from a few localities in central Albania and makes up the J Clade together with one population of *M. tomorosi tomorosi* (Mto-670, Mto-663 and Mto-234), which is found more than 100 km southwards, surrounded by several other *M. tomorosi* s.l. populations that fall into the K Clade. Unfortunately, the *M. tomorosi* populations of the J Clade were not available for dissection and no anatomical data can therefore currently be incorporated. *Montenegrina minuscula* shows a totally unique genital morphology that clearly distinguishes the species from all the remaining *Montenegrina* taxa (Figure 39). Its status as a valid species is, indeed, also well supported by its position in the phylogenetic tree, although its strange phylogenetic relationship with distant *M. tomorosi* populations calls for further investigation.

#### Fehér & Szekeres, 2016

*Montenegrina minuscula* Eröss and Szekeres, 2006

#### De Mattia et al., 2020

*Montenegrina minuscula* Eröss and Szekeres, 2006

### *Montenegrina minuscula* Eröss and Szekeres, 2006

Figures 39.1–39.7

*Montenegrina janinensis* – Dhora & Welter-Schultes, 1999: 16.

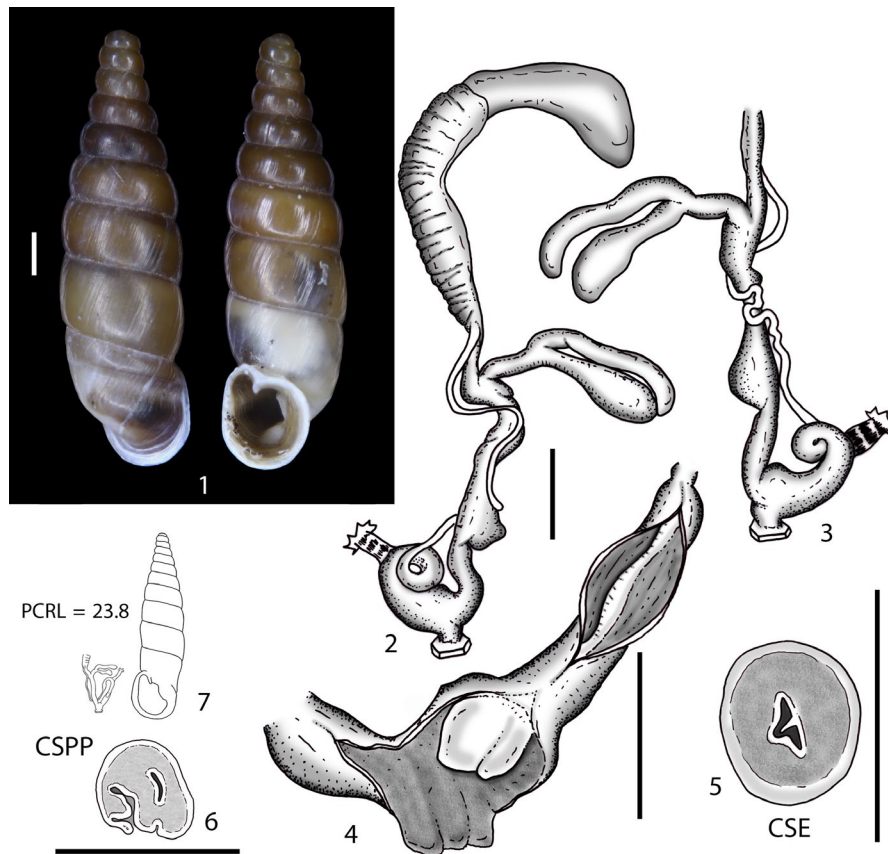
*Montenegrina minuscula* Eröss and Szekeres, 2006 in Eröss et al., 2006: 184–185, fig. 2. – Nordsieck, 2009: 75.

*Montenegrina minuscula* – Fehér & Szekeres, 2016: 67, fig. 19L, distribution map fig. 22.

#### **Examined material: three dissected specimens (paratypes).**

Albania, Mat District, 3 km W of the Qafa e Murrës, gorge of the Lumi i Varoshit near the Shkëmb i Skanderbeut, 970 m, 41.6465°N, 20.1898°E [type locality], leg. ZE, ZF, JK, DM, 26.vi.2003 (HNHM 94833, Mmn-206-01 [16S: KU308135, 12S: KU307963]).

**External genitalia (Figures 39.2–39.3):** The whole genital complex is medium-sized (PCRL = 23.8). The FO is short (FO/V = 0.13) and slender. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.29). The bursa copulatrix is short (DB/V = 0.53), club-like, moderately wide and with a more or less visible transition area between the second duct and the bursa itself. The bursa is big, elongated and the apex is rounded. The diverticulum is short (D/V = 0.41), cylindrical, thinner, and shorter than the bursa copulatrix (D/BC = 0.76). The apex is pointed. The vagina is very long (VRL = 31.7) with a very particular swelling along its midlength. The atrium is short and narrow. The PC is shorter than the vagina (PC/V = 0.75). The penis (and the whole PC) shows unique features among all the *Montenegrina* taxa. The penis is extremely short and very wide



**FIGURE 39** *Montenegrina minuscula* Erőss and Szekeres, 2006 HNHM 94832. 39.1 shell. 39.2–39.3 whole distal genitalia. 39.4 inner distal genitalia. 39.5 cross section of epiphallus. 39.6 cross section of penial papilla. 39.7 shell-genitalia ratio

distally. Its whole volume is completely filled by a very large penial papilla. The epiphallus is much longer than the penis ( $E/P = 2.00$ ) and gradually tapers towards the vas deferens. It merges into the vas deferens without a distinct transitional area. The retractor muscle is short and very strong.

**Inner genitalia (Figures 39.4–39.6):** The atrium is smooth. The whole vagina is completely smooth without the vaginal pilaster. The penis is completely smooth, without any sculpturing. The big penial papilla is globose. Its surface is smooth and the aperture is lateral and very small. The epiphallus has only one simple, smooth pleat originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina nana* Fehér & Szekeres, 2006 sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

*Montenegrina nana* s.l. forms a subclade within Clade I and is paraphyletic due to the population Mcs-441 that, based on its shell, resembles *M. perstriata callistoma*. The latter is, in genital morphology, very similar to *M. nana nana*, with a bulky shape of the external

genitalia and a complex inner sculpturing. Since this *M. perstriata callistoma* population (Mcs-441) is geographically very close to *M. nana nana* (i.e., Mna-442, about 1 km), hybridization between the two taxa is the most reasonable explanation for this phenomenon. *Montenegrina nana barinai* and *M. nana gracilis* fall together into a separate subclade, showing very small genetic distances but clearly distinguishable based on their shells. They also show a nearly identical genital anatomy, namely extremely thin and elongated genitalia with an almost smooth inner sculpturing (Figure 41), but *M. nana barinai* lacks the penial papilla.

Taking into account the phylogenetic results and the substantial differences of the genital anatomy between *M. nana nana* and the *M. nana gracilis*–*M. nana barinai* pair, we consider *Montenegrina nana* and *Montenegrina gracilis* stat. nov. as separate species, with *M. gracilis barinai* comb. nov. as a subspecies.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina nana nana</i> Fehér & Szekeres, 2006	<i>Montenegrina nana</i> Fehér & Szekeres, 2006
<i>Montenegrina nana barinai</i> Fehér & Szekeres, 2016	<i>Montenegrina gracilis barinai</i> Fehér & Szekeres, 2016 comb. nov.
<i>Montenegrina nana gracilis</i> Erőss and Szekeres, 2006	<i>Montenegrina gracilis gracilis</i> Fehér & Szekeres, 2006 stat. nov.



**Montenegrina nana** Fehér & Szekeres, 2006

Figures 40.1–40.6

*Montenegrina perstriata nana* Fehér & Szekeres, 2006 in Eröss et al., 2006: 202–203, fig. 24. – Nordsieck, 2009: 74, plate 3, fig. 17.

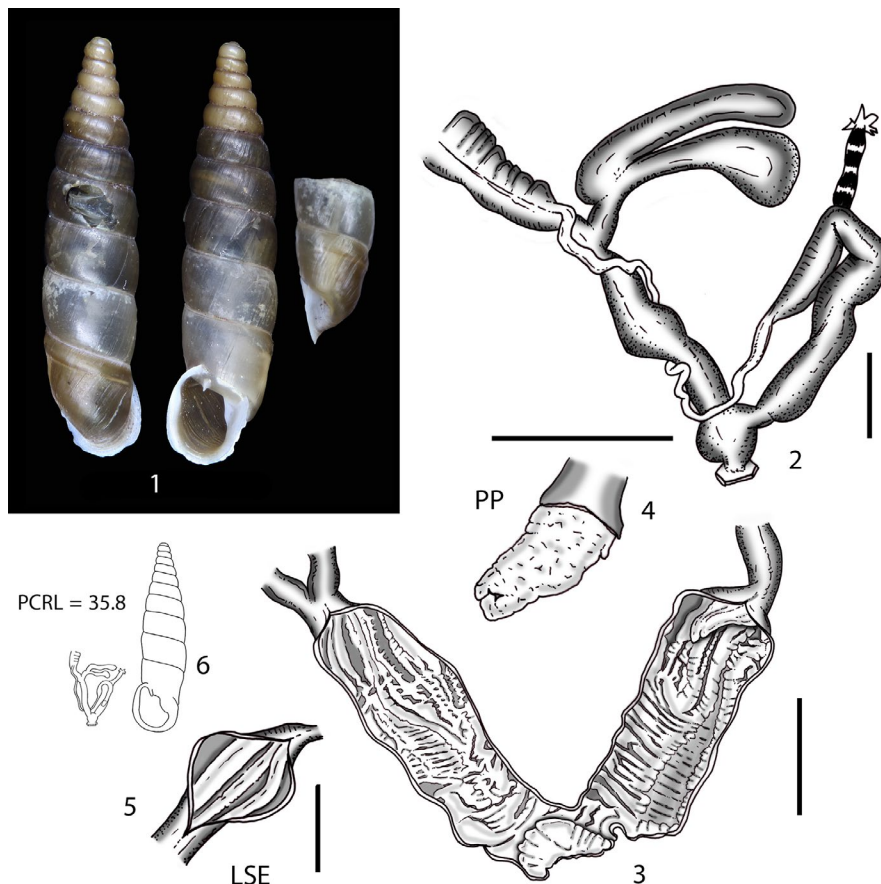
*Montenegrina nana nana* – Fehér & Szekeres, 2016: 68, fig. 24A, distribution map fig. 25A.

**Examined material:** two dissected specimens. Albania, Librazhd District, 3 km NE of Lunik, on the Librazhd–Peshkopi road, 1,050 m, 41.2966°N, E20.3741°E [type locality], leg. ZF, TN, EM, 13.iv.2014 (HNHM 98973, Mna-439-01 [COI: KU307720, 16S: KU308142]).

**External genitalia (Figure 40.2):** The whole genital complex is large (PCRL = 35.8). The FO is very short (FO/V = 0.19). The vas deferens is thin along its whole course, only slightly swollen proximally. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.23). The bursa copulatrix is long (DB/V = 0.96), club-like, wide, and with a more or less visible transitional area between the second duct and the bursa itself. The bursa is swollen, elongated and the apex is rounded. The diverticulum is long (D/V = 1.19), uniformly cylindrical and longer than the bursa copulatrix (D/BC = 1.23). The apex is rounded. The vagina is medium-sized (VRL = 17.9), with a swelling at its midlength. The atrium is short but large, with a distinct swelling at the vaginal side of likely

glandular origin. The PC is longer than the vagina (PC/V = 2.00). The penis is cylindrical, only slightly tapering along its distal part. The epiphallus is longer than the penis (E/P = 1.25), wider along its distal portion and only slightly swollen proximally. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 40.3–40.5):** The atrium has a big, irregular, polylobated fold originating directly at the genital aperture. The fold occupies the complete atrial volume. The distal vagina shows a set of transversal pleats, oblique and irregularly splitting and merging into one another. The proximal vagina has many smooth, fine, fringed pleats that are irregularly arranged. The pleats are connected by many small, fleshy bridges. The vaginal pilaster is present and randomly connected with the pleats by many small, fleshy bridges. The proximal penis has a variable number of oblique, rough, and irregularly lobated longitudinal pleats that distally merge into one another. The distal penis bears a variable number of irregular, smooth transversal pleats, arranged into two or three main cords. The smooth background is usually visible. The medium-sized, conical penial papilla has a pointed apex and a granulated surface. The aperture reaches the papilla's tip. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.



**FIGURE 40** *Montenegrina nana* Fehér & Szekeres, 2006 HNHM 98973. 40.1 shell. 40.2 whole distal genitalia. 40.3 inner distal genitalia. 40.4 penial papilla. 40.5 longitudinal section of epiphallus. 40.6 shell-genitalia ratio

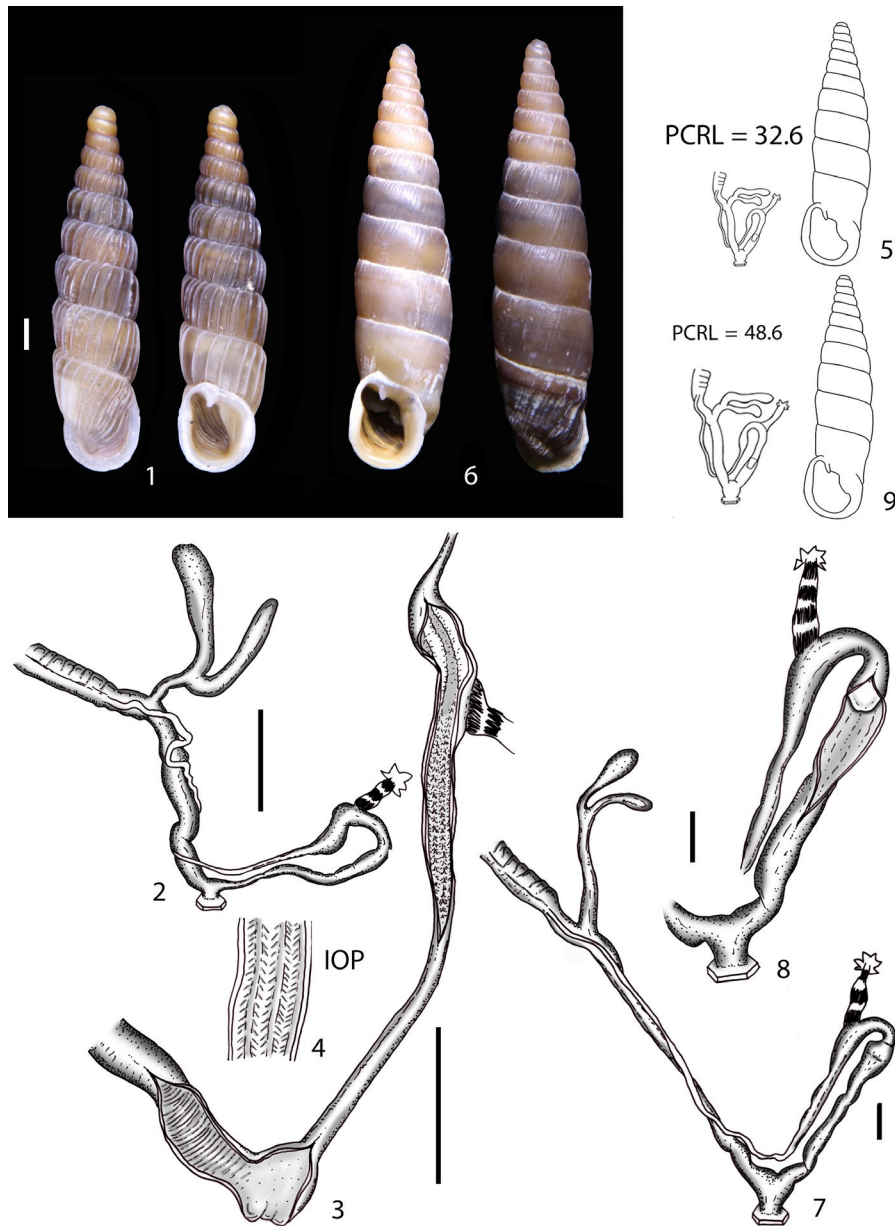
***Montenegrina gracilis barinai* Fehér & Szekeres, 2016  
comb. nov.**

Figures 41.1–41.5

*Montenegrina nana barinai* – Fehér & Szekeres, 2016: 69, fig. 24B, distribution map fig. 25A.

**Examined material: two dissected specimens (paratypes).**  
Albania, Bulqizë District, Valikardhë, S slope of the Maja e Temshisit, 770 m, 41.514°N, 20.316°E [type locality], leg. ZF, TN, EM, 15.iv.2014 (HNHM 99008, Mba-453-01 [COI: KU307539, 16S: KU308018]; Mba-453-02 [COI: MT251514]).

**External genitalia (Figure 41.2):** The whole genital complex is large (PCRL = 32.6), but the overall appearance is very slender. The FO is very short (FO/V = 0.26) but wide. The vas deferens is thin along its whole course, only slightly swollen at its proximal end. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.23) and slender. The bursa copulatrix is short (DB/V = 0.68), club-like to slightly cylindrical, wide and without a clearly visible transitional area between the second duct and the bursa itself. The apex is rounded. The diverticulum is short (D/V = 0.74), uniformly cylindrical, less wide and slightly longer (D/BC = 1.08) than the bursa copulatrix. The apex is pointed. The vagina is medium-sized (VRL = 14.7), uniformly cylindrical. The atrium is very small. The PC is much longer



**FIGURE 41** 41.1–41.5 *Montenegrina gracilis barinai* Fehér & Szekeres, 2016 comb. nov. HNHM 99008. 41.1 shell, 41.2 whole distal genitalia, 41.3 inner distal genitalia, 41.4 magnification of the inner ornamentation of proximal penis, 41.5 shell-genitalia ratio. 41.6–41.9 *Montenegrina gracilis gracilis* Eröss and Szekeres, 2006 stat. nov. HNHM 94887. 41.6 shell, 41.7 whole distal genitalia, 41.8 inner proximal penis and penial papilla, 41.9 shell-genitalia ratio

than the vagina ( $PC/V = 2.21$ ). The penis is thin, long and widens only slightly towards the epiphallus. The epiphallus is shorter than the penis ( $E/P = 0.5$ ), wider than the penis, and only slightly swollen proximally. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 41.3–41.4):** The small atrium is completely smooth. The distal vagina is almost smooth, only with very fine transversal wrinkles. The proximal vagina is smooth. The vaginal pilaster is absent. The distal penis is completely smooth, although the walls are very finely granulated. The proximal penis bears 3–5 rows of chevron-like, fine longitudinal striae. The penial papilla is absent and the transition between the penis and the epiphallus is marked by the change insculpturing. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina gracilis gracilis* Eröss and Szekeres, 2006 stat. nov.**

Figures 41.6–41.9

*Montenegrina perstriata gracilis* Eröss and Szekeres, 2006 in Eröss et al., 2006: 202, fig. 23. – Nordsieck, 2009: 74.

*Montenegrina nana gracilis* – Fehér & Szekeres, 2016: 70, fig. 24C, distribution map fig. 25A.

**Examined material: three dissected specimens.** Albania, Bulqizë District, 10 km E of Bulqizë, bank of Lumi i Zalli i Qytetit, 620 m, 41.5096°N, 20.3149°E [type locality], leg. LD, ZE, ZF, 30.vi.2007 (HNHM 99624, Mgc-277-01 [COI: KU307676, 16S: KU308109]; Mgc-277-02 [COI: KU307677, 16S: KU308110]).

**External genitalia (Figure 41.7):** The whole genital complex is large ( $PCRL = 48.6$ ) but its overall appearance is very slender. The FO is very short ( $FO/V = 0.14$ ) but wide. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is extremely long ( $DBC/DB = 1.32$ ). The complex of the bursa copulatrix is unusually small for the genus. The bursa copulatrix is very short ( $DB/V = 0.28$ ), club-like and lacks a clearly visible transition area between the second duct and the bursa itself. The apex is rounded. The diverticulum is extremely short ( $D/V = 0.20$ ), uniformly cylindrical, less wide than the bursa copulatrix and slightly shorter ( $D/BC = 0.73$ ). The apex is pointed. The vagina is extremely long ( $VRL = 43.2$ ) and uniformly cylindrical. The atrium is small. The PC is longer than the vagina ( $PC/V = 1.13$ ). The penis is thin, long and with a distinct swelling at the level of the penial papilla. The epiphallus is slightly wider than the penis and only moderately swollen proximally. It merges into the vas deferens without a distinct transitional area. The retractor muscle is short and strong. The epiphallus is shorter than the penis ( $E/P = 0.82$ ).

**Inner genitalia (Figure 41.8):** The atrium is smooth. Both the distal and proximal vagina are almost smooth with very fine transversal wrinkles. The vaginal pilaster is absent. The penis is completely smooth without any sculpturing. The medium-sized penial papilla is

globose with a blunt apex and a smooth surface. The aperture extends laterally, reaching the apical area. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is coarse.

### ***Montenegrina perstriata* (Wagner, 1919) sensu Fehér & Szekeres (2016)**

#### **Taxonomic and systematic remarks**

The distributional area of *M. perstriata* sensu Fehér and Szekeres (2016) includes eastern central Albania and the western part of North Macedonia next to the Albanian border. Fehér and Szekeres (2016) recognized 12 subspecies. Undeep, this species-group shows an extraordinary variability of the shell, which is matched by an equally remarkable variability in genital morphology. Following Mason et al. (2020), these taxa are scattered among four different main clades of the phylogenetic tree, thus turning out to be polyphyletic without any clear geographic partition.

The nominal subspecies, *M. perstriata perstriata*, is embedded within Clade L, forming a strongly supported group together with three other subspecies, *M. perstriata diminuta*, *M. p. mavrovoensis* and *M. perstriata subcristatula*. Geographically, all populations of this clade are located in the same area in the western part of North Macedonia. These taxa are quite similar in shell morphology and in the arrangement of both male and female genital parts, displaying only slight differences of the same general pattern. Considering the phylogenetic tree as well, we propose to maintain their conspecific status, comprising four subspecies as already proposed by Fehér and Szekeres (2016).

Interpreting the genetic and anatomical results together, we can state that all remaining *M. perstriata* subspecific taxa, sensu Fehér and Szekeres (2016), distributed among the phylogenetically distant clades H, L, and I (which also display different genital arrangements), should not be considered as being conspecific with *M. perstriata*. They will be discussed in the following, starting with the taxa in Clade I.

*Montenegrina perstriata callistoma*, *M. perstriata ochridensis* and *M. perstriata tenebrosa* form a highly supported subclade in Clade I. The only exception is one population of *M. perstriata callistoma*, which was already discussed above (in the *M. nana* section). The two highly distinct subclades comprising these taxa show a similar problematic situation. Both contain isolated mountain populations represented by varying anatomical arrangements, and in both, some mountain populations were assigned to *M. perstriata ochridensis*.

*Montenegrina perstriata tenebrosa* consists of two very closely related mt lineages (Mte-440, Moh-453), the latter one so far considered as *M. perstriata ochridensis*. They are similar in shell morphology but different in anatomy. We propose to treat *M. tenebrosa* stat. nov. as a good species and the population Moh-453 (Figure 42) as its subspecies *M. tenebrosa szekeresi* n. ssp.

Concerning the *M. perstriata callistoma*/*M. perstriata ochridensis* subclade, three populations of *M. perstriata callistoma* were

dissected: HHNM 98977 (AL Bulqizë district, Zabzun), HHNM 98954 (AL, Librazhd district, Funarës) and HHNM 98986 (AL, Bulqizë district, Ostreni i Madh). Leaving aside HHNM 98977 (which was treated in the *M. nana* section), HHNM 98954 and HHNM 98986 are very different, particularly regarding the male organs, whereas the population of *M. perstriata ochridensis* from the shore of Lake Ohrid (HHNM 94434) is very similar to HHNM 98986. Unfortunately, specimens from population HHNM 94434 were not included in the genetic analysis, but it closely neighbors HHNM 94434 (Moh-213-02) from the lake shore. Thus, population HHNM 94434 can be regarded as a representative for the genital morphology of *M. perstriata ochridensis* from the lake shore. All populations from the shoreline (HHNM 94434 [Moh-213-02], HHNM 94428 [Moh-214-01], NHMW 110430/MN/0079 [Moh-535-01]) so far analyzed are genetically nested together with mountain populations, one of them assigned to *M. perstriata ochridensis* (HHNM 99006, Moh-452-01), the other to *M. perstriata callistoma* (HHNM 98953, Mcs-433-01). Interpreting this phylogeographic pattern together with the finding that the anatomical arrangements from the lake shore specimens are also present in the mountain populations, the lake shore populations were most probably recently derived from the mountain *M. perstriata callistoma* populations. Based on our results, we propose to consider *Montenegrina ochridensis* stat. nov. as a valid species with two subspecies. *Montenegrina ochridensis callistoma* comb. nov. comprises the mountain populations, whereas, considering the slight differences in shell morphology and the detached distribution, we propose the name *Montenegrina ochridensis ochridensis* stat. nov. for the population at Lake Ohrid.

The remaining *M. perstriata* taxa are positioned in Clades H and K, and *M. perstriata drimica* is present in both. The high genetic distance between the two clades implies that *M. perstriata drimica* sensu Fehér and Szekeres (2016) includes more than one species, although there is some overlap in genital morphology, as will be outlined in the following. High intraspecific distances within land snail species have been reported for some taxa (e.g., Thomaz, Guiller, & Clarke, 1996; Gittenberger, Piel, & Groenenberg, 2004; Haase et al., 2003; Watanabe and Chiba, 2001; Sauer and Hausdorf 2012; Scheel & Hausdorf, 2012; Harl, Duda, Kruckenhauser, Sattmann, & Haring, 2014; Kruckenhauser et al., 2014) and per se are not a sufficient argument for splitting. Yet, both clades H and K are themselves composed of various species in the tree, and a number of species are located between them. Accordingly, maintaining the *M. perstriata* taxa in Clades H and K in a conspecific status would require assuming massive budding speciation and/or mitochondrial capture. Nordsieck (1972: 32) provided the locus typicus for *M. perstriata drimica* as "Lukovo". Most of the *M. perstriata drimica* populations of Clade H are located north of Lukovo, with the closest population 1.5 km away. All populations of Clade K are located south of Lukovo. We thus applied the name *drimica* to the populations included in Clade H, which are now proposed as a valid species *M. drimica* stat. nov. The populations included in Clade K are described as a new species, *Montenegrina globocica* n. sp..

Starting with *M. perstriata drimica*, seven populations distributed in a small area along the Black Drin Valley from Lukovo to

Debar in North Macedonia were dissected. Five different genital arrangements (referred to as "*drimica* genital group": DGG) were detected. DGG1 is represented by population NHMW 110430/MN/0088, Mdr-520, embedded within Clade K, (3.7 km south of Lukovo). Its inner genitalia are totally smooth. It is designated in the following sections as *M. globocica* n. sp.. The DGG2 is represented by the population HHNM 41149, Mdr-220 (N of Lukovo). The external genitalia are very elongated and the inner surface of the penis and vagina exhibit many fine, fringed longitudinal pleats. DGG3 is represented by the populations NHMW110430/MN/0087, Mdr-519 (S of Debar, at the dam of the Crni Drin River), NHMW110430/MN/0097, Mdr-529 (S of Modrić junction) and HHNM 98990 M40 448 (Gradec). Those three populations fall together into clade H, but into two separated subclades, and exhibit an almost identical anatomical arrangement (exception: population Mdr-448), which differs slightly in the sculpturing of the inner proximal penis. This difference alone does not justify the creation of an additional DGG group. Despite of this minor difference, the population Mdr-448 seems to be phylogenetically closer to Mdr-519 than to Mdr-529. It is also phylogenetically more distant to Mdr-529, with which it shares an identical anatomy. DGG4 is represented by the population HHNM 36712 (SE of Džepišta), which shows an intermediate genital arrangement between DGG2 and DGG3. Unfortunately, the lack of suitable material made it impossible to determine the phylogenetic relationships of this population. Finally, DGG5 was found in HHNM36711 Mcr 221 (N of Lukovo). It resembles DGG1, but completely lacks the big atrial fold.

While three of the DGGs were located exclusively in Clade H (DGG3, DGG5) and one was present only in Clade K (DGG1), DGG2 was found in both of them (Mdr-220-02, Mcr-221-01) (no genetic data were available for DGG4). Mdr-220-02 was recorded in the northern most population of Clade K "*drimica*" co-occurring with individual Mdr-523-01 (Clade H). This finding, together with the fact that individual Mdr-217-01, which was found in the southern part of the Drin Valley, has a Clade H haplotype, shows that the distributions of the two taxa overlap. This implies sporadic gene flow between the two lineages.

Although in our analysis *M. drimica* stat. nov. exhibited three different genital arrangements (DGG2, 3, 5) and is distributed in two subclades (with *M. perstriata plenostoma* being part of one), we refrain from proposing new taxa within *M. drimica*. Nonetheless, the status of the two existing subspecies within this group (*M. perstriata plenostoma*, *M. perstriata occidentalis*) must be evaluated: *M. perstriata plenostoma* inhabits the western side of Lake Ohrid in the Pogradec district, 2 km E of Qafa e Thanës (Albania), about 30 km south of the closest *M. drimica* population. This taxon (HHNM 98945, Mpl-430) is monophyletic but closely related to one of the *M. drimica* subclades. Its shell and genital arrangement differ from all the investigated *M. drimica* populations (Clade H). Considering these results and waiting for further investigations, we prefer to keep this taxon at subspecific rank: *M. drimica plenostoma* comb. nov.

Unfortunately, no preserved specimens of *M. perstriata occidentalis* were suitable for anatomical investigations (juvenile or damaged

samples), so no data about genital morphology are available. This taxon is included in Clade H, within the subclade that contains the slender form of *M. drimica*. We provisionally keep it as a valid subspecies, *M. drimica occidentalis* comb. nov., until more data becomes available.

*Montenegrina perstriata radikae* (population Mra-518) and the *M. cfr. perstriata* ssp. population M\_55-675 fall together in a subclade of Clade K, the sister group of *M. globocica* n. sp.. Their genital anatomy shows some similarity regarding the penial papilla and the inner walls of the vagina, even though the penial inner walls differ somewhat. Also for these two taxa, isolation may have enabled genital-anatomical differentiation. As for most of the previously taxa deemed as subspecies of *M. perstriata*, *M. radikae radikae* stat. nov. must be considered as a valid species, not phylogenetically related with *M. perstriata* but merely showing shell morphology convergence. Population M55-675, despite showing a phylogenetic proximity with *M. radikae radikae* and a partially similar genital anatomy, lives about 60 km apart. Nevertheless, we prefer to consider the M55-675 population as belonging to a new subspecies of *M. radikae* that is here described as *M. radikae paparistoeae* n. sp.

Due to vague locality data, no *M. perstriata steffeki* specimen was available for both anatomical investigation and DNA analysis (Fehér & Szekeres, 2016: 83). For these reasons the identity of this taxon cannot be evaluated with the integrative approach, and its current status is retained until new data become available.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina perstriata callistoma</i> Fehér & Szekeres, 2006	<i>Montenegrina ochridensis callistoma</i> Fehér & Szekeres, 2006 comb. nov.
<i>Montenegrina perstriata diminuta</i> Fehér & Szekeres, 1999	<i>Montenegrina perstriata diminuta</i> Fehér & Szekeres, 1999
<i>Montenegrina perstriata drimica</i> Nordsieck, 1972	<i>Montenegrina drimica drimica</i> Nordsieck, 1972 stat. nov. <i>Montenegrina globocica</i> n. sp.
<i>Montenegrina perstriata mavrovoensis</i> Nordsieck, 2009	<i>Montenegrina perstriata mavrovoensis</i> Nordsieck, 2009
<i>Montenegrina perstriata occidentalis</i> Nordsieck, 1977	<i>Montenegrina drimica occidentalis</i> Nordsieck, 1977 comb. nov.
<i>Montenegrina perstriata ochridensis</i> (Wagner, 1925)	<i>Montenegrina ochridensis ochridensis</i> (Wagner, 1925) stat. nov.
<i>Montenegrina perstriata perstriata</i> (Wagner, 1919)	<i>Montenegrina perstriata perstriata</i> (Wagner, 1919)
<i>Montenegrina perstriata plenostoma</i> Fehér & Szekeres, 2006	<i>Montenegrina drimica plenostoma</i> Fehér & Szekeres, 2006 comb. nov.
<i>Montenegrina perstriata radikae</i> Nordsieck, 1972	<i>Montenegrina radikae radikae</i> Nordsieck, 1972 <i>Montenegrina radikae paparistoeae</i> n. ssp.
<i>Montenegrina perstriata subcrisatula</i> Nordsieck, 1977	<i>Montenegrina perstriata subcrisatula</i> Nordsieck, 1977
<i>Montenegrina perstriata steffeki</i> Eröss and Szekeres, 1999	<i>Montenegrina perstriata steffeki</i> Eröss and Szekeres, 1999

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina perstriata tenebrosa</i> Nordsieck, 2009	<i>Montenegrina tenebrosa tenebrosa</i> Nordsieck, 2009 stat. nov. <i>Montenegrina tenebrosa szekeresi</i> n. ssp.

### *Montenegrina perstriata perstriata* (Wagner, 1919)

Figures 42.1–42.7

*Delima laxa perstriata* Wagner, 1919: 71–72.

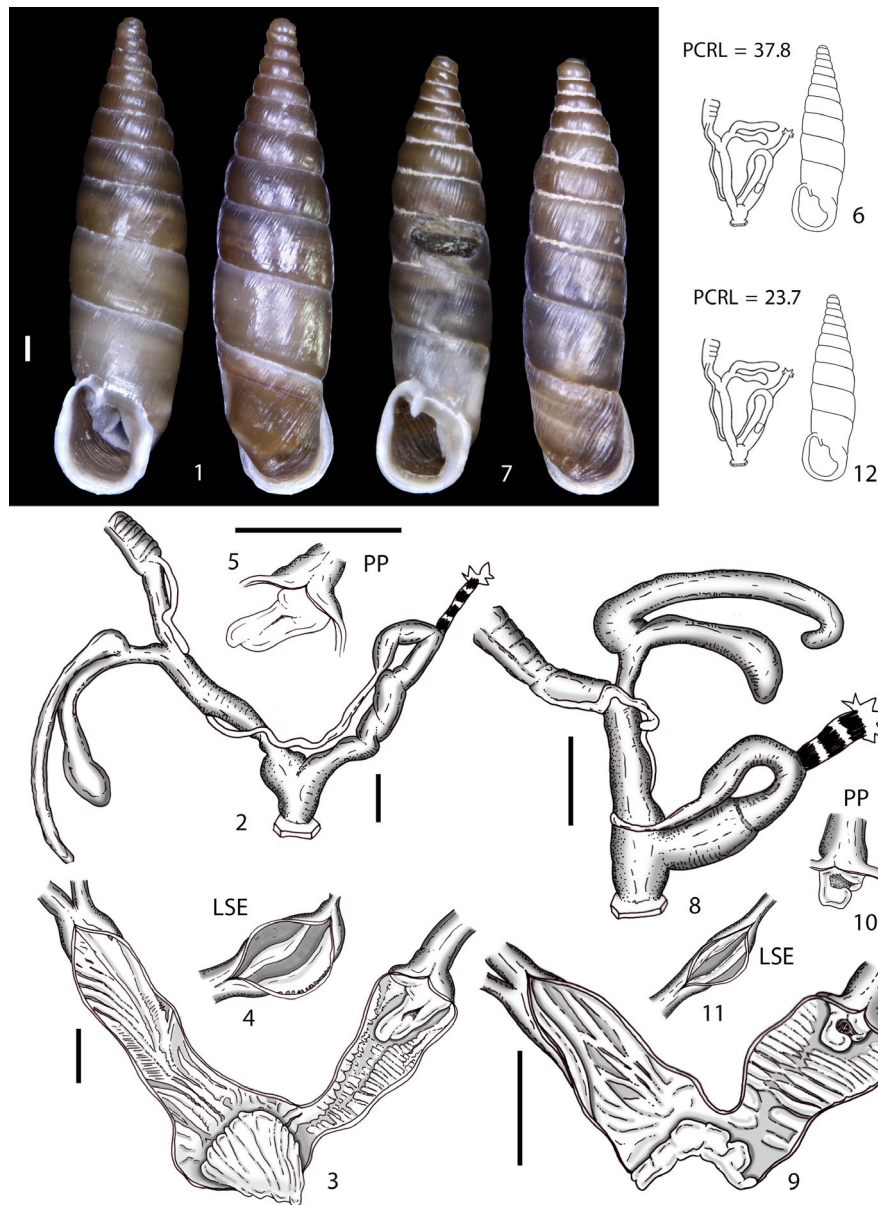
*Delima* (*Albanodelima*) *perstriata* – Wagner, 1924: 120. – Wagner, 1925: 61, plate 14, figs 97a–b.

