



DISSERTATION | DOCTORAL THESIS

Titel | Title

Testing genital anatomical characters in clausiliid systematics
on the example of Alopiinae (Gastropoda: Stylommatophora:
Clausiliidae)

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"Can there be a better reason for studying Zoology? We are the most complicated and most perfectly designed machines in the known universe. It is hard to understand why anyone would study anything else!"

Richard Dawkins

"I have a debt, a loyalty to the museum; the best place for me to do what I wanted to do."

George Gaylord Simpson

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Abstract

The taxonomy and systematics of the door snail genera *Montenegrina* Boettger, 1877 and *Siciliaria* Vest, 1867 were revised, based on a comprehensive genital anatomical investigation combined with shell morphology and DNA sequence data. The genital morphology of 405 specimens of 124 taxa from 174 populations of *Montenegrina* was investigated. The genus revealed an astonishing variability in genital morphology, with distinctive combinations of anatomical features for each taxon. *Siciliaria* revealed a remarkable variability in genital morphology as well with taxon-specific distinctive combinations of anatomical features. The genital morphology of 120 specimens of 22 taxa from 44 populations was investigated. Phylogenetic trees, based on *COI* and *ITS2* sequences, showed that the species clustered within two separate highly supported, clades.

Montenegrina quantitative (morphometric measurements) and qualitative (categorization of traits) data were statistically analyzed by a multivariate ordination and clustering approach, to test if genitalia and shell morphological traits correspond to the phylogeny based on DNA sequences. Neighbour Joining trees (NJ), based on Euclidean distances including both the shell and genital measurements, and NJ trees based on Hamming distances from qualitative categorization of traits, highlight the non-concordance between morphological characters and phylogenetic reconstruction depicted in the BI (Bayesian Inference) phylogenetic trees. The topologies of these morphological trees have hardly any branching in common with the DNA-based tree. Thus, despite the morphological characters are essential for alpha-taxonomy, they apparently appear randomly throughout the range of taxa, making their contribution to the phylogenetic reconstruction apparently very limited.

The research results presented here are explanatory and should serve as a stimulus to investigate further obliged rock/dwelling clausiliid species e.g. of the genera *Medora*, *Muticaria* or *Charpentieria* or even other families (e.g. Chondrinidae) that occupy the same ecological niche.

Zusammenfassung

Die Taxonomie und Systematik der Schließmundschneckengattungen *Montenegrina* Boettger, 1877 und *Siciliaria* Vest, 1867 wurden auf der Grundlage einer umfassenden genitalanatomischen Untersuchung in Kombination mit Schalenmorphologie und DNA-Sequenzdaten überarbeitet. Die Genitalmorphologie von 405 Exemplaren von 124 Taxa aus 174 Populationen von *Montenegrina* wurde untersucht. Die Gattung *Montenegrina* wies eine erstaunliche Variabilität in der Genitalmorphologie auf, wobei die Kombinationen anatomischer Merkmale bei jedem Taxon unterschiedlich waren.

Siciliaria zeigte ebenfalls eine bemerkenswerte Variabilität in der Genitalmorphologie mit taxonspezifisch ausgeprägten Kombinationen von anatomischen Merkmalen. Die Genitalmorphologie von 120 Exemplaren von 22 Taxa aus 44 Populationen wurde untersucht. Phylogenetische Bäume, die auf *COI*- und *ITS2*-Sequenzen basieren, zeigten, dass die Arten in zwei getrennten, stark unterstützten Kladen vorkommen.

Die quantitativen (morphometrische Messungen) und qualitativen (Kategorisierung von Merkmalen) Daten von *Montenegrina* wurden mittels eines multivariaten Ordnungs- und Clusterungsansatzes statistisch analysiert, um zu prüfen, ob die Genitalien und die morphologischen Merkmale der Schale mit der auf den DNA-Sequenzen basierenden Phylogenie übereinstimmen.

Neighbour-Joining-Bäume (NJ) auf der Grundlage euklidischer Abstände, die sowohl die Schalen- als auch die Genitalabmessungen enthalten, und NJ-Bäume auf der Grundlage von Hamming-Distanzen, die auf einer qualitativen Kategorisierung der Merkmale beruhen, verdeutlichen die

Nichtübereinstimmung zwischen morphologischen Merkmalen und der phylogenetischen Rekonstruktion, die in den phylogenetischen Bäumen der BI (Bayes'sche Inferenz) dargestellt wird.

Die Topologien dieser morphologischen Bäume haben kaum eine Verzeigung mit dem DNA-basierten Baum gemeinsam. Obwohl die morphologischen Merkmale für die Alpha-Taxonomie von wesentlicher Bedeutung sind, erscheinen sie anscheinend zufällig im gesamten Spektrum der Taxa verteilt, so dass ihr Beitrag zur phylogenetischen Rekonstruktion offensichtlich äußerst begrenzt ist.

Die hier vorgestellten Forschungsergebnisse sind beispielhaft und sollen als Anregung dienen, weitere felsbewohnende Arten der Familie Clausiliidae zu untersuchen, z.B. der Gattungen *Medora*, *Muticaria* oder *Charpentieria* oder auch Vertreter anderer Familien (z.B. Chondrinidae), die dieselbe ökologische Nische besetzen.

Part A

1. General Introduction to Clausiliidae (Gastropoda: Stylommatophora)

Clausiliidae is a family of the Stylommatophora land snails characterized by mostly sinistral, turreted shells with interior wall folds that function as a closing mechanism, known as the clausilial apparatus (Nordsieck, 2007). The family is primarily distributed across Europe, East Asia, and South America. The presence of the clausilial apparatus, a feature unique to Clausiliidae among land snails, strongly supports the monophyly of this family, as confirmed by molecular genetic studies (Wade et al., 2001; Van Moorsel, 2001; Uit De Weerd, 2004; Wade et al., 2006; Hausdorf & Neiber, 2022; Uit De Weerd et al., 2023; Magonyi et al., 2024). No known synapomorphies link Clausiliidae to other groups. The family is divided into 11 subfamilies and 211 genera, of which 38 are extinct and 173 are extant (Bouchet et al., 2005; Nordsieck, 2007; De Mattia et al., 2021; Becher et al., 2025; Colomba et al., 2025; Molluscabase, 2025). The subfamily Alopiinae, the most species-rich in the Central and Eastern Mediterranean and adjacent areas of Asia and Africa, is mainly classified based on shell features, though some genera also show distinct differences in genital apparatus (Nordsieck, 2007). Alopiinae comprises 23 genera, 31 subgenera, and 896 currently valid species and subspecies (Nordsieck, 2007; De Mattia et al., 2020; De Mattia et al., 2021; Nordsieck, 2022/2024; Molluscabase, 2025).

Hartmut Nordsieck (1940–2022) dedicated much of his scientific career to the study of Clausiliidae, contributing significantly to the taxonomy of Alopiinae (Nordsieck, 1963a, 1963b, 1970, 1972, 1977, 1997, 1999, 2002, 2007, 2008, 2011, 2012, 2013a, 2013b, 2022/2024). Other key contributors to Alopiinae systematics include Douris et al. (1998), Welter-Schultes (2000), Uit de Weerd (2004), Uit de Weerd & Gittenberger (2005), Fehér et al. (2013), and Fehér & Szekeres (2016). Alopiinae exhibit considerable diversity in shell morphology, likely due to their low dispersal ability and habitat-specificity, which promotes isolation and limited gene flow. Gittenberger (1991) suggested a nonadaptive radiation model for Alopiinae, with extreme species richness arising from geographic isolation and the resulting lack of gene flow, as seen in the genus *Montenegrina*. The extreme species richness of *Montenegrina* can be attributed to the patchy distribution of calcareous rocks, which act as isolated "limestone islands" (Gittenberger, 2002). Given the considerable changes in systematics observed in the genera *Montenegrina* and *Siciliaria* from integrative studies, several other hyper-speciose genera such as *Delima*, *Albinaria*, and *Stigmatica* also require major revisions.

Before the advent of molecular phylogenetics, systematics was primarily based on shell morphology, with little attention given to genital anatomy. However, shell-based taxonomy has limitations in defining land snail taxa, as highlighted by Giusti & Manganelli (1992). While genital morphology was often overlooked for taxonomic purposes, it plays a crucial role in the taxonomy of other western Palearctic pulmonates (e.g., Zonitidae, Oxychilidae, Geomitridae) and Architaenioglossa families (e.g., Hydrobiidae, Cochostomatidae) (Giusti & Manganelli, 1992).

This remarkable lack in literature of genital data at the genus and species level in Alopiinae (and Clausiliidae in general) is probably due to the dissecting skills and time-consuming procedures required to study clausiliid genital anatomy. Anyhow, this lack of data does not mean that genital morphology could not play an important role, as well as together with molecular genetic and biogeographic analyses. Sure enough, genital morphology (outer and internal traits) is of fundamental importance concerning the taxonomy of most of the other western Palaearctic Pulmonata families (e.g. Zonitidae, Oxychilidae, Geomitridae, Limacidae, Milacidae, Agriolimacidae etc.) and in most Architaenioglossa (e.g. Hydrobiidae, Cochostomatidae etc).

2. Brief Description of Taxa and Methods

This thesis focuses on two speciose genera of Alopiinae:

- *Montenegrina* O. Boettger, 1877 - 106 taxa, occurring in an area of about 50.000 km² in the southern Dinarids, Croatia, Montenegro, Albania, North Macedonia, Greece, recent revisions by Mason et al. (2020), De Mattia et al. (2020) and Mason et al. (2023).
- *Siciliaria* Vest, 1867 - 22 taxa, occurring in an area of about 2.000 km² in the southern Tyrennids, endemic to Sicily, Italy, recent revision by De Mattia et al. (2021).

These genera share several ecological features but also exhibit fundamental differences:

- Both genera inhabit similar habitat, they are found exclusively in calcareous rock massifs, particularly on limestone walls, boulders, and rocky debris. They primarily feed on endolithic crustose lichens and rupicolous microflora. Their populations are distributed in isolated patches, where the limestone peaks and boulders act as ecological "islands," leading to limited gene flow and genetic drift.
- Both genera have recently undergone morphological revisions: *Montenegrina* (Fehér & Szekeres, 2016) and *Siciliaria* (Beckmann, 2004; Liberto et al., 2016).
- A significant number of ethanol-preserved specimens are available from various sources, including my personal collection, NHMW, HNHM, and other private/public collections.
- Phylogenetic studies based on mitochondrial and nuclear DNA sequences for both *Montenegrina* and *Siciliaria* were conducted in parallel with the morphological analysis (Mason et al., 2020; De Mattia et al., 2021). This enabled an integrative approach combining shell, genitalia, and molecular data.
- The range of *Montenegrina* spans nearly 50,000 km², while *Siciliaria* (together with *Sicania*) occupies an area of just 2,000 km².

Morphological methods include photographic documentation, measurement of shell characteristics, and dissection of genitalia using micro-surgical techniques. Genitalia were depicted through drawings

to highlight key taxonomic features. Datasets were created for qualitative, quantitative (morphometric), molecular, and geographic data, including dimensional values for shell and genital traits and non-measurable parameters like morphological arrangements. Statistical analyses included univariate (normality tests, Mantel test), multivariate (ordination and clustering), and model-based (bivariate regression) approaches.

3. Key Research Questions

The data presented here address unresolved issues in the taxonomy and systematics of Alopiinae. Currently, taxa are primarily delimited by shell morphology, but the role of other soft part features, particularly genital anatomy, is unclear. It is also unknown whether morphological traits of the shell and genitalia correlate with phylogenetic relationships as inferred from genetic data. Furthermore, the geographical distribution of taxa and its relationship to phylogenetic patterns has not been explored yet. The key research questions are:

- Can genital and shell morphology provide clearer taxonomic boundaries than shell morphology alone?
- Do these morphological traits carry phylogenetic signals consistent with genetic analysis?
- How does geographical distribution correlate with phylogenetic relationships?

3.1 Genital Morphology for Taxa Delimitation

The current systematics of Alopiinae rely heavily on shell morphology, but this often results in ambiguous or inconsistent taxonomic information. Some characters traditionally used in shell-based taxonomy show high variability. For instance, taxa with markedly different shells may be considered subspecies of the same species due to similarities in buccal armature (e.g., Pall-Gergely, 2010), while taxa with similar shells may be treated as distinct species based on small differences (e.g., Nordsieck, 2007). By incorporating genital anatomy into the analysis, this research aims to refine species delimitation. The goal is to determine whether genital traits, both qualitative and quantitative, can provide more reliable taxonomic boundaries than shell morphology alone.

3.2 Phylogenetic Signal of Morphological Traits and Geographic Distribution

Recent phylogenetic studies on *Montenegrina* and *Siciliaria* (Mason et al., 2020; De Mattia et al., 2020, 2021) have clarified the relationships among taxa. However, it remains uncertain whether morphological traits correspond to phylogenetic distances. This research investigates whether genital and shell morphology, as well as geographical distribution, carry phylogenetic signals. By transforming morphological data into mathematical distances and comparing them with genetic distances, the study will test the correlation between phylogeny, morphology, and geography.

Additionally, the role of geographic isolation in driving speciation will be examined, especially in relation to isolation by distance.

3.3 Morphological Variation and Geographic Distance

The extensive morphometric data on genitalia and shells provide an opportunity to explore correlations between morphological traits and geographic distribution. This includes investigating potential relationships between genitalia and shell traits, as well as examining how geographical isolation influences morphological differentiation. For taxa with syntopic populations, the concept of reproductive character displacement (RCD) will be considered, as natural selection may act to reduce interspecific mating through changes in reproductive traits when species come into secondary contact.

4. Aims and Objectives

To address the research questions outlined above, a comprehensive study of both genital (internal and external) and shell traits was conducted on two genera of Alopiinae: *Montenegrina* O. Boettger, 1877, and *Siciliaria* Vest, 1867. The results were integrated with DNA-based phylogenies and biogeographical analyses in Publications 1 and 2, to achieve a robust taxonomic system via molecular phylogenetics in both genera. Furthermore, diagnostic and phylogenetic signal in the shell and genitalia data should be assessed and we aimed to find explanations for emerging patterns in these data. The latter goals were addressed in Publication 3, where the genital and shell morphology of *Montenegrina* was analyzed to test for correlations, species identification suitability, and phylogenetic signals.

5. Conclusion: Key Findings, Synthesis, and Future Perspectives

This study introduces a new taxonomic approach to Alopiinae clausiliids, where distinctions traditionally based on subtle shell morphology are reconsidered. Historically, taxa were described based on variations like secondary folds or lamellae in the buccal armature, and differences in teleoconch ornamentation. These shell-based traits have often been used to justify the introduction of new taxa, contributing to an overburdened nomenclature. The discovery that genital morphology exhibits variability, similar to shell morphology, allows for a more comprehensive taxonomic approach. We also obtained a meaningful molecular phylogenetic system. This work integrates shell traits, genital morphology, and molecular genetic data, leading to the description of new species and subspecies, and nomenclatural changes (synonymizations, new combinations, and status revisions), finally resulting in the taxonomic revision of *Montenegrina* and *Siciliaria*. Major changes in the latter genus were the reclassification of *Sicania* as a junior synonym of *Siciliaria* and the identification of *Mauritanica* in Europe, previously only known from North Africa.

This study is the first of its kind in Clausiliidae. Although a high number of taxa were anatomically investigated, the sample size per taxon remains limited, and the intra-taxon range of character variability is still insufficiently understood. Further studies should use larger samples to refine taxon delimitation by analyzing genital anatomical traits within species, subspecies, and populations. A matrix of quantitative and qualitative morphological data for *Montenegrina* allowed statistical analysis to test correlations among genital traits, shell traits, and shell-genital traits. The analysis revealed that shell size does not correspond to genitalia size, suggesting that these character complexes are influenced by independent selective pressures. The shell may be more affected by environmental and microclimatic factors, while genital traits may evolve due to isolation-driven divergence. This study also assessed that, while shell and genital traits form the foundation of alpha-taxonomy, they do not appear to carry a phylogenetic signal.

The incongruence between morphometric trees and molecular phylogeny (Mason et al., 2020) suggests that similar genital morphology among phylogenetically distant *Montenegrina* taxa could be homoplasy rather than a result of evolutionary constraints.

Combining shell, genitalia, and DNA sequence data has provided a more integrative approach to Aloiinae systematics that could potentially be applied to the entire Clausiliidae family.

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Part B

7. Publications

The present doctoral thesis is submitted as a cumulative dissertation based on three published articles in peer-reviewed scientific journals with impact factor. The original reprints are provided hereafter.

8. Publication 1

De Mattia, W., Fehér, Z., Mason, K. & Haring, E. (2020). An integrative approach to the taxonomy and systematics within the genus *Montenegrina* Boettger, 1877 (Mollusca, Gastropoda, Clausiliidae). *Journal of Zoological Systematics and Evolutionary Research*, Special Issue 58: 691-808. <http://dx.doi.org/10.1111/jzs.12407>



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 Manganeli (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 genitals 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-atrium 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.

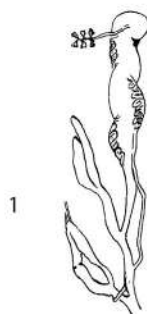


Abb. 2. Genitalorgan von *Montenegrina* (*Beieriella*) *irmengardis* nov. spec. Platanusa im Epirus.

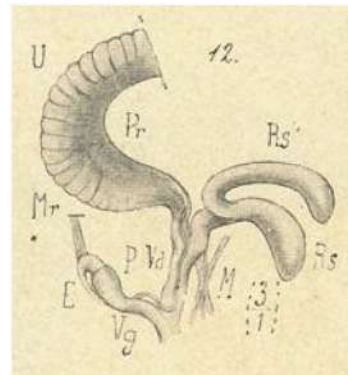


Fig. 23 [№ 366] *Delima* (*Albanodelima*) *subcristata* K. von Cetinje; Sexualorgane.

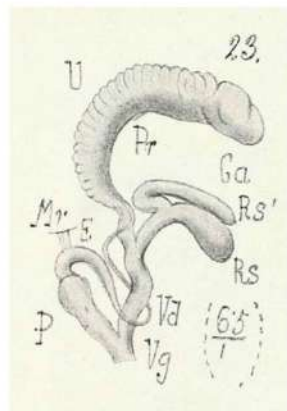


Fig. 12 [№ 377] *Delima* (*Albanodelima*) *apfelbecki* A. J. Wagner vom Mali Senjt (Mali-Sheit) bei Orosht; Sexualorgane.

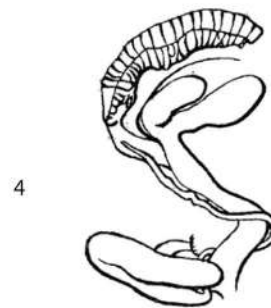


Fig. 3. Genital organs of *Cl. (Delima) skipetarica* n. sp.

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 ± 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

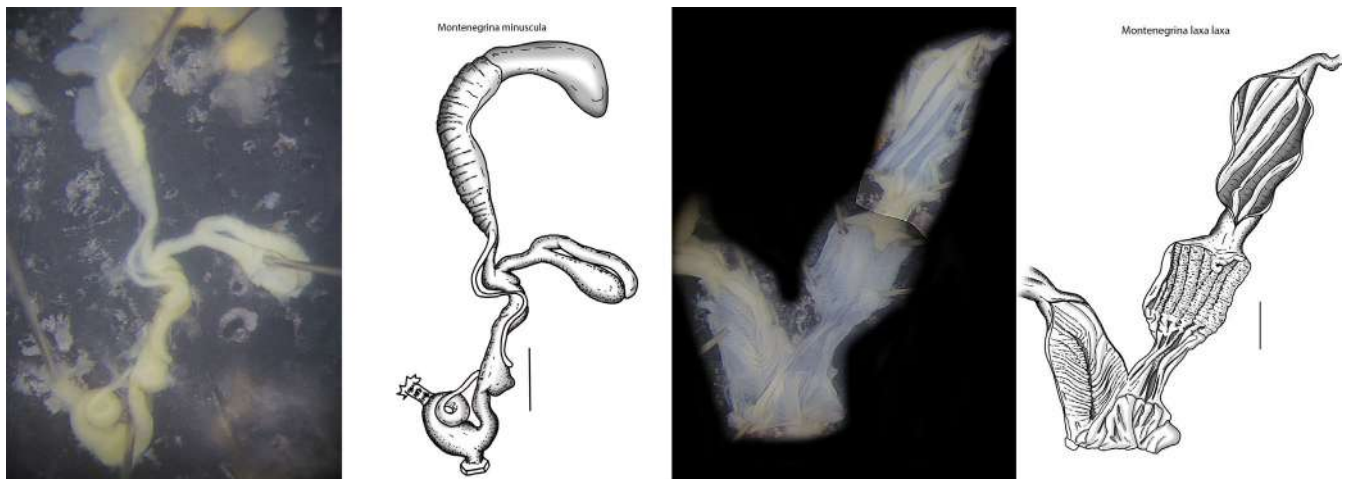


FIGURE 2 Direct comparison between the real sample and the iconography of both external and inner genitalia

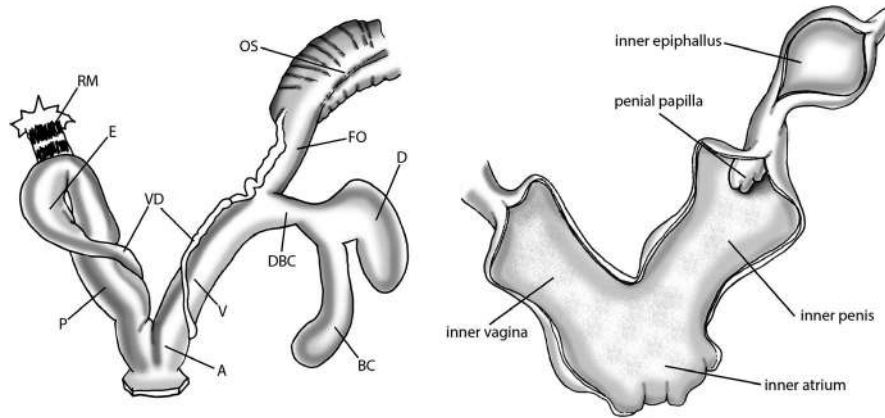


FIGURE 3 General scheme of the distal external and inner genitalia of the genus *Montenegrina*

TABLE 1 Categorized ratios of genital parts

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

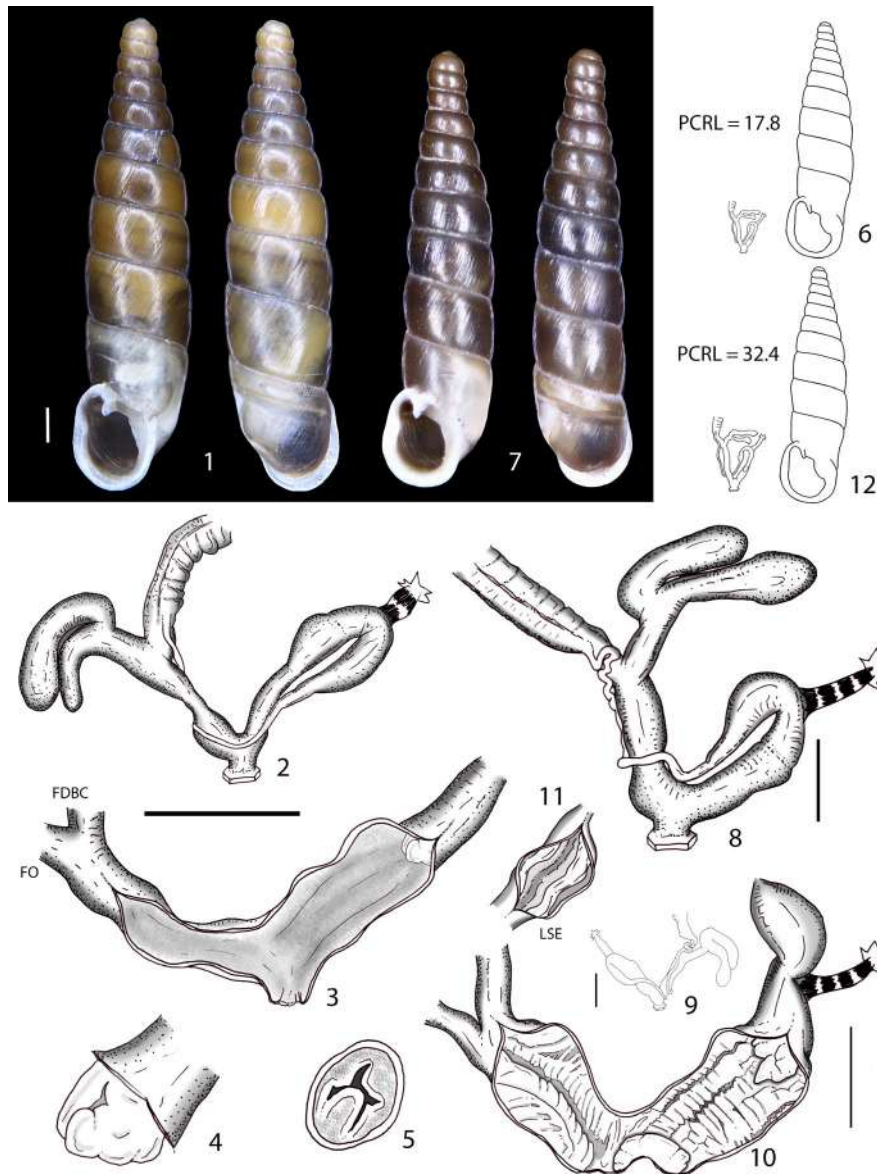


FIGURE 4 4.1–4.6 *Montenegrogrina attemsi* (Wagner, 1914), I. Dedov coll. MK311. 4.1 shell 4.2 whole genitalia except gonads and proximal spermooviduct, 4.3 inner distal genitalia, 4.4 penial papilla, 4.5 cross section of the proximal epiphallus, 4.6 shell-genitalia ratio. 4.7–4.12 *Montenegrogrina jakupicensis*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

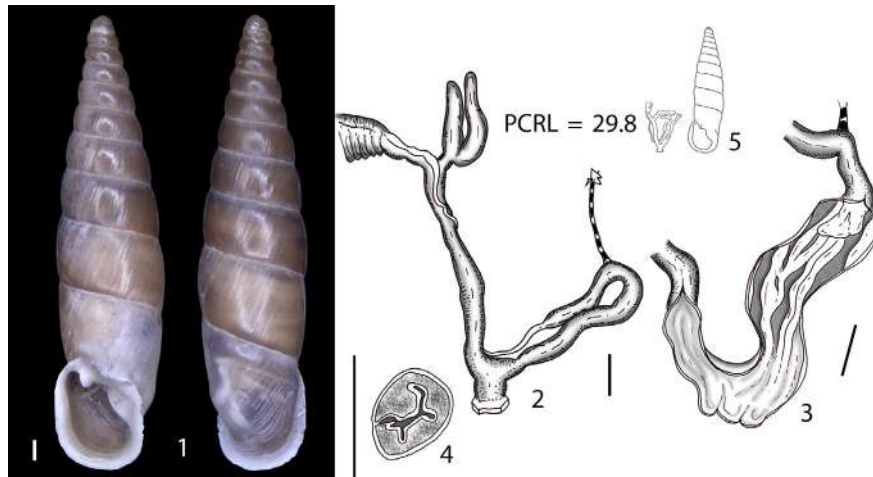


FIGURE 5 *Montenegrina cattaroensis* (Rossmässler, 1835) HNHM 43127. 5.1 shell. 5.2 whole genitalia except gonads and proximal spermoviduct. 5.3 inner distal genitalia. 5.4 cross section of the proximal epiphallus. 5.5 shell-genitalia ratio

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

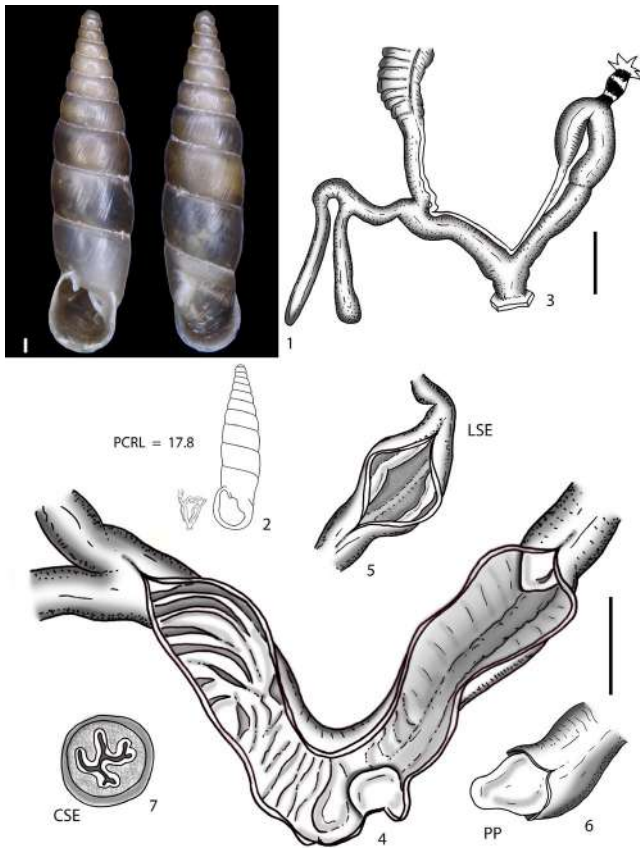


FIGURE 6 *Montenegro umbilicata umbilicata* (Boettger, 1879) stat. nov. NHMW 110430/MN/0152. 6.1 shell. 6.2 shell-genitalia ratio. 6.3 whole genitalia except gonads and proximal spermoviduct. 6.4 inner distal genitalia. 6.5 longitudinal section of the proximal epiphallus. 6.6 penial papilla. 6.7 cross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

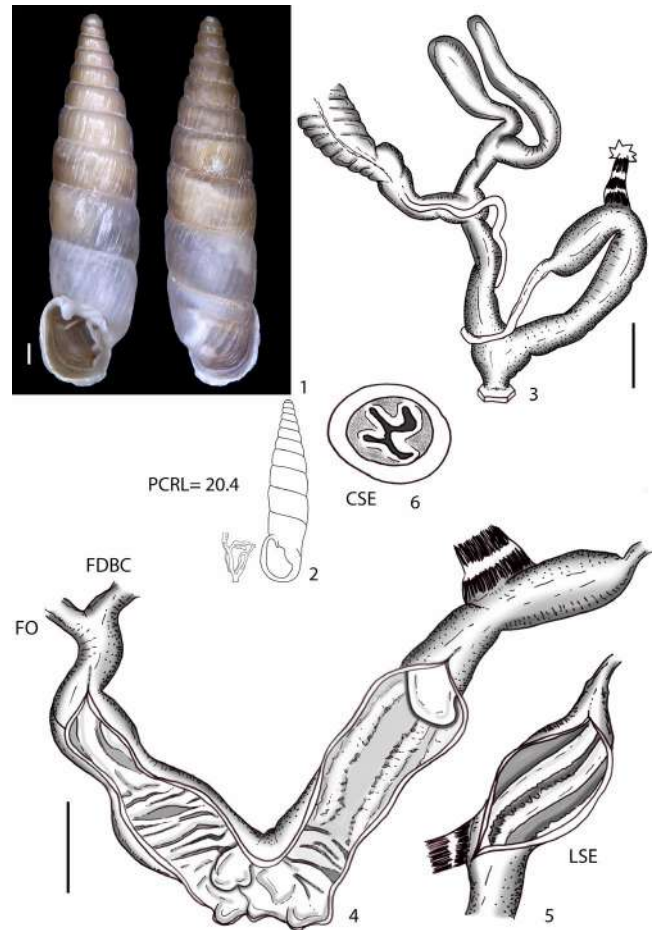


FIGURE 7 *Montenegro umbilicata antivariocostata* (Fehér & Szekeres, 2016) comb. nov. NHMW 110430/MN/0155. 7.1 shell. 7.2 shell-genitalia ratio. 7.3 whole genitalia except gonads and proximal spermoviduct. 7.4 inner distal genitalia. 7.5 longitudinal section of the proximal epiphallus. 7.6 cross section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

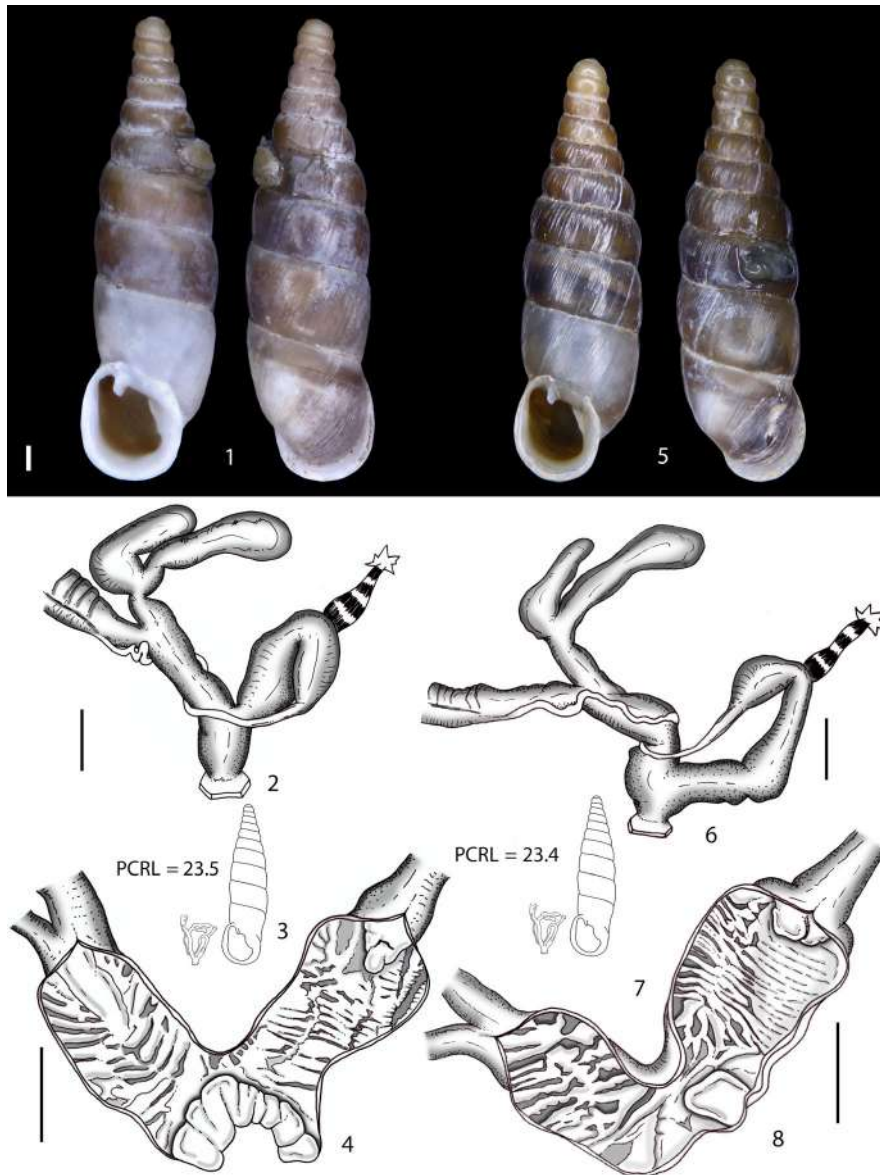


FIGURE 8 8.1–8.4 *Montenegrina dofleini dofleini* (Wagner, 1928) NHMW 110430/MN/0040. 8.1 shell, 8.2 shell-genitalia ratio, 8.3 whole genitalia except gonads and proximal spermoviduct, 8.4 inner distal genitalia. 8.5–8.8 *Montenegrina dofleini fagorum* Nordsieck, 1974 NHMW 110430/MN/0052. 8.5 shell,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

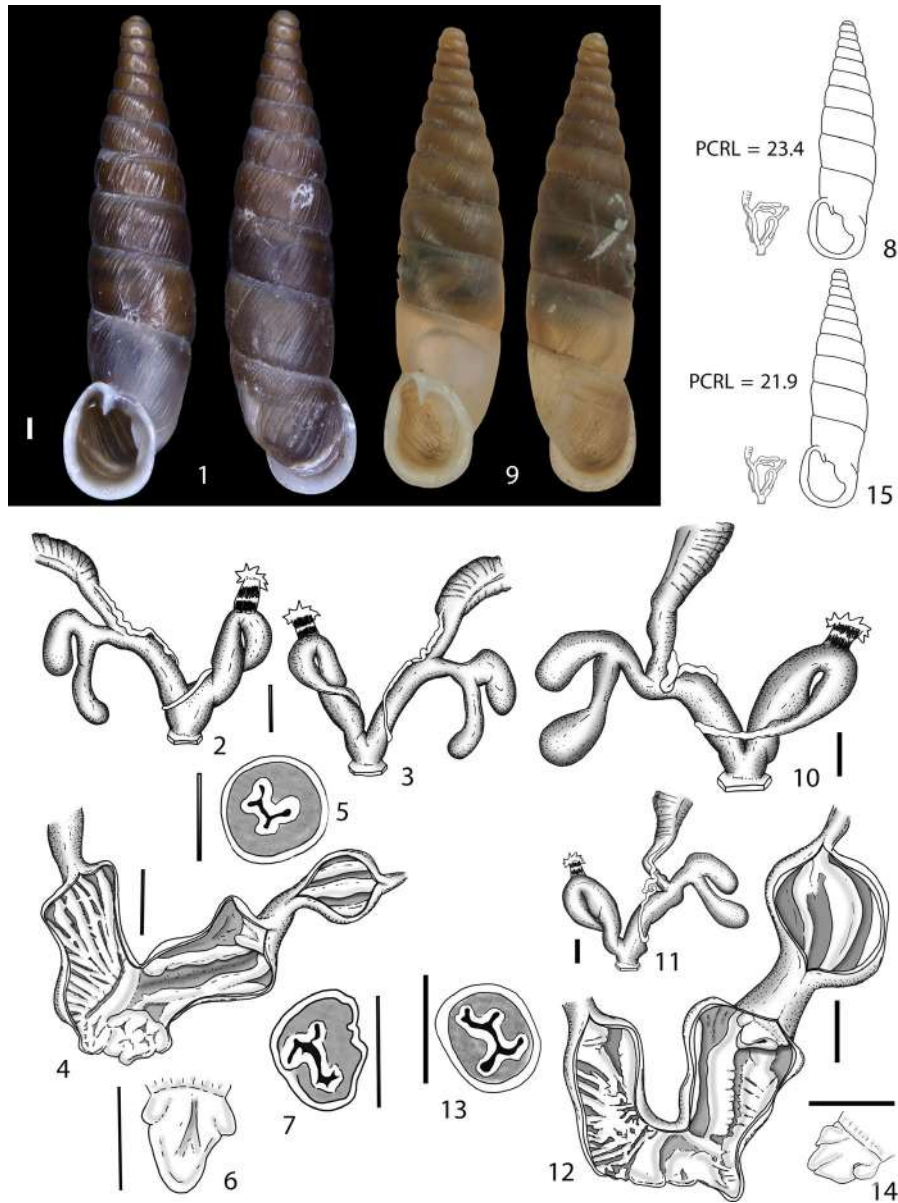


FIGURE 9 *Montenegrina kastoriae kastoriae* Nordsieck, 1972 stat. nov. HNHM 99570. 9.1 shell. 9.2–9.3 whole genitalia except gonads and proximal spermoviduct. 9.4 inner distal genitalia. 9.5 cross section of epiphallus. 9.6 penial papilla. 9.7 cross section of penial papilla. 9.8 shell-genitalia ratio. 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

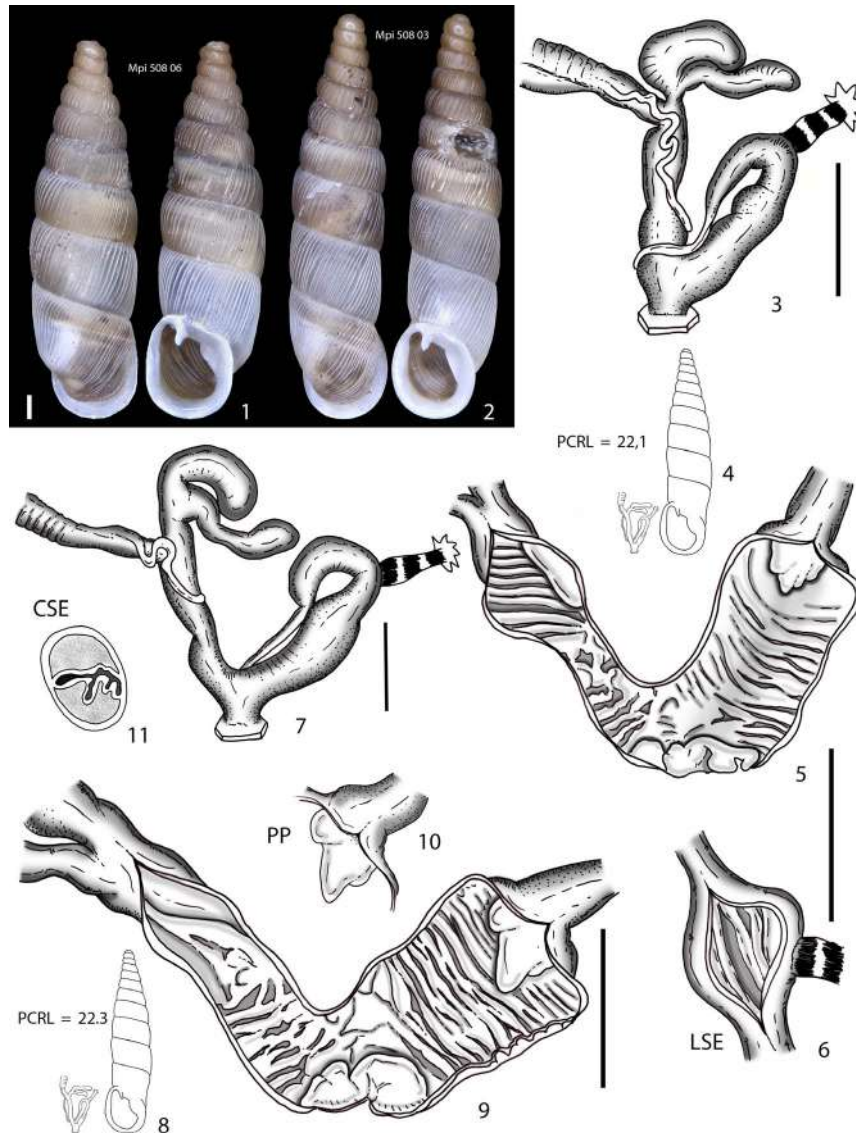


FIGURE 10 *Montenegrina pinteri* Nordsieck, 1974 stat. nov. NHMW 110430/MN/0051. 10.1–10.2 shells. 10.3 whole genitalia except gonads and proximal spermoviduct specimen Mpi-508-6. 10.4 shell-genitalia ratio specimen Mpi-508-6. 10.5 inner distal genitalia specimen Mpi-508-6. 10.6 longitudinal section 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

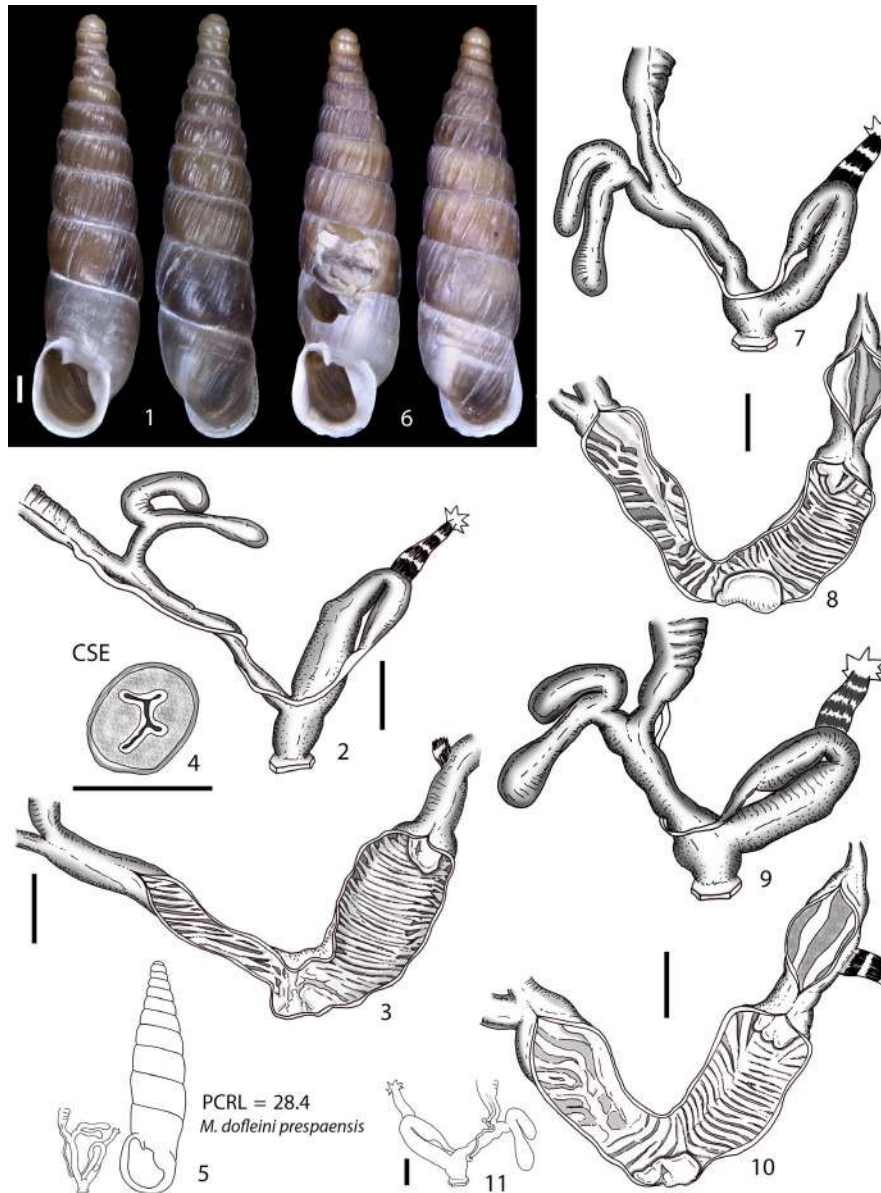


FIGURE 11 *Montenegroa prespaensis prespaensis* Nordsieck, 1988 stat. nov. HNHM 99573. 11.1 shell. 11.2 whole distal genitalia. 11.3 inner distal genitalia. 11.4 cross section of the epiphallus. 11.5 shell-genitalia ratio. NHMW 110430/MN/0134 Mrp-616_04. 11.6 shell. 11.7 whole distal genitalia. 11.8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

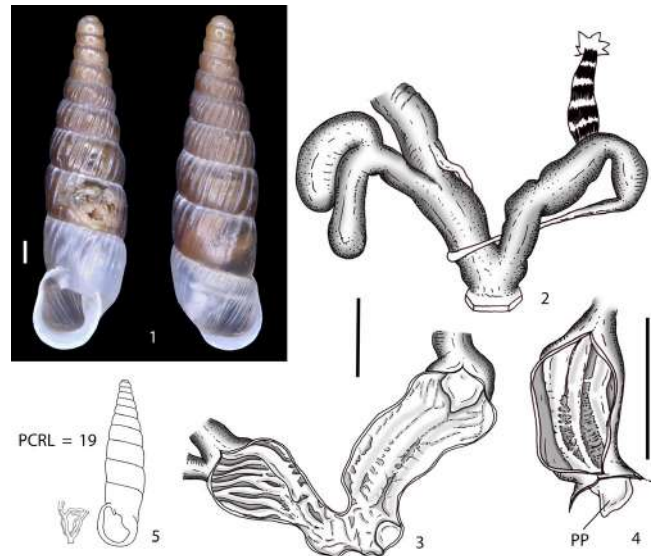


FIGURE 12 *Montenegrina prespaensis sinosi* Páll-Gergely, 2010 comb. nov. NHMW 110430/MN/0058. 12.1 shells. 12.2 whole distal genitalia. 12.3 inner distal genitalia. 12.4 longitudinal section of the epiphallus. 12.5 shell-genitalia ratio

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 & 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.

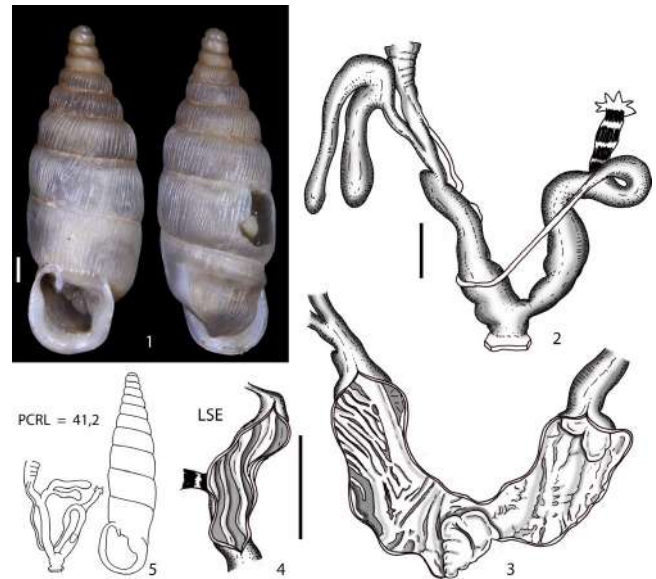


FIGURE 13 *Montenegrina drimmeri* Fehér & Szekeres, 2006 HNHM 94830. 13.1 shells. 13.2 whole distal genitalia. 13.3 inner distal genitalia. 13.4 longitudinal section of the epiphallus. 13.5 shell-genitalia ratio

***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.

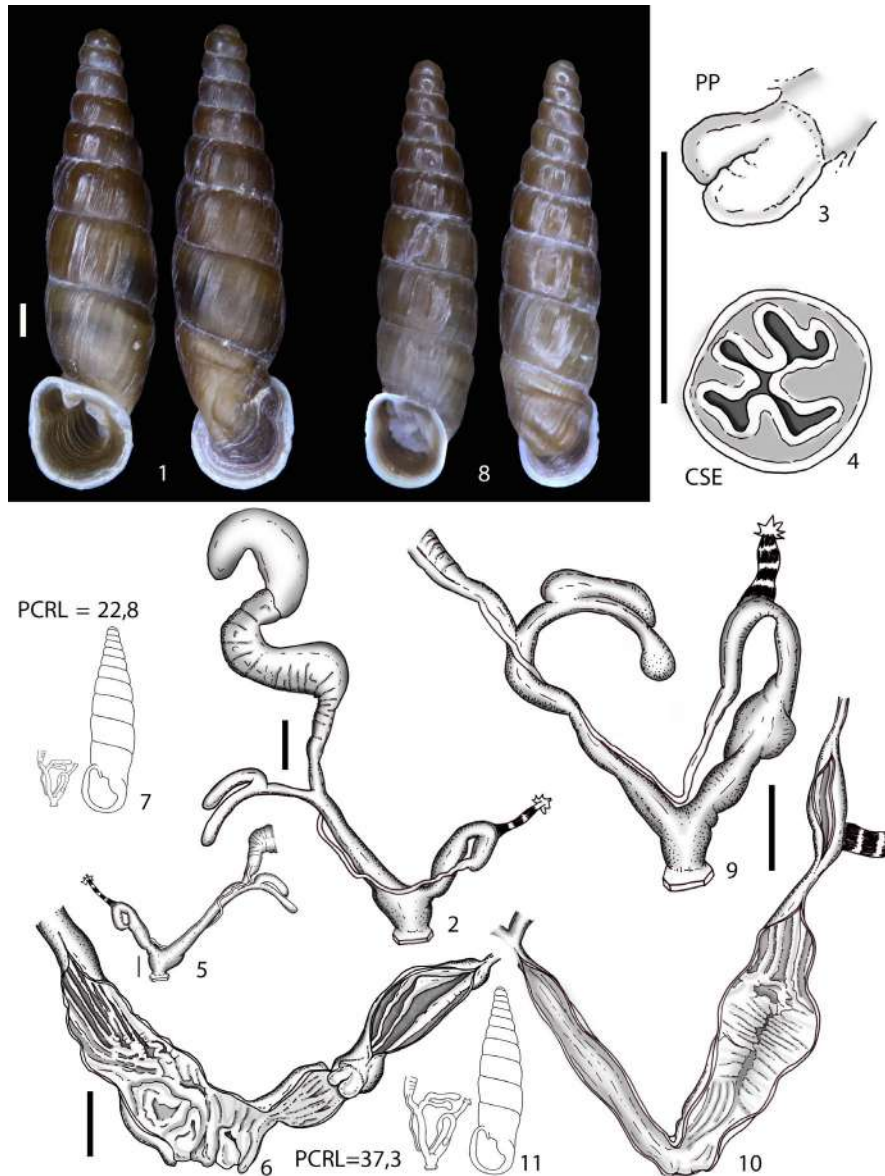


FIGURE 14 14.1–14.7 *Montenegrogrina fuchsi* Brandt, 1961 NHMW 110430/MN/0036. 14.1 shells. 14.2 whole distal genitalia. 14.3 penial papilla. 14.4 cross section of epiphallus. 14.5 whole distal genitalia. 14.6 inner distal genitalia. 14.7 shell-genitalia ratio. 14.8–14.11 *Montenegrogrina klemmi* Brandt, 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]).