*Montenegrina perstriata perstriata* – Nordsieck, 1977: 84, plate 4, fig. 13 – Zilch, 1981: 130. – Nordsieck, 2009: 74. – Fehér & Szekeres, 2016: 74, fig. 27A, distribution map fig. 25A.

**Examined material: three dissected specimens.** North Macedonia, Galičnik, 1,440 m, 41.5936°N, 20.6575°E [type locality], leg. ZF, EH, KJ, HS, 14.x.2014 (NHMW 110430/MN/0105, Mpe-512-01 [COI: KU307740, 16S: KU308162]).

**External genitalia (Figures 42.2–42.3):** The whole genital complex is long (PCRL = 37.8) but the overall appearance is slender. The FO is medium-sized (FO/V = 0.55). The vas deferens is moderately thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.22). The bursa copulatrix is long (DB/V = 1.02), slender, club-like and with a more or less clearly visible transition area between the second duct and the bursa itself. The apex is moderately swollen and rounded. The diverticulum is very long (D/V = 1.45), uniformly cylindrical, very slender, slightly thinner than the bursa copulatrix and much longer (D/BC = 1.42). The apex is pointed. The vagina is long (VRL = 21.1) wide, cylindrical and slightly tapered distally. The atrium is very large at the vaginal side. The PC is much longer than the vagina (PC/V = 1.80). The penis is wide, irregular, and long, with a distinct swelling at the level of the penial papilla. The epiphallus is shorter and thinner than the penis (E/P = 0.84) and only slightly swollen along its proximal part. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long.

**Inner genitalia (Figures 42.4–42.6):** The atrium shows a very big, irregular, polylobated fold originating directly at the genital aperture. The fold is markedly fan-like and occupies almost the whole atrial volume. The distal vagina has 6–10 irregular, fringed longitudinal pleats that continue into the atrium. The proximal vagina shows many oblique, elevated, irregular, transversal pleats. The background walls are smooth. The vaginal pilaster is present. The penis has two main large, smooth and polylobated pleats. The pleats are divided by a smooth longitudinal section of the wall surface. These pleats extend from the proximal part as far as the atrium. The medium-sized, conical penial papilla has a pointed apex and a pleated surface. The aperture is lateral and does not reach the papilla's tip. The apical apertureless part



**FIGURE 42** 42.1–42.7 *Montenegrina perstriata perstriata* (Wagner, 1919) NHMW 110430/MN/0105. 42.1 shell, 42.2–42.3 whole distal genitalia, 42.4 inner distal genitalia, 42.5 cross section of penial papilla, 42.6 penial papilla. 42.7 shell-genitalia ratio. 42.8–42.12 *Montenegrina perstriata diminuta* Fehér & Szekeres, 1999 NHMW 110430/MN/0101. 42.7 shell. 42.8 whole distal genitalia, 42.9 inner distal genitalia, 42.10 penial papilla, 42.11 longitudinal section of epiphallus, 42.12 shell-genitalia ratio

is smaller in diameter. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina perstriata diminuta* Fehér & Szekeres, 1999

Figures 42.8–42.12

*Montenegrina perstriata diminuta* Fehér & Szekeres, 1999 in Erőss et al., 1999: 446–448, fig. 2 – Nordsieck, 2009: 74, plate 3, fig. 12 – Fehér & Szekeres, 2016: 77, fig. 27C, distribution map fig. 25A.

**Examined material:** two dissected specimens. North Macedonia, Ohrid District, 2.2 km to Rečica from the Ohrid–Resen road, 940 m, 41.2202°N, 20.9115°E, leg. ZF, EH, KJ, HS, 15.x.2014 (NHMW 110430/MN/0101, Mdm-533-01 [COI: KU307633]).

**External genitalia (Figure 42.8):** The whole genital complex medium-sized (PCRL = 23.7). The FO is also medium-sized (FO/V = 0.56). The vas deferens is thin but gradually tapers proximally. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.30). The bursa copulatrix is long (DB/V = 1.11), with a wide second duct. The bursa itself is not particularly swollen. There is no clearly visible transitional area. The diverticulum is very long (D/V = 2.28), uniformly cylindrical, slender and much longer than the bursa copulatrix (D/BC = 2.05). The apex is blunt. The vagina

is medium-sized (VRL = 10.7), wide and uniformly cylindrical. The atrium is long and large. The PC is much longer than the vagina (PC/V = 2.22). The penis is strongly swollen and thick-walled. The epiphallus is longer than the penis (E/P = 1.86), almost uniformly cylindrical and thinner than the penis. It merges into the vas deferens without a distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 42.9–42.11):** The atrium bears anirregular, polylobated fold originating directly at the genital aperture. The distal vagina shows scattered, irregularly arranged pleats. The proximal vagina has four or five elevated longitudinal pleats (the vaginal pilaster is included). These pleats are irregular and randomly connected by small fleshy bridges. The background is smooth. The whole penis shows two main large, smooth and polylobated pleats. The metamers are transversely oriented. The two pleats are longitudinally divided by a smooth section of the wall surface. These pleats extend as far as the atrium. The medium-sized penial papilla is globose, irregular, with a blunt apex. The aperture extends laterally, reaching the apical area. The surface is smooth. The epiphallus has two simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background walls are irregular, yielding jagged edges on the pleats.

### ***Montenegrina ochridensis callistoma* Fehér & Szekeres, 2006 comb. nov.**

Figures 43.1–43.13

*Montenegrina perstriata callistoma* Fehér & Szekeres, 2006 in Eröss et al., 2006: 200–202, fig. 22 – Nordsieck, 2009: 74, plate 3, fig. 16.

*Montenegrina perstriata crassa* – Fehér & Eröss, 2009: 11.

*Montenegrina perstriata "crassa"* – Nordsieck, 2009: 75, plate 3, fig. 15.

*Montenegrina perstriata callistoma* – Fehér & Szekeres, 2016: 75, fig. 27B, distribution map fig. 25B.

**Examined material: six dissected specimens.** Albania, Librazhd district, Funarës W 3.5 km (9 km from the Librazhd–Peshkopi road to Oranjë), 660 m asl., 41.2748°N 20.2679°E, leg. ZF, LN, EM, 12.4.2014 (HNHM 98954, Mcs-434-01 [COI: KU307611, 16S: KU308067, 12S: KU307938]; Mcs-434-02 [COI: MT251536]).

Albania, Bulqizë District, W of Zabzun, 4 km from the Librazhd to Peshkopi road towards Sebisht, 1,230 m, 41.3462°N, 20.3904°E, leg. ZF, 13.iv.2014 (HNHM 98977, M37-441-01 [COI: KU307564, 16S: KU308036]; M37-441-02 [COI: MT251537]).

**External genitalia (Figures 43.2–43.3, 43.9–43.10):** The whole genital complex is medium-sized (PCRL = 29.1). The FO is short (FO/V = 0.37). The vas deferens is very thin along its whole course. The first duct of the bursa copulatrix complex is very short (DBC/DB = 0.13). The bursa copulatrix is also short (DB/V = 0.69) with

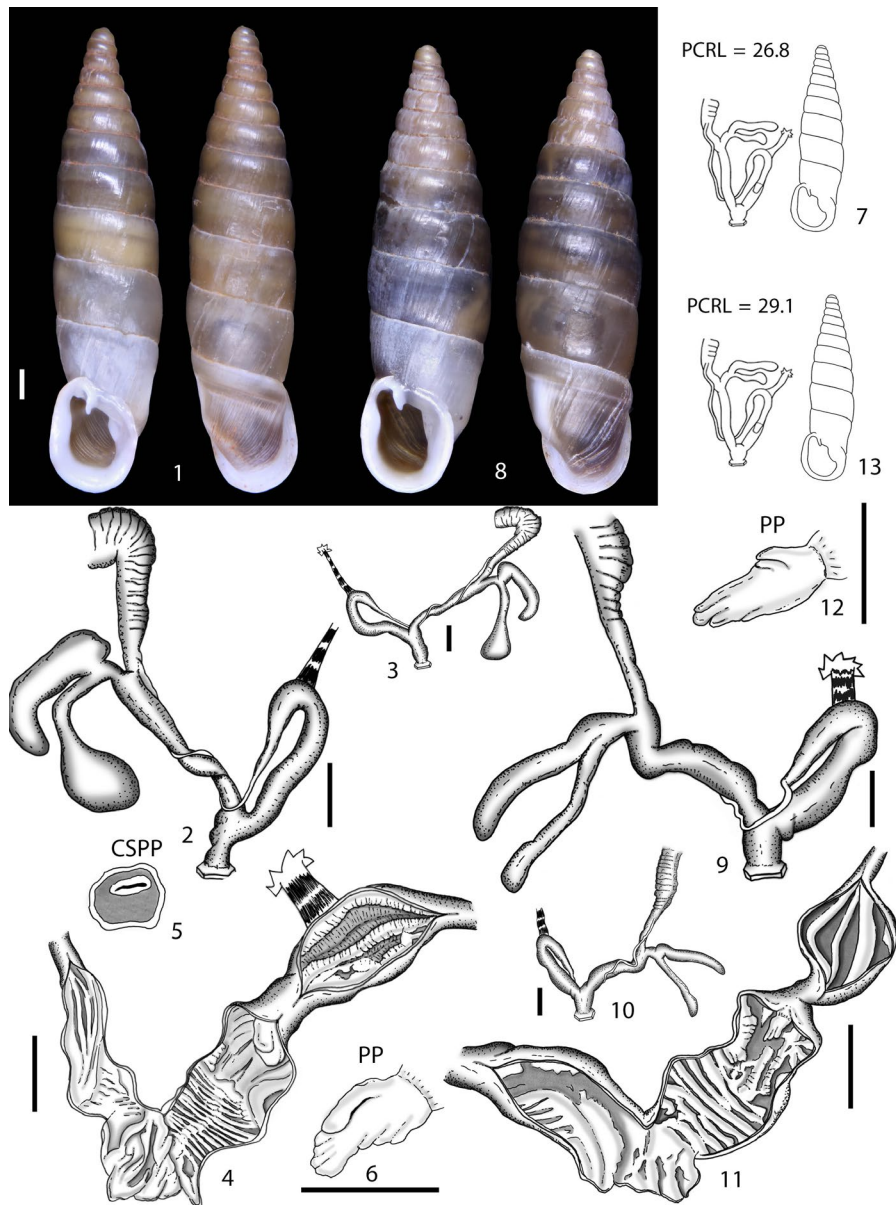
a slender second duct and a very swollen and rounded bursa, with a clearly visible transitional area. The diverticulum is also short (D/V = 0.69), uniformly cylindrical, very wide and roughly as long as the bursa copulatrix (D/BC = 1). The apex is blunt. The vagina is medium-sized (VRL = 19.6), wide, cylindrical and slightly tapering at its distal end. The atrium is long and slightly swollen at its vaginal side. The PC is longer than the vagina (PC/V = 1.49). The penis is slender, cylindrical, without any swelling at the level of the penial papilla. The epiphallus is longer than the penis (E/P = 1.89) and cylindrical. It merges into the vas deferens without a distinct transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 43.4–43.6, 43.11–43.12):** The atrium has an irregular set of 4–7 fleshy, often overlapping, large folds, which are very irregular and discontinuous with a smooth surface. The distal vagina is smooth but with traces of flat, minimally elevated, branched and oblique pleats. The proximal vagina bears 5–8 elevated longitudinal pleats. The pleats can be connected with small fleshy bridges of variable thickness. The vaginal pilaster is present. The distal penis has 8–14 fine, elevated and smooth transversal pleats that are very densely arranged. These pleats merge along the central axis, forming kind of a “backbone-like” arrangement. The proximal penis shows few irregularly arranged fringed pleats. The smooth background is well visible. The medium-sized penial papilla is globular, bilobated. The aperture extends between the two lobes. The epiphallus has two simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is irregular with pleats with jagged edges.

**Examined material: two dissected specimens.** Albania, Bulqizë District, 1.2 km S of Ostreni i Madh, 870 m, 41.4199°N, 20.4633°E, leg. ZF, TN, EM, 14.iv.2014 (HNHM 98986, Mcs-446-02 [COI: KU307614, 16S: KU308070]).

**External genitalia (Figure 44.2):** The whole genital complex is medium-sized (PCRL = 28.9). The FO is short (FO/V = 0.32). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is very short (DBC/DB = 0.14). The bursa copulatrix is very long (DB/V = 1.91), with a wide second duct and a wider bursa, swollen and rounded. There is no clearly visible transition area. The diverticulum is medium-sized (D/V = 1.23), very wide, uniformly cylindrical, wider and shorter than the bursa copulatrix (D/BC = 0.64). The apex is blunt. The vagina is medium-sized (VRL = 12.7), wide and uniformly cylindrical. The atrium is long and slightly swollen at its vaginal side. The PC is much longer than the vagina (PC/V = 2.27). The penis is swollen. The epiphallus is longer than the penis (E/P = 1.27), cylindrical, wider along its distal part and gradually tapering towards the vas deferens. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 44.3–44.5, 44.8):** The atrium bears a large, irregular, pad-like pleat. The surface is smooth. The distal vagina has 6–10 smooth transversal pleats. These pleats are irregular, randomly



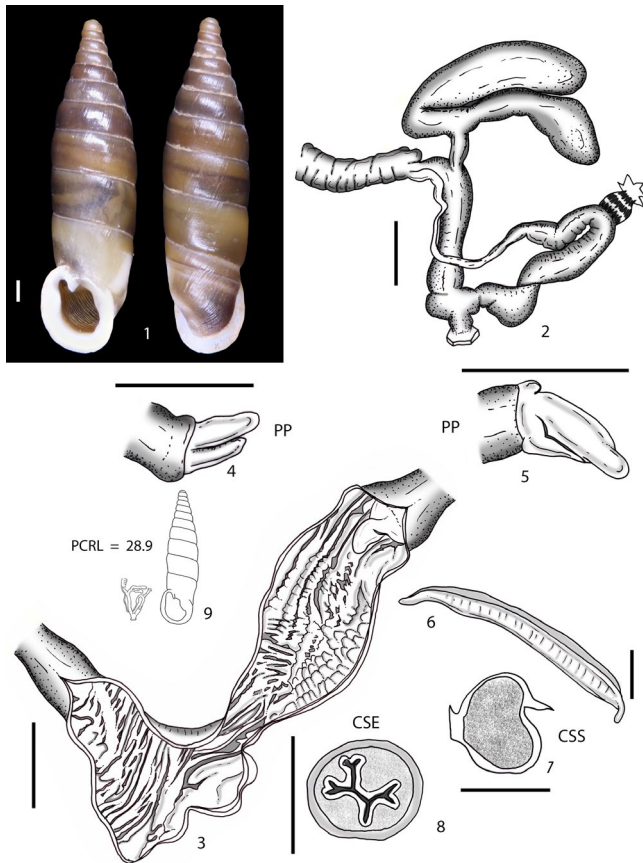
**FIGURE 43** *Montenegrina ochridensis callistoma* Fehér & Szekeres, 2006 comb. nov. HNHM 98977. 43.1 shell. 43.2–43.3 whole distal genitalia. 43.4 inner distal genitalia. 43.5 cross section of penial papilla. 43.6 penial papilla. 43.7 shell-genitalia ratio. HNHM 98954. 43.8 shell. 43.9–43.10 whole distal genitalia. 43.11 inner distal genitalia. 43.12 penial papilla. 43.13 shell-genitalia ratio

splitting and merging into one another. The proximal vagina has one main longitudinal pleat surrounded by many minor transversal pleats originating directly from it. These transversal pleats are also irregular. The main pleat is a direct continuation of the vaginal pilaster. The background walls are smooth. The proximal penis shows 5–7 irregular, pearl-necklace-like longitudinal pleats with few irregular, oblique, minor folds. Many small, irregular transversal pleats extend through the distal penis. The medium-sized, conical penial papilla has a pointed apex and an irregular surface. The aperture is lateral, not reaching the papilla's tip. The apical, apertureless part is smaller in diameter. The epiphallus has two simple, jagged pleats originating proximally from the end of the vas deferens and fading before the

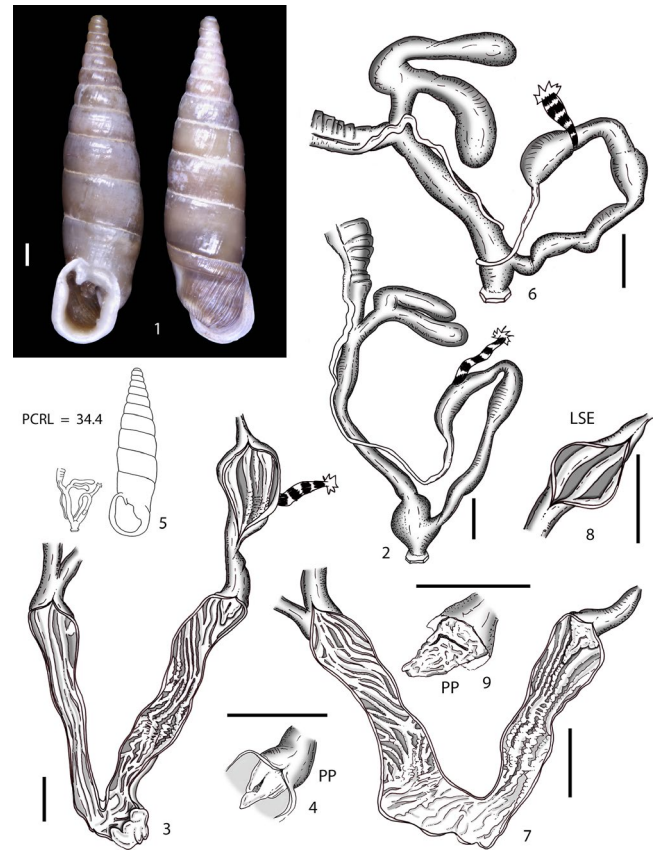
origin of the penial papilla. The background is irregular and finely granulated.

**Spermatophore (Figures 44.6–44.7):** The spermatophore is straight with a narrow head and tail. The head is narrow but not pointed, with the apex slightly bent downwards. The tail is narrow but rounded and also slightly bent downwards. The lower carina is absent. The upper carina starts approximately behind the head and extends almost as far as the tail. The lateral surface shows a weak rib-like sculpturing. The cross section is roundish with two lateral sharp keels. The largest one has a large base and it is rectangular in cross section, with a sharp lateral edge. The smaller one is high and sharp. The spermatophore is 4.6 mm long and 0.7 mm in diameter.





**FIGURE 44** *Montenegro ochridensis callistoma* Fehér & Szekeres, 2006 stat. nov. HNHM 98986. 44.1 shell. 44.2 whole distal genitalia. 44.3 inner distal genitalia. 44.4–44.5 penial papilla. 44.6 spermatophore, 44.7 cross section of spermatophore. 44.8 cross section of epiphallus. 44.9 shell-genitalia ratio



**FIGURE 45** *Montenegro drimica* Nordsieck, 1972 stat. nov. DGG2 HNHM 41149/43. 45.1 shell. 45.2 whole distal genitalia. 45.3 inner distal genitalia. 45.4 penial papilla. 45.5 shell-genitalia ratio. DGG5 HNHM 36711/41. 45.6 whole distal genitalia. 45.7 inner distal genitalia. 45.8 longitudinal section of epiphallus. 45.9 penial papilla

### *Montenegro drimica* Nordsieck, 1972 stat. nov.

Figures 45.1–45.9, 46.1–46.12, 47.1–47.6, 48.1–48.6

*Montenegro perstriata drimica* Nordsieck, 1972: 32, plate 4, fig. 38. – Zilch, 1981: 130, plate 14, fig. 31 – Nordsieck, 2009: 74, plate 1, fig. 3 – Dedov & Neubert, 2009: 91, plate 1, figs 3 and 4.

*Montenegro perstriata crassa* Eröss and Szekeres, 1999 in Eröss et al., 1999: 448, fig. 3 – Nordsieck, 2009: 75.

*Montenegro perstriata drimica* – Fehér & Szekeres, 2016: 78, fig. 27D, E, distribution map fig. 25B.

### DGG2

**Examined material:** five dissected specimens. North Macedonia, north of Lukovo, 610 m 41.3545°N, 20.6124°E, leg. EK, LP,5.vii.1985 (HNHM 41149/43, 97383, no DNA sequence data).

**External genitalia (Figure 45.2):** The whole genital complex is long (PCRL = 34.4), whereas the FO is short (FO/V = 0.28). The vas deferens is thin along its whole course, except for its proximal end, where it is slightly swollen. The first duct of the bursa copulatrix complex is

short (DBC/DB = 0.25). The bursa copulatrix is short (DB/V = 0.75), with a wide second duct and a wide actual bursa. There is no clear transitional area. The diverticulum is short (D/V = 0.94), uniformly cylindrical, slightly thinner but on average longer than the bursa copulatrix (D/BC = 1.25). The apex is blunt. The vagina is medium-sized (VRL = 17.8) and uniformly cylindrical. The atrium is moderately large and long. The PC is much longer than the vagina (PC/V = 1.94). The penis is thin and irregular along its whole course, only slightly swollen at the level of the penial papilla. The epiphallus is shorter than the penis (E/P = 0.77), slightly swollen along both its proximal and distal part. It merges into the vas deferens with a more or less clear transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 45.3–45.4):** The atrium has some irregular smooth, flat, and pad-like pleats that are irregularly arranged. The distal vagina shows many smooth, scattered, irregularly arranged pleats. The pleats are fringed and connected to each other by small fleshy bridges. The proximal vagina exhibits many irregularly arranged pleats (oblique or longitudinal), randomly splitting and merging into one another. The proximal penis has 5–8 fine, longitudinal metameric pleats, arranged in a pearl-necklace-like manner with a few irregular, oblique minor folds. Small, irregular transversal

pleats run through the distal penis, extending into the atrium. The medium-sized, conical penial papilla has a pointed apex with more or less irregular surface. The aperture is lateral and does not reach the papilla's tip. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### DGG3

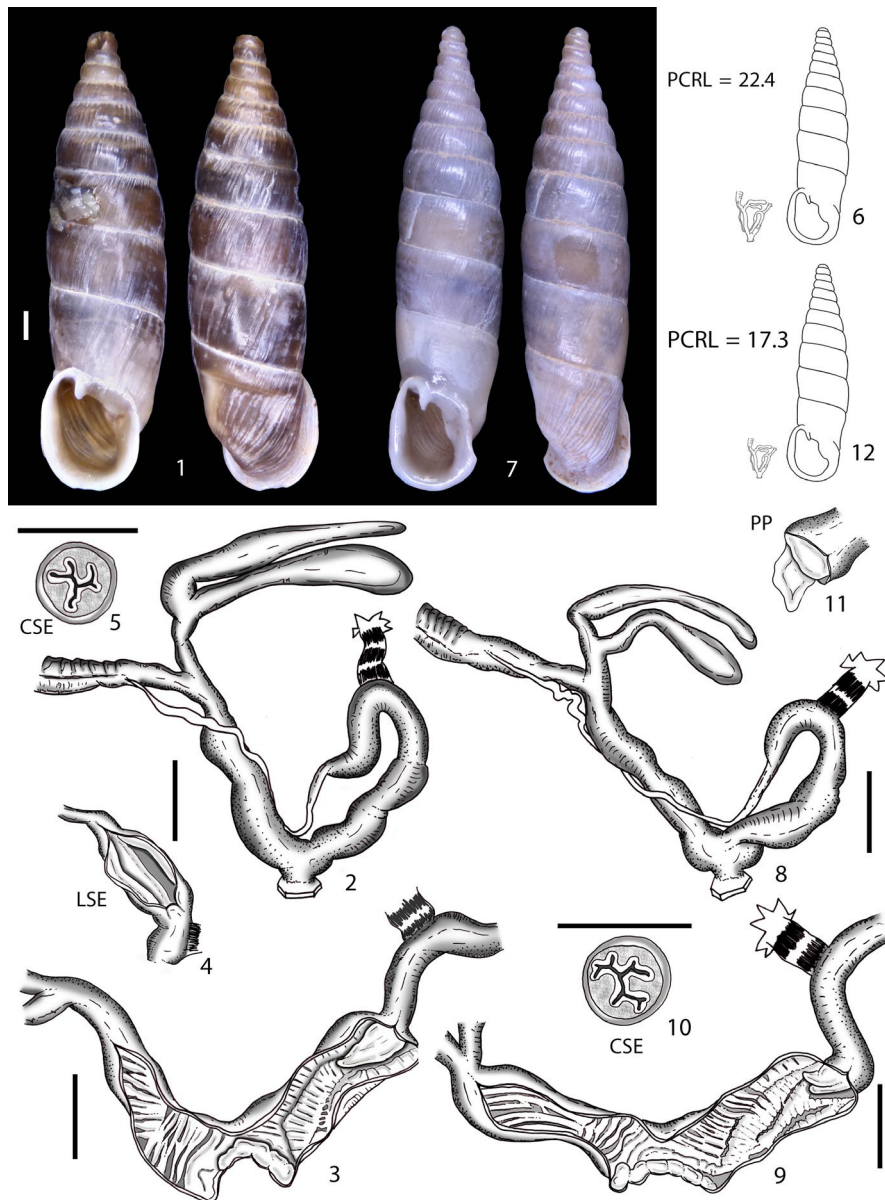
**Examined material:** seven dissected specimens. North Macedonia, Debar District, S of Debar, at the dam of the Crni Drin, 590 m, 41.4948°N, 20.5052°E, leg. ZF, EH, KJ, HS, 14.x.2014

(NHMW 110430/MN/0087, Mra-519-01 [COI: KU307771, 16S: KU308173]).

North Macedonia, Prov. Struga, Crni Drin Valley, S of Modrić junction, Lukovo N 2.4 km, 610 m [roadside rocks], 41.3705°N, 20.5979°E, leg. ZF, EH, KJ, HS, 15.x.2014 (NHMW 110430/MN/0097, Mdr-529-01 [COI: KU307655]).

North Macedonia, Dibrë district, Gradec (near Grazhdan) gorge of Lumi i Drinit te Zi, 440 m asl. [limestone rocks], 41.6097°N, 20.4431°E, leg. ZF, EM, 14.4.2014 (HNHM 98990, M40-448-01 [COI: KU307567, 16S: KU308038]; Mdr-448-02 [COI: MT251560]).

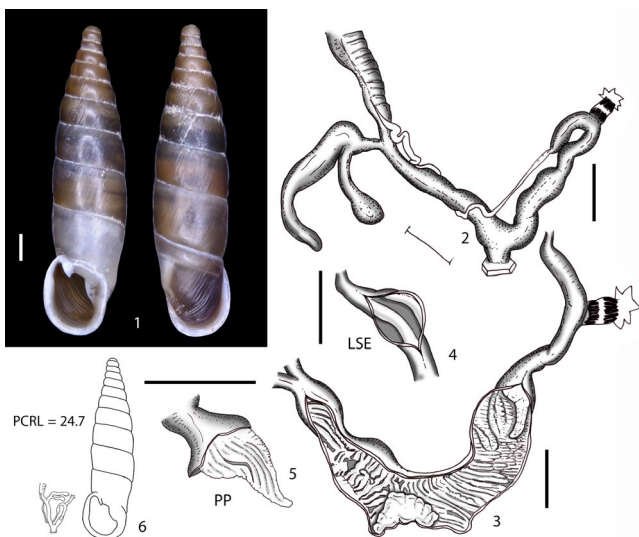
**External genitalia (Figures 46.2, 46.7, 47.2):** The whole genital complex is medium-sized (PCRL = 19.8). The FO is also medium-sized (FO/V = 0.6). The vas deferens is thin along its whole course. The first



**FIGURE 46** *Montenegro drimica* Nordsieck, 1972 stat. nov. DGG3 NHMW 110430/MN/0087. 46.1 shell. 46.2 whole distal genitalia. 46.3 inner distal genitalia. 46.4 longitudinal section of epiphallus. 46.5 cross section of epiphallus. 46.6 shell-genitalia ratio. DGG3 NHMW 110430/MN/0097. 46.7 shell. 46.8 whole distal genitalia. 46.9 inner distal genitalia. 46.10 cross section of epiphallus. 46.11 penial papilla. 46.12 shell-genitalia ratio

duct of the bursa copulatrix complex is quite short ( $DBC/DB = 0.20$ ). The bursa copulatrix is long ( $DB/V = 1.5$ ), with a thin second duct and an elongated and pointed bursa proper. The transition area is more or less distinct. The diverticulum is short ( $D/V = 1.1$ ), uniformly cylindrical, slightly wider but on average shorter than the bursa copulatrix ( $D/BC = 0.7$ ). The apex is pointed. The vagina is medium-sized ( $VRL = 11.5$ ) and cylindrical. The atrium is moderately large. The PC is longer than the vagina ( $PC/V = 1.7$ ). The penis is slightly swollen and wide. The epiphallus is slightly shorter than the penis ( $E/P = 0.9$ ), almost uniformly cylindrical, thinner than the penis and only slightly swollen along its proximal part. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 46.3–46.4, 46.8–46.10, 47.3–47.5):** The atrium has a big, irregular, polylobated fold originating directly at the genital aperture. The distal vagina shows 5–8 big and smooth transversal pleats, all irregularly merging together and forming a medial longitudinal pleat. The proximal vagina has many oblique, elevated transversal pleats, all extending towards the vaginal pilaster and eventually merging in it. The background walls are smooth. The penis has two main large longitudinal pleats extending from the base of the penial papilla as far as the beginning of the atrium. A third, smaller pleat can be present proximally. These large pleats have a comb-like shape with the metamers often separated by a shallow aperture. The medium-sized, conical penial papilla presents a pointed but nonetheless broad apex and a smooth surface. The aperture is lateral, does not reach the papilla's tip and is transversely oriented. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.



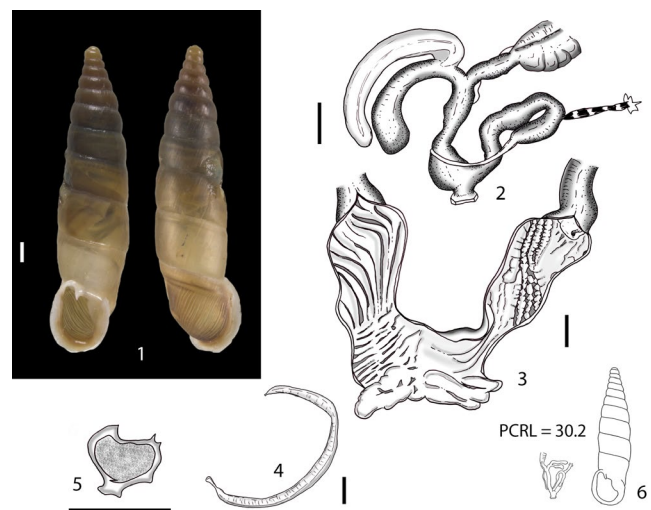
**FIGURE 47** *Montenegrogrina drimica* Nordsieck, 1972 stat. nov. DGG3 HNHM 98990. 47.1 shell. 47.2 whole distal genitalia. 47.3 inner distal genitalia. 47.4 longitudinal section of epiphallus. 47.5 penial papilla. 47.6 shell-genitalia ratio

## DGG4

**Examined material: two dissected specimens.** North Macedonia, Debar District, 1 km SE of Džepište, 414432°N 205374°E, leg. LP, PS, AS, 17.vii.1972 (HNHM 36712, no DNA sample).

**External genitalia (Figure 48.2):** The whole genital complex is long ( $PCRL = 30.2$ ), whereas the FO is medium-sized ( $FO/V = 0.50$ ). The vas deferens is thin along its whole course except for its proximal end, where it is slightly swollen. The first duct of the bursa copulatrix complex is very short ( $DBC/DB = 0.15$ ). The bursa copulatrix is very long ( $DB/V = 1.38$ ), club-like, with a second duct abruptly widening into the broad bursa itself, which is rounded. The diverticulum is long ( $D/V = 1.79$ ), uniformly cylindrical and slightly wider but on average longer than the bursa copulatrix ( $D/BC = 1.30$ ). The apex is blunt. The vagina is medium-sized ( $VRL = 13.4$ ) and gradually widens towards the atrium. The atrium is very large. The PC is much longer than the vagina ( $PC/V = 2.25$ ). The penis is cylindrical, irregular along its whole course, only slightly swollen at the level of the penial papilla. The epiphallus is shorter than the penis ( $E/P = 0.54$ ), slightly swollen along its proximal part. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figure 48.3):** The atrium has a set of irregular fleshy, often overlapping large pleats. The surface is smooth but irregular. The distal vagina has up to 10 smooth transversal pleats, merging into a backbone-like median longitudinal pleat. The proximal vagina has many oblique, elevated transversal pleats splitting proximally and merging into one another. The background walls are smooth. The vaginal pilaster is present. The penis has three pearl-necklace-like, oblique pleats, extending from the proximal penis and fading into smooth pleats before entering into the atrium. These pleats are surrounded on both sides by irregular, fleshy pleats with fringed edges. The medium-sized penial papilla is globose with a blunt apex. The aperture extends laterally, reaching the apical area.



**FIGURE 48** *Montenegrogrina drimica* Nordsieck, 1972 stat. nov. DGG4 NHMW 36712. 48.1 shell. 48.2 whole distal genitalia. 48.3 inner distal genitalia. 48.4 spermatophore. 48.5 cross section of the spermatophore. 48.6 shell-genitalia ratio

The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

**Spermatophore (Figures 48.4–48.5):** The spermatophore is straight and slender with a narrowhead and tail. The head is narrow with a narrow neck and a slightly swollen and rounded apex. The tail is narrow, almost straight and pointed. The lower carina is absent. The upper carina starts approximately behind the head and extends almost as far as 3/4 of the total length towards the tail. The lateral surface has a weak but somewhat dense, rib-like sculpturing. The cross section is oval-roundish with five lateral keels. The largest one has a large base, it is roughly rectangular in section, with two sharp lateral edges. The smallest one is high and sharp. There are three more minor keels that are spiny in cross section. The spermatophore is 7.2 mm long and 0.6 mm wide.

## DGG5

**Examined material: two dissected specimens.** North Macedonia, Crni Drim River left bank, north of Lukovo, 41.3544°N, 20.6107°E, leg. LP, PS, AS, 17.vii.1972 (HNHM 36711/41, Mcr-221-01 [COI: KU307607]; Mcr-221-02 [COI: KU307608]).

**External genitalia (Figure 45.6):** The whole genital complex is large (PCRL = 34.4) with a slender appearance. The FO is also small-sized (FO/V = 0.28) and wide in diameter. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is quite short (DBC/DB = 0.25). The bursa copulatrix is bulky, short (DB/V = 0.75), with a thin second duct and a small bursa proper. There is nodistinct transition area. The diverticulum is short (D/V = 0.94), almost cylindrical, slightly wider and longer than the bursa copulatrix (D/BC = 1.15). The apex is blunt. The vagina is medium-sized (VRL = 17.8) with an irregular shape and swollen at its distal end in connection with the atrium. The atrium is moderately large. The PC is much longer than the vagina (PC/V = 1.94). The penis is almost uniformly cylindrical. The epiphallus is shorter than the penis (E/P = 0.77), almost uniformly cylindrical, as wide as the penis and only slightly swollen proximally. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long and strong.

**Inner genitalia (Figures 45.7–45.8):** The atrium has some irregular, smooth, flat, and pad-like pleats irregularly arranged without any atrial fold. The distal vagina shows many smooth, scattered, irregularly arranged pleats. The pleats are usually fringed and connected to each other by small fleshy bridges. The proximal vagina exhibits many irregularly arranged pleats randomly splitting and merging into one another. The proximal penis has 5–8 irregular, longitudinal metameric fine pleats, usually pearl-necklace-like with few irregular minor folds. Small, irregular transversal pleats run through the distal penis, ending into the atrium. The medium-sized, conical penial papilla has a pointed apex, is pleated and exhibits a more or less irregular surface. The aperture is lateral and does not reach the papilla's tip. The apical, apertureless part

is smaller in diameter. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

## *Montenegrina globocica* n. sp.

urn:lsid:zoobank.org:act:C9EFEB92-71CD-4407-B2E5-A6F-89CE5904E.