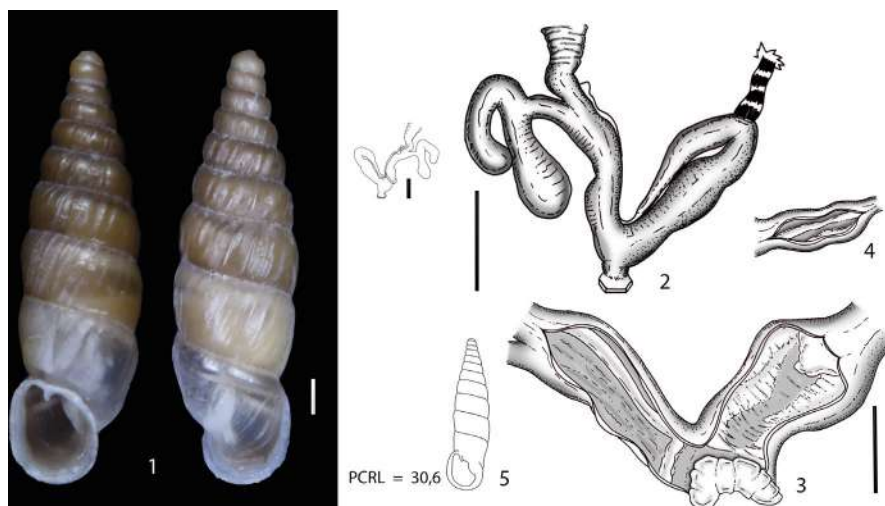


FIGURE 15 *Montenegrina pallida* Fauer, 1993 stat. nov. HNHM 99566. 15.1 shell. 15.2 whole distal genitalia. 15.3 inner distal genitalia. 15.4 longitudinal section of epiphallus. 15.5 shell-genitalia ratio

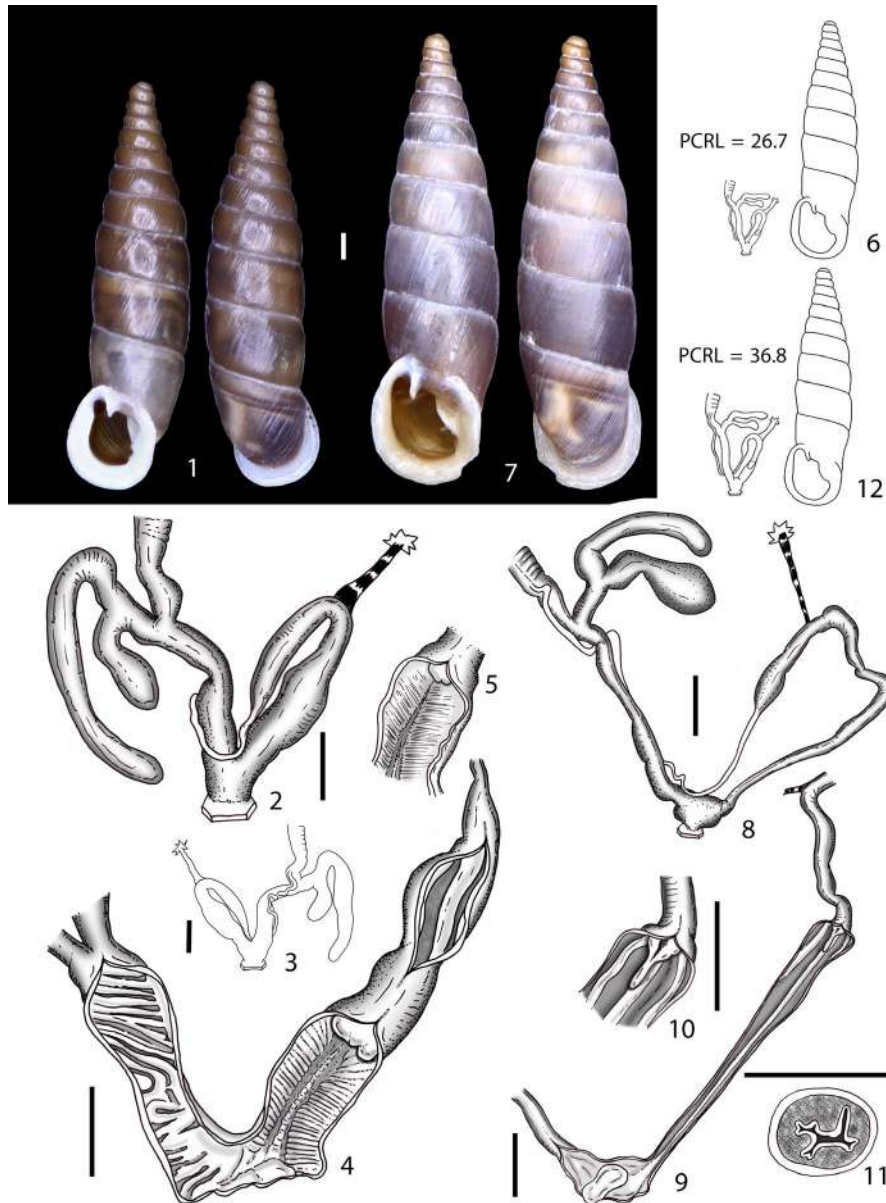


FIGURE 16 16.1–16.6 *Montenegroina rugilabris rugilabris* (Mousson, 1859) HNHM 99547. 16.1 shell. 16.2–16.3 whole distal genitalia. 16.4 inner distal genitalia. 16.5 penial papilla and inner proximal penis. 16.6 shell-genitalia ratio. 16.7–16.12 *Montenegroina edmundi* Szekeres, 2006 stat. nov. HNHM 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

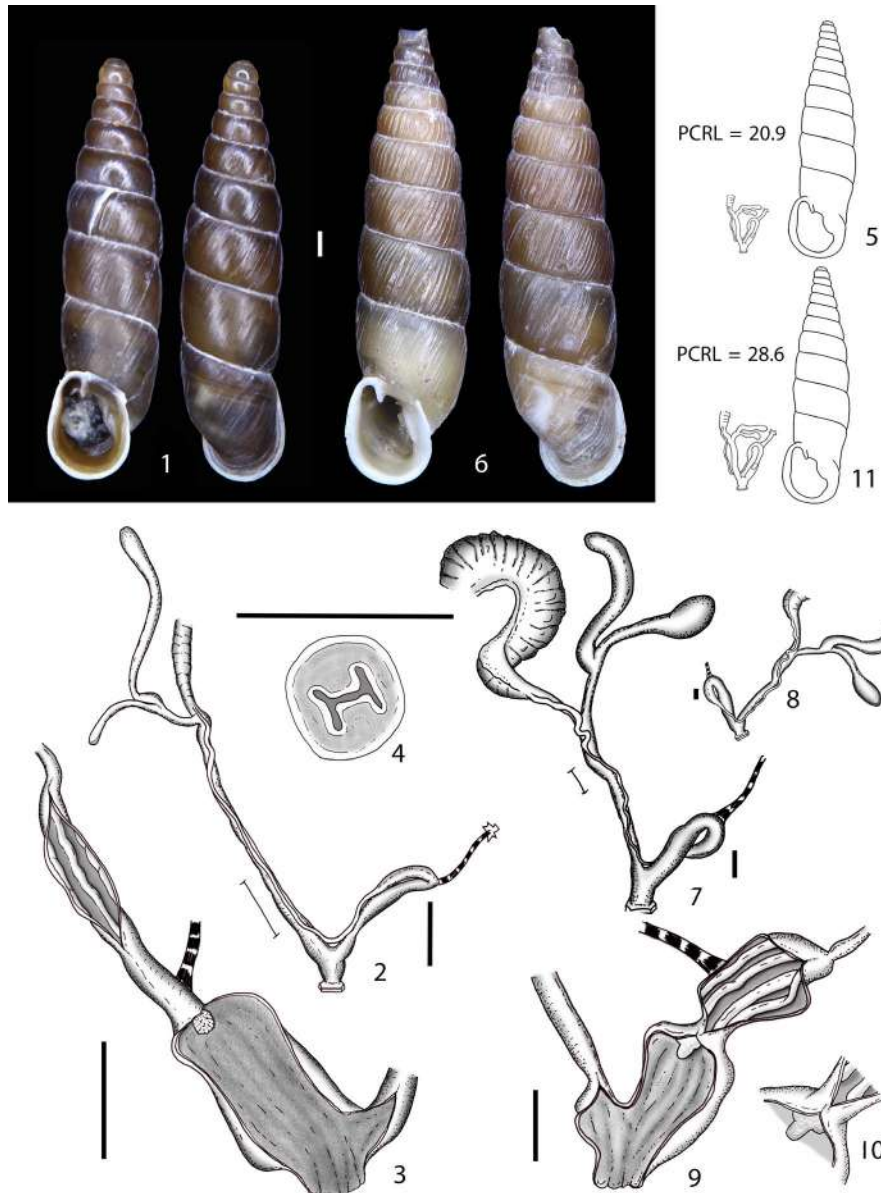


FIGURE 17 17.1–17.5 *Montenegroa golikutensis* Fehér & Szekeres, 2016 stat. nov. NHMW 111215. 17.1 shell. 17.2 whole distal genitalia. 17.3 inner distal genitalia. 17.4 cross section of epiphallus. 17.5 shell-genitalia ratio. 17.6–17.11 *Montenegroa gregoi* Fehér & Szekeres, 2016 stat. nov. HHNM 99475. 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.

Montenegroa rugilabris irmengardis Klemm, 1962

Figures: 18.1–18.6

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

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

Montenegroa skipetarica irmengardis – Nordsieck, 2009: 73.

Montenegroa 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,

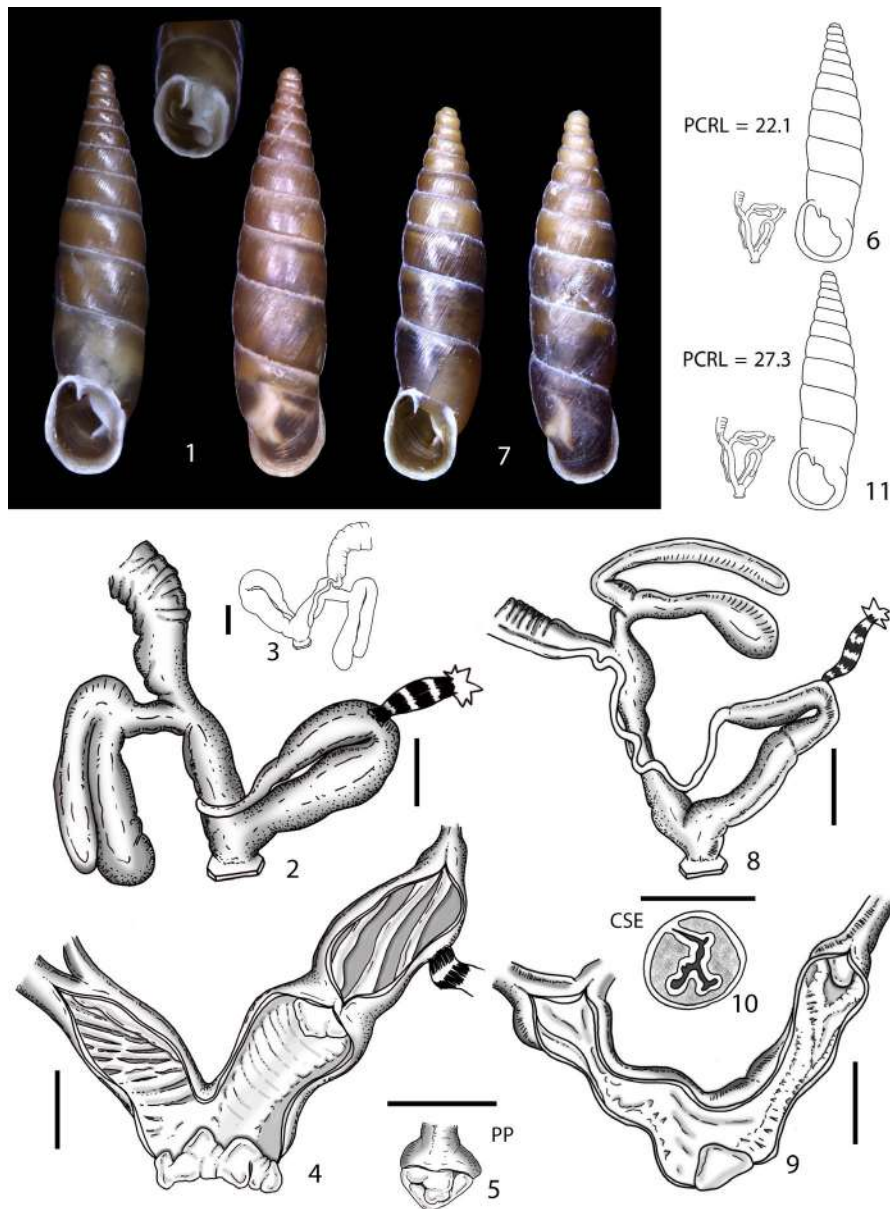


FIGURE 18 18.1–18.6 *Montenegrina rugilabris irmengardis* Klemm, 1962 HNHM 99552. 18.1 shell. 18.2–18.3 whole distal genitalia. 18.4 inner distal genitalia. 18.5 penial papilla. 18.6 shell-genitalia ratio. 18.7–18.11 *Montenegrina lambdaformis welterschultesi* Fehér & Szekeres, 1999 NHMW 110430/MN/0316.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

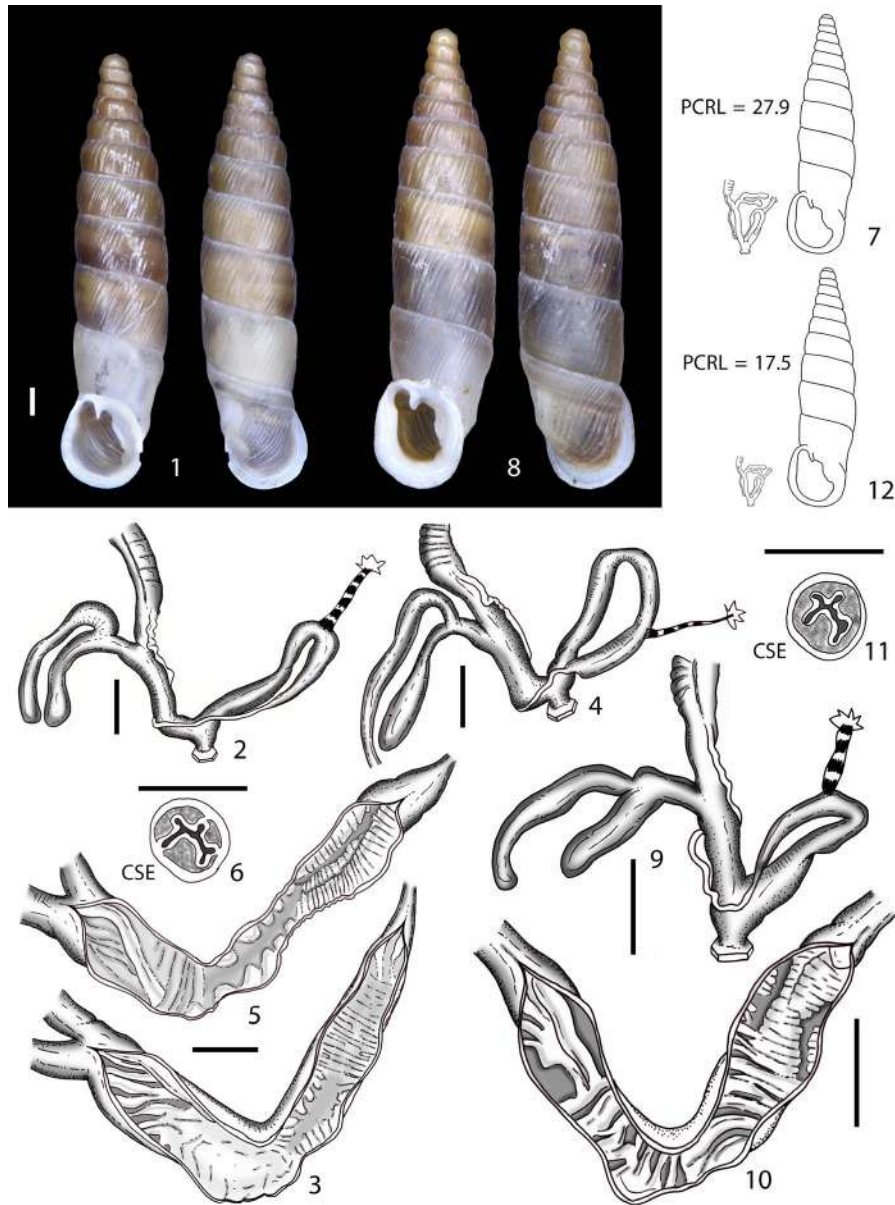


FIGURE 19 19.1–19.7 *Montenegrina janinensis* (Mousson, 1859) HNHM 99560. 19.1 shell. 19.2 whole distal genitalia. 19.3 inner distal genitalia. 19.6 cross section of epiphallus. 19.7 shell-genitalia ratio. 19.8–19.12 HNHM 99561 *M. janinensis crassilabris* morphotype. 19.8 shell. 19.9 whole distal genitalia.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

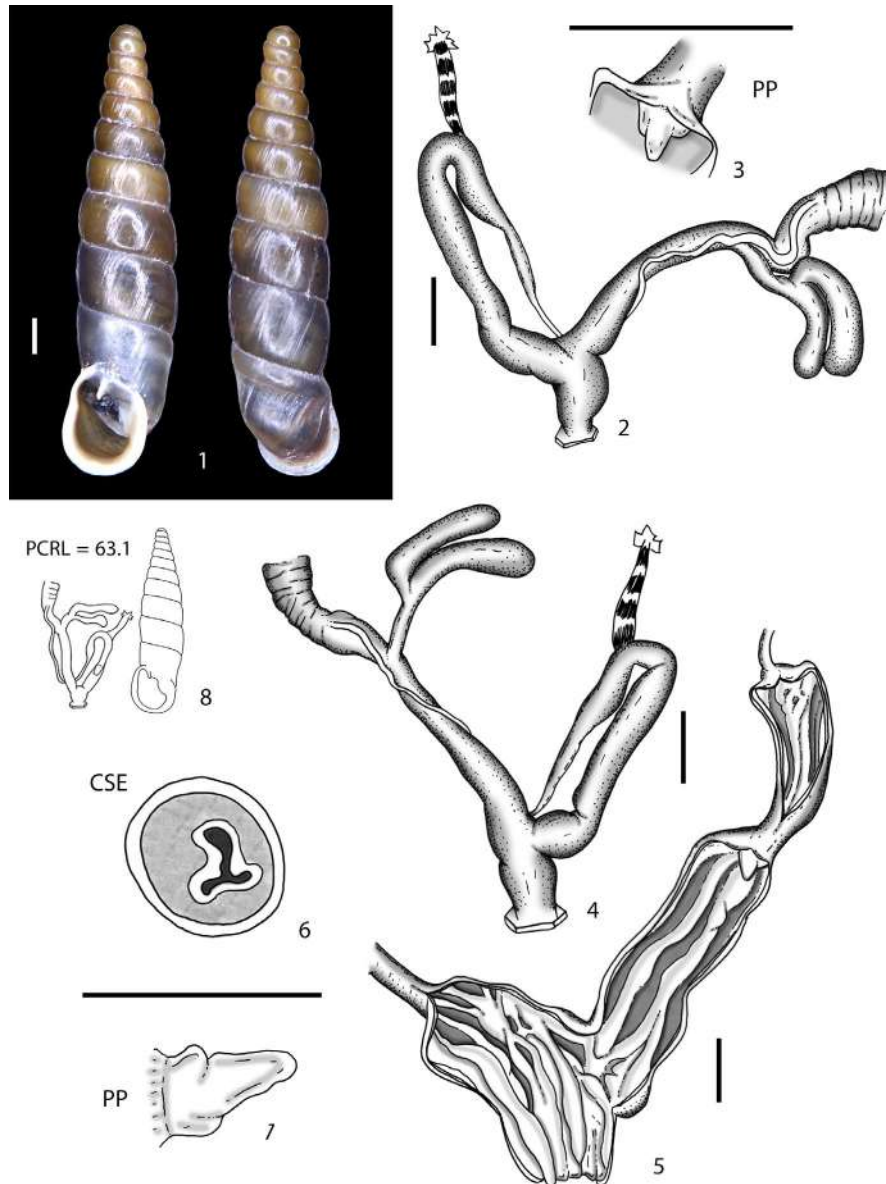


FIGURE 20 *Montenegrina improvisa* Fehér & Szekeres, 2016 stat. nov. HHNM 99019. 20.1 shell. 20.2 whole distal genitalia. 20.3 penial papilla. 20.4 whole distal genitalia. 20.5 inner distal genitalia. 20.6 cross section of epiphallus. 20.7 penial papilla. 20.8 shell-genitalia ratio

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.

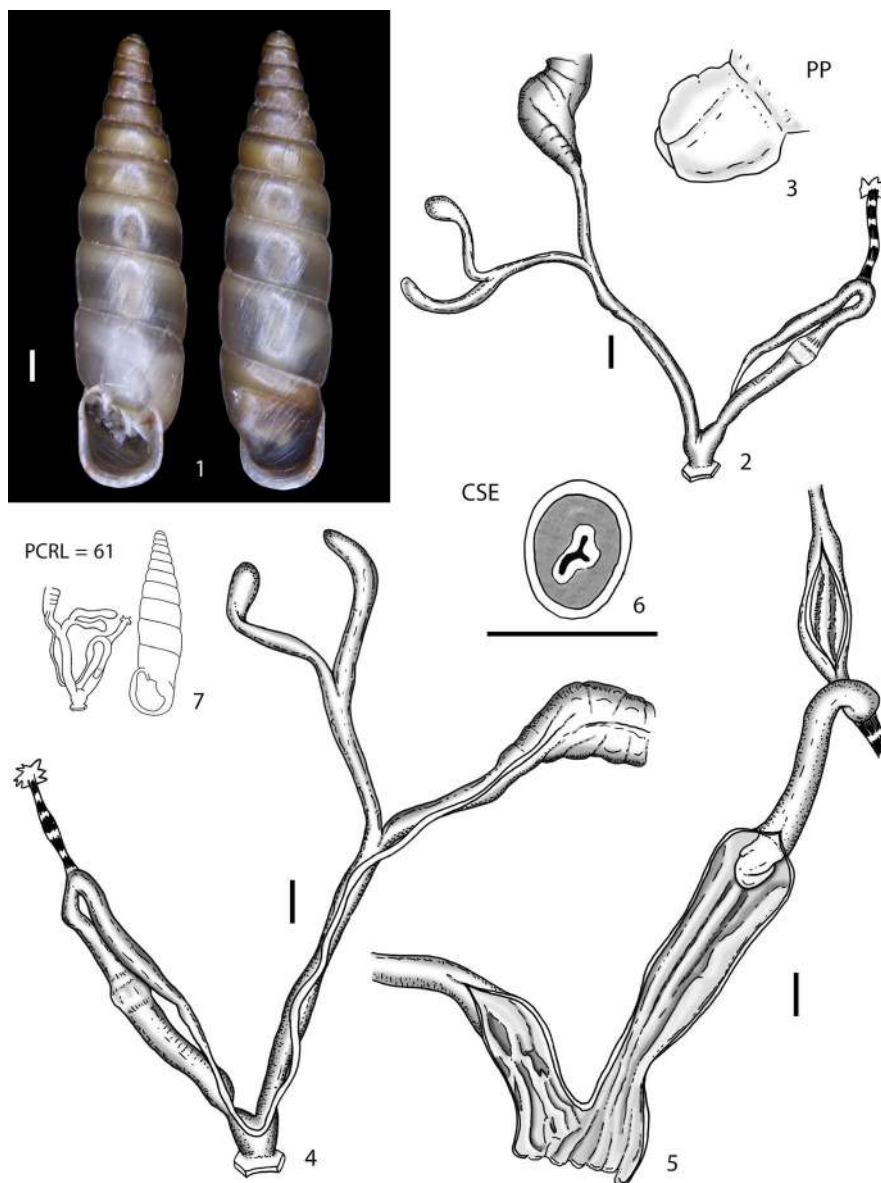


FIGURE 21 *Montenegrina haringae* Fehér & Szekeres, 2016 NHMW 111220. 21.1. shell. 21.2 whole distal genitalia. 21.3 penial papilla. 21.4 whole distal genitalia. 21.5 inner distal genitalia. 21.6 cross section of epiphallus. 21.7 shell-genitalia ratio

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,

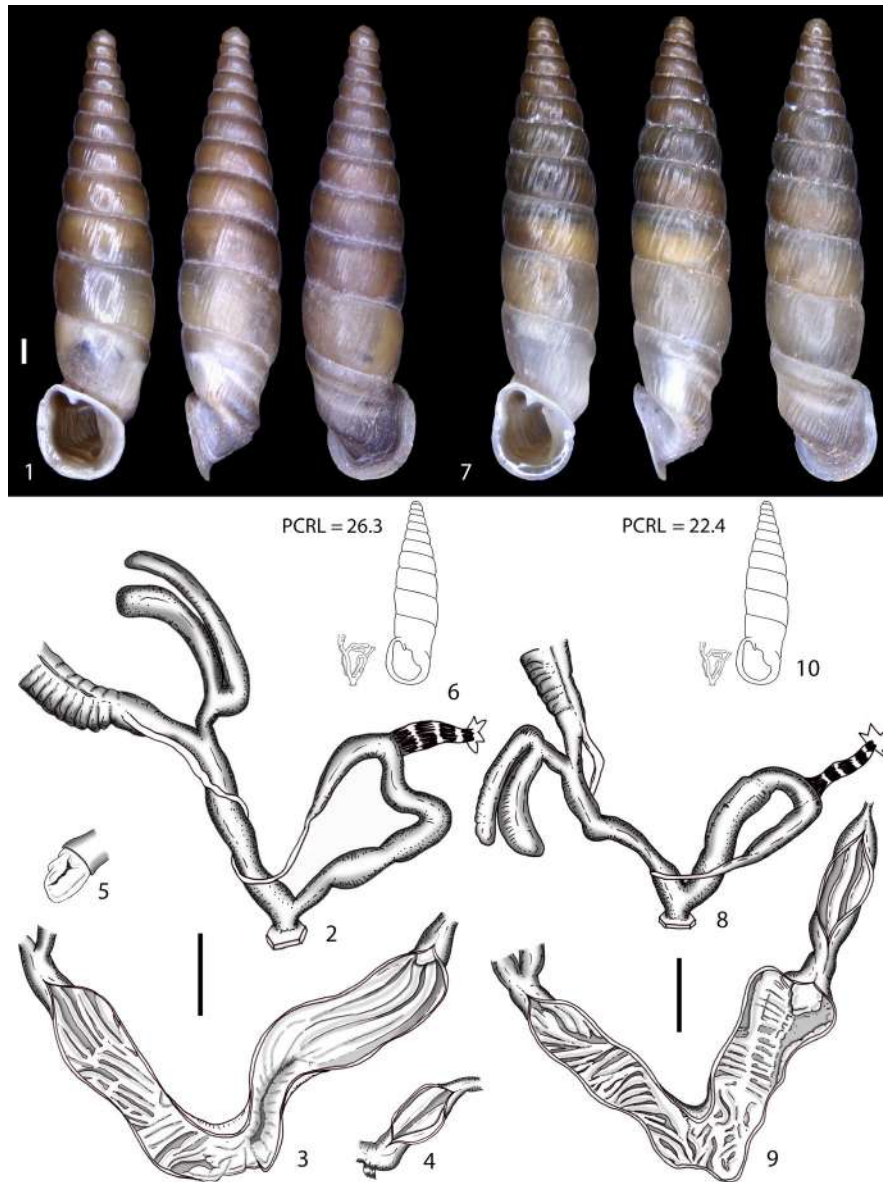


FIGURE 22 22.1–22.6 *Montenegrina helvola carinata* Erőss and Szekeres, 1999 HNHM 99618. 22.1 shell. 22.2 whole distal genitalia. 22.3 inner distal genitalia. 22.4 longitudinal section of epiphallus. 22.5 penial papilla. 22.6 shell-genitalia ratio. 22.7–22.10 *Montenegrina helvola magna* Fehér & Szekeres,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

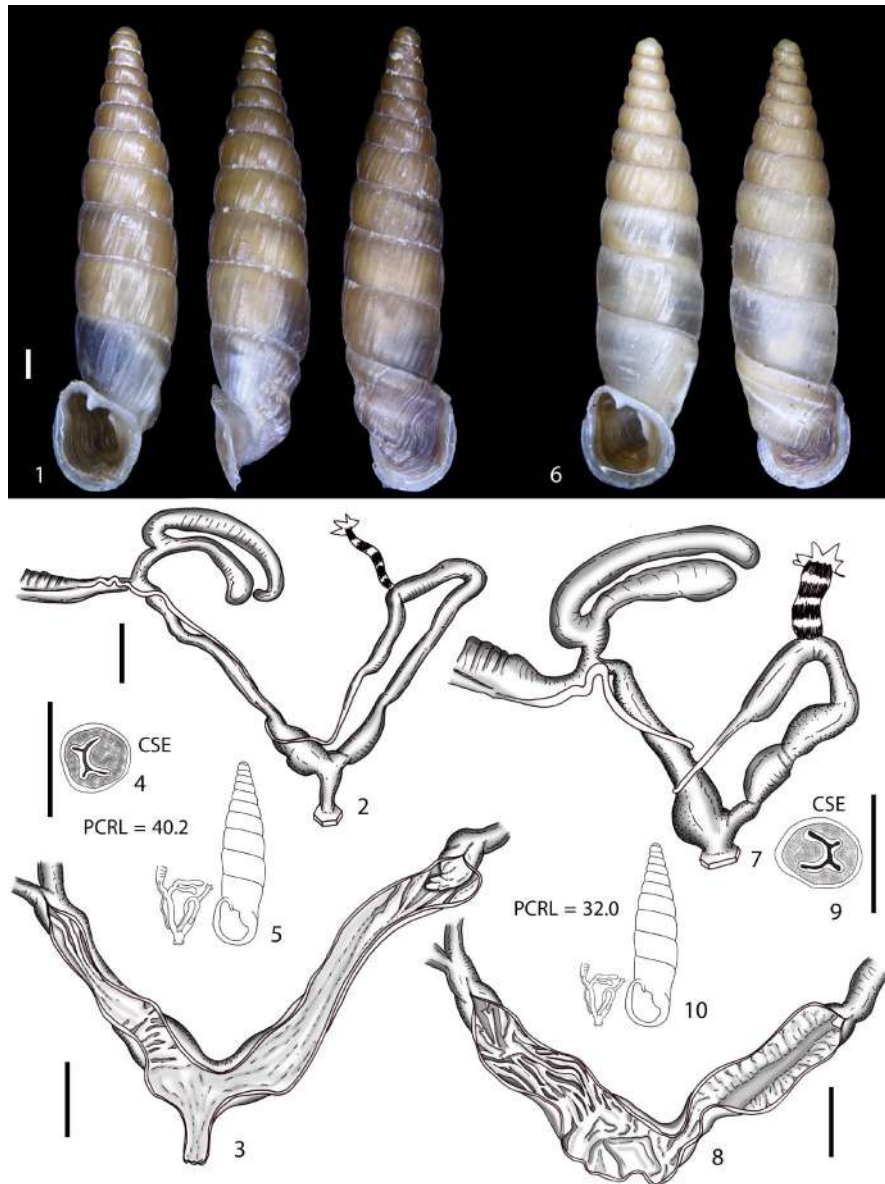


FIGURE 23 23.1–23.5 *Montenegro helvola ornata* Eröss and Szekeres, 1999 HNHM 99617. 23.1. shell 23.2 whole distal genitalia. 23.3 inner distal genitalia. 23.4 cross section of epiphallus. 23.5 shell-genitalia ratio. 23.6–23.10 *Montenegro helvola pageti* Brandt, 1962 NHMW 110430/MN/0077. 23.6 shell.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

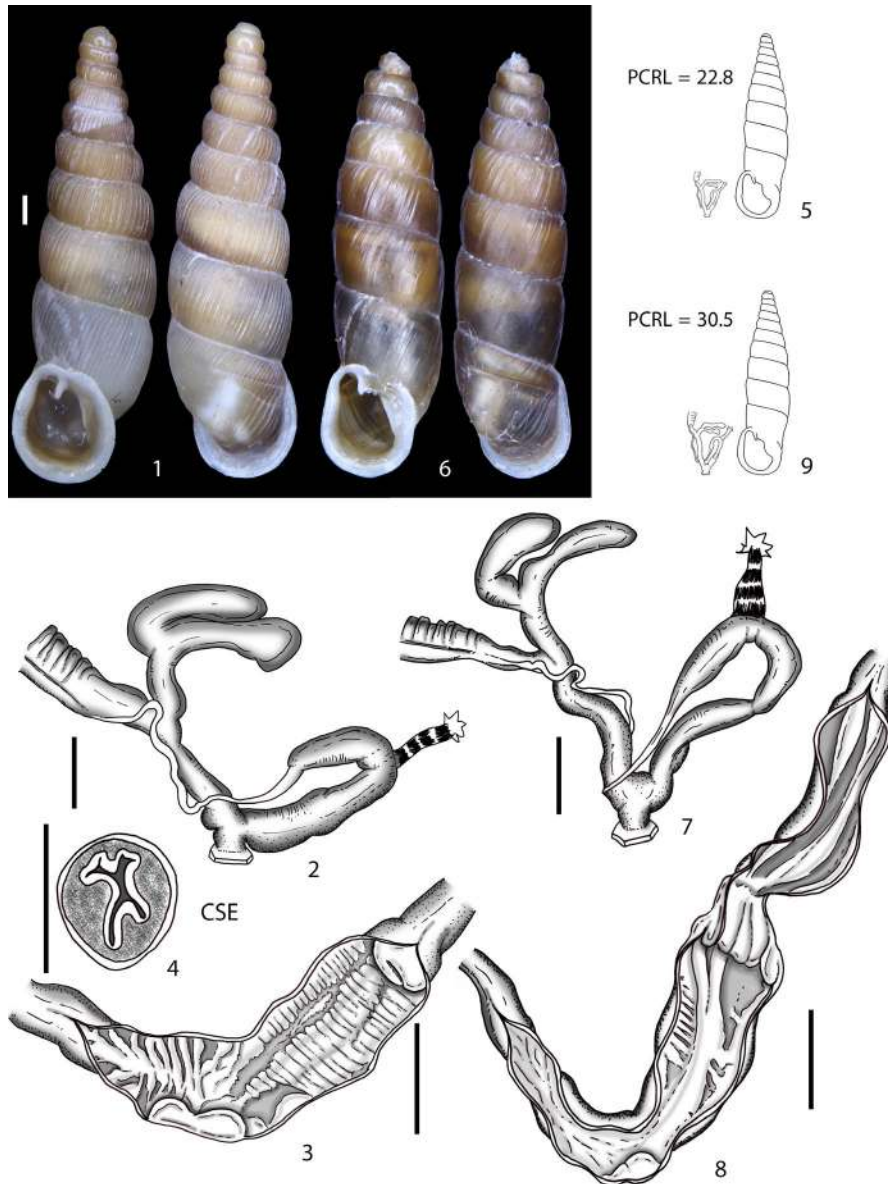


FIGURE 24 24.1–24.5 *Montenegrina hiltrudae costulata* Erőss and Szekeres, 2006 comb. nov. HNHM 99590. 24.1 shell. 24.2 whole distal genitalia. 24.3 inner distal genitalia. 24.4 cross section of epiphallus. 24.5 shell-genitalia ratio. 24.6–24.9 *Montenegrina dennisi dennisi* Gittenberger, 2002 stat.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

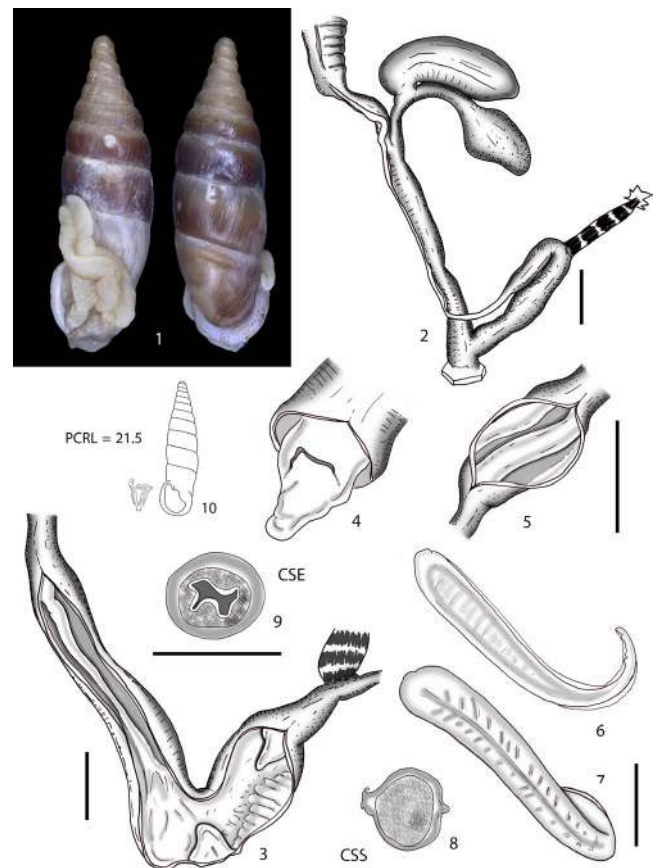


FIGURE 25 *Montenegrina hiltrudae densicostulata* Nordsieck, 1974 HNHM 99583. 25.1 shell. 25.2 whole distal genitalia. 25.3 inner distal genitalia. 25.4 penial papilla. 25.5 longitudinal section of epiphallus. 25.6–25.7 spermatophore. 25.8 cross section of spermatophore. 25.9 cross section of epiphallus.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

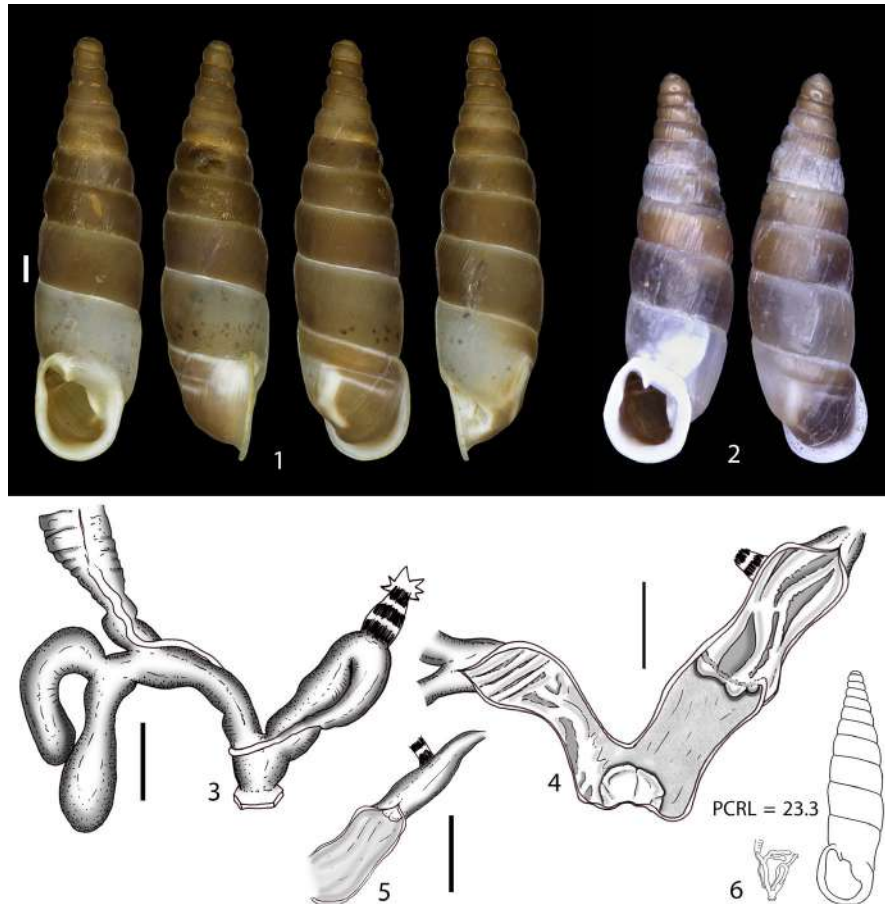


FIGURE 26 *Montenegrina atansiensis* n. sp. HNHM 99587 Mds-408-07. 26.1 shell of the Holotype. 26.2 shell of the dissected specimen HNHM 99587 Msa-408-01. 26.3 whole distal genitalia and inner distal genitalia. 26.4 inner distal genitalia. 26.5 penial papilla and proximal inner penis. 26.6 shell-genitalia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

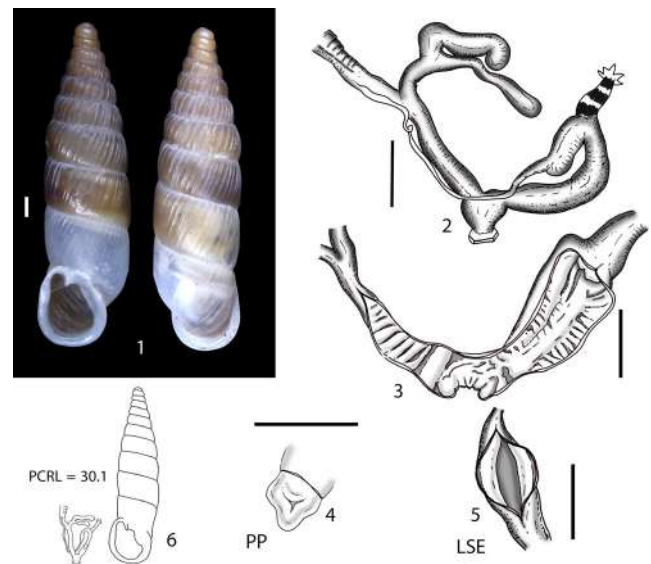


FIGURE 27 *Montenegrina desaretica* Fehér & Szekeres, 2016 stat. nov. NHMW 111251. 27.1 shell. 27.2 whole distal genitalia. 27.3 inner distal genitalia. 27.4 longitudinal section of epiphallus. 27.5 penial papilla. 27.6 shell-genitalia ratio

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.

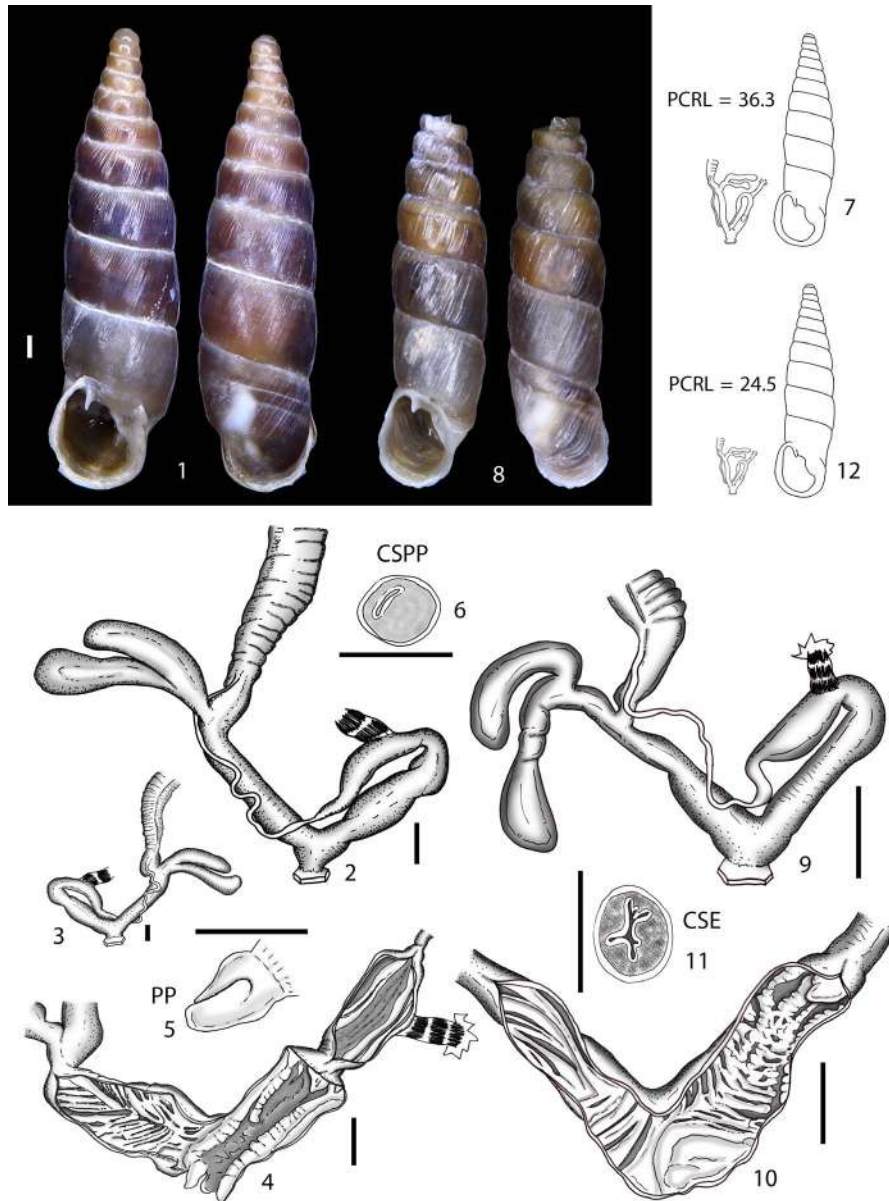


FIGURE 28 28.1–28.7 *Montenegrogrina fusca* Fehér & Szekeres, 2006 stat. nov. HNHM 99596. 28.1 shell. 28.2–28.3 whole distal genitalia. 28.4 inner distal genitalia. 28.5 penial papilla. 28.6 cross section of penial papilla. 28.7 shell-genitalia ratio. 28.8–28.12 *Montenegrogrina dennis maasseni* Gittenberger,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

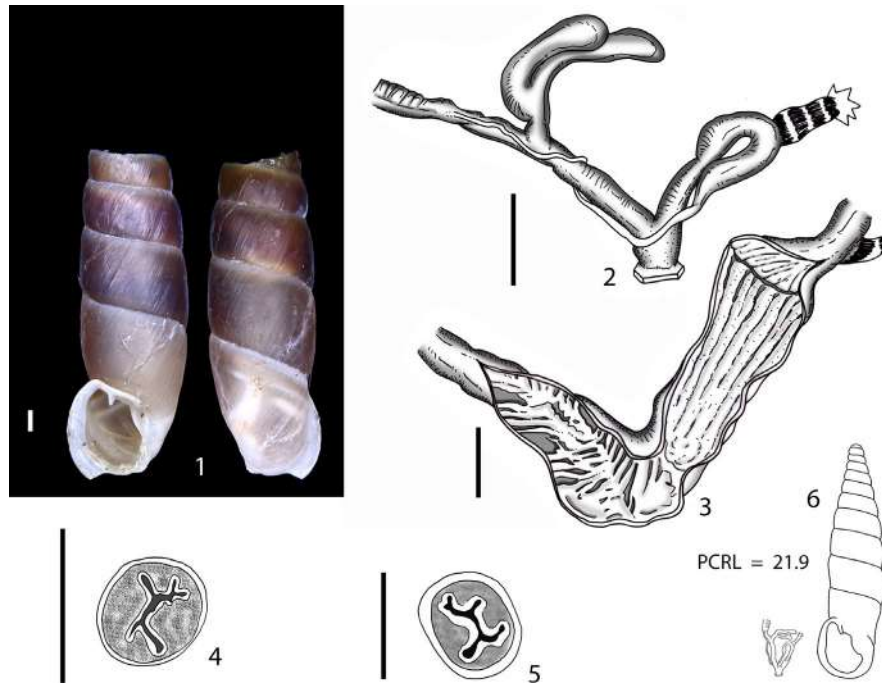


FIGURE 29 29.1–29.5 *Montenegrina hiltrudae protruda* Gittenberger, 2002 HNHM 99593. 29.1 shell, 29.2 whole distal genitalia, 29.3 inner distal genitalia, 29.4 cross section of epiphallus. 29.5 shell-genitalia ratio

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

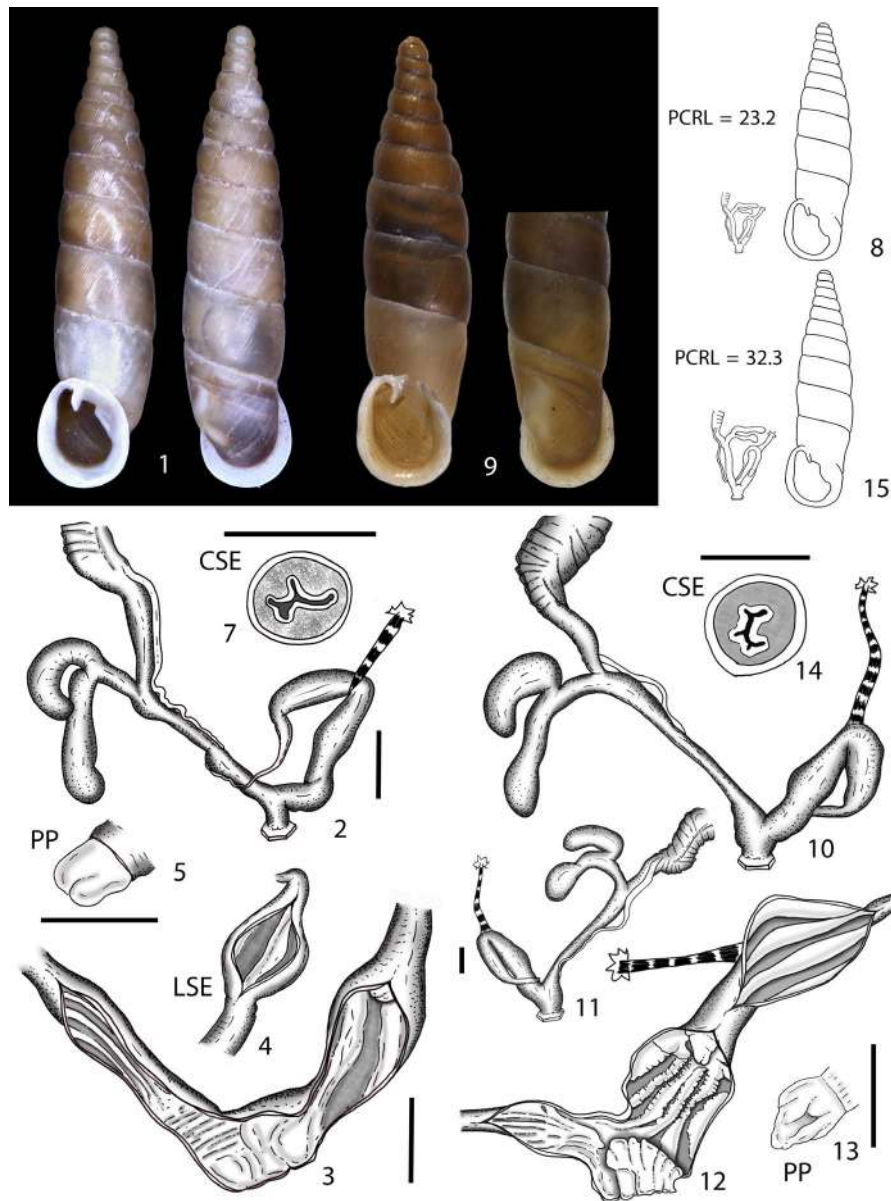


FIGURE 30 30.1–30.6 *Montenegrogrina sattmanni sattmanni* Nordsieck, 1988 stat. nov. HHNM 99585, 30.1 shell, 30.2 whole distal genitalia, 30.3 inner distal genitalia, 30.4 longitudinal section of epiphallus, 30.5 penial papilla, 30.6 cross section of epiphallus. 30.7 shell-genitalia ratio. 30.7–30.14 *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.

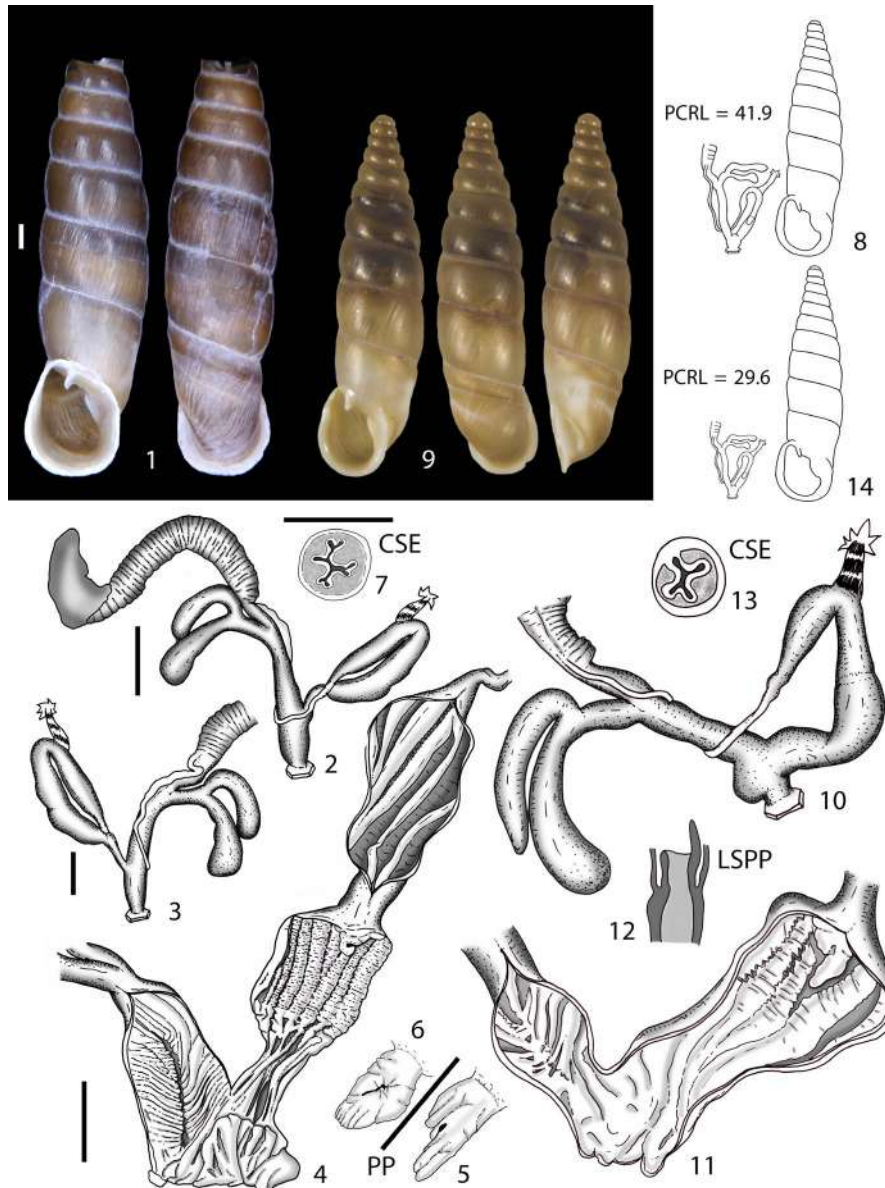


FIGURE 31 31.1–31.8 *Montenegro laxa* (Küster, 1861) HNHM 99033. 31.1 shell. 31.2–31.3 whole distal genitalia. 31.4 inner distal genitalia. 31.5–31.6 penial papilla. 31.7 cross section of epiphallus. 31.8 shell-genitalia ratio. 31.9–31.14 *Montenegro miraka dedovi* Nordsieck, 2009 comb. nov. DED-580,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

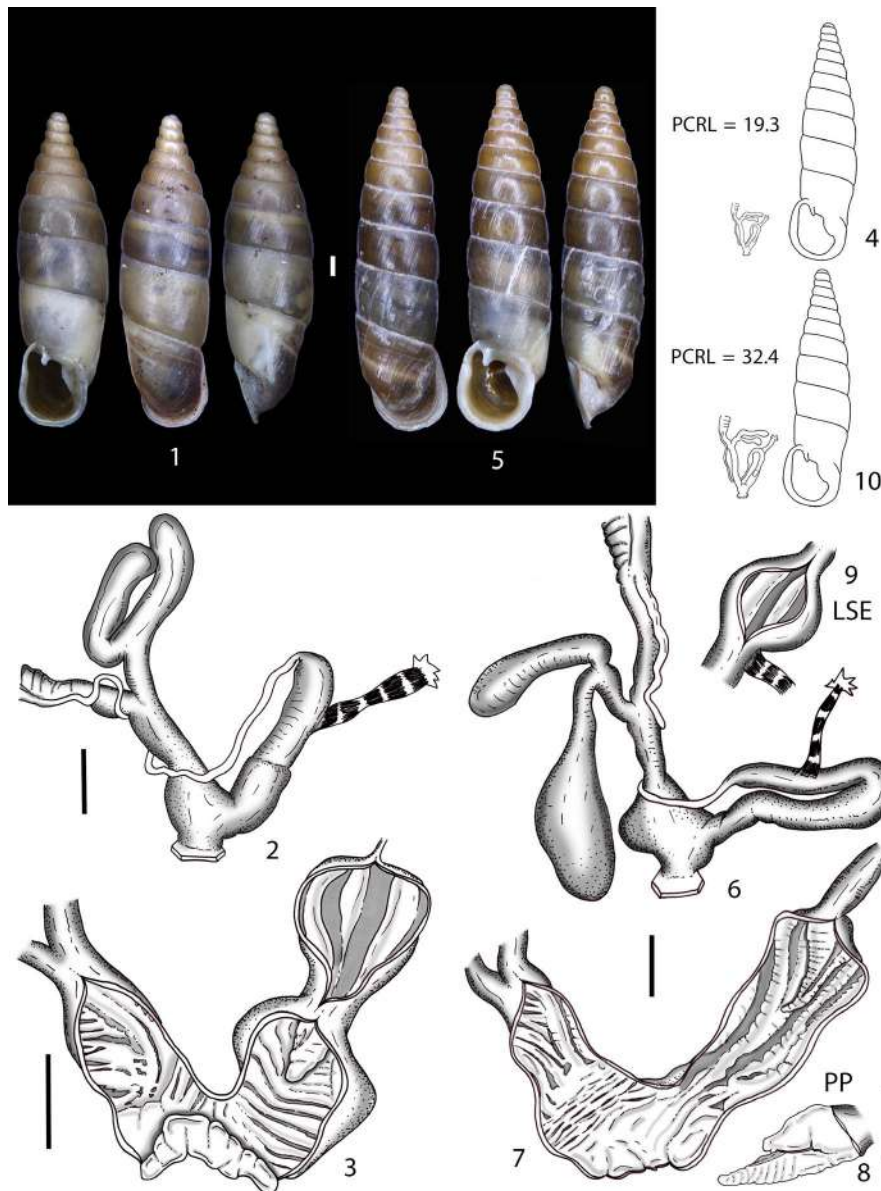


FIGURE 32 32.1–32.4 *Montenegrina miraka delii* Fehér & Szekeres, 2016 comb. nov. NHMW 111235. 32.1 shell, 32.2 whole distal genitalia, 32.3 inner distal genitalia, 32.4 shell-genitalia ratio. 32.5–32.10 *Montenegrina miraka disjuncta* Fehér & Szekeres, 2006 comb. nov. HNHM 99000. 32.5 shell, 32.6 whole 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.