Figures 49.1–49.6

*Montenegrina perstriata drimica* – Nordsieck, 1972: 32–33. (partim) – Fehér & Szekeres, 2016: 78 (partim).

**Type locality.** North Macedonia, Struga District, valley of the Crni Drin, 3.7 km S of Lukovo, 700 m, 41.3299°N, 20.6369°E.

**Type material.** Type locality, leg. ZF, EH, KJ, HS, 15.x.2014, holotype in ethanol (NHMW 111676 = Mdr-520-02 [COI: MT251561]), paratypes (NHMW 110430/MN/0088/12a including Mdr-520-01 [COI: KU307646, 16S: KU308091, 12S: KU307948] and Mdr-520-03 to Mdr-520-11); same locality, leg. ZE, ZF, AH, 8.iv.2004 (HNHM 94448/24 + 5fr+3ja incl Mdr-217-01).

**Other material.** Brana Globočica, 3 km S of Lukovo, 41.3355°N, 20.6345°E, leg. ZE, ZF, AH, 8.iv.2004 (HNHM 94447); 2 km S of Lukovo, S of the viaduct, 690 m, 41.3397°N, 20.6273°E, leg. ZF, EH, KJ, HS, 15.x.2014 (NHMW 110430/MN/0089); same locality, N of the viaduct, 690 m, 41.3406°N, 20.6266°E, leg. ZF, EH, KJ, HS, 15.x.2014 (NHMW 110430/MN/0090); same locality, leg. ZE, ZF, AH, 8.iv.2004 (HNHM 94446).

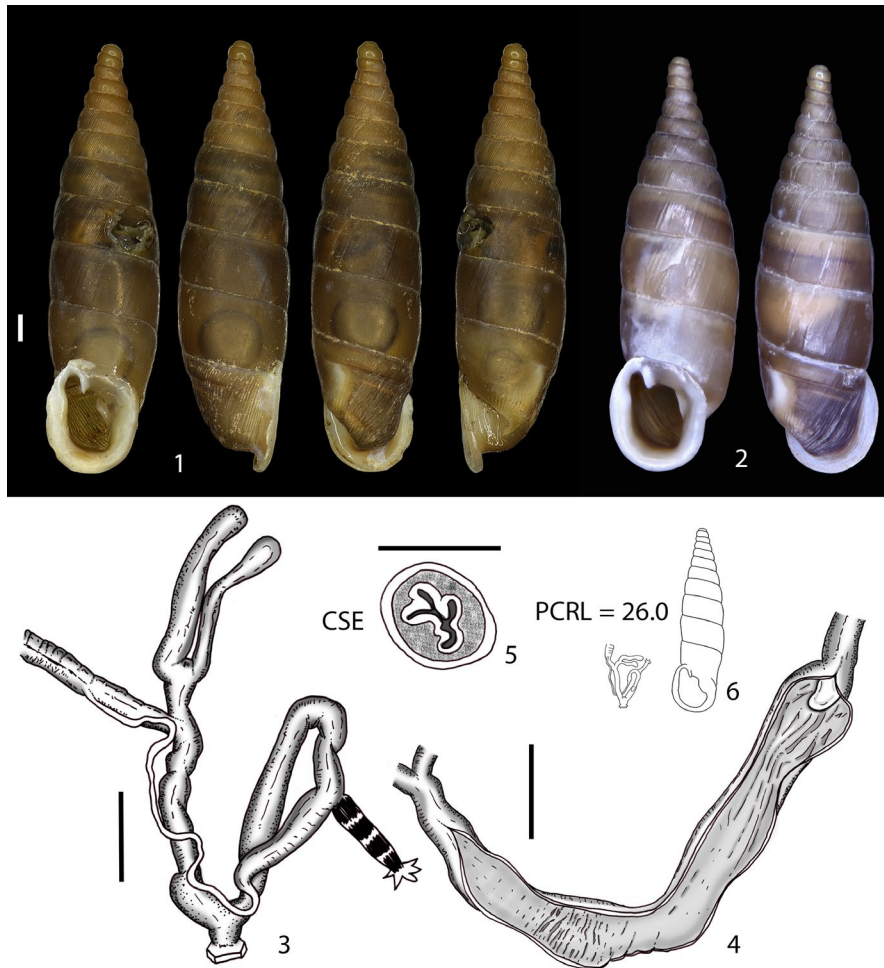
**Distribution:** This taxon inhabits the Black Drin River Valley, along the Globočica Reservoir, ca. 4 km south of Lukovo village.

**Shell differential diagnosis:** it can be distinguished from the nearby occurring *M. drimica* by its mitochondrial sequences. It belongs to clade K in contrast to *M. drimica*, which is positioned in the genetically distant clade H (Mason et al., 2020). Furthermore, it exhibits a long anterior plica superior.

**Diagnosis:** *Montenegrina globocica* n. sp. is a large tumid species with thick white peristome, and its whorls are very finely ribbed and usually bear a long anterior plica superior. The genitalia exhibit a completely smooth vagina atrium and distal penis. Only weak wrinkles are present along the distal vagina. The penial papilla is conical with a rounded apex. *Montenegrina globocica* n. sp. belongs to the DGG1 genital group. Furthermore, it belongs to the mitochondrial clade K in contrast to *M. drimica*, which is positioned in the genetically very distantly related clade H (Mason et al., 2020).

**Dimensions** (in mm): Holotype Hs: 20.4,  $W_s$ : 5.3,  $H_a$ : 5.4,  $W_a$ : 4.4; paratypes Hs: 17.5–22.0,  $W_s$ : 4.8–5.5,  $H_a$ : 4.8–5.6 mm,  $W_a$ : 3.9–4.5 mm.

**Shell description (Figures 49.1–49.2):** The shell is large, horn-brown and tumid, with 10½–12 whorls. The upper whorls are finely striated and somewhat convex, the lower ones are almost smooth and flattened. The neck is moderately inflexed, distinctly



**FIGURE 49** *Montenegroglobocica* n. sp. 49.1 Holotypeshell, NHMW 111676 (=Mdr-520-02) specimen Mdr-520-02. 49.2 shell paratype NHMW 110430/MN/0088, specimen Mdr-520-01. 49.3 whole distal genitalia, 49.4 inner distal genitalia. 49.5 cross section of epiphallus. 49.6 shell-genitalia ratio

striate-costate. The basal and peripheral crests are distinct. The aperture is ovoid, margin attached, strongly deflexed, swollen and whitish. The lamella superior is long and overlaps with the spiralis. In front view, the lamella columellaris is barely emerged, and the lamella subcolumellaris is visible. The lunella is lateral and separate from the basalis. The subclaustralis is short and the sulcalis is present. The anterior plica superior is usually long but separate from the lunella complex. The clausilium plate is not visible through the aperture.

**External genitalia (Figure 46.3):** The whole genital complex is medium-sized (PCRL = 26.0) with a slender appearance. The FO is also medium-sized (FO/V = 0.44) and wide in diameter. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is quite short (DBC/DB = 0.20). The bursa copulatrix is short (DB/V = 0.74), with a thin second duct and a small actual bursa. There is no distinct transition area. The diverticulum is short (D/V = 0.85), uniformly cylindrical, slightly wider and longer than the bursa copulatrix (D/BC = 1.15). The apex is blunt. The vagina is medium-sized (VRL = 13.0), irregularly shaped and swollen at its distal end in connection with the atrium. The atrium is moderately large.

The PC is much longer than the vagina (PC/V = 2.0). The penis is almost uniformly cylindrical. The epiphallus is longer than the penis (E/P = 1.45), almost uniformly cylindrical, as wide as the penis and only slightly swollen proximally. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long and strong.

**Inner genitalia (Figures 49.4–49.5):** The atrium is smooth with a few weak, flat wrinkles. A big atrial fold is present. The distal vagina is smooth with only traces of a few irregular, smooth and flat transversal pleats. The proximal vagina is completely smooth and lacks the vaginal pilaster. The penis is mainly smooth but has traces of flat, minimally elevated longitudinal pleats, especially along the proximal part. The small penial papilla is globose and rounded. The aperture extends laterally and reaches the apical area. The surface is smooth. The epiphallus has up to five simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background walls are smooth.

**Etymology:** The new taxon is named after the Globočica Reservoir in the Drim Valley.

**Montenegrina perstriata mavrovoensis** Nordsieck, 2009

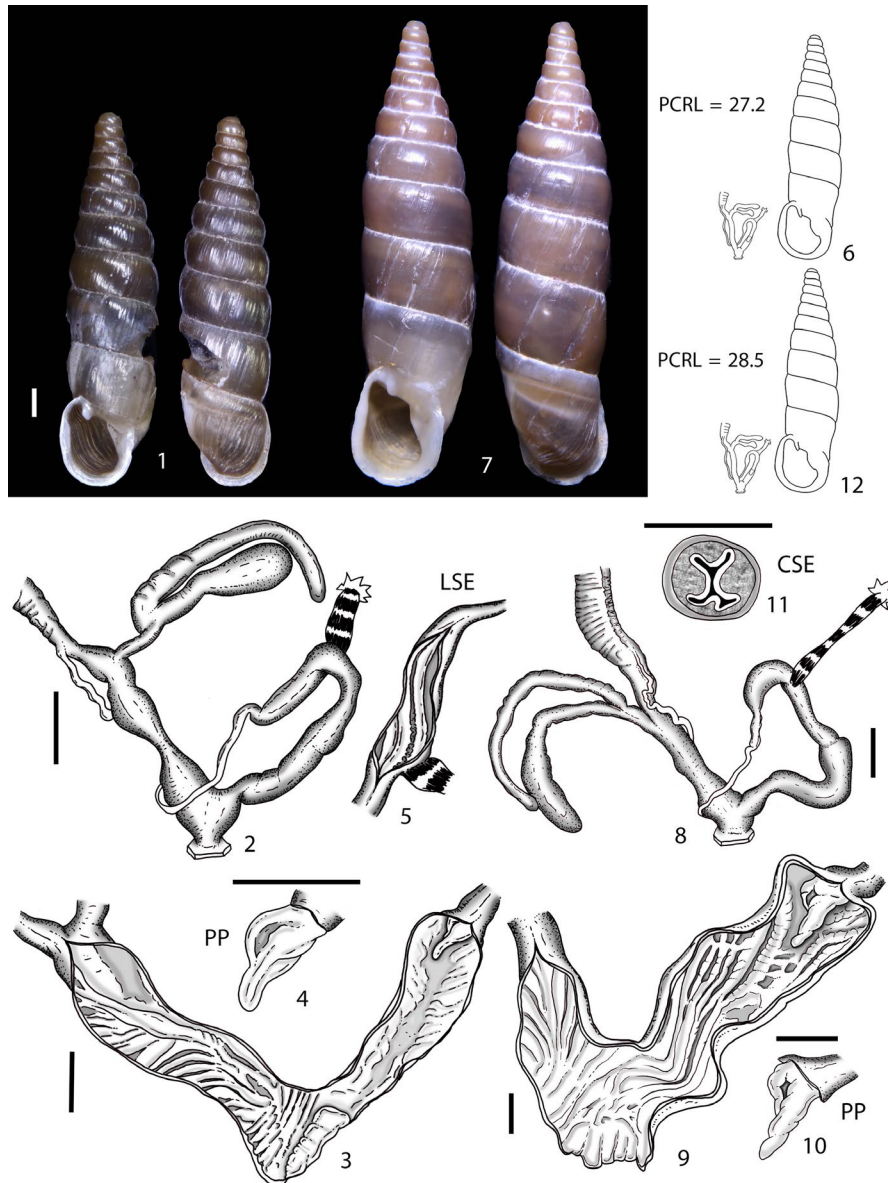
Figures 50.1–50.6

*Montenegrina perstriata mavrovoensis* Nordsieck, 2009: 78, plate 3, fig. 11. – Fehér & Szekeres, 2016: 79, fig. 27F, distribution map fig. 25A.

**Examined material: two dissected specimens.** North Macedonia, Bistra Mts, Mavrovo, 6 km to Galicnik, 1,720 m, 41.6459°N, 20.7069°E, leg. EH, 17.viii.2016 (NHMW 110430/MN/0148, Mmv-658-01 [COI: MT251666, 16S: MT160795, 12S: MT249807]; Mmv-658-03 [COI: MT251668, 16S: MT160797, 12S: MT249809]).

**External genitalia (Figure 50.2):** The whole genital complex is medium-sized (PCRL = 27.2), whereas the FO is short (FO/V = 0.28). The

vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.38). The bursa copulatrix is medium-sized (DB/V = 0.84), club-like, with a wide second duct and a rounded bursa itself. There is a more or less distinct transitional area. The diverticulum is generally long (D/V = 1.6), uniformly cylindrical, thinner than the bursa copulatrix and generally much longer (D/BC = 1.9). The apex is pointed. The vagina is medium-sized (VRL = 14.8), swollen at its proximal and distal ends with a narrow midsection. The atrium is very large. The PC is longer than the vagina (PC/V = 1.84). The penis is cylindrical, swollen and irregular along its whole course, also swollen at the level of the penial papilla. The epiphallus is longer than the penis (E/P = 1.42), on average uniformly cylindrical and slightly thinner than the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.



**FIGURE 50** 50.1–50.6 *Montenegrina perstriata mavrovoensis* Nordsieck, 2009 NHMW 110430/MN/0148. 50.1 shell, 50.2 whole distal genitalia, 50.3 inner distal genitalia, 50.4 penial papilla, 50.5 longitudinal section of epiphallus, 50.6 shell-genitalia ratio. 50.7–50.12 *Montenegrina radikae radikae* Nordsieck, 1972 stat. nov. HNHM 31107. 50.7 shell, 50.8 whole distal genitalia, 50.9 inner distal genitalia, 50.10 penial papilla, 50.11 cross section of epiphallus, 50.12 shell-genitalia ratio

**Inner genitalia (Figures 50.3–50.5):** The atrium has an irregular, polylobated fold originating directly at the genital aperture. The distal vagina shows a series of fine, irregular, obliquetransversal pleats, all of them randomly merging into a backbone pattern. The proximal vagina has many elevated, oblique, transversal pleats. The background walls are smooth. The vaginal pilaster is present. The proximal penis presents two main, large, smooth and polylobated longitudinal pleats. The pleats are separated by a smooth section of the wall surface. These pleats are pad-like, flat and extend as far as the atrium. The medium-sized, conical penial papilla has a pointed apex and finely pleated surface. The aperture is lateral. The apical, apertureless part is smaller in diameter. The epiphallus has three fringed pleats with jagged edges, originating proximally from the end of the vas deferens and fading before the penial papilla. The background is transversely irregularly fringed.

***Montenegrina radikae radikae* Nordsieck, 1972  
stat. nov.**

Figures 50.7–50.12

*Montenegrina perstriata radikae* Nordsieck, 1972: 32, plate 4, fig. 37 – Zilch, 1981: 130, plate 14, fig. 32 – Nordsieck, 2009: 74. – Fehér & Szekeres, 2016: 82, fig. 27J, distribution map fig. 25B.

**Examined material: two dissected specimens.** North Macedonia, Mavrovo District, Radika Valley, 6 km from Trnica towards Debar, 41°69'2"N 20°64'77"E [type locality], leg. LP, PS, AS, 12.vii.1972 (HNHM 31107, no DNA data available).

**External genitalia (Figure 50.8):** The whole genital complex is medium-sized (PCRL = 28.5) with a slender appearance. The FO is long (FO/V = 0.61). The vas deferens is thin along its whole course. The first duct of the complex of the bursa copulatrix is very short (DBC/DB = 0.1). The bursa copulatrix is extremely long (DB/V = 2.39), usually cylindrical, or slightly club-like, very thin and with the actual bursa itself very elongated. There is no clearly visible transitional area. The diverticulum is also generally long (D/V = 1.96), uniformly cylindrical, thinner but generally shorter (D/BC = 0.82) than the bursa copulatrix. The apex is blunt. The vagina is medium-sized (VRL = 10.4), uniformly cylindrical, or slightly swollen distally. The atrium is large. The PC is much longer than the vagina (PC/V = 2.74). The penis is cylindrical and slightly swollen along its whole course. The transitional section with the epiphallus is clearly marked by an abrupt constriction in the diameter. The epiphallus is slightly longer than the penis (E/P = 1.1), moderately swollen along its proximal part and wider than the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long but strong.

**Inner genitalia (Figures 50.9–50.11):** The atrium shows an irregular set of many fleshy, overlapping, flat pleats. The surface of the pleats is smooth. The distal vagina has 5–7 smooth and flat transversal pleats. The proximal vagina has up to 10 smooth, oblique or longitudinal pleats. The background walls are smooth. The vaginal pilaster is present. The proximal penis has 7–11 irregular

“pearl-necklace”-like longitudinal pleats, more irregular towards the proximal part. Along the distal penis they turn into a set of smooth and flat longitudinal pleats gradually fading towards the atrium. The penial papilla is elongated, slim, with a narrow and pointed apex. The surface is irregular. The aperture is lateral and transversely opens near the base. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

***Montenegrina drimica occidentalis* Nordsieck, 1977  
comb. nov.**

*Montenegrina dofleini occidentalis* Nordsieck, 1977: 85, plate 4, fig. 15 – Zilch, 1981: 127, plate 15, fig. 38 – Nordsieck, 2009: 74. – Fehér & Szekeres, 2016: 80, fig. 27G, distribution map fig. 25A.

No alcohol-preserved specimens were available for anatomical investigations.

***Montenegrina ochridensis ochridensis* (Wagner, 1925)  
stat. nov.**

Figures 51.1–51.6

*Delima (Albanodelima) perstriata ochridensis* – Wagner, 1924: 120. (*nomen nudum*).

*Delima (Delima) perstriata ochridensis* Wagner, 1925: 62, plate 14, figs 98a–c.

*Delima (Montenegrina) perstriata ochridensis* – Loosjes, 1966: 122, fig. 1 (genital anatomy).

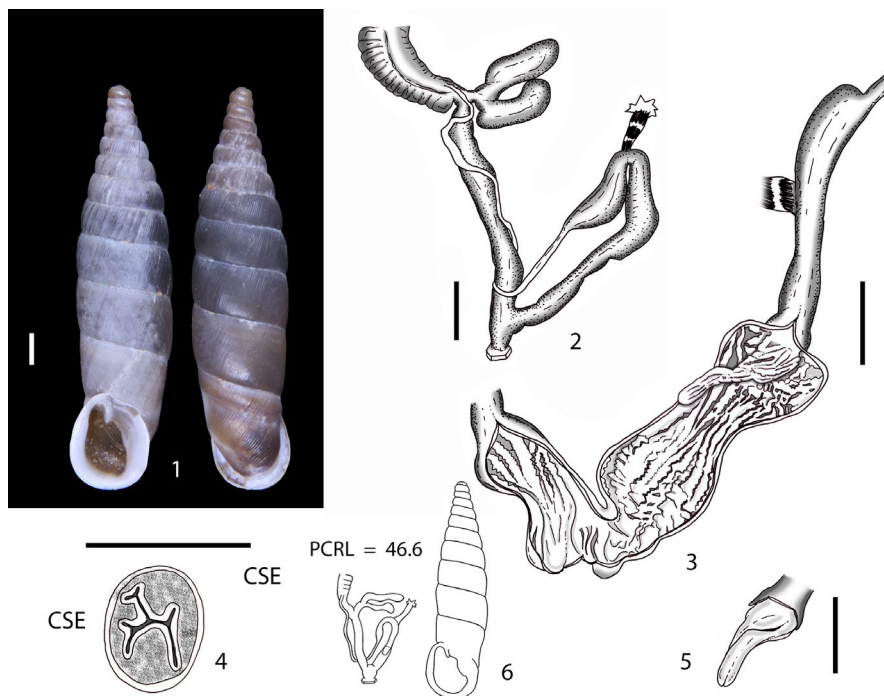
*Montenegrina perstriata ochridensis* – Nordsieck, 1972: 32–33, plate 4, fig. 39 – Zilch, 1981: 130. – Erőss et al., 1999: 448. – Nordsieck, 2009: 74.

*Montenegrina ochridensis* – Nordsieck, 1988: 201.

*Montenegrina perstriata ochridensis* – Fehér & Szekeres, 2016: 80, fig. 27H, distribution map fig. 25B.

**Examined material: two dissected specimens.** North Macedonia, Ohrid, at shore of Lake Ohrid approx 25 km S of Peštani, 40.99°N, 20.8007°E, leg. LP, PS, AS, 16.vii.1972 HNHM 94434, Moh-213-02 [COI: KU307724, 16S: KU308148, 12S: KU307969].

**External genitalia (Figure 51.2):** The whole genital complex is very long (PCRL = 46.6). The FO is very short (FO/V = 0.13). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is extremely short (DBC/DB = 0.06). The bursa copulatrix is short (DB/V = 0.38), bulky, uniformly cylindrical with a blunt apex. There is no visible transition area. The diverticulum is also generally very short (D/V = 0.33), uniformly cylindrical, as wide as the bursa copulatrix and generally shorter (D/BC = 0.88). The apex is blunt. The vagina is very long (VRL = 30.8) and almost uniformly cylindrical. The atrium is moderately large and long. The PC is longer than the vagina (PC/V = 1.51). The penis is cylindrical,



**FIGURE 51** *Montenegrina ochridensis ochridensis* (Wagner, 1925) stat. nov. HNHM 94434. 51.1 shell. 51.2 whole distal genitalia. 51.3 inner distal genitalia. 51.4 cross section of epiphallus. 51.5 penial papilla. 51.6 shell-genitalia ratio

thin, slightly swollen at the level of the penial papilla. The epiphallus is shorter than the penis ( $E/P = 0.70$ ), swollen proximally and wider than the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 51.3–51.5):** The atrium has few, irregular, flat and fleshy large pleats. The vagina has 6–10 fringed longitudinal pleats. The vaginal pilaster is absent and the background is smooth. The whole penis shows 7–11 irregular, fringed longitudinal pleats, gradually becoming more irregular proximally. The papilla is elongated, slim and slender, with a narrow but blunt apex. The surface is irregular, with many fine, fringed longitudinal pleats. The aperture is lateral and opens near the papilla's base. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina drimica plenostoma* Fehér & Szekeres, 2006 comb. nov.

Figures 52.1–52.8

*Montenegrina dofleini plenostoma* Fehér & Szekeres, 2006 in Eröss et al., 2006: 188, fig. 7. – Nordsieck, 2009: 74.

*Montenegrina perstriata plenostoma* – Fehér & Szekeres, 2016: 81, fig. 271, distribution map fig. 25A.

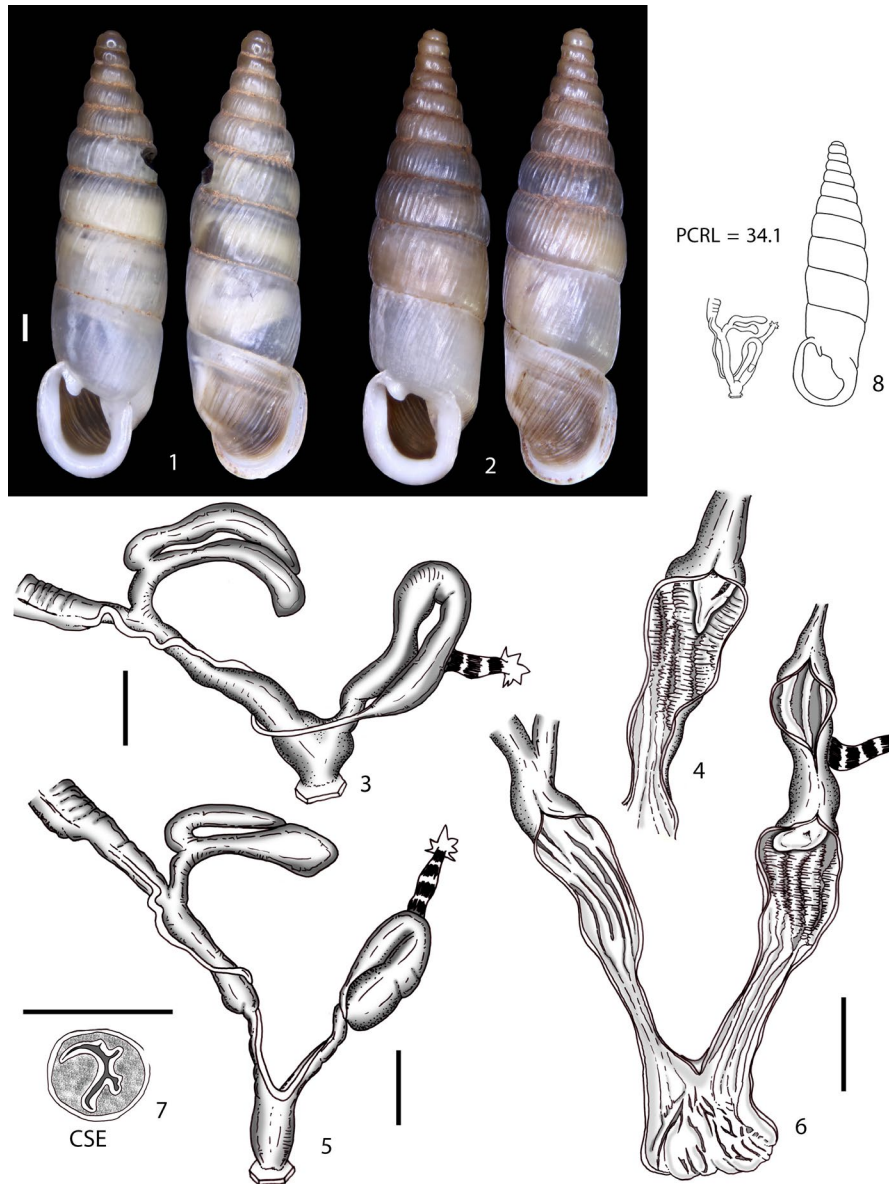
**Examined material:** four dissected specimens. Albania, Pogradec district, 2 km E of Qafa e Thanës, along the Elbasan–Pogradec main road, 830 m asl. [rocky grassland], 41.0632°N,

20.6253°E [type locality], leg. ZF, TN, EM, 12.iv.2014 (HNHM 98945, Mpl-430-01 [COI: KU307748, 16S: KU308165]; Mpl-430-03 [COI: MT251701]).

**External genitalia (Figures 52.3 and 52.5):** The whole genital complex is long ( $PCRL = 30.2$ ). The FO is short ( $FO/V = 0.4$ ). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized ( $DBC/DB = 0.33$ ). The bursa copulatrix is short ( $DB/V = 0.6$ ), usually cylindrical, or slightly club-like. The bursa itself can be swollen or narrow with a blunt apex. There is no clearly visible transitional area. The diverticulum is also generally short ( $D/V = 0.7$ ), uniformly cylindrical, thinner than the bursa copulatrix and generally longer ( $D/BC = 1.3$ ). The apex is pointed. The vagina is medium-sized ( $VRL = 16.9$ ), almost uniformly cylindrical or slightly swollen towards its distal end. The atrium is large. The PC is longer than the vagina ( $PC/V = 1.9$ ). The penis is cylindrical and slightly swollen along its whole course. The epiphallus is longer than the penis ( $E/P = 1.2$ ), swollen proximally and wider than the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 52.4–52.7):** The atrium has an irregular set of smooth pleats, branching and forming a net-like pattern. The smooth background is visible. The distal vagina is smooth but with traces of flat longitudinal pleats. The proximal vagina shows many irregularly arranged longitudinal pleats, randomly splitting and merging into one another, especially proximally. The proximal penis has four main, elevated, strongly fringed longitudinal pleats. The pleats are well spaced and a smooth background is visible. Before entering into the distal penis, they abruptly become a set of four smooth and well-spaced pleats that stop before entering the atrium. The medium-sized,





**FIGURE 52** *Montenegrina drimica plenostoma* Fehér & Szekeres, 2006 comb. nov. HHNM 98945. 52.1–52.2 shells. 52.3–52.5 whole distal genitalia. 52.4 penial papilla and inner proximal penis, 52.6 inner distal genitalia, 52.7 cross section of epiphallus, 52.8 shell-genitalia ratio

conical penial papilla has a pointed but nonetheless broad apex and a smooth surface. The aperture is lateral and does not reach the papilla's tip. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina perstriata steffeki* Eröss and Szekeres, 2006

*Montenegrina perstriata steffeki* Eröss and Szekeres, 2006 in Eröss et al., 2006: 203, fig. 25.

*Montenegrina dofleini steffeki* – Nordsieck, 2009: 74.

*Montenegrina perstriata steffeki* – Fehér & Szekeres, 2016: 83, fig. 27K.

No alcohol-preserved specimens were available for anatomical investigations.

### *Montenegrina perstriata subcristatula* Nordsieck, 1977 stat. nov.

Figures 53.1–53.5

*Montenegrina perstriata perstriata* – Nordsieck, 1972: 31, plate 4, fig. 36.

*Montenegrina perstriata subcristatula* Nordsieck, 1977: 84, plate 4, fig. 14. – Zilch, 1981: 130, plate 14, fig. 33 – Nordsieck, 2009: 74, plate 3, fig. 13.

*Montenegrina perstriata subcristatula* – Fehér & Szekeres, 2016: 83, fig. 27L, distribution map fig. 25A.

**Examined material: two dissected specimens.** North Macedonia, Mavrovo District, Radika Valley, along the Debar to Gostivar road at the Ničpur junction, 930 m, 41.7203°N, 20.6682°E, leg. ZF, EH, KJ, HS, 14.x.2014 (NHMW 110430/MN/0107, Msl-514-01 [COI: KU307800, 16S: KU308192, 12S: KU307984]).

**External genitalia (Figure 53.2):** The whole genital complex is medium-sized (PCRL = 25.7) with a slender appearance. The FO is short (FO/V = 0.38). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is very long (DBC/DB = 0.64). The bursa copulatrix is medium-sized (DB/V = 0.85), usually club-like, with a thin second duct and the bursa itself apparently elongated. There is no clearly visible transition area. The diverticulum is also on average long (D/V = 1.62), uniformly cylindrical, thinner, and on average longer (D/BC = 1.91) than the bursa copulatrix. The apex is pointed. The vagina is medium-sized (VRL = 14.5) and uniformly cylindrical. The atrium is large and swollen at the vaginal side. The PC is longer than the vagina (PC/V = 1.77). The penis is cylindrical and slightly swollen distally. The transitional section with the epiphallus is clearly marked by a sudden, ring-shaped constriction in diameter. A cecum is visible at the level of the penial papilla. The epiphallus is slightly longer than the penis (E/P = 1.19), moderately swollen proximally and thinner than the penis. It merges into the vas deferens without a distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 53.3–53.4):** The atrium is smooth with very weak traces of flat pleats. The vagina is completely smooth and, as the atrium, has weak traces of flat pleats. The whole penis is smooth with very light and poorly visible transversal lines. The medium-sized, conical penial papilla is pointed with a smooth surface. The aperture is lateral, not reaching the papilla's tip. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina tenebrosa tenebrosa* Nordsieck, 2009 stat. nov.**

Figures 53.6–53.11

*Montenegrina perstriata* – Dhora & Welter-Schultes, 1999: 16.

*Montenegrina perstriata tenebrosa* Nordsieck, 2009: 78–79, plate 3, fig. 14 – Fehér & Szekeres, 2016: 84, fig. 27M, distribution map fig. 25B.

**Examined material: two dissected specimens.** Albania, Bulqizë District, Maja a Zyllit (= Maja e Shullanit), 6 km from the Librazhd to Peshkopi road towards Sebisht, 1,360 m, 41.3611°N, 20.3967°E, leg. ZF, 13.iv.2014 (HNHM 98975, Mte-440-01 [COI: KU307849, 16S: KU308210]; Mte-440-02 [COI: MT251831]).

**External genitalia (Figure 53.7):** The whole genital complex is long (PCRL = 35.7) with a slender appearance. The FO is medium-sized (FO/V = 0.46) and wide in diameter. The vas deferens is thin along its distal course but swollen proximally. The first duct

of the bursa copulatrix complex is medium-sized (DBC/DB = 0.35). The bursa copulatrix is short (DB/V = 0.63), cylindrical, or slightly club-like. There is no clearly visible transition area. The diverticulum is also on average short (D/V = 0.76), uniformly cylindrical, slightly wider on average longer (D/BC = 1.19) than the bursa copulatrix and. The apex is slightly pointed. The vagina is medium-sized (VRL = 19.8), uniformly cylindrical and wide in diameter. The atrium is large, swollen at the penial side. The PC is longer than the vagina (PC/V = 1.80). The penis is irregular and swollen along its distal course and at the level of the penial papilla. The epiphallus is slightly longer than the penis (E/P = 1.31), moderately swollen proximally and thin distally. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and thin.

**Inner genitalia (Figures 53.8–53.10):** The atrium shows a set of flat and fleshy, irregularly arranged pleats. The whole distal vagina has many smooth, fine pleats that are irregularly arranged. The background is smooth. The whole proximal vagina shows many fine, fringed pleats that are irregularly arranged and form an irregular net-like pattern. The vaginal pilaster is present and connected with the pleats with many small fleshy bridges. The proximal penis has a variable number of oblique rough, irregular longitudinal pleats that distally merge into one another. The distal penis exhibits a variable number of irregular, smooth transversal pleats. The medium-sized, conical penial papilla is pointed with a smooth surface. The aperture is lateral. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina tenebrosa szekeresi* n. ssp.**

urn:lsid:zoobank.org:act:9FF41A74-153B-40A4-B36F-F6AC-37CE92F6.

Figures 54.1–54.9

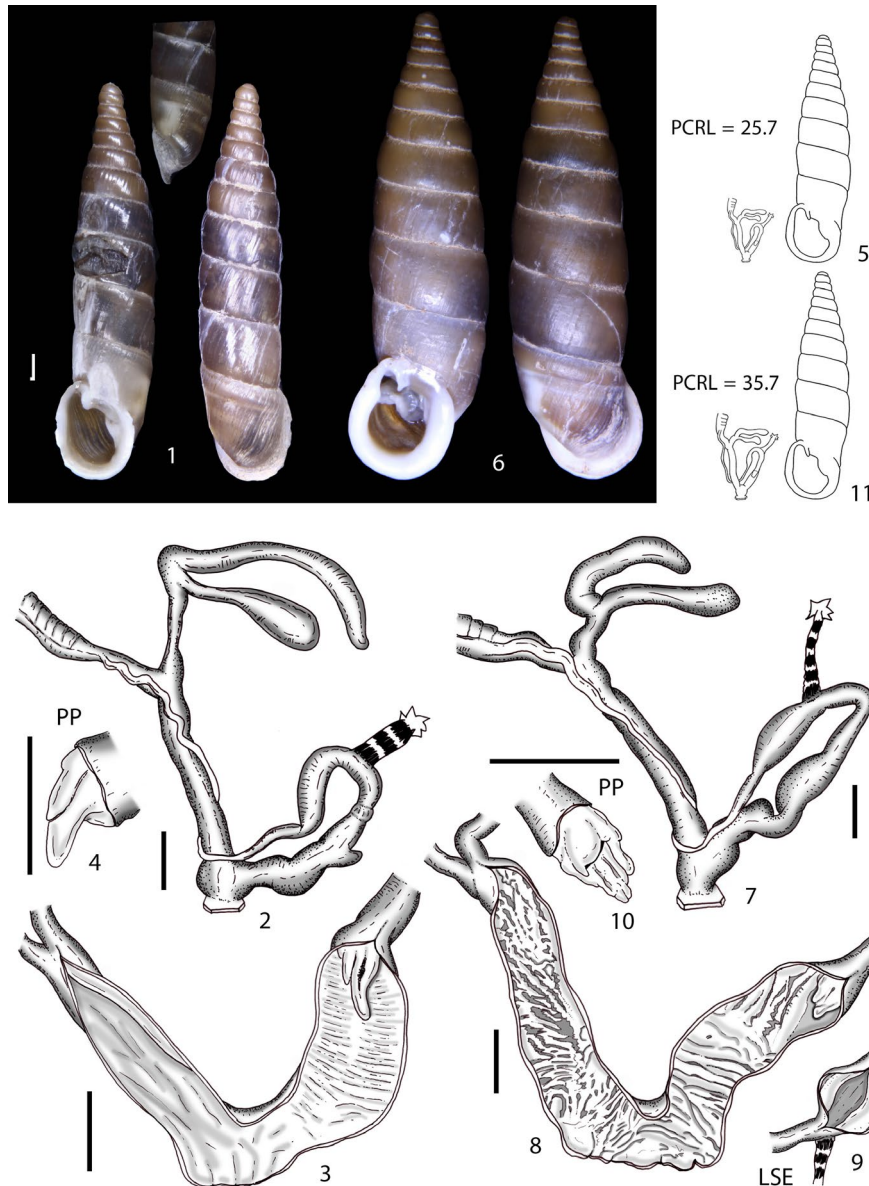
*Montenegrina perstriata ochridensis* – Fehér & Szekeres, 2016: 80–81 (partim).

**Type locality:** Albania, Bulqizë District, Valikardhë, S slope of the Maja e Temlishit, 770 m, 41.5140°N, 20.3160°E.

**Type material:** type locality, leg. ZF, TN, EM, 15.iv.2014 holotype in ethanol (HNHM 104158), paratypes (HNHM 99007/21 + 19a+17a juv including Moh-453-01 [COI: KU307727, 16S: KU308151]; Moh-453-02 [COI: MT251679]; Moh-453-03 [COI: MT251680]).

**Distribution:** *Montenegrina tenebrosa szekeresi* n. ssp. is known only from the type locality.

**Shell differential diagnosis:** The shell is similar to *M. ochridensis ochridensis* stat. nov. but differs by a weaker surface sculpture and the basal, which is separate from the lunella complex. The genital anatomy is remarkably different from its nominal subspecies *M. tenebrosa tenebrosa* stat. nov. but resembles *M. ochridensis ochridensis* stat. nov.



**FIGURE 53** 53.1–53.5 *Montenegrina subcristatula subcristatula* Nordsieck, 1977 stat. nov. NHMW 110430/MN/0107. 53.1 shell, 53.2 whole distal genitalia, 53.3 inner distal genitalia, 53.4 penial papilla, 53.5 shell-genitalia ratio. 53.6–53.11 *Montenegrina tenebrosa tenebrosa* Nordsieck, 2009 stat. nov. HHNM 98975. 53.6 shell, 53.7 whole distal genitalia, 53.8 inner distal genitalia, 53.9 longitudinal section of epiphallus, 53.10 penial papilla, 53.11 shell-genitalia ratio

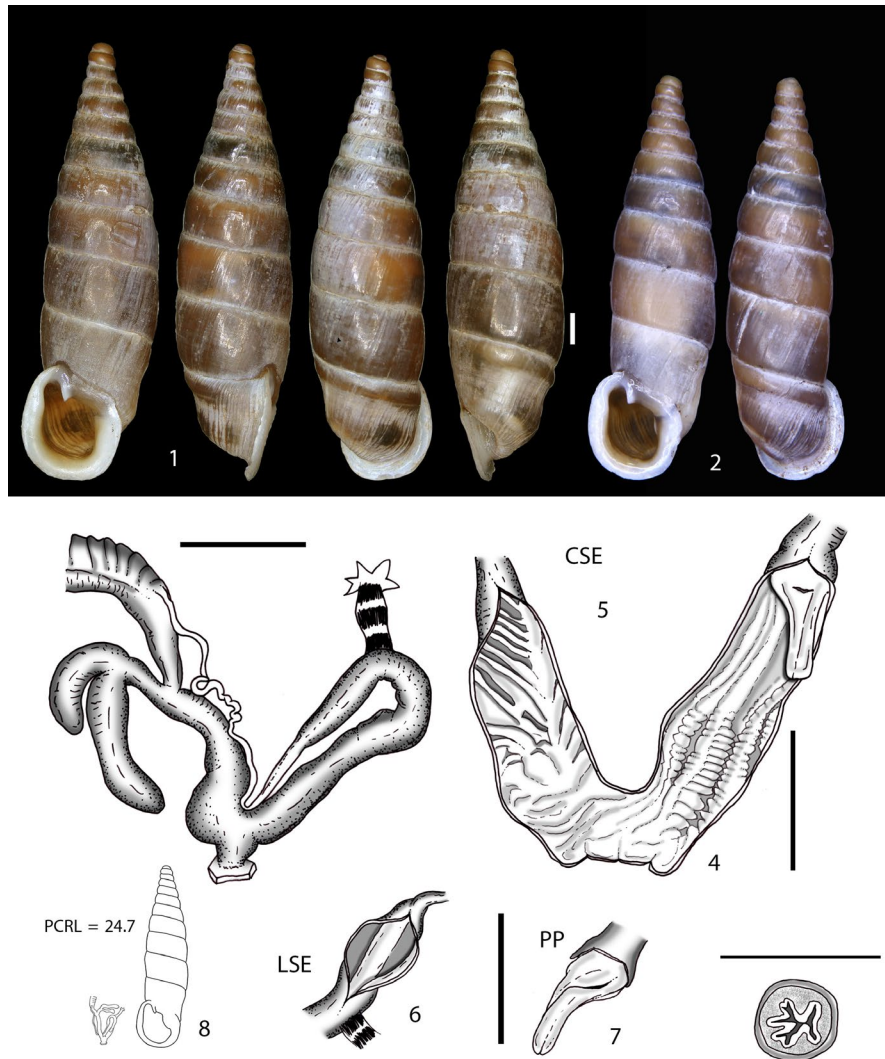
**Diagnosis:** The diverticulum of the bursa copulatrix complex is generally very short, whereas the PC is long. The pleats extending longitudinally throughout the inner penis are smooth and regular along the distal part, becoming metameric and fleshy cords distally. The penial papilla is long, conical and with a blunt apex.

**Dimensions** (in mm): Holotype Hs: 18.5,  $W_s$ : 5.4,  $H_a$ : 4.8,  $W_a$ : 4.3; paratypes Hs: 14.9–20.2,  $W_s$ : 4.2–5.6,  $H_a$ : 4.2–4.7;  $W_a$ : 3.5–4.1.

**Shell description (Figures 54.1–54.2):** The shell is light corneous, consists of 10–11 whorls. The lower whorls are smooth, the upper ones densely striate, the neck moderately inflexed, densely costulate. The peristome is angular, swollen and reflexed with the margin attached. The lamella superior is short and does not overlap with lamella spiralis. In front view, the lamella columellaris is barely

emerged, the lamella subcolumellaris is not visible. The lunella lateral is separate from the basalis. The subclaustralis and sulcalis are present. The anterior plica superior is usually long but typically separate from the lunella complex.

**External genitalia (Figure 54.3):** The whole genital complex is medium-sized (PCRL = 24.7), as is the FO (FO/V = 0.60). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.24). The bursa copulatrix is long (DB/V = 1.05), uniformly cylindrical with a pointed apex. There is no transitional area. The diverticulum is generally very short (D/V = 0.40), uniformly cylindrical, as wide as the bursa copulatrix and shorter (D/BC = 0.76). The apex is pointed. The vagina is medium-sized (VRL = 11.5) and swollen at its distal end. The atrium is very large and



**FIGURE 54** *Montenegrogrina tenebrosa* szekeres in. ssp. 54.1 shell of the Holotype HHNM 99007. 54.2 shell. 54.3 whole distal genitalia. 54.4 inner distal genitalia. 54.5 cross section of epiphallus. 54.6 penial papilla. 54.7 longitudinal section of epiphallus. 54.9 shell-genitalia ratio

moderately long. The PC is much longer than the vagina ( $PC/V = 2.15$ ). The penis is cylindrical, wide, slightly swollen at the level of the penial papilla. The epiphallus is uniformly cylindrical, much longer ( $E/P = 3.30$ ) and slightly thinner than the penis. It merges into the vas deferens without a distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 54.3–54.7):** The atrium has a few, irregular, flat and fleshy large pleats. Both the atrium and the distal vagina show smooth, scattered, irregularly arranged pleats. The proximal vagina has many elevated, obliquetransversal pleats. The background walls are smooth. The vaginal pilaster is present. The proximal penis bears 4–6 flat and smooth pleats that run longitudinally and merge into a set of three or four big, and fleshy metameric cords that reach the atrium. The medium-sized, conical penial papilla has a pointed apex and finely pleated surface. The aperture is lateral, transversal and does not reach the papilla's tip. The apical, apertureless part is smaller in diameter. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

**Etymology:** The new taxon is named after our colleague and friend Miklós Szekeres, who made a major contribution to our knowledge of the Balkan Clausiliidae.

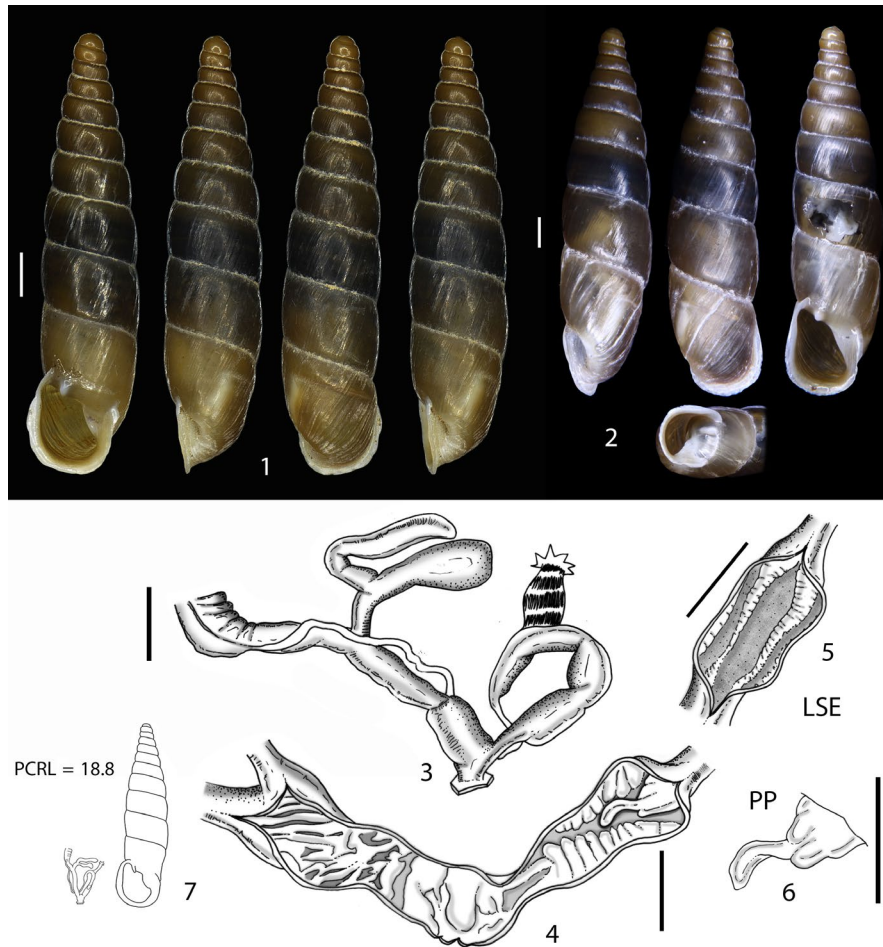
#### *Montenegrogrina radikae* paparistoe n. ssp.

urn:lsid:zoobank.org:act:E0FC7CAA-0A0B-4477-BD57-1B6E810663D1.

Figures 55.1–55.7

**Type locality.** Albania, Burreli District, Shkalla e Drenit, (between Gurra e vogël and Mner i Sipërm), 41.5168°N 19.9300°E.

**Type material.** Type locality, leg. A. Papparisto, 19.vii.2017, holotype in ethanol (NHMW 111675), paratypes (NHMW 110430/MN/0963 /6a incl. M55-675-01 [COI: MT251501] + Univ. Tirana/12a + 7ja); same locality, leg. A. Papparisto, 23.vii.2016, paratypes (NHMW 110430/MN/0261/1a (= Mto-661-01 [COI: MT251500])); Univ. Tirana/3a + 3ja).



**FIGURE 55** *Montenegrina radikae paparistoe* n. ssp. 55.1 shell of the Holotype NHMW 110430/MN/0261\_2 NHMW 110430/MN/0261\_3. 55.2 shell, 55.3 whole distal genitalia and inner distal genitalia, 55.4 inner distal genitalia, 55.5 longitudinal section of epiphallus, 55.6 penial papilla, 55.7 shell-genitalia ratio

**Distribution:** *Montenegrina radikae paparistoe* n. ssp. is known only from the type locality in Central Albania.

**Shell differential diagnosis:** This subspecies differs from the nominal subspecies by a smaller, thinner and more slender shell.

**Diagnosis:** The shell is small, almost fragile, very finely ribbed with a lateral lunella. The peristome is weak. The external genitalia exhibit a long FO and a broader section of distal vagina. The bursa copulatrix is large and slightly club-like. The inner vagina presents an irregular pattern of smooth pleats, whereas the inner portion of the penis shows two main, big metameric cords. The penial papilla has a very long tip with two basal lobes.

**Dimensions** (in mm): Holotype Hs: 18.6 W<sub>s</sub>: 4.6 H<sub>a</sub>: 4.4, W<sub>a</sub>: 3.9; H<sub>s</sub>: 16.0–18.8, W<sub>s</sub>: 4.4–4.8, H<sub>a</sub>: 4.2–4.8, W<sub>a</sub>: 3.1–4.0.

**Shell description (Figures 55.1–55.2):** The light brownish-corneous shell consists of  $9\frac{1}{2}$ – $10\frac{1}{2}$  bulging whorls. Except for the finely costate neck, the entire shell surface is smooth and glossy. The neck is only weakly inflected. The basal crest is weak, the peripheral one is not recognizable. The subquadrangular peristome has a simple, weakly reflexed margin, which is missing at the upper columellar side of the aperture. The weak lamella superior is wide and separated from the spiralis. The moderately emerged lamella inferior descends

steeply, ending well behind the peristome margin. The medium-bent lamella subcolumellaris is not visible through the aperture. The plica principalis spans one third of a whorl from the dorsolateral–lateral side. The vertical lunella, originating under, and separate from the inner end of the principalis, forms a nearly straight fusion with the short basalis. The subclaustralis is short, lump-like, the sulcalis is very weak. The anterior plica superior is absent. The clausilium plate is not visible through the aperture.

**External genitalia (Figure 55.3):** The whole genital complex is short (PCRL = 18.8) with a bulky appearance. The FO is medium-sized (FO/V = 0.50). The vas deferens is thin distally but slightly swollen proximally. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.28). The bursa copulatrix is medium-sized (DB/V = 0.82), large and slightly club-like. There is a more or less clearly visible transition area. The diverticulum is on average longer (D/V = 1.63), uniformly cylindrical, thinner, and on average shorter (D/BC = 1.22) than the bursa copulatrix. The apex is slightly pointed. The vagina is medium-sized (VRL = 15.4), uniformly cylindrical and wide in diameter. The atrium is moderately large. The PC is longer than the vagina (PC/V = 1.64). The penis is slimmer along its distal section close to the atrium. It abruptly widens along its central and proximal parts. The epiphallus is twice as

long as the penis ( $E/P = 2.0$ ) and almost uniformly cylindrical. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 55.4–55.6):** The atrium shows a set of irregular, large, smooth pleats that continue upward along the distal vagina. The proximal vagina bears many more oblique, irregular pleats, including the vaginal pilaster. The penis bears two main, big metameric cords originating from the proximal part at the level of the penial papilla. Only the lower cord usually reaches the atrium. The penial papilla is long with a pointed apex. The aperture is longitudinally oriented. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

**Etymology:** The new taxon is dedicated to Anila Paparisto (University of Tirana), who first found it.

### *Montenegrina skipetarica* (Soós, 1924) sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

The *M. skipetarica* includes 15 subspecific taxa. In the mt phylogenetic tree, all these taxa are positioned in the Clades B and C (Mason et al., 2020). All Clade B populations are in N Albania except for *M. skipetarica pindica* (Mpn), and all C Clade populations are in S Albania-Epirus, except for *M. skipetarica csikii* (Mck). The nominal subspecies *M. skipetarica skipetarica* (Msk) falls into Clade B. This taxon is known from the Q. Murre Gorge and from another remote site (Ura e Lapavës, the type locality) (Fehér & Szekeres, 2016: 98). Since all the known *M. skipetarica skipetarica* populations are genetically very similar, this might be a recent jump dispersal case. The genital morphology (population HNHM 99522, Msk-205) is very peculiar, showing a long genital apparatus (PCRL 87.6, one of the highest PCRL in the genus *Montenegrina*) with an extremely long PC and vagina (Figure 56.3). The inner walls are almost smooth except for a thin and long pleat running along the penial wall. The bursa copulatrix complex is very small compared to the remaining genitalia. The penial papilla is very thin and pointed. Its overall anatomy strictly resembles that of *M. edmundi* (Figures 16.8–16.11), which is phylogenetically distant. In the mt tree, its sister taxon is *M. skipetarica remota* (HNHM 99021, Mre-459), which shows a similar shell morphology (Figure 61.1), but the genital anatomy shows only a slight resemblance (elongated genitalia as Msk-205-01), presenting instead overall shorter and thicker genitalia in which the inner walls of both the penis and vagina are considerably sculptured with an irregular pattern of pleats. Despite the close phylogenetic relationship with the nominal subspecies, due to the strikingly different genital anatomy we consider *M. skipetarica* and *M. remota* stat. nov. as separate and valid species.

*Montenegrina skipetarica pindica* forms a subclade, the sister group of the *M. skipetarica/M. remota* subclade. Its genital anatomy strictly resembles *M. remota* both regarding the external shape and the inner sculpturing. It also differs considerably from *M. s. skipetarica*

(Figure 60). Although its shell morphology and genital arrangement put this taxon very close to *M. remota*, its separated geographic distribution (ca. 170 km SE of the *M. skipetarica/M. remota* area, Fehér & Szekeres, 2016: 98) as well as its position in the mitochondrial tree support its status as a valid species: *M. pindica* stat. nov.

*Montenegrina skipetarica pifkoi* also belongs to Clade B and is monophyletic, except one specimen (Mpf-298-01) that stands out (Mason et al., 2020). The assignment of this specimen/population was based on shell features and no specimens were dissected. Thus, the final assignment of this population requires careful investigation and the awaited results should be discussed as soon as more data become available. The shell morphology of *M. skipetarica pifkoi* (Fehér & Szekeres, 2016: 103) and, above all, its genital arrangement are very different from the previous taxa. In comparison, the genitalia are shorter, with a sturdier shape and a very different inner sculpturing of both the male and female parts (Figures 59.7–59.9). Based on the previous results, we here treat *M. pifkoi* stat. nov. as a valid species.

The taxa *M. skipetarica gurelurensis* and *M. skipetarica puskasi* are both found near the village Gurë-Lurë (Albania). Along the Setës gorge, the two taxa occur in close contact with *M. skipetarica gurelurensis*, which inhabits the western part of the gorge, whereas *M. skipetarica puskasi* occurs along the eastern part. The latter taxon, however, is also known from other localities E and S of the Setës gorge (Fehér & Szekeres, 2016: 98). The two taxa have been separated based on shell differences, whereby *M. skipetarica gurelurensis* has a costate-ribbed shell and *M. skipetarica puskasi* an almost entirely smooth one (Fehér & Szekeres, 2016: 96–97). This strict geographic-distributional relationship is also reflected in the mt tree and in the genital morphology. These two taxa are intermingled within a subclade and their genital arrangement is the same (Figures 58 and 67). The genetic and anatomical data also strongly support that both taxa should not be considered as subspecies of *M. skipetarica*. Based on these results, we consider *M. puskasi puskasi* stat. nov. as a valid species. The populations with ribbed shell, which represent a restricted morphotype and are described as *M. skipetarica gurelurensis*, are now considered as a subspecies: *M. puskasi gurelurensis* comb. nov.

Unfortunately, no alcohol-preserved specimen was available for *M. skipetarica danyii*, but its position in the phylogenetic tree shows its close relationship to *M. puskasi*. It is phylogenetically separated from *M. puskasi* s.l. as previously considered in Fehér and Szekeres (2016). For the moment, we propose to treat it as *M. puskasi danyii* comb. nov.

Clade C contains eight subspecies of *M. skipetarica* sensu Fehér and Szekeres (2016). Considering the high genetic distances, all these taxa should no longer be considered as conspecific with *M. skipetarica*.

*Montenegrina nobilis* stat. nov. and *M. ersekensis* stat. nov., both monophyletic in the tree, live approximately 3 km apart in the surroundings of Barmash (southern Albania). Their distribution of the two taxa clearly points to sister taxa. Their strikingly different genital anatomy could be evidence for a genetic isolation. *Montenegrina nobilis* has bulky genitalia with a large bursa copulatrix complex and short vagina, as opposed to *M. ersekensis* with slender genitalia, small CBC and long vagina. Regarding the inner sculpturing of the male

parts, *M. nobilis* has type of grid sculpturing with a large penial papilla, whereas *M. ersekensis* exhibits smooth longitudinal pleats and lacks a penial papilla.

The taxa *M. "skipetarica" voidomatis* (Mvo), *M. "skipetarica" konitsae* (Mkn) and *M. "skipetarica" thysi* (Mty) form together a monophyletic group. These three taxa inhabit the area surrounding the Ethnikos Drimos mountain in northern Greece (Fehér & Szekeres, 2016: 98). The widest distributed *M. "skipetarica" voidomatis* is paraphyletic, while Mkn and Mty are monophyletic. *Montenegrina voidomatis voidomatis* stat. nov. is thus considered as a valid species. The genitalia of *M. "skipetarica" konitsae* and *M. "skipetarica" thysi* proved to be identical and both differ from *M. voidomatis voidomatis*. Based on the anatomical traits and the mt tree, we consider the new combinations: *M. voidomatis konitsae* comb. nov. and *M. voidomatis thysi* comb. nov. The different subspecific status of these two taxa is retained on the basis of shell morphology, where *M. voidomatis thysi* represents a ribbed microendemic morphotype, which is one population within the range of *M. voidomatis voidomatis* at the large scale and almost parapatric with that at the local scale.

*Montenegrina skipetarica rugosa* is known from a few isolated populations in southern Albania (Fehér & Szekeres, 2016: 98). It forms a subclade together with the Mvo-Mkn-Mty clade (taxa located 80 km SE). No alcohol-preserved specimen was available for dissection, but its position in the phylogenetic tree lead us to propose it as a subspecies of *M. voidomatis*, *M. voidomatis rugosa* comb. nov.

*Montenegrina skipetarica flava* and *M. skipetarica csikii* also fall into Clade C. The first taxon is known by one isolated population in southern Albania, and the latter is found ca. 150 km far away in northern Albania. The two taxa have remarkably different arrangements of the genitalia, especially as regards the inner sculpturing of both the male and female parts. The two taxa are here considered as valid species: *M. csikii* Eröss and Szekeres, 2006 stat. nov. and *M. flava* Eröss and Szekeres, 2006 stat. nov.

Fehér & Szekeres, 2016	De Mattia, Fehér, Mason & Haring, 2020
<i>Montenegrina skipetarica skipetarica</i> (Soós, 1924)	<i>Montenegrina skipetarica</i> (Soós, 1924)
<i>Montenegrina skipetarica csikii</i> Eröss and Szekeres, 2006	<i>Montenegrina csikii</i> Eröss and Szekeres, 2006 stat. nov.
<i>Montenegrina skipetarica danyii</i> Fehér & Szekeres, 2016	<i>Montenegrina puskasi danyii</i> Fehér & Szekeres, 2016 comb. nov.
<i>Montenegrina skipetarica ersekensis</i> Nordsieck, 1996	<i>Montenegrina ersekensis</i> Nordsieck, 1996 stat. nov.
<i>Montenegrina skipetarica flava</i> Eröss and Szekeres, 2006	<i>Montenegrina flava</i> Eröss and Szekeres, 2006 stat. nov.
<i>Montenegrina skipetarica gurelurensis</i> Fehér & Szekeres, 2016	<i>Montenegrina puskasi gurelurensis</i> Fehér & Szekeres, 2016 comb. nov.
<i>Montenegrina skipetarica konitsae</i> Nordsieck, 1972	<i>Montenegrina voidomatis konitsae</i> Nordsieck, 1972 comb. nov.
<i>Montenegrina skipetarica nobilis</i> Eröss and Szekeres, 2006	<i>Montenegrina nobilis</i> Eröss and Szekeres, 2006 stat. nov.

Fehér & Szekeres, 2016	De Mattia, Fehér, Mason & Haring, 2020
<i>Montenegrina skipetarica pifkoi</i> Fehér & Szekeres, 2016	<i>Montenegrina pifkoi</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina skipetarica pindica</i> Nordsieck, 1998	<i>Montenegrina pindica</i> Nordsieck, 1998 stat. nov.
<i>Montenegrinaskipetarica puskasi</i> Fehér & Szekeres, 2016	<i>Montenegrina puskasi puskasi</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina skipetarica remota</i> Fehér & Szekeres, 2006	<i>Montenegrina remota</i> Fehér & Szekeres, 2006 stat. nov.
<i>Montenegrina skipetarica rugosa</i> Fehér & Szekeres, 2006	<i>Montenegrina voidomatis rugosa</i> Fehér & Szekeres, 2006 comb. nov.
<i>Montenegrina skipetarica thysi</i> Loosjes & Loosjes-van Bommel, 1988	<i>Montenegrina voidomatis thysi</i> Loosjes & Loosjes-van Bommel, 1988 comb. nov.
<i>Montenegrina skipetarica voidomatis</i> Nordsieck, 1974	<i>Montenegrina voidomatis voidomatis</i> Nordsieck, 1974 stat. nov.

### Montenegrina skipetarica (Soós, 1924)

Figures 56.1–56.6

*Clausilia (Delima) skipetarica* Soós, 1924: 181–183, fig. 2 (shell), 3 (genital anatomy).

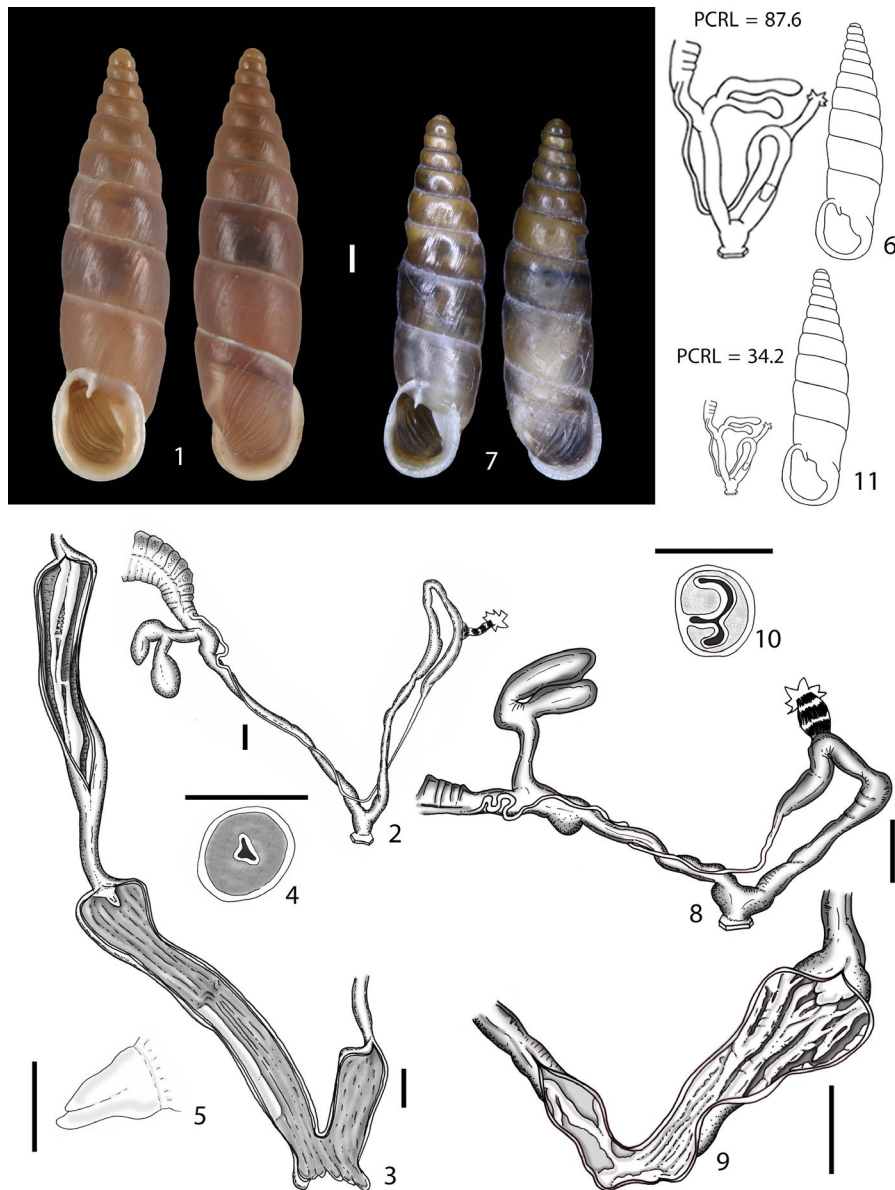
*Delima (Albanodelima) skipetarica* – Wagner, 1924: 120.

*Montenegrina perstriata skipetarica* – Eröss et al., 2006: 203, fig. 26 – Nordsieck, 2009: 73, plate 1, fig. 1.

*Montenegrina skipetarica skipetarica* – Fehér & Szekeres, 2016: 95, fig. 30E, distribution map fig. 31B.

**Examined material: two dissected specimens.** Albania, Mat District, 3 km W of the Qafa e Murrës, Shkëmb i Skanderbeut, gorge of the Lumi i Varoshit, 970 m, 41.6465°N, 20.1901°E, leg. ZE, ZF, JK, DM, 26.vi.2003 (HNHM 99522, Msk-301-01 [COI: KU307798, 16S: KU308186, 12S: KU307983]).

**External genitalia** (Figure 56.2): The whole genital complex is extremely long (PCRL = 87.6) – the longest recorded for the genus *Montenegrina*. The FO is very short (FO/V = 0.03). The vas deferens is very thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.63). The bursa copulatrix is very short (DB/V = 0.18). The proper bursa is bulky, club-like with a big rounded apex. There is a more or less visible transitional area. The diverticulum is also on average very short (D/V = 0.24), uniformly cylindrical, as wide as and on average shorter (D/BC = 0.88) than the bursa copulatrix. The apex is pointed. The vagina is very long (VRL = 54.6), uniformly thin and cylindrical. The atrium is moderately large and long. The PC is longer than the vagina (PC/V = 1.60). The penis is cylindrical, very thin, only slightly swollen at the level of the penial papilla. The epiphallus is shorter than the penis (E/P = 0.79), swollen along its proximal



**FIGURE 56** 56.1–56.6 *Montenegrina skipetarica* (Soós, 1924) HNHM 99522. 56.1 shell, 56.2 whole distal genitalia, 56.3 inner distal genitalia, 56.4 cross section of epiphallus, 56.5 penial papilla, 56.6 shell-genitalia ratio. 56.7–56.11 *Montenegrina csikii* Eröss and Szekeres, 2006 stat. nov. HNHM 96845. 56.7 shell, 56.8 whole distal genitalia, 56.9 inner distal genitalia, 56.10 cross section of epiphallus, 56.11 shell-genitalia ratio

part and wider than the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 56.3–56.5):** The atrium is mainly smooth, with only traces of very weak longitudinal pleats. The whole vagina is also smooth, and the vaginal pilaster is absent. The whole penis is smooth, with only a long, longitudinal pleat extending along the distal penis. The penial papilla is very small, shark-tooth shaped with a pointed apex, and the aperture is lateral but transversely oriented. The epiphallus has three fringed pleats with jagged edges, originating proximally from the end of the vas deferens and fading before the base of the penial papilla. The background is transversely irregular.

***Montenegrina csikii* Eröss and Szekeres, 2006 stat. nov.**

Figures 56.7–56.11

*Montenegrina apfelbecki csikii* Eröss and Szekeres, 2006 in Eröss et al., 2006: 185–186, fig. 4.

*Montenegrina janinensis csikii* – Nordsieck, 2009: 75.

*Montenegrina skipetarica csikii* – Fehér & Szekeres, 2016: 97, fig. 30K, distribution map fig. 31b.

**Examined material: two dissected specimens.** Albania, Kukës District, Bicaj, gorge of the Përroi i Tershanës, 500 m, 41.9897°N, 20.4202°E [type locality], leg. LD, ZE, ZF, AH, DM, 25.vi.2007



(HNHM 96845, Mck-275-01 [COI: KU307599]; Mck-275-02 [COI: KU307600, 16S: KU308061, 12S: KU307936]).

**External genitalia (Figure 56.8):** The whole genital complex is long (PCRL = 34.2). The FO is short (FO/V = 0.25). The vas deferens is very thin along its whole course. The first duct of the bursa copulatrix complex is extremely long (DBC/DB = 1.0). The bursa copulatrix is short (DB/V = 0.31), bulky, uniformly cylindrical with a blunt apex. There is no visible transitional area. The diverticulum is generally very short (D/V = 0.56), uniformly cylindrical, wider than the bursa copulatrix and generally longer (D/BC = 1.82). The apex is blunt. The vagina is very long (VRL = 23.7), irregular in shape with a roundish swelling at its proximal end. The atrium is moderately large. The PC is longer than the vagina (PC/V = 1.44). The penis is cylindrical, irregular, only slightly swollen at the level of the penial papilla. The epiphallus is shorter than the penis (E/P = 0.79), almost uniformly cylindrical, only slightly swollen proximally, and wider than the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 56.9–56.10):** The atrium has one small, smooth fold originating from the aperture. The background is completely smooth. The distal vagina shows only one smooth, “Y” shaped pleat. This pleat is the direct continuation of the vaginal pilaster. The proximal vagina exhibits only the vaginal pilaster and one or two minor, oblique accessory pleats originating from it. The background is smooth. The penis bears a set of many irregular, large longitudinal pleats connected by minor small transversal/oblique pleats. Along the distal penis the pleats gradually become a set of minimally elevated longitudinal pleats fading towards the atrium. The background walls are smooth. The medium-sized, conical penial papilla has three protruding but blunt apexes and a smooth surface. The aperture is lateral. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina puskasi danyii* Fehér & Szekeres, 2016 comb. nov.**

*Montenegrina skipetarica danyii* – Fehér & Szekeres, 2016: 98, fig. 30N, distribution map fig. 31b.

No alcohol-preserved specimens were available for anatomical investigations.

### ***Montenegrina ersekensis* Nordsieck, 1996 stat. nov.**

Figures 57.1–57.5

*Montenegrina ersekensis* Nordsieck, 1996: 9–10, plate 2, fig. 3.

*Montenegrina skipetarica ersekensis* – Nordsieck, 2009: 73.

*Montenegrina skipetarica ersekensis* – Fehér & Szekeres, 2016: 99, fig. 30F, distribution map fig. 31A.

**Examined material: two dissected specimens.** Albania, Ersekë District, 4 km S of Barmash, 920 m, 40.2656°N, 20.6001°E, leg. DA, ZE, ZF, JG, 29.vi.2014 (HNHM 99375, NHMW 110430/MN/0031, Mek-477-01 [COI: KU307660, 16S: KU308097, 12S: KU307950]; Mek-477-02 [COI: MT251588]).

**External genitalia (Figure 57.2):** The whole genital complex is very long (PCRL = 54.0) with a very slender appearance. The FO is extremely short (FO/V = 0.03). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.21). The bursa copulatrix is bulky, short (DB/V = 0.41), uniformly cylindrical with a blunt apex. There is no visible transitional area between the second duct and the bursa itself. The diverticulum is generally very short (D/V = 0.32), uniformly cylindrical, as wide as the bursa copulatrix and on average shorter (D/BC = 0.76). The apex is blunt. The vagina is very long (VRL = 49.2), almost uniformly cylindrical and very thin. The atrium is moderately large and long. The PC is slightly longer than the vagina (PC/V = 1.1). The penis is uniformly cylindrical and thin. The epiphallus is longer than the penis (E/P = 1.24), cylindrical and thin. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 57.3–57.4):** The atrium has many irregular, smooth pleats that split randomly, forming a net-like pattern. The distal vagina is smooth but with traces of flat, branched longitudinal pleats. The proximal vagina is completely smooth, and the vaginal pilaster is absent. The penis bears an irregular set of smooth longitudinal pleats, which branch to form a net-like pattern. The penial papilla is absent, but the transition area between epiphallus and proximal penis bears a small but well-visible pseudopapilla. The pseudopapilla does not show any channel or aperture. The epiphallus has three fringed pleats with jagged edges, originating proximally from the end of the vas deferens and fading before the base of the penial papilla. The background is transversely irregular.