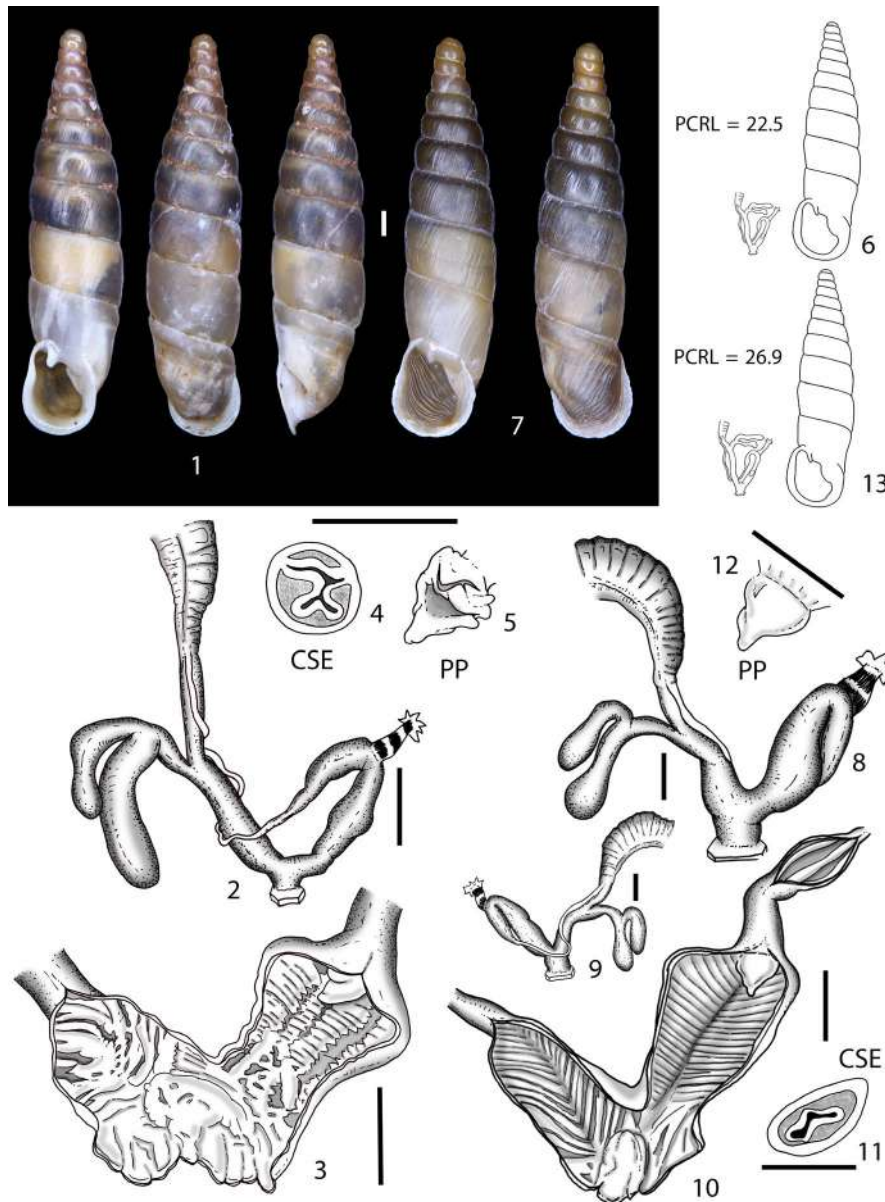


FIGURE 33 33.1–33.6 *Montenegrina miraka errans* Erőss and Szekeres, 2006 comb. nov. HNHM 98950. 33.1 shell, 33.2 whole distal genitalia, 33.3 inner distal genitalia. 33.4 cross section of epiphallus, 33.5 penial papilla, 33.6 shell-genitalia ratio. 33.7–33.13 *Montenegrina iba* Nordsieck, 1972 stat.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

Figures 34.1–34.5

Montenegrina laxa kotschani Erőss and Szekeres, 2006 in Erőss 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.

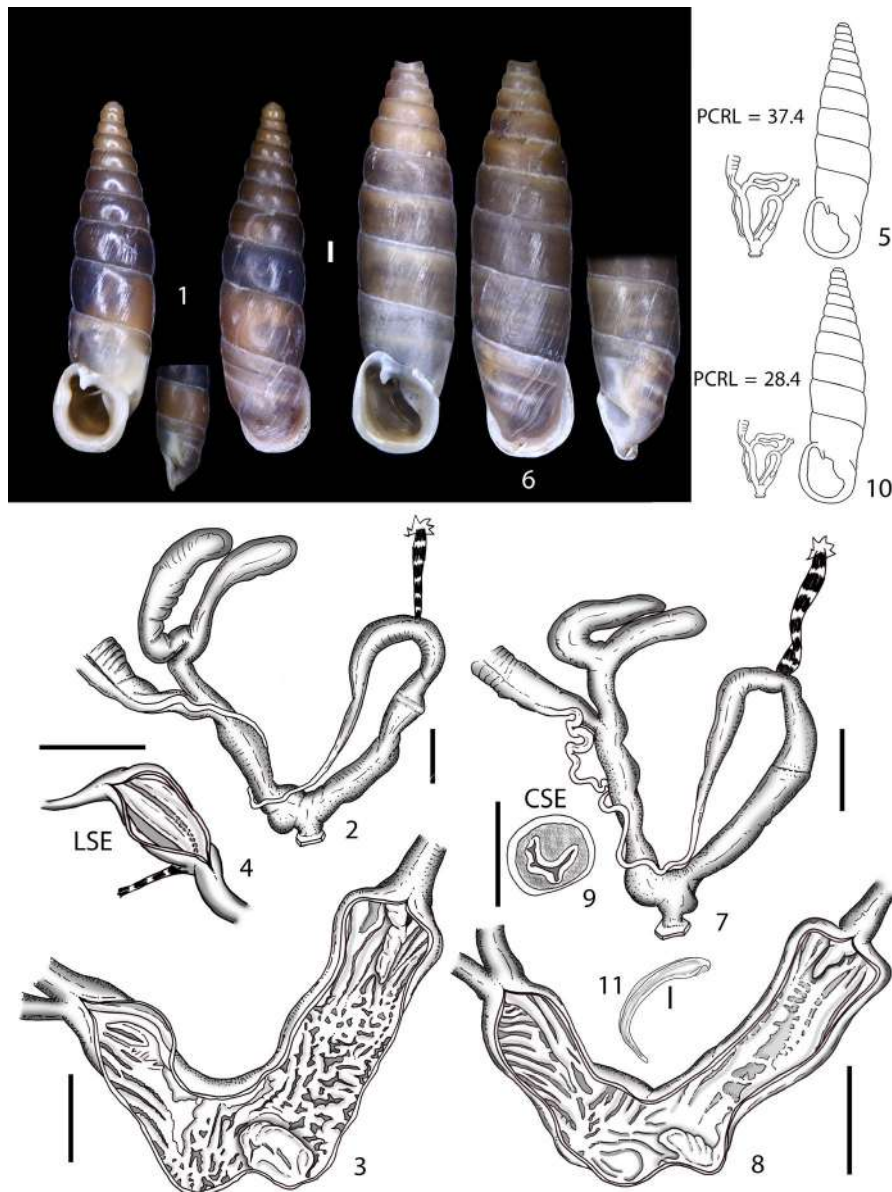


FIGURE 34 34.1–34.5 *Montenegrina miraka kotschani* Eröss and Szekeres, 2006 comb. nov. HNHM 99634. 34.1 shell, 34.2 whole distal genitalia, 34.3 inner distal genitalia, 34.4 longitudinal section of epiphallus, 34.5 shell-genitalia ratio. 34.6–34.10 *Montenegrina miraka miraka* Nordsieck, 1996 stat. 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 okolenis* 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. okolenis* 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. okolenis* 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 & 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 & Szekeres, 2016

Montenegrina sporadica tropojana
Fehér & Szekeres, 2016

Montenegrina okolenis okolenis
Szekeres, 2006

Montenegrina okolenis 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 okolenis okolenis
Szekeres, 2006

Montenegrina okolenis 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]).

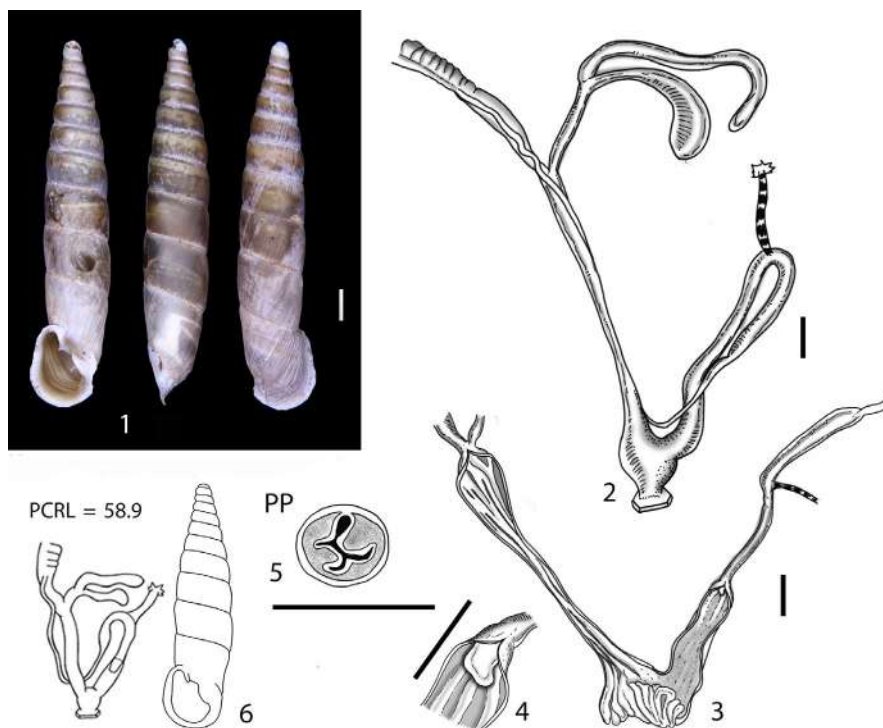


FIGURE 35 *Montenegrina lillae* Fehér & Szekeres, 2016 NHMW 11043/MN/0594. 35.1 shell. 35.2 whole distal genitalia. 35.3 inner distal genitalia. 35.4 penial papilla and proximal inner penis. 35.5 cross section of epiphallus. 35.6 shell-genitalia ratio

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

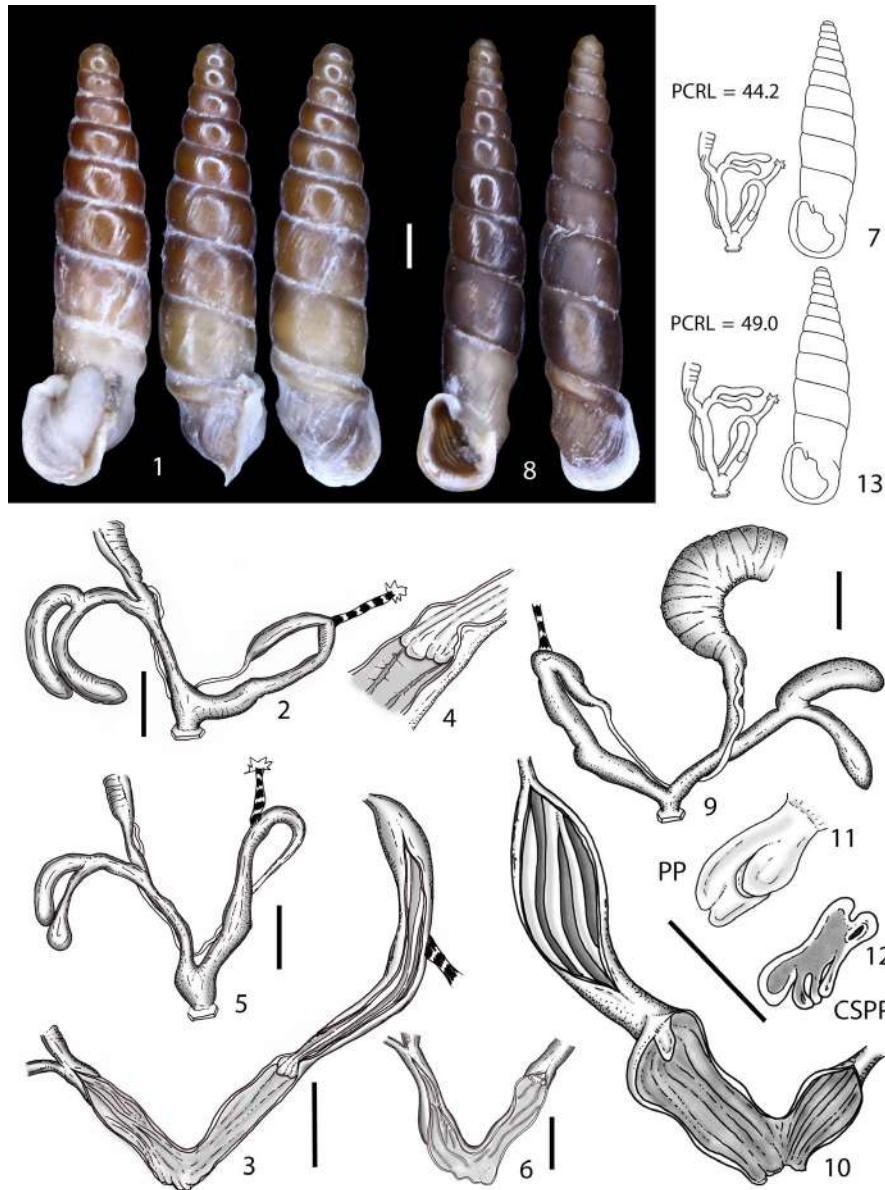


FIGURE 36 36.1–36.7 *Montenegrina prokletiana prokletiana* Fehér & Szekeres, 2016 NHMW 110430/MN/0184. 36.1 shell, 36.2 whole distal genitalia, 36.3 inner distal genitalia, 36.4 transition zone between proximal penis and epiphallus. NHMW 110430/MN/0185. 36.5 whole distal genitalia, 36.6 inner distal genitalia, 36.7 shell-genitalia ratio. 36.8–36.13 *Montenegrina prokletiana kovacsorum* Fehér & Szekeres, 2016 HHNM 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.

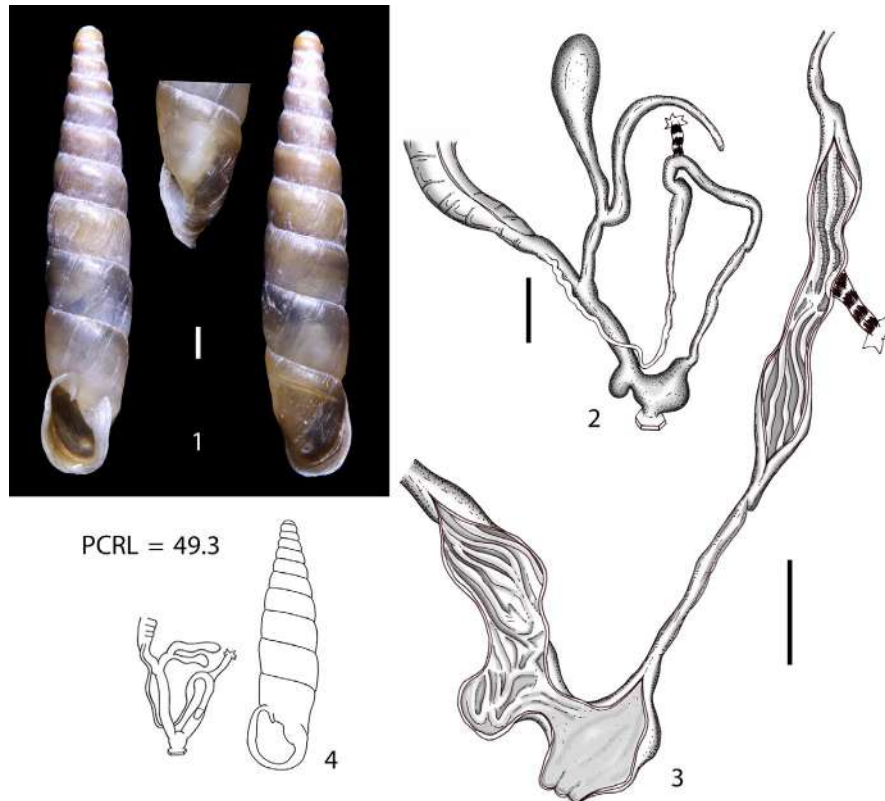


FIGURE 37 *Montenegro tropojana* Fehér & Szekeres, 2016 stat. nov. NHMW 111225. 37.1 shell. 37.2 whole distal genitalia. 37.3 inner distal genitalia. 37.4 shell-genitalia ratio

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

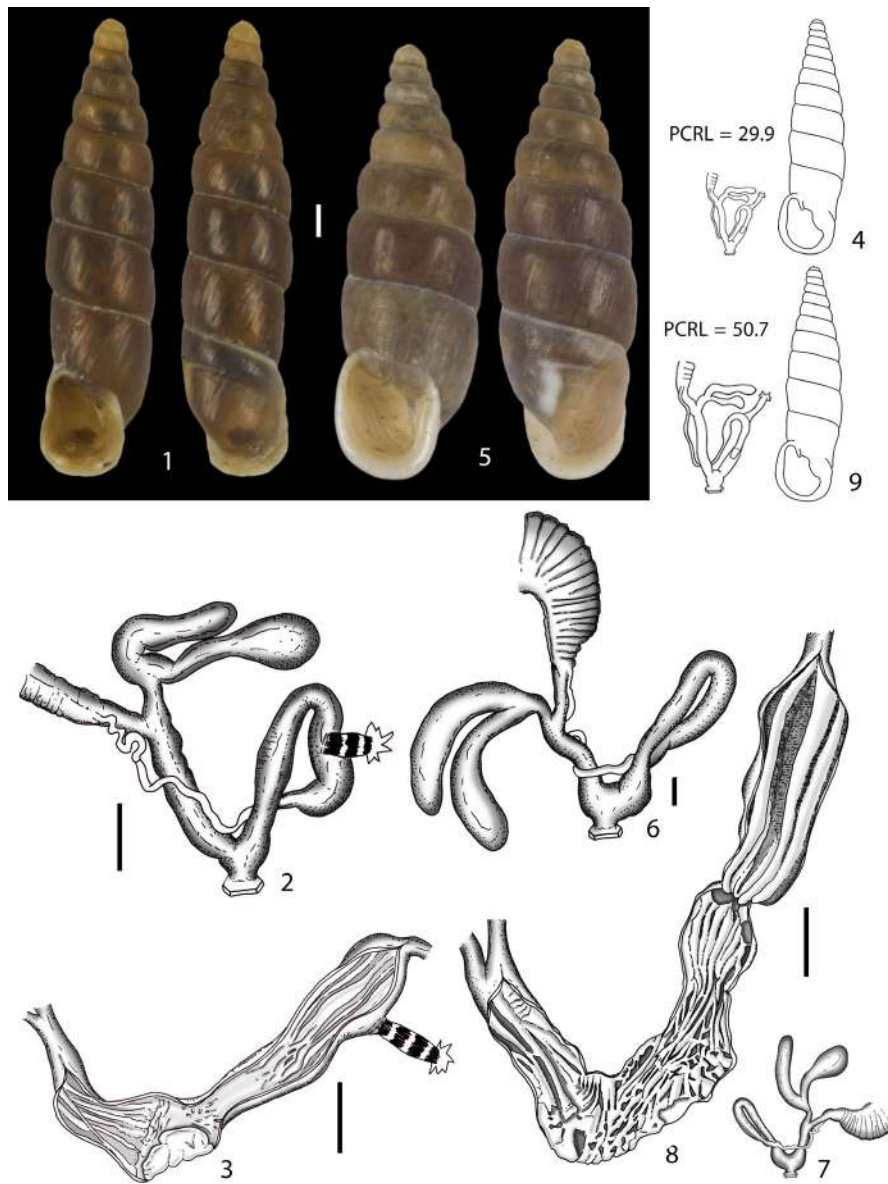


FIGURE 38 38.1–38.4 *Montenegrina okolenis okolenis* Szekeres, 2006 HNHM 99614. 38.1 shell, 38.2 whole distal genitalia, 38.3 inner distal genitalia, 38.4 shell-genitalia ratio. 38.5–38.9 *Montenegrina okolenis caesia* Fehér & Szekeres, 2006 HNHM 94836. 38.5 shell, 38.6–38.7 whole distal genitalia, 38.8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

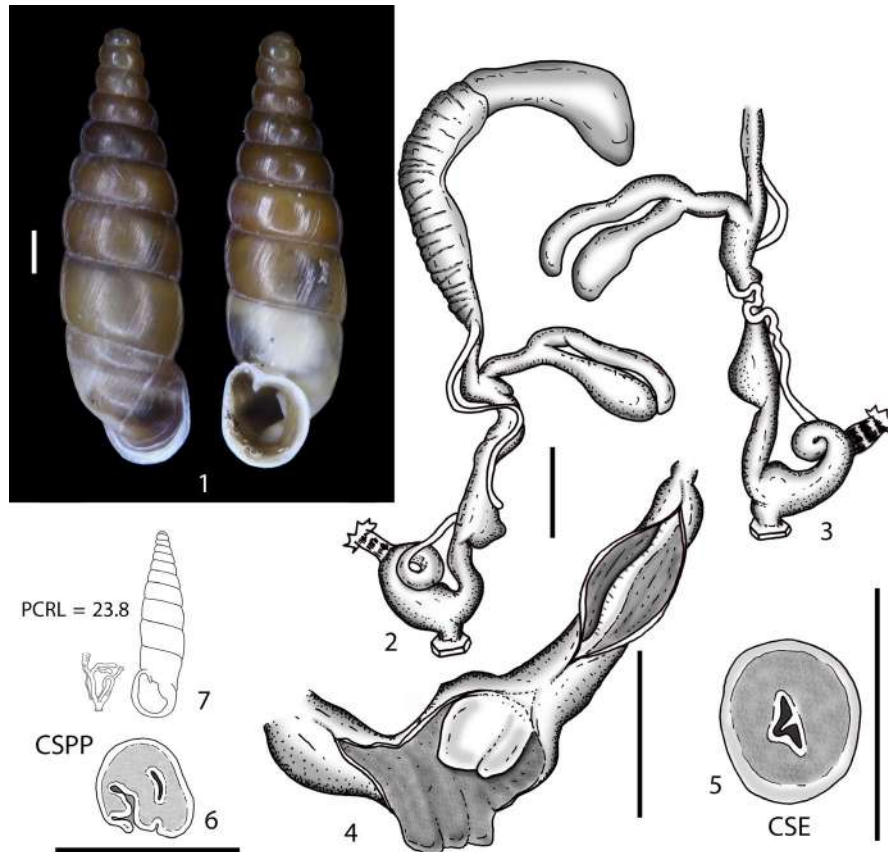


FIGURE 39 *Montenegrina minuscula* Erőss and Szekeres, 2006 HNHM 94832. 39.1 shell. 39.2–39.3 whole distal genitalia. 39.4 inner distal genitalia. 39.5 cross section of epiphallus. 39.6 cross section of penial papilla. 39.7 shell-genitalia ratio

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.

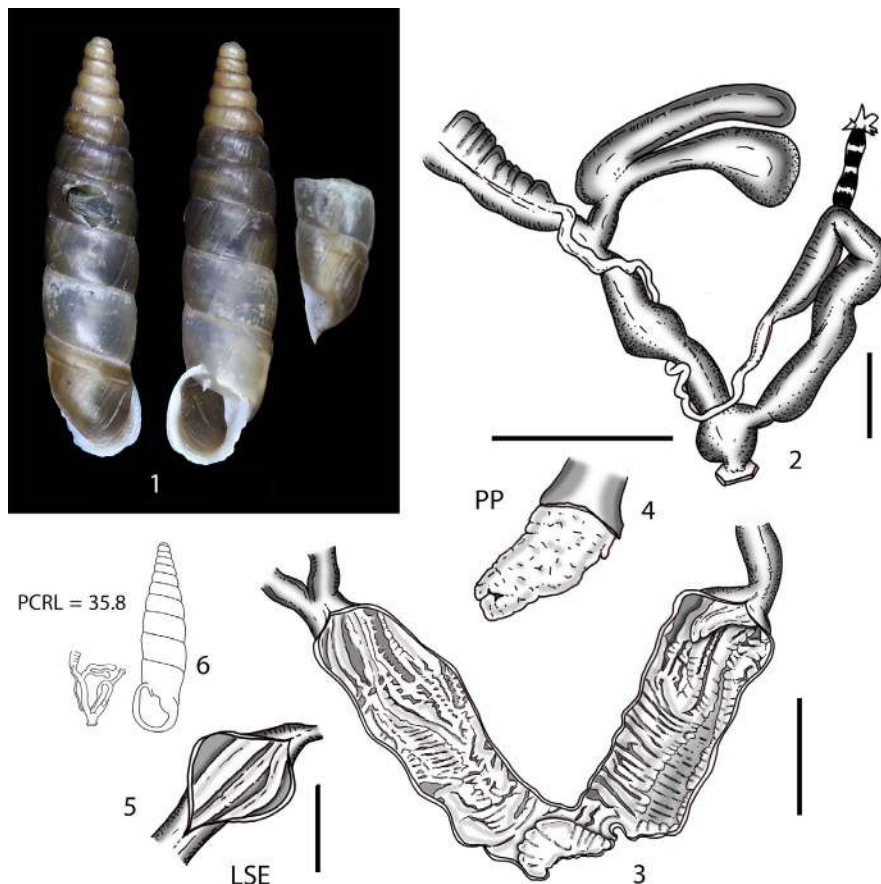


FIGURE 40 *Montenegrina nana* Fehér & Szekeres, 2006 HNHM 98973. 40.1 shell. 40.2 whole distal genitalia. 40.3 inner distal genitalia. 40.4 penial papilla. 40.5 longitudinal section of epiphallus. 40.6 shell-genitalia ratio

***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 Temlishit, 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

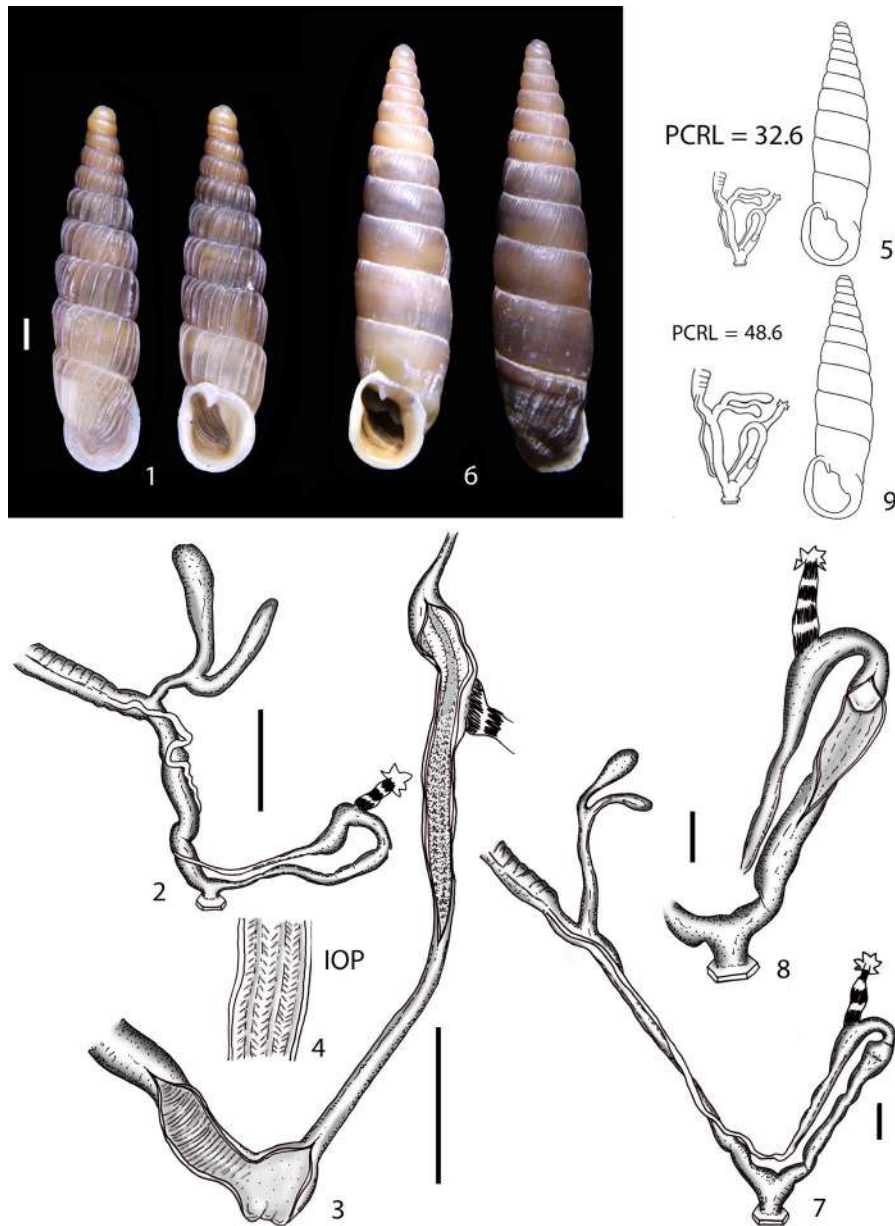


FIGURE 41 41.1–41.5 *Montenegrina gracilis barinai* Fehér & Szekeres, 2016 comb. nov. HNHM 99008. 41.1 shell, 41.2 whole distal genitalia, 41.3 inner distal genitalia, 41.4 magnification of the inner ornamentation of proximal penis, 41.5 shell-genitalia ratio. 41.6–41.9 *Montenegrina gracilis gracilis* Erőss 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. Undeem, 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

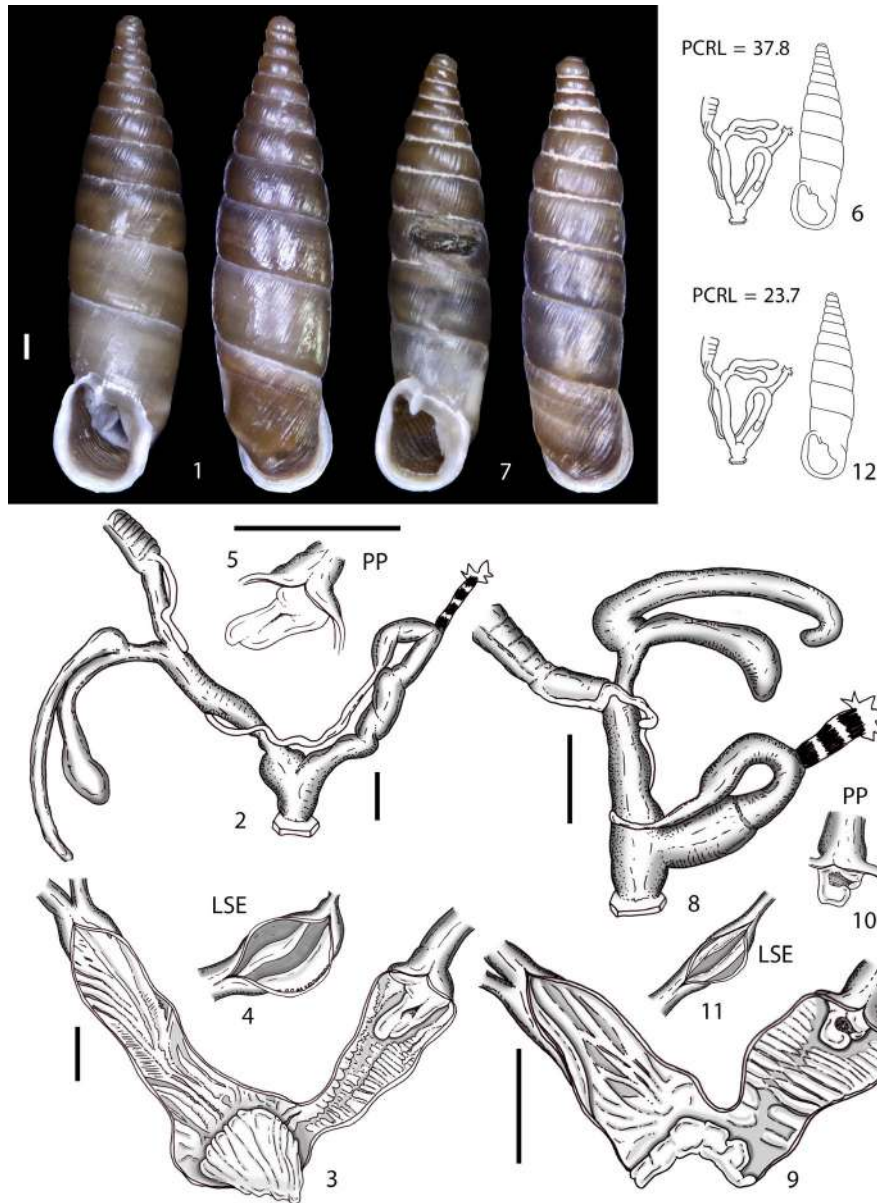


FIGURE 42 42.1–42.7 *Montenegrina perstriata perstriata* (Wagner, 1919) NHMW 110430/MN/0105. 42.1 shell, 42.2–42.3 whole distal genitalia, 42.4 inner distal genitalia, 42.5 cross section of penial papilla, 42.6 penial papilla. 42.7 shell-genitalia ratio. 42.8–42.12 *Montenegrina perstriata diminuta* 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

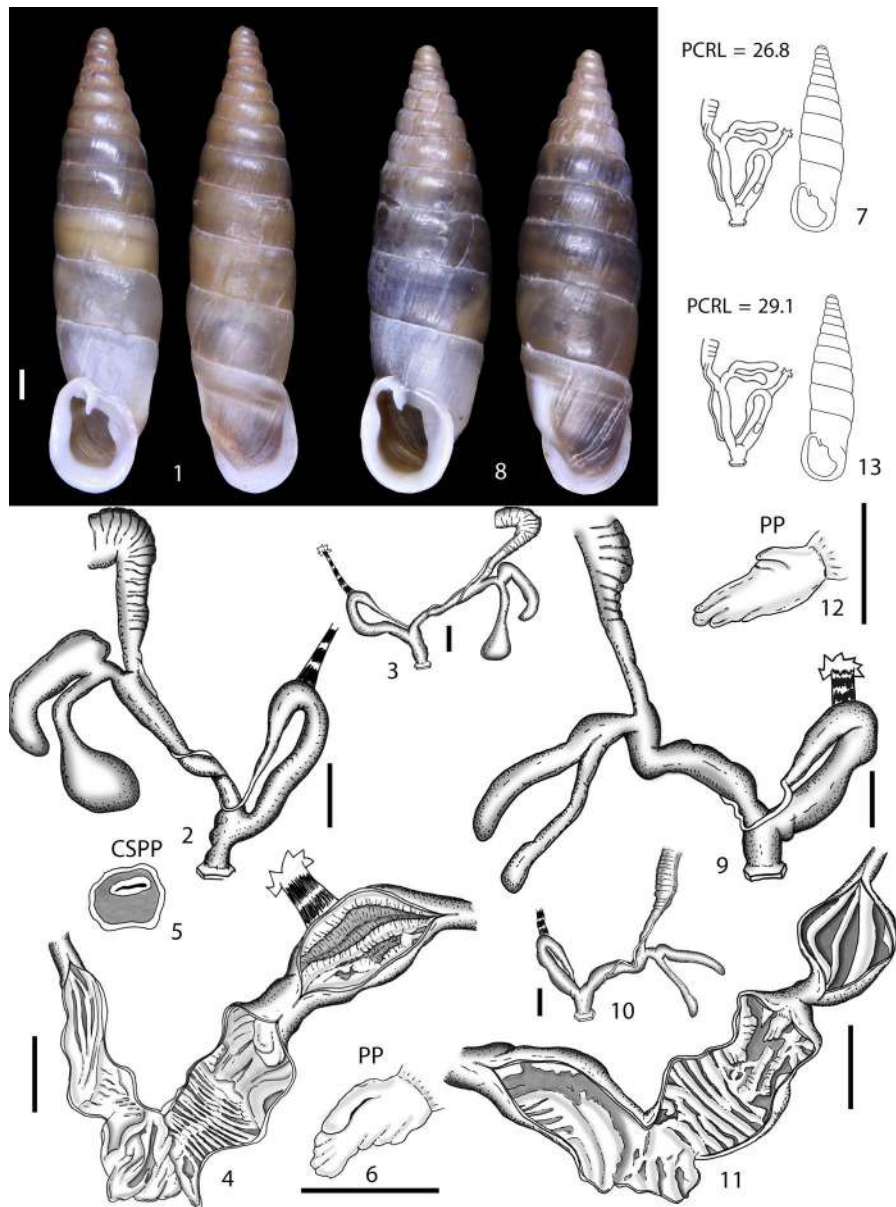


FIGURE 43 *Montenegrina ochridensis callistoma* Fehér & Szekeres, 2006 comb. nov. HNHM 98977. 43.1 shell. 43.2–43.3 whole distal genitalia. 43.4 inner distal genitalia. 43.5 cross section of penial papilla. 43.6 penial papilla. 43.7 shell-genitalia ratio. HNHM 98954. 43.8 shell. 43.9–43.10 whole distal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

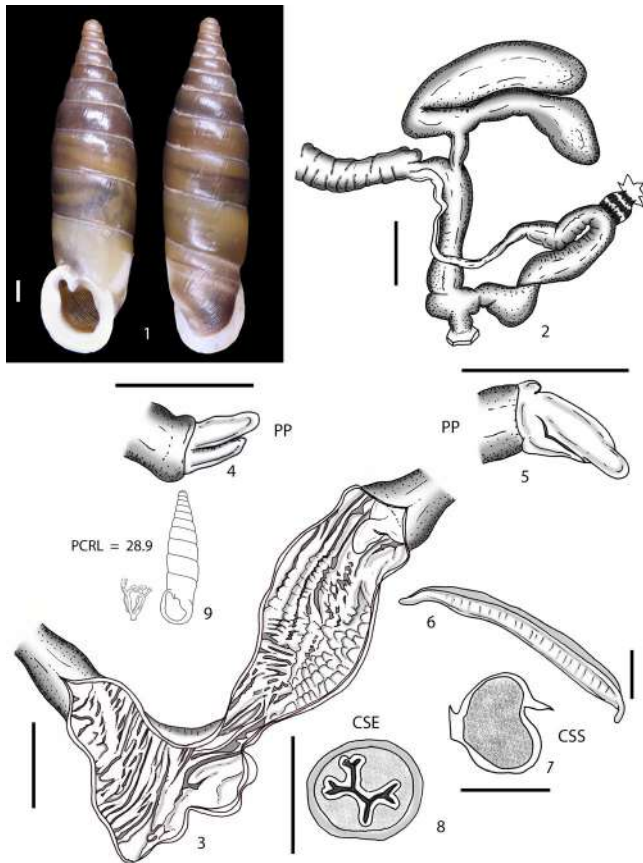


FIGURE 44 *Montenegro ochridensis callistoma* Fehér & Szekeres, 2006 stat. nov. HNHM 98986. 44.1 shell. 44.2 whole distal genitalia. 44.3 inner distal genitalia. 44.4–44.5 penial papilla. 44.6 spermatophore, 44.7 cross section of spermatophore. 44.8 cross section of epiphallus. 44.9 shell-genitalia ratio

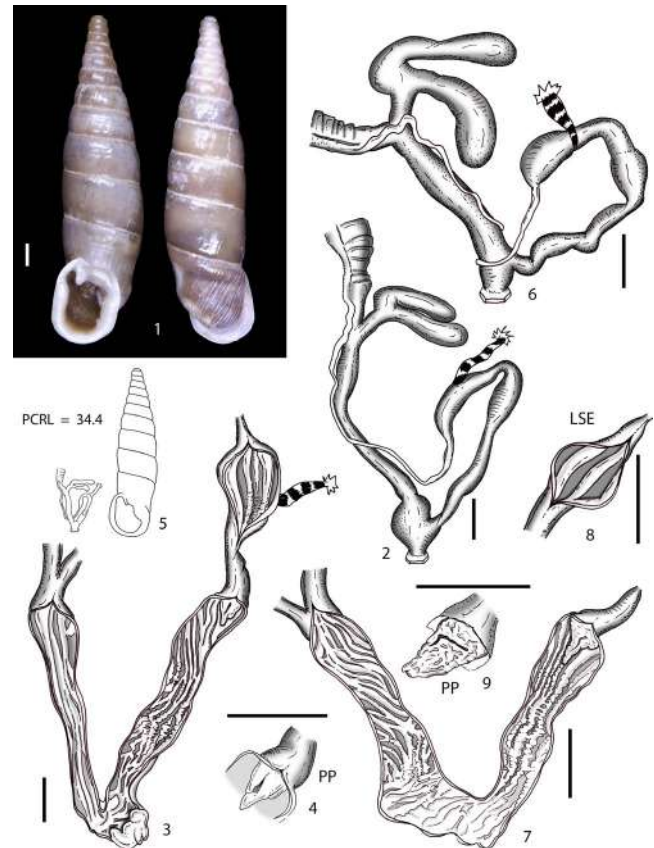


FIGURE 45 *Montenegro drimica* Nordsieck, 1972 stat. nov. DGG2 HNHM 41149/43. 45.1 shell. 45.2 whole distal genitalia. 45.3 inner distal genitalia. 45.4 penial papilla. 45.5 shell-genitalia ratio. DGG5 HNHM 36711/41. 45.6 whole distal genitalia. 45.7 inner distal genitalia. 45.8 longitudinal section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

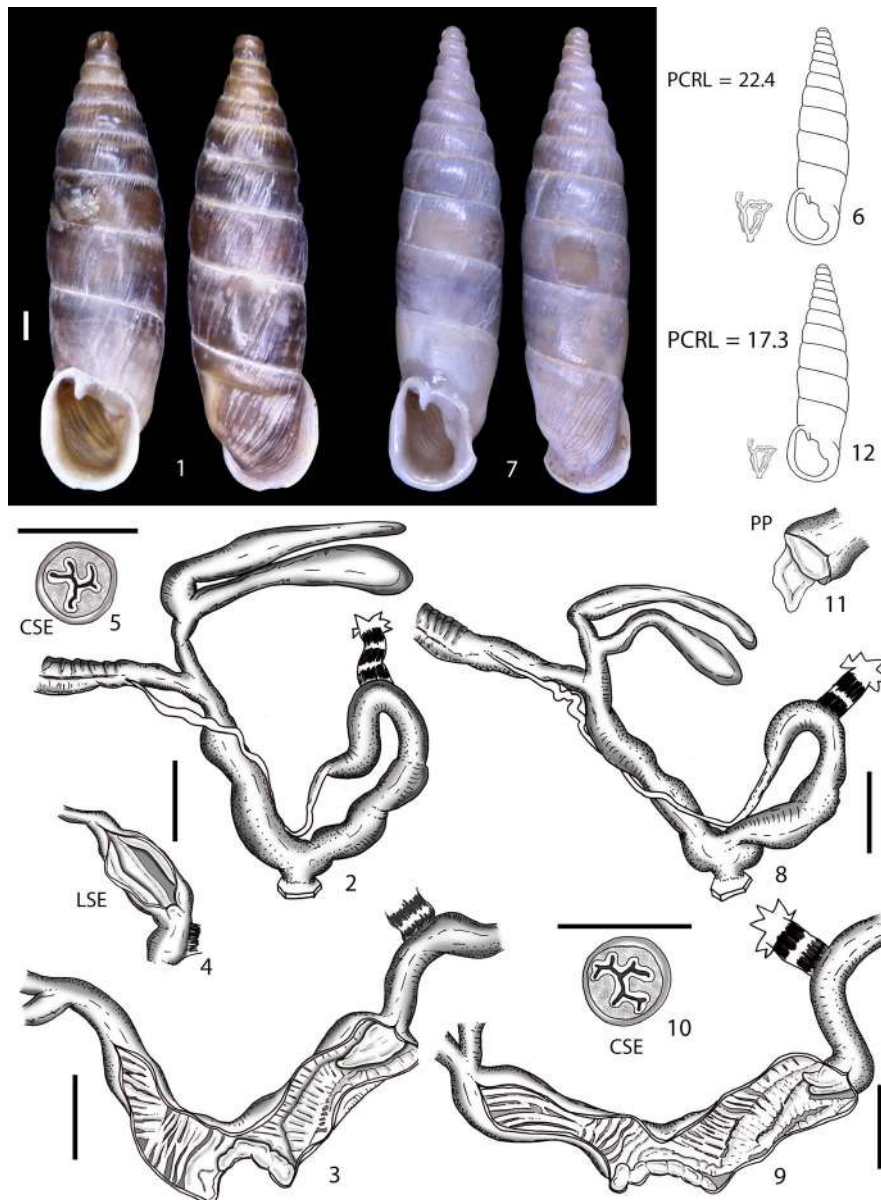


FIGURE 46 *Montenegrina drimica* Nordsieck, 1972 stat. nov. DGG3 NHMW 110430/MN/0087. 46.1 shell. 46.2 whole distal genitalia. 46.3 inner distal genitalia. 46.4 longitudinal section of epiphallus. 46.5 cross section of epiphallus. 46.6 shell-genitalia ratio. DGG3 NHMW 110430/MN/0097. 46.7 shell. 46.8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

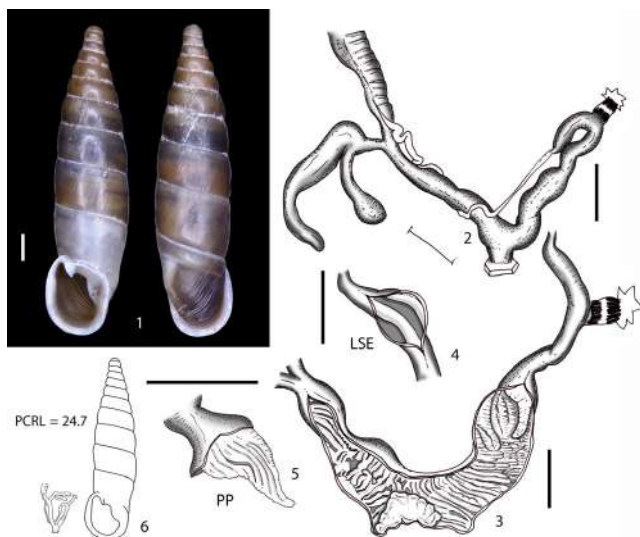


FIGURE 47 *Montenegrogrina drimica* Nordsieck, 1972 stat. nov. DGG3 HNHM 98990. 47.1 shell. 47.2 whole distal genitalia. 47.3 inner distal genitalia. 47.4 longitudinal section of epiphallus. 47.5 penial papilla. 47.6 shell-genitalia ratio

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.

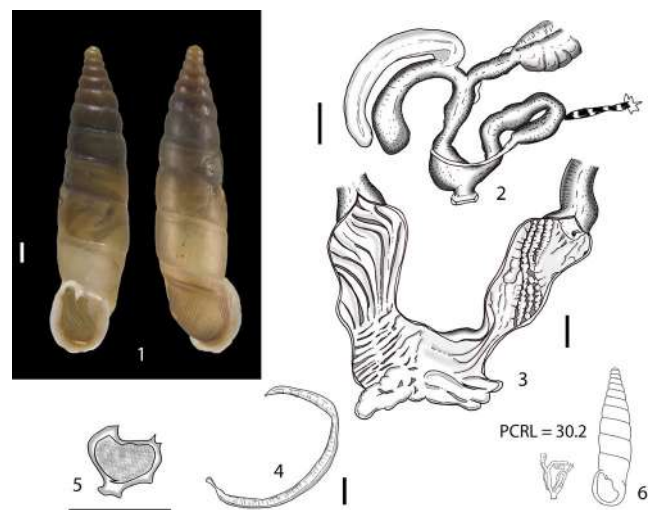


FIGURE 48 *Montenegrogrina drimica* Nordsieck, 1972 stat. nov. DGG4 NHMW 36712. 48.1 shell. 48.2 whole distal genitalia. 48.3 inner distal genitalia. 48.4 spermatophore. 48.5 cross section of the spermatophore. 48.6 shell-genitalia ratio

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

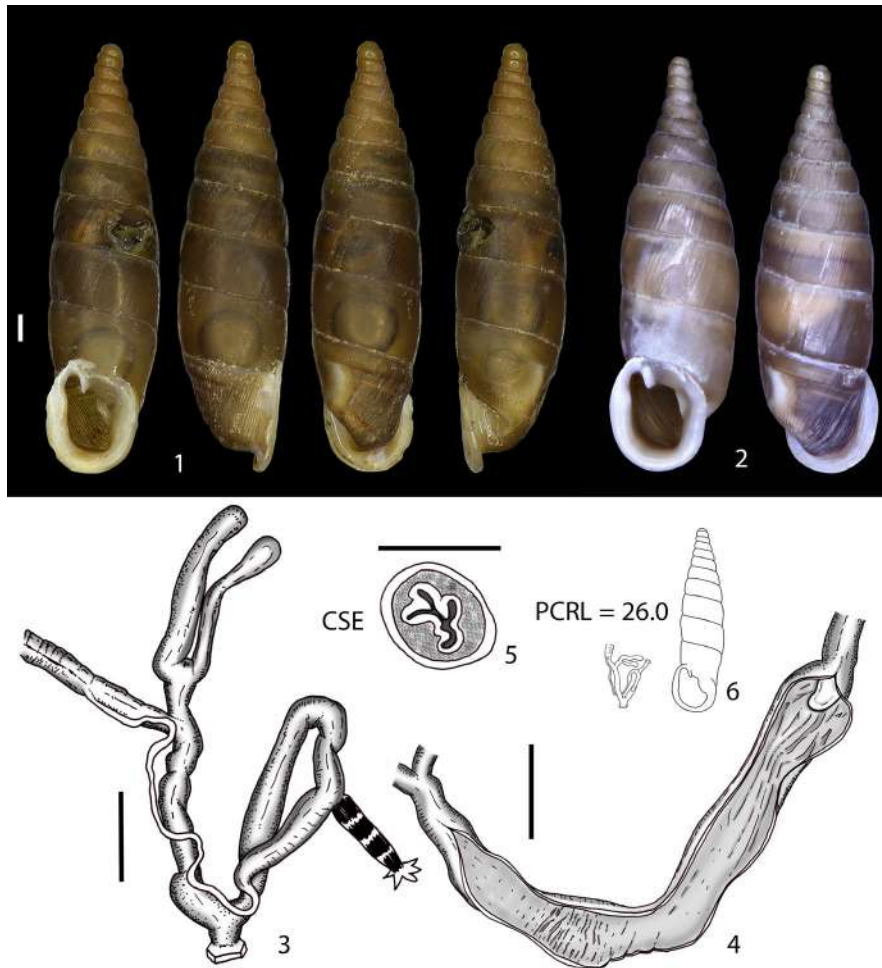


FIGURE 49 *Montenegroglobocica* n. sp. 49.1 Holotypeshell, NHMW 111676 (=Mdr-520-02) specimen Mdr-520-02. 49.2 shell paratype NHMW 110430/MN/0088, specimen Mdr-520-01. 49.3 whole distal genitalia, 49.4 inner distal genitalia. 49.5 cross section of epiphallus. 49.6 shell-genitalia ratio

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.