### ***Montenegrina flava* Eröss and Szekeres, 2006 stat. nov.**

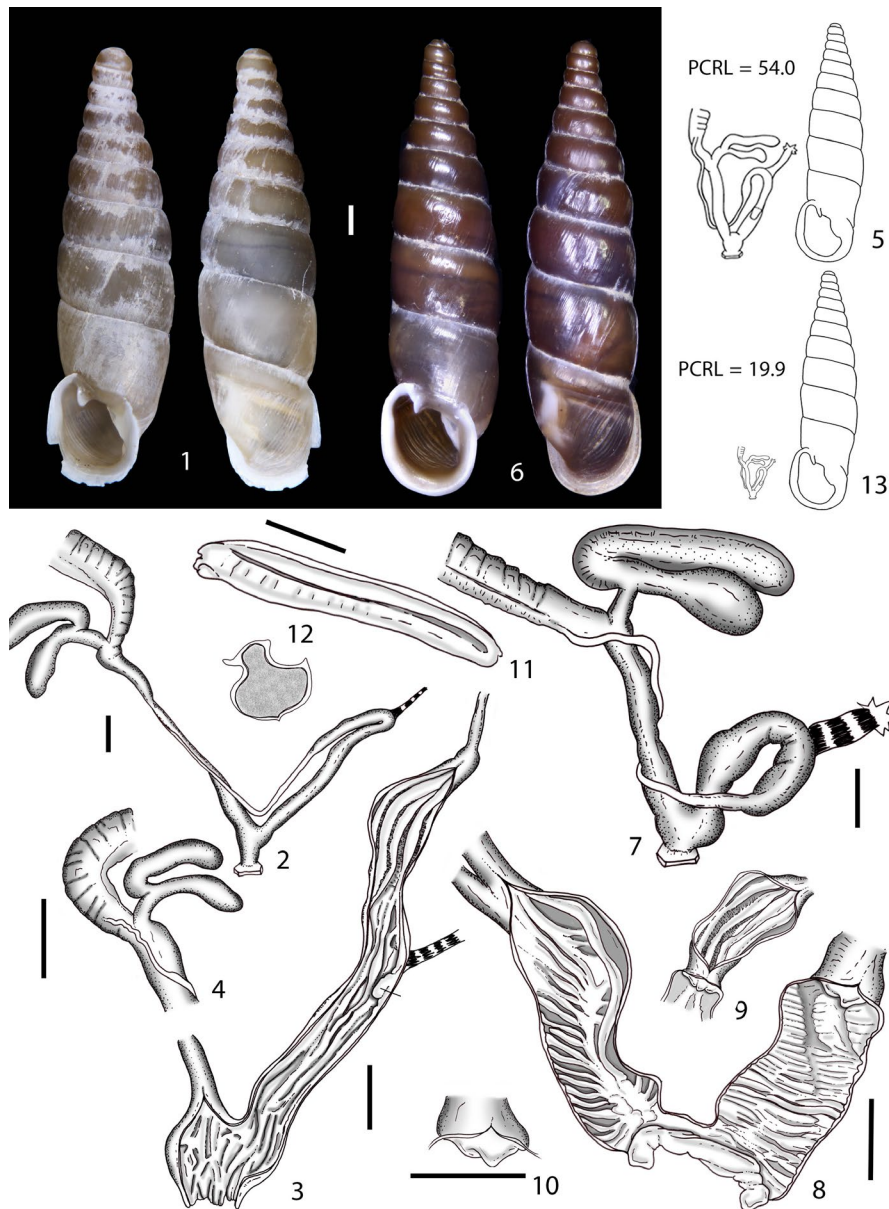
Figures 57.6–57.13

*Montenegrina irmengardis flava* Eröss and Szekeres, 2006 in Eröss et al., 2006: 192, fig. 12.

*Montenegrina skipetarica flava* – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 100, fig. 30J, distribution map fig. 31A.

**Examined material: two dissected specimens.** Albania, Korçë District, gorge of the Lumi i Devollit at the Gjnikas junction, 25 km W of Maliq, along the Korçë to Gramsh road, 750 m, 40.6921°N, 20.5003°E [type locality], leg. PJ, TK, DM, GP, 16.x.2013 (HNHM 99544, Mfl-428-01 [COI: KU307672, 16S: KU308105]; Mfl-428-02 [COI: MT251601]).

**External genitalia (Figure 57.7):** The whole genital complex is short (PCRL = 19.9). The FO is short (FO/V = 0.30) but very wide. The vas deferens is moderately wide along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.32) and thin compared to the rest of the complex. The bursa copulatrix is short (DB/V = 0.63), bulky, slightly club-like, very wide



**FIGURE 57** 57.1–57.5 *Montenegrina ersekensis* Nordsieck, 1996 stat. nov. HNHM 99375, NHMW 110430/MN/0031. 57.1 shell, 57.2 whole distal genitalia, 57.3 inner distal genitalia, 57.4 bursa copulatrix complex, 57.5 shell-genitalia ratio. 57.6–57.13 *Montenegrina skipetarica flava* Eröss and Szekeres, 2006 HNHM 99544. 57.6 shell, 57.7 whole distal genitalia, 57.8 inner distal genitalia, 57.9 penial papilla and longitudinal section of epiphallus, 57.10 penial papilla, 57.11 spermatophore, 57.12 cross section of spermatophore, 57.13 shell-genitalia ratio

and with a wide bursa itself. There is no distinct transitional area. The diverticulum is on average medium-sized ( $D/V = 1.23$ ), uniformly cylindrical, wider, and longer ( $D/BC = 1.95$ ) than the bursa copulatrix. The apex is big but blunt. The vagina is medium-sized ( $VRL = 16.1$ ) and almost uniformly cylindrical. The atrium is large. The PC is slightly longer than the vagina ( $PC/V = 1.23$ ). The penis is cylindrical and slightly swollen at the level of the penial papilla. The epiphallus is much longer than the penis ( $E/P = 2.36$ ) and narrower than the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 57.8–57.10):** The atrium has a big, irregular, polylobated fold originating directly at the genital aperture. The distal

vagina shows 5–7 big, smooth transversal pleats converging into a medial longitudinal pleat. The proximal vagina has many oblique, slightly transversal pleats converging towards the vaginal pilaster. The background walls are smooth. The proximal penis bears three main large and metameric cords that are slightly oblique, with portions of the smooth background visible. These three cords merge together at mid-penial length, forming a pattern of irregular transversal cords that randomly split and merge as far as the atrium. The medium-sized, conical penial papilla is pointed but with a broad apex and a smooth surface. The aperture is lateral, not reaching the papilla's tip. The epiphallus has five smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The distal

portions of the cords become markedly fringed. The background is proximally smooth and distally fringed.

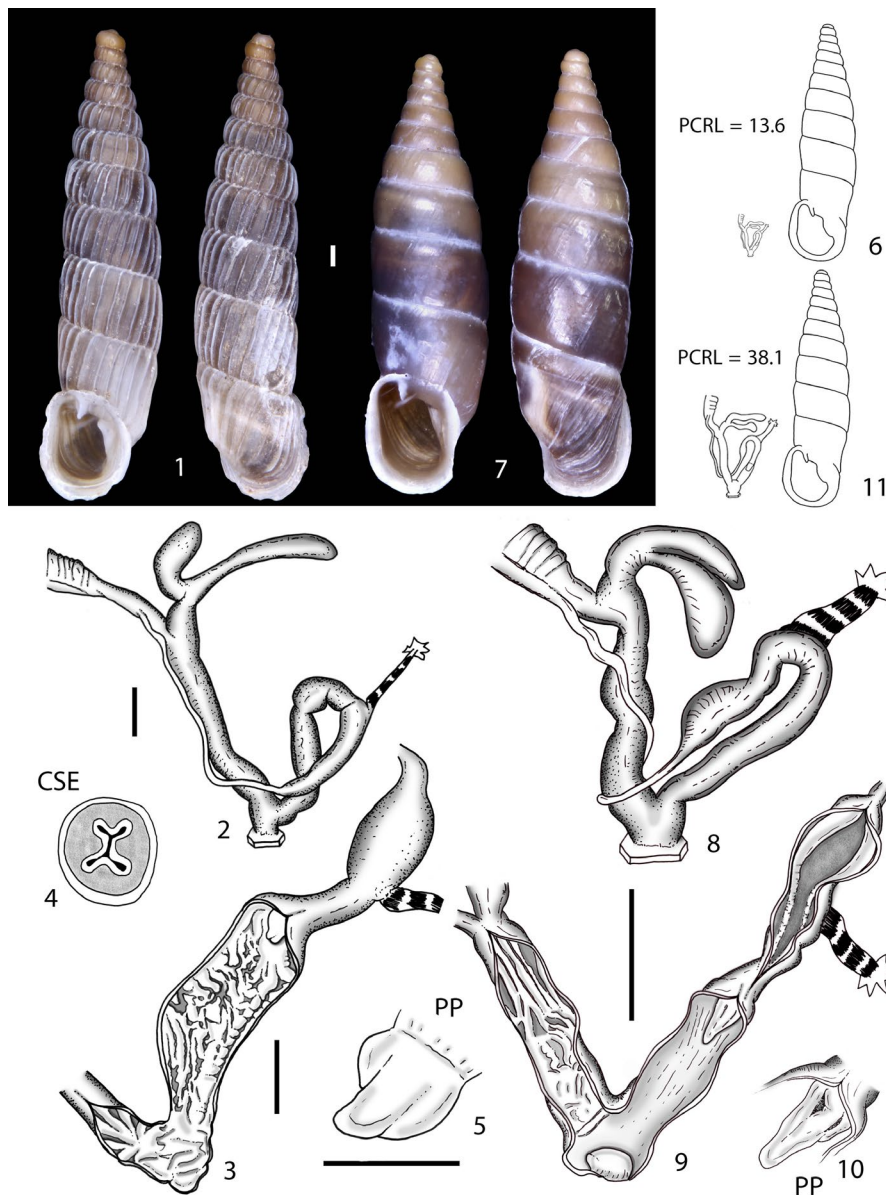
**Spermatophore (Figures 57.11–57.12):** The spermatophore is almost straight, and the head is almost as big as the tail, with no evident narrowing towards the ends. Both the head and the tail are blunt. The lower carina is extremely small and barely visible (only from the perspective of the cross section). The upper carina begins immediately behind the head and extends as far as the tip of the tail. The ventral surface has a weak fishbone-like sculpturing with a longitudinal line running along the midbody. The cross section is pear-shaped, with the upper carina slightly set off from the main longitudinal axis. The spermatophore is 3.8 mm long and 0.6 mm wide.

***Montenegrina puskasi gurelurensis* Fehér & Szekeres, 2016 comb. nov.**

Figures 58.1–58.8

*Montenegrina skipetarica gurelurensis* – Fehér & Szekeres, 2016: 101, fig. 30O, distribution map fig. 31b.

**Examined material: four dissected specimens (paratypes).** Albania, Dibrë District, ca. 2 km W of Cidhnë along the footpath to Gurë-Lurë, gorge of the Përroi i Setës, 780 m, 41.7525°N, 20.2484°E [type locality], leg. ZE, DM, 10.x.2005 (HNHM 99461, Mgu-249-01 [COI: KU307901]); along the Cidhnë-Gurrë-Lurë footpath, 1.9 km from the hydroelectric station, 690 m [rocks], 41.7524°N,



**FIGURE 58** 58.1–58.6 *Montenegrina puskasi gurelurensis* Fehér & Szekeres, 2016 comb. nov. HNHM 99461. 58.1 shell, 58.2 whole distal genitalia, 58.3 inner distal genitalia, 58.4 cross section of epiphallus, 58.5 penial papilla, 58.6 shell-genitalia ratio. 58.7–58.11 *Montenegrina voidomatis konitsae* Nordsieck, 1972 comb. nov. HNHM 99528. 58.7 shell, 58.8 whole distal genitalia, 58.9 inner distal genitalia, 58.10 penial papilla, 58.11 shell-genitalia ratio

20.24838°E, leg. ZE, ZF, JG, 1.vii.2015 (NHMW 111208, Mgu-631-03 [COI: MT251621]).

**External genitalia (Figure 58.2):** The whole genital complex is short (PCRL = 13.6). The FO is short (FO/V = 0.26). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is long (DBC/DB = 0.58). The bursa copulatrix is short (DB/V = 0.63), slender, uniformly cylindrical, or slightly club-like with a blunt apex. There is no visible transition area. The diverticulum is also on average very short (D/V = 0.39), bulky, uniformly cylindrical, wider than the bursa copulatrix and on average much shorter (D/BC = 0.52). The apex is blunt. The vagina is medium-sized (VRL = 13.6) and almost uniformly cylindrical. The atrium is moderately large and long. The PC is as long as the vagina (PC/V = 1.0). The penis is cylindrical, only slightly swollen. The epiphallus is longer than the penis (E/P = 1.82), swollen distally, cylindrical proximally part and slightly thinner than the penis. It merges into the vas deferens without a distinct transitional area. The retractor muscle is long and thin.

**Inner genitalia (Figures 58.3–58.5):** The atrium shows many irregular smooth and fleshy, pad-like, large pleats. The distal vagina has 5–10 smooth longitudinal pleats. The background is smooth. The proximal vagina has few elevated, oblique, transversal pleats converging towards the vaginal pilaster. The background walls are smooth. The whole penis shows a variable number of irregularly arranged, smooth pleats. The pleats are variable in shape and length, forming a sort of “random” net-like pattern. The medium-sized penial papilla is pyramidal, pointed but with a blunt apex. The aperture extends laterally, not reaching the apical area. The surface is smooth with two small, roundish basal lobes. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina voidomatis konitsae* Nordsieck, 1972 comb. nov.

Figures 58.7–58.11

*Montenegrina irmengardis konitsae* Nordsieck, 1972: 35, plate 4, fig. 35. – Zilch, 1981: 129, plate 15, fig. 41.

*Montenegrina skipetarica konitsae* – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 102, fig. 30b, distribution map fig. 31A.

**Examined material: two dissected specimens.** Greece, Epirus, Sarantaporos Gorge near the Exochi to Agia Varvara road, 530 m, 40.1102°N, 20.7203°E, leg. ZE, ZF, JG, 26.vi.2013 (HNHM 99528, Mkn-393-01 [COI: KU307696, 16S: KU308122]; Mkn-393-02 [COI: MT251633]).

**External genitalia (Figures 58.8):** The whole genital complex is long (PCRL = 38.1). The FO is very short (FO/V = 0.24). The vas deferens is thin along its whole course and slightly swollen proximally. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.18). The bursa copulatrix is also short (DB/V = 0.68), bulky, club-like with a wide actual bursa. There is no clearly visible transition area. The diverticulum is generally very short

(D/V = 0.59), uniformly cylindrical, thinner than the bursa copulatrix (D/BC = 0.86). The apex is pointed. The vagina is medium-sized (VRL = 19.5), wide, and irregularly cylindrical. The atrium is large. The PC is longer than the vagina (PC/V = 1.95). The penis is cylindrical, thin and not swollen at the level of the penial papilla. The epiphallus is longer than the penis (E/P = 1.58), swollen proximally and cylindrical distally. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 58.9–58.10):** The atrium has one small, smooth fold directly originating from the aperture. The background is completely smooth. The distal vagina shows many smooth, scattered, irregularly arranged pleats. The proximal vagina bears four or five longitudinal pleats, including the vaginal pilaster. The background is smooth. The penis is completely smooth. The medium-sized, conical penial papilla has a pointed apex and smooth surface. The aperture is lateral and does not reach the papilla's tip. The epiphallus presents two simple pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. Along their distal part they become fringed with irregular jagged edges. The background is irregular.

### *Montenegrina nobilis* Erőss and Szekeres, 2006 stat. nov.

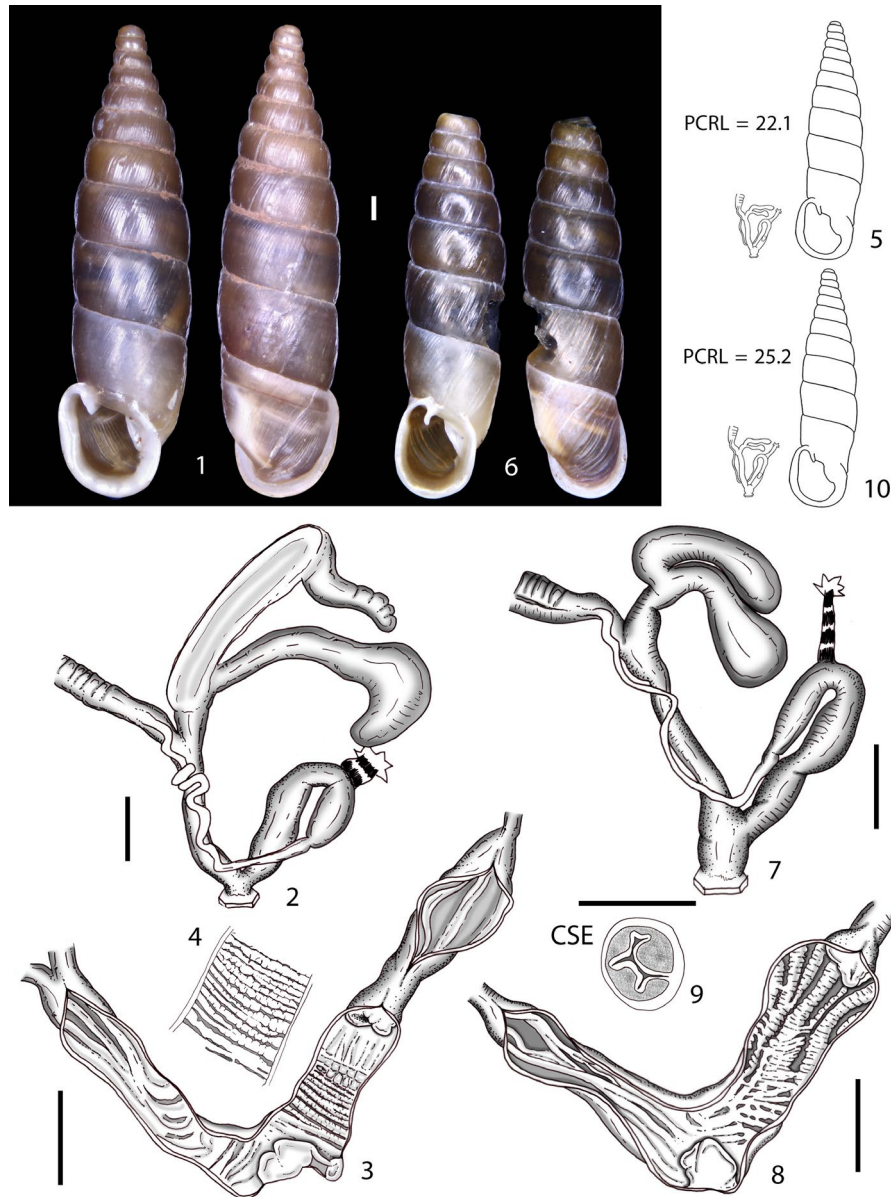
Figures 59.1–59.5

*Montenegrina ersekensis nobilis* Erőss and Szekeres, 2006 in Erőss et al., 2006: 189, fig. 8.

*Montenegrina skipetarica nobilis* – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 102, fig. 30H, distribution map fig. 31A.

**Examined material: two dissected specimens.** Albania, Ersekë District, 4 km S of Borovë, NE of Barmash, on the Ersekë to Leskovik road, 1,040 m, 40.2913°N, 20.6273°E [type locality], leg. PJ, TK, DM, GP, 15.x.2013 (HNHM 99536, Mno-427-01 [COI: MT251671, 16S: KU308143]; Mno-427-02 [COI: MT251672]).

**External genitalia (Figure 59.2):** The whole genital complex is medium-sized (PCRL = 22.1). The FO is also medium-sized (FO/V = 0.42). The vas deferens is moderately thick along its whole course. The first duct of the bursa copulatrix complex is extremely short (DBC/DB = 0.17). The bursa copulatrix is very long (DB/V = 2.0), club-like and irregular. There is no clearly visible transitional area between the second duct and the bursa proper. The diverticulum is also on average very long (D/V = 2.33), uniformly cylindrical, thinner and on average longer (D/BC = 1.17) than the bursa copulatrix. The apex is pointed. The vagina is medium-sized (VRL = 11.3) and uniformly cylindrical. The atrium is small. The PC is longer than the vagina (PC/V = 1.96). The penis is cylindrical and swollen. The epiphallus is longer than the penis (E/P = 1.24), swollen along its proximal part and as wide as the penis (except for its distal part, which is thinner). It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is very short and strong.



**FIGURE 59** 59.1–59.5 *Montenegrina nobilis* Eröss and Szekeres, 2006 stat. nov. HHNM 99536. 59.1 shell, 59.2 whole distal genitalia, 59.3 inner distal genitalia, 59.4 magnification of the inner sculpturing of the proximal penis, 59.5 shell-genitalia ratio. 59.6–59.10 *Montenegrina pifkoi* Fehér & Szekeres, 2016 stat. nov. HHNM 99466. 59.6 shell, 59.7 whole distal genitalia, 59.8 inner distal genitalia, 59.9 cross section of epiphallus, 59.10 shell-genitalia ratio

**Inner genitalia (Figures 59.3–59.4):** The atrium has a big, unilobate irregular fold originating directly at the genital aperture. The distal vagina shows a set of irregular, pad-like, flat, transversal and oblique pleats. The proximal vagina shows four or five longitudinal pleats including the vaginal pilaster. These pleats tend to distally merge into one another. The background is smooth. The proximal penis is smooth around the penial papilla, gradually turning into large and smooth longitudinal pleats. These pleats end, forming two or three rows of square-like, smooth tubercles that are transversely arranged and gradually decrease in size. Distally, a variable number of small transversal pleats extend as far as the borders with the atrium. These pleats are fringed, following a square-like pattern. The wide

but very short penial papilla has a central opening. The surface is smooth with some moderate swelling. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

***Montenegrina pifkoi* Fehér & Szekeres, 2016 stat. nov.**

Figures 59.6–59.10

*Montenegrina skipetarica pifkoi* – Fehér & Szekeres, 2016: 103, fig. 30L, distribution map fig. 31B.

**Examined material: two dissected specimens (paratypes).** Albania, Mat District, Mali i Dejës, Macukull, rocky forest E (above) of the village, 1,280 m, 41.6971°N, 20.1362°E [type locality], leg. ZF, DM, ZU, 19.v.2010 (HNHM 99466, Mpf-304-01 [COI: KU307521]).

**External genitalia (Figure 59.7):** The whole genital complex is medium-sized (PCRL = 25.2). The FO is very short (FO/V = 0.24). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.38). The bursa copulatrix is also medium-sized (DB/V = 0.84), bulky, club-like with a wide bursa proper. There is no visible transition area. The diverticulum is short (D/V = 0.92), uniformly cylindrical and generally longer (D/BC = 1.10). The apex is blunt. The vagina is medium-sized (VRL = 16.6) almost uniformly cylindrical, only slightly swollen proximally. The atrium is large and long. The PC is longer than the vagina (PC/V = 1.52). The penis is cylindrical, slightly swollen at the level of the penial papilla. The epiphallus is longer than the penis (E/P = 1.24), moderately swollen along its proximal part and thinner than the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 59.8–59.9):** The atrium shows a big, unilobate fold originating directly at the genital aperture. The distal vagina has 5–8 smooth longitudinal pleats that are the direct continuation of the proximal vagina's pleats. The proximal vagina bears two or three longitudinal pleats (vaginal pilaster included) that continue and eventually split in the distal vagina. The background is smooth. The proximal penis shows six or seven main, fringed, metameric longitudinal pleats that merge via fleshy, smooth bridges. Along the distal penis, these fringes merge all together, forming an irregular reticulate pattern. The medium-sized, conical penial papilla has a pointed but nonetheless broad apex and smooth surface. The aperture is lateral, not reaching the papilla's tip. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina pindica* Nordsieck, 1988 stat. nov.**

Figures 60.1–60.6

*Montenegrina dofleini pindica* Nordsieck, 1988: 199, fig. 3 – Nordsieck, 2009: 74.

*Montenegrina skipetarica pindica* – Fehér & Szekeres, 2016: 104, fig. 30M, distribution map fig. 31A.

**Examined material: two dissected specimens.** Greece, Epirus, Gramos Mts, W of the Epano Arena summit, 2000 m, 40.3090°N, 20.8981°E, leg. ZE, ZF, JG, 27.vi.2013 (HNHM 99524, Mpn-396-01 [COI: KU307749, 16S: KU308166, 12S: KU307973]).

**External genitalia (Figure 60.2):** The whole genital complex is long (PCRL = 30.5). The FO is very short (FO/V = 0.23) and very thin. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.47)

but wide. The bursa copulatrix is short (DB/V = 0.57), bulky, swollen with a blunt apex. There is no visible transition area between the second duct and the bursa itself. The diverticulum is also generally very short (D/V = 0.63), uniformly cylindrical, as wide as and usually much shorter (D/BC = 1.12) than the bursa copulatrix. The apex is blunt. The vagina is medium-sized (VRL = 19.5), almost uniformly cylindrical except for the proximal part, which slightly increases in width. The atrium is very large and long. The PC is longer than the vagina (PC/V = 1.57). The penis is cylindrical and wide. The epiphallus is shorter than the penis (E/P = 0.88), swollen along its proximal part but very thin distally. It merges into the vas deferens without a distinct transitional area. The retractor muscle is long and strong.

**Inner genitalia (Figures 60.3–60.5):** The atrium shows a set of irregular, smooth and fleshy pleats. The distal vagina has many scattered, irregularly arranged pleats. The proximal vagina bears many irregular, longitudinal or oblique pleats that randomly split and merge. The background walls are smooth and the vaginal pilaster is present. The whole penis shows a variable number of irregularly arranged, smooth pleats. The pleats are variable in shape and length, forming a sort of randomly arranged pattern. The medium-sized pyramidal penial papilla is pointed but with a blunt apex. The aperture is lateral. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

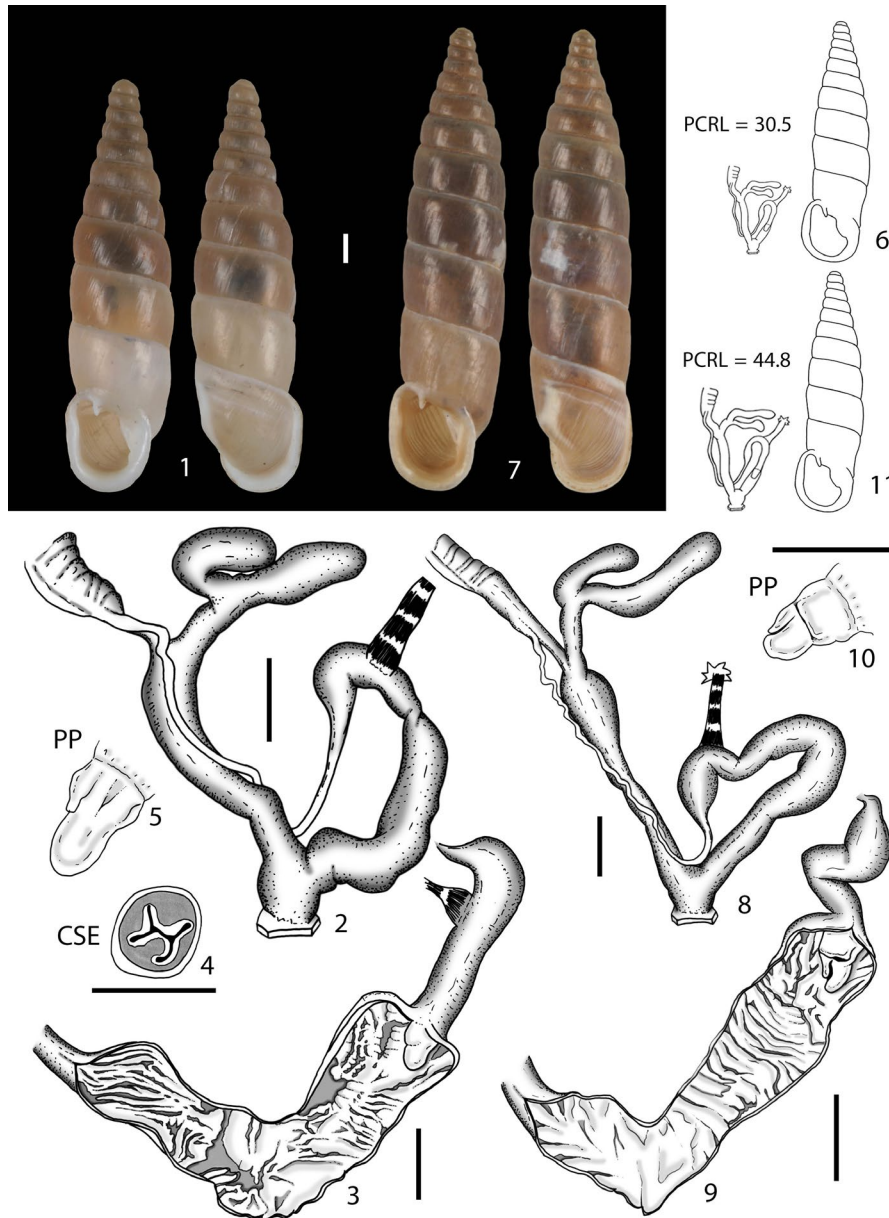
### ***Montenegrina puskasi puskasi* Fehér & Szekeres, 2016 stat. nov.**

Figures 60.7–60.11

*Montenegrina skipetarica puskasi* – Fehér & Szekeres, 2016: 105, fig. 30A, distribution map fig. 31b.

**Examined material: three dissected specimens.** Albania, Dibrë District, 0.1–1.5 km W of Cidhnë, leg. ZE, ZF, JG, 1.vii.2015 (HNHM 99458, Mpu-628-01 [COI: MT251753]).

**External genitalia (Figure 60.8):** The whole genital complex is long (PCRL = 44.8). The FO is short (FO/V = 0.29) and thin. The vas deferens is very thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.31) and thinner than the bursa copulatrix. The bursa copulatrix is short (DB/V = 0.78), uniformly cylindrical with a blunt apex. No transition area is visible between the second duct and the actual bursa. The diverticulum is also generally short (D/V = 0.42), uniformly cylindrical, slightly thinner and generally much shorter (D/BC = 0.54) than the bursa copulatrix. The apex is blunt. The vagina is long (VRL = 24.6), almost uniformly cylindrical but with a distinct swelling along its proximal part. The atrium is moderately large. The PC is longer than the vagina (PC/V = 1.82). The penis is cylindrical, slightly swollen at the level of the penial papilla. The epiphallus is longer than the penis (E/P = 1.65), swollen along its proximal part and wider than the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is long and strong.



**FIGURE 60** 60.1–60.6 *Montenegro pindica* Nordsieck, 1988 stat. nov. HNHM 99524. 60.1 shell, 60.2 whole distal genitalia, 60.3 inner distal genitalia, 60.4 cross section of epiphallus, 60.5 penial papilla, 60.6 shell-genitalia ratio. 60.7–60.11 *Montenegro puskasi puskasi* Fehér & Szekeres, 2016 stat. nov. NHMW 111207. 60.7 shell, 60.8 whole distal genitalia, 60.9 inner distal genitalia, 60.10 penial papilla, 60.11 shell-genitalia ratio

**Inner genitalia (Figures 60.9–60.10):** The atrium has an irregular, smooth and fleshy, large pleat. The distal vagina bears 5–10 smooth longitudinal or slightly oblique pleats that distally merge into a common longitudinal pleat. The proximal vagina bears many transversal pleats. The background walls are smooth and the vaginal pilaster is present. The proximal penis shows a set of irregularly arranged, smooth pleats that are variable in shape and length, forming a sort of “random” pattern. The distal penis bears a few large, smooth transversal pleats. These pleats randomly split and merge into one another. The background is smooth. The medium-sized, conical penial papilla has a pointed apex and smooth surface. The aperture is lateral. The apical aperture less part is thinner in diameter. The epiphallus has two or three simple smooth pleats

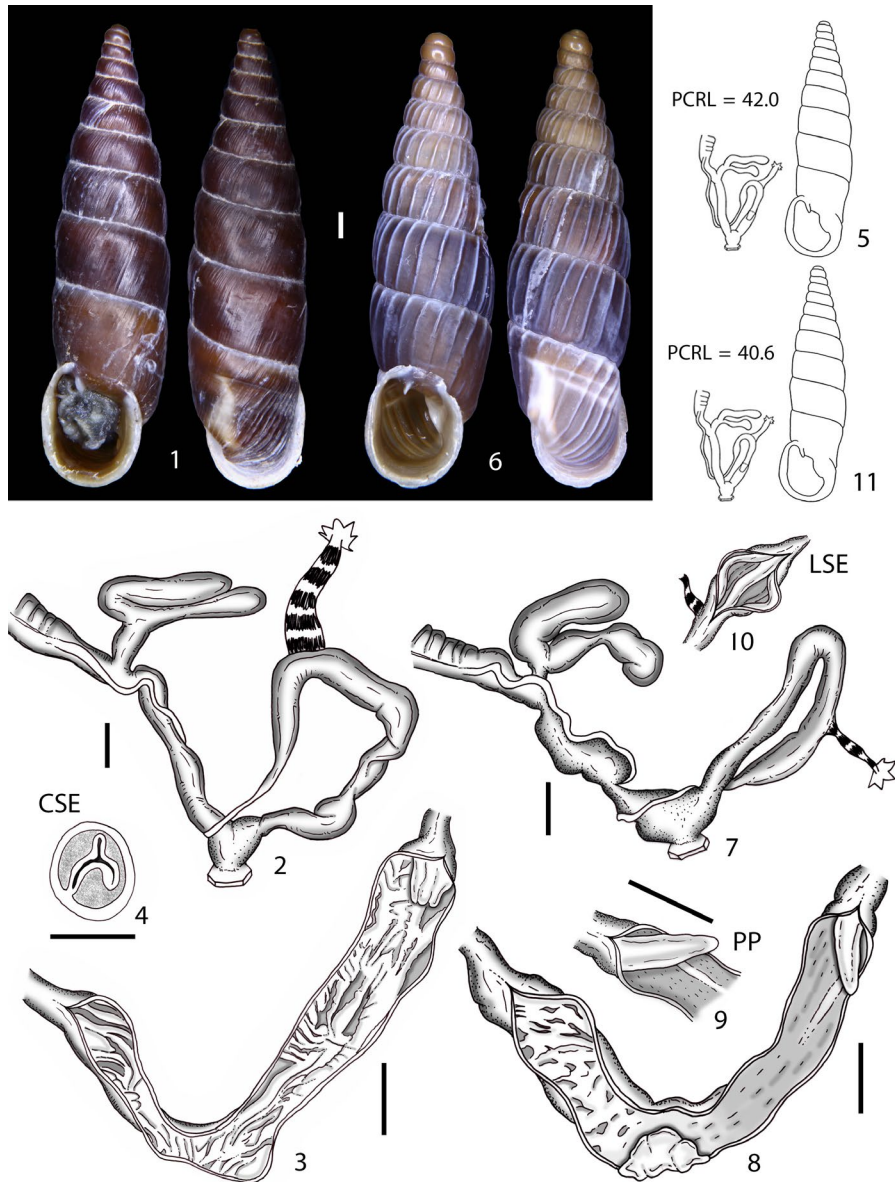
originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

***Montenegro remota* Fehér & Szekeres, 2006 stat. nov.**

Figures 61.1–61.5

*Montenegro irmengardis remota* Fehér & Szekeres, 2006 in Erőss et al., 2006: 192–194, fig. 13.

*Montenegro skipetarica remota* – Nordsieck, 2009: 73, plate 1, fig and. – Fehér & Szekeres, 2016: 106, fig. 30I, distribution map fig. 31B.



**FIGURE 61** 61.1–61.5 *Montenegrina remota* Fehér & Szekeres, 2006 stat. nov. HNHM 99021. 61.1 shell, 61.2 whole distal genitalia, 61.3 inner distal genitalia, 61.4 cross section of epiphallus, 61.5 shell-genitalia ratio. 61.6–61.11 *Montenegrina voidomatis thysi* Loosjes & Loosjes-van Bemmelen, 1988 comb. nov. HNHM 99532. 61.6 shell, 61.7 whole distal genitalia, 61.8 inner distal genitalia, 61.9 penial papilla, 61.10 longitudinal section of epiphallus, 61.11 shell-genitalia ratio

**Examined material:** two dissected specimens. Albania, gorge of the Mat River, 11 km W of the Ulëz junction, along the Burrel to Milot road, 100 m, 41.6919°N, 19.8318°E [type locality], leg. ZF, TN, EM, 16.iv.2014 (HNHM 99021, Mre-459-01 [COI: MT251756]; Mre-459-01 [COI: MT251757]).

**External genitalia (Figure 61.2):** The whole genital complex is long (PCRL = 42.0). The FO is short (FO/V = 0.32) but wide. The vas deferens is thin along its whole course except for the proximal part, where it is wider. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.39) and wide. The bursa copulatrix is short (DB/V = 0.56), with a slender second duct, slightly club-like and without a distinct transitional zone between the duct and the actual bursa. The apex is rounded. The diverticulum is on

average short ( $D/V = 0.78$ ), almost uniformly cylindrical, wider than the bursa copulatrix and on average longer ( $D/BC = 1.39$ ). The apex is pointed. The vagina is medium-sized ( $VRL = 18.7$ ), almost uniformly cylindrical but irregular in shape with a little swelling along its course. The atrium is moderately large and long. The PC is much longer than the vagina ( $PC/V = 2.24$ ) and slender. The penis is cylindrical. The epiphallus is shorter than the penis ( $E/P = 0.67$ ), almost uniformly cylindrical and wider than the penis. It merges into the vas deferens without a distinct transitional area. The retractor muscle is long and strong.

**Inner genitalia (Figures 61.3–61.4):** The atrium shows many irregular, smooth pleats forming a random pattern. The distal vagina is mainly smooth, with only weak traces of a few transversal



or irregular, smooth, oblique pleats. The proximal vagina has many oblique or transversal pleats that split and merge irregularly. The background walls are smooth and the vaginal pilaster is present. The whole penis shows an irregular arrangement, with a set of irregular, large longitudinal pleats often connected with many minor, small, transversal or oblique pleats. Some main longitudinal pleats can show signs of a metameric structure. The medium-sized, conical penial papilla has three elevated but blunt apices and a smooth surface. The aperture is lateral. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### ***Montenegrina voidomatis rugosa* Fehér & Szekeres, 2006 comb. nov.**

*Montenegrina irmengardis rugosa* Fehér & Szekeres, 2006 in Erőss et al., 2006: 194, fig. 14.

*Montenegrina skipetarica rugosa* – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 106, fig. 30G, distribution map fig. 31A.

No alcohol-preserved specimens were available for anatomical investigations.

### ***Montenegrina voidomatis voidomatis* Nordsieck, 1974**

Figures 62.1–62.5

*Montenegrina irmengardis voidomatis* Nordsieck, 1974: 155, plate 6, fig. 38. – Zilch, 1981: 129, plate 15, fig. 42.

*Montenegrina skipetarica voidomatis* – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 108, fig. 30C, distribution map fig. 31A.

**Examined material: two dissected specimens.** Greece, Epirus, Ioannina District, Tymfi Mts, Vikos Gorge at the Oxia viewpoint, 1,330 m, 39.9067°N, 20.7519°E, leg. ZE, ZF, JG, 25.vi.2013 (HNHM 99529, Mvo-389-01 [COI: KU307863, 16S: KU308216, 12S: KU307991]; Mvo-389-02 [COI: MT251865]).

**External genitalia (Figure 62.2):** The whole genital complex is medium-sized (PCRL = 27.3). The FO is long (FO/V = 0.60). The vas deferens is moderately thick along its whole course. The first duct of the bursa copulatrix complex is long (DBC/DB = 0.59). The bursa copulatrix is medium-sized (DB/V = 0.90), bulky, uniformly cylindrical, or only slightly club-like, with a rounded apex. There is no visible transition area between the second duct and the bursa itself. The diverticulum is on average short to medium-sized (D/V = 0.93), uniformly cylindrical, slightly wider and on average longer (D/BC = 1.04) than the bursa copulatrix. The apex is blunt. The vagina is medium-sized (VRL = 12.2), wide and almost uniformly cylindrical. The atrium is small. The PC is much longer than the vagina (PC/V = 2.23). Distally, the penis is thin, gradually increasing in width and reaching

its maximum diameter at the level of the penial papilla. The epiphallus is shorter than the penis (E/P = 0.86) and slightly swollen along its proximal part. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 62.3–62.4):** The atrium has few irregular, smooth and fleshy, pad-like pleats. The distal vagina shows five or six smooth transversal pleats that do not continue into the atrium. These pleats are irregular. The proximal vagina shows many oblique, transversal pleats that start from both sides of the very large vaginal pilaster. The background walls are smooth. The penis shows three or four main, fringed, metameric cords that extend longitudinally from the penial papilla's base as far as the distal penis. The cords distally merge into one another and rather abruptly become smooth. The background walls are smooth. The medium-sized, conical penial papilla has a pointed shape and a smooth surface. The aperture is lateral, not reaching the papilla's tip. Three smooth pleats originating proximally from the end of the vas deferens fade towards the proximal penis. Along their distal part they gradually become fringed with jagged edges. The background presents a fine chevron-like pattern.

### ***Montenegrina voidomatis thysi* Loosjes & Loosjes-van Bommel, 1988 comb. nov.**

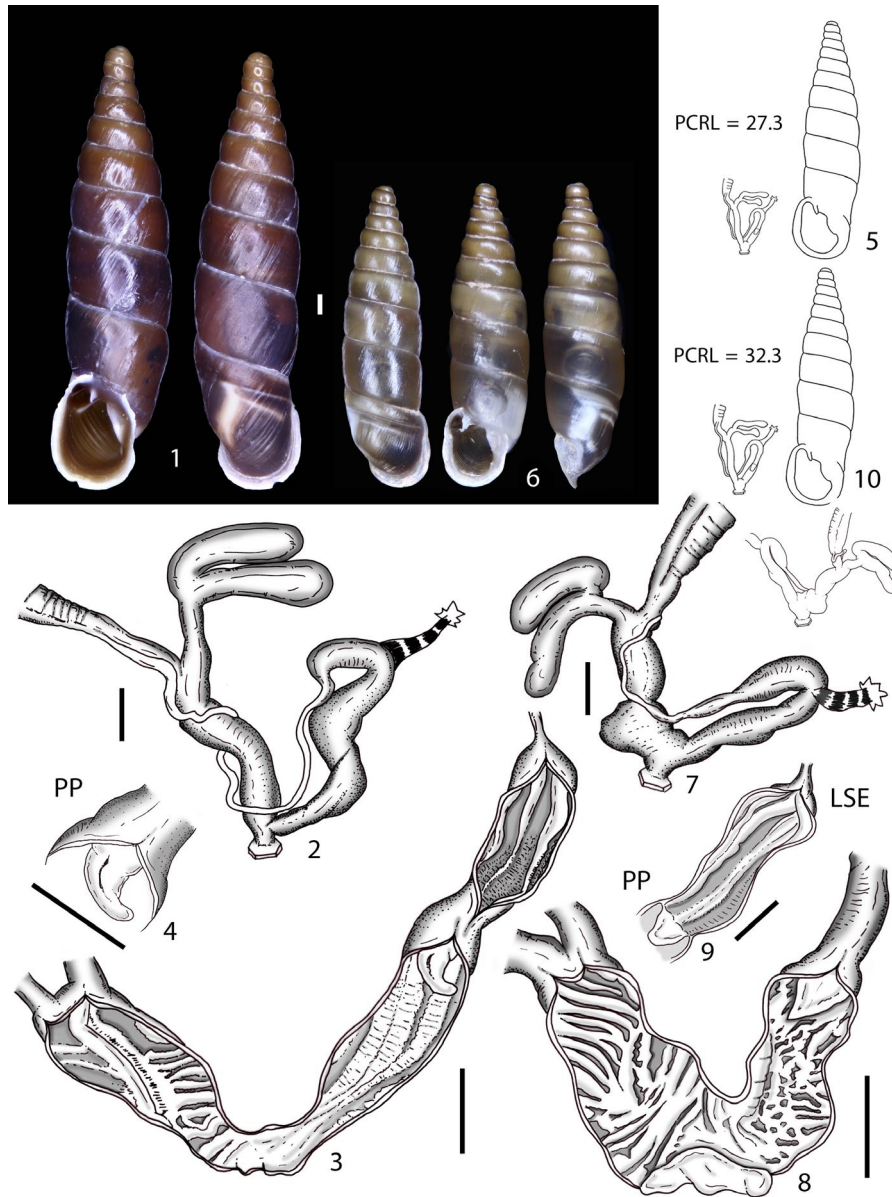
Figures 61.6–61.11

*Montenegrina thysi* Loosjes & Loosjes-van Bommel, 1988: 189–191, fig. 1.

*Montenegrina skipetarica thysi* – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 107, fig. 30D, distribution map fig. 31A.

**Examined material: two dissected specimens.** Greece, Epirus, Tymfi Mts, Vikos Gorge near the Agia Paraskevi Monastery, 1,030 m, 39.8910°N, 20.7538°E [type locality], leg. ZE, ZF, JG, 25.vi.2013 (HNHM 99532, Mty-388-01 [COI: KU307857, 16S: KU308214, 12S: KU307989]; Mty-388-02 [COI: MT251855]).

**External genitalia (Figure 61.7):** The whole genital complex is long (PCRL = 40.6). The FO is medium-sized (FO/V = 0.46) and wide in diameter. The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is very short (DBC/DB = 0.13) and thin. The bursa copulatrix is short (DB/V = 0.76), irregular in shape with a rounded apex. There is no visible transitional area between the second duct and the actual bursa. The diverticulum is also short (D/V = 0.90), wide, and wider and longer (D/BC = 1.19) than the bursa copulatrix. The apex is blunt. The vagina is medium-sized (VRL = 18.7) and irregular in shape with a swollen portion along its course. The atrium is large but short. The PC is much longer than the vagina (PC/V = 2.17). The penis is uniformly cylindrical and thin. The epiphallus is longer than the penis (E/P = 1.28), swollen along its proximal part and wider than the penis. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is moderately long.



**FIGURE 62** 62.1–62.5 *Montenegrina voidomatis voidomatis* Nordsieck, 1974 stat. nov. HHNM 99529. 62.1 shell, 62.2 whole distal genitalia, 62.3 inner distal genitalia, 62.4 penial papilla, 62.5 shell-genitalia ratio. 62.6–62.10 *Montenegrina soosi* Eröss and Szekeres, 2006 NHMW 110430/MN/0115. 62.6 shell, 62.7 whole distal genitalia, 62.8 inner distal genitalia, 62.9 penial papilla and proximal inner part of penis, 62.10 shell-genitalia ratio

**Inner genitalia (Figures 61.8–61.10):** The atrium has a big, polylobated fold originating directly at the genital aperture. The distal vagina is mainly smooth with only weak traces of a few irregular, flat transversal pleats. The proximal vagina bears many smooth, irregularly arranged pleats that randomly split and merge. The vaginal pilaster is absent. The penis is smooth but with a trace of one flat, longitudinal pleat that ends before entering the distal penis. The medium-sized, conical penial papilla has a pointed apex and a smooth surface. The aperture is lateral. The epiphallus shows three simple, smooth pleats originating proximally from the end of the vas deferens and fading towards the origin of the penial papilla. The background is smooth.

### *Montenegrina soosi* Eröss and Szekeres, 2006 sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

*Montenegrina soosi* is known from a small area in northern Albania in the Kukës District. It is monophyletic, forming a distinct subclade within the main Clade L. Its genital anatomy resembles that of *M. pinteri*, which, considering the phylogenetic and the geographic distance between the two taxa, is interpreted to be due to homoplasy rather than introgression or incomplete lineage sorting. Its status as a valid species is here confirmed.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina soosi</i> Eröss and Szekeres, 2006	<i>Montenegrina soosi</i> Eröss and Szekeres, 2006

## *Montenegrina soosi* Eröss and Szekeres, 2006

Figures 62.6–62.10

*Montenegrina janinensis soosi* Eröss and Szekeres, 2006 in Eröss et al., 2006: 197, fig. 18 – Nordsieck, 2009: 75.

*Montenegrina soosi* – Fehér & Szekeres, 2016: 108, fig. 28H, distribution map fig. 32.

**Examined material: two dissected specimens.** Albania, Kukës District, 1.3 km S of the mouth of the Përroi i Bushtricës, 400 m, 41.9254°N, 20.3569°E, leg. ZE, ZF, JG, 2.vii.2015 (NHMW 110430/MN/0115, Mso-413-01 [COI: KU307806, 16S: KU308196, 12S: KU307986]).

**External genitalia (Figure 62.7):** The whole genital complex is long (PCRL = 32.3), whereas the FO is short (FO/V = 0.29). The vas deferens is moderately thick along its whole course and becomes considerably wider towards the epiphallus. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.28). The bursa copulatrix is long (DB/V = 1.06), wide, uniformly cylindrical with a blunt apex. There is no visible transitional area between the second duct and the bursa itself. The diverticulum is short (D/V = 0.94), uniformly cylindrical, wider, and generally shorter (D/BC = 0.89) than the bursa copulatrix. The apex is blunt. The vagina is medium-sized (VRL = 12.8), remarkably wide and swollen along its whole course. The atrium is very large with a very large swelling along the vaginal side. The PC is much longer than the vagina (PC/V = 2.53). The penis is thinner than the vagina and slightly swollen at the level of the penial papilla. The epiphallus is much longer than the penis (E/P = 2.86), slightly swollen proximally and thinner distally. It merges into the vas deferens with a more or less distinct transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figures 62.8–62.9):** The atrium has a big, irregular, unilobate fold originating directly at the genital aperture. The distal vagina shows 6–10 smooth transversal pleats that do not continue into the atrium. The pleats are irregular, splitting, and merging into one another. The proximal vagina shows many smooth, oblique or transversal pleats that converge into a central longitudinal pleat. The background walls are smooth. The vaginal pilaster is present. The whole penis presents a variable number of smooth, randomly arranged pleats, variable in shape and length, forming sort of a net-like pattern. The medium-sized, conical penial papilla has a sharp, pointed apex, and smooth surface. The aperture is lateral. The epiphallus has up to five simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The distal background walls are fringed with a chevron-like pattern. The proximal background walls are smooth.

## *Montenegrina stankovici* (Urbański, 1960) sensu Fehér & Szekeres, 2016

### Taxonomic and systematic remarks

The taxonomy of *M. stankovici* is discussed in the *M. dofleini* remarks.

## *Montenegrina stankovici* (Urbański, 1960)

Figures 63.1–63.7

*Delima* (*Delima* [*Heteroptycha*]) *stankovici* Urbański, 1960: 51–54, plate la–c, fig. 1.

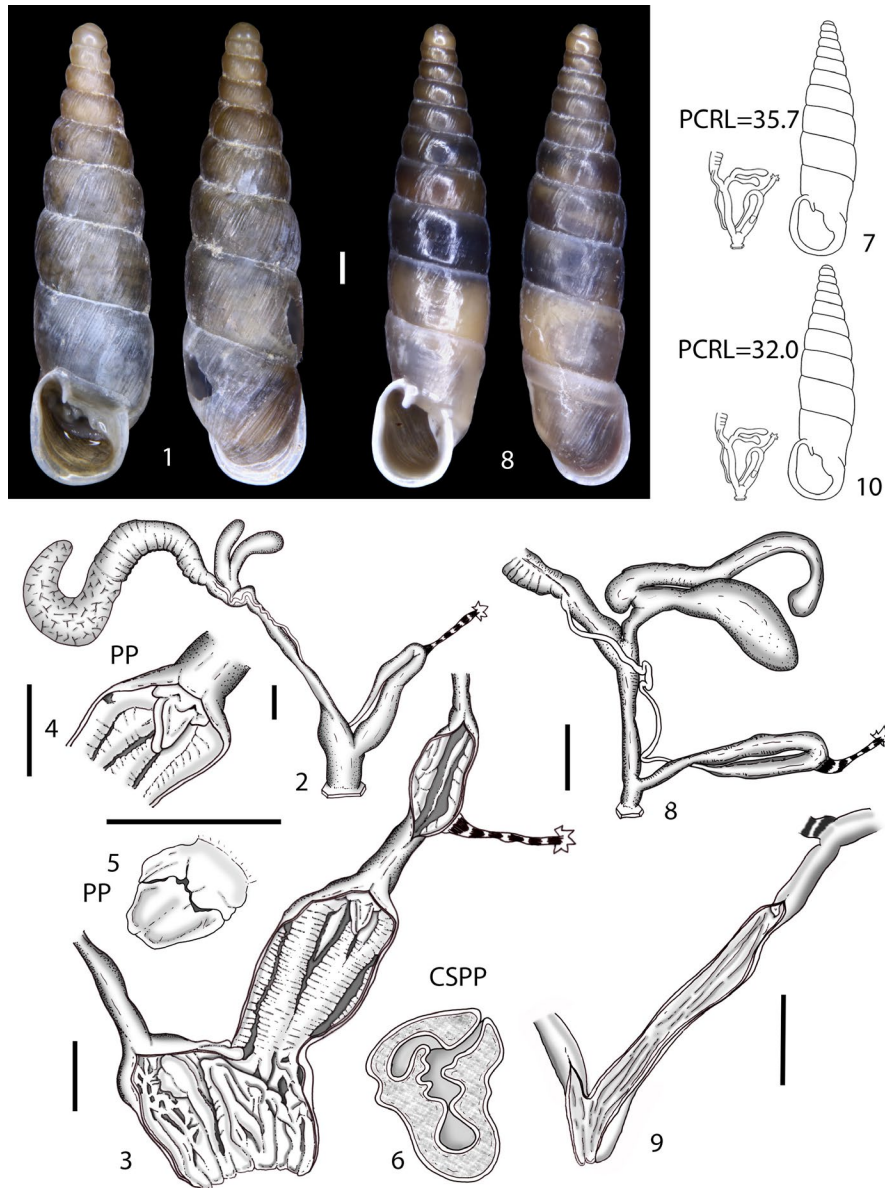
*Montenegrina stankovici* – Nordsieck, 1969b: 259. (genital anatomy) – Nordsieck, 1974: 135, plate 6, fig. 36 – Zilch, 1981: 132. – Nordsieck, 2009: 73.

*Montenegrina stankovici* – Fehér & Szekeres, 2016: 111, fig. 28I.

**Examined material: two dissected specimens.** North Macedonia, Ohrid District, Ohrid, N foot of the castle hill, 700 m, 41.1147°N, 20.7876°E, leg. ZF, LT, 10.viii.2014 (NHMW 110430/MN/0061, Mst-510-01 [COI: KU307846, 16S: KU308208]; Mst-510-02 [COI: KU307847, 16S: KU308209]).

**External genitalia (Figure 63.2):** The whole genital complex is long (PCRL = 35.7) with a slender appearance. The FO is very short (FO/V = 0.25). The vas deferens is very thin along its whole course. The first duct of the bursa copulatrix complex is extremely short (DBC/DB = 0.14). The bursa copulatrix is also extremely short (DB/V = 0.39), cylindrical with a blunt apex. There is no visible transitional area between the second duct and the bursa itself. The diverticulum is short (D/V = 0.34), uniformly cylindrical, slightly thinner and generally shorter (D/BC = 0.86) than the bursa copulatrix. The apex is blunt. The vagina is very long (VRL = 36.4) and thin. The atrium is very large and long. The PC is slightly shorter than the vagina (PC/V = 0.98). The penis is wider than the vagina and only gradually narrows proximally. The epiphallus is approximately as long as the penis (E/P = 0.96) and gradually narrows towards the vas deferens, without a clear transition zone. The retractor muscle is long and thin.

**Inner genitalia (Figures 63.3–63.6):** The atrium bears 9–12 small longitudinal pleats that branch and merge. The proximal portion of the atrium has a more irregular pattern of pleats. The distal vagina shows smooth, scattered, irregularly arranged pleats. The proximal vagina has 5–10 elevated longitudinal pleats connected by small fleshy bridges of varying thickness. The vaginal pilaster is present. The penis shows two main, fringed, metameric cords that extend from the penial papilla base as far as the atrium. The cords can merge at a very proximal level. Some smaller fringed cords can also be visible. The background is smooth. The penial papilla is medium-sized, conical, with a pointed apex and a smooth surface. The aperture is lateral but transversely oriented. The apical, aperture less part is smaller in diameter. The epiphallus shows two main, fringed pleats divided by a small, smooth pleat. The background is smooth.



**FIGURE 63** 63.1–63.7 *Montenegrina stankovici* (Urbański, 1960) NHMW 110430/MN/0061. 63.1 shell, 63.2 whole distal genitalia, 63.3 inner distal genitalia, 63.4 penial papilla and proximal inner part of penis, 63.5 penial papilla, 63.6 cross section penial papilla. 63.7 shell-genitalia ratio, 63.8–63.10 *Montenegrina gropana* Fehér & Szekeres, 2016 stat. nov. HNHM 99503. 63.8 shell, 63.9 whole distal genitalia, 63.10 shell-genitalia ratio

***Montenegrina sturanyana* Fehér & Szekeres, 2016 sensu Fehér & Szekeres, 2016 and *Montenegrina timeae* Eröss and Szekeres, 2006**

**Taxonomic and systematic remarks**

*Montenegrina sturanyana* and *M. timeae* are included in one of the two main subclades of Clade H. This subclade contains a paraphyletic *M. sturanyana* and a monophyletic *M. timeae*. These taxa are known to occur in central Albania with *M. timeae* in the north and *M. sturanyana. ostrovcensis* about 100 km southward.

*Montenegrina sturanyana* has three subspecies: *M. sturanyana sturanyana*, *M. sturanyana gropana*, and *M. sturanyana ostrovcensis*.

Unfortunately, no alcohol-preserved specimens of *M. sturanyana sturanyana* were available for anatomical investigation, but its position in the mt tree clearly supports the view that it is not conspecific with *M. sturanyana gropana* and *M. sturanyana ostrovcensis*. No alcohol-preserved specimen was available for *M. sturanyana ostrovcensis* as well. The lack of anatomical data prevents a more in-depth taxonomic analysis, and thus, we retain it as *M. sturanyana ostrovcensis*.

Concerning *M. timeae* and *M. sturanyana gropana*, their genitalia show a certain degree of similarity, both of them being slender and more or less smooth as regards the inner sculpturing of the male and female parts. *M. timeae*, however, completely lacks the penial papilla (Figures 57 and 63). Unfortunately, the pivotal genital anatomy of

the population HNHM 99504 (Mop-317) is missing. Nonetheless, their similarity implies a quite recent split. We consider *M. gropana* stat. nov. as a valid species, confirming the status of *M. timeae* as a valid species, even though more data are necessary to better understand the relationships between these taxa.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina sturanyana sturanyana</i> Fehér & Szekeres, 2016	<i>Montenegrina sturanyana</i> Fehér & Szekeres, 2016
<i>Montenegrina sturanyana gropana</i> Fehér & Szekeres, 2016	<i>Montenegrina gropana</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina sturanyana ostrovicensis</i> Fehér & Szekeres, 2016	<i>Montenegrina sturanyana ostrovicensis</i> Fehér & Szekeres, 2016
<i>Montenegrina timeae</i> Eröss and Szekeres, 2006	<i>Montenegrina timeae</i> Eröss and Szekeres, 2006

### *Montenegrina sturanyana* Fehér & Szekeres, 2016

*Montenegrina sturanyana sturanyana* – Fehér & Szekeres, 2016: 112, fig. 34K, distribution map fig. 33.

No alcohol-preserved specimens were available for anatomical investigations.

### *Montenegrina gropana* Fehér & Szekeres, 2016 stat. nov.

Figures 63.8–63.10

*Montenegrina sturanyana gropana* – Fehér & Szekeres, 2016: 114, fig. 34M, distribution map fig. 3.

**Examined material: two dissected specimens (paratypes).** Albania, Tiranë District, Gropa Mts, Bizë, gorge of the Kaprol Stream near a military camp, 1,250 m, 41.3392°N, 20.1989°E [type locality], leg. ZF, TK, DM, 20.vi.2012 (HNHM 99503, Mop-316-01 [COI: KU307531]).

**External genitalia (Figure 63.8):** The whole genital complex is long (PCRL = 32.0) with a very slender appearance. The FO is also long (FO/V = 0.67). The vas deferens is thin along its whole course. The whole bursa copulatrix complex is very large compared to the remaining distal genitalia. The first duct of the complex of the bursa copulatrix is short (DBC/DB = 0.19). The bursa copulatrix is extremely long (DB/V = 1.50), huge, and wide, markedly club-like with a big and rounded apex. There is no transition area between the second duct and the bursa itself. The diverticulum is extremely long (D/V = 2.28), uniformly cylindrical, much thinner, and much longer (D/BC = 1.52) than the bursa copulatrix. The apex is swollen and rounded. The vagina is medium-sized or short (VRL = 11.8), thin, and uniformly cylindrical. The atrium is small but long. The PC is much longer than the vagina (PC/V = 2.72). The penis is approximately as

wide as the vagina and uniformly cylindrical. The epiphallus is longer (E/P = 1.72) and as thin as the penis and cylindrical along its whole course. The retractor muscle is long and thin.

**Inner genitalia (Figure 63.9):** The atrium is as smooth as the whole vagina. The vaginal pilaster is absent. The penis is completely smooth, with only weak traces of flat longitudinal pleats. The penial papilla is very small, with a smooth surface, pointed, and with a lateral opening. The epiphallus shows three simple, smooth pleats originating proximally from the end of the vas deferens and fading towards the base of the penial papilla. The background is smooth.

### *Montenegrina sturanyana ostrovicensis* Fehér & Szekeres, 2016

*Montenegrina sturanyana ostrovicensis* – Fehér & Szekeres, 2016: 114, fig. 34L, distribution map fig. 33.

No alcohol-preserved specimens were available for anatomical investigations.

### *Montenegrina timeae* Eröss and Szekeres, 2006

Figures 69.1–69.6

*Montenegrina irmengardis timeae* Eröss and Szekeres, 2006 in Eröss et al., 2006: 194–196, fig. 15.

*Montenegrina skipetarica timeae* – Nordsieck, 2009: 73.

*Montenegrina timeae* – Fehér & Szekeres, 2016: 122, fig. 34F, distribution map fig. 36.

**Examined material: two dissected specimens.** Albania, Mat District, 6.7 km NE of Gurri i Bardhë, along the road from Klos to Elbasan, 650 m, 41.4682°N 20.0903°E, HNHM 94857, leg. ZF, JK, DM09.x.2004 (HNHM 94856, Mti-239-01 [COI: KU307850]).

**External genitalia (Figure 69.2):** The whole genital complex is medium-sized (PCRL = 22.6) with a slender appearance. The FO is medium-sized (FO/V = 0.42). The vas deferens is thin along its whole course. The first duct of the bursa copulatrix complex is medium-sized (DBC/DB = 0.32). The bursa copulatrix is short (DB/V = 0.7), slim, and cylindrical with a slightly swollen apex. There is no clear transition area between the second duct and the bursa itself. The diverticulum is short (D/V = 0.8), slim and uniformly cylindrical, thinner, and longer (D/BC = 1.3) than the bursa copulatrix. The apex is swollen and rounded. The vagina is medium-sized or short (VRL = 17.1), thin and uniformly cylindrical. The atrium is large with a swelling along the vaginal side. The PC is longer than the vagina (PC/V = 1.32). The penis is slightly wider than the vagina and uniformly cylindrical. The epiphallus is shorter (E/P = 0.95) and thinner than the penis and cylindrical along its whole course. The retractor muscle is short but large.

**Inner genitalia (Figures 69.3–69.5):** The atrium is completely smooth, as is the whole vagina. The vaginal pilaster is absent.

The penis is completely smooth. The penial papilla is absent. The epiphallus has two or three simple, smooth pleats with jagged edges, originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina subcristata* (Pfeiffer, 1848) sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

*Montenegrina subcristata* has the widest distributional area, which includes western Montenegro and northwestern Albania. The species is highly variable in shell size, shape, and the position of the lunella complex. At least seven different names have been introduced to describe this variability (Fehér & Szekeres, 2016). Nordsieck (2007, 2009) in its revisions accepted only two valid subspecies. According to Fehér and Szekeres (2016) and the molecular genetic data (Mason et al., 2020), no subspecies were delimited because no clear borders were detected among taxa. Thus, only the nominal taxon was considered as valid and the other names were synonymized. This conclusion is strongly supported by the anatomical-genital data. Despite its large distributional range and high shell variability (dimensions, shape, clausiliar apparatus), *M. subcristata* shows a remarkable stability of the genital features, which supports the recent vision of Fehér and Szekeres (2016) to merge all the former subspecific taxa and to synonymize them into the nominal taxon.

#### Fehér & Szekeres, 2016

*Montenegrina subcristata*  
(Pfeiffer, 1848)

#### De Mattia et al., 2020

*Montenegrina subcristata*  
(Pfeiffer, 1848)

### *Montenegrina subcristata* (Pfeiffer, 1848).

Figures 64.1–64.14, 65.1–65.13, 66.1–66.13, 67.1–67.12, 68.1–68.12

*Clausilia subcristata* Pfeiffer, 1848: 438. – Küster, 1844–1862: 39–40, plate 4, figs 10–13 – Schmidt, 1868: 70.

*Clausilia cattaroënsis* (partim) – Walderdorff, 1864: 509.

*Clausilia cattaroënsis* var. *minor* Boettger, 1877: 66.

*Clausilia* (*Herilla*) *klecaki* (sic!) Westerlund, 1881: 55.

*Clausilia subcristata* *Clausilia* (*Delima*) *subcristata* – Westerlund, 1884: 54. – Clessin, 1885: 182. – Wohlberedt, 1907: 551–552. – Wohlberedt, 1909: 675, plate 14, figs 158–161.

*Clausilia* (*Delima*) *kleciaki* – Westerlund, 1884: 54.

*Clausilia* (*Delima*) *wohlberedti* Möllendorff, 1899: 169–170.

*Clausilia* (*Delima*) *wohlberedti* var. – Möllendorff, 1899: 170.

*Delima wohlberedti* var. *sublabiata* v. Möll. – Wohlberedt, 1901: 198, 206. (*nomen nudum*).

*Clausilia* (*Delima*) *kleciaki* var. *brunnea* Boettger, 1907 in Wohlberedt, 1907: 553. – Wohlberedt, 1909: 676–677.

*Clausilia* (*Delima*) *subcristata* var. *interior* Boettger in Wohlberedt, 1907: 552. – Wohlberedt, 1909: 675, plate 14, fig. 162–163.

*Clausilia* (*Delima*) *subcristata* var. *sublabiata* Wohlberedt, 1907: 553. – Wohlberedt, 1909: 676.

*Clausilia* (*Delima*) *subcristata* f. *minor* – Wohlberedt, 1907: 552.

*Clausilia* (*Delima*) *subcristata wohlberedti* – Wohlberedt, 1907: 552–553. – Wohlberedt, 1909: 675–676, plate 14, figs 164–169.

*Delima* (*Delima*) *cattaroënsis* – Sturany & Wagner, 1915: 73.

*Delima* (*Delima*) *cattaroënsis kleciaki* – Sturany & Wagner, 1915: 73.

*Delima* (*Albanodelima*) *subcristata* – Wagner, 1924: 118. – Wagner, 1925: 67, plate 2, fig. 23. (genital anatomy).

*Delima* (*Albanodelima*) *kleciaki* – Wagner, 1924: 118. – Wagner, 1925: 67, plate 3, fig. 26. (genital anatomy).

*Delima* (*Albanodelima*) *subcristata wohlberedti* – Wagner, 1924: 119.

*Delima* (*Albanodelima*) *subcristata interior* – Wagner, 1924: 119.

*Clausilia laxa* – Wagner, 1924: 119.

*Montenegrina subcristata* – Nordsieck, 1969b: 259. (genital anatomy).

*Montenegrina subcristata subcristata* – Zilch, 1981: 131, plate 13, fig. 19. – Nordsieck, 2009: 73.

*Montenegrina subcristata wohlberedti* – Zilch, 1981: 131, plate 13, figs 20–22 – Nordsieck, 2009: 73.

*Montenegrina subcristata* – Fehér & Szekeres, 2016: 116, fig. 34A–E, distribution map fig. 35.

**Examined material: 26 dissected specimens.** Albania, Shkodër, Rozafa Hill, S side, 42.0451°N, 19.4902°E, leg. TD, ZE, ZF, 28.v.2015 (NHMW 110430/MN/0143, Mwo-603-01 [COI: KU307892]).

Montenegro, Njeguši, near the church, 880 m, 42.4316°N, 18.8126°E, leg. TD, ZE, ZF, 29.v.2015 (NHMW 110430/MN/0149, Msr-609-01 [COI: KU307836]).

Montenegro, Nikšić, Prekornica, Bogateci, 450 m, 42.6862°N, 18.994°E, leg. MD, EH HS, 5.iv.2017 (NHMW 11030/MN/0258, Msr-659-01 [COI: MT251807]).

Montenegro, Zeta Valley, ca. 2 km S of Nikšić along the road to Podgorica, 620 m, 42.7319°N, 18.9382°E, leg. TD, ZE, ZF, 30.v.2015 (NHMW 110430/MN/0150, Msr-610-01).

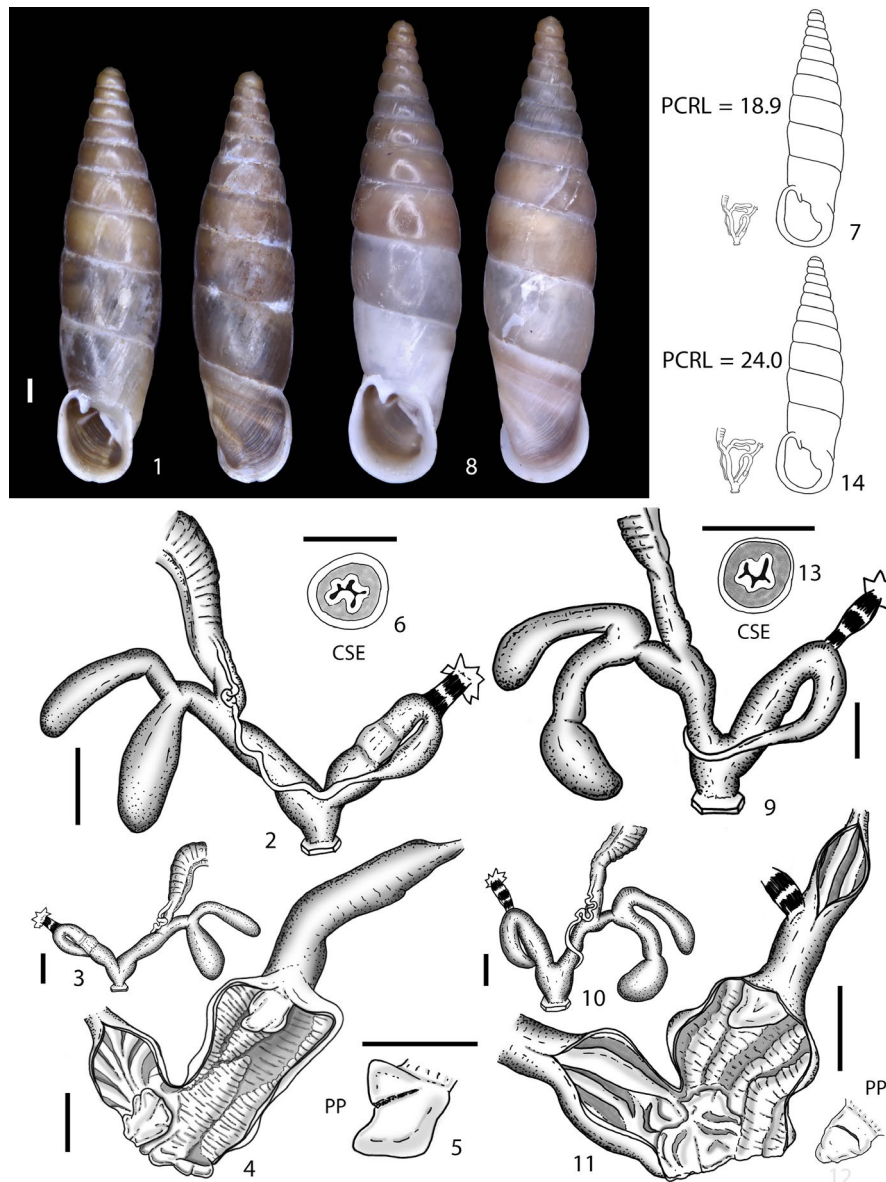
Montenegro, Podgorica District, Vitoja Spring, 42.3252°N, 19.3623°E, leg. MD, EH, KJ, HS, 8.vii.2015 (NHMW 110430/MN/0158, Msr-640-01 [COI: KU307837]; Msr-640-02 [COI: MT251801]).