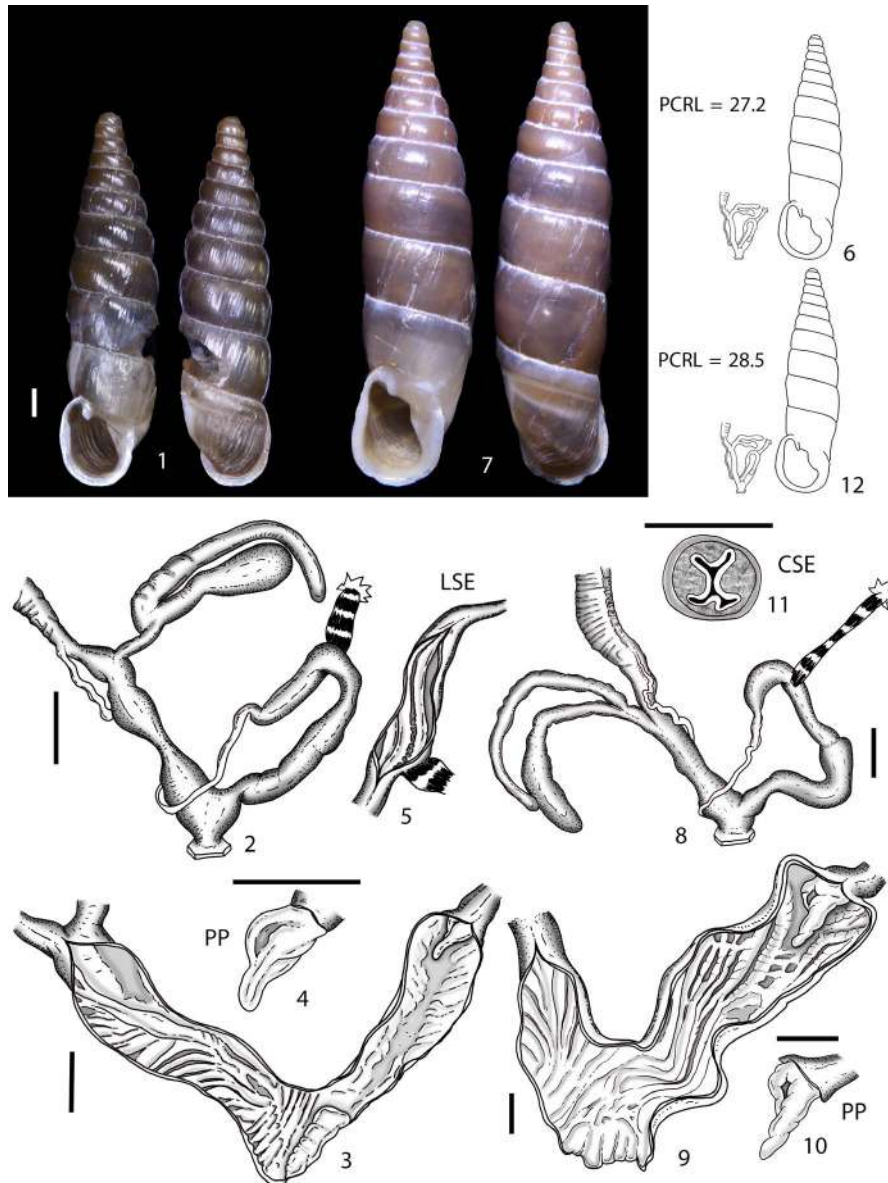


FIGURE 50 50.1–50.6 *Montenegrina perstriata mavrovoensis* Nordsieck, 2009 NHMW 110430/MN/0148. 50.1 shell, 50.2 whole distal genitalia, 50.3 inner distal genitalia, 50.4 penial papilla, 50.5 longitudinal section of epiphallus, 50.6 shell-genitalia ratio. 50.7–50.12 *Montenegrina radikae radikae* Nordsieck, 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,

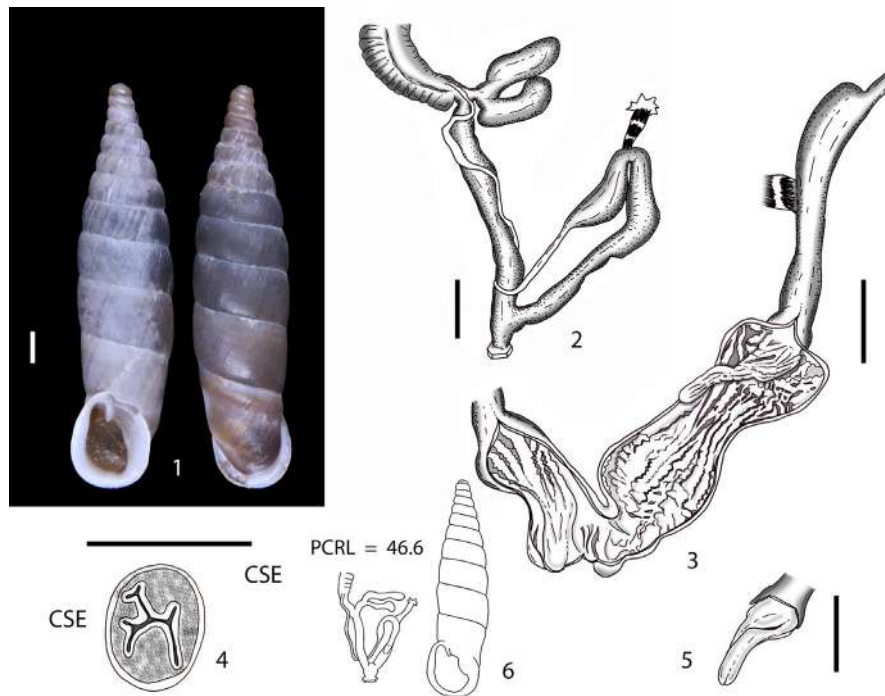


FIGURE 51 *Montenegrina ochridensis ochridensis* (Wagner, 1925) stat. nov. HNHM 94434. 51.1 shell. 51.2 whole distal genitalia. 51.3 inner distal genitalia. 51.4 cross section of epiphallus. 51.5 penial papilla. 51.6 shell-genitalia ratio

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,

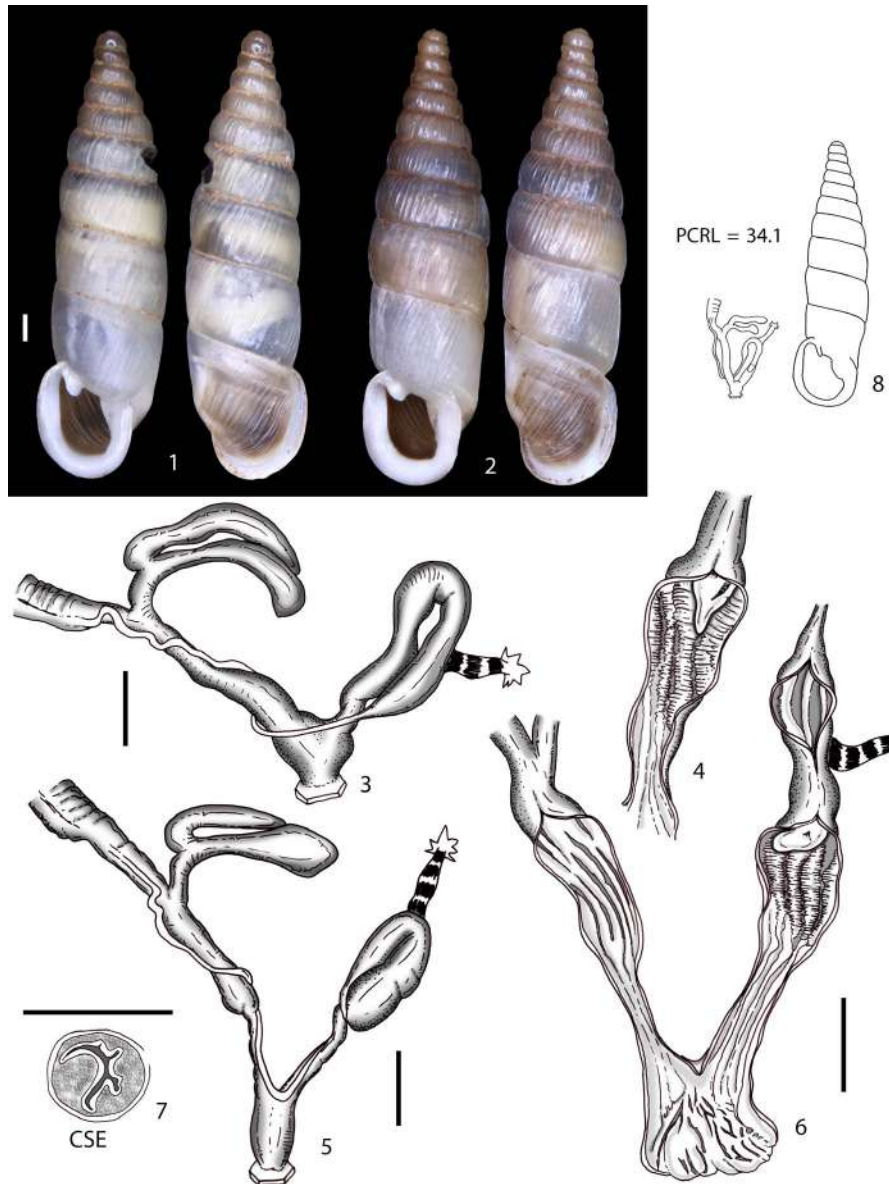


FIGURE 52 *Montenegrina drimica plenostoma* Fehér & Szekeres, 2006 comb. nov. HHNM 98945. 52.1–52.2 shells. 52.3–52.5 whole distal genitalia. 52.4 penial papilla and inner proximal penis, 52.6 inner distal genitalia, 52.7 cross section of epiphallus, 52.8 shell-genitalia ratio

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.

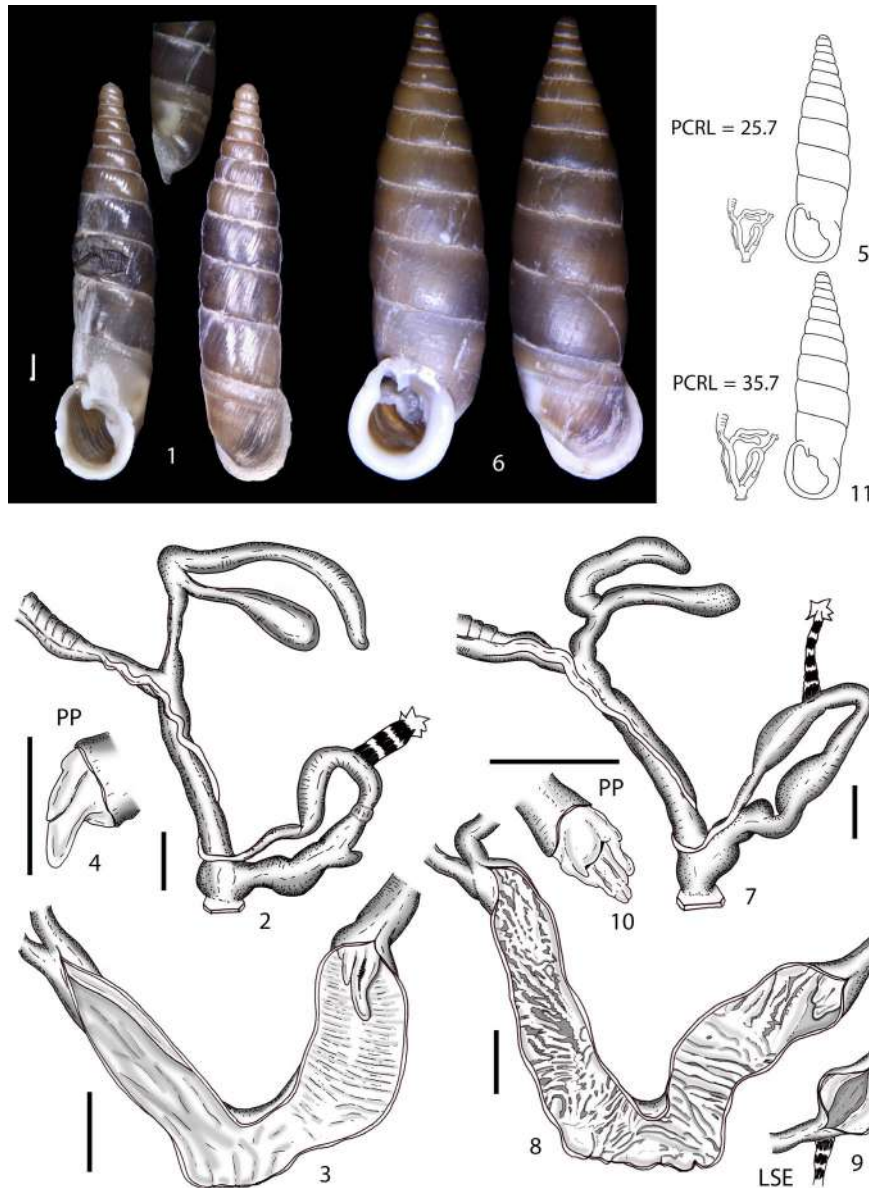


FIGURE 53 53.1–53.5 *Montenegrina subcristatula subcristatula* Nordsieck, 1977 stat. nov. NHMW 110430/MN/0107. 53.1 shell, 53.2 whole distal genitalia, 53.3 inner distal genitalia, 53.4 penial papilla, 53.5 shell-genitalia ratio. 53.6–53.11 *Montenegrina tenebrosa tenebrosa* Nordsieck, 2009 stat. nov. 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

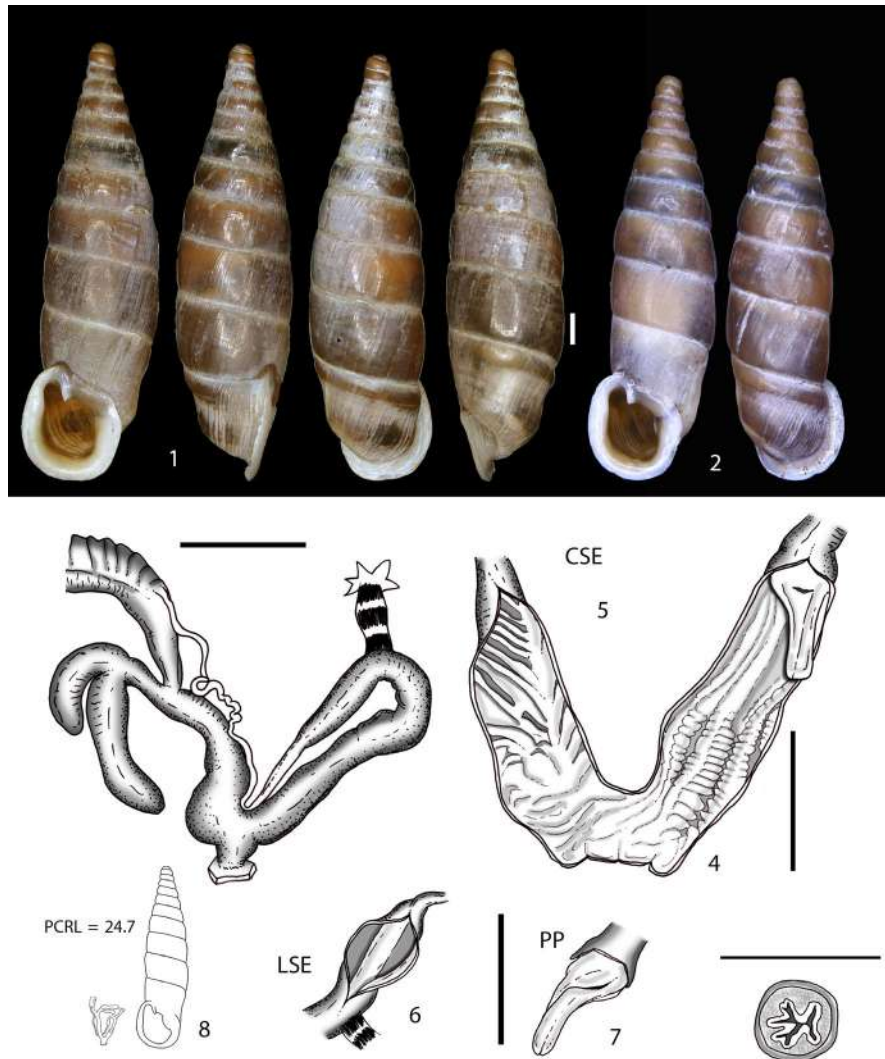


FIGURE 54 *Montenegrina tenebrosa* szekeres in. ssp. 54.1 shell of the Holotype HHNM 99007. 54.2 shell. 54.3 whole distal genitalia. 54.4 inner distal genitalia. 54.5 cross section of epiphallus. 54.6 penial papilla. 54.7 longitudinal section of epiphallus. 54.9 shell-genitalia ratio

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.

Montenegrina 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).

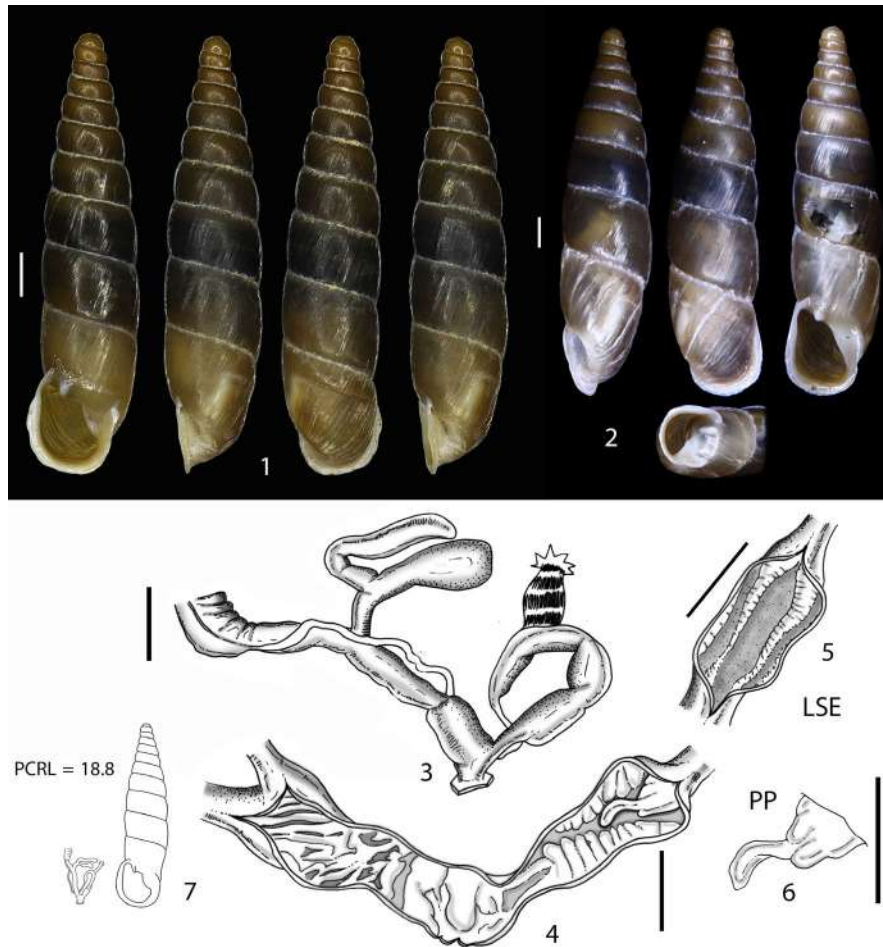


FIGURE 55 *Montenegrina radikae paparistoeae* n. ssp. 55.1 shell of the Holotype NHMW 110430/MN/0261_2 NHMW 110430/MN/0261_3. 55.2 shell, 55.3 whole distal genitalia and inner distal genitalia, 55.4 inner distal genitalia, 55.5 longitudinal section of epiphallus, 55.6 penial papilla, 55.7 shell-genitalia ratio

Distribution: *Montenegrina radikae paparistoeae* 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_s: 4.6 H_a: 4.4, W_a: 3.9; H_s: 16.0–18.8, W_s: 4.4–4.8, H_a: 4.2–4.8, W_a: 3.1–4.0.

Shell description (Figures 55.1–55.2): The light brownish-corneous shell consists of 9¹/₂–10¹/₂ 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

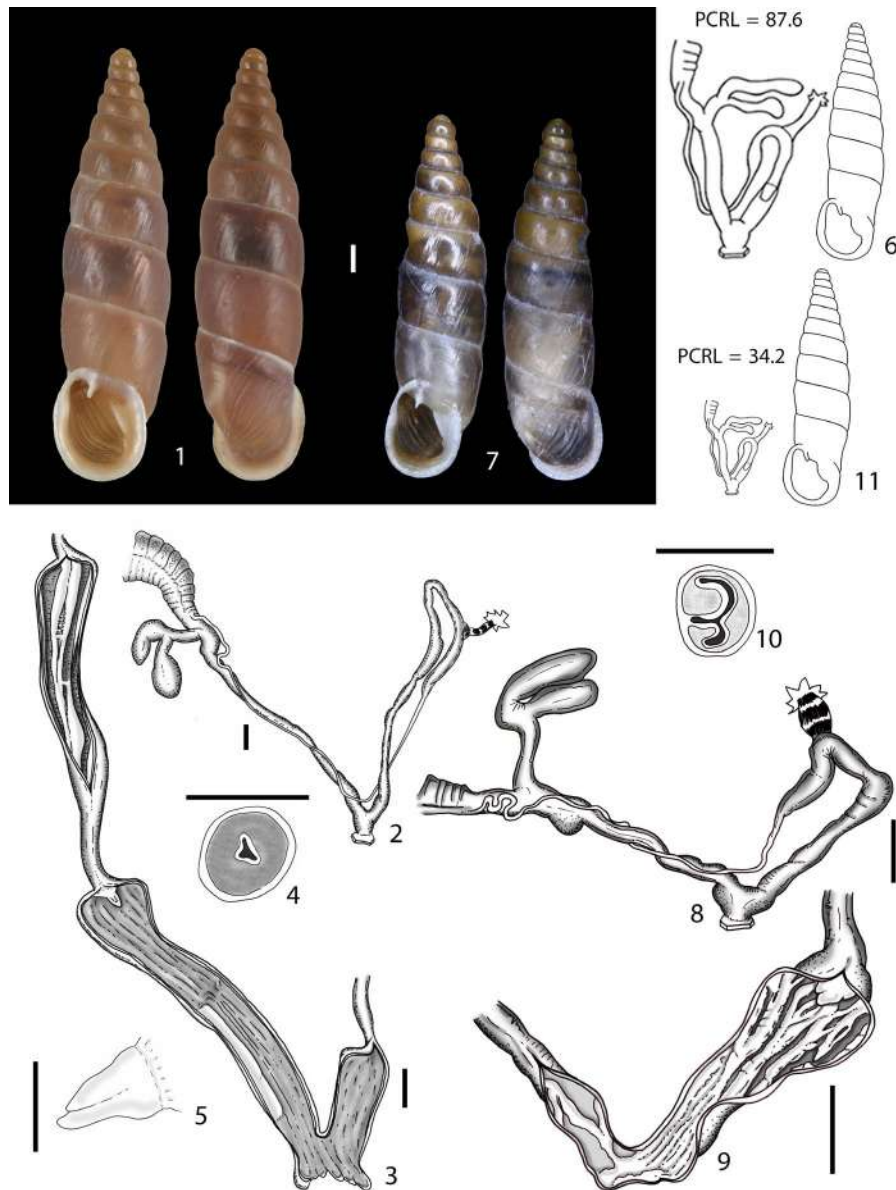


FIGURE 56 56.1–56.6 *Montenegrina skipetarica* (Soós, 1924) HNHM 99522. 56.1 shell, 56.2 whole distal genitalia, 56.3 inner distal genitalia, 56.4 cross section of epiphallus, 56.5 penial papilla, 56.6 shell-genitalia ratio. 56.7–56.11 *Montenegrina csikii* Eröss and Szekeres, 2006 stat. nov. HNHM 96845. 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

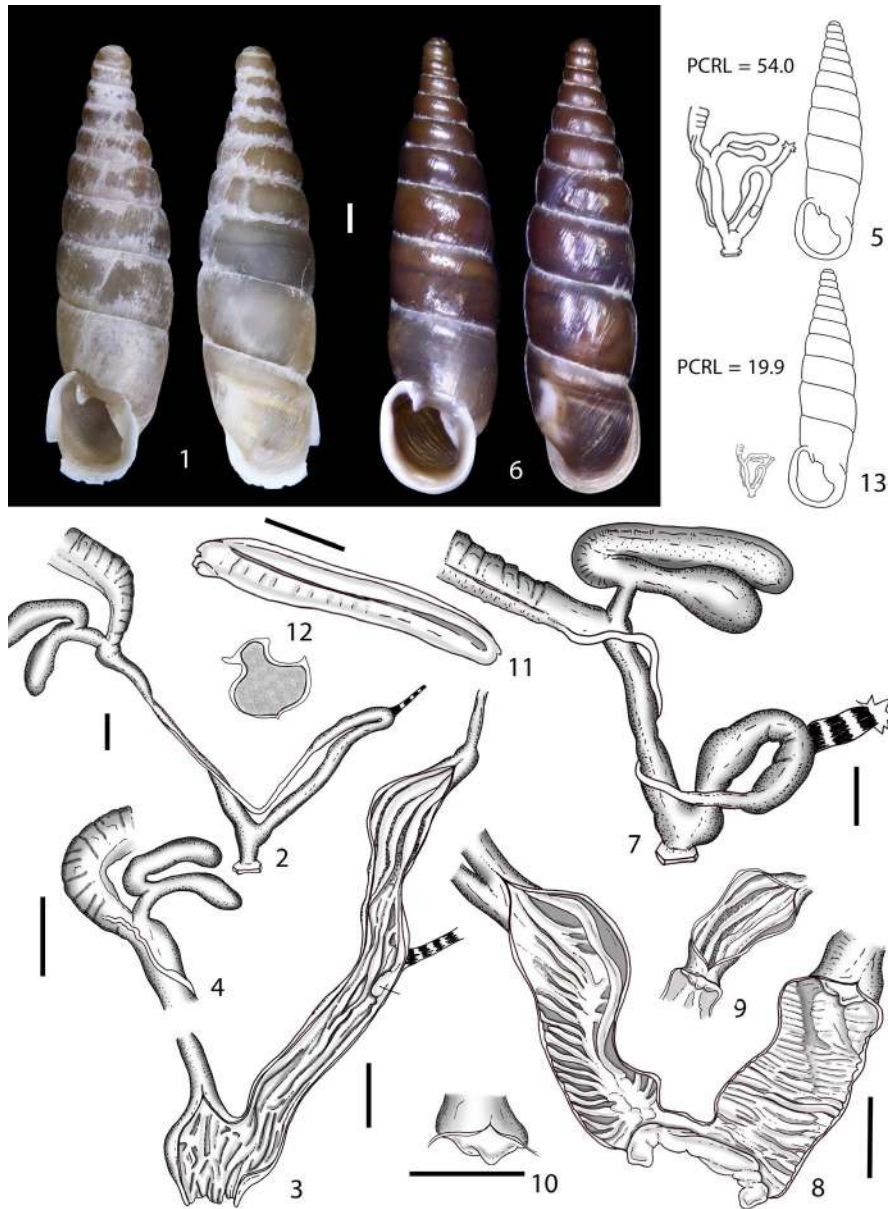


FIGURE 57 57.1–57.5 *Montenegrina ersekensis* Nordsieck, 1996 stat. nov. HHNM 99375, NHMW 110430/MN/0031. 57.1 shell, 57.2 whole distal genitalia, 57.3 inner distal genitalia, 57.4 bursa copulatrix complex. 57.5 shell-genitalia ratio. 57.6–57.13 *Montenegrina skipetarica flava* Eröss and Szekeres, 2006 HHNM 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,

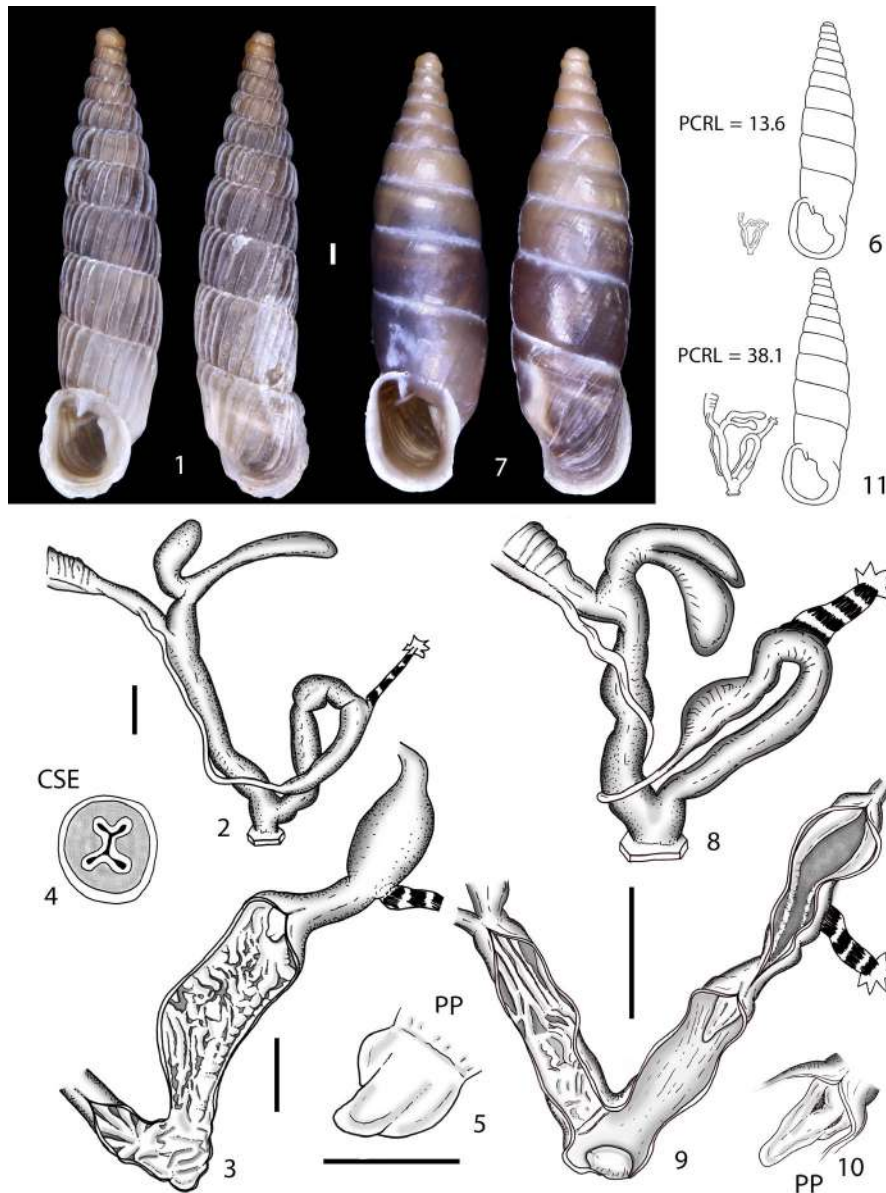


FIGURE 58 58.1–58.6 *Montenegrina puskasi gurelurensis* Fehér & Szekeres, 2016 comb. nov. HNHM 99461. 58.1 shell, 58.2 whole distal genitalia, 58.3 inner distal genitalia, 58.4 cross section of epiphallus, 58.5 penial papilla, 58.6 shell-genitalia ratio. 58.7–58.11 *Montenegrina voidomatis konitsae* 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.

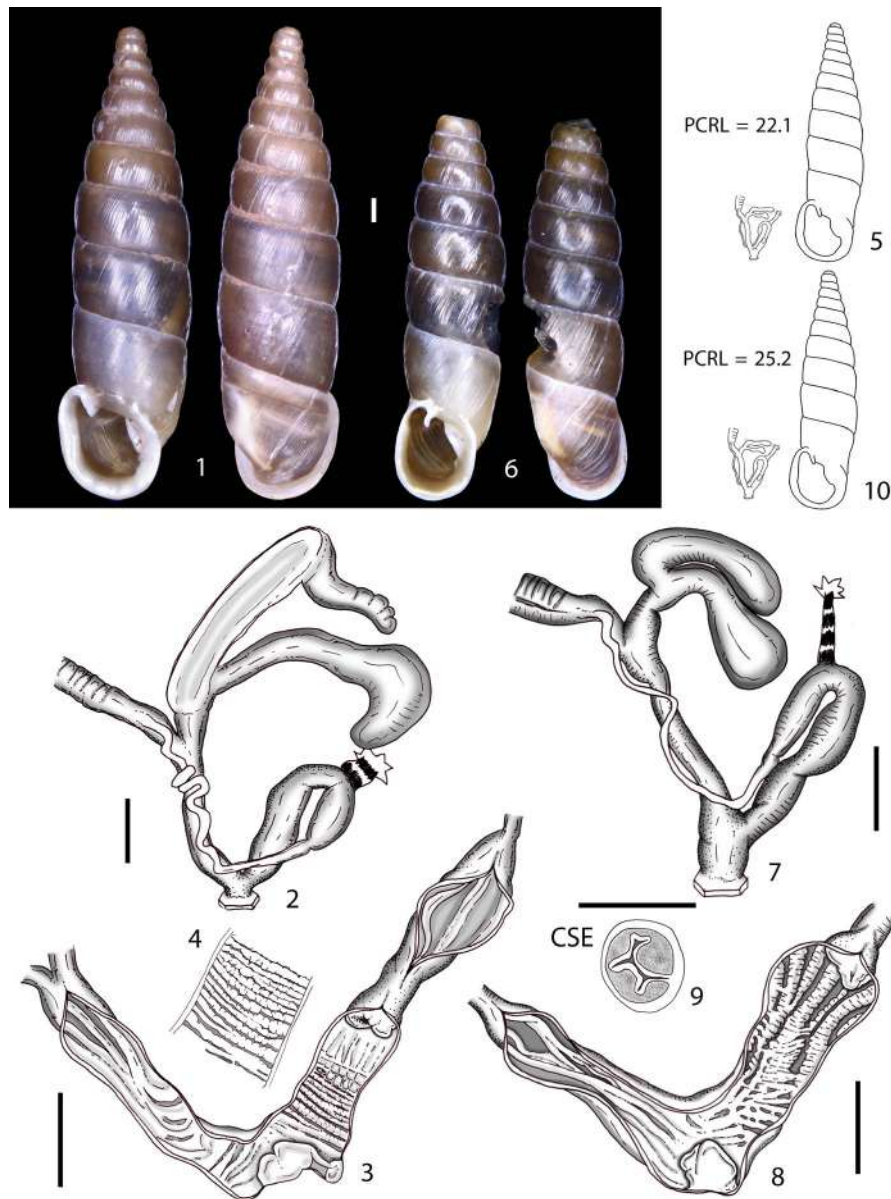


FIGURE 59 59.1–59.5 *Montenegrina nobilis* Eröss and Szekeres, 2006 stat. nov. HHNM 99536. 59.1 shell, 59.2 whole distal genitalia, 59.3 inner distal genitalia, 59.4 magnification of the inner sculpturing of the proximal penis, 59.5 shell-genitalia ratio. 59.6–59.10 *Montenegrina pifkoi* Fehér & Szekeres, 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.

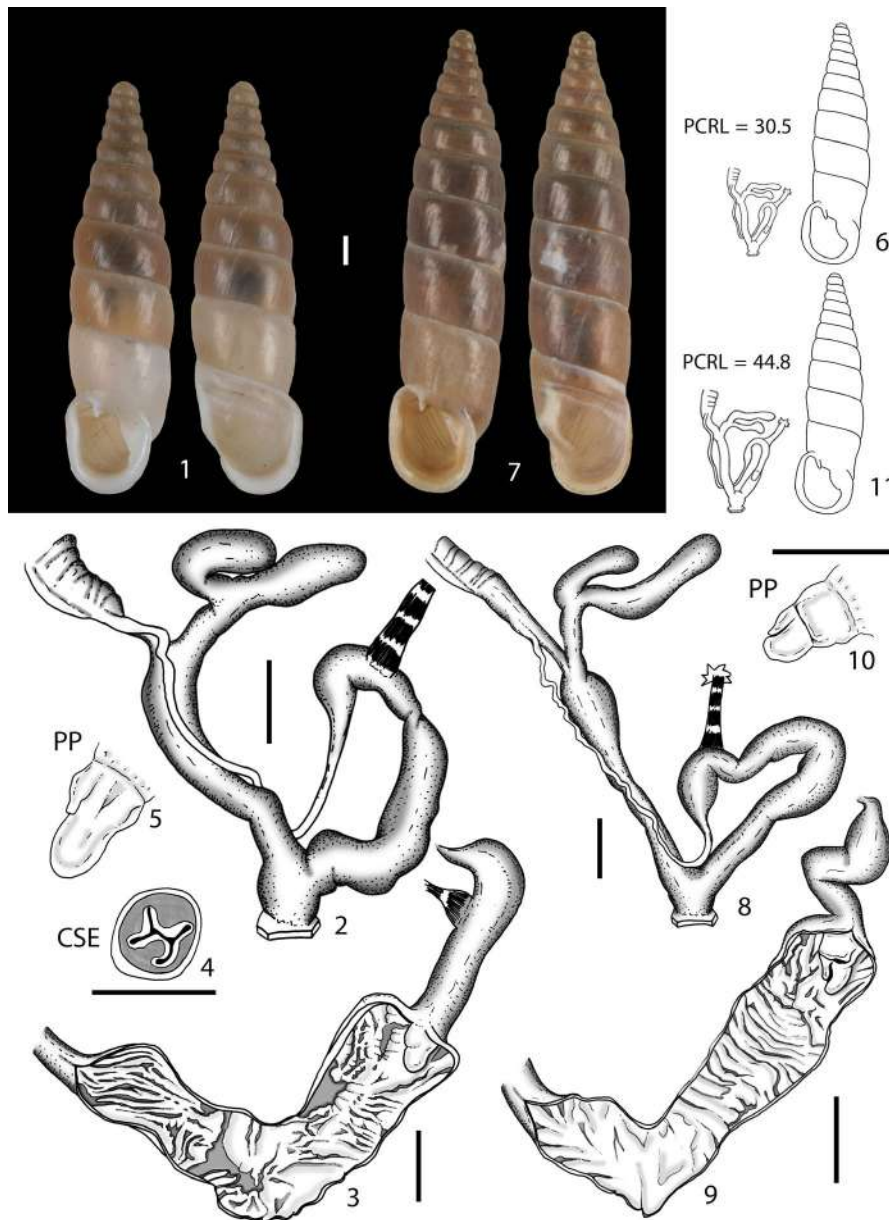


FIGURE 60 60.1–60.6 *Montenegrina pindica* Nordsieck, 1988 stat. nov. HNHM 99524. 60.1 shell, 60.2 whole distal genitalia, 60.3 inner distal genitalia, 60.4 cross section of epiphallus, 60.5 penial papilla, 60.6 shell-genitalia ratio. 60.7–60.11 *Montenegrina pusikasi pusikasi* Fehér & Szekeres, 2016 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.

***Montenegrina remota* Fehér & Szekeres, 2006 stat. nov.**

Figures 61.1–61.5

Montenegrina irmengardis remota Fehér & Szekeres, 2006 in Erőss et al., 2006: 192–194, fig. 13.

Montenegrina skipetarica remota – Nordsieck, 2009: 73, plate 1, fig and. – Fehér & Szekeres, 2016: 106, fig. 30I, distribution map fig. 31B.

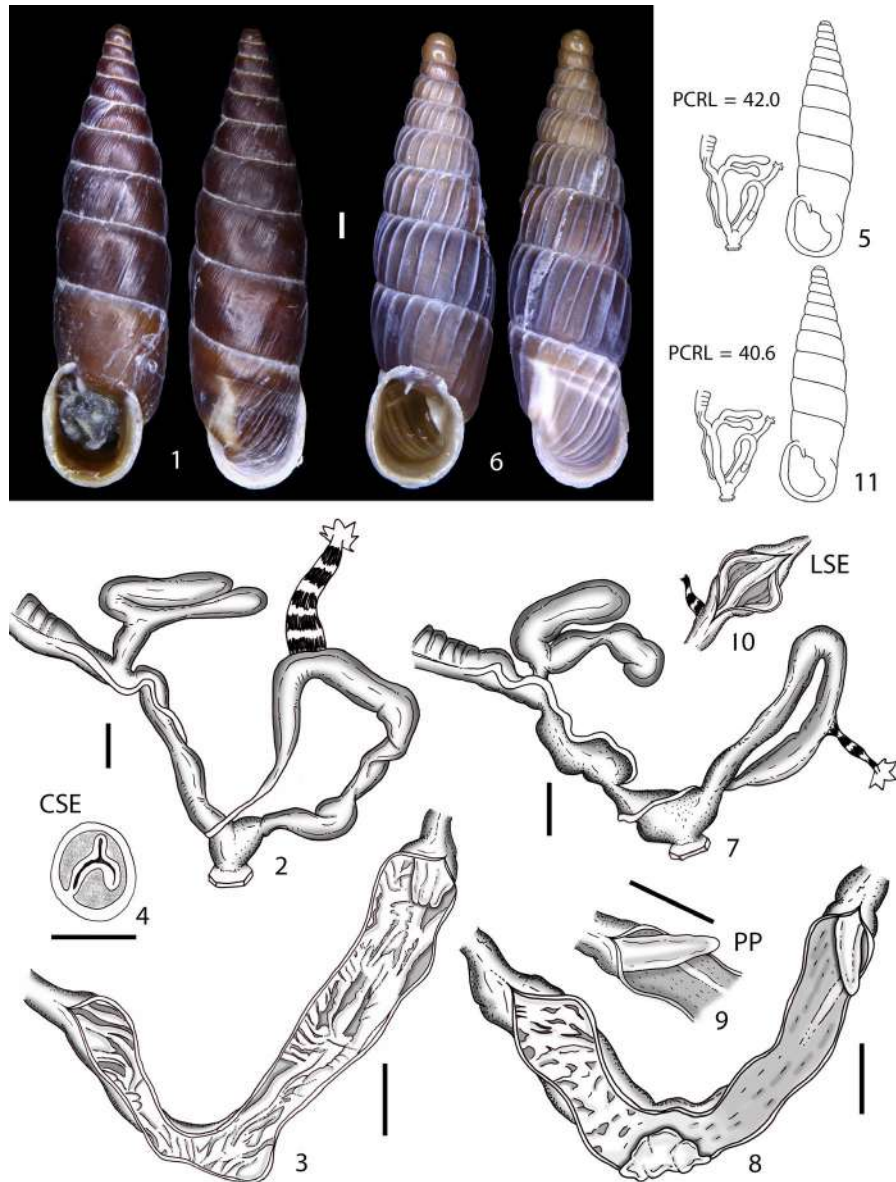


FIGURE 61 61.1–61.5 *Montenegrina remota* Fehér & Szekeres, 2006 stat. nov. HNHM 99021. 61.1 shell, 61.2 whole distal genitalia, 61.3 inner distal genitalia, 61.4 cross section of epiphallus, 61.5 shell-genitalia ratio. 61.6–61.11 *Montenegrina voidomatis thysi* Loosjes & Loosjes-van Bemmelen, 1988 comb. 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.

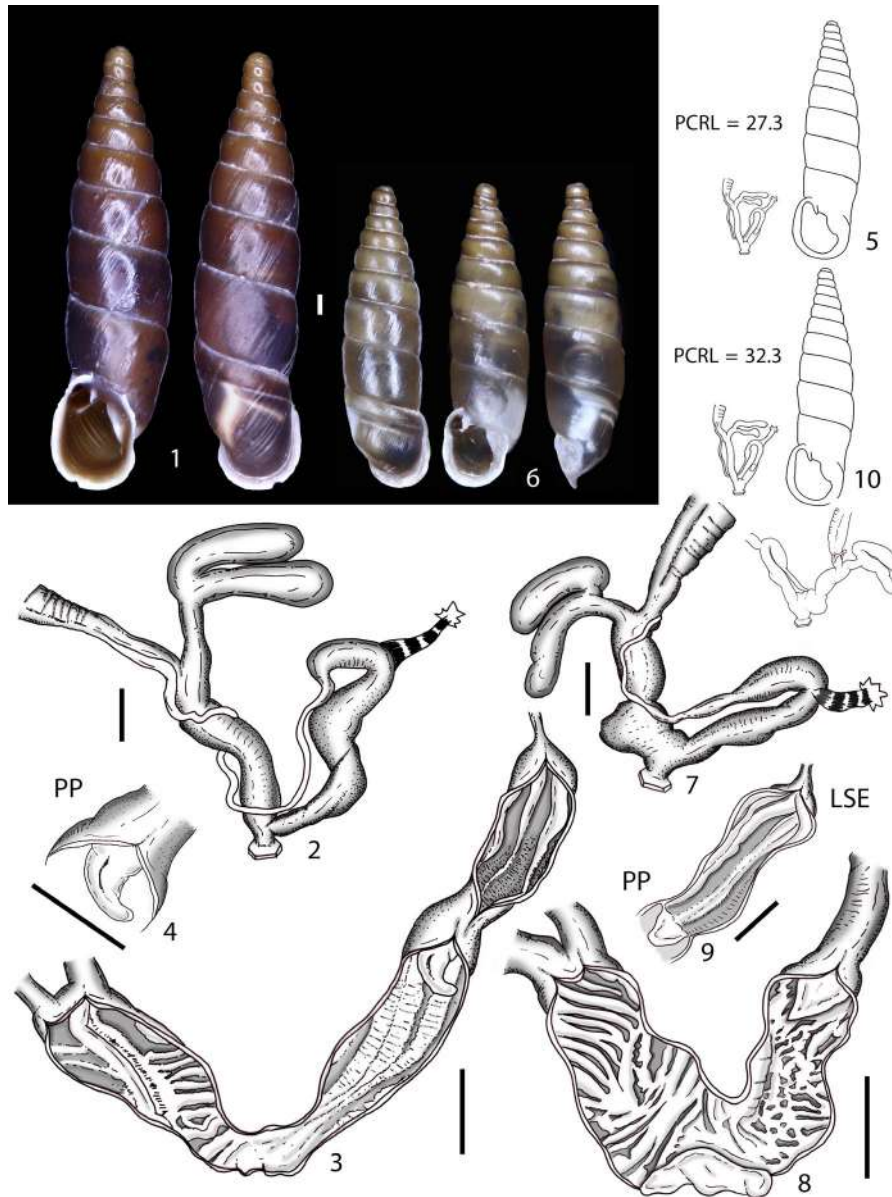


FIGURE 62 62.1–62.5 *Montenegrina voidomatis voidomatis* Nordsieck, 1974 stat. nov. HHNM 99529. 62.1 shell, 62.2 whole distal genitalia, 62.3 inner distal genitalia, 62.4 penial papilla, 62.5 shell-genitalia ratio. 62.6–62.10 *Montenegrina soosi* Eröss and Szekeres, 2006 NHMW 110430/MN/0115. 62.6 shell, 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.

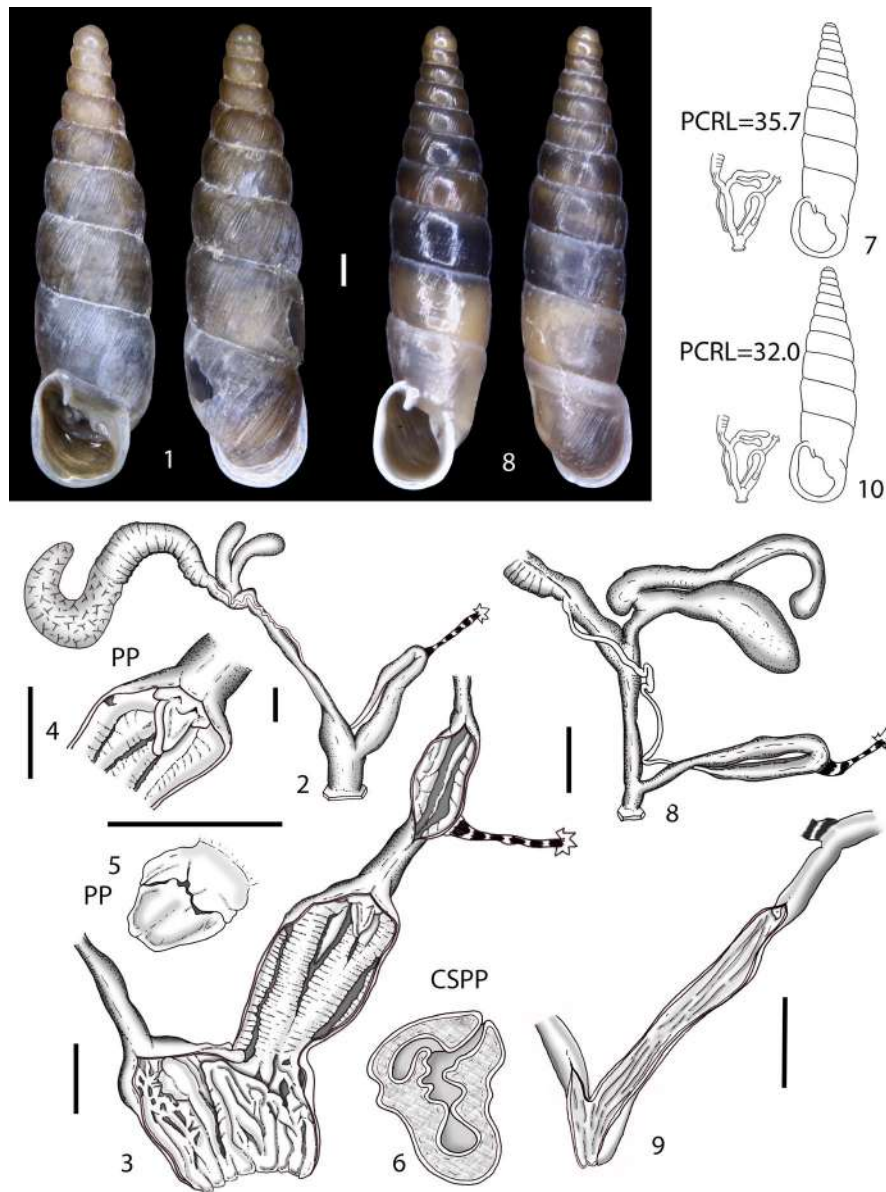


FIGURE 63 63.1–63.7 *Montenegrina stankovici* (Urbański, 1960) NHMW 110430/MN/0061. 63.1 shell, 63.2 whole distal genitalia, 63.3 inner distal genitalia, 63.4 penial papilla and proximal inner part of penis, 63.5 penial papilla, 63.6 cross section penial papilla. 63.7 shell-genitalia ratio, 63.8–63.10 *Montenegrina gropana* Fehér & Szekeres, 2016 stat. nov. HNHM 99503. 63.7 shell, 63.8 whole distal genitalia, 63.9 inner 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).

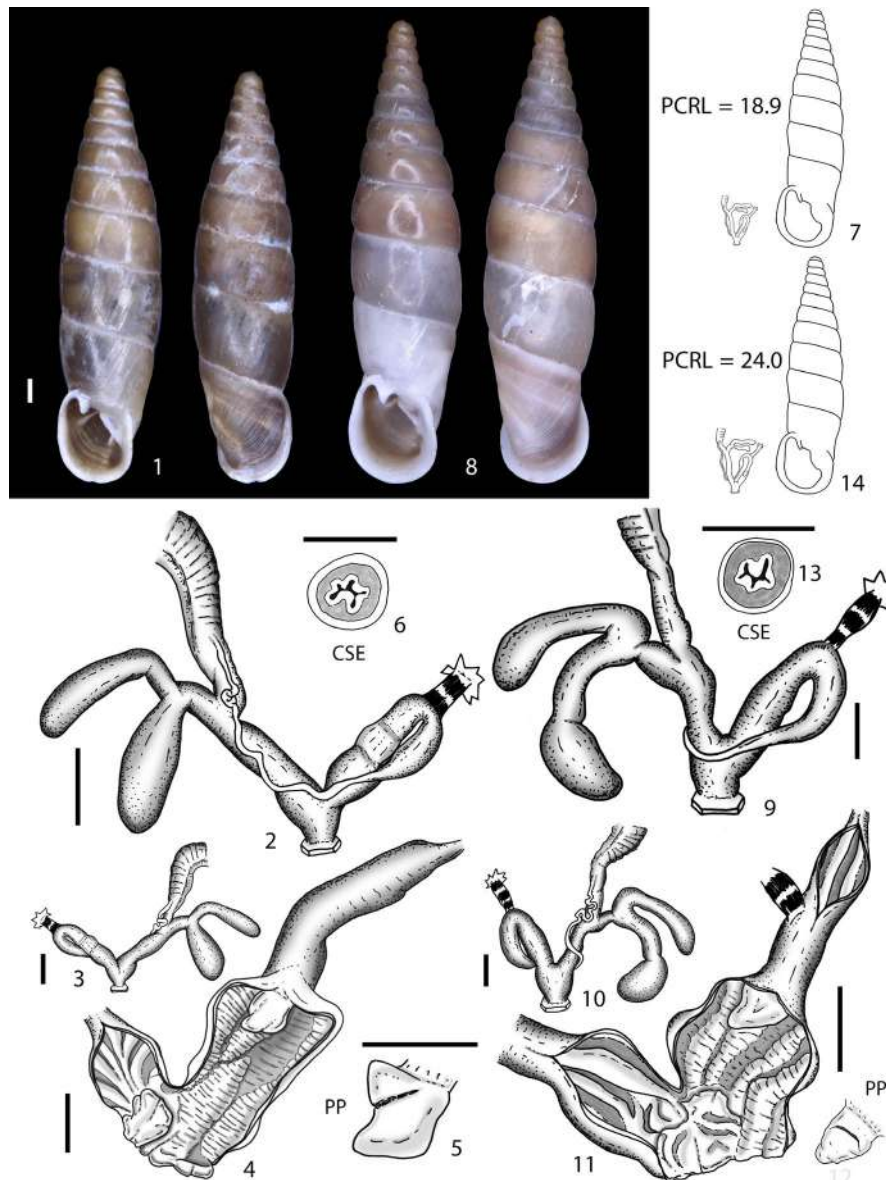


FIGURE 64 *Montenegrina subcristata* (Pfeiffer, 1848) NHMW 110430/MN/0143. 64.1 shell. 64.2–64.3 whole distal genitalia. 64.4 inner distal genitalia, 64.5 penial papilla, 64.6 cross section of epiphallus, 64.7 shell-genitalia ratio. NHMW 110430/MN/0150. 64.8 shell. 64.9–64.10 whole distal genitalia. 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

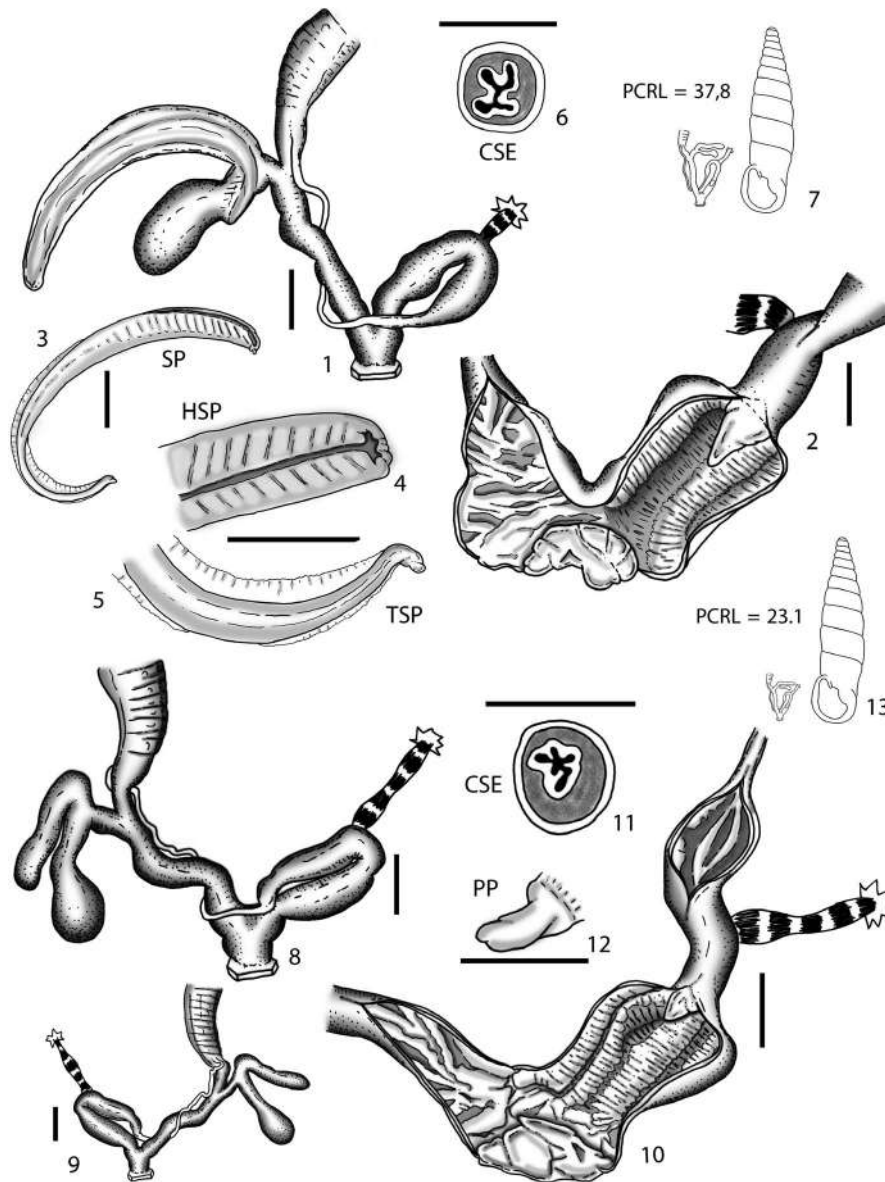


FIGURE 65 *Montenegrogrina subcristata* (Pfeiffer, 1848) NHMW 110430/MN/0149. 65.1 whole distal genitalia. 65.2 inner distal genitalia. 65.3 spermatophore. 65.4 head of spermatophore. 65.5 tail of spermatophore. 65.6 cross section of epiphallus. 65.7 shell-genitalia ratio. NHMW 110430/MN/0122. 65.8–65.9 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

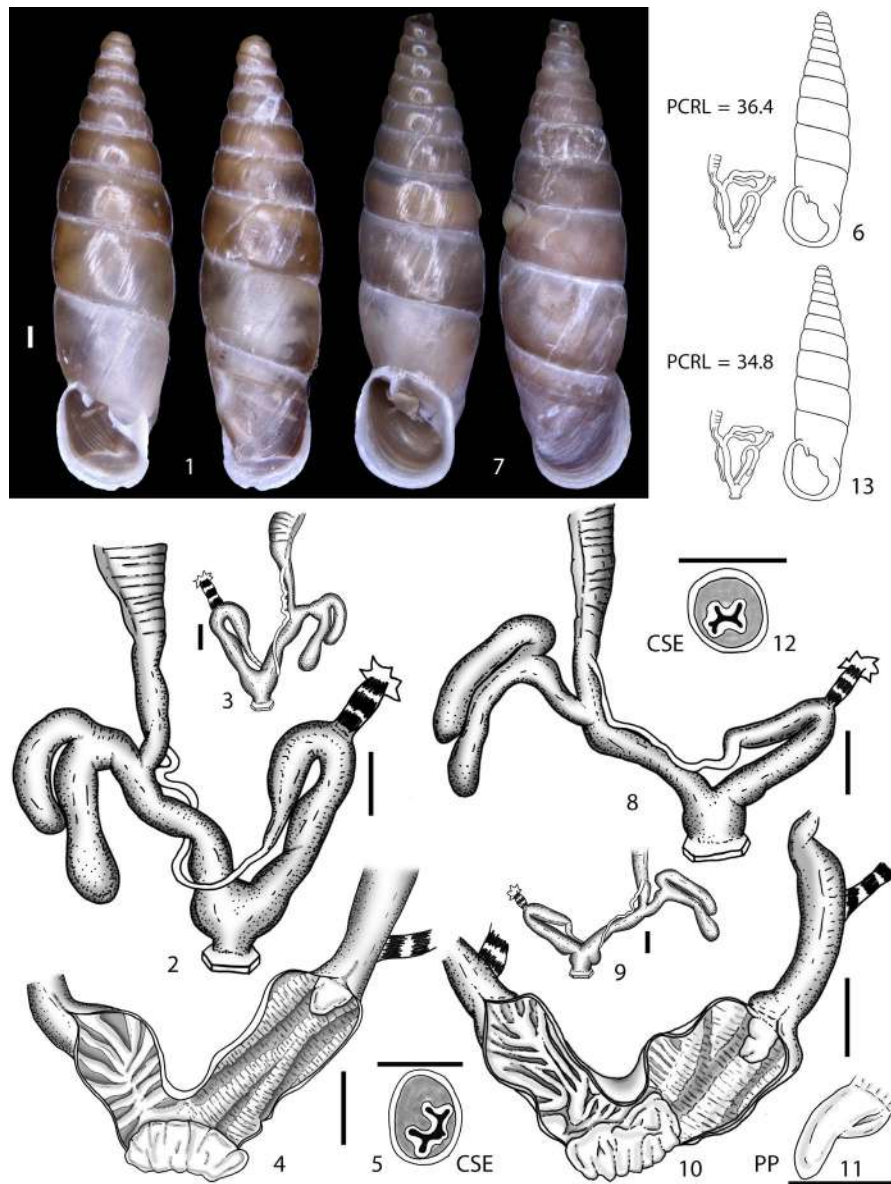


FIGURE 66 *Montenegrina subcristata* (Pfeiffer, 1848) NHMW 110430/MN/0158. 66.1 shell. 66.2–66.3 whole distal genitalia. 66.4 inner distal genitalia. 66.5 cross section of epiphallus. 66.6 shell-genitalia ratio. NHMW 110430/MN/0121. 66.7 shell. 66.8–66.9 whole distal genitalia. 66.10 inner distal genitalia. 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,

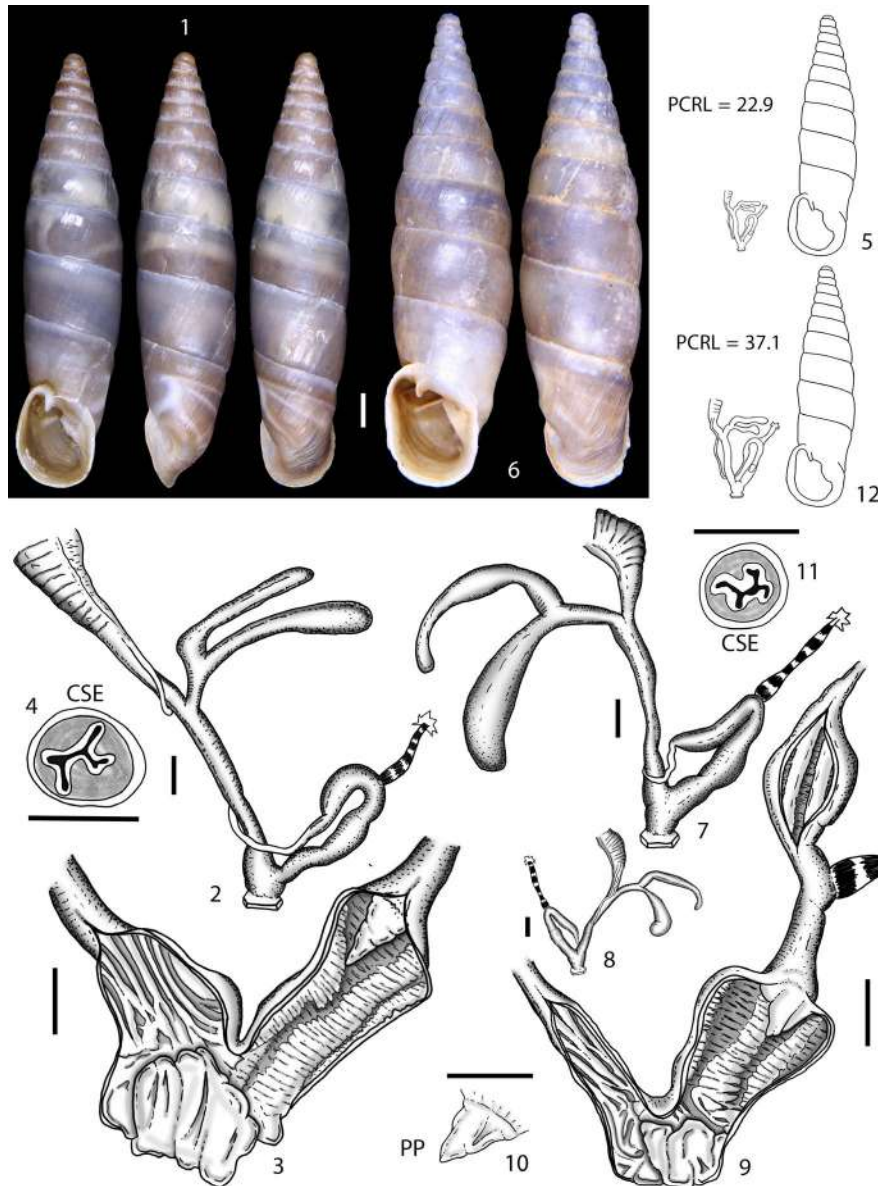


FIGURE 67 *Montenegrina subcristata* (Pfeiffer, 1848) WDM 7269. 67.1 shell. 67.2 whole distal genitalia. 67.3 inner distal genitalia. 67.4 cross section of epiphallus. 67.5 shell-genitalia ratio. WDM 723167.6 shell 67.7–67.8 whole distal genitalia. 67.9 inner distal genitalia. 67.10 penial papilla. 67.11 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

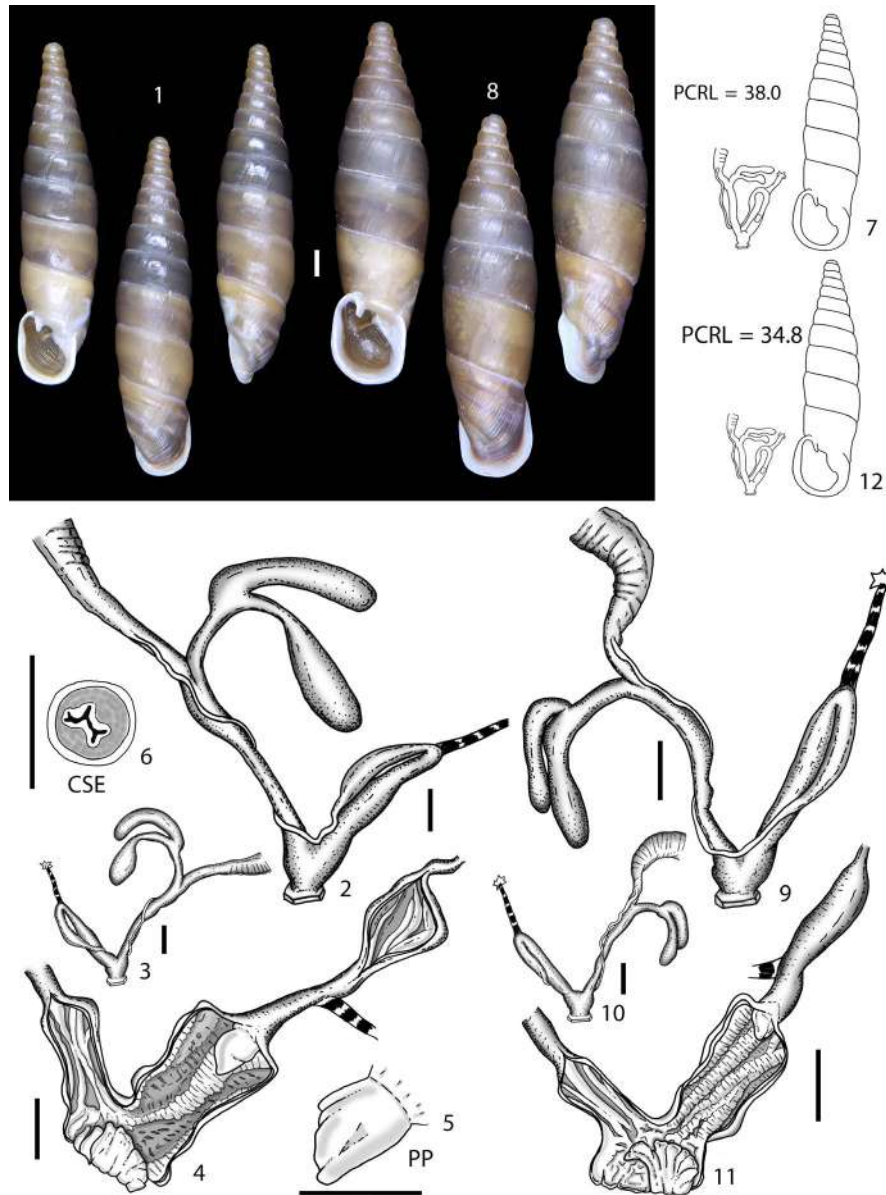


FIGURE 68 *Montenegrina subcristata* (Pfeiffer, 1848) WDM 7273. 68.1 shell. 68.2–68.3 whole distal genitalia. 68.4 inner distal genitalia. 68.5 penial papilla. 68.6 cross section of epiphallus. 68.7 shell-genitalia ratio. WDM 7235. 68.8 shell. 68.9–68.10 whole distal genitalia. 68.11 inner distal genitalia. 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.,

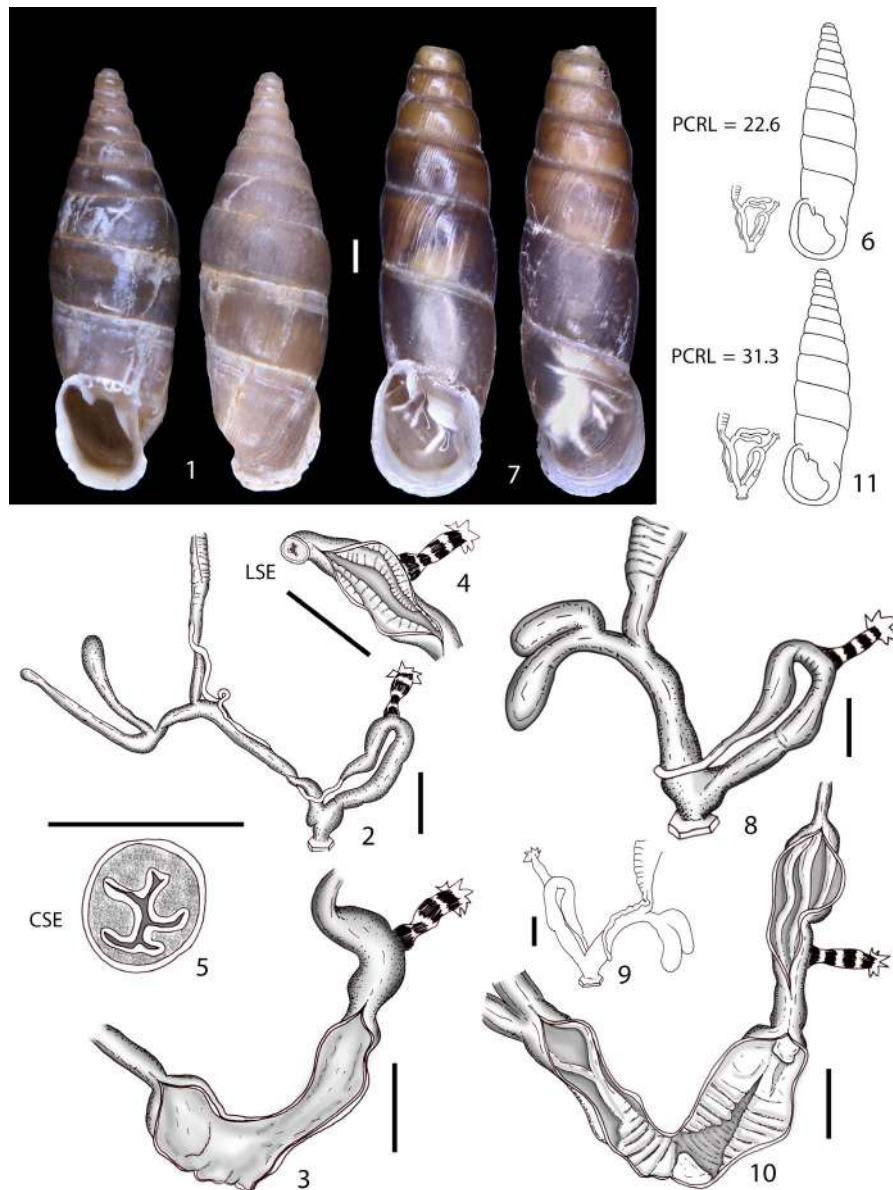


FIGURE 69 69.1–69.6 *Montenegrina timeae* Eröss and Szekeres, 2006 HNHM 94856. 69.1 shell. 69.2 whole distal genitalia. 69.3 inner distal genitalia. 69.4 longitudinal section of epiphallus. 69.5 cross section of epiphallus. 69.6 shell-genitalia ratio. 69.7–69.11 *Montenegrina zilchi* Nordsieck, 1974 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

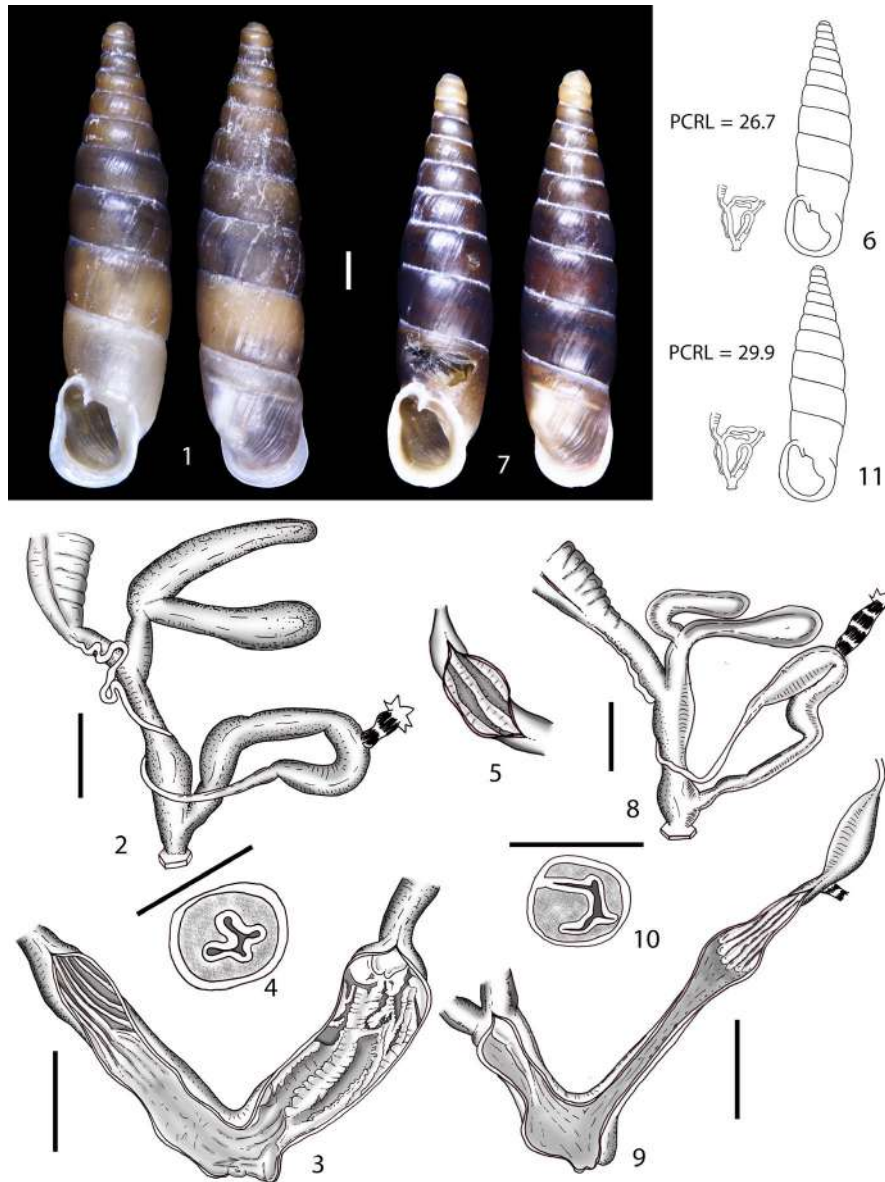


FIGURE 70 70.1–70.6 *Montenegrina tomorosi tomorosi* Brandt, 1961 HNHM 99724. 70.1 shell. 70.2 whole distal genitalia. 70.3 inner distal genitalia. 70.4 cross section of epiphallus. 70.5 longitudinal section of epiphallus. 70.6 shell-genitalia ratio. 70.7–70.11 *Montenegrina tomorosi coerulescens* Nordsieck, 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

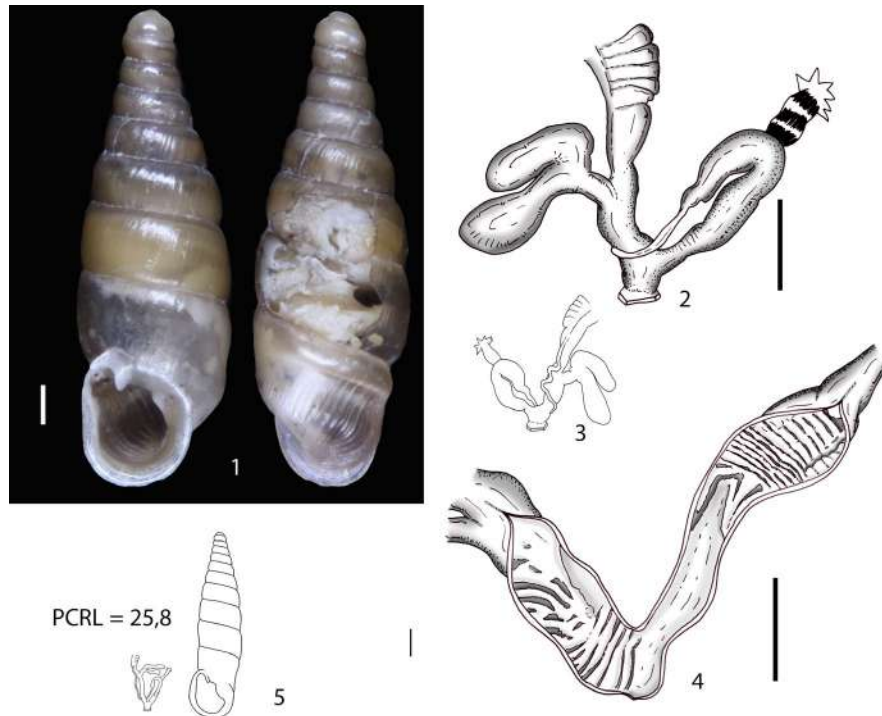


FIGURE 71 71.1–71.5 *Montenegrogrina tomorosi muranyii* Fehér & Szekeres, 2006 comb. nov. HHNM 94847. 71.1 shell. 71.2–71.3 whole distal genitalia. 71.4 inner distal genitalia. 71.5 shell-genitalia ratio

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 trojopjana*, 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 cataroensis cataroensis</i> (Rossmässler, 1835)	<i>Montenegrina cataroensis</i> (Rossmässler, 1835)
<i>Montenegrina cataroensis umbilicata</i> (Boettger, 1879)	<i>Montenegrina umbilicata umbilicata</i> (Boettger, 1879) stat. nov.
<i>Montenegrina cataroensis antivariocostata</i> (Boettger, 1907)	<i>Montenegrina umbilicata antivariocostata</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.

(Continues)

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.

(Continues)

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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9. Publication 2

De Mattia, W., Reier, S. & Haring, E. (2021). Morphological investigation of genital organs and first insights into the phylogeny of the genus *Siciliaria* Vest, 1867 as a basis for a taxonomic revision (Mollusca, Gastropoda, Clausiliidae). *Zookeys* 1077: 1–175.

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Morphological investigation of genital organs and first insights into the phylogeny of the genus *Siciliaria* Vest, 1867 as a basis for a taxonomic revision (Mollusca, Gastropoda, Clausiliidae)

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Abstract

The taxonomy and systematics of the door snail genus *Siciliaria* was revised based on an integrative approach including a comprehensive genital anatomical investigation, which was combined with shell morphology and DNA sequence data (mitochondrial COI, nuclear ITS2 sequences). The genital morphology of 120 specimens of 22 taxa from 44 populations was investigated, and a new general description of the genital morphology of the genus is provided. Additionally, 26 specimens of 14 taxa of five genera (MolluscaBase 2021) of Aloiinae (*Mauritanica*, *Charpentieria*, *Stigmatica*, *Gibbularia*, *Papillifera*) were included in the genetic analyses. New anatomical structures are described: the parapseudopapilla for *Charpentieria dyodon* and the hemipapilla for *Charpentieria stenzii*. In the phylogenetic tree based on COI sequences, the species of the genus *Siciliaria* s. l. from northwestern Sicily were found within two separate highly supported main clades. In the tree based on the nuclear ITS2 marker sequence, resolution was considerably lower but it partially confirmed the mitochondrial tree. The genus *Sicania* Tomlin, 1929 (corresponding to main clade II in the trees) is re-introduced. *Siciliaria scarificata* did not appear in one of the two main clades but clustered together with *Mauritanica perinni polygyra*. Concerning monophyly of species, only the widely distributed *S. calcarae* was paraphyletic in the COI tree, a finding that has to be investigated further with multiple marker sequences. For the other genera (*Mauritanica*, *Charpentieria*, *Stigmatica*,

Gibbularia, and *Papillifera*) detailed descriptions of the anatomy of the genital organs of 46 taxa for a total amount of 133 dissected specimens are also provided here. Some of these taxa could be included in the phylogenetic analysis. Although the taxon sampling of these taxa was far from being complete, the comprehensive data provided here (concerning morphology, genetics, and distribution) provide first insights into the phylogenetic relationships of this diverse group of clausiliid taxa. The following six taxa new to science are described: *Siciliaria grobmanniana addaurae* **ssp. nov.**, *Siciliaria calcarae borgettensis* **ssp. nov.**, *Siciliaria calcarae jatinensis* **ssp. nov.**, *Siciliaria calcarae parajatinensis* **ssp. nov.**, *Siciliaria calcarae cruenta* **ssp. nov.**, and *Siciliaria tiberii armettensis* **ssp. nov.**

Keywords

Anatomy of genital organs, Clausiliidae, phylogeny, *Siciliaria*, systematics, taxonomy

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Introduction

Siciliaria Vest, 1867 is a genus of the family Clausiliidae that is distributed along the calcareous ranges of northwestern Sicily (Italy). It is distributed from Egadi Islands and Trapani in the west to western Madonie in the east. The southern boundaries are represented by the line (west to east) Trapani, Calatafimi, Bosco Ficuzza and Monte San Calogero.

Vest (1867: 166) introduced the genus name *Siciliaria* (type species *Clausilia grohmanniana* Rossmässler 1836) for a group of Sicilian rock-dwelling clausiliids species also including *Clausilia syracusana* Philippi, 1836 [currently *Muticaria syracusana* (Philippi, 1836)] from the Iblean Peninsula. Schmidt (1868: 40–43) proposed a first rearrangement, creating the “Formenkreis” of *Clausilia septemplexata*, that included all the northwestern Sicilian species, oddly neglecting the genus name *Siciliaria* Vest (1867).

Later, Boettger (1877: 33) split the species into two groups based on the shape of the clausilium, shell sculpture and the development of the plicae and lamellae (Nordsieck 2013b). The “Gruppe der *septemplexata* Phil.” for the *Siciliaria* s. s. species [namely. *Siciliaria grohmanniana*, *Siciliaria (Siciliaria) septemplexata*, *Siciliaria (Siciliaria) calcarae*, *Siciliaria adelina* (currently a junior synonym of *Siciliaria calcarae*), *Siciliaria (Siciliaria) confinata* (currently *Mauritanica scarificata* comb. nov.) and *Siciliaria (Siciliaria) tiberii*], which he characterised by “Clausilium vorn am Aussenrand stark umgeschlagen”. The “Gruppe der *crassicostata* Ben”, for which he introduced the name *Trinacria* [namely *Siciliaria (Trinacria) crassicostata*, *Siciliaria (Trinacria) crassicostata* var. *eminens* (currently *Sicania eminens* comb. nov.), *Siciliaria (Trinacria) leucophryna* (currently *Siciliaria leucophryna*) and *Siciliaria (Trinacria) nobilis*] and which he described with “Clausilium tief rinnenförmig, vorn dick und schräg abgestutzt, schwach ausgerandet”.

The name *Sicania* had been introduced in order to replace the pre-occupied name *Trinacria* Boettger 1877 (the senior homonym is *Trinacria* Mayer, 1868; Bivalvia: Glycymerididae). Few additional contributions dealt with northwestern Sicilian *Siciliaria*, namely Benoit (1881: 101–120) with a synonym list and some information about distribution of species and Westerlund (1892: 47–48) who simply reported a species list. The genital organs of representatives of *Siciliaria* were treated for the first time by Wagner (1913, 1925), who depicted three northwestern Sicilian species [as *Delima* (*Siciliaria*): *S. septemplicata*: Wagner 1913: pl. 572, fig. 14; *S. grobmanniana*: Wagner 1925: pl. 1, fig. 8, *S. calcarae*: Wagner 1925: pl. 3, fig. 25. Wagner's genital anatomical drawings are reproduced in Fig. 1A–C.

More recently, Brandt (1961: 13) depicted the distal genital organs of *Siciliaria ferrox* Brandt, 1961 (Fig. 1D). Brandt (1961) introduced five new taxa and made a few systematic arrangements, but his results are inconclusive due to unidentified or wrong localities reported on the material's labels housed at SMF (mainly provided by Monterosato). Alzona (1971: 90–92) did not list Brandt's new taxa, although his paper was cited. Nordsieck (1979: 259–260) united Boettger's groups, because he considered *S. calcarae* (Philippi, 1844) conchologically as an intermediate form. Nordsieck (1984: 202) described *Siciliaria spezialensis*. Later, Nordsieck (2002: 29) considered *Siciliaria* as a subgenus of *Charpentieria* Stabile, 1864 and listed 12 species. Within the genus *Charpentieria*, he grouped many other genera as subgenera, viz. *Stigmatica* Boettger, 1877, *Gibbularia* Monterosato, 1908 and *Mauritanica* Boettger, 1879, creating a new system based on shell characters (Fig. 2). Beckmann (2004) introduced two new subspecies (*Siciliaria tiberii scalettensis*, *Siciliaria septemplicata hemmeni*), both considered to be conchologically intermediate “hybrid forms”. Nordsieck (2007) kept *Siciliaria* (and all the above-mentioned genera) as subgenus of *Charpentieria*. In the last two decades, contributions to the knowledge of the distribution of species were provided by Reitano et al. (2007: 326) [*Siciliaria ferrox* (Brandt, 1961)]; Reitano et al. (2012) [*Siciliaria leucophryna* (Pfeiffer, 1862)] and Liberto et al. (2015) [*Siciliaria scarificata* (L. Pfeiffer, 1856)] and two new subspecies were recently described: *Siciliaria calcarae orlandoii* Liberto, Reitano, Giglio, Colomba & Sparacio, 2016 and *Siciliaria leucophryna microinsularis* Sparacio, Surdo, Viviano, Liberto & Reitano, 2021. For a comprehensive recap about the systematics and the nomenclatural history of *Siciliaria* see Nordsieck (2013b: 1–2). This system changed in the following Nordsieck's papers (2013a; 2013b) where *Charpentieria* and *Siciliaria* were treated again as separated genera and *Stigmatica*, *Gibbularia* and *Mauritanica* were considered as subgenera of *Siciliaria*. Nordsieck (2013b: 2) stated that the genital morphology of all *Siciliaria* species was similar. While that analysis concentrated on the external characters of genital organs (shape, proportions among anatomical parts) and, to some extent, to the pseudopapilla, the internal morphology was not investigated.

Nordsieck (2013a: 4) again separated *Siciliaria* from *Charpentieria* and listed the presence/absence of the thickening as a delimitation of the proximal part of the penis, being distinct or not as the main differences in the morphology of genital organs among *Charpentieria*, *Siciliaria*, *Stigmatica*, and *Mauritanica*. In detail, he stated that

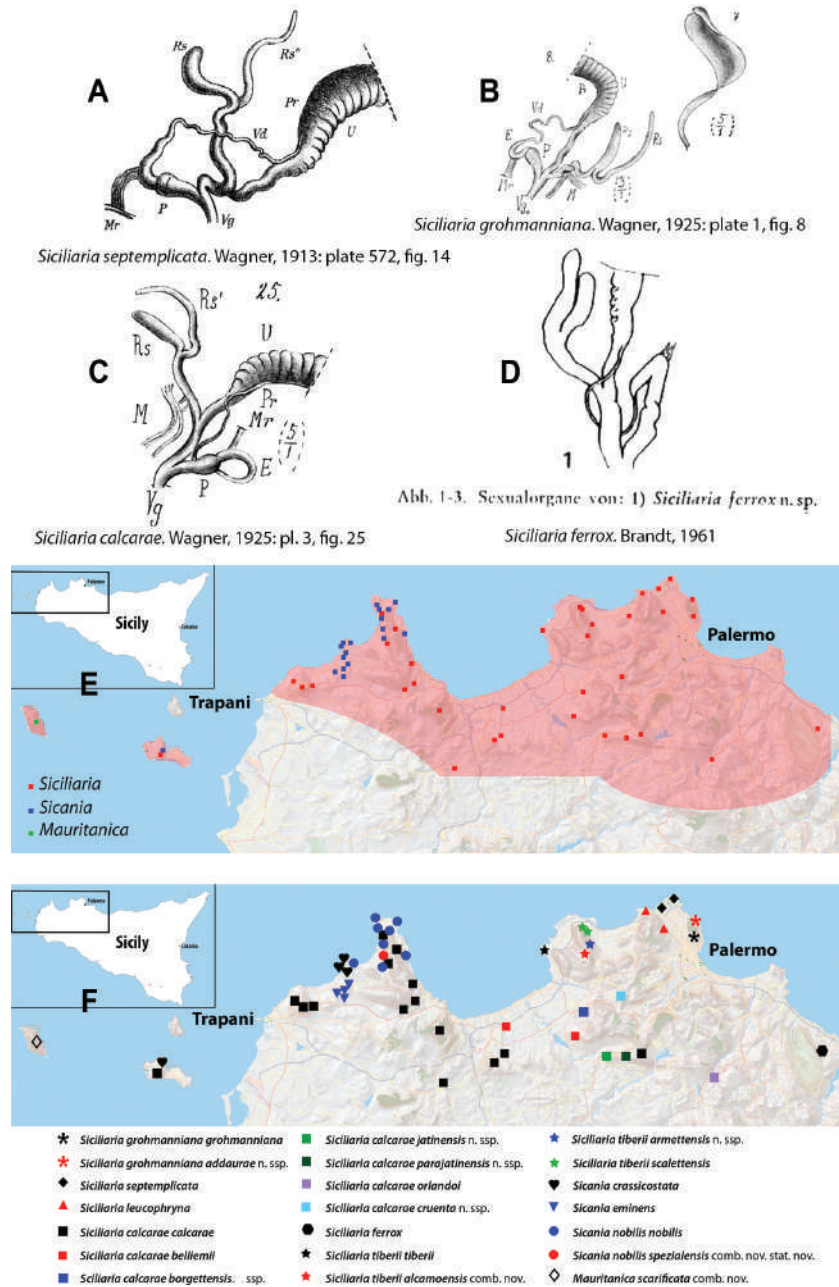


Figure 1. Wagner's (1913, 1925) and Brandt's (1961) *Siciliaria* genital drawings **A** *Siciliaria septemplicata*, Wagner, 1913: plate 572, fig. 14 **B** *Siciliaria grohmanniana grohmanniana*, Wagner, 1925: plate 1, fig. 8 **C** *Siciliaria calcarae calcarae*, 1925: plate 3, fig. 25 **D** *Siciliaria ferrox*, Brandt, 1961: fig. 1 **E** overall *Siciliaria/Sicania* and Sicilian *Mauritanica* distribution **F** *Siciliaria/Sicania* and Sicilian *Mauritanica* distribution of taxa.

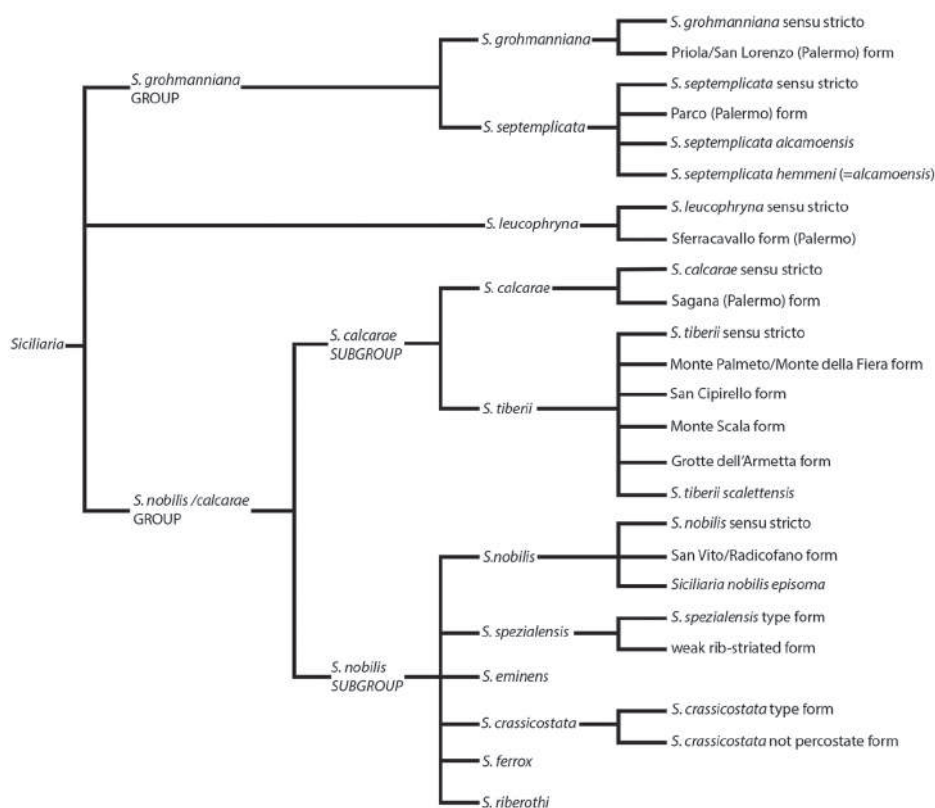


Figure 2. Qualitative shell-based tree depicting Nordsieck's (2013b) *Siciliaria* system.

in *Charpentieria* the "epiphallar thickening at the transition epiphallus-penis was missing" and "the delimitation of the proximal part of the penis was distinct". In *Siciliaria* s. l. the epiphallar thickening should be present [except for *S. (Gibbularia)*] and the delimitation of the proximal part of the penis was described to be indistinct. *Mauritanica* was deemed as belonging to *Siciliaria* because it exhibits the same characters. Moreover, he stated that *Siciliaria* could be morphologically distinguished from *Charpentieria* only "by the defined characters". Yet, Nordsieck (2013a: 4) introduced the term "epiphallar thickening" without providing a clear explanation for this term. Given that it concerns the transition between penis and epiphallus, it is not clear whether the epiphallar thickening was an external or internal character of the genital organs. Most likely, it concerns the external appearance of the transition penis-epiphallus, where the epiphallar thickening reveals a clear distinction between penis and epiphallus; it was already depicted by Wagner (1913, 1925) (Fig. 1). In his paper dealing with southern Alpine *Charpentieria* (Nordsieck 1963b), which includes a good number of genital drawings, the concept of epiphallar thickening was not mentioned nor depicted. Our genital anatomical investigations of the internal arrangement of the distal genital or-

gans revealed an intriguing, diversified, and complex situation that may not be summarised by the character states dichotomy proposed by Nordsieck (1963a: 95, figs 9–10; 97, fig. 11; 1963b: 185, figs 4751; 189: figs 52–54; 193: figs 55–56; 1979, 2013).

According to the currently accepted system (MolluscaBase 2021), *Siciliaria* is deemed as a subgenus of the all-inclusive genus *Charpentieria*, with 12 species and 17 subspecies. It currently comprises six subgenera with 29 taxa and ~ 70 subspecific taxa. The phylogenetic relationships among *Siciliaria*, *Charpentieria*, *Stigmatica*, *Gibbularia* and *Mauritanica* are still unclear. Scheel and Hausdorf (2012), Uit de Weerd and Gittenberger (2013) and Xu and Hausdorf (2021) included Delimini species in their phylogenetic analyses, but those articles concentrated on other aims (south Alpine *Charpentieria*, general Clausiliidae phylogeny) and thus the phylogeny of Delimini is still largely incomplete. Nordsieck (2020) summarised these results by proposing that *Siciliaria* and *Charpentieria* should be separate genera and by recognising a geographic split within *Siciliaria*. He thus introduced again the name *Sicania* as a subgenus of *Siciliaria*, but stressing that there is no morphological evidence supporting such a dichotomy. Moreover, *Mauritanica* was deemed as a subgenus of *Siciliaria*, whereas for *Stigmatica* the need for further research was emphasised.

Aims of the study

In the present study a comprehensive investigation of the genus *Siciliaria* Vest, 1867 (type species: *Clausilia grohamnniana* Rossmässler, 1836) was performed, including morphology of the genital organs and DNA sequence analyses, which were interpreted in the light of the current taxonomic system (Nordsieck 2007, 2013a; MolluscaBase 2021). In addition to *Siciliaria* (*sensu* MolluscaBase 2021), 14 taxa belonging to genera related to *Siciliaria* (namely *Charpentieria*, *Stigmatica*, *Gibbularia*, *Papillifera* and *Mauritanica*) were included in the molecular genetic study as a first attempt to elucidate their relationships using *Papillifera* as outgroup. Yet, we were well aware that the low number of samples would provide only a preliminary insight. We systematically introduced new genital anatomical characters for the above listed genera. This study follows the strategy and methods of the recently published integrative approach to the taxonomy and systematics within *Montenegrina* Boettger, 1877 (De Mattia et al. 2020; Mason et al. 2020a), where DNA-based phylogenetic trees together with morphological characters (both shell and morphology of genital organs) were the basis for a taxonomic revision.

Materials and methods

Most of the Sicilian material (mainly *Siciliaria* and *Papillifera*), unless differently stated, was collected during four field collecting trips by the first author (WDM) and currently kept in the Willy De Mattia collection (Syracuse, Italy). The type material of the newly described taxa was deposited in the Natural History Museum in Vienna. Part of the material was made available by other private collections. In order to increase the sample (n) for shell measurements, also dead material was extensively collected. In

this study we investigated the anatomy of the genital organs of 120 specimens from 44 populations representing 16 of the 17 taxa presently listed in MolluscaBase eds. (2021). The identification of taxa was based following Nordsieck (2013b) and personal communications with H. Nordsieck.

The non-Sicilian specimens were also collected mostly by the first author (WDM) during collecting trips throughout the central and eastern southern Alps, Italian peninsula, and western Balkans from 1992 to date, though interesting specimens belonging to *Stigmatica* and *Papillifera* were provided by other collectors. As regards the other genera (*Mauritanica*, *Charpentieria*, *Stigmatica*, *Gibbularia*, and *Papillifera*), 133 specimens of 46 taxa were anatomically investigated.

Ninety-four specimens comprising *Siciliaria*, *Charpentieria*, *Gibbularia*, *Stigmatica*, *Mauritanica*, and *Papillifera* were genetically analyzed (see Table 1). The remaining DNA is stored in the DNA/Tissue collection of the Natural History Museum Vienna.

The DNA extraction was performed in a sterile room using the QIAmp DNeasy Blood and Tissue Kit (QIAGEN, Hilden, Germany) following the protocol of the manufacturer. A 655 bp long fragment of the mitochondrial (mt) cytochrome c oxidase subunit 1 gene (COI) was amplified using the primers LCO1490_ABOL_Moll_1 (5'-TCAACAAAYCATAARGAYATTGG-3') and HCO2198_ABOL_Moll_1 (5'-TAAACTTCTGGRTGACCAAAAAAYCA-3') (Duda et al. 2017). As nuclear (nc) marker sequence we analyzed the internal transcribed spacer 2 (ITS2) between the two nuclear rRNA genes (5.8S rRNA gene and 28S rRNA gene).

Using the primers 5.8S_LSU-1fw (5'-CTAGCTGCGAGAATTAATGTGA-3') and 28S_LSU-3rv (5'-ACTTTCCTCACGGTACTTG-3') (Wade and Mordan 2000), which bind in the flanking rRNA genes, fragments with varying lengths (911–957 bp) were amplified (this fragment, hereafter named ITS2, comprised besides ITS2 also short partial sequences of the two rRNA genes). PCR reactions were performed in a final volume of 25 µl containing, 2.5 µl 10× PCR buffer, 1.5 mM MgCl₂, 0.2 mM of each dNTP, 0.5 µM of each primer, 0.5 units TopTaq Polymerase and 1 µl template DNA. Each PCR had the following conditions: 94 °C for 3 min, 35 cycles of (94 °C for 30 s, 50 °C for 30 s and 72 °C for 60 s) and 72 °C for 7 min.

The ITS2 PCR fragments proved to be length-variable due to insertions/deletion, and most individuals were heterozygous. To avoid unreadable sequences, PCR products were cloned. For this task, additional PCRs were performed using the proofreading Platinum® Taq DNA Polymerase High Fidelity (Invitrogen, Carlsbad, CA, USA). These PCRs were conducted with different PCR conditions: 95 °C for 2 min, 5 cycles (94 °C for 15 s, 60 °C for 30 s, 72 °C for 1 min), 35 cycles (94 °C for 15 s, 50 °C for 30 s, 72 °C for 1 min) and without final elongation. PCR fragments were purified with the QIAquick Gel Extraction Kit (QIAGEN, Hilden, Germany) and cloned with the TOPO-TA© cloning kit (Invitrogen, Carlsbad, CA, USA). Three to five clones per individual were sequenced.

Sequencing was performed at Microsynth (Balgach, Switzerland) in both directions using the original PCR primers or, for cloned PCR products, using M13 uni-

versal primers. Sequences were processed in Geneious 2.10.3 (<https://www.geneious.com>). COI sequences were unambiguously aligned (605 sites, no missing data), while the alignments of ITS2 sequences was performed in Geneious 2.10.3 using the MAFFT algorithm (Katoh and Standley 2013), resulting in a 985 bp alignment (no missing data). Alignments of both markers were concatenated using Geneious 2.10.3. Neighbour joining (NJ) trees were calculated in MEGA 10.0.5 (Kumar et al. 2018). In addition, Bayesian inference (BI) trees were calculated using MrBayes v.3.2.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). The best-fit models using Bayesian Information Criterion (BIC) were evaluated for each gene using ModelFinder (Kalyaanamoorthy et al. 2017), which were GTR+F+I+G4 (COI) and K2P+G4 (ITS2) respectively. BI analyses were performed with three runs for 30×10^6 generations and four chains each. Trees and parameters were sampled every 1000th generation. The first 25% of trees were discarded as burn-in and a 50% majority rule consensus tree was built from the remaining trees. Inter- and intraspecific uncorrected p-distances were calculated using MEGA 10.0.5 (Kumar et al. 2018).

The shells of all dissected specimens were photographed in multiple views (front, back, lateral and internal mouth), including the clausilium distal part, with a Canon EOS camera equipped with 60 mm macro lenses mounted on a Kaiser microslide frame for multi-image stacking. Maximum shell height was measured with a digital caliper (accuracy ± 0.05 mm). For each population at least two specimens were dissected (except for *Mauritanica perinni polygyra*) in order to reduce the possibility of being misled by abnormalities or single freak specimens (Nordsieck 2007).

Anatomical examinations and dissections were performed under a Zeiss stereoscope with a ring LED illumination apparatus, connected to a digital, high-resolution camera and a camera lucida. The genital organs were separated from the rest of the body after a careful crushing of the shell. Dissections were made using a pair of very fine and pointed micro-tweezers (Dumostar Biology 55) and a micro-scissor (FST 150000, Aesculap OC series) in a Petri dish with black paraffin on the bottom and filled with 70% ethanol. The genital organs were fixed with very fine steel micro-pins (commonly used for the preparation of microlepidopteran specimens in entomology). Internal characters of the genital organs (based on cross and longitudinal sections) were examined after dissection with micro-tweezers or a pair of micro-scissors. Measurements were taken using a millimetric measurement scale. The genital organs were photographed in different positions (40–50 high-resolution images) to create an image database. Drawings were prepared by tracing the most representative digital images after contrast enhancement with picture editing software.

Measurements of anatomical features (e.g., length of P, V, BC+SDBC) were taken using image editing software directly on the high-resolution photographs. The anatomical nomenclature partially follows Nordsieck (1969a, 1972, 2009) and Giusti et al. (1995). The anatomical partition and acronyms are depicted in Fig. 3. Gonads, albumen glands, the first hermaphroditic duct, and most ovispermiducts are neither described nor depicted in drawings as they are deemed as not carrying any reliable taxonomical characters. The VR was found in the same position in all the investigated

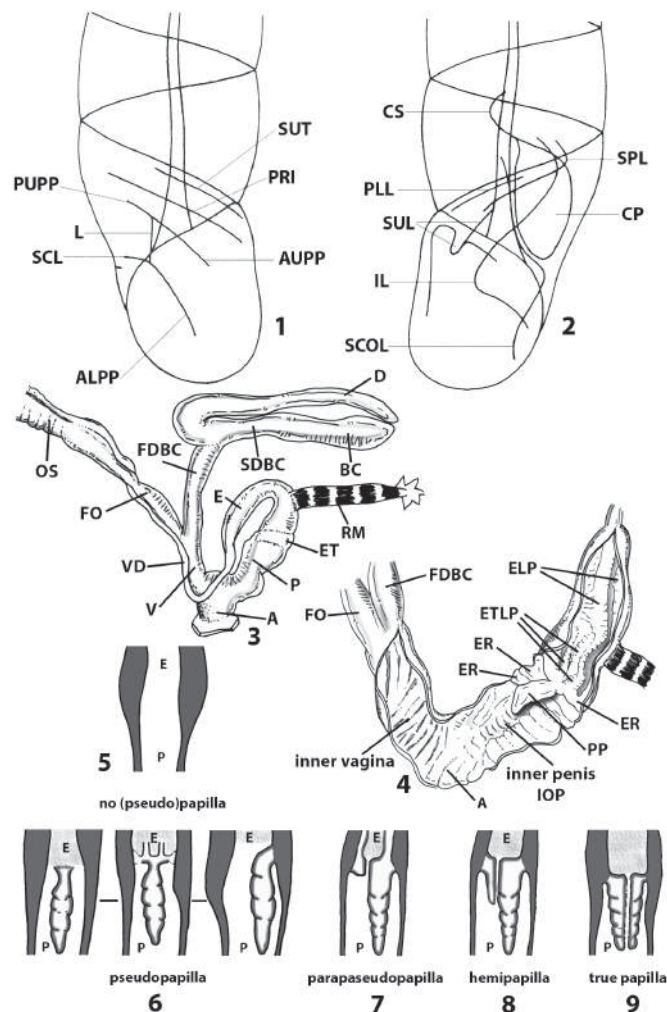


Figure 3. **3.1, 2** *Siciliaria/Sicania* clausilial apparatus (from hnords.de, modified): **3.1** plicae **3.2** lamellae **3.3,4** *Siciliaria/Sicania* anatomy of the genital organs general scheme and **(3.5–9)** variability of the pseudopapilla within genera *Siciliaria*, *Sicania*, *Mauritanica*, *Charpentieria*, *Stigmatica*, *Gibbularia* and *Papillifera* **3.5** no (pseudo)papilla **3.6** pseudopapilla **3.7** parapseudopapilla **3.8** hemipapilla **3.9** eupapilla (true penial papilla).

specimens: thus, in order to render the anatomical drawings clearer and focus on key taxonomic features, it is not depicted.

In order to highlight the proportions among the genital parts, the measurements were converted into relative values (ratios). All the ratios are based on measures of at least two specimens. The ratios are FO/V , $D/BC+SDBC$, $BC+SDBC/V$, $D/BC+SDBC$, $P+E/V$, and E/P . The measurements of both shell and genital organs are always given in mm. The proximal/distal indications refer as seen from the gonads. The subdivision of the genital apparatus in anatomical parts follows De Mattia et al. (2020).

Acronyms

A	atrium;	OELP	occupied epiphallar longitudinal plate;
ALPP	anterior lower palatal plica;	OS	ovispermiduct (second hermaphroditic duct);
AUPP	anterior upper palatal plica;	P	penis;
BC	actual bursa copulatrix;	PC	penial complex (P+E);
CP	clausiliar plate;	PCL	penial complex length;
CS	clausiliar stalk;	PG	prostatic gland;
CSP	cross section of the penial pseudopapilla;	PLL	parallelis;
CSE	cross section of the epiphallus;	PP	penial pseudopapilla;
D	diverticulum of the bursa copulatrix;	PPP	parapseudopapilla;
E	epiphallus;	PR	penial retractor muscle;
EF	epiphallar funnel;	PRI	principalis;
ELP	epiphallar longitudinal pleats;	PUPP	posterior upper palatal plica;
ER	epiphallar ring;	SCL	subclaustralis;
ETLP	epiphallar transitional longitudinal pleats;	SCOL	subcolumellatis;
EO	epiphallar outlet of the hemipapilla;	SDBC	second duct of the bursa copulatrix;
ET	epiphallar thickening;	SG	sperm groove;
FDBC	first duct of the bursa copulatrix;	SPL	spiralis;
FELP	free epiphallar longitudinal plate;	spm	specimen(s);
FO	free oviduct;	SUL	sulcalis or parietalis;
H_a	aperture height;	SUT	suturalis;
H_s	shell height;	TP	transition passage;
HG	hermaphroditic gland;	V	vagina;
H_s	shell height;	VD	vas deferens;
IOP	internal sculpturing of penis;	VR	vaginal retractor;
IL	columellaris or inferior lamella;	W_a	aperture width;
L	lunella;	W_s	shell last whorl width (body whorl).
CWDM	malacological collection of Willy De Mattia;		
NHMW	Natural History Museum Vienna (Naturhistorisches Museum Wien);		
SMF	Senckenberg Museum Frankfurt.		

Structure and rationale of *Siciliaria/Sicania* taxonomic analysis

In the first part of the Results we describe the molecular genetic data. For clarity, and in view of the various taxonomic changes in the past, a comprehensive table is presented at the end of the taxonomic part including the new full checklist of the taxa so far considered as *Siciliaria* (Table 12). In the following, we refer to these taxa as belong-

ing to “*Siciliaria/Sicania*”. We decided to apply the new taxonomic system already in the phylogenetic trees and their discussion, as well as in the morphological descriptions of the taxonomic part. In the general discussion we interpret the molecular and anatomical results and give an overview on the, so far, unidentified or enigmatic taxa mentioned in the literature.

The taxonomic part of the results comprises the descriptions of the taxa with a detailed list of examined specimens and the principal systematic and/or faunistic publications. For the specimens investigated genetically, the identifier is listed together with the GenBank accession numbers (in square brackets) for sequences of the mt cytochrome c oxidase subunit 1 gene (COI) and where available for the internal transcribed spacer 2 (ITS2). The descriptions of the shells and the clausiliar apparatus of those taxa that are currently valid (MolluscaBase 2021) were already provided and discussed by Nordsieck (2013b). We report here only the descriptions provided by Nordsieck (2013b). For the newly described taxa, the shell and clausiliar apparatus are described with full details.

Results

Phylogenetic trees

The collection numbers, voucher numbers, GenBank accession numbers and geographical coordinates for the specimens used in the molecular genetic analyses are listed in Table 1. *Papillifera* was used as outgroup for the phylogenetic trees calculated from the three data sets (COI, ITS2, combined). BI and NJ analyses yielded the same overall topologies (not shown). The BI tree based on COI sequences comprising 92 individuals is shown in Figure 4. In this tree, the species from northwestern Sicily so far comprising the genus *Siciliaria* were found within two separate highly supported main clades. Albeit the two clades (I and II) emerge as sister groups in the combined tree, this grouping is not well supported, and it remains unclear whether *Siciliaria* and *Sicania* together form a monophylum. There is only one exception, *Siciliaria scarificata* (in the tree designated as *Mauritanica scarificata* comb. nov.), which forms the sister group of *Mauritanica perinni polygyra*. This branch is the sister clade of clade II, although this relationship is very weakly supported. The mean p distance between clades I and II was 19.6% (range 18.9–21.6%). The two clades correspond to the division into the two genera *Siciliaria* and *Sicania* as proposed by Boettger (1877).

The taxa comprising the two main clades I and II cluster in a geographic pattern (maps in Fig. 1E, F). Clade I includes species that are found in limited areas in the eastern part of the distribution area, plus the widely distributed *Siciliaria calcarae*. The latter is found in several occurrences in the southern parts of the distribution range from west to east. Along the eastern part of its distribution area, the nominate subspecies of *S. calcarae* is sometimes replaced by local costate forms. Clade II comprises

Table 1. Specimens used in the molecular genetic analyses. Collection numbers, laboratory IDs, GenBank accession numbers, and geographical coordinates are listed. More than one ITS2 sequence was obtained from some individuals.

Taxon	Collection No.	Lab ID	GenBank Accession No.		Coordinates
			COI	ITS2	
<i>Sicania crassicostrata</i> (L. Pfeiffer, 1856)	WDM Siciliaria 1	1_1	MW758912	MW757114, MW757113	38°05'40.91"N, 12°40'10.98"E
	WDM Siciliaria 1	L_4	MW758924	no	38°05'40.91"N, 12°40'10.98"E
<i>Mauritanica scarificata</i> (L. Pfeiffer 1856)	WDM Siciliaria 2	2_1	MW758915	MW757112, MW757111	37°58'11.08"N, 12°03'59.36"E
	WDM Siciliaria 2	2_2	MW758916	no	37°58'11.08"N, 12°03'59.36"E
<i>Siciliaria calcarae calcarae</i> (Philippi 1844)	WDM Siciliaria 5	5_1	MW758925	MW757125, MW757126, MW757127	37°57'29.40"N, 12°57'33.64"E
<i>Suania nobilis nobilis</i> (L. Pfeiffer, 1848)	WDM Siciliaria 14	14_1	MW758875	MW757128, MW757129, MW757130	38°10'51.85"N, 12°43'37.70"E
<i>Siciliaria tiberii scalatensis</i> Beckmann, 2004	WDM Siciliaria 17	17_2	MW758923	MW757110, MW757109, MW757108	38°10'35.53"N, 13°07'27.22"E
<i>Suania nobilis nobilis</i> (L. Pfeiffer, 1848)	WDM Siciliaria 18	18_1	MW758918	MW757107, MW757106	38°10'30.07"N, 12°46'14.09"E
<i>Siciliaria tiberii tiberii</i> (A. Schmidt, 1868)	WDM Siciliaria 19	19_1	MW758919	MW757117, MW757116	38°08'19.06"N, 13°03'14.01"E
	WDM Siciliaria 19	19_2	MW758920	no	38°08'19.06"N, 13°03'14.01"E
<i>Siciliaria ferrox</i> (Brandt, 1961)	WDM Siciliaria 21	Sf_1	MW758922	MW757115	37°59'17.62"N, 13°36'51.11"E
	WDM Siciliaria 21	Sf_2	MW758917	no	37°59'17.62"N, 13°36'51.11"E
<i>Suania crassicostrata</i> (L. Pfeiffer, 1856)	WDM Siciliaria 33	33_1	MW758876	no	38°06'44.89"N, 12°40'34.27"E
<i>Sicilia crassicostrata</i> (L. Pfeiffer, 1856)	WDM Siciliaria 33	33_2	MW758877	MW757105, MW757104, MW757131, MW757103	38°06'44.89"N, 12°40'34.27"E
	WDM Siciliaria 34	34_1	MW758878	no	37°58'15.07"N, 13°12'2.23"E
<i>Sicilia calcarae jatinensis</i> ssp. nov.	WDM Siciliaria 34	34_2	MW758879	MW757118, MW757120, MW757119, MW757121	37°58'15.07"N, 13°12'2.23"E
	WDM Siciliaria 34	34_3	MW758926	no	37°58'15.07"N, 13°12'2.23"E
<i>Sicilia calcarae calcarae</i> (Liberto et al., 2016)	WDM Siciliaria 34	34_4	MW758927	no	37°58'15.07"N, 13°12'2.23"E
	WDM Siciliaria 36	36_1	MW758921	MW757132, MW757133	37°55'46.42"N, 13°23'5.22"E
<i>Sicilia tiberii alcamoensis</i> Brandt, 1961	WDM Siciliaria 37	37_1	MW758928	MW757102, MW757101	38°07'48.60"N, 13°08'26.94"E
<i>Sicilia tiberii armattensis</i> ssp. nov.	WDM Siciliaria 38	38_1	MW758880	MW757100, MW757099, MW757098	38°08'58.56"N, 13°09'25.83"E
	WDM Siciliaria 38	38_2	MW758881	no	38°08'58.56"N, 13°09'25.83"E
<i>Sicilia tiberii scalatensis</i> Beckmann, 2004	WDM Siciliaria 39	39_1	MW758882	MW757097, MW757096, MW757095	38°10'42.45"N, 13°07'34.50"E
	WDM Siciliaria 40	40_1	no	no	38°10'35.53"N, 13°07'27.22"E
<i>Sicilia grobmanniana addaure</i> ssp. nov.	WDM Sicilia 41	41_1	MW758883	MW757094, MW757093	38°11'13.01"N, 13°21'6.91"E
	WDM Sicilia 41	41_2	MW758884	no	38°11'13.01"N, 13°21'6.91"E
<i>Sicilia grobmanniana grobmanniana</i> (Rossmässler, 1836)	WDM Sicilia 41	41_3	MW758929	no	38°11'13.01"N, 13°21'6.91"E
	WDM Sicilia 42	42_1	MW758886	no	38°10'4.41"N, 13°21'2.60"E
<i>Sicilia leucophryna</i> (L. Pfeiffer, 1862)	WDM Sicilia 42	42_2	MW758887	MW757092, MW757091	38°10'4.41"N, 13°21'2.60"E
	WDM Sicilia 42	42_3	MW758885	no	38°10'4.41"N, 13°21'2.60"E
	WDM Sicilia 43	43_1	MW758888	no	38°12'1.32"N, 13°16'3.05"E

Taxon	Collection No.	Lab ID	GenBank Accession No.		Coordinates
			COI	ITS2	
<i>Sicilia calcarae bellieni</i> (Brandt, 1961)	WDM Sicilia 44	44_1	MW758889	MW757122, MW757123	38°00'54.80"N, 12°59'13.35"E
	WDM Sicilia 44	44_2	MW758913	no	38°00'54.80"N, 12°59'13.35"E
	WDM Sicilia 44	44_3	MW758930	no	38°00'54.80"N, 12°59'13.35"E
<i>Sicilia calcarae boegttensis</i> sp. nov.	WDM Sicilia 44	44_4	MW758931	no	38°00'54.80"N, 12°59'13.35"E
	WDM Sicilia 46	46_1	MW758890	MW757090, MW757089, MW757080	38°02'59.53"N, 13°08'58.55"E
	WDM Sicilia 46	46_2	MW758891	no	38°02'59.53"N, 13°08'58.55"E
	WDM Sicilia 46	46_3	MW758932	no	38°02'59.53"N, 13°08'58.55"E
	WDM Sicilia 47	47_1	MW758933	MW757079, MW757078	38°03'37.03"N, 13°12'38.53"E
<i>Sicilia calcarae orientis</i> sp. nov.	WDM Sicilia 47	47_2	MW758934	MW757088, MW757087, MW757077	38°03'37.03"N, 13°12'38.53"E
	WDM Sicilia 47	47_3	MW758935	no	38°03'37.03"N, 13°12'38.53"E
	WDM Sicilia 47	47_4	MW758936	no	38°03'37.03"N, 13°12'38.53"E
	WDM Sicilia 49	49_1	MW758892	no	38°04'0.52"N, 12°41'1.34"E
	WDM Sicilia 49	49_2	MW758893	no	38°04'0.52"N, 12°41'1.34"E
<i>Sicilia eminentis</i> (A. Schmidt, 1868)	WDM Sicilia 50	50_1	MW758894	MW757076, MW757075, MW757074, MW757073	38°04'6.38"N, 12°41'48.68"E
	WDM Sicilia 50	50_2	MW758895	no	38°04'6.38"N, 12°41'48.68"E
	WDM Sicilia 51	51_1	MW758896	MW757072	38°04'55.97"N, 12°40'9.91"E
	WDM Sicilia 51	51_2	MW758897	no	38°04'55.97"N, 12°40'9.91"E
	WDM Sicilia 52	52_1	MW758898	no	38°05'18.10"N, 12°40'17.18"E
<i>Sicilia calcarae bellieni</i> (Brandt, 1961)	WDM Sicilia 52	52_2	MW758899	MW757086, MW757071, MW757085	38°05'18.10"N, 12°40'17.18"E
	WDM Sicilia 54	54_1	MW758900	MW757134, MW757135, MW757136	38°00'22.47"N, 13°06'37.79"E
	WDM Sicilia 54	54_2	MW758901	no	38°00'22.47"N, 13°06'37.79"E
	WDM Sicilia 55	55_1	MW758902	MW757124	38°11'13.61"N, 13°16'44.68"E
	WDM Sicilia 55	55_2	MW758903	no	38°11'13.61"N, 13°16'44.68"E
<i>Sicilia septemlocata</i> (Philippi, 1836)	WDM Sicilia 56	56_1	MW758904	MW757137, MW757138	38°12'39.27"N, 13°17'21.26"E
	WDM Sicilia 57	57_1	MW758937	MW757070	38°13'5.61"N, 13°18'4.76"E
	WDM Sicilia 59	59_1	MW758905	MW757084, MW757069, MW757068	38°02'54.18"N, 12°48'26.61"E
	WDM Sicilia 60	60_1	MW758906	MW757067, MW757066, MW757139, MW757065	38°06'25.71"N, 12°44'33.37"E
	WDM Sicilia 60	60_2	MW758907	no	38°06'25.71"N, 12°44'33.37"E
<i>Sicilia calcarae calcarae</i> (Philippi 1844)	WDM Sicilia 60	60_4	MW758938	no	38°06'25.71"N, 12°44'33.37"E
	WDM Sicilia 60	60_5	MW758939	no	38°06'25.71"N, 12°44'33.37"E
	WDM Sicilia 61	61_1	MW758908	MW757140, MW757141	38°06'25.71"N, 12°44'33.37"E
	WDM Sicilia 61	61_2	MW758909	MW757142, MW757143, MW757144	38°06'25.71"N, 12°44'33.37"E
	WDM Sicilia 62	62_2	MW758914	no	38°08'48.81"N, 12°44'6.61"E
<i>Sicilia nobilis nobilis</i> (L. Pfeiffer, 1848)	WDM Sicilia 62	62_3	MW758940	no	38°08'48.81"N, 12°44'6.61"E

Taxon	Collection No.	Lab ID	GenBank Accession No.		Coordinates
			COI	ITS2	
<i>Sicaria nobilis spezialensis</i> (Nordsteck, 1984)	WDM Siciliaria 63	63_1	MW758910	MW757040, MW757039	38°07'41.78"N, 12°44'9.24"E
	WDM Siciliaria 63	63_2	MW758911	no	38°07'41.78"N, 12°44'9.24"E
<i>Charpentieria itula borinae</i> (Gredler, 1869)	WDM Charpentieria 3	C3_2	MW758954	no	45°50'23.18"N, 10°36'49.06"E
<i>Charpentieria stenizi cincta</i> (Brumati, 1838)	WDM Charpentieria 2	C2_2	MW758953	MW757050, MW757049	46°11'40.51"N, 12°38'14.26"E
<i>Charpentieria itula itula</i> (G. von Martens, 1824)	WDM Charpentieria 1	Cl_1	MW758952	no	45°24'22.30"N, 11°31'11.93"E
<i>Charpentieria stenizi letochanae</i> (Gredler, 1874)	WDM Charpentieria 19	C19_1	MW758957	no	46°36'27.42"N, 12°12'20.01"E
<i>Charpentieria itula baldensis</i> (Strobel, 1851)	WDM Charpentieria 20	C20_1	MW758955	no	45°44'25.95"N, 10°51'13.69"E
<i>Charpentieria epydon epydon</i> (S. Studer, 1820)	WDM Charpentieria 44	C44_1	MW758956	MW757052, MW757051	46°12'29.53"N, 8°12'46.18"E
	WDM Charpentieria 44	C44_3	MW758951	no	46°12'29.53"N, 8°12'46.18"E
<i>Gibbularia gibbula gibbula</i> (Rossmässler, 1836)	Nordsteck 12167	12167_1	MW758947	no	41°47'1.22"N, 15°26'39.92"E
	Nordsteck 12167	12167_2	MW758948	MW757057, MW757056, MW757055	41°47'1.22"N, 15°26'39.92"E
	WDM Gibbularia 64	G64_1	MW758958	MW757048, MW757083, MW757082	45°36'8.91"N, 13°46'0.72"E
	WDM Gibbularia 64	G64_2	MW758959	no	45°36'8.91"N, 13°46'0.72"E
<i>Mauritanica perinmi polygyna</i> (O. Boettger, 1879)	SME335011/1	SME	MW758966	MW757045, MW757044	36°22'2.45"N, 10°07'11.81"E
	Nordsteck 11786	11786_1	MW758941	MW757063, MW757062, MW757064	42°01'4.58"N, 12°54'19.30"E
	Nordsteck 11786	11786_2	MW758942	no	42°01'4.58"N, 12°54'19.30"E
<i>Papillifera solida solida</i> (Draparnaud, 1805)	Nordsteck 12100	12100_1	MW758944	no	40°40'1.62"N, 16°37'16.08"E
<i>Papillifera papillaris transitans</i> (Paulucci, 1878)	Nordsteck 12147	12147_1	MW758945	no	38°28'45.91"N, 16°27'48.05"E
	Nordsteck 12147	12147_2	MW758946	MW757059, MW757058	38°28'45.91"N, 16°27'48.05"E
<i>Papillifera papillaris affinis</i> (Philippi, 1836)	WDM Papillifera 2	P2_1	MW758960	no	37°58'2.36"N, 13°11'45.19"E
	WDM Papillifera 2	P2_2	MW758961	no	37°58'2.36"N, 13°11'45.19"E
	WDM Papillifera 3	P3_1	MW758962	MW757081, MW757047, MW757046	37°57'58.18"N, 12°58'9.06"E
	WDM Papillifera 4	P4_1	MW758963	no	37°57'58.18"N, 13°13'14.57"E
	Nordsteck 12194	12194_1	MW758949	MW757054, MW757053	40°40'31.60"N, 17°56'40.44"E
	Nordsteck 12194	12194_2	MW758950	no	40°40'31.60"N, 17°56'40.44"E
	Nordsteck 12068	12068_2	MW758943	MW757061, MW757060	39°17'2.08"N, 16°15'30.22"E
<i>Stigmatica vulcanica vulcanica</i> (Benoit, 1860)	WDM Stigmatica 11	St11_1	MW758965	no	39°07'58.01"N, 16°15'01.92"E
<i>Stigmatica kobeltiana</i> (Küster, 1876)	WDM Stigmatica 9	St9_2	MW758964	MW757042, MW757043, MW757041	39°46'18.23"N, 19°50'47.23"E
<i>Stigmatica pantocratoris pantocratoris</i> (O. Boettger, 1889)					

the western species distributed in a comparatively small area from San Vito Lo Capo Peninsula, Monte Cofano to Cornino-Custonaci area. Within the main clades, the various (generally highly supported) subclades are mostly consistent with taxa and reflect their distribution. Specimens from the same locality delivered very similar or identical sequences. Intraspecific distances (summarised in Table 3) within both *Siciliaria* and *Sicania* were moderately low mean distances up to 7.0% with the highest values found in *S. calcarae* (7.0%) and *S. grobmanniana* (5.1%). Besides the main clades I and II, the tree contains several quite distinct lineages representing other taxa [belonging to *Stigmatica*, *Charpentieria*, as well as *Gibbularia*, which are separated by high p distances from each other (mean distances ranging from 18.6–23.8%), as well as from clades I and II (18.3–23.1%). In this tree, the genera *Stigmatica* and *Gibbularia* are not monophyletic. *Charpentieria* forms one clade but the support values are very low. The relationships between the two main clades and the other genera remain unresolved and appear as a polytomy in the tree. The low resolution in the deeper nodes is not surprising given the high distances, as substitutional saturation might blur the relationships among lineages. The average p distance between the outgroup *Papillifera* and the ingroup sequences was 24.6% (range of means between groups 23.8–25.6%). Even within some genera remarkably high distances were found (up to 25.8% *Papillifera*, 22.6% *Charpentieria itala*, 18% *Charpentieria stenzii*), while distances within *Siciliaria* and *Sicania* were lower (mean p distance 13.4 and 11.4%, respectively) (see Table 2).

The ITS2 sequences were obtained from 42 individuals (Table 1) and comprised altogether 106 sequences (due to up to five cloned sequences per individual; see Materials and methods). The BI tree (Fig. 5) shows all sequence variants isolated from those individuals. The variation among ITS2 copies is due to the fact that for some individuals, more than one clone was sequenced (due to the genomic arrangement of the rRNA genes in repeats of clustered units, more than two alleles can be expected). Generally, small distances were found among ITS2 sequences, resulting in a low resolution in the ITS2 tree. Most branches did not obtain sufficient support, but the tree reflects to some extent the COI tree. The western taxa (corresponding to main clade II, *Sicania*) appear as separated group including no representatives of main clade I (*Siciliaria*).

Table 2. Mean genetic distances (p-distances in %) for the COI dataset between the genera and/or lineages analysed. Mean genetic distances within the genera *Siciliaria* and *Sicania* are in bold. *Gibbularia* 1 = *Gibbularia gibbula gibbula* from Apricena; *Gibbularia* 2 = *Gibbularia gibbula gibbula* from Muggia.

	1	2	3	4	5	6	7	8	9	10
1 <i>Siciliaria</i>	13.4									
2 <i>Sicania</i>	19.6	11.4								
3 <i>Mauritanica</i>	20.5	17.0								
4 <i>Stigmatica pantocratis</i>	21.5	18.3	17.1							
5 <i>Stigmatica vulcanica</i>	21.3	21.3	20.7	18.6						
6 <i>Stigmatica sturmii</i>	22.1	19.9	19.8	19.5	22.4					
7 <i>Charpentieria itala</i>	21.7	21.4	20.8	20.7	22.5	21.9				
8 <i>Charpentieria stenzi</i>	21.3	21.8	20.2	18.6	21.0	21.9	20.7			
9 <i>Gibbularia</i> 1	21.0	21.4	19.4	19.4	20.7	22.8	22.3	20.1		
10 <i>Gibbularia</i> 2	23.1	23.1	22.2	20.7	22.4	23.8	22.3	21.9	20.5	
11 <i>Papillifera</i>	24.5	24.5	24.0	24.1	25.7	23.9	25.6	24.4	23.8	25.3

One subgroup contains only *S. nobilis* and the other subgroup contains *S. crassicos-tata*, *S. eminens*, and a few sequences of *S. nobilis* (from San Vito). Various clones of *S. crassicos-tata* differed slightly and for the specimen 33, clones 2 and 3 appeared in a subclade separate from the remaining sequences of *S. crassicos-tata* (including those from the same individual). The taxa corresponding to main clade I are found within several mixed clades/haplogroups with no apparent taxonomic or geographic pattern. Sequences from specimens of the same population cluster together with low distances. Sequences of the other genera appear as various separate branches. *Stigmatica* and *Gib-bularia* are not monophyletic.

The tree based on the combined data set (COI plus ITS2; 45 individuals) is shown in Fig. 6. It has the same overall topology as the COI tree, but with high support of several nodes, but fewer individuals represented. The apparent sister group relationship between clades I and II received no considerable support and thus, the relationship between the two clades remains open. The species are monophyletic and most of them well supported. Concerning the other genera, it should be mentioned that this tree provides less information as the number of individuals is lower than in the COI tree. As in the COI tree, *C. stenzii* and *C. itala/dyodon* cluster, highly supported, but in the combined tree of this clade only *C. stenzi* and *C. dyodon* were included. *Mauritanica* (including the former *S. scarificata*) is highly supported as well.

Specimens from the same locality delivered very similar or identical sequences. Intraspecific distances (summarised in Table 3) within both clades I and II (i.e., *Sicili-aria* and *Sicania*) show moderately low mean distances, up to 7.0% with the highest values found in *S. calcarae* (7.0%) and *S. grohmanniana* (5.1%). With one exception, all species were highly supported in the COI tree and in the combined tree. Within *Siciliaria/Sicania* only *S. calcarae* was found in two subclades, which formed together with *Siciliaria leucophryna* an unresolved trichotomy within one clade. In some cases, subspecies formed slightly separated lineages (e.g., *Siciliaria tiberii tiberii*), while generally this was not the case.

Phylogeography: distribution and phylogeny of *Siciliaria/Sicania* with analysis of the sympatries among taxa

The taxa comprising the two main clades I (*Siciliaria*) and II (*Sicania*) cluster in a geographic pattern (maps in Fig. 1E, F). Most taxa show well defined and delimited

Table 3. Intra- and interspecific mean genetic distances (p-distances in %) among the main clades of *Siciliaria* and *Sicania* calculated from the COI sequences. Intraspecific mean distances are in bold.

	1	2	3	4	5	6	7	8
1 <i>Siciliaria calcarae</i>	7.0							
2 <i>Siciliaria leucophryna</i>	11.3	0.4						
3 <i>Siciliaria tiberii</i>	14.3	14.4	0.5					
4 <i>Siciliaria ferrox</i>	17.0	16.6	17.8	0.4				
5 <i>Siciliaria septemplicata / grohmanniana</i>	16.9	17.3	17.3	16.4	5.1			
6 <i>Sicania eminens</i>	20.8	21.3	20.8	20.8	19.7	2.8		
7 <i>Sicania crassicos-tata</i>	21.4	20.3	21.3	20.2	20.2	12.2	2.5	
8 <i>Sicania nobilis</i>	20.9	20.5	21.6	19.7	18.9	13.3	12.5	4.3

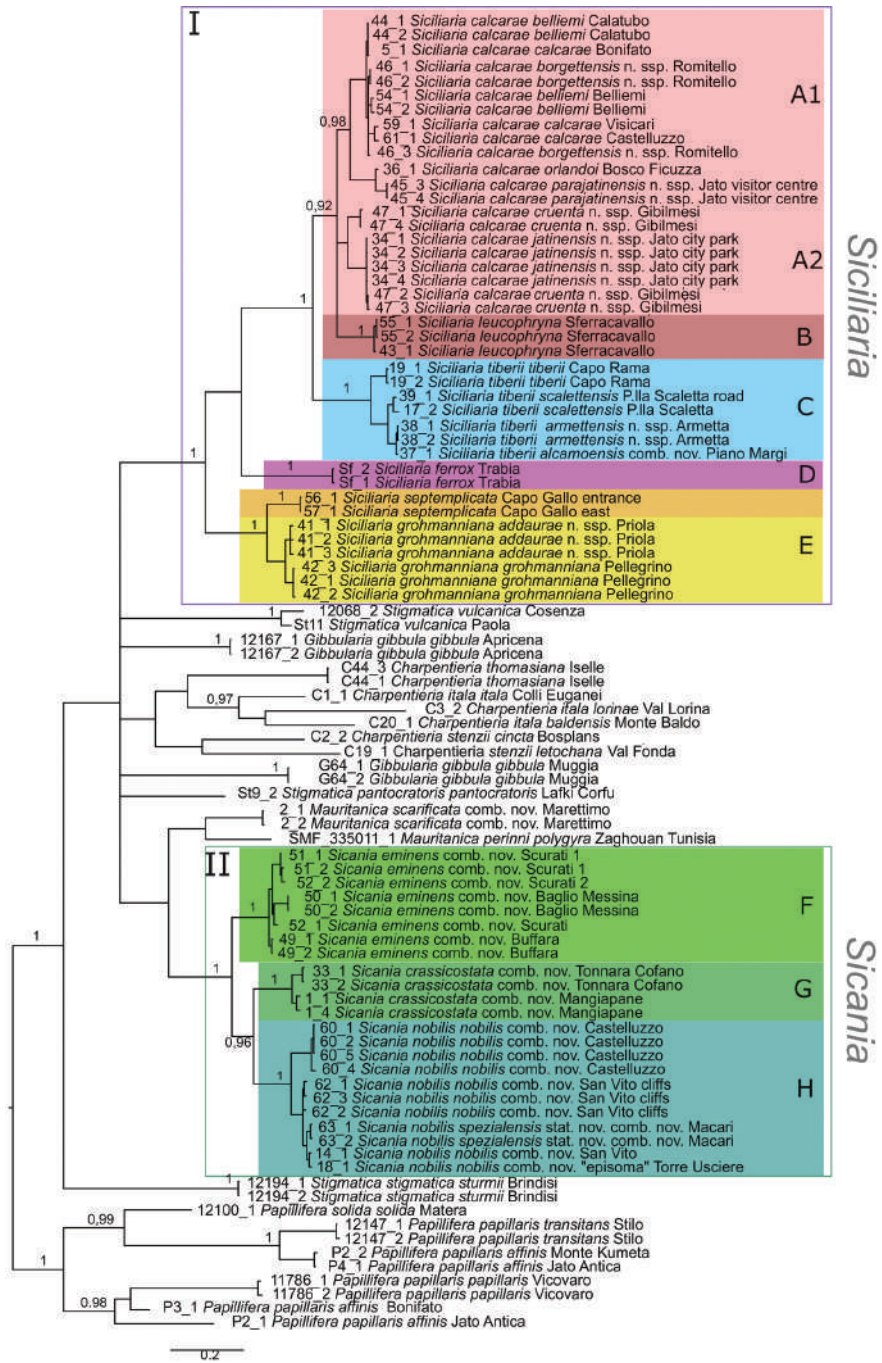


Figure 4. BI tree of based on the COI data set of *Siciliaria*, *Sicania* and related genera. BI posterior probability values (> 0.90) of major nodes are indicated.

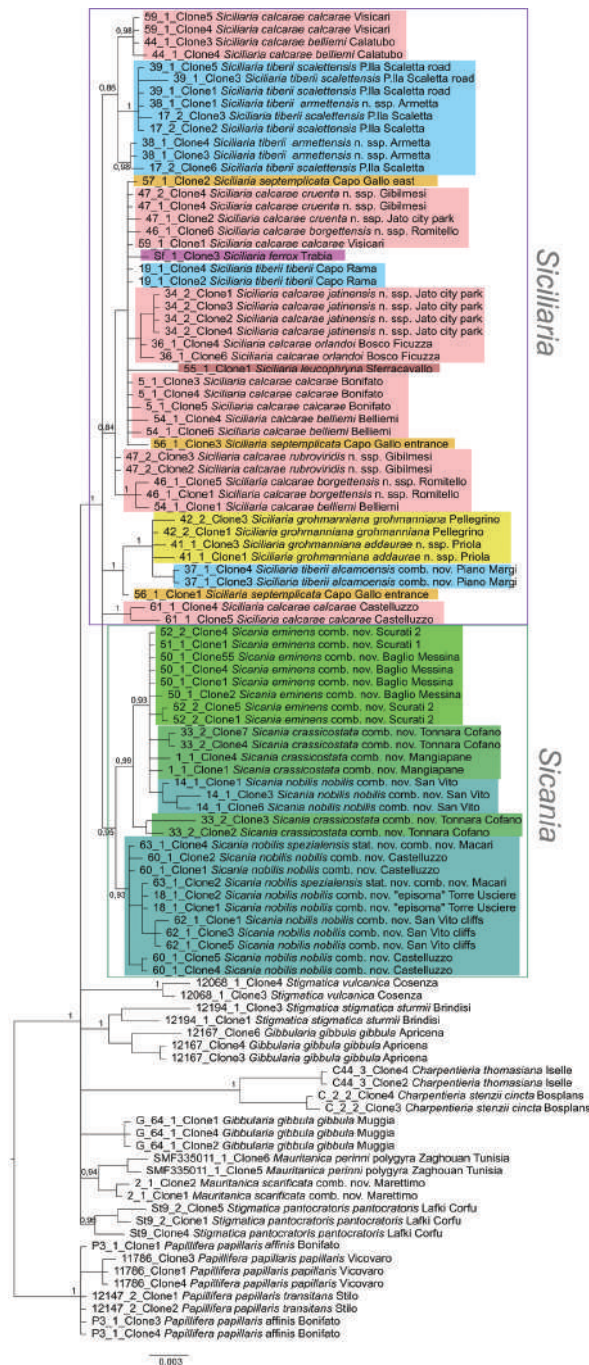


Figure 5. BI tree of based on the ITS2 data set of *Siciliaria*, *Sicania* and related genera. Colours of *Siciliaria* and *Sicania* clades correspond to those in the distribution maps (Figs 1E, F). BI posterior probability values (> 0.90) of major nodes are indicated.

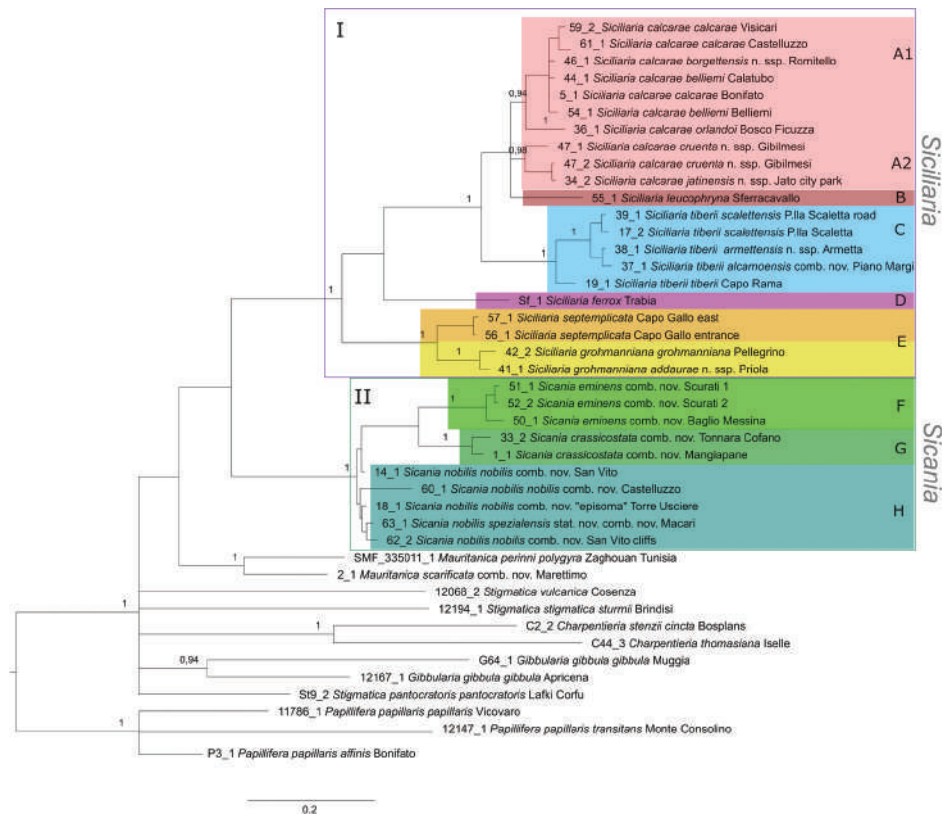


Figure 6. BI tree of based on the concatenated COI and ITS2 data set of *Siciliaria*, *Sicania* and related genera. Colours of *Siciliaria* and *Sicania* clades correspond to those in the distribution maps (Fig. 1 E, F). BI posterior probability values (> 0.90) of major nodes are indicated.

distributions, with some exceptions (of both *Siciliaria* and *Sicania*). The widely distributed *Siciliaria calcarae* has a partially overlapping distribution with either *Sicania n. nobilis* or *Sicania eminens*. Moreover, along the eastern part of the distribution area, the nominate subspecies of *Siciliaria calcarae* is locally replaced by other subspecies that differ by virtue of the costate shells or details of the clausiliar apparatus. The distribution records of *Sicania crassicosata* and *Sicania eminens* overlap in a small area near Contrada Scurati/Grotta Mangiapane, where the two species are, hardly distinguishable by their shell but show differences in the morphology of the genital organs and the genetic results (see *Sicania eminens* comb. nov.).

Siciliaria leucophryna shows a narrow distribution, limited to Isola delle Femmine, Pizzo Mollica, and Pizzo Manolfo. *Siciliaria tiberii* is restricted to the calcareous massif of Monte Palmeto, Pizzo di Mezzo, Monte Pecoraro and Montagna Longa and its northwestern coastline. *Siciliaria ferrox* occurs in the Trabia-S. Onofrio area. The closely related *Siciliaria grohmanniana* and *Siciliaria septemplicata* are in-

deed geographically close, the former occurring exclusively along the southern slopes of Monte Gallo and on Monte Pellegrino and the latter found along the northern slopes of Monte Gallo and scattered localities south of Palermo (Nordsieck 2013b). Syntopy seems to be very rare among *SiciliarialSicania* taxa. To our current knowledge, *Siciliaria calcarae* is sympatric with *Siciliaria septemPLICATA* (south and west of Palermo area), with *Siciliaria grohmanniana* (Monte Pellegrino), with *Sicania eminens* (Custonaci and Castellammare del Golfo Area) and with *Sicania nobilis* (San Vito lo Capo area). The sympatry of *Siciliaria calcarae* and *Sicania crassicosTATA* from Favignana Island seems to be due to antropochorous dispersal of the latter taxon. The southern part of the *SiciliarialSicania* distribution area so far seems to be occupied only by *Siciliaria calcarae* as also supported by the molecular genetic results. In one locality only (Castelluzzo) *Siciliaria calcarae* and *Sicania nobilis* were found together at the same spot: shady limestone walls in a *Quercus ilex* shrub. Nonetheless, a clear ecological niche separation of these two taxa syntopic at this locality was detected. The actual and detailed distribution ranges of the *Siciliaria* taxa still have to be clarified. Moreover, further field research must still verify undetermined or uncertain old literature citations, and thoroughly investigate a diverse and heterogenous territory with an amazing endemism rate.

Autecology: *Siciliaria* and *Sicania* taxa are not obligate rock-dwelling snails

SiciliarialSicania taxa show a remarkable adaptation and capability to colonise not only dry, open and exposed limestone walls and cliffs but also a huge variety of habitats and ecological niches. The most stenoecious species are, in order, *Sicania nobilis*, *Siciliaria ferrox*, and *Siciliaria septemPLICATA*, which are found exclusively on limestone walls or limestone boulders. *Sicania crassicosTATA* is found on limestone walls or under rocks. More euryoecious habits were recorded for *Siciliaria grohmanniana grohmanniana*, which is found on exposed limestone walls hiding in cracks and under crags. It is also found in *Pinus* sp. forest on decaying woods and tree trunks, including shady and humid spots on mosses and ferns. Interestingly, its subspecies *Siciliaria grohmanniana addaurae* ssp. nov. is found exclusively on limestone walls. *Siciliaria leucophryna* and *Sicania eminens* colonise limestone cliffs hiding in cracks or under stones. They are very common on isolated boulders and tree trunks and barks in the xerophilic scrub. The most euryoecious species is *Siciliaria calcarae*, which colonises all the habitats until now described but also is commonly found in anthropogenic environments as stone walls, road walls, ruins and disturbed habitats.

External morphology of the genital organs

The high number of *SiciliarialSicania* specimens dissected during this study (n = 120) provided an accurate overall description of the genital organs of these genera.

No seasonal variations were detected concerning shape or internal sculpturing of genital organs. The only clear distinction was between adult specimens with full-de-

veloped genital organs and immature, subadult specimens with extremely reduced, vestigial genital organs.

The general external morphology of the genital organs is the same in all taxa of *Siciliaria/Sicania*. The relative dimensions (ratio between the shell height and the length of the penial complex $H_3/PCL \times 100$) do not substantially differ among taxa, ranging from 25% to 35%, revealing a great dimension stability of genital organs in relationship to the shell dimensions. The genus *Montenegrina* (De Mattia et al. 2020) showed a higher variability, ranging from 13.9% to 87.6%. The overall appearance of the genital organs of *Siciliaria/Sicania* is always balanced [“mesomorphic” as defined in De Mattia et al. (2020)], without showing the extreme variability found in *Montenegrina* where extremely elongated and thin or short and bulky genital organs were found.

The hermaphroditic gland (HG) has many consolidated acini and it is found along the two apical whorls of the animal's body. The first hermaphroditic duct (FHD) is very thin along its proximal portion but abruptly turns into a highly coiled, skin-like structure. The diameter of the FHD is much larger along the coiled part, and the number of whorls ranges from six to eleven. The distal uncoiled part of the FHD is very thin, straight and ends directly in the fertilisation chamber-spermatheca complex. The albumen gland (AG) is slender. The general scheme of the FHD is stable among all the *Siciliaria* taxa. The AG is very variable in size compared to the ovispermiduct (OS). In full-grown adult specimens, it can be larger or as long as the OS or barely reaching $1/4$ of its length. The OS consists of a female and a male part including the seminal groove, which is not visible from outside. Externally, it is irregularly spaced by smooth constrictions and it is whitish to cream in colour. The male, prostatic part consists of the visible prostatic gland (PG) and the sperm groove (SG), light to dark grey in colour and clearly distinguishable from the lighter female part. The overall size of the OS is very stable among the *Siciliaria/Sicania* taxa. The free oviduct (FO) is usually thin and long and its length is stable in relation to the length of the vagina (V), and its average ratio (FO/V) is ~ 1 . The V is simple, usually cylindrical, without any appendix or caecum. The vaginal retractor (VR) is strong; it is always present and attached to the second duct of the bursa copulatrix (SDBC). It was not depicted in the anatomical drawing due to its low taxonomic value. The V is stable in length in relation both to shell height and penis length. The ratio between the length of the penial complex (PC) and the length of the V (PC/V) is also stable, ranging from two to three. The BC+SDBC complex (CBC) consists of the FDBC, a second duct (SDBC), a well-developed D (diverticulum) and the actual BC+SDBC. The D is always longer than the SDBC+BC. The transitional section between the BC and the SDBC can range from clearly visible to completely missing (with all degrees of transitional states). The PC comprises the penis (P) and the epiphallus (E). The transition between P and E does not always show the epiphallar thickening (ET), as stated in Nordsieck (2013b). More than 50% of the dissected specimens did not present the ET. The presence of the ET is not species-specific as it is randomly present or missing also in specimens of the same population of one given taxon. The flagellum is absent. The retractor muscle (RM) is single and undivided and usually strong. The P is usually uniformly cylindrical

or slightly swollen proximally, without caecum or penial appendix. The E is usually as long as the P. It can be cylindrical to thin and spindly. The transitional area between the E and the distal portion of the vas deferens (VD) is usually smooth or barely visible. The atrium (A) is usually large and short.

Internal morphology of the genital organs

In contrast to the external morphology of the genital organs, the internal sculpturing differs between the various taxa of *Siciliaria* and *Sicania*, but is stable within the taxa, with only minor population/individual variability. The penis shows the highest variability, which involves the combination (or the absence) of pleats arranged in a longitudinal, transversal, or oblique direction or creating irregular patterns. The epiphallus shows different types of sculpturing, with longitudinal pleats or without any structure. The internal transition between the epiphallus and the vas deferens is very clear due to the clear change of the sculpturing. The structure and the variability of the penial pseudopapilla and the morphology of the internal transition between penis and epiphallus will be discussed in detail in the following. The atrium can exhibit different configurations, from completely smooth to variable pleats. In contrast to what was found in *Montenegrina* (De Mattia et al. 2020), a large atrial fold has never been detected. The internal V shows few different configurations. Similar to the penis, its variability lies in the combination (or absence) of pleats arranged either in a longitudinal, transversal or oblique direction.

Two specimens were found with the spermatophore intact and embedded into the diverticulum of the bursa copulatrix complex or in the vagina and partially inside the first duct of the complex of the bursa copulatrix. The spermatophore of *Siciliaria calcarae calcarae* (Philippi, 1844) and *Mauritanica perinni polygyra* (O. Boettger, 1879) are described for the first time. The spermatophores are slender and slightly longer than the diverticulum. The overall shape is slightly to markedly bent. These preliminary observations revealed a difference between *Siciliaria* with both upper and lower keel and *Mauritanica* with only the upper keel.

All the genera *Siciliaria*, *Sicania*, *Mauritanica*, *Stigmatica*, *Gibbularia*, and *Papillifera* exhibit a pseudopapilla. The pseudopapilla (PP) is a “false” penial papilla, found at the transition between the penis and the epiphallus, slightly distally to the insertion of the retractor muscle. The pseudopapilla, conversely to the actual penial papilla [as in the genus *Montenegrina*, depicted in De Mattia et al. (2020)], originates from one side of the penial wall and totally lacks a penial channel. Its lumen is filled with loose spongy tissue (Fig. 3.6). The shape and dimensions of the pseudopapilla are extremely variable, from conical and blunt to elongated and cylindrical. Sometimes it is extremely reduced or totally missing. Presumably the absence of the pseudopapilla represents the apomorphic state. The base of the pseudopapilla can be simple, thus it directly originates from the penial wall. Otherwise, the pseudopapilla can originate from a fleshy structure emerging from the penial wall. This structure is circular, fleshy, ring-like, usually smooth and more or less robust. We name this genital structure “epiphall-

lar ring” (ER). The ER can be missing or up to three. When detectable from outside, the transition between penis and epiphallus presents a more or less sudden narrowing of the proximal penis, distally to the base of the retractor muscle and corresponding to the area where the pseudopapilla originates. The genital portion immediately distal to the narrowing could be seen as a thickening and could represent what Nordsieck (2013a) introduced as the ”epiphallar thickening“ (ET).

In *Siciliaria/Sicania* one to three strong epiphallar rings are always present (only one being the origin of the pseudopapilla). *Charpentieria* and *Stigmatica* present only one epiphallar ring which is the origin of the pseudopapilla. In *Gibbularia* the epiphallar ring was found only in *Gibbularia gibbula* cf. *sanctangeli* (Fig. 56.6). *Papillifera* never shows an epiphallar ring and the pseudopapilla is either isolated (thus directly originating from the wall) or directly originating from the distal end of one epiphallar longitudinal pleat.

In the Southern Alpine *Charpentieria* the genital investigations revealed two undescribed structures of the transition between P and E: in *C. dyodon* s. l. it is named “parapseudopapilla” (PPP) and in *C. stenzii* s. l. it is named “hemipapilla” (HP) and are described in the following sections. In order to describe and classify the huge variety of PP-ER-ELP combinations found in all the taxa, we created a pseudopapillar formula. This formula will be provided for each taxon and population dissected, in order to highlight the extreme variable situation of this part of the genital organs. In this formula the parentheses () mean direct connection (continuity/contiguity of anatomical traits), whereas the plus + means interruption of the anatomical continuity. For example, the formula 1ER(PP)+2ER(ELP) means that PP originates from the distal (first) ER and the proximal ER (second ER) is directly connected with the ELP.

Diagnoses of the shell and distal genital organs of the genera *Siciliaria* and *Sicania*

Shell. Shell elongated, fusiform, sinistral, can be either decollate or non-decollate, with or without well-developed white surface layer. Apex subacute when present, whitish to dark brick red in colour. Protoconch smooth. Spire slowly and regularly growing with 9.5–11.5 whorls. Umbilicus closed, sutures shallow. Aperture subovoid to subquad-rangular. Peristome continues to be interrupted. Average shell height 19.9 ± 2.1 mm ($n = 630$, decollate and not decollate shells), average last whorl width 4.5 ± 0.4 mm ($n = 630$), average aperture height 4.6 ± 0.5 mm ($n = 630$), average aperture width 2.9 ± 0.4 mm ($n = 630$). Whorls weakly rib-striated, rib-striated, ribbed to percostate without or with evident to barely recognisable sutural papillae. Dorsal keel missing, mostly indistinct to prominent. Lunella always present, dorsal to dorso-lateral, more or less developed. Inferior lamella low, moderately high, high to very high. Missing, one or two anterior upper palatal plica; when two are present: upper one mostly separated from upper palatal plica; when one is present: separated from or connected with upper posterior palatal plica. Rarely, lower anterior upper palatal plica is present, separated from or connected with upper palatal plica. ALPP tending to be shortened to almost missing. Spiralis overlapping or not overlapping parietalis. Posterior lower palatal plica

missing more or less reduced. Palatal edge of clausilium plate distally receding, slightly or not receding. Clausilium palatal edge against distal end not bent upwards, or bent upwards to strongly bent upwards.

External distal part of the genital organs. Free oviduct slightly shorter to remarkably longer than the vagina. Vas deferens thin. First duct of the bursa copulatrix slightly shorter to much longer than second duct of bursa copulatrix + the actual bursa. Distinction between the actual bursa and second duct of bursa copulatrix clear to missing. Diverticulum of the bursa copulatrix longer to much longer than the vagina and second duct of bursa copulatrix + the actual bursa. The vagina is long or short and the atrium usually large. Penial complex always longer to much longer than the vagina. Retractor muscle short to long, usually robust. Epiphallar thickening present or missing. Epiphallus slightly shorter to much longer than the penis. Transition between epiphallus and vas deferens clearly visible to totally indistinguishable.

Internal distal part of the genital organs. Vagina and penis with internal sculpturing 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 pattern. Atrium simple or pleated. Pseudopapilla originating from epiphallar wall or epiphallar ring, elongated to roundish, with smooth or coarse surface. Epiphallar rings up to three to completely missing. Proximal epiphallar ring connected or not with the epiphallar pleats. Epiphallus with or without longitudinal pleats, both smooth or fringed. Epiphallar walls almost smooth, finely granulated or with small transverse papillae.

General discussion

The alpha-taxonomy of *Siciliaria/Sicania* was based on shell morphology. However, the variability of the shell characters reflects the complicate nomenclatural history (Nordsieck 2013b). After a brief general discussion, the Taxonomic part will provide in-depth discussion of the results regarding taxonomy and taxonomic decisions.

The external shape of the genital organs was found to be of low taxonomic value, because no particular configuration is exclusive and distinctive of one taxon or a group of taxa. On the other side, the internal sculpturing is highly variable, but stable at the population level and the morphology of the genital organs delimits (sub)species, similar to what was found in the genus *Montenegrina* (De Mattia et al. 2020). Different (sub)species can share a similar morphology of one or more sections of the genital organs (atrium, penis, epiphallus, penial papilla, distal vagina, proximal vagina), but no taxon, both at specific and subspecific level, was found to show an identical overall anatomical arrangement with another one. Even closely related taxa differ in their anatomy of the genital organs (e.g., *Siciliaria calcarae* complex). Isolation plus time (i.e., drift + microenvironmental conditions) may be the “engine” of morphological diversification (anatomy of the genital organs, shell) in *Siciliaria* and *Sicania* (and also in related genera, e.g., *Stigmatica* and *Charpentieria*). Furthermore, preliminary results indicated that even in *Papillifera*, the morphology of the genital organs, which was thought to

be “stable”, shows a much higher diversity (see Fig. 65). Nevertheless, homoplasies in parts of the anatomy of the genital organs may be expected. It is worth stressing that despite the high anatomical variability found, no diagnostic traits of the external or internal genital organs were found distinguishing *Siciliaria* from *Sicania*. Furthermore, our anatomical investigation proved that morphological characters proposed by Nordsieck (2013a: 4), to differentiate *Siciliaria* (sensu MolluscaBase 2021) from other genus-groups (*Charpentieria*, *Stigmatica*, *Gibbularia*, and *Papillifera*), namely the presence/absence of the ET and the delimitation of the proximal part of the penis (may it be “distinct” or “indistinct”) revealed to be not valid. Character combinations, both external and internal, were not found exclusively in any given (sub)genus.

Nordsieck (2013b) proposed *Mauritanica* as a subgenus of *Siciliaria* Vest, 1867 based on the preliminary molecular data of Scheel and Hausdorf (2012) and Uit de Weerd and Gittenberger (2013) and on some common morphological characters of the genital organs, such as the presence of a thickening in the passage (ET) from the penis to the epiphallus (missing in *Charpentieria*) and for an indistinct delimitation between proximal and distal penis (distinct in *Charpentieria*). Our genital investigations did not confirm the observations of Nordsieck, namely that the epiphallar thickening (ET) is always missing in *Charpentieria* and always present in *Siciliaria*. The external shape of the transition between penis and epiphallus is highly variable in *Siciliaria/Sicania* and *Charpentieria*, in taxa of both genera the ET may be present or missing. The characters presented by Nordsieck as the “indistinct delimitation between proximal and distal penis (distinct in *Charpentieria*)” was also not verified in the present genital investigations, which is probably due to the lower sample size analysed by Nordsieck (1963a; 1963b).

Species delimitation in *Siciliaria* and *Sicania*

The principal rationale of our integrative strategy was whether phylogenetic relationships confirm morphogroups found in a specific area and whether or not they correspond with current taxonomy. We deliberately refrained from applying automated species delimitation methods, for which larger sample sizes would have been necessary. Furthermore, in various land snail species as it was shown such methods may deliver discordant results (e.g., Prevot et al. 2013; Modica et al. 2016; Batomalaque et al. 2019; Mason et al. 2020a), there may be a lot of factors hampering straightforward delimitation solely based on genetic clades and the concept of the DNA barcoding gap (Meier et al. 2008). First, intra specific distances were found to vary considerably among various land snail species and are sometimes higher than commonly reported interspecific distances (Davison et al. 2009). Further examples for high intraspecific distances are the clausiliid genera *Montenegrina* (Mason et al. 2020a) and *Clausilia* (Mason et al. 2020b), the genus *Schileykula* (Harl et al. 2019) and the genetically highly diverse hairy snail *Trochulus hispidus* where even budding speciation was observed (Kruckenhauser et al. 2011).

So far, mostly mitochondrial marker sequences were used successfully in phylogenetic studies of land snails. The quite frequently used nuclear encoded histone genes H3 and H4 (including the spacer region in-between) often did not add much informa-

tion or even resulted in confusing trees, probably due to multiple paralogous copies of these genes that escaped homogenisation and/or recombination events after hybridisation (e.g., Harl et al. 2019; Mason et al. 2020a). Indication for interspecific hybridisation, even (at least sporadically) over wide phylogenetic distances were reported for several species, e.g., in the clausiliid genus *Montenegrina* (Mason et al. 2020a). Further examples were found e.g., in the bradybaenid land snail genera *Ainohelix* and *Ezohelix* (Morii et al. 2015) or the orculid genus *Schileykula* (Harl et al. 2019). Likewise, the internal transcribed spacer ITS2 used in the present study did not yield a well resolved tree and showed too low variation to unambiguously elucidate the phylogenetic relationships within *Siciliaria* and *Sicania*. Anyhow, several mt lineages were confirmed in the ITS2 tree. The ITS2 marker sequence showed some problems caused by paralogous copies as indicated by the various positions the sequences from single individuals took in the tree. Based on the presently available data it cannot be decided whether this is solely due to incomplete lineage sorting. Intraspecific hybridisation would result in similar patterns and there are some cases where this explanation appears likely (e.g., *alcamoensis*; see Taxonomic part).

In summary, in the COI tree the species were monophyletic except the widely distributed *S. calcarae*. Clustering of subspecies is mentioned in the taxonomic part, albeit this aspect is of minor relevance, (1) because subspecies would not necessarily be expected to be monophyletic and (2) because they were represented by too small samples.

Unidentified taxa, enigmatic species and the hybridisation concept within *Siciliaria* and *Sicania*

Potiez and Michaud (1838: 181–182) introduced *Clausilia decollata* and *Clausilia deshayesii* with a broad distribution indication: "Hab. La Sicilie". These names probably belong to *Siciliaria/Sicania*, but their specific status was not yet clarified. Benoit (1876: 151; 1881: 106) mentioned *Clausilia deshayesii*, providing a precise distribution ("vive nelle campagne di Palermo; l'abbiamo pure ricevuta dai dintorni di Prizzi"). As synonyms, Benoit (1876) listed *Clausilia calcarae*, *Clausilia assimilis* (= ?) and *Clausilia castanea* (= ?) and Benoit (1881) listed *Clausilia calcarae*, *Clausilia septemPLICATA* and *Clausilia castanea* (= ?) thus, as already suggested by Nordsieck (2020: 6) this name could be regarded as a junior synonym of *Siciliaria calcarae* or *Siciliaria septemPLICATA*. As a matter of fact, both taxa are known to occur in the surroundings of Palermo. On the other hand, Prizzi is currently considered remarkably outside of the known distribution of *Siciliaria/Sicania*, and further research in this area is needed in order to clearly assess the identity of this name. Its synonymy with *Clausilia calcarae* and *Clausilia septemPLICATA* can only be speculated until additional data are available. Benoit (1876, 1881) introduced three taxa that currently are unidentified. The first is *Clausilia trina-crina* (Benoit 1876: 151) or also cited as *Clausilia trinaclina* (Benoit 1881: 105), erroneously cited by Nordsieck (2013b: 4) as *C. trinacliana* that he arbitrarily considered as a misprint of *trinacriana*. The distribution of this taxon (Benoit 1881: 106) is the area surrounding Palermo and Calatafimi. De Stefani (1895: 186) cited the species with

its proper name, which is *Clausilia trinacrina*, as he received the correct name spelling directly from Benoit: “nel detto catalogo (Benoit 1881) Benoit la chiama *trinaclina*, ciò per errore di stampa come risulta dalla correzione a penna fatta da lui stessa nella copia donatami”. Moreover, De Stefani (1895: 187) provided a precise locality for the species: Monte Cuccio near Palermo. The differential diagnosis provided by Benoit and Boettger’s opinion (Boettger 1881: 106) makes the synonymy with *Siciliaria calcare* very plausible. Benoit (1876: 151) cited *Clausilia panormitana* from Monte Cuccio, east of Palermo as a synonym of *Siciliaria grohmanniana*. Our field research confirmed that *Siciliaria grohmanniana* is not present on Monte Cuccio and its surrounding peaks. For *Clausilia trinacrina*, the synonymy with *Siciliaria calcare* is very plausible.

Finally, Benoit (1876: 152) cited *Clausilia laudabilis* from San Fratello. This locality is probably an old toponym from the surroundings of Bagheria (Palermo) as San Fratello near Messina is totally out of the distribution range of *Siciliaria/Sicania*. *Clausilia laudabilis* is considered by Nordsieck (2013b: 7) as a synonym of *Siciliaria leucophryna* despite the locality provided by Benoit doesn’t match with the current known distribution of this species. Thus, both the exact position of the locality and the identity of *Clausilia laudabilis* remain to be assessed.

Benoit (1881: 117) introduced also *Clausilia rubra* from San Fratello, and San Fratello near Messina cannot be excluded in this case. *Clausilia rubra* Benoit, 1881 could be referred to *Stigmatica incerta* (Küster, 1861), which is known to occur from the area (WDM personal data). Despite Boettger’s opinion that considered *Clausilia rubra* as a form of *Siciliaria septemplicata*, Benoit (1881: 117) disagreed with his opinion, by virtue of a differential diagnosis that highlights important differences. The given locality is found remarkably outside of the currently known distribution of both, *Siciliaria* and *Sicania* (Nordsieck 2013b: 2). More field and taxonomical research are needed in order to properly assess the status of this species and, at the moment, no synonymy is conceivable.

Clausilia subdiaphana was introduced by Benoit (1881: 118), who stated that this taxon is conchologically similar to *Siciliaria grohmanniana* but differs by a different arrangement of the lamelle and plicae and by a very fragile, not decollate shell. The collecting locality is “montagna Buon Riposo presso Palermo”. This old toponym is currently almost forgotten, but Scinà (1818: 51, 57) identified this hill at the western foot of Monte Cuccio, east of Palermo. Yet, the lithological substratum of that hill and its surroundings is composed by quartzite, gres, and sandstones, thus an unusual habitat for *Siciliaria/Sicania*. The fragile shell could represent an adaptation to a soil extremely poor in limestone contents. Monterosato (1894: 170) assumed the snails from Monte Pellegrino to be “Var. ex forma: *subdiaphana*, Ben.”, a variety of *Siciliaria grohmanniana*. Monterosato neither justified the synonymy, nor stated that he actually found Benoit’s taxon at Monte Pellegrino. At the moment, no synonymy is conceivable.

The status of *Siciliaria riberothi*, introduced by Brandt (1961: 8 as *Siciliaria leucophryna riberothi*) was thoroughly discussed by Nordsieck (2013b: 14). The taxon is based on a specimen provided by Monterosato labelled as *Clausilia riberothi*, collected from a valley north of Ribera (Agrigento) (currently outside of the known distribution

of *Siciliaria* and *Sicania*), housed at the Senckenberg Natural History Museum (SMF 163947). This specimen was depicted by Brandt (1961: 20–21). Brandt (1961: 8), as additional material, listed a "Paratypoid" from his own collection (Cl. 2518/5) but the origin of this sample(s) is not specified. Probably, the collecting data provided by Monterosato on the original label was wrong as was also stated by Beckmann (2004: 188) after a field survey.

Nordsieck (2013b: 5) depicted another specimen from Monterosato's collection, labelled as *Clausilia remota* (SMF 232084) collected by Monterosato from an unidentified locality, namely Monte della "Terrazza" or "Torrazza". As stated by Beckmann (2004: 188), it is unlikely that this locality is Torrazza, east of San Vito lo Capo as from this locality only *Siciliaria calcarae* and *Siciliaria nobilis* were found. Considering the overall shell shape, the prominent dorsal keel and the arrangement of the plicae and lamellae (AUPP and ALPP developed and visible from the frontal view of the mouth), both *Siciliaria riberothi* and Monterosato's samples from Monte della "Terrazza" or "Torrazza" could be provisionally referred to *Siciliaria tiberii* ssp.

The concept of interspecies hybridisation (or geographic forms) introduced by Nordsieck (Nordsieck 2007: 99–101; 2013b: 10) refers to populations that share certain shell characters and have to some extent overlapping distribution [such as *calcarae-septemPLICATA* (e.g., Parco, south of Palermo; Sagana near Borghetto), *septemPLICATA-grohmanniana* (Punta Priola), *tiberii-calcarae* (Monte della Fiera), *leucophryna-calcarae* (Sferracavallo), *crassicosata-eminens* (Monte Cofano) etc]. When available, such populations were analysed anatomically and genetically in the present study. Hybridisation and gene flow proved to provide no suitable explanation for sharing common shell characters. The results did not support close relationships or hybridisation between these taxon pairs. The "hybridisation" cases will be discussed taxon by taxon in the taxonomic part.

Taxonomic part

The list of the examined specimens of *Siciliaria* and *Sicania* is depicted in Table 4.

We isolated and depicted the clausiliar plates in order to verify the morphology described by Boettger (1877) for the two clausiliar types. The results are displayed in Table 5. Unexpectedly and in contrast to Boettger (1877), the "deep gutter-shaped" clausiliar plate, deemed by Boettger as being exclusive to the "Gruppe der *crassicosata*", was found to be present only in few taxa of the "Gruppe der *septemPLICATA*", namely *Siciliaria grohmanniana* s. l., *Siciliaria septemPLICATA* and *Siciliaria calcarae orlandoi* (see Table 5) but not present in any representative of the "Gruppe of *crassicosata*". Despite this inconsistency, the "Gruppe of *crassicosata*" showed a stable structure of the clausiliar plate, which is, for all the taxa, distally not receding, not gutter-like and distally not bent upwards. The "Gruppe der *septemPLICATA*" presents a variable situation, with the taxa that present a combination of the three characters states. The genera *Siciliaria* and *Sicania* cannot be distinguished by any

Table 4. *Siciliaria/Sicania* taxa examined (anatomy and/or molecular genetic data) with description of the variable penis-epiphallus transition: epiphallar formula. DNA = molecular genetic data available (Yes/No).

Taxon	Locality	DNA	Epiphallar formula
<i>Siciliaria grobmanniana grobmanniana</i> (Rossmässler, 1836)	Italy, Sicily, Palermo, Monte Pellegrino, N side of the top plateau, 380 m asl, 38°10'55.26"N, 13°21'1.66"E, leg. W. De Mattia and J. Macor leg.	Y	1ER(PP+ELP)
	Italy, Sicily, Palermo, Monte Pellegrino, Santuario Santa Rosalia, 420 m asl, 38°10'4.41"N, 13°21'2.60"E, leg. W. De Mattia and J. Macor leg.	Y	1ER(PP+ELP)
<i>Siciliaria grobmanniana addaurae</i> ssp. nov. De Mattia, Reier & Haring	Italy, Sicily, Palermo, N side of Monte Pellegrino, Punta Priola, Grotte dell'Addaura, 115 m asl, 38°11'13.01"N, 13°21'6.91"E, W. De Mattia and J. Macor leg.	Y	1ER(PP)+ELP
<i>Siciliaria septemplicata</i> (Philippi, 1836)	Italy, Sicily, Palermo, N side of Monte Gallo near Sferracavallo, 40 m asl, 38°12'39.27"N, 13°17'21.26"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP+ELP)
	Italy, Sicily, Palermo, E side of Monte Gallo, 140 m asl, 38°13'5.61"N, 13°18'4.76"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP+ELP)
<i>Siciliaria leucophryna</i> (L. Pfeiffer, 1862)	Italy, Sicily, Palermo, Grotta Conza, 150 m asl, 38°11'13.61"N, 13°16'44.68"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP+ELP)
	Italy, Sicily, Palermo, Sferracavallo, via Plauto, 50 m asl, 38°11'13.01"N, 13°21'6.91"E, W. De Mattia and J. Macor leg.	Y	1ER(PP)+ELP
<i>Siciliaria calcarae calcarae</i> (Philippi, 1844)	Italy, Sicily, Alcamo, Monte Bonifato, top of the mountain, 640 m asl, 37°57'29.40"N, 12°57'33.64"E, A. Margelli leg.	N	1ER(PP)+ELP
	Italy, Sicily, Alcamo, Monte Bonifato, top of the mountain, 640 m asl, 37°57'29.40"N, 12°57'33.64"E, I. Niero leg.	Y	1ER(PP)+ELP
	Italy, Sicily, Alcamo, Monte Bonifato, west side of the mountain, over the quarry, 550 m asl, 37°57'16.92"N, 12°58'9.06"E, W. De Mattia and J. Macor leg.	N	1ER(PP)+ELP
	Italy, Sicily, Piana degli Albanesi, 500 m south of Portella Ginestra, northern cliffs of Monte Kumeta, 970 m asl, 37°58'13.35"N, 13°15'22.06"E, W. De Mattia and J. Macor leg.	N	1ER(PP)+2ER(ELP)
	Italy, Sicily, Castellammare del Golfo, Castello di Baida, W of the town along the road to Visicari, 300 m asl, 38°02'41.64"N, 12°48'14.34"E, W. De Mattia and J. Macor leg.	N	1ER(PP)+2ER(ELP)
	Italy, Sicily, San Vito lo Capo, Castelluzzo, west cliffs E of town, 120 m asl, 38°06'25.71"N, 12°44'33.37"E, W. De Mattia and J. Macor leg.	Y	1ER(PP)+ELP
	Italy, Sicily, Castellammare del Golfo, Visicari, 395 m asl, 38°02'54.18"N, 12°48'26.61"E, W. De Mattia and J. Macor leg.	Y	1ER(PP)+ELP
<i>Siciliaria calcarae calcarae</i> (Philippi, 1844) (= <i>adelina</i> Küster, 1847)	Italy, Sicily, Calatafimi, Castello Eufemio, 395 m asl, 37°57'45.67"N, 12°51'21.13"E, W. De Mattia and J. Macor leg.	N	1ER+2ER(PP)+ELP
<i>Siciliaria calcarae belliemi</i> (Brandt, 1961)	Italy, Sicily, Partinico, W side of the Mount Belliemi, 440 m asl, 38°00'22.47"N, 13°06'37.79"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP)+ELP
	Italy, Sicily, Alcamo, E side of the Calatubo Castle, 75 m asl, 38°00'54.80"N, 12°59'13.35"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP+ELP)
<i>Siciliaria calcarae borgettensis</i> ssp. nov. De Mattia, Reier & Haring	Italy, Sicily, Municipality of Borghetto, road to Romitello, 400 m asl, 38°02'59.53"N, 13°08'58.55"E, W. De Mattia and J. Macor leg.	Y	1ER(PP)+ELP
	Italy, Sicily, San Giuseppe Jato, quarry E of the town, 630 m asl, 37°58'15.07"N, 13°12'2.23"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP+ELP)
<i>Siciliaria calcarae parajatinensis</i> ssp. nov. De Mattia, Reier & Haring	Italy, Sicily, Monreale, W part of Monte Kumeta toward Jato Antica, 630 m asl, 37°57'8.18"N, 13°13'14.57"E, W. De Mattia and J. Macor leg.,	Y	1ER+2ER(PP+ELP)
<i>Siciliaria calcarae orlandoi</i> Liberto, Reitano, Giglio, Colomba & Sparacio, 2016	Italy, Sicily, Monreale, Bosco Ficuzza, Ponte Arcere, 470 m asl, 37°55'46.42"N, 13°23'5.22"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP+ELP)
<i>Siciliaria calcarae cruenta</i> ssp. nov. De Mattia, Reier & Haring	Italy, Sicily, Monreale, N side of Monte Gibilmesì, 890 m asl, 38°03'37.03"N, 13°12'38.53"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP)+ELP

Taxon	Locality	DNA	Epiphallar formula
<i>Siciliaria ferox</i> Brandt, 1961	Italy, Sicily, Trabia, Contrada Sant'Onofrio, 170 m asl, 37°59'17.62"N, 13°36'51.11"E, W. De Mattia and J. Macor leg.	Y	?ER+PP(ELP)
<i>Siciliaria tiberi tiberi</i> (A. Schmidt, 1868)	Italy, Sicily, Terrasini, Capo Rama, 30 m asl, 38°08'19.06"N, 13°03'14.01"E, W. De Mattia and J. Macor leg.	Y	ER+PP(ELP)
<i>Siciliaria tiberii alcamoensis</i> Brandt, 1961 comb. nov.	Italy, Sicily, Cinisi, Piano Margi, 670 m asl, 38°08'58.56"N, 13°09'25.83"E, W. De Mattia and J. Macor leg.	Y	1ER(PP+ELP)
<i>Siciliaria tiberii armettensis</i> ssp. nov. De Mattia, Reier and Haring	Italy, Sicily, Carini, Grotta dei Puntali o dell'Armetta, 90 m asl, 38°08'58.56"N, 13°09'25.83"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER+3ER(PP+ELP)
<i>Siciliaria tiberii scalettensis</i> Beckmann, 2004	Italy, Sicily, Cinisi, Portella Scaletta [locus typicus], 90 m asl, 38°10'35.53"N, 13°07'27.22"E, W. De Mattia and J. Macor leg.	Y	1ER+PP(ELP)
	Italy, Sicily, Cinisi, along the SS113 road from Villagrazia di Carini to Cinisi, 70 m asl, 38°10'42.45"N, 13°07'34.50"E, W. De Mattia and J. Macor leg.	Y	1ER+PP(ELP)
<i>Sicania crasscostata</i> (Pfeiffer, 1856)	Italy, Sicily, Castelluzzo, cliffs W of the Tonnara di Monte Cofano, 50 m asl, 38°6'44.89"N, 12°40'34.27"E, W. De Mattia and J. Macor leg.	Y	1ER+PP(ELP)
	Italy, Sicily, Custonaci, cliffs N of the Mangiapane cave, 63 m asl, 38°05'40.91"N, 12°40'10.98"E, W. De Mattia and J. Macor leg.	Y	1ER(PP)+ELP
<i>Sicania eminens</i> (A. Schmidt, 1868), comb. nov.	Italy, Sicily, Custonaci, Baglio Messina, 340 m asl, 38°4'06.38"N, 12°41'48.68"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP+ELP)
	Italy, Sicily, Custonaci, Buffara, NE side of the hollow, 150 m asl, 38°04'0.52"N, 12°41'1.34"E, W. De Mattia and J. Macor leg.	Y	1ER(PP)+ELP
	Italy, Sicily, Custonaci, contrada Scurati, crossing with Strada Provinciale 18, 65 m asl, 38°04'56.04"N, 12°40'9.86"E, W. De Mattia and J. Macor leg.	Y	1ER(PP)+2ER(ELP)
	Italy, Sicily, Custonaci, contrada Scurati, 60 m asl, 38°05'18.10"N, 12°40'17.18"E, W. De Mattia and J. Macor leg.	Y	1ER(PP)+2ER(ELP)
	Italy, Sicily, Custonaci, contrada Scurati, limestone cliffs S of the village, 60 m asl, 38°06'44.89"N, 12°40'34.27"E, W. De Mattia and J. Macor leg.	Y	1ER(PP)+2ER(ELP)
<i>Sicania nobilis nobilis</i> (L. Pfeiffer, 1848), comb. nov.	Italy, Sicily, Castelluzzo, Monte Cofano E of Tonnara di Monte Cofano, 80 m asl, 38°06'22.04"N, 12°40'59.77"E, W. De Mattia and J. Macor leg.	N	1ER+2ER+3ER(PP+ELP)
	Italy, Sicily, San Vito lo Capo, boulders W of the town, 50 m asl, 38°10'51.85"N12°43'37.70"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER+3ER(PP+ELP)
	Italy, Sicily, San Vito lo Capo, Castelluzzo, west cliffs E of town, 120 m asl, 38°06'25.71"N, 12°44'33.37"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP)+ELP
	Italy, Sicily, San Vito lo Capo, cliffs S of "El-Bahira" camping, 60 m asl, 38°08'48.81"N12°44'06.61"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP)+ELP
<i>Sicania nobilis nobilis</i> (L. Pfeiffer, 1848), comb. nov. (= <i>episoma</i> Brandt, 1961)	Italy, Sicily, San Vito lo Capo, Torre delle Usciore, 5 m asl, 38°10'30.07"N, 12°46'14.09"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER+3ER(PP+ELP)
<i>Sicania nobilis spezialensis</i> (Nordsieck 1984), stat. nov., comb. nov.	Italy, Sicily, San Vito Lo Capo, Macari, E side of Monte Speciale, 75 m asl, 38°07'41.78"N, 12°44'09.24"E, W. De Mattia and J. Macor leg.	Y	1ER+2ER(PP+ELP)

shell or genital character. No morphological character of the shell (surface, shape, decollation or dimensions), of the clausiliar apparatus and of the external/internal shape and sculpturing of the genital organs was found that is exclusively present in one genus. The main differences in shell and genital organs between *Siciliaria* and *Sicania* are listed in Table 6.

Table 5. Distribution of the clausilium character states within the *Siciliaria/Sicania* taxa. n = number of specimens analysed.

Taxon	n	Boettger's groups: Gruppe der <i>septemplicata</i> / Gruppe der <i>crassicosata</i>	Clausiliar plate distally receding/not receding	Clausiliar plate gutter- like/not gutter like	Clausiliar plate bent upwards/ not bent upwards
<i>Siciliaria grohmanniana grohmanniana</i> (Rossmässler, 1836)	22	<i>septemplicata</i>	receding	gutter-like	bent
<i>Siciliaria grohmanniana addaurae</i> ssp. nov.	18	<i>septemplicata</i>	receding	gutter-like	bent
<i>Siciliaria septemplicata</i> (Philippi, 1836)	15	<i>septemplicata</i>	receding	gutter-like	bent
<i>Siciliaria leucophryna</i> (L. Pfeiffer, 1862)	20	<i>septemplicata</i>	not receding	not gutter-like	not bent
<i>Siciliaria calcarae calcarae</i> (Philippi 1844)	36	<i>septemplicata</i>	not receding	not gutter-like	bent
<i>Siciliaria calcarae belliemi</i> (Brandt, 1961)	25	<i>septemplicata</i>	not receding	not gutter-like	bent
<i>Siciliaria calcarae borgettensis</i> ssp. nov.	12	<i>septemplicata</i>	not receding	not gutter-like	bent
<i>Siciliaria calcarae jatinensis</i> ssp. nov.	21	<i>septemplicata</i>	not receding	not gutter-like	bent
<i>Siciliaria calcarae parajatinensis</i> ssp. nov.	15	<i>septemplicata</i>	not receding	not gutter-like	bent
<i>Siciliaria calcarae orlando</i> Liberto, Reitano, Giglio, Colomba & Sparacio, 2016	9	<i>septemplicata</i>	partially receding	gutter-like	bent
<i>Siciliaria calcarae cruenta</i> ssp. nov.	7	<i>septemplicata</i>	not receding	not gutter-like	bent
<i>Siciliaria ferrox</i> (Brandt, 1961)	11	<i>septemplicata</i>	partially receding	partially gutter-like	not bent
<i>Siciliaria tiberii tiberii</i> (A. Schmidt, 1868)	31	<i>septemplicata</i>	not receding	not gutter-like	bent
<i>Siciliaria tiberii armettensis</i> ssp. nov.	33	<i>septemplicata</i>	not receding	not gutter-like	bent
<i>Siciliaria tiberii hemmeni</i> (Beckmann, 2004), comb. nov.	6	<i>septemplicata</i>	not receding	not gutter-like	not bent
<i>Siciliaria tiberii scalettensis</i> Beckmann, 2004	27	<i>septemplicata</i>	not receding	not gutter-like	not bent
<i>Sicania crassicosata</i> (L. Pfeiffer, 1856), comb. nov.	19	<i>crassicosata</i>	not receding	not gutter-like	not bent
<i>Sicania eminens</i> (A. Schmidt, 1868), comb. nov.	29	<i>crassicosata</i>	not receding	not gutter-like	not bent
<i>Sicania nobilis nobilis</i> (L. Pfeiffer, 1848), comb. nov.	35	<i>crassicosata</i>	not receding	not gutter-like	not bent
<i>Sicania nobilis spezialensis</i> (Nordsieck, 1984), comb. nov., stat. nov.	21	<i>crassicosata</i>	not receding	not gutter-like	not bent

Order Stylommatophora
Infraordo Clausilioidei Gray, 1855
Superfamilia Clausilioidea Gray, 1855
Familia Clausiliidae Gray, 1855
Subfamilia Alopiinae A.J. Wagner, 1913
Tribus Delimini R.A. Brandt, 1956
Genus *Siciliaria* Vest, 1867

***Siciliaria grohmanniana* (Rossmässler, 1836) s. l.**

Remarks. *Siciliaria grohmanniana* forms a subclade with its sister group *Siciliaria septemplicata* (mean p distance 9.0%). The two subspecies of *S. grohmanniana* appear monophyletic in the mt tree (Fig. 4), albeit each represented by only a small number of samples: *Siciliaria grohmanniana grohmanniana* (one population with three samples), *Siciliaria grohmanniana addaurae* ssp. nov. (one population with three samples). Mean distance between the two subspecies was found to be 3.3%.

Table 6. Main morphological differences between *Siciliaria* and *Sicania*.

Character	<i>Siciliaria</i>	<i>Sicania</i>
Shell – waxy surface	not present	only in <i>Sicania nobilis nobilis</i>
Shell – percostate	not present	only in <i>Sicania crasscostata</i>
Shell – clausiliar plate gutter-like	only in <i>S. grobmanniana s. l.</i> and <i>S. septemPLICATA</i>	not present
Shell – clausiliar plate receding	only in <i>S. grobmanniana s. l.</i> and <i>S. septemPLICATA</i>	not present
Ganitalia – penial internal papillose sculpturing	not present	only in <i>Sicania nobilis nobilis</i>

The shell of *Siciliaria grobmanniana addaurae* ssp. nov. was at first considered by Nordsieck (2013b: 6), as an "intermediate geographic form" of *S. grobmanniana* s. s. with "shell not decollate and whorls more weakly ribbed" and (2013b: 10) as: "a *S. grobmanniana* with characters of *S. septemPLICATA*" but without stating what these characters are. He introduced it as the: "Priola form from Priola (= Punta Priola) and San Lorenzo near Palermo" and depicted a shell (Nordsieck 2013b: 12, fig. 8). The internal penial sculpturing of *Siciliaria grobmanniana grobmanniana* is similar to *Siciliaria septemPLICATA* (internal penial sculpturing showing a more or less fringed longitudinal pleats) although the sculpturing of epiphallus and vagina shows greater variability.

***Siciliaria grobmanniana grobmanniana* (Rossmässler, 1836)**

Figs 1.F, 7.1–7.3, 8.1–8.4, 13.1–13.4

Clausilia grobmanniana Rossmässler 1836: 7.

Clausilia grobmanniana var. *minor* A. Schmidt 1868: 40 [non Rossmässler].

Clausilia grobmanniana [sic!] – Benoit 1876: 151.

Clausilia grobmanniana [sic!] – Benoit 1881: 108.

Clausilia (Siciliaria) grobmanniana – Monterosato 1894: 170.

Delima (Siciliaria) grobmanniana – Wagner 1925: 67.

Siciliaria grobmanniana – Schileyko 2000: 665.

Charpentieria grobmanniana – Beckmann 2004: 188.

Siciliaria grobmanniana – Nordsieck 2007: 53.

Siciliaria grobmanniana – Welter-Schultes 2012: 340.

Siciliaria grobmanniana – Nordsieck 2013b: 6.

Charpentieria grobmanniana – De Mattia 2017a.

Specimens examined. ITALY, Sicily, Palermo, Monte Pellegrino, N side of the top plateau, 380 m asl, 38°10'55.26"N, 13°21'1.66"E, W. De Mattia and J. Macor leg., 20.xii.2003. 15 live spm, 3 dissected spm. ITALY, Sicily, Palermo, Monte Pellegrino, Santuario Santa Rosalia, 420 m asl, 38°10'4.41"N, 13°21'2.60"E, [Lab ID 42_1, COI: MW758886; Lab ID 42_2, COI: MW758887, ITS2: MW757091 MW757092; Lab ID 42_3, COI: MW758885], W. De Mattia and J. Macor leg., 15.iv.2017. 12 live spm, 3 dissected spm.

Shell (Figs 8.1–8.4, 13.1–13.4). Shell mostly decollate; whorls ribbed; dorsal keel indistinct or missing; inferior lamella very high; two anterior upper palatal plicae present, upper one mostly separated from upper palatal plica; palatal edge of clausilium plate distally receding, plate gutter-like narrowed, palatal edge against distal end bent upwards and more or less pointed (as in Nordsieck 2013b).

Measurements (n = 25, decollate): shell height 19.4 ± 0.8 , whorl width 5.1 ± 0.2 , aperture height 3.9 ± 0.2 , aperture width 2.7 ± 0.2 .

External morphology of the genital organs (Fig. 7.1). The FO is longer than the V (FO/V range from 1.6 to 1.8). The VD is thin along its whole course. The FD BC is shorter than the BC+SDBC (FD BC/BC+SDBC range from 0.7 to 0.8). The BC+SDBC is cylindrical or club-like and slightly longer than the V (BC+SDBC/V range 1.3–1.4), with no clear distinction between the SDBC and the BC. The apex is wide and round or pointed. The D is longer than the V (D/V range 2.0–2.1) and longer than the BC+SDBC (D/BC+SDBC range 1.4–1.7), thinner than the BC+SDBC and with a pointed apex. The V is short and cylindrical. The A is large. The PC is longer than the V (P+E/V range 2.4–2.6). The PR is long and robust. There is a clear distinction between P and E as there is a visible ER and a proximal narrowing. The E is thinner but longer than the P (E/P range 1.1–1.3), almost gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 7.2, 7.3). The A is smooth or with weak traces of the distal penial pleats. The P presents 4–6 longitudinal and very irregular pleats. These pleats are very variable in thickness and sculpture, being both smooth or segmented along the same pleat. These pleats often split (proximally, distally or both) into smaller pleats. The fine structure of the wall is smooth. The PP is big, irregular, wrinkly and pointed. It can be smooth or with small tubercles. The P-E transition presents one ER with the PP and ELP originating from the ER. The epiphallar formula is: 1ER(PP+ELP). The E shows 4 to 6 main longitudinal finely fringed pleats. The V is almost completely smooth. The wall is finely granulated.

Ecology. *Siciliaria grohmanniana grohmanniana* is widespread and common throughout its range. It is found to live on exposed limestone walls hiding in cracks and under crags. It is also found in *Pinus* sp. forest on decaying woods and tree trunks, including shady and humid spots on mosses and ferns. According to De Mattia (2017a) *Siciliaria grohmanniana grohmanniana* is considered as Endangered following the IUCN criteria B1ab(i,ii,iii,v)+2ab(i,ii,iii,v). The whole area of distribution is currently included in protected areas.

Distribution. The taxon is limited to the calcareous mountains northern of Palermo: Monte Pellegrino and the southern slopes of Monte Gallo.

***Siciliaria grohmanniana addaurae* ssp. nov.**

<http://zoobank.org/47B512C7-4087-41F2-8781-EB2A56803C95>

Figs 1.F, 7.4–7.6, 8.5–8.9, 13.5–13.8

Type locality. ITALY, Sicily, Palermo, N side of Monte Pellegrino, Punta Priola, Grotte dell'Addaura, 115 m asl, 38°11'13.01"N, 13°21'6.91"E.

Type material. 1 *Holotype* (NHMW 113611) [Lab ID 41_1, COI: MW758883, ITS2: MW757093, MW757094] and 8 *Paratypes* (NHMW 113612): Italy, Sicily, Palermo, N side of Monte Pellegrino, Punta Priola, Grotte dell'Addaura, 115 m asl, 38°11'13.01"N, 13°21'6.91"E, [Lab ID 41_2, COI: MW758884; Lab ID 41_3 COI: MW758929], W. De Mattia and J. Macor leg., 15.iv.2017. 3 dissected spm. 10 *Paratypes* (CWDM 18222): same locality.

Shell diagnosis. Shell decollate; whorls ribbed; dorsal keel weak but distinguishable; inferior lamella very high; two anterior upper palatal plicae present, both of them separated from the lunella; parietalis short ends before the beginning of the spiralis; palatal edge of clausilium plate distally receding, plate gutter-like narrowed, palatal edge against distal end bent upwards and more or less pointed.

Shell description (Figs 8.5–8.9, 13.5–13.8). The shell is elongated, fusiform, sinistral and decollate, rarely not decollate. It is brown to reddish brown in colour. The external surface has small raised ribs almost equally arranged in all whorls of the teleoconch. The spire slowly and regularly grows with eight or nine whorls that are only slightly convex. The sutures are moderately shallow with very rare whitish papillae

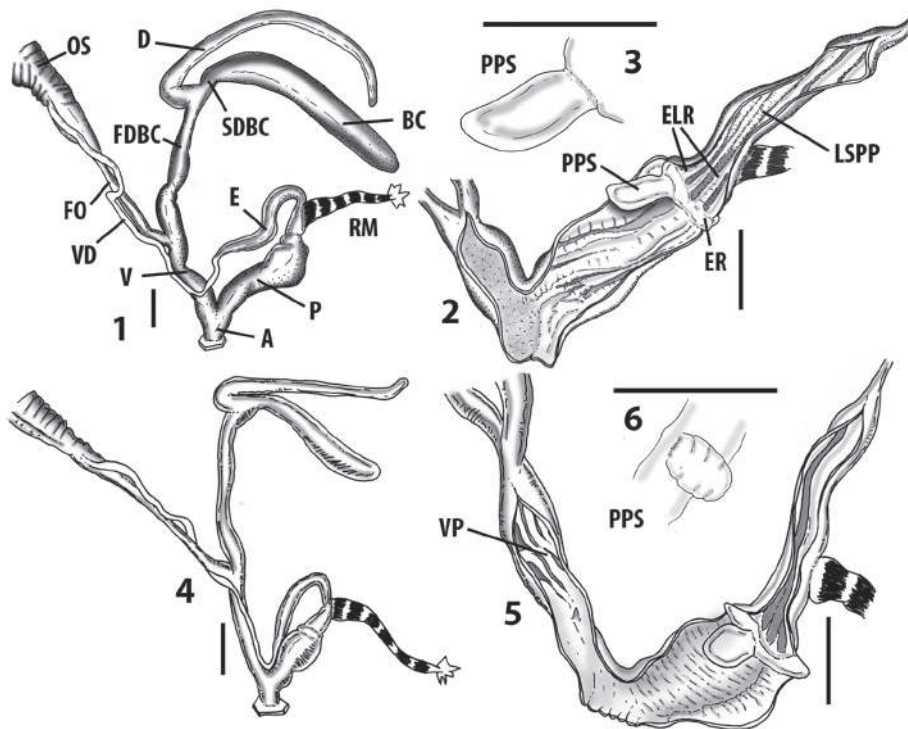


Figure 7. *Siciliaria grobmanniana grobmanniana* (Rossmässler, 1836), Monte Pellegrino, Palermo **7.1** whole distal genital organs **7.2** internal distal part of genital organs **7.3** penial pseudopapilla detail. *Siciliaria grobmanniana addaurae* ssp. nov. Grotta dell'Addaura, Punta Priola **7.4** whole distal genital organs **7.5** internal distal part of genital organs **7.6** penial pseudopapilla detail.

present towards the apex. The basal and the cervical keels are weak but distinguishable. The umbilicus is closed. The aperture width is $\sim \frac{1}{4}$ of shell height and subovoid in shape. The PRI is long and raised, wider along its posterior part and not fused with the L. The PRI is not visible from the aperture. The L is antero-lateral, with a reduced, knob-like PUPP connected to it. There are two AUPP, both of them detached from the L and barely visible from the aperture. The upper AUPP is stronger and longer than the lower one. The ALPP (BAS) starts directly from the L and it is long and strong, clearly visible from the aperture. The SCL is present and robust. It is connected to the L. The IL is high to very high. The SUL is short, tooth-like and ends before the beginning of the SPL that is wider along its posterior part. The SCOL is not emergent. The peristome is continuous, markedly thickened and reflected. It is not superiorly fused to the wall of the first whorl. The palatal edge of the clausilium is distally receding and bent upwards. The plate is narrow and gutter-like.

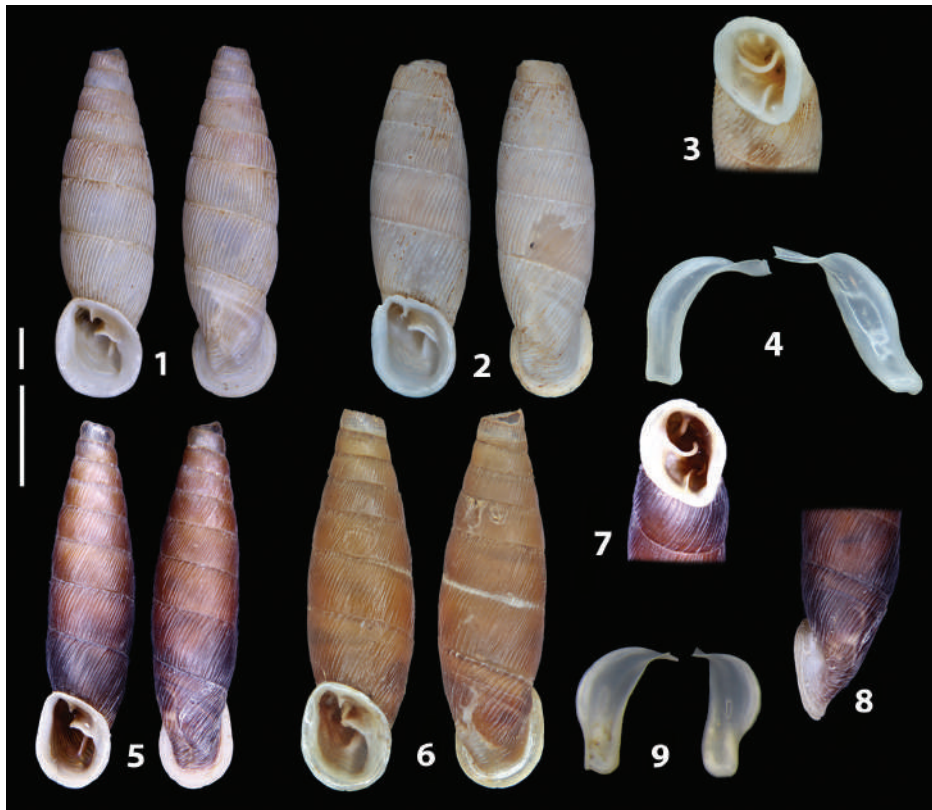


Figure 8. *Siciliaria grohmanniana grohmanniana* (Rossmässler, 1836), Monte Pellegrino, Palermo **8.1** shell **8.2** shell **8.3** detail of the aperture **8.4** clausiliar plate double side. *Siciliaria grohmanniana addaurae* ssp. nov. Grotta dell'Addaura, Punta Priola **8.5** shell **8.6** shell **8.7** detail of the aperture **8.8** detail of the columellar side of last whorl **8.9** clausiliar plate double side.

Measurements *Holotype*: decollate shell height 17.3, whorl width 4.5, aperture height 4, aperture width 2.5. ***Paratypes*** (n = 20, decollate): shell height 17.2 ± 0.6 , whorl width 4.4 ± 0.1 , aperture height 3.9 ± 0.3 , aperture width 2.9 ± 0.3 .

External morphology of the genital organs (Fig. 7.4). The FO is longer than the V (FO/V range 1.5–1.7). The VD is thin along its whole course. The FDBC is longer than the BC+SDBC (FDBC/BC+SDBC range 1.0–1.3). The BC+SDBC is cylindrical or club-like and slightly longer than the V (BC+SDBC/V = 1.1), with no clear distinction between the SDBC and the BC. The apex is wide and round. The D is longer than the V (D/V range 1.3–1.5) and longer than the BC+SDBC (D/BC+SDBC range 1.1–1.3), thinner than the BC+SDBC and with a small apex. The V is long and cylindrical and thin in diameter. The A is small. The PC is longer than the V (P+E/V range 1.6–1.8). The PR is long and thin. There is a clear distinction between P and E as there is a visible ER and a proximal narrowing. The E is much thinner but longer than the P (E/P range 1.2–1.5), gradually shrinking and turning into the vas deferens.

Internal morphology of the genital organs (Figs 7.5, 7.6). The A is smooth. The P presents very smooth and scarcely elevated weak transverse pleats. The fine structure of the wall is smooth. The PP is big, rounded and smooth. It originates from the big epiphallar ring. The P-E transition presents one ER with the PP originating from it. The ELP are not connected with the ER. The epiphallar formula is: 1ER(PP)+ELP. The E shows three or four main smooth longitudinal pleats. The proximal V shows an irregular set of smooth longitudinal pleats that, distally, turn into a smooth fold that goes as far as the atrium.

Comparative analysis. *Siciliaria grohmanniana addaurae* ssp. nov. differs from *Siciliaria grohmanniana grohmanniana* by its slender shape and darker shell colour and its denser ribbing (Fig. 8.5, 8.6). The two AUPP are longer and stronger. The basal and the cervical keels are more prominent. The internal wall of the P presents different sculpturing: smooth and scarcely elevated weak transverse pleats versus 4 to 6 longitudinal and very irregular pleats (Fig. 7.5). *Siciliaria grohmanniana addaurae* ssp. nov. differs from *Siciliaria septemplicata* by its more ribbed surface and the stronger ALPP. The SCL is much longer and more robust. The internal wall of the P presents different sculpturing: smooth and scarcely elevated weak transverse wrinkles versus four to five smooth longitudinal or fringed pleats. (Fig. 7.5).

Distribution. *Siciliaria grohmanniana addaurae* ssp. nov. is exclusively known from the type locality, along the limestone cliffs around the Addaura caves near Punta Priola, Palermo. It is likely to be present in other spots along the northeastern limestone cliffs of the Monte Pellegrino, but more research is needed to define its distribution.

Ecology. *Siciliaria grohmanniana addaurae* ssp. nov. is an obligate rock-dweller and inhabits the limestone cliffs, on open walls or hiding in cracks in humid spots, around the Addaura caves. This subspecies has a very limited distribution range with an area of much less than 1 km². Although, the area is included in the Riserva Naturale Orientata Monte Pellegrino and the Addaura caves are fenced, the habitat quality is inferred to be declining due to no access regulation nor restriction, resulting in dumping, littering and murals on the limestone walls (Ferrante 2011).

Etymology. The taxon is named after the Addaura caves, a complex of three natural caverns where wall engravings dated to the Paleolithic and the Mesolithic were discovered.

***Siciliaria septemplicata* (Philippi, 1836)**

Figs 1.F, 9.1–9.2, 10.1–10.7, 13.9–13.11

- Clausilia septemplicata* Philippi 1836: 139.
Clausilia sericina Rossmässler 1836: 7.
Clausilia septemplicata – Calcara 1840: 15.
Clausilia septemplicata var. *prasina* A. Schmidt 1868: 41.
Clausilia septemplicata – Benoit 1876: 151.
Clausilia prasina Benoit 1876: 151.
Clausilia septemplicata – Monterosato 1882: 102.
Clausilia (*Siciliaria*) *septemplicata* – Monterosato 1894: 170.
Delima (*Siciliaria*) *septemplicata prasina* – Wagner 1913: plate 572, fig. 14.
Charpentieria septemplicata – Beckmann 2004: 188.
Siciliaria septemplicata – Welter-Schultes 2012: 343.
Siciliaria septemplicata – Nordsieck 2013b: 6.
Charpentieria septemplicata – De Mattia 2017b.

Taxonomical and phylogenetic remarks. The case of *Siciliaria septemplicata* and its alleged subspecies (“geographic forms” following Nordsieck 2013b: 7) highlights the weakness of a entirely shell-based taxonomy at the species level.

Specimens examined. ITALY, Sicily, Palermo, N side of Monte Gallo near Sferacavallo, 40 m asl, 38°12'39.27"N, 13°17'21.26"E, [Lab ID 56_1, COI: MW758904, ITS2: MW757137, MW757138], W. De Mattia and J. Macor leg., 16.iv.2017. 5 live spm, 2 dissected spm. ITALY, Sicily, Palermo, E side of Monte Gallo, 140 m asl, 38°13'5.61"N, 13°18'4.76"E, [Lab ID 57_1, COI: MW758937, ITS2: MW757070], W. De Mattia and J. Macor leg., 16.iv.2017. 4 live spm, 2 dissected spm.

Shell (Figs 10.1–10.7, 13.9–13.11). Shell mostly not decollate; whorls rib-striated, with sutural papillae; dorsal keel indistinct or missing; inferior lamella very high; two anterior upper palatal plicae present, upper one mostly separated from upper palatal plica; palatal edge of clausilium plate distally receding, plate gutter-like narrowed, palatal edge against distal end bent upwards and more or less pointed (as in Nordsieck 2013b).

Measurements (n = 18, not decollate): shell height 17.9 ± 0.6 , whorl width 4.2 ± 0.2 , aperture height 3.9 ± 0.2 , aperture width 2.9 ± 0.4 .

External morphology of the genital organs (Fig. 9.1). The FO is longer than the V (FO/V range from 1.1 to 3.9). The VD is thin along its whole course. The FDBC is slightly longer than the BC+SDBC (FDBC/BC+SDBC range 1.1–1.9). The BC+SDBC is cylindrical to spindle-like and longer than the V (BC+SDBC/V range 1.1–1.3), with no clear distinction between the SDBC and the actual BC.

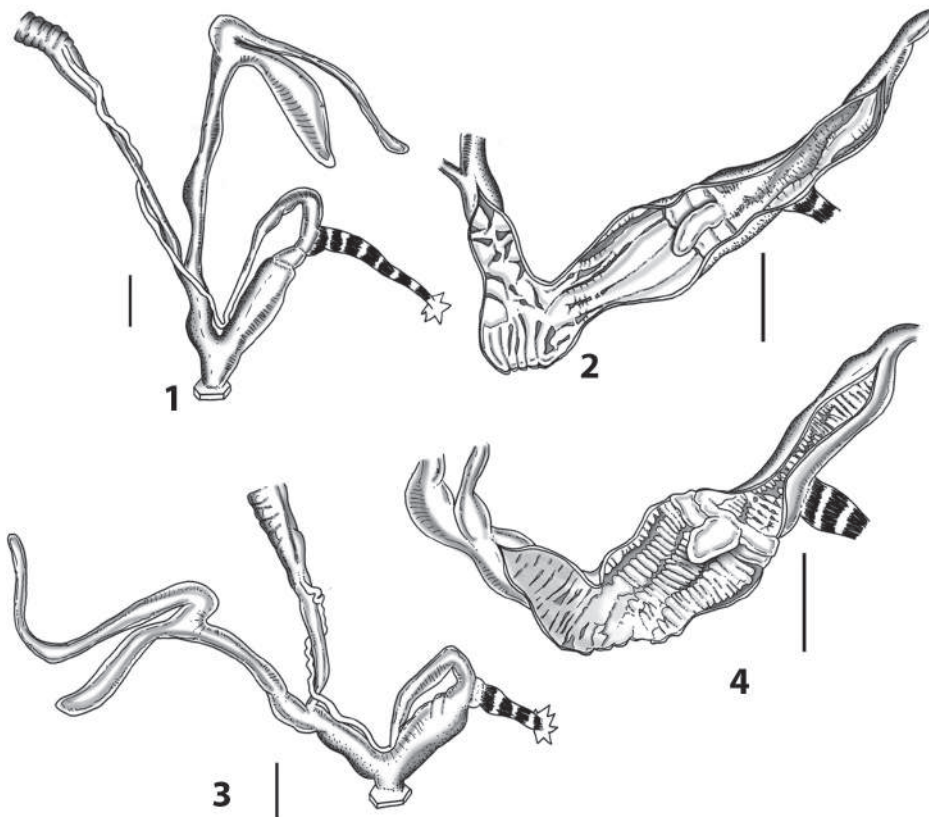


Figure 9. *Siciliaria septemplexata* (Philippi, 1836), Monte Gallo, Sferracavallo **9.1** whole distal genital organs **9.2** internal distal part of genital organs **9.3** whole distal genital organs **9.4** internal distal part of genital organs.

The apex is big and pointed. The D is longer than the V ($D/V = 1.9$) and longer than the BC+SDBC ($D/BC+SDBC$ range 1.6–1.7), thinner than the BC+SDBC and with a small and round apex. The V is cylindrical. The A is large. The PC is longer than the V ($P+E/V$ range 2.0–2.4). The PR is long and thin or short and strong. The E is as long as the P ($E/P = 1.0$), gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Fig. 9.2). The A shows a set of longitudinal irregular pleats. The P presents four to five smooth longitudinal or slightly fringed pleats. The fine structure of the wall is smooth. The PP is small to medium in dimensions and elongated. The P-E transition presents a first distal ER, PP and ELP originate from the second proximal ER. The epiphallar formula is: 1ER+2ER (PP+ELP). The E shows one main longitudinal slightly segmented pleat that fades out before the VD. Few additional small, weak, elevated pleats can also be present. The wall of the E is coarsely granulated. The V presents a set of irregular fleshy folds.

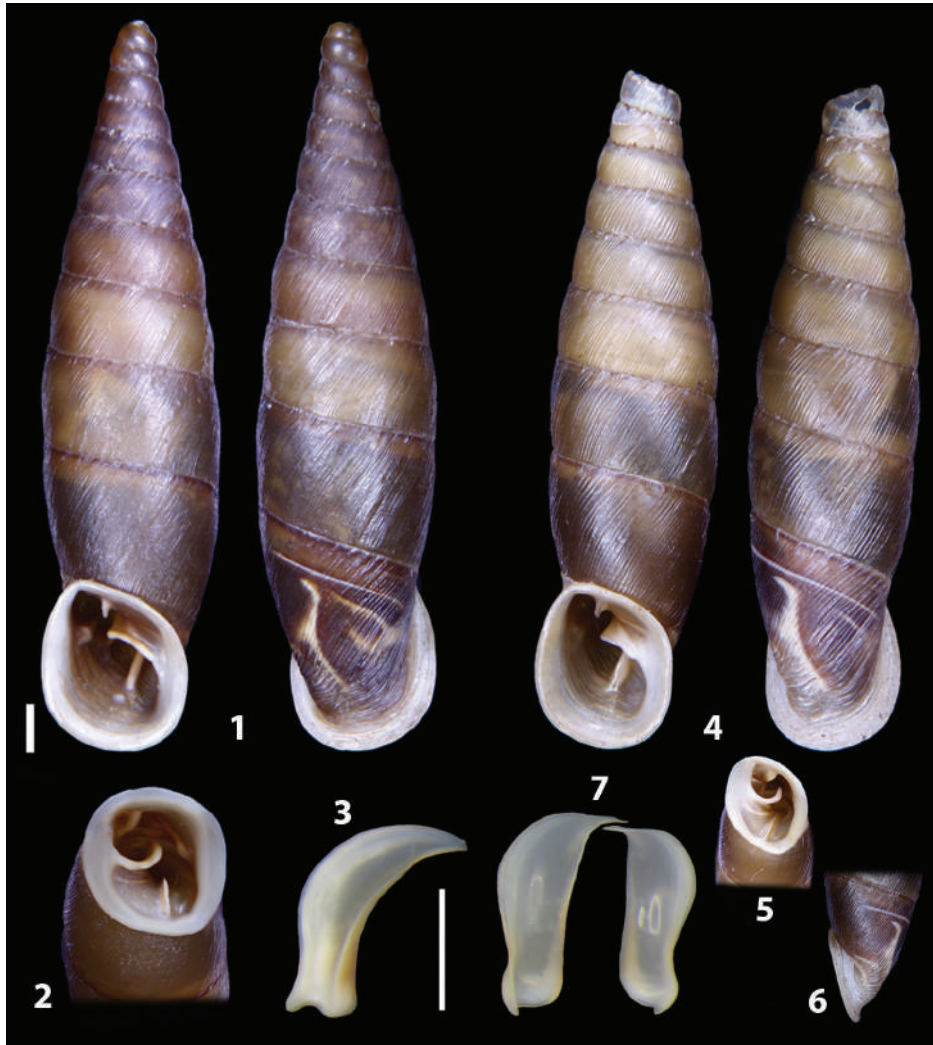


Figure 10. *Siciliaria septemPLICATA* (Philippi, 1836), Monte Gallo, Sferracavallo **10.1** shell **10.2** detail of the aperture **10.3** clausiliar plate **10.4** shell **10.5** detail of the aperture **10.6** detail of the columellar side of last whorl **10.7** clausiliar plate double side.

Ecology. *Siciliaria septemPLICATA* was found dwelling on limestone cliffs, hiding in cracks in exposed or shady spots. According to De Mattia (2017b) the species is Near Threatened.

Distribution. Following the new taxonomical results, the distribution of *Siciliaria septemPLICATA*, must be reconsidered. Beckmann (2004: 188) and Nordsieck (2013b: 7) described a wide area from Cinisi in the west and Monte Gallo in the north to Piana degli Albanesi in the south and Monte Catalfano in the east. At least the area of Cinisi must be removed from the distribution list of *Siciliaria septemPLICATA*, it is occupied by *S. tiberii alcamoensis* comb. nov.

***Siciliaria leucophryna* (L. Pfeiffer, 1862)**

Figs 1.F, 11.1–11.5, 12.1–12.6, 13.12–13.14

Clausilia leucophryna Pfeiffer 1862: 204.*Siciliaria leucophryne* [sic!] – Boettger 1877: 34.*Clausilia leucophryne* var. *laudabilis* [sic!] Boettger 1879: 34.*Clausilia leucophryna* [sic!] – Benoit 1881: 108.*Clausilia confinata merens* Westerlund 1892: 47.*Clausilia leucophryne laudabilis* [sic!] – Westerlund 1892: 48.*Charpentieria leucophryna* – Beckmann 2004: 188.*Siciliaria leucophryna* – Welter-Schultes 2012: 341.*Siciliaria leucophryna* – Liberto et al. 2012: 560.*Siciliaria leucophryna* – Nordsieck 2013b: 7.*Siciliaria leucophryna* – Liberto et al. 2015: 489.*Charpentieria leucophryna* – De Mattia 2017c.*Siciliaria leucophryna microinsularis* Sparacio et al. 2021: 598.

Remarks. *Siciliaria leucophryna* in the mt tree forms a separate subclade within the big *S. calcarae* clade (mean p distance 11.3%). As depicted in the combined tree (Fig. 6), the close relationship of this species with *S. calcarae* appears clear. *Siciliaria leucophryna microinsularis* Sparacio, Surdo, Viviano, Liberto & Reitano, 2021 was recently introduced from the island of Isola delle Femmine (Palermo). In the comparative notes provided by Sparacio et al. (2021: 599), the character states reveal to fall into the variability we detected for the topotypical specimens from Grotta Conza (Palermo), both regarding shell and genital morphology. In the type locality, small specimens ($H_s = 14.7$ mm) and light brown colour of the shell are also known. The same applies for the connection between the AUPP and PUPP where specimens from the type locality also show a “wide” spacing. Following the pictures provided by Sparacio et al. (2021: figs 43, 44), the PP of *S. leucophryna microinsularis* does not appear longer if compared to the PP of the specimens from the type locality (Figs 11.2, 11.3, 11.5). The variability of the sculpturing of the internal walls of the vagina refrains us to consider it a reliable taxonomic character for the whole genus *Siciliaria*. The status of *S. leucophryna microinsularis* should be further investigated morphologically as well as genetically. Anyhow, *Siciliaria leucophryna microinsularis* Sparacio, Surdo, Viviano, Liberto & Reitano, 2021 is here deemed as a local form, thus a junior synonym of *Siciliaria l. leucophryna*.

The population from Via Plauto, concerning the shell, matches with the “Sferracavallo form” described by Nordsieck (2013b: 7), showing a lower inferior lamella and the palatal edge of the clausilium plate more strongly bent upwards.

Specimens examined. ITALY, Sicily, Palermo, Grotta Conza, 150 m asl, 38°11'13.61"N, 13°16'44.68"E, [Lab ID 55_1, COI: MW758902, ITS2: MW757124; Lab ID 55_2, COI: MW758903], W. De Mattia and J. Macor leg., 15.iv.2017. 15 live spm, 3 dissected spm. ITALY, Sicily, Palermo, Sferracavallo, via Plauto, 50 m asl,

38°12'1.32"N, 13°16'3.05"E, [Lab ID 43_1, COI: MW758888], W. De Mattia and J. Macor leg., 15.iv.2017. 7 live spm, 2 dissected spm.

Shell (Figs 12.1–12.6, 13.12–13.14). Shell decollate; whorls ribbed; dorsal keel mostly indistinct or missing; inferior lamella moderately high; anterior upper palatal plica present, widely separated from or connected with upper palatal plica; palatal edge of clausilium plate distally slightly or not receding, palatal edge distally bent upwards (as in Nordsieck 2013b) or not.

Measurements (n = 35, decollate): shell height 18.2 ± 2.1 , whorl width 4.3 ± 0.2 , aperture height 4.5 ± 0.2 , aperture width 3.4 ± 0.2 .

External morphology of the genital organs (Figs 11.1, 11.4). The FO is longer than the V (FO/V range 2.1–2.4). The VD is thin along its whole course. The FDBC of the BC+SDBC is longer than the BC+SDBC (D/BC+SDBC = 2.1). The BC+SDBC is club-like to cylindrical and longer than the V (BC+SDBC/V range 1.4–1.6), with no clear distinction between the SDBC and the BC. The apex is wide and rounded. The D is longer than the V (D/V range 2.7–2.8) and longer than the BC+SDBC (D/

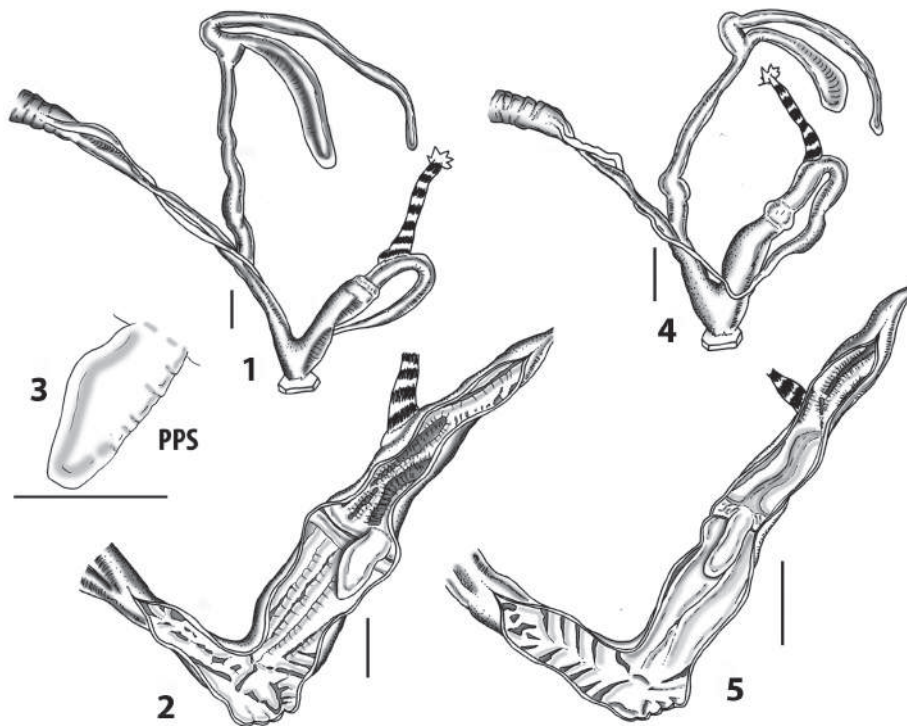


Figure 11. *Siciliaria leucophryna* (L. Pfeiffer, 1862), Grotta Conza, Palermo **11.1** whole distal genital organs **11.2** internal distal part of genital organs **11.3** pseudopapilla detail. Sferracavallo, via Plauto **11.4** whole distal genital organs **11.5** internal distal part of genital organs.



Figure 12. *Siciliaria leucophryna* (L. Pfeiffer, 1862), Grotta Conza, Palermo **12.1** shell **12.2** detail of the aperture **12.3** clausiliar plate double side. Sferracavallo, via Plauto **12.4** shell **12.5** detail of the aperture **12.6** detail of the columellar side of last whorl.

BC+SDBC range 1.9–2.4), thinner than the BC+SDBC and with a pointed apex. The V is short and cylindrical. The A is very large. The PC is much longer than the V (P+E/V range 2.4–3.9). The PR is long and thin. There is a clear distinction between P and E as there is a visible ER and a proximal narrowing. The E is thinner but longer than the P (E/P range 1.4–1.8), almost gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 11.11.2–11.2, 11.4). The A shows a set of irregular fleshy folds. The P presents two big smooth longitudinal pleats that occupy almost the whole internal penial space. The fine structure of the wall is

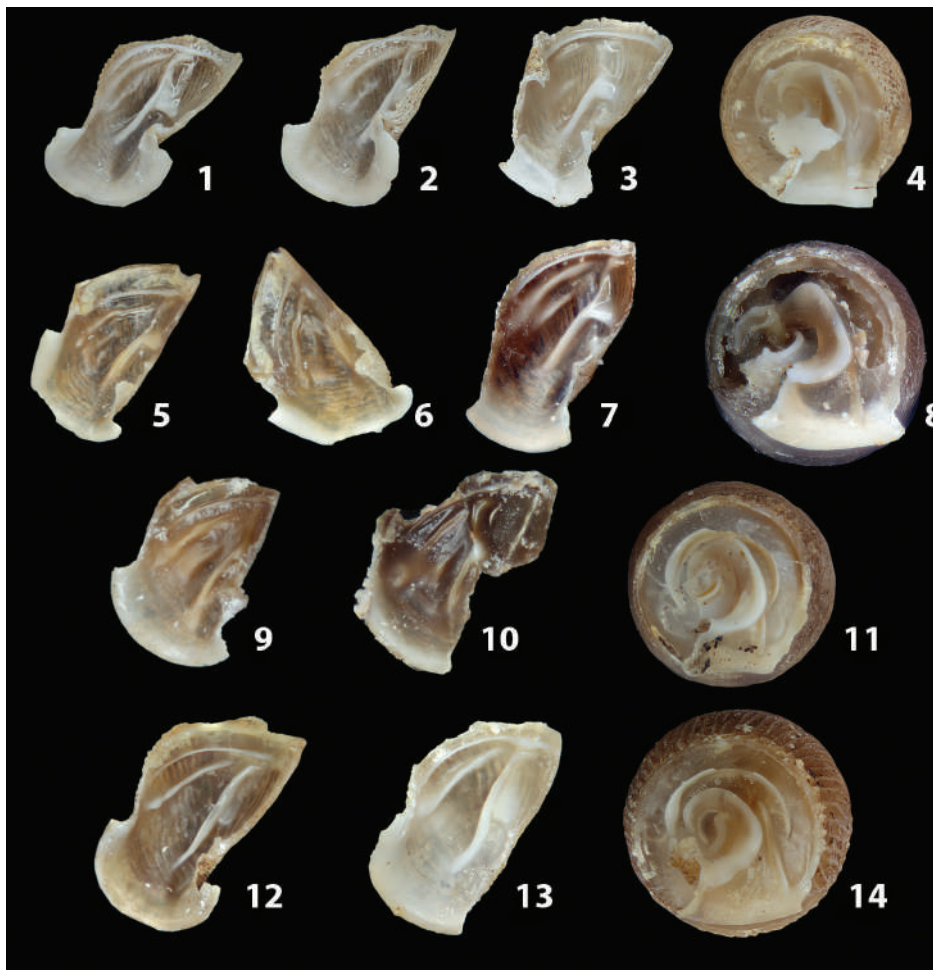


Figure 13. *Siciliaria grohmanniana grohmanniana* (Rossmässler, 1836), Monte Pellegrino, Palermo. **13.1–13.3** palatal plicae **13.4** parietal lamellae *Siciliaria grohmanniana addaurae* ssp. nov., Grotta dell'Addaura, Punta Priola **13.5–13.7** palatal plicae **13.8** parietal lamellae. *Siciliaria septemplicata* (Philippi, 1836), Monte Gallo, Sferracavallo **13.9–13.10** palatal plicae **13.11** parietal lamellae. *Siciliaria leucophryna* (L. Pfeiffer, 1862), Grotta Conza, Palermo **13.12–13.13** palatal plicae **13.14** parietal lamellae.

smooth. The PP is very elongated and smooth with a pointed tip. The P-E transition presents two slightly different structures. The population from the L.T. (Grotta Conza) presents a first distal ER, the PP and ELP originate from the second proximal ER. The epiphallar formula is: 1ER+2ER(PP+ELP). The V presents irregular, transverse to slightly longitudinal pleats. The population from Sferracavallo presents one ER with the PP originating from it. The ELP are not connected with the ER. The epiphallar formula is: 1ER(PP)+ELP. Distally, the E shows two main ELP that, at its mid length abruptly become finely fringed. The V presents a set of transverse-oblique smooth pleats that merge together one into another forming a kind of chevron or irregular pattern.

Ecology. *Siciliaria leucophryna* colonises limestone cliffs hiding in cracks or under stones. It is very common on isolated boulders and tree trunks and barks in the xerophilic scrub around Grotta Conza. The species is quite abundant where found. According to De Mattia (2017c) the species is Endangered following the IUCN criteria B1ab(iii,v)+2ab(iii,v). The map provided by De Mattia (2017) partially misses a portion of the actual distribution area, as the western part was left out from the perimeter (Pizzo Mollica and Isola delle Femmine).

Distribution. *Siciliaria leucophryna* is known to occur from a small area from Isola delle Femmine to Sferracavallo, including the northernmost sides of Pizzo Mollica and Pizzo Manolfo (where Grotta Conza is located) [(Sparacio et al. (2021)]. Nordsieck (2013b) reports also Monte Gallo, despite recent field collecting failed to find it there. Further field research throughout the whole Pizzo Manolfo-Pizzo Castellaccio-Cozzo San Rocco massif is required to precisely define the distribution of this species.

Siciliaria calcarae (Philippi, 1844) s. l.

Remarks. In the COI tree two subclades of *Siciliaria calcarae* s. l. appear together with *S. leucophryna* in an unresolved trichotomy. The subspecies of *Siciliaria calcarae* are distributed within two haplogroups, one (haplogroup 1) comprising the nominate subspecies as well as *S. c. belliemi*, *S. c. borgettensis* ssp. nov., *S. c. orlandoi*, *S. c. parajatinensis* ssp. nov. and the other one (haplogroup 2) consisting of *S. c. cruenta* ssp. nov. and *S. c. jatinensis* ssp. nov. Unfortunately, *S. parajatinensis* could not be included into the ITS2 analysis. Yet, given the low distances among all representatives of *S. calcarae* in the ITS2 tree (and the resulting bad resolution), this data set does not tell us much concerning these relationships. Thus, presently the close relationship between *S. c. orlandoi* and *S. c. parajatinensis* has to rely on mt data only. Concerning the anatomy of the genital organs, shell morphology, distribution, ecology and haplogroup of *Siciliaria calcarae*, two general types can be distinguished for each category.

Genital organs. Two main anatomical types of male (penial) internal sculpturing are found. The first type presents clear longitudinal pleats that run from the origin of penial pseudopapilla down to (or almost to) the atrium. These longitudinal pleats can be either (almost) completely smooth (Monte Belliemi) or more or less markedly

fringed (Calatubo, Romitello, Ficuzza, Jato city park, Monte Kumeta, and Castelluzzo). The second type presents transverse and strong smooth pleats (Bonifato, Gibilmese, and Visicari).

Sculpturing of the surface of the teleoconch. The first type corresponds to *S. calcarae calcarae* (Philippi, 1844) morphotype, which is more or less striated (Bonifato, Ficuzza, Romitello, Visicari, Gibilmese, and Castelluzzo), whereas the second type presents a markedly ribbed shell (Calatubo, Jato city park, Monte Kumeta, and Monte Belliemi).

Distribution. Throughout the whole *S. calcarae* distribution, the nominate subspecies *S. calcarae calcarae* has the widest distribution, whereas all the remaining subspecies have an isolated, punctiform distribution. The populations from Alcamo, Visicari and Castelluzzo belong to the widely distributed nominate subspecies (1) whereas the remaining populations (Ficuzza, Calatubo, Monte Kumeta, Jato city park, Romitello, Gibilmese and Monte Belliemi) belong to limited, punctiform populations (2).

Ecology. The populations belonging to this subclade were collected in two main ecological niches. Most of them (type 1) were found on limestone rocks and cliffs (Jato city park, Bonifato, Calatubo, Gibilmese, Monte Kumeta, Romitello, Monte Belliemi and Visicari), whereas the other populations (type 2), from Ficuzza and Castelluzzo, were exclusively found on tree trunks.

Haplotypes. Concerning the haplogroups of the *calcarae* clade, eight populations fall into subclade 1 (Bonifato, Calatubo, Romitello, Monte Belliemi, Visicari and Castelluzzo, Monte Kumeta, Ficuzza), whereas two populations (Gibilmese, and Jato city park) fall in to the subclade 2. *Siciliaria calcarae orlandoi* Liberto et al., 2016 was recently described from a few scattered localities restricted to Bosco Ficuzza (Corleone, Sicily) (Liberto et al. 2016: 371). The arrangement of the internal penial sculpturing of the holotype seems not matching with what was found by our dissection, where, instead of "two long weak longitudinal furrows" (Liberto et al. 2016: 372) a set of transverse, interrupted fleshy smooth pleats were found instead. Yet, the authors provided besides pictures and description of the external morphology of the genital organs, only very few details on the internal morphology of the genital organs, namely: "internal walls of penis show two long weak longitudinal furrows; conic penial papilla, with slightly pointed apex and a restriction to the base". The brief description and the quality of the images (Liberto et al. 2016: 375) do not allow accurate comparison of the internal features with those found in the present analysis. Moreover, the pseudopapilla was erroneously considered as a true penial papilla.

The position of *S. calcarae orlandoi* in the COI tree within haplogroup 1 is close to sequences of a population of *Siciliaria* from the western slopes of Monte Kumeta. Despite the close phylogenetic relationship of this population with *S. calcarae orlandoi*, the differences in the arrangement of the internal male genital organs (a set of transverse, interrupted fleshy smooth pleats and epiphallus with two main fringed chords vs. smooth longitudinal pleats and smooth proximal epiphallus) as well as the remarkable differences concerning shell morphology (see also Liberto et al. 2016: 372 for a comparative discussion with conspecific taxa) we propose the population from Monte Kumeta as *S. calcarae parajatensis* ssp. nov.

Two additional new subspecies of *Siciliaria calcarae* will be described in the following sections: *S. calcarae borgettensis* ssp. nov. and *S. calcarae cruenta* ssp. nov. Both taxa, despite showing close phylogenetic relationships with the other *Siciliaria calcarae* taxa, present distinctive shell and genital characters strong enough to propose their description as new subspecies.

***Siciliaria calcarae calcarae* (Philippi, 1844)**

Figs 1.F, 14.1–14.10, 15.1–15.17, 16.1–16.6, 24.1, 24.2

Clausilia calcarae Philippi 1844: 107.

Clausilia adelina Küster 1847: 298.

Clausilia adelina – Benoit 1876: 152.

Clausilia brugnoneana Pini 1884: 379.

Clausilia calcarae var. *nodosa* Westerlund 1892: 48.

Clausilia adelina var. *subsolida* Monterosato 1892: 28.

Delima (*Siciliaria*) *calcarae* – Wagner 1925: pl. 3, fig. 25.

Charpentieria calcarae – Beckmann 2004: 188.

Siciliaria calcarae – Welter-Schultes 2012: 338.

Siciliaria calcarae – Nordsieck 2013b: 7.

Siciliaria (*Siciliaria*) *calcarae calcarae* – Liberto et al. 2015: 489.

Siciliaria (*Siciliaria*) *calcarae calcarae* – Liberto et al. 2016: 372.

Charpentieria calcarae – De Mattia 2017d.

Specimens examined. ITALY, Sicily, San Vito lo Capo, Castelluzzo, west cliffs E of town, 120 m asl, 38°6'25.71"N, 12°44'33.37"E, [Lab ID 61_1, COI: MW758908, ITS2: MW757140 MW757141; Lab ID 61_2, COI: MW758909, ITS2: MW757142 MW757143 MW757144], W. De Mattia and J. Macor leg., 14.iv.2017. 2 dissected spm. ITALY, Sicily, Castellammare del Golfo, Visicari, 395 m asl, 38°02'54.18"N, 12°48'26.61"E, [Lab ID 59_1, COI: MW758905, ITS2: MW757068 MW757069 MW757085], W. De Mattia and J. Macor leg., 15.iv.2017. 2 dissected spm. ITALY, Sicily, Alcamo, Monte Bonifato, top of the mountain, 640 m asl, 37°57'29.40"N, 12°57'33.64"E, [Lab ID 5_1, COI: MW758925, ITS2: MW757125, MW757126, MW757127], I. Niero leg., 15.vi.2010. 2 dissected spm. ITALY, Sicily, Alcamo, Monte Bonifato, top of the mountain, 640 m asl, 37°57'29.40"N, 12°57'33.64"E, A. Margelli leg., 15.vi.2010. 2 dissected spm. ITALY, Sicily, Alcamo, Monte Bonifato, west side of the mountain, over the quarry, 550 m asl, 37°57'16.92"N, 12°58'9.06"E, W. De Mattia and J. Macor leg., 10.iv.2017. 2 dissected spm. ITALY, Sicily, Castellammare del Golfo, Castello di Baida, W of the town along the road to Visicari, 300 m asl, 38°2'41.64"N, 12°48'14.34"E, W. De Mattia and J. Macor leg., 15.iv.2017. 2 dissected spm. ITALY, Sicily, Piana degli Albanesi, 500 m south of Portella Ginestra, northern cliffs of Monte Kumeta, 970 m asl, 37°58'13.35"N, 13°15'22.06"E, W. De Mattia and J. Macor leg., 18.iv.2017. 2 dissected spm. ITALY, Sicily, Calatafimi, Castello Eu-

femio, 395 m asl, 37°57'45.67"N, 12°51'21.13"E, W. De Mattia and J. Macor leg., 18.vi.2020. 2 dissected spm.

Shell (Figs 14.1–14.10, 15.1–15.17, 24.1–24.2). Shell not decollate; whorls striated, with sutural papillae; dorsal keel indistinct or missing; inferior lamella moderately high or low; anterior upper palatal plica present, mostly separated from upper palatal plica, rarely lower anterior upper palatal plica present; palatal edge of clausilium plate distally not receding, palatal edge distally more or less strongly bent upwards (Nordsieck 2013b).

Measurements (n = 50, not decollate). shell height 19.7 ± 0.8 , whorl width 4.3 ± 0.3 , aperture height 4.1 ± 0.2 , aperture width 2.6 ± 0.1 .

External morphology of the genital organs (Figs 14.1, 14.3, 14.5, 14.7, 14.9). The FO is slim and long. The ratio FO/V ranges from 0.9 to 1.8. The VD is very thin along its whole course. The FDBC is shorter or longer than the BC+SDBC (FDBC/BC+SDBC) ranges from 0.9 to 1.8. The BC+SDBC can be either cylindrical or club-like, with either a pointed or a blunt apex. Its ratio with the V (BC+SDBC/V) ranges from 0.9 to 1.8. The transition between the BC and then SDBC can be clearly visible or almost indistinguishable. The D is moderately to extremely long, with a ratio with the V (D/V) that ranges from 1.3 to 4.1. It is thinner than the BC+SDBC, cylindrical in shape, with a rounded thin apex. The ratio D/BC+SDBC ranges from 1.4 to 2.5. The V is thick, cylindrical or hourglass-like in shape and shorter than the PC. The A can be short and narrow or large and long. The PC is longer than the V, with a range (P+E/V) that goes from 2.1 to 4.8. The P is wider than the V, cylindrical or distally swollen. The PR can be both long and thin or short and strong. The distinction between P and E with a visible ER is not always present as it appears randomly among the populations. The E is thinner than the P and can be slightly shorter or longer than the P, with a ratio (E/P) that ranges from 0.9 to 3.0. The actual transition area between E and the VD can be clearly visible or almost indistinguishable and it is clearly visible only from inside.

Internal morphology of the genital organs (Figs 14.2, 14.4, 14.6, 14.8, 14.10). The internal wall of the A presents a variety of sculpture. It can be almost smooth, or with the distal part of the penial longitudinal pleats that gradually fade. Otherwise, it presents longitudinal broad and poorly elevated fleshy pleats or an irregular pattern of fleshy lumps. The internal sculpturing of the P can be distinguished in two main arrangements. The first is represented by 3 to 6 longitudinal fleshy smooth or irregularly segmented pleats that reach the A. The second arrangement presents large fleshy transverse pleats that are interrupted in the median part of the internal P. These pleats become smaller and continuous as approaching the A. The PP is big, elongated or nipple-like/roundish in shape, smooth, with a rounded apex and sometimes slightly depressed in the middle. The P-E transition presents three different structures among the examined populations. The populations from the top of Monte Bonifato and Castelluzzo present one ER with the PP originating from it. The ELP are not connected with the ER. The epiphallar formula is: 1ER(PP)+ELP. The populations from Monte Bonifato, from Monte Bonifato near the quarry and Visicari present one ER with both

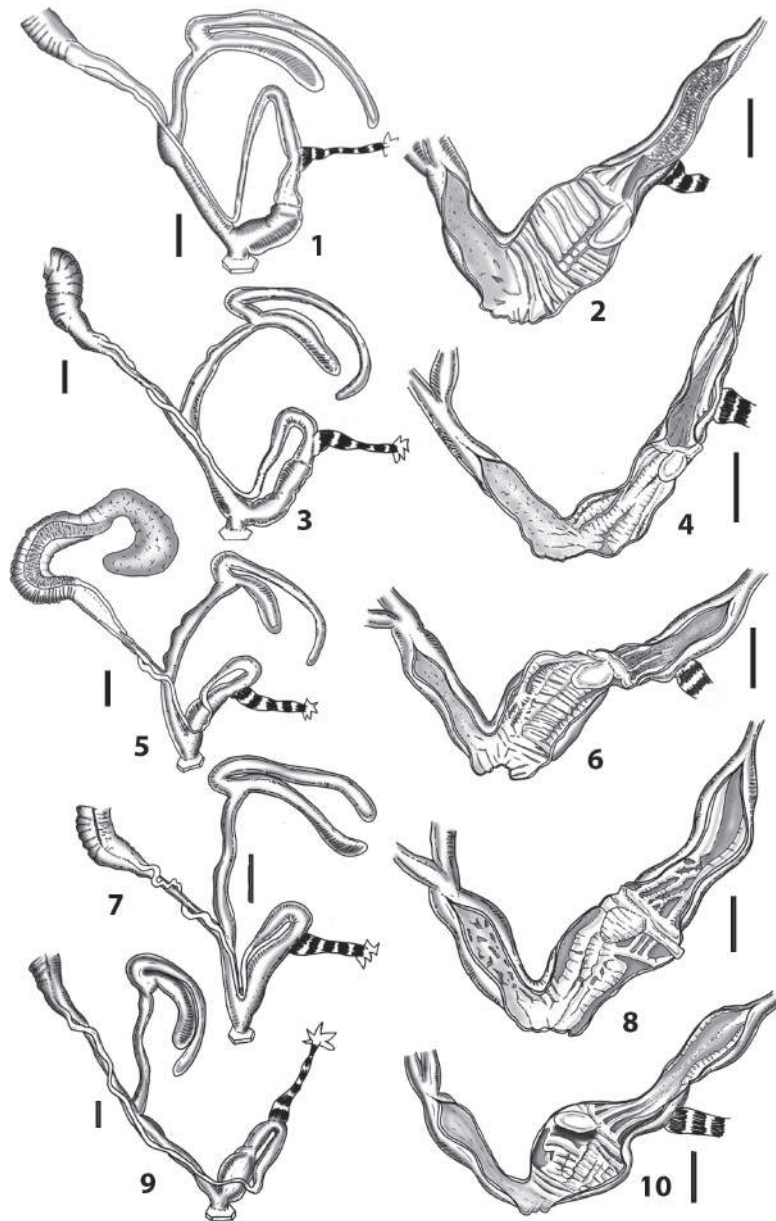


Figure 14. *Siciliaria calcarae calcarae* (Philippi, 1844), Visicari, Castellammare del Golfo **14.1** whole distal genital organs **14.2** internal distal part of genital organs. Castelluzzo, San Vito Lo Capo **14.3** whole distal genital organs **14.4** internal distal part of genital organs. Castello di Baida, Castellammare del Golfo **14.5** whole distal genital organs **14.6** internal distal part of genital organs. Piana delle Ginestre, Monte Kumeta **14.7** whole distal genital organs **14.8** internal distal part of genital organs. Calatafimi, Castello Eufemio. (= *adelina* Küster, 1847) **14.9** whole distal genital organs **14.10** internal distal part of genital organs.

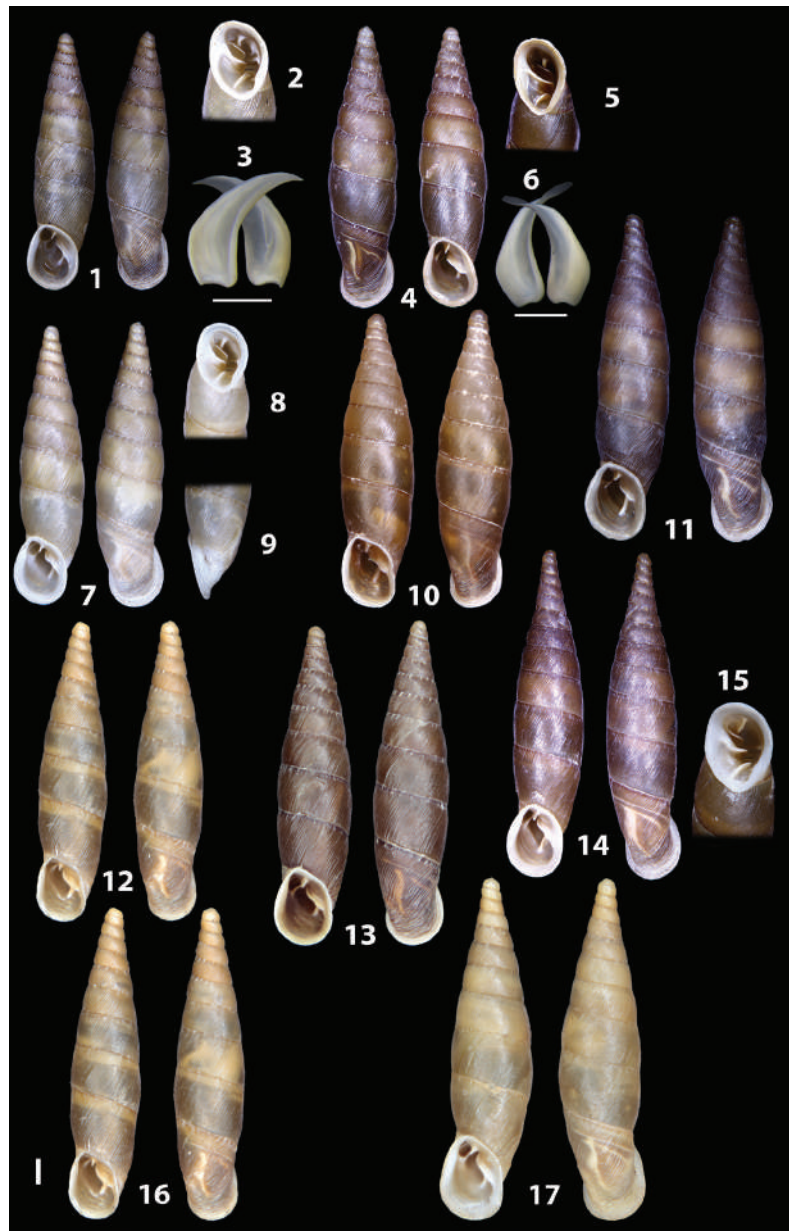


Figure 15. *Siciliaria calcarae calcarae* (Philippi, 1844), Visicari, Castellammare del Golfo **15.1** shell **15.2** detail of the aperture **15.3** clausiliar plate double side. Castelluzzo, San Vito Lo Capo **15.4** shell **15.5** detail of the aperture **15.6** clausiliar plate double side. Castello di Baida, Castellammare del Golfo **15.7** shell **15.8** detail of the aperture **15.9** detail of the columellar side of last whorl. Monte Bonifato, Alcamo **15.10–15.12** shells. Calatafimi, Castello Eufemio, (= *adelina* Küster, 1847) **15.13** shell. Piana delle Ginestre, Monte Kumeta **15.14** shell **15.15** detail of the aperture. Monte Erice, western slopes **15.16** shell. Scopello **15.17** shell.

the PP and the ELP originating from it. The epiphallar formula is: 1ER(PP+ELP). Two additional populations from Portella Ginestra and Castello di Baida present a slightly more complex structure, namely a first distal ER with the PP originating from it and the ELP originating from a second proximal ER. The epiphallar formula is: 1ER(PP)+2ER(ELP).

The E internal sculpturing presents a variety of arrangements, as: two main large smooth or fringed longitudinal pleats that gradually disappear toward the distal origin of the vas deferens or 4 thin smooth longitudinal pleats that abruptly disappear turning into an irregular texture of small dense papillae. The V can be either smooth and showing a very fine granulation or showing a coarse chevron pattern made of large fleshy pleats, merging together along the median longitudinal axis.

Spermatophore (Figs 16.3–16.4). The spermatophore is thin and elongated. It is 6.7 mm long and 0.7 mm wide at its widest point. The tail and the head are missing as probably already digested. The upper and the lower keels are simple and run throughout the known length of the spermatophore. The lower keel is half as tall as the upper one.

Ecology. *Siciliaria calcarae calcarae* was found on south exposed limestone walls (Alcamo, Monte Bonifato), shady and humid north exposed limestone walls (Piana degli Albanesi, 500 m south of Portella Ginestra), shady habitats on decaying woods and tree trunks of *Quercus ilex* (Castelluzzo, west cliffs E of town) or among grass and shrub nearby a cave entrance (Castellammare del Golfo, Visicari). *Siciliaria calcarae calcarae* appeared to be adapted to many different habitats and niches and it is not an obliged rock-dwelling taxon. According to De Mattia (2017d), *Siciliaria calcarae* is Least Concern. The nominate subspecies is common and widespread all over its range and it is somewhere replaced by local rib/striated forms.

Distribution. *Siciliaria calcarae calcarae* presents the widest distributional area among the species of the genus *Siciliaria*. It is found from Trapani-Erice in the west to Montagna Grande and Bagheria in the east and Calatafimi-Piana degli Albanesi-Castelvetrano in the south. It is also known from the islands of Favignana and Levanzo (Nordsieck 2013b; Liberto et al. 2016: 382).

Remarks. *Siciliaria calcarae calcarae* shows minor shell differences among the populations which were described by the introduction of new names, such as a well-developed whole UPP (in *Clausilia adelina* var. *subsolida*), a well-developed AUPP in *Clausilia adelina*) or the presence of a knob as a second AUPP (*Clausilia calcarae* var. *nodosa*) (Liberto et al. 2016: 382).

***Siciliaria calcarae belliemii* (Brandt, 1961)**

Figs 1.F, 16.7–16.11, 17.1–17.6, 24.4

Siciliaria (*Siciliaria*) *calcarae belliemii* Brandt 1961: 9.

Charpentieria calcarae belliemii – Nordsieck 2007: 53.

Siciliaria calcarae belliemii – Nordsieck 2013b: 8.

Siciliaria (Siciliaria) calcarae belliemi – Liberto et al. 2016: 371.

Specimens examined. ITALY, Sicily, Partinico, W side of the Mount Belliemi, 440 m asl, 38°00'22.47"N, 13°6'37.79"E, [Lab ID 54_1, COI: MW758900, ITS2: MW757134, MW757135, MW757136; Lab ID 54_2, COI: MW758901], W. De Mattia and J. Macor leg., 12.iv.2017. 15 live spm, 3 dissected spm. ITALY, Sicily, Alcamo, E side of the Calatubo Castle, 75 m asl, 38°00'54.80"N, 12°59'13.35"E, [Lab ID 44_1, COI: MW758889, ITS2: MW757122, MW757123; Lab ID 44_2, COI: MW758913; Lab ID 44_3, COI: MW758930; Lab ID 44_4, COI: MW758931], W. De Mattia and J. Macor leg., 14.iv.2017. 18 live spm, 2 dissected spm.

Shell (Figs 17.1–17.6, 24.4). Shell not decollate; whorls ribbed, with sutural papillae; dorsal keel indistinct or missing; inferior lamella moderately high to low; anterior upper palatal plica present, separated from upper palatal plica, sometimes lower anterior upper palatal plica present; palatal edge of clausilium plate distally not receding, palatal edge distally more or less strongly bent upwards.

Measurements (n = 40, not decollate, Monte Belliemi): shell height 17.6 ± 1.2 , whorl width 3.1 ± 0.1 , aperture height 2.9 ± 0.2 , aperture width 2.0 ± 0.1 . (n = 22, not decollate, Calatubo): shell height 19.6 ± 1.4 , whorl width 3.9 ± 0.2 , aperture height 3.4 ± 0.2 , aperture width 3.0 ± 0.2 .

External morphology of the genital organs (Figs 16.7, 16.9). The FO is slim and long. The ratio FO/V ranges from 2.0 to 2.2. The VD is very thin along its whole course. The ratio of the BC+SDBC with the BC+SDBC+the second duct (FDBC/BC+SDBC) ranges from 1.4 to 2.1. The BC+SDBC can be either cylindrical or club-like, with either a pointed or a blunt apex. It is slightly shorter or as long as the V, with a ratio (SDBC+BC/V) that ranges from 0.9 to 1.0. The transition between the BC and then SDBC is little visible or almost indistinguishable. The D is long, with a ratio with the V (D/V) that ranges from 2.9 to 3.1. It is thinner or as thin as the SDBC+BC, cylindrical in shape with a rounded thin apex. The ratio D/BC+SDBC ranges from 2.1 to 2.4. The V is short and cylindrical. The A is short but wide. The PC is much longer than the V, with range (PC/V) 2.8–3.1. The P is wider than the V, cylindrical or distally swollen. The PR is robust. The E is thin and slightly shorter or as long as the P, with the ratio E/P ranging 0.9–1. It gradually shrinks and turns into the VD. The actual transition area between E and the VD can be clearly visible or almost indistinguishable and it is clearly visible only from inside.

Internal morphology of the genital organs (Figs 16.8, 16.10, 16.11). The A shows 3–5 large longitudinal pleats oriented towards the P. The P presents 4–6 longitudinal fleshy and smooth pleats, gradually narrowing towards the A. Sometimes the lower pleats gradually become irregularly segmented. The fine structure of the wall is smooth. The PP is big, nipple-like in shape, smooth with a rounded apex. The P-E transition presents two slightly different structures in the two examined populations. The population from Monte Belliemi (type locality) presents a first distal ER, the PP originates from the second proximal ER. The ELP are not connected to the second

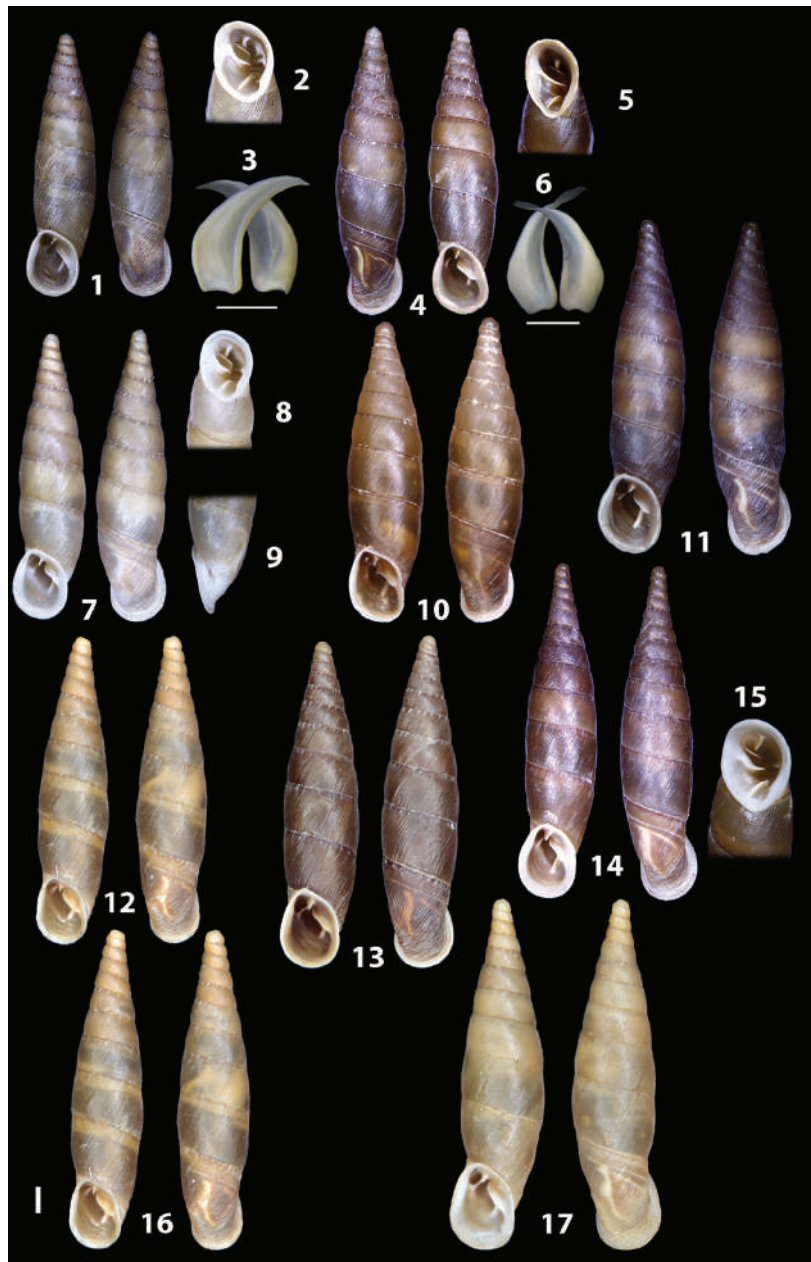


Figure 16. *Siciliaria calcarae calcarae* (Philippi, 1844), Monte Bonifato **16.1** whole distal genital organs **16.2** internal distal part of genital organs **16.3** cross section of the spermatophore **16.4** spermatophore **16.5** whole distal genital organs **16.6** internal distal part of genital organs. *Siciliaria calcarae belliemi* (Brandt, 1961), Monte Belliemi, Partinico **16.7** whole distal genital organs **16.8** internal distal part of genital organs. *Siciliaria calcarae belliemii* (Brandt, 1961), Castello Calatubo, Alcamo **16.9** whole distal genital organs **16.10** internal distal part of genital organs **16.11** penial pseudopapilla.

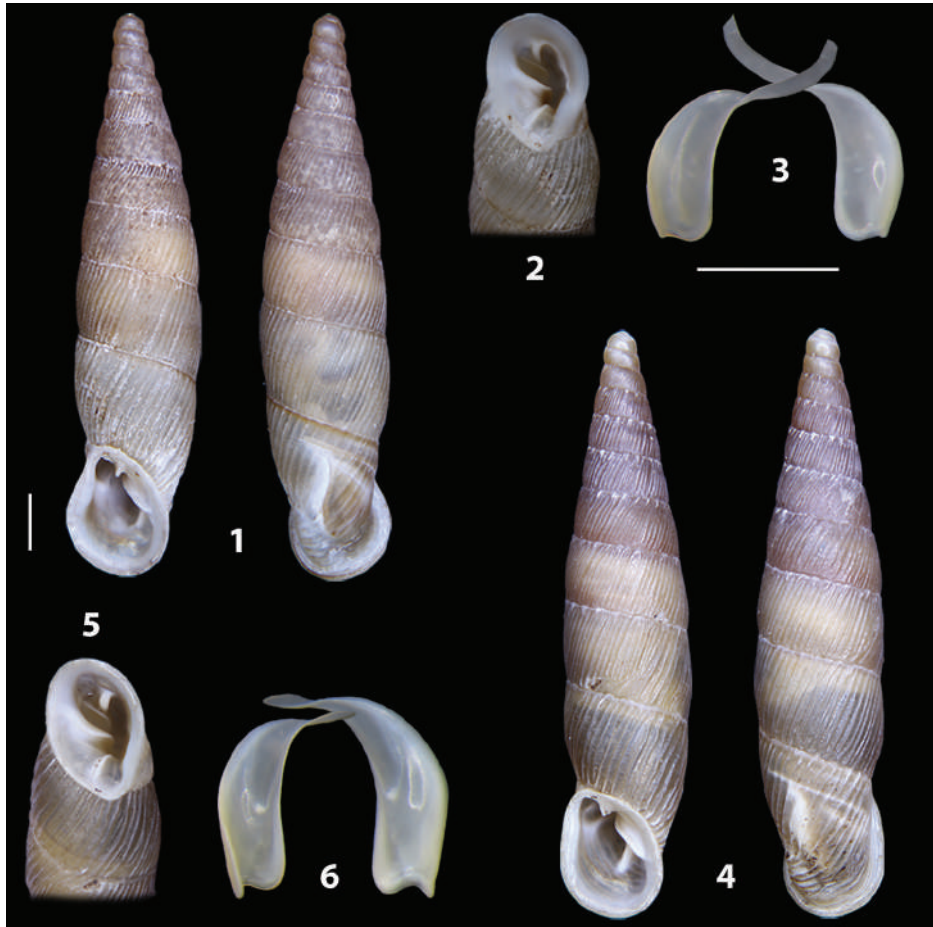


Figure 17. *Siciliaria calcarae belliemi* (Brandt, 1961), Monte Belliemi, Partinico **17.1** shell **17.2** detail of the aperture **17.3** clausiliar plate double side. Castello di Calatubo, Alcamo **17.4** shell **17.5** detail of the aperture **17.6** clausiliar plate double side.

proximal ER. The epiphallar formula is: 1ER+2ER(PP)+ELP. The population from Calatubo presents a first distal ER, while the PP and ELP originate from the second proximal ER. The epiphallar formula is: 1ER+2ER(PP+ELP). The E shows 4–6 irregular metameric longitudinal and irregular pleats that gradually disappear toward the distal origin of the vas deferens. The V shows a coarse chevron pattern made of large fleshy pleats, merging together along the median longitudinal axis or sometimes presents an irregular pattern made of small irregular fleshy pleats.

Ecology. The subspecies inhabits both scattered isolated boulders (Monte Belliemi) or limestone cliffs (Calatubo Castle). This subspecies is known only from two localities with very limited size, although it is abundant. Both localities are not included in protected areas.

Distribution. *Siciliaria calcarae belliemi* is known from Monte Belliemi near Partinico and from the limestone cliffs of the Calatubo Castle near Alcamo.

Remarks. The Calatubo population is bigger than the population from the type locality (Monte Belliemi). The average shell heights are 19.6 ± 1.4 vs. 17.6 ± 1.2 . The two populations occupy remarkably different ecological niches: high cliffs vs isolated small boulders scattered throughout open fields. Could the different ecology of the two populations be the origin or cause of such different dimensions of the shell? This interesting hypothesis could be tested also including other *Siciliaria calcarae* ssp. populations found both on limestone cliffs or different niches as tree's barks (Visicari, Castelluzzo and Ficuzza).

***Siciliaria calcarae borgettensis* ssp. nov.**

<http://zoobank.org/A092D144-BDF7-4F35-A104-5E8AE27B1BD8>

Figs 1.F, 18.1–18.2, 19.1–19.5, 24.5, 24.6

Type locality. ITALY, Sicily, Municipality of Borgetto, Anime Sante hill, road to Romitello, 400 m asl, $38^{\circ}02'59.53''\text{N}$, $13^{\circ}08'58.55''\text{E}$.

Type material. 1 *Holotype* (NHMW 113613) [Lab ID 46_1, COI: MW758890, ITS2: MW757080, MW757089, MW757090] and two *Paratypes* (NHMW 113614): ITALY, Sicily, Municipality of Borgetto, Anime Sante hill, road to Romitello, 400 m asl, $38^{\circ}02'59.53''\text{N}$, $13^{\circ}08'58.55''\text{E}$, [Lab ID 46_2, COI: MW758891; Lab ID 46_3, COI: MW758932], W. De Mattia and J. Macor leg., 22.vi.2015. 3 dissected spm. 3 *Paratypes* (CWDM 18223): same locality.

Shell diagnosis. Shell not decollate; whorls rib-striated; dorsal keel not distinguishable; inferior lamella very high; anterior upper palatal plicae present detached from the lunella; parietalis short partially overlapping of the spiralis; palatal edge of clausilium plate distally receding, plate gutter-like narrowed, palatal edge against distal end bent upwards and more or less pointed.

Shell description (Figs 19.1–19.5, 24.5, 24.6). The shell is elongated, fusiform to slightly pyriform, sinistral and not decollate. It is light reddish-brown in colour. The external surface is irregularly ribbed and striated. The spire is slowly and regularly growing with $9\frac{1}{2}$ – $10\frac{1}{4}$ slightly convex whorls. The sutures are shallow with whitish papillae, mainly present along the 4th–8th whorls. The whitish papillae become much less dense along the first four whorls of the teleoconch. The suture is dark red in colour, forming a darker line along it. The basal and the cervical keels are almost indistinguishable or not present. The umbilicus is closed. The aperture is $\sim \frac{1}{4}$ of shell height and subovoid in shape. The PRI is long and moderately raised, wider along its posterior part and not fused with the L. The PRI is not visible from a frontal view of the aperture. The L is anterior, with a very reduced, knob-like PUPP connected to it. The AUPP is strong, detached from the L and well visible from the aperture. The BAS starts directly from the L and it is long and strong, clearly visible from the aperture. The SCL is vestigial to absent. The IL is very high. The SUL is tooth-like and partially

overlaps with the spiralis. The SCOL is not emergent. The peristome is continuous, markedly thickened and reflected. It is not superiorly fused to the wall of the first whorl. The palatal edge of the clausilium is distally receding and bent upwards. The plate is narrow and gutter-like. The palatal edge against distal end is bent upwards and more or less blunt.

Measurements. *Holotype*: not decollate shell height 18.7, whorl width 4.2, aperture height 3.9, aperture width 2.8. *Paratypes* (n = 20, not decollate): shell height 19.0 ± 0.3 , whorl width 4.3 ± 0.1 , aperture height 3.8 ± 0.1 , aperture width 2.9 ± 0.1 .

External morphology of the genital organs (Fig. 18.1). The FO is as long as or slightly longer than the V (FO/V range 1.0–1.1). The VD is thin along its whole course. The FDBC is longer than the BC+SDBC (FDBC/BC+SDBC range 1.5–1.8). The BC+SDBC is club-like to cylindrical and as long as the V (BC+SDBC/V = 1.0), with no clear distinction between the SDBC and the BC. The apex is big and rounded. The D is longer than the V (D/V range 2.2–2.7) and longer than the BC+SDBC (D/BC+SDBC range 2.1–2.5), slightly thinner than BC+SDBC and with a small and round apex. The V is cylindrical. The A is very large. The PC is longer than the V (PC/V range 2.1–2.2). The PR is long and robust. The transition P-E does not show any ET. The E is almost as long as the P (E/P range 0.8–0.9), gradually shrinking and turning into the VD. The transition area between the E and the VD is not clearly visible outside.

Internal morphology of the genital organs (Fig. 18.2). The A shows a set of irregular fleshy folds. The P presents four to five large longitudinal fleshy segmented pleats. These pleats distally become weak and irregular entering in the A. The fine structure of the penial wall is smooth. The PP is big, rhombus-shaped and smooth. The P-E transition presents one ER with the PP originating from it. The ELP are not connected with the ER. The epiphallar formula is: 1ER(PP)+ELP. The E shows a pattern of 3 to 4 irregular longitudinal extremely fringed pleats. These pleats abruptly fade and most of the epiphallus is smooth. The V is smooth with a finely granulated surface.

Comparative and taxonomical remarks. *Siciliaria calcarae borgettensis* ssp. nov. was reported as “Sagana form” in Nordsieck (2013b: 8; personal communication), which differs from the nominate subspecies by a higher inferior lamella, a lower anterior upper palatal plica more or less developed and the palatal edge of the clausilium less strongly bent upwards. The type locality (Anime Sante hill along the Borghetto-Romitello road) is very close to Sagana, which is found 3.5 km eastward. This taxon is similar to the *Siciliaria calcarae cruenta* ssp. nov. (described below) from Monte Gibilmese, that is also found at short distance from Sagana (1.5 km northeast) but differs from the latter by its more striated shell, lighter colour and the more developed AUPP which is always visible from the frontal view. *Siciliaria calcarae cruenta* ssp. nov. belongs to haplogroup 2, whereas *Siciliaria calcarae borgettensis* ssp. nov. belongs to haplogroup 1.

Distribution. *Siciliaria calcarae borgettensis* ssp. nov. is exclusively known from the type locality. It is likely to be present along the whole northern limestone slopes of the Anime Sante hill (Romitello) as far as Sagana, thus further field investigations are needed in order to clearly define its actual distribution range.

Ecology. The subspecies is found on limestone boulders and under scattered rocks.

Etymology. *Siciliaria calcarae borgettensis* ssp. nov. is named after the nearby Borgetto town (Borgetto-Partinico), where the new subspecies was discovered.

***Siciliaria calcarae jatinensis* ssp. nov.**

<http://zoobank.org/56D36819-7A84-41DE-8820-966CB683B61E>

Figs 1.F, 18.3–18.7, 19.6–19.8, 24.7–24.8

Type locality. ITALY, Sicily, San Giuseppe Jato, quarry E of the town, 630 m asl, 37°58'15.07"N, 13°12'2.23"E.

Type material. 1 *Holotype* (NHMW 113615) [Lab ID 34_2, COI: MW758879, ITS2: MW757118, MW757119, MW757120, MW757121] and 5 *Paratypes* (NHMW 113616): ITALY, Sicily, San Giuseppe Jato, quarry E of the town, 630 m asl, 37°58'15.07"N, 13°12'2.23"E, [Lab ID 34_1, COI: MW758878; Lab ID 34_3, COI: MW758926; Lab ID 34_4, COI: MW758927], W. De Mattia and J. Macor leg., 22.iv.2017. 3 dissected spm. 8 *Paratypes* (CWDM 18224): same locality.

Shell diagnosis. Shell decollate, rarely not decollate; whorls ribbed; dorsal keel weak but distinguishable; inferior lamella very high; anterior upper palatal plicae present and detached from the lunella; parietalis long; palatal edge of clausilium plate distally receding, plate gutter-like, narrowed, palatal edge against distal end bent upwards and more or less pointed.

Shell description (Figs 19.6–19.8, 24.7, 24.8). The shell is elongated, fusiform, sinistral, decollate but rarely not decollate. It is reddish-brown in colour. The external surface is regularly ribbed. The spire is slowly and regularly growing with (decollate) 8 to 9 ¼ slightly convex whorls. The sutures are moderately deep with whitish papillae present all along the teleoconch, moderately denser along the last whorls. The basal and the cervical keels are distinguishable. The umbilicus is closed. The aperture is ~ 1/5 of shell height and roundish to subovoid in shape. The PRI is short and ends at the level of the L. It is not fused with the L. The PRI is not visible from a frontal view of the aperture. The L is dorso-lateral, thick and somehow irregular. There is a very reduced, knob-like PUPP connected to it. The AUPP is strong to moderately weak, detached from the L and barely visible from the aperture. The BAS starts directly from the L and it is long and strong, well visible from the aperture. The SCL is absent. The IL is high to very high. The SUL is tooth-like, long and partially overlaps with the SPL. The SCOL is not emergent. The peristome is continuous, markedly thickened and reflected. It is not superiorly fused to the wall of the first whorl. The palatal edge of the clausilium is distally receding and bent upwards. The plate is narrow and gutter-like. The palatal edge against distal end is bent upwards and more or less blunt.

Measurements. *Holotype*: not decollate shell height 20.3, whorl width 4.3, aperture height 3.8, aperture width 2.4. *Paratypes* (n = 25, decollate): shell height 20.9 ± 1.0 , whorl width 4.4 ± 0.1 , aperture height 3.9 ± 0.2 , aperture width 2.4 ± 0.2 .

External morphology of the genital organs (Figs 18.3, 18.6). The FO is longer than the V with a FO/V ratio ranging from 2.0 to 2.1. The VD is thin along its whole

course. The ratio of the FDBC with the BC+SDBC (FDBC/BC+SDBC) ranges from 1.1 to 1.3. The BC+SDBC is club-like and longer than the V, with a blunt apex. It is slightly longer than the V, with a ratio (BC+SDBC/V) that ranges from 1.6 to 1.8. There is a clear distinction between the SDBC and the BC. The D is longer than the V (with a D/V ranging from 2.1 to 2.3) and slightly longer than BC+SDBC (D/BC+SDBC ratio 1.2–1.3). It is thinner than the BC+SDBC and with a small and round apex. The V is big and cylindrical. The A is large. The PC is longer than the V (P+E/V ratio 2.1–2.4). The PR is very short and robust. The ET is weak. The E is longer than the P (E/P ratio 1.1–1.2) and almost abruptly shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 18.4, 18.7). The A shows few irregular pleats. The P presents 4 to 6 heavily segmented longitudinal pleats that begin directly from the PP and run as far as the A, becoming irregular as approaching their distal sections. The penial wall is smooth. The PP is big, rounded to rhomboid, smooth with a round to blunt apex. The P-E transition presents a first distal ER, while both the PP and ELP originate from the second proximal ER. The epiphallar formula is: 1ER+2ER(PP+ELP). The E shows a pattern of 4 to 6 smooth longitudinal pleats. These pleats merge one into another forming two main smooth pleats that run as far as the vas deferens. The V shows a weak irregular pattern of smooth pleats.

Comparative and taxonomical remarks. The shell of *Siciliaria calcarae jatinensis* ssp. nov. is very similar to the shells of *Siciliaria calcarae belliemi* and *Siciliaria calcarae parajatinensis* spp. nov. The three taxa have markedly ribbed shells. The density of the ribs along the body whorl is similar, with overlapping ranges: 32 ± 5 for *Siciliaria calcarae belliemi* (n = 25), 35 ± 6 for *Siciliaria calcarae jatinensis* ssp. nov. (n = 21) and 34 ± 5 for *Siciliaria calcarae parajatinensis* spp. nov. (n = 15). The PRI are short and stop at the level of the L, whereas the AUPP is strong to moderately weak and detached from the L. Slight differences are observed concerning the dimensions and the colour of the shell: *Siciliaria calcarae jatinensis* ssp. nov. is dark reddish to dark brown with an average height of 20.9 ± 1.0 whereas *Siciliaria calcarae parajatinensis* ssp. nov. (average height: 21.7 ± 1.4) and *Siciliaria calcarae belliemi* (average height: 17.6 ± 1.2 , type locality) are light yellowish to light brown. The three subspecies show just slight differences in their anatomy of the genital organs, which fit into the intraspecific variability of *S. calcarae* and do not allow a certain separation. The different subspecific status of these populations is mainly supported by the phylogenetic results in connection to their patchy and isolated distribution. *Siciliaria calcarae jatinensis* ssp. nov. is included in the haplogroup 2 whereas *Siciliaria calcarae parajatinensis* n. spp. and *Siciliaria calcarae belliemi* both belong to haplogroup 1.

Nordsieck (2013a) recently supplemented his *Siciliaria* web article (May 2021) after receiving samples we collected from Monte Jato (*S. calcarae jatinensis* ssp. nov.) and the W side of Monte Kumeta (*S. calcarae parajatinensis* ssp