Montenegro, Podgorica, Ljubović hill, SE slope, 42.430598°N, 19.25468°E, leg. WDM, JM 15.v.2014 (WDM 7231, no DNA material).

Montenegro, Virpazar, 42.2460°N, 19.0917°E, leg. TD, ZE, ZF, 25.v.2015 (NHMW 110430/MN/0122, Mwo-581-01 [COI: KU307882]).

Montenegro, Virpazar, abandoned quarry SW of the town, 42.2430°N, 19.0860°E, leg. WDM, JM, 15.v.2014 (WDM 7242, no DNA material).

Montenegro, Virpazar, town's walls, 42.2447°N, 19.0917°E, leg. WDM, JM, 15.v.2014 (WDM 7269, no DNA material).



**FIGURE 64** *Montenegrina subcristata* (Pfeiffer, 1848) NHMW 110430/MN/0143. 64.1 shell. 64.2–64.3 whole distal genitalia. 64.4 inner distal genitalia, 64.5 penial papilla, 64.6 cross section of epiphallus, 64.7 shell-genitalia ratio. NHMW 110430/MN/0150. 64.8 shell. 64.9–64.10 whole distal genitalia. 64.11 inner distal genitalia. 64.12 penial papilla. 64.13 cross section of epiphallus. 64.14 shell-genitalia ratio

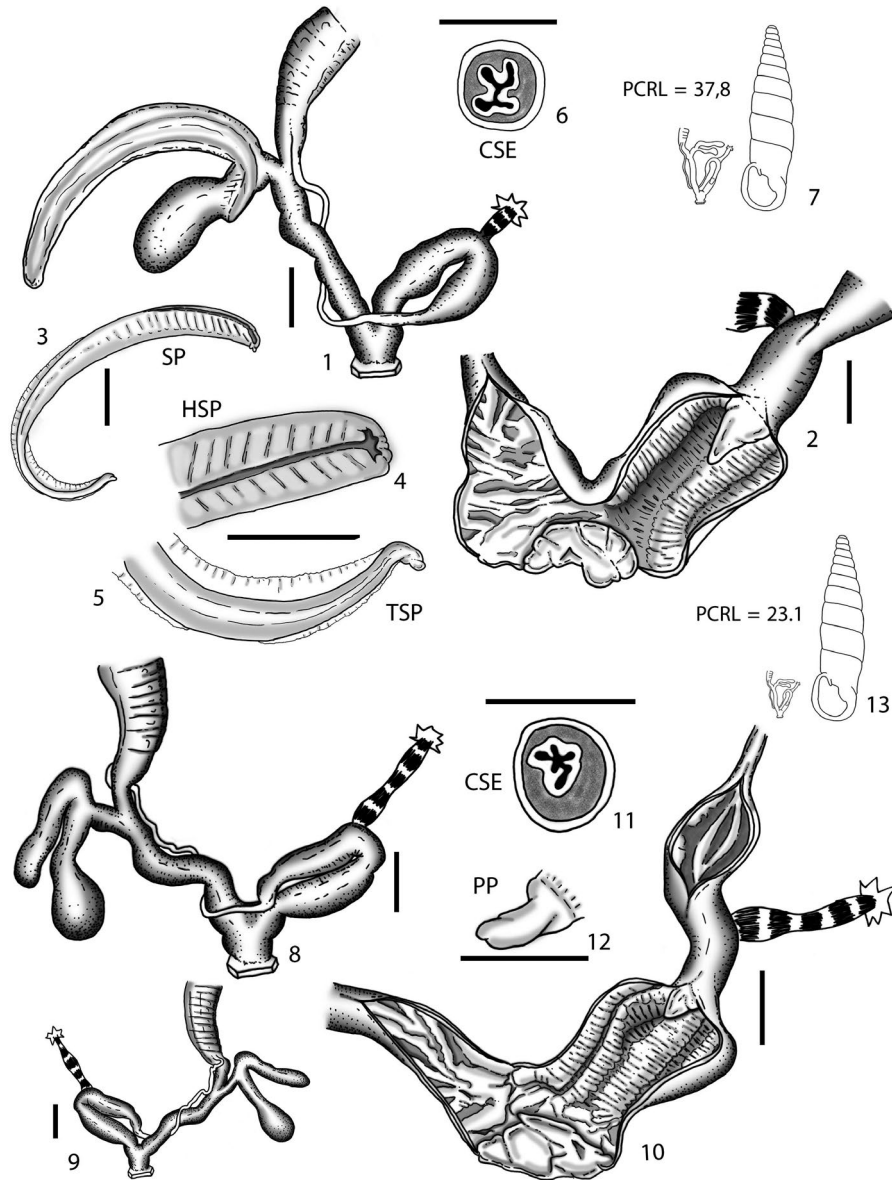
Montenegro, Žabljak Crnojevića, fortress, 50 m, 42.3172°N, 19.1567°E, leg. TD, ZE, ZF, 25.v.2015 (NHMW 110430/MN/0121, Mwo-580-02 [COI: KU307880]).

Montenegro, Rijeka Crnojevića, 24 m, 42.3562°N, 19.0330°E, leg. WDM, JM, 16.v.2014 (WDM 7235, no DNA material).

Montenegro, Cetinje, limestone walls W of the town, 845 m, 42.4045°N, 18.8876°E, leg. WDM, JM, 18.v.2014 (WDM 7273, no DNA material).

**External genitalia (Figures 64.2–64.3, 64.9–64.10, 65.1, 65.8–65.9, 66.2–66.3, 66.8–66.9, 67.2, 67.7–67.8, 68.2–68.3, 68.9–68.10):** The whole genital complex is long (PCRL = 30.0, 20.5–36.4). The FO is short (FO/V = 0.4, 0.14–1.0). The vas deferens is thin along its whole course. The whole bursa copulatrix complex is very large compared to the rest of the distal genitalia. The first duct of

the bursa copulatrix complex is short (DBC/DB = 0.3, 0.08–0.57). The bursa copulatrix is medium-sized to long (DB/V = 1.0, 0.5–2.07), very large, and wide, markedly club-like with a big and rounded apex. There usually is a distinct transitional area between the second duct and the bursa itself. The diverticulum is medium-sized (D/V = 1.0, 0.45–2.67), uniformly cylindrical, or slightly club-like, usually as wide as the bursa copulatrix and as long or slightly longer (D/BC = 1.0, 0.81–1.29). The apex is rounded. The vagina is of variable length (VRL = 18.1, 7.5–27.1), thin, and uniformly cylindrical. The atrium is big and long. The PC is usually longer than the vagina (PC/V = 1.8, 0.84–3.2). The penis is approximately as wide as the vagina and uniformly cylindrical. The epiphallus is usually longer (E/P = 1.3, 0.66–1.72). ( $n = 26$ ) and thinner than the penis and cylindrical along its whole course. There is no clear transitional zone between the



**FIGURE 65** *Montenegrogrina subcristata* (Pfeiffer, 1848) NHMW 110430/MN/0149. 65.1 whole distal genitalia. 65.2 inner distal genitalia. 65.3 spermatophore. 65.4 head of spermatophore. 65.5 tail of spermatophore. 65.6 cross section of epiphallus. 65.7 shell-genitalia ratio. NHMW 110430/MN/0122. 65.8–65.9 whole distal genitalia. 65.10 inner distal genitalia. 65.11 cross section of epiphallus. 65.12 penial papilla. 65.13 shell-genitalia ratio

epiphallus and the vas deferens. The retractor muscle is short and strong.

**Inner genitalia (Figures 64.4–64.6, 64.11–64.13, 65.6, 65.11–65.12, 66.4–66.5, 66.10–66.12, 67.3–67.4, 67.9–67.11, 68.4–68.6, 68.11):** The atrium has a big, polylobated fold originating directly at the genital aperture. The distal vagina shows 5–10 smooth transversal or slightly oblique pleats that merge medially to form a backbone pattern. The proximal vagina presents 5–10 elevated longitudinal pleats. The pleats can be connected with small fleshy bridges. The vaginal pilaster is present. The penis has three or four main, fringed, irregularly metameric cords that extend from the penial papilla base as far as the atrium. The cords merge into one another, especially at the very proximal or distal ends. The background is transversely

fringed. The penial papilla is medium-sized, conical, with a pointed but nonetheless broad apex and a smooth surface. The aperture is lateral and does not reach the papilla's tip, opening half way to the tip. The epiphallus has two or three simple, smooth pleats with jagged edges, originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is transversely irregular.

**Spermatophore (Figures 65.3–65.5):** The spermatophore is slender with a narrow head and tail. It is uniformly bent from the head to the tail. The head is large with a “mouth” resulting from the junction of the right and left sides. The mouth continues towards the tail with an open channel that closes almost where the dorsal keel begins. The tail is narrow but irregularly rounded, almost bilobate.



The lower carina is present only along the first quarter of the spermatophore length. The upper carina is present only three quarters of the length of the spermatophore. A small, minor dorsal carina is present along the tail. Along the anterior part of the spermatophore the lateral surface presents a weak, but slightly dense, rib-like sculpturing. The cross section is oval-roundish with two lateral keels. The largest one has a large base, it is roughly rectangular in section, with one sharp lateral edge. The smaller one is rounded. The spermatophore is 5.1 mm long and 0.6 mm wide.

### *Montenegrina tomorosi* Brandt, 1961 sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

All the subspecific taxa of *M. tomorosi* s.l. are positioned in Clade K. As already stated in the *M. minuscula* section, a few populations identified as *M. tomorosi* from the peak of Mount Tomor unexpectedly fall into Clade J. No anatomical data are available for this set of populations and, thus, no integrative approach is possible. As a consequence, the status and the systematic position of those populations (Mto-234, Mto-663 and Mto-670), provisionally deemed as *M. cfr tomorosi* (based on shell morphology; Fehér & Szekeres, 2016: 123), will be discussed as soon as new data becomes available.

The remaining *M. tomorosi* s.l. populations are all very closely grouped together and mixed up in the phylogenetic tree. Anatomical data are also lacking for most of these populations, with only two populations dissected: *M. t. tomorosi* Mto-648 and *M. t. coeruleus* Mce-664. The genitalia of these two taxa show major differences in the inner structure and sculpturing. *Montenegrina t. tomorosi* exhibits a pleated male part and a penial papilla, whereas *M. t. coeruleus* has a smooth inner penis and lacks the penial papilla (Figure 70.9).

*Montenegrina fuchsi muranyii* falls into the *M. tomorosi* s.l. clade. Fehér and Szekeres (2016: 35) placed it conchologically into *M. fuchsi* due to its "fuchsoid" shell, although this taxon is found ca. 50 km north of the nearest *M. fuchsi* s.l. population (Fehér & Szekeres, 2016: 33). Its position in the tree shows its close phylogenetic relationship with *M. tomorosi*, and the shell similarity to *M. fuchsi* could merely be a homoplasy. While its genital anatomy is markedly different from *M. tomorosi tomorosi*, it is similar to *M. t. coeruleus*. It completely lacks the penial papilla and the distal penis is smooth (Figure 71.4). Nonetheless, the results allow considering *M. fuchsi muranyii* as a subspecies of *M. tomorosi*: *M. tomorosi muranyii* comb. nov.

The differences in genital morphology reveal a certain degree of separation/isolation among the *M. tomorosi* populations. This also appears in the phylogenetic tree (Mason et al., 2020). Still, the currently available data does not allow a proper integrative evaluation of the systematic position of the subspecific taxa. We thus leave the nomenclature as presented in Fehér and Szekeres (2016) until new data becomes available.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina tomorosi tomorosi</i> Brandt, 1961	<i>Montenegrina tomorosi tomorosi</i> Brandt, 1961
<i>Montenegrina tomorosi ampla</i> Fehér & Szekeres, 2006	<i>Montenegrina tomorosi ampla</i> Fehér & Szekeres, 2006
<i>Montenegrina tomorosi coeruleus</i> Nordsieck, 1996	<i>Montenegrina tomorosi coeruleus</i> Nordsieck, 1996
<i>Montenegrina tomorosi hunyadii</i> Fehér & Szekeres, 2016	<i>Montenegrina tomorosi hunyadii</i> Fehér & Szekeres, 2016
<i>Montenegrina fuchsi muranyii</i> Fehér & Szekeres, 2006	<i>Montenegrina tomorosi muranyii</i> Fehér & Szekeres, 2006 comb. nov.

### *Montenegrina tomorosi tomorosi* Brandt, 1961

Figures 70.1–70.6

*Montenegrina (Montenegrina) janinensis tomorosi* Brandt, 1961: 3–4, plate 1, fig. 2.

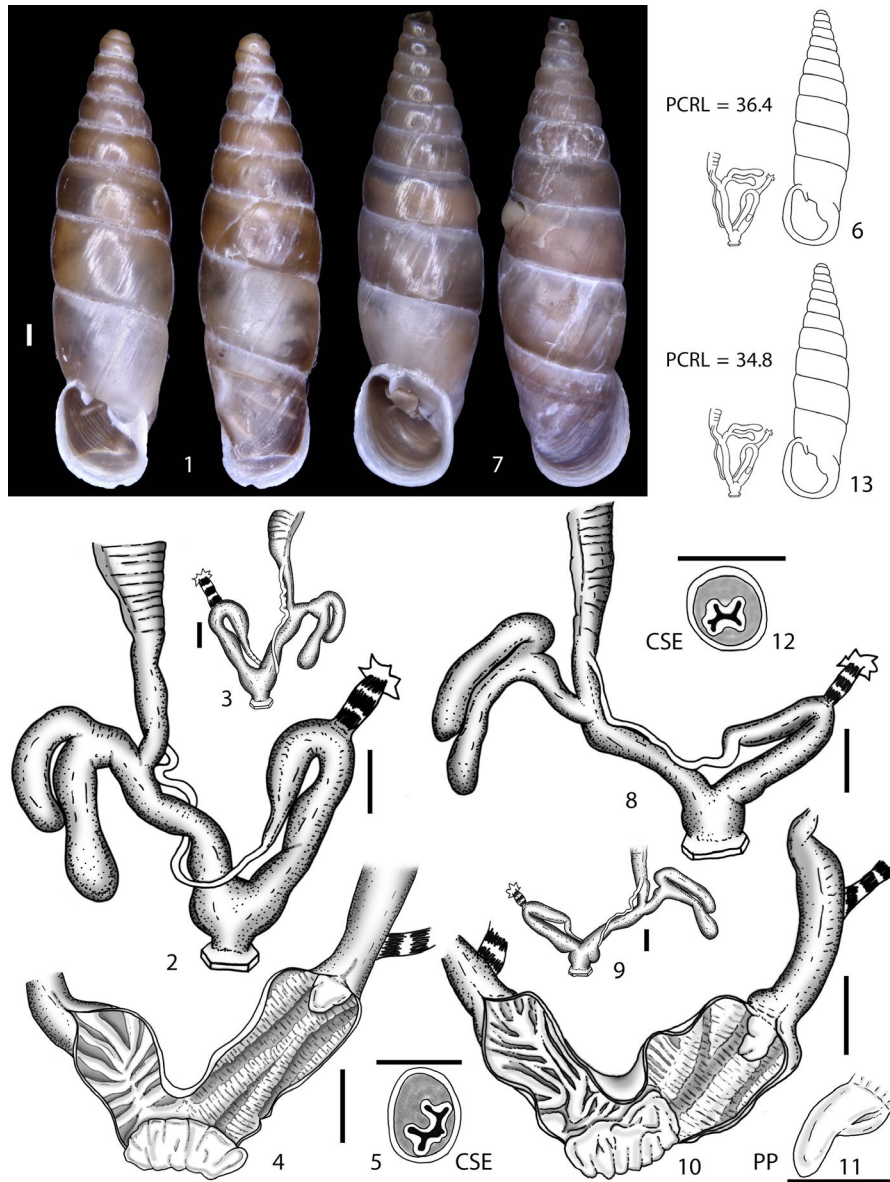
*Montenegrina janinensis tomorosi* – Zilch, 1981: 129, plate 14, fig. 2. – Nordsieck, 2009: 75.

*Montenegrina tomorosi tomorosi* – Fehér & Szekeres, 2016: 124, fig. 34G, distribution map fig. 36.

**Examined material:** two dissected specimens. Albania, Skrapar District, between Tomorr and Kulmak Mts, rock with small caves, 1,280 m, 40.597°N, 20.204°E, leg. GP, G., MS, JU, BV, 23.ix.2015 (HNHM 99724, Mto-648-01 [COI: MT251841]; Mto-648-02 [COI: MT251842]).

**External genitalia (Figure 70.2):** The whole genital complex is medium-sized (PCRL = 26.7) and bulky. The FO is medium-sized (FO/V = 0.41). The vas deferens is long and thin along its whole course. The first duct of the bursa copulatrix complex is short to medium-sized (DBC/DB = 0.30). The bursa copulatrix is very long (DB/V = 1.35), wide in diameter, almost completely cylindrical, only slightly swollen at the apex. There is no clear transitional area between the second duct and the bursa itself. The diverticulum is medium-sized (D/V = 1.3), wide, and uniformly cylindrical, gradually narrowing towards the apex and slightly shorter than the bursa copulatrix (D/BC = 0.95). The apex is pointed. The vagina is medium-sized or short (VRL = 10.6), proximally thin and gradually swelling towards the distal portion. The atrium is large. The PC is much longer than the vagina (PC/V = 2.53). The penis is as wide as the vagina. The epiphallus is shorter (E/P = 0.79) and thinner than the penis and gradually narrows towards the vas deferens. There is a more or less distinct transition zone between the epiphallus and the vas deferens. The retractor muscle is short but large.

**Inner genitalia (Figures 70.3–70.5):** The atrium is smooth with only sparse, irregular, smooth, flat pleats. The distal vagina is mostly smooth. The proximal vagina has 5–10 slim, elevated longitudinal pleats. The vaginal pilaster is present. The proximal penis shows an irregular pattern of fringed cords. Along the distal penis there are



**FIGURE 66** *Montenegrina subcristata* (Pfeiffer, 1848) NHMW 110430/MN/0158. 66.1 shell. 66.2–66.3 whole distal genitalia. 66.4 inner distal genitalia. 66.5 cross section of epiphallus. 66.6 shell-genitalia ratio. NHMW 110430/MN/0121. 66.7 shell. 66.8–66.9 whole distal genitalia. 66.10 inner distal genitalia. 66.11 penial papilla. 66.12 cross section of epiphallus. 66.13 shell-genitalia ratio

two or three irregular, main metameric cords. The penial papilla is small, globose and rounded. The aperture extends laterally, reaching the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

#### ***Montenegrina tomorosi ampla* Fehér & Szekeres, 2006**

*Montenegrina janinensis ampla* Fehér & Szekeres, 2006 in Eröss et al., 2006: 196, fig. 16. – Nordsieck, 2009: 75.

*Montenegrina tomorosi ampla* – Fehér & Szekeres, 2016: 125, fig. 34I, distribution map fig. 36.

No alcohol-preserved specimens were available for anatomical investigations.

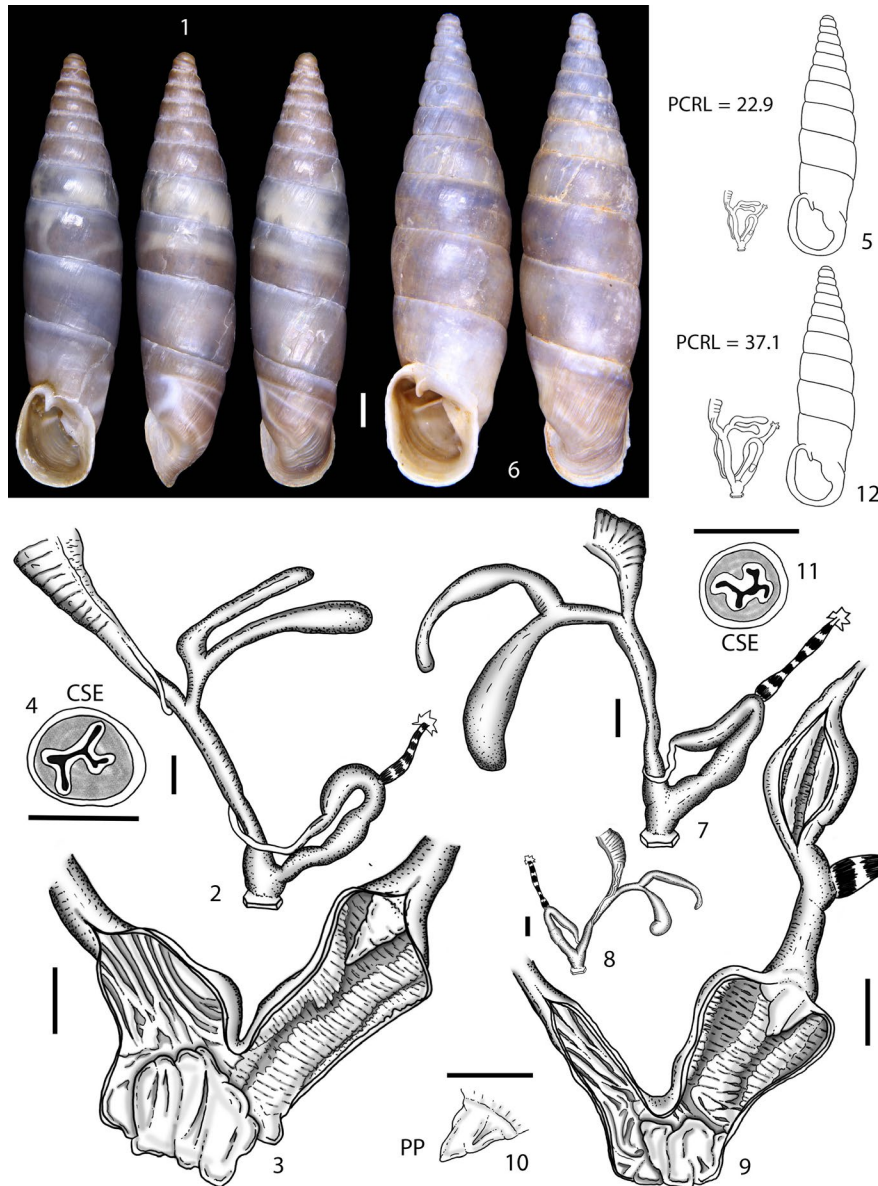
#### ***Montenegrina tomorosi coerulescens* Nordsieck, 1996**

Figures 70.7–70.11

*Montenegrina janinensis coerulescens* Nordsieck, 1996: 10, plate 3, fig. 4 – Nordsieck, 2009: 75.

*Montenegrina tomorosi coerulescens* – Fehér & Szekeres, 2016: 126, fig. 34H, distribution map fig. 36.

**Examined material:** two dissected specimens. Albania, Tomorr Mts., eastern slopes, above Roms, 2,178 m 40.6972°N 20.1486° E,



**FIGURE 67** *Montenegrina subcristata* (Pfeiffer, 1848) WDM 7269. 67.1 shell. 67.2 whole distal genitalia. 67.3 inner distal genitalia. 67.4 cross section of epiphallus. 67.5 shell-genitalia ratio. WDM 723167.6 shell 67.7–67.8 whole distal genitalia. 67.9 inner distal genitalia. 67.10 penial papilla. 67.11 cross section of epiphallus. 67.12 shell-genitalia ratio

leg. AP, 21.vii.2016 (NHMW 110430/MN/0264, Mce-664-04 [COI: MT251524]; Mce-664-05 [COI: MT251525]).

**External genitalia (Figure 70.8):** The whole genital complex is medium-sized (PCRL = 29.9). The FO is long (FO/V = 0.73). The vas deferens is long and thin along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.24). The bursa copulatrix is long (DB/V = 1.13), wide in diameter and almost uniformly cylindrical along its whole course. There is no clear transitional area between the second duct and the bursa itself. The diverticulum is medium-sized (D/V = 1.20), wide and club-like with a blunt apex and only slightly longer than the bursa copulatrix (D/BC = 1.06). The vagina is short (VRL = 10.4), wide in diameter and slightly wider proximally. The atrium is large and slightly larger at the vaginal side. The PC is much longer than the vagina (PC/V = 2.87). The penis is thinner

than the vagina and almost uniformly cylindrical. The epiphallus is longer than the penis (E/P = 1.26) and slightly swollen along its proximal part. There is a more or less distinct transitional zone between the epiphallus and the vas deferens. The retractor muscle is short but large.

**Inner genitalia (Figures 70.9–70.10):** The atrium, the vagina, and the penis are almost completely smooth. Along all the three parts, only very weak longitudinal smooth pleats are barely visible. Along the proximal vagina, the vaginal pilaster is clearly visible. The penial papilla is absent. The transitional area between the penis and the epiphallus shows a set of longitudinal pleats, forming a sort of fleshy crown but not a true penial papilla. The epiphallus has two or three simple, smooth pleats with jagged edges, originating proximally from the end of the vas deferens and

fading before the origin of the penial papilla. The background is transversely irregular.

### *Montenegrina tomorosi hunyadii* Fehér & Szekeres, 2016

*Montenegrina tomorosi hunyadii* – Fehér & Szekeres, 2016: 127, fig. 34J, distribution map fig. 36.

No alcohol-preserved specimens were available for anatomical investigations.

### *Montenegrina tomorosi muranyii* Fehér & Szekeres, 2006 comb. nov.

Figures 71.1–71.5

*Montenegrina fuchsi muranyii* Fehér & Szekeres, 2006 in Eröss et al., 2006: 189–190, fig. 9 – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 35, fig. 15D, distribution map fig. 16.

**Examined material: two dissected specimens (paratypes).** Albania, Berat District, Tomorr Mts, Kalaja e Tomorrit, 1100 m, 40.7025°N, 20.1093°E [type locality], leg. DM, 26.v.2004, (HNHM 94847, Mmu-226-02 [COI: KU307717]; Mmu-226-04 [COI: KU307718]).

**External genitalia (Figures 71.2–71.3):** The whole genital complex is medium-sized (PCRL = 25.8). The FO is long (FO/V = 1.29). The vas deferens is uniformly thin. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.28). The bursa copulatrix is long (DB/V = 2.57), very wide, club-like with a swollen and rounded apex. A transition zone between the second duct and the bursa itself is poorly visible. The diverticulum is long (D/V = 1.71), but much shorter (D/BC = 0.67) and as wide as the bursa copulatrix. It is more or less uniformly cylindrical. The vagina is extremely short (VRL = 5.8), bulky, and cylindrical. The atrium is large. The PC is considerably longer than the vagina (PC/V = 4.43), thinner distally and gradually swelling towards the epiphallus. The cylindrical epiphallus, slightly longer than the penis (E/P = 1.07), merges into the vas deferens with a visible transitional area. The retractor muscle is short and strong.

**Inner genitalia (Figure 71.4):** The atrium is almost completely smooth. The distal vagina shows 6–10 smooth transversal pleats that do not continue into the atrium. These pleats often merge along their midportion. The proximal vagina bears 5–10 elevated, irregular longitudinal pleats that can be connected with fleshy bridges and can be more or less broad. The vaginal pilaster is present. The proximal penis shows 12 to 14 smooth transversal pleats that gradually narrow in width distally. The last pleat gradually stretches and fades towards the distal penis, which is completely smooth. The penial papilla is small, globose, and rounded. The aperture extends laterally, reaching the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is smooth.

### *Montenegrina zilchi* Nordsieck, 1974 sensu Fehér & Szekeres, 2016

#### Taxonomic and systematic remarks

*Montenegrina zilchi* falls in the E clade with *M. apfelbecki*, *M. hiltrudae* s.l., and *M. wagneri* and forms a monophyletic group. Its anatomy is depicted in Figure 63. Its clear phylogenetic position, its shell morphology and its unique genital anatomy strongly support its status as a valid species.

Fehér & Szekeres, 2016	De Mattia et al., 2020
<i>Montenegrina zilchi</i> Nordsieck, 1974	<i>Montenegrina zilchi</i> Nordsieck, 1974

### *Montenegrina zilchi* Nordsieck, 1974

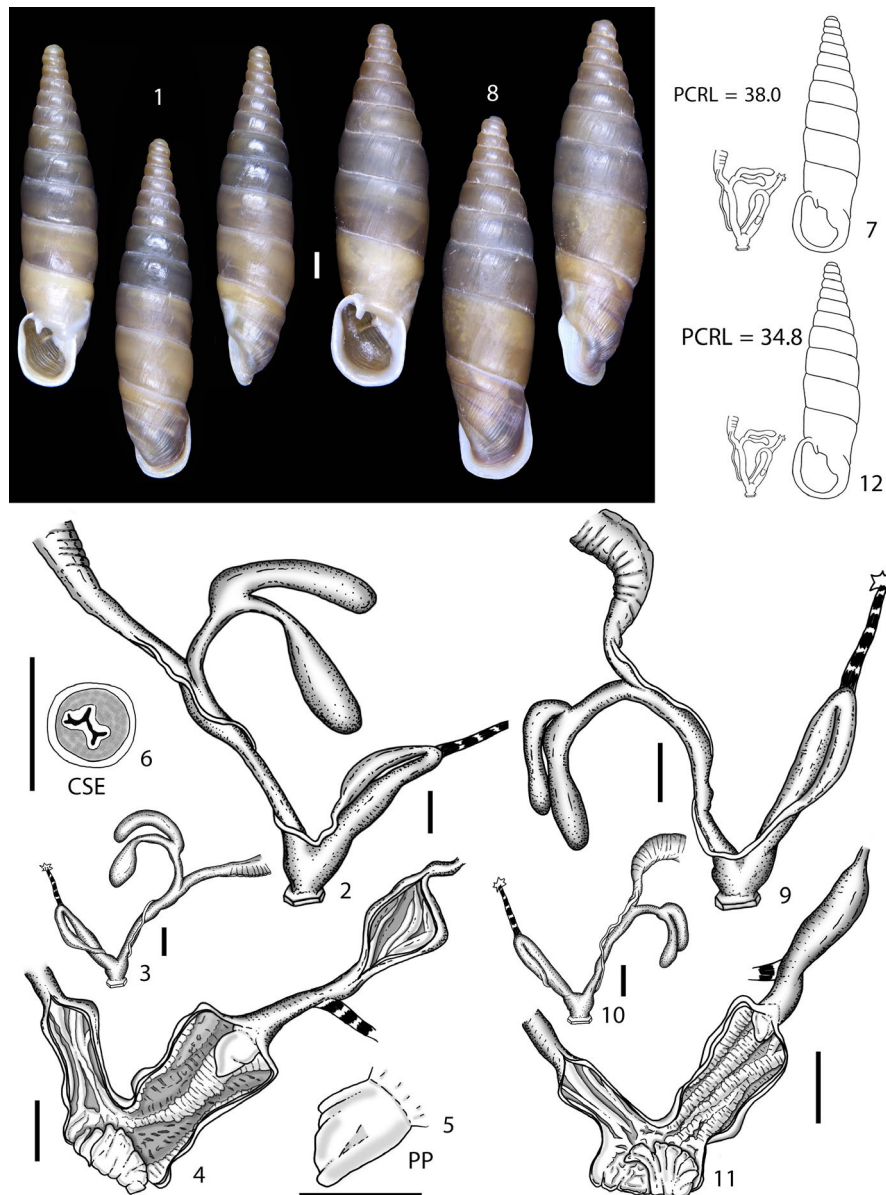
Figures 69.7–69.11

*Montenegrina zilchi* Nordsieck, 1974: 156, plate 6, fig. 39 – Zilch, 1981: 132, plate 15, fig. 43 – Nordsieck, 2009: 73. – Fehér & Szekeres, 2016: 127, fig. 34N, distribution map fig. 36.

**Examined material: two dissected specimens.** Greece, Thessaly, Trikala, Pili near ancient bridge, 235 m, 39.4603°N 21.6008°E [type locality], leg. ZE, ZF, JG, 22.vi.2013 (HNHM 99598, Mzi-371-02 [COI: KU307916, 16S: KU308244]; Mzi-371-03 [COI: KU307917, 16S: KU308245]).

**External genitalia (Figures 69.8–69.9):** The whole genital complex is long (PCRL = 31.3). The FO is short (FO/V = 0.33). The vas deferens is long and rather wide along its whole course. The first duct of the bursa copulatrix complex is short (DBC/DB = 0.27). The bursa copulatrix is medium-sized (DB/V = 0.92), wide in diameter, only slightly swollen at the apex. There is no clear transition area between the second duct and the bursa itself. The diverticulum is short (D/V = 0.63), wide, uniformly cylindrical with a blunt apex, and much shorter than the bursa copulatrix (D/BC = 0.68). The vagina is short (VRL = 12.5) but wide in diameter. The atrium is large and slightly larger at the vaginal side. The PC is much longer than the vagina (PC/V = 2.5). The penis is thinner than the vagina and almost uniformly cylindrical. The epiphallus is longer than the penis (E/P = 1.4) and slightly swollen proximally. There is a more or less distinct transitional zone between the epiphallus and the vas deferens. The retractor muscle is short but large.

**Inner genitalia (Figure 69.10):** The atrium shows one smooth fold originating from the genital aperture. The distal vagina has 6–10 smooth, large transversal pleats that do not continue into the atrium. The background is smooth. The proximal vagina is smooth and has two large, smooth pleats (one is the vaginal pilaster). These two pleats merge and eventually merge into the transversal distal pleats. The proximal penis shows a fleshy, smooth pleat covering the whole surface. This pleat abruptly splits into two main cords, gradually narrowing towards the atrium. The cords are composed by



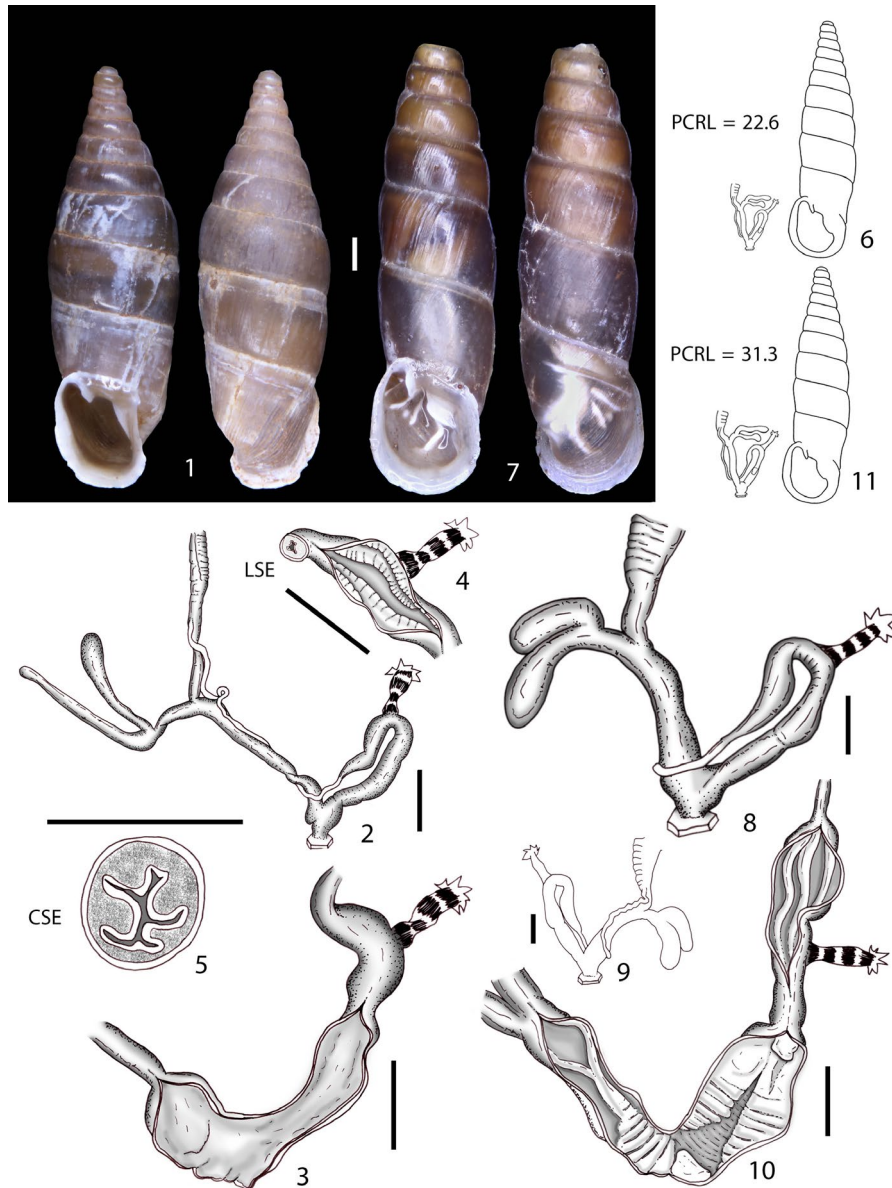
**FIGURE 68** *Montenegrina subcristata* (Pfeiffer, 1848) WDM 7273. 68.1 shell. 68.2–68.3 whole distal genitalia. 68.4 inner distal genitalia. 68.5 penial papilla. 68.6 cross section of epiphallus. 68.7 shell-genitalia ratio. WDM 7235. 68.8 shell. 68.9–68.10 whole distal genitalia. 68.11 inner distal genitalia. 68.12 shell-genitalia ratio

large metamers. The background penial wall exhibits fine transversal striae. The penial papilla is medium-sized, globose but irregular, with blunt apex. The aperture extends laterally, reaching the apical area. The surface is smooth. The epiphallus has two or three simple, smooth pleats with jagged edges, originating proximally from the end of the vas deferens and fading before the origin of the penial papilla. The background is transversely irregular.

## 5 | DISCUSSION

The revised system of *Montenegrina* that we propose here is based on an integrative approach that combines information on genital morphology, DNA sequence data (Mason et al., 2020) and shell

characters as summarized in the latest revision by Fehér & Szekeres (2016) together with geographic distributions. This combination of approaches led us to a revision of the current systematics and nomenclature (Fehér & Szekeres, 2016). We are well aware that our revised taxonomy is based on limited knowledge and that, for some taxa, this taxonomy remains arbitrary to some extent. We recognized that there is no single, straightforward, universally applicable rationale about how species should be delimited in *Montenegrina*. Monophyly in genetic trees, genetic distances, morphological characters, geographic distribution – all are important information, but not always congruent. High intraspecific distances have been reported in land snails (e.g., Thomaz et al., 1996; Watanabe and Chiba, 2001; Haase et al., 2003; Sauer and Hausdorf 2012; Scheel & Hausdorf, 2012; Harl et al., 2014; Kruckenhauser et al.,



**FIGURE 69** 69.1–69.6 *Montenegrina timeae* Eröss and Szekeres, 2006 HNHM 94856. 69.1 shell. 69.2 whole distal genitalia. 69.3 inner distal genitalia. 69.4 longitudinal section of epiphallus. 69.5 cross section of epiphallus. 69.6 shell-genitalia ratio. 69.7–69.11 *Montenegrina zilchi* Nordsieck, 1974 HNHM 99598. 69.7 shell. 69.8–69.9 whole distal genitalia. 69.10 inner distal genitalia. 69.11 shell-genitalia ratio

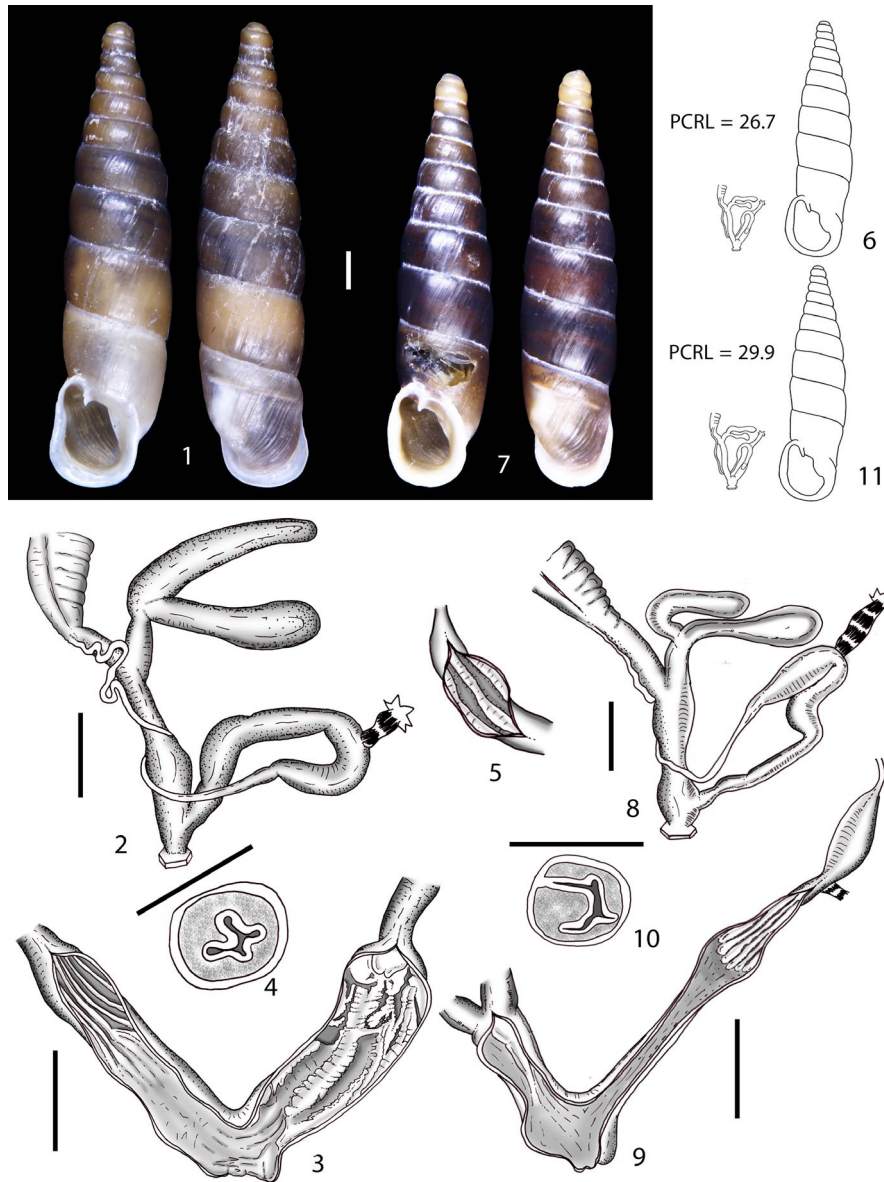
2014), but distances alone are insufficient to define species. The same is true for monophyly. It is well known that non-monophyly in genetic trees is not a decisive argument for separating taxa. Lack of monophyly can have various causes (Funk & Omland, 2003) including insufficient DNA sequence information (e.g., single-locus versus multi-locus as discussed in Sauer and Hausdorf, 2012), incomplete lineage sorting, introgression (e.g., Harl, Haring, & Páll-Gergely, 2020; Koch et al., 2017; Lammers et al., 2013), or budding speciation (e.g., Kruckenhauser et al., 2014). Furthermore, with regard to our genetic data, we currently still have only mt sequences available, because the histone genes analyzed proved to be uninformative or inconclusive (Mason et al., 2020). Nevertheless, for most taxa we achieved a considerable increase of information that was not available previously. The comprehensive analysis of genital

anatomy presented here arose from the need for further morphological characters to evaluate the systematics of *Montenegrina*.

Unfortunately, for a few taxa, not every type of information was available: Thus, only dry shells were available for two taxa (*M. chiasma*, *M. steffeki*), for a further 18 taxa only the DNA sequence analysis was possible but no suitable material was available for dissection. Further revisions will be necessary when information concerning the presently missing data becomes available.

The updated checklist of the new systematics and nomenclature is summarized in Table 2.

Out of 106 taxa accepted by Fehér and Szekeres (2016), 37 subspecies were raised to the status of valid species (stat. nov.), 21 subspecies were moved to a different species (comb. nov.), and four new taxa were described. The status of 48 taxa remained



**FIGURE 70** 70.1–70.6 *Montenegrina tomorosi tomorosi* Brandt, 1961 HNHM 99724. 70.1 shell. 70.2 whole distal genitalia. 70.3 inner distal genitalia. 70.4 cross section of epiphallus. 70.5 longitudinal section of epiphallus. 70.6 shell-genitalia ratio. 70.7–70.11 *Montenegrina tomorosi coeruleascens* Nordsieck, 1996 NHMW 110430/MN/0264. 70.7 shell. 70.8 whole distal genitalia. 70.9 inner distal genitalia. 70.10 cross section of epiphallus. 70.11 shell-genitalia ratio

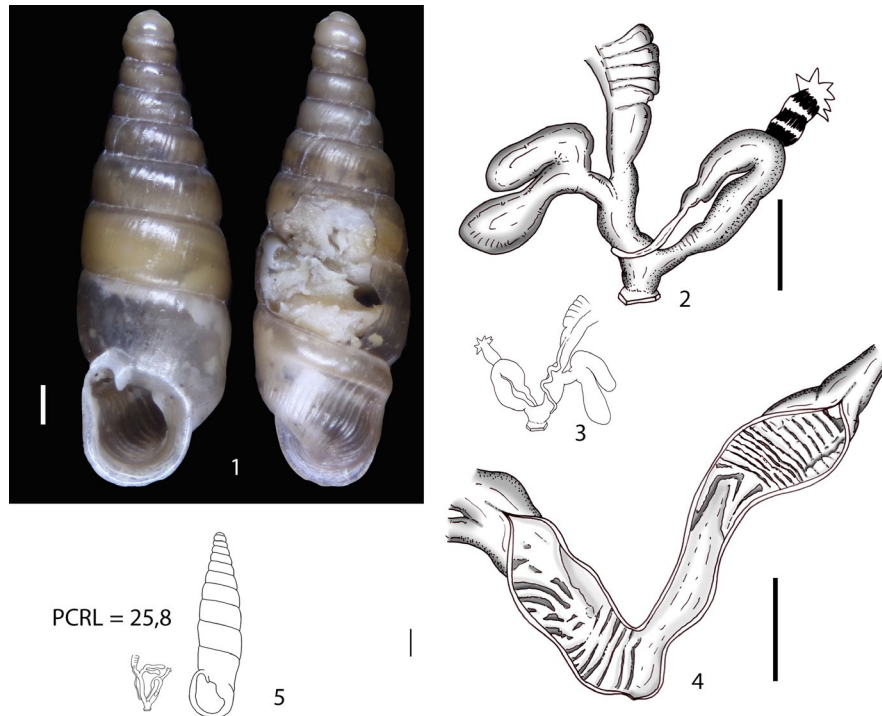
unchanged, as our results supported the current taxonomy. In only two cases out of 48 taxa the taxonomy was not changed because of lack of data.

Contrary to what was held to be true prior to this study, the genus *Montenegrina* revealed an astonishing variability in genital morphology. The most variable and thus the taxonomically more informative features were found in the inner genitalia. The descriptions of the anatomical parts of the various taxa highlight that the most variable features are (in decreasing magnitude of variability):

1. the inner sculpturing of the penis, with about 68 different arrangements,
2. the shape and dimension of the penial papilla, with about 22 different arrangements,

3. the inner sculpturing of the distal vagina, with about 19 different arrangements,
4. the inner sculpturing of the atrium, with about 19 different arrangements,
5. the inner sculpturing of the proximal vagina, with about 16 different arrangements, and
6. the inner sculpturing of the epiphallus, with about nine different arrangements.

In general, the overall external shape and dimensions of the *Montenegrina* genitalia proved to be very stable, as depicted in Figure 3. This contrasts with other clausiliid genera such as *Alopi* and *Delima*, where the overall shape and parts are variable (WDM, personal unpublished data). The taxonomic/systematic weight of



**FIGURE 71** 71.1–71.5 *Montenegrogrina tomorosi muranyii* Fehér & Szekeres, 2006 comb. nov. HHNM 94847. 71.1 shell. 71.2–71.3 whole distal genitalia. 71.4 inner distal genitalia. 71.5 shell-genitalia ratio

this variability (the various characters and their states) will be evaluated in upcoming studies.

In the genus *Montenegrogrina* we identified three general shape types:

1. the extremely elongated and thin (“ectomorphic”) genitalia such as in *Montenegrogrina skipetarica* and *Montenegrogrina lillae*,
2. the balanced (“mesomorphic”) genitalia such as in *Montenegrogrina drimmeri*, and
3. the bulky and solid (“endomorphic”) genitalia such as in *Montenegrogrina nobilis*.

The huge number of specimens (259) analyzed enabled comparing the sizes of anatomical (genital) parts. The relative dimensions of the genitalia (PCRL) are remarkably variable, from a minimum average of the 13% of the shell height in *Montenegrogrina puskasi gurelurensis* to a maximum average of 87% in *Montenegrogrina skipetarica*. The taxa with ectomorphic genitalia usually exhibit higher PCRL. The proportions among the different parts also are very variable. As an example, the ratio between the length of the penis and vagina (PC/V) ranges from 0.75 in *Montenegrogrina minuscula* to 4.5 in *Montenegrogrina trojajana*, or the ratio between the penis and the epiphallus (P/E) ranges from 0.5 in *Montenegrogrina lillae* to 4.5 in *Montenegrogrina kastoriae*.

Moreover, the length of the PC in general and the epiphallus in particular seem to show a positive correlation with the vagina, the first duct of the bursa copulatrix and the diverticulum of the bursa. This might be due to the size of the spermatophore, which is produced in the epiphallus and, after mating, moves into the receiving diverticulum of the bursa via the vagina and the first duct of the

bursa copulatrix. These findings and their significance will be the subject of a future study.

The morphology of the genitalia delimits (sub)species. Different (sub)species can share a similar morphology of one or more sections of the genitalia (atrium, penis, epiphallus, penial papilla, distal vagina, proximal vagina), but no taxon was found to show an identical overall anatomical arrangement with another one. The inner sculpturing of the penis can serve as an example: 10 taxa show perfectly smooth walls (*M. attemsi*, *M. desaretica*, *M. gracilis gracilis*, *M. prokletiana prokletiana*, *M. golikutensis*, *M. gregoi*, *M. voidomatis konitsae*, *M. gropana*, and *M. timeae*) but differ in other anatomical characters (i.e., *M. attemsi* and *M. gracilis gracilis* show an identical inner atrium, inner penis, and penial papilla, but differ regarding the inner epiphallus and vagina). Even very closely related taxa differ in their genital anatomy: *Montenegrogrina dennis dennis* and *M. dennis maaseni*, which are extremely intermingled in the mt tree, nonetheless presented quite a different morphology of the external and inner genitalia (Figures 24.6–9 and 28.8–12). Another striking example is the two phylogenetically closely related species *M. densicostulata*/*M. protruda*, which showed extreme differences in genital anatomy.

The morphology of the genitalia proved to be stable within a (sub) species. Even a large number of populations of *Montenegrogrina subcristata*, distributed over a wide area, exhibited a stable genital morphology. Interestingly, the shell morphology of *M. subcristata* seems to show a much greater variability, and this is indicated by the number of names that had been formerly introduced to describe this variability (at least six as summarized in Fehér & Szekeres, 2016: 116).

As noted above, the inner features of both male and female genitalia show great diversity in *Montenegrogrina*. The external features,



**TABLE 2** Recapitulatory checklist table of the nomenclatural changes of the *Montenegrina* taxa from Fehér & Szekeres, 2016 to the present paper

Fehér & Szekeres, 2016	De Mattia, Fehér, Mason & Haring, 2020
<i>Montenegrina apfelbecki</i> (Sturany, 1907)	<i>Montenegrina apfelbecki</i> (Sturany, 1907)
<i>Montenegrina attemsi attemsi</i> (Wagner, 1914)	<i>Montenegrina attemsi</i> (Wagner, 1914)
<i>Montenegrina attemsi jakupicensis</i> Fauer, 1993	<i>Montenegrina jakupicensis</i> Fauer, 1993 stat. nov.
<i>Montenegrina cattaroensis cattaroensis</i> (Rossmässler, 1835)	<i>Montenegrina cattaroensis</i> (Rossmässler, 1835)
<i>Montenegrina cattaroensis umbilicata</i> (Boettger, 1879)	<i>Montenegrina umbilicata umbilicata</i> (Boettger, 1879) stat. nov.
<i>Montenegrina cattaroensis antivaricostata</i> (Boettger, 1907)	<i>Montenegrina umbilicata antivaricostata</i> (Boettger, 1907) comb. nov.
<i>Montenegrina chiasma</i> Nordsieck, 1972	<i>Montenegrina chiasma</i> Nordsieck, 1972
<i>Montenegrina dofleini dofleini</i> (Wagner, 1928)	<i>Montenegrina dofleini dofleini</i> (Wagner, 1928)
<i>Montenegrina dofleini fagorum</i> Nordsieck, 1974	<i>Montenegrina dofleini fagorum</i> Nordsieck, 1974
<i>Montenegrina dofleini kastoriae</i> Nordsieck, 1972	<i>Montenegrina kastoriae</i> Nordsieck, 1972 stat. nov.
<i>Montenegrina dofleini pinteri</i> Nordsieck, 1974	<i>Montenegrina pinteri</i> Nordsieck, 1974 stat. nov.
<i>Montenegrina dofleini prespaensis</i> Nordsieck, 1988	<i>Montenegrina prespaensis prespaensis</i> Nordsieck, 1988 stat. nov.
<i>Montenegrina dofleini sinosi</i> Páll-Gergely, 2010	<i>Montenegrina prespaensis sinosi</i> Páll-Gergely, 2010 comb. nov.
<i>Montenegrina dofleini wagneri</i> Szekeres, 2006	<i>Montenegrina wagneri</i> Szekeres, 2006 stat. nov.
<i>Montenegrina drimmeri</i> Fehér & Szekeres, 2006	<i>Montenegrina drimmeri</i> Fehér & Szekeres, 2006
<i>Montenegrina fuchsi fuchsi</i> Brandt, 1961	<i>Montenegrina fuchsi</i> Brandt, 1961
<i>Montenegrina fuchsi klemmi</i> Brandt, 1962	<i>Montenegrina klemmi</i> Brandt, 1962 stat. nov.
<i>Montenegrina fuchsi pallida</i> Fauer, 1993	<i>Montenegrina pallida</i> Fauer, 1993 stat. nov.
<i>Montenegrina janinensis janinensis</i> (Mousson, 1859)	<i>Montenegrina janinensis</i> (Mousson, 1859)
<i>Montenegrina grammica grammica</i> Nordsieck, 1988	<i>Montenegrina grammica grammica</i> Nordsieck, 1988
<i>Montenegrina grammica erosszoltani</i> Fehér & Szekeres, 2016	<i>Montenegrina grammica erosszoltani</i> Fehér & Szekeres, 2016
<i>Montenegrina grammica improvisa</i> Fehér & Szekeres, 2016	<i>Montenegrina improvisa</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina haringae</i> Fehér & Szekeres, 2016	<i>Montenegrina haringae</i> Fehér & Szekeres, 2016
<i>Montenegrina helvola helvola</i> (Küster, 1860)	<i>Montenegrina helvola helvola</i> (Küster, 1860)
<i>Montenegrina helvola carinata</i> Eröss and Szekeres, 1999	<i>Montenegrinahelvola carinata</i> Eröss and Szekeres, 1999
<i>Montenegrina helvola magna</i> Fehér & Szekeres, 2006	<i>Montenegrina helvola magna</i> Fehér & Szekeres, 2006
<i>Montenegrina helvola ornata</i> Eröss and Szekeres, 1999	<i>Montenegrina helvola ornata</i> Eröss and Szekeres, 1999
<i>Montenegrina helvola pageti</i> Brandt, 1962	<i>Montenegrina helvola pageti</i> Brandt, 1962
<i>Montenegrina hiltrudae hiltrudae</i> Nordsieck, 1972	<i>Montenegrina hiltrudae hiltrudae</i> Nordsieck, 1972
<i>Montenegrina hiltrudae costulata</i> Eröss and Szekeres, 2006	<i>Montenegrina sattmanni costulata</i> Eröss and Szekeres, 2006 comb. nov.
<i>Montenegrina hiltrudae desaretica</i> Fehér & Szekeres, 2016	<i>Montenegrina desaretica</i> Fehér & Szekeres, 2016 stat. nov.
	<i>Montenegrina atansiensis</i> n. sp.
<i>Montenegrina hiltrudae densicostulata</i> Nordsieck, 1974	<i>Montenegrina hiltrudae densicostulata</i> Nordsieck, 1974
<i>Montenegrina hiltrudae dennisi</i> Gittenberger, 2002	<i>Montenegrina dennisi dennisi</i> Gittenberger, 2002 stat. nov.
<i>Montenegrina hiltrudae fusca</i> Fehér & Szekeres, 2006	<i>Montenegrina fusca</i> Fehér & Szekeres, 2006 stat. nov.
<i>Montenegrina hiltrudae maaseni</i> Gittenberger, 2002	<i>Montenegrina dennisi masseni</i> Gittenberger, 2002 comb. nov.
<i>Montenegrina hiltrudae robusta</i> Nordsieck, 2009	<i>Montenegrina kastoriae robusta</i> Nordsieck, 1972 comb. nov.
<i>Montenegrina hiltrudae protruda</i> Gittenberger, 2002	<i>Montenegrina protruda</i> Gittenberger, 2002, stat. nov.
<i>Montenegrina hiltrudae sattmanni</i> Nordsieck, 1988	<i>Montenegrina sattmanni sattmanni</i> Nordsieck, 1988 stat. nov.
<i>Montenegrina hiltrudae selcensis</i> Fehér & Szekeres, 2016	<i>Montenegrina selcensis</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina janinensis</i> (Mousson, 1859)	<i>Montenegrina janinensis</i> (Mousson, 1859)
<i>Montenegrina laxa laxa</i> (Küster, 1861)	<i>Montenegrina laxa</i> (Küster, 1861)
<i>Montenegrina laxa dedovi</i> Nordsieck, 2009	<i>Montenegrina miraka dedovi</i> Nordsieck, 2009 comb. nov.
<i>Montenegrina laxa delii</i> Fehér & Szekeres, 2016	<i>Montenegrina miraka delii</i> Fehér & Szekeres, 2016 comb. nov.

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TABLE 2 (Continued)

Fehér & Szekeres, 2016	De Mattia, Fehér, Mason & Haring, 2020
<i>Montenegrina laxa disjuncta</i> Fehér & Szekeres 2006	<i>Montenegrina miraka disjuncta</i> Fehér & Szekeres 2006 comb. nov.
<i>Montenegrina laxa iba</i> Nordsieck, 1972	<i>Montenegrina iba</i> Nordsieck, 1972 stat. nov.
<i>Montenegrina laxa kotschani</i> Eröss and Szekeres, 2006	<i>Montenegrina miraka kotschani</i> Eröss and Szekeres, 2006 comb. nov.
<i>Montenegrina laxa errans</i> Eröss and Szekeres, 2006	<i>Montenegrina miraka errans</i> Eröss and Szekeres, 2006 comb. nov.
<i>Montenegrina laxa lakmosensis</i> Nordsieck, 2009	<i>Montenegrina miraka lakmosensis</i> Nordsieck, 2009 comb. nov.
<i>Montenegrina laxa miraka</i> Nordsieck, 1996	<i>Montenegrina miraka miraka</i> Nordsieck, 1996 stat. nov.
<i>Montenegrina lillae</i> Fehér & Szekeres, 2016	<i>Montenegrina lillae</i> Fehér & Szekeres, 2016
<i>Montenegrina minuscula</i> Eröss and Szekeres, 2006	<i>Montenegrina minuscula</i> Eröss and Szekeres, 2006
<i>Montenegrina nana nana</i> Fehér & Szekeres, 2006	<i>Montenegrina nana</i> Fehér & Szekeres, 2006
<i>Montenegrina nana barinai</i> Fehér & Szekeres, 2016	<i>Montenegrina gracilis barinai</i> Fehér & Szekeres, 2016 comb. nov.
<i>Montenegrina nana gracilis</i> Eröss and Szekeres, 2006	<i>Montenegrina gracilis gracilis</i> Fehér & Szekeres, 2006 stat. nov.
<i>Montenegrina okolensis okolensis</i> Szekeres, 2006	<i>Montenegrina okolensis okolensis</i> Szekeres, 2006
<i>Montenegrina okolensis caesia</i> Fehér & Szekeres, 2006	<i>Montenegrina okolensis caesia</i> Fehér & Szekeres, 2006
<i>Montenegrina perstriata callistoma</i> Fehér & Szekeres, 2006	<i>Montenegrina ochridensis callistoma</i> Fehér & Szekeres, 2006 comb. nov.
<i>Montenegrina perstriata diminuta</i> Fehér & Szekeres, 1999	<i>Montenegrina perstriata diminuta</i> Fehér & Szekeres, 1999
<i>Montenegrina perstriata drimica</i> Nordsieck, 1972	<i>Montenegrina drimica drimica</i> Nordsieck, 1972 stat. nov. <i>Montenegrina globocica</i> n. sp.
<i>Montenegrina perstriata mavrovoensis</i> Nordsieck, 2009	<i>Montenegrina perstriata mavrovoensis</i> Nordsieck, 2009
<i>Montenegrina perstriata occidentalis</i> (Wagner, 1925)	<i>Montenegrina drimica occidentalis</i> (Wagner, 1925) comb. nov.
<i>Montenegrina perstriata ochridensis</i> (Wagner, 1925)	<i>Montenegrina ochridensis ochridensis</i> (Wagner, 1925) stat. nov.
<i>Montenegrina perstriata perstriata</i> (Wagner, 1919)	<i>Montenegrina perstriata perstriata</i> (Wagner, 1919)
<i>Montenegrina perstriata plenostoma</i> Fehér & Szekeres, 2006	<i>Montenegrina drimica plenostoma</i> Fehér & Szekeres, 2006 comb. nov.
<i>Montenegrina perstriata radikae</i> Nordsieck, 1972	<i>Montenegrina radikae radikae</i> Nordsieck, 1972 stat. nov. <i>Montenegrina radikae paparistoeae</i> n. ssp.
<i>Montenegrina perstriata subcratatula</i> Nordsieck, 1977	<i>Montenegrina perstriata subcratatula</i> Nordsieck, 1977
<i>Montenegrina perstriata steffeki</i> Eröss and Szekeres, 1999	<i>Montenegrina perstriata steffeki</i> Eröss and Szekeres, 1999
<i>Montenegrina perstriata tenebrosa</i> Nordsieck, 2009	<i>Montenegrina tenebrosa tenebrosa</i> Nordsieck, 2009 stat. nov. <i>Montenegrina tenebrosa szekeresi</i> n. ssp.
<i>Montenegrina prokletiana prokletiana</i> Fehér & Szekeres, 2016	<i>Montenegrina prokletiana prokletiana</i> Fehér & Szekeres, 2016
<i>Montenegrina prokletiana kovacsorum</i> Fehér & Szekeres, 2016	<i>Montenegrina prokletiana kovacsorum</i> Fehér & Szekeres, 2016
<i>Montenegrina rugilabris rugilabris</i> (Mousson, 1859)	<i>Montenegrina rugilabris</i> (Mousson, 1859)
<i>Montenegrina rugilabris edmundi</i> Szekeres, 2006	<i>Montenegrina edmundi</i> Szekeres, 2006 stat. nov.
<i>Montenegrina rugilabris golikutensis</i> Fehér and Szekeres, 2016	<i>Montenegrina golikutensis</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina rugilabris gregoi</i> Fehér and Szekeres, 2016	<i>Montenegrina gregoi</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina rugilabris irmengardis</i> Klemm, 1962	<i>Montenegrina rugilabris irmengardis</i> Klemm, 1962
<i>Montenegrina rugilabris welterschultesi</i> Fehér and Szekeres, 1999	<i>Montenegrina lambdaformis welterschultesi</i> Fehér & Szekeres, 1999 comb. nov.
<i>Montenegrina rugilabris lambdaformis</i> Reischütz and Sattmann, 1990	<i>Montenegrina lambdaformis lambdaformis</i> Reischütz and Sattmann, 1990 stat. nov.
<i>Montenegrina skipetarica skipetarica</i> (Soós, 1924)	<i>Montenegrina skipetarica</i> (Soós, 1924)
<i>Montenegrina skipetarica csikii</i> Eröss and Szekeres, 2006	<i>Montenegrina csikii</i> Eröss and Szekeres, 2006 stat. nov.
<i>Montenegrina skipetarica danyii</i> Fehér & Szekeres, 2016	<i>Montenegrina puskasi danyii</i> Fehér & Szekeres, 2016 comb. nov.
<i>Montenegrina skipetarica ersekensis</i> Nordsieck, 1996	<i>Montenegrina ersekensis</i> Nordsieck, 1996 stat. nov.
<i>Montenegrina skipetarica flava</i> Eröss and Szekeres, 2006	<i>Montenegrina flava</i> Eröss and Szekeres, 2006 stat. nov.
<i>Montenegrina skipetarica gurelurensis</i> Fehér & Szekeres, 2016	<i>Montenegrina puskasi gurelurensis</i> Fehér & Szekeres, 2016 comb. nov.

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TABLE 2 (Continued)

Fehér & Szekeres, 2016	De Mattia, Fehér, Mason & Haring, 2020
<i>Montenegrina skipetarica konitsae</i> Nordsieck, 1972	<i>Montenegrina voidomatis konitsae</i> Nordsieck, 1972 comb. nov.
<i>Montenegrina skipetarica nobilis</i> Eröss and Szekeres, 2006	<i>Montenegrina nobilis</i> Eröss and Szekeres, 2006 stat. nov.
<i>Montenegrina skipetarica pifkoi</i> Fehér & Szekeres, 2016	<i>Montenegrina pifkoi</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina skipetarica pindica</i> Nordsieck, 1998	<i>Montenegrina pindica</i> Nordsieck, 1998 stat. nov.
<i>Montenegrina skipetarica puskasi</i> Fehér & Szekeres, 2016	<i>Montenegrina puskasi puskasi</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina skipetarica remota</i> Fehér & Szekeres, 2006	<i>Montenegrina remota</i> Fehér & Szekeres, 2006 stat. nov.
<i>Montenegrina skipetarica rugosa</i> Fehér & Szekeres, 2006	<i>Montenegrina voidomatis rugosa</i> Fehér & Szekeres, 2006 comb. nov.
<i>Montenegrina skipetarica thysi</i> Loosjes & Loosjes-van Bommel, 1988	<i>Montenegrina voidomatis thysi</i> Loosjes & Loosjes-van Bommel, 1988 comb. nov.
<i>Montenegrina skipetarica voidomatis</i> Nordsieck, 1974	<i>Montenegrina voidomatis voidomatis</i> Nordsieck, 1974 stat. nov.
<i>Montenegrina soosi</i> Eröss and Szekeres, 2006	<i>Montenegrina soosi</i> Eröss and Szekeres, 2006
<i>Montenegrina sporadica sporadica</i> Nordsieck, 1974	<i>Montenegrina sporadica</i> Nordsieck, 1974
<i>Montenegrina sporadica tropojana</i> Fehér & Szekeres, 2016	<i>Montenegrina tropojana</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina stankovici</i> (Urbański, 1960)	<i>Montenegrina stankovici</i> (Urbański, 1960)
<i>Montenegrina sturanyana sturanyana</i> Fehér & Szekeres, 2016	<i>Montenegrina sturanyana</i> Fehér & Szekeres, 2016
<i>Montenegrina sturanyana gropana</i> Fehér & Szekeres, 2016	<i>Montenegrina gropana</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina sturanyana ostrovicensis</i> Fehér & Szekeres, 2016	<i>Montenegrina ostrovicensis</i> Fehér & Szekeres, 2016 stat. nov.
<i>Montenegrina subcristata</i> (Pfeiffer, 1848)	<i>Montenegrina subcristata</i> (Pfeiffer, 1848)
<i>Montenegrina timeae</i> Eröss and Szekeres, 2006	<i>Montenegrina timeae</i> Eröss and Szekeres, 2006
<i>Montenegrina tomorosi tomorosi</i> Brandt, 1961	<i>Montenegrina tomorosi tomorosi</i> Brandt, 1961
<i>Montenegrina tomorosi ampla</i> Fehér & Szekeres, 2006	<i>Montenegrina tomorosi ampla</i> Fehér & Szekeres, 2006
<i>Montenegrina tomorosi coeruleascens</i> Nordsieck, 1996	<i>Montenegrina tomorosi coeruleascens</i> Nordsieck, 1996
<i>Montenegrina tomorosi hunyadii</i> Fehér & Szekeres, 2016	<i>Montenegrina tomorosi hunyadii</i> Fehér & Szekeres, 2016
<i>Montenegrina fuchsi muranyii</i> Fehér & Szekeres, 2006	<i>Montenegrina tomorosi muranyii</i> Fehér & Szekeres, 2006 comb. nov.
<i>Montenegrina zilchi</i> Nordsieck, 1974	<i>Montenegrina zilchi</i> Nordsieck, 1974

such as the shape and ratio among parts, also presented some variability among taxa but stability inside single taxa. Although for many taxa only two or three individuals were anatomically investigated per population, we included several populations of a number of taxa. As a first impression, the absence/presence, dimension, and shape of each single genital anatomical character seemed to show no correlation or relationship with any geographic, altitudinal, climatic, shell-morphological, or phylogenetic parameter. This is valid both for external and inner features of the genitalia. Taxa that are phylogenetically related often presented very different genital arrangements. A comprehensive data matrix with all the morphometric conchological and genital measurements, ratios, and categorized inner genital features will be presented in an upcoming cladistic paper, where correlations among these variables are currently being tested.

Sauer and Hausdorf (2010) stated that “the success of morphological species delimitation results from the potential to focus on characters that are directly involved in the speciation process”. Genital anatomy might be considered as an important character system in this regard. It remains to be tested in a future study whether the genital morphology of *Montenegrina* was shaped by random effects or sexual selection as already suggested by

Schilthuizen (2003) for shell diversity. Within *Montenegrina* species, genital characters revealed extreme stability even over a large geographic range, for example the inner sculpturing of the male part in *M. subcristata*. At the same time, quite similar genital arrangements are found in taxa that are phylogenetically extremely distant, for example, *M. lillae* and *M. tropojana*, a finding that can be plausibly explained by parallelism rather than plesiomorphy as shown by Fehér et al. (2018). This confirms assumptions of Gittenberger (1991), who showed that *Montenegrina* radiation was mainly non-adaptive. We therefore conclude that isolation plus time (i.e. drift) are the “engine” of morphological differentiation (genital anatomy, shell) in *Montenegrina* and that homoplasies are to be expected in such a huge genus. On the other hand, this does not mean that genital anatomical traits are not under selection within a population. Otherwise, it would be difficult to explain the stability within taxa. The present analyses suggest that the morphology of the genitalia, while important for alpha-taxonomy and thus for systematics and nomenclature, have no or little phylogenetic information in *Montenegrina*. Future cladistic analyses will be necessary to test the phylogenetic value of these morphological characters in detail.

## 6 | CONCLUSIONS

Our study allowed us to compare and integrate different taxonomically relevant data, yielding a considerable change in the systematics and nomenclature of the genus *Montenegrina*. The systematic position of 63 taxa out of 106 (59%) has been modified. The study revealed that the contribution of genital anatomical characters is essential for alpha-taxonomy, although their contribution to the phylogenetic reconstruction appears limited because the character states seem to randomly appear throughout the range of taxa. Many gray areas remain. More data are necessary to shed light on the phylogeny of and speciation within the genus *Montenegrina*, both in terms of a molecular genetics (in particular informative nuclear genes) and an anatomical approach. This study represents a first integrative taxonomic study within Clausiliidae attempting to combine genetic data, genital and shell-morphological characters along with distributional data, and it will be followed by many more.

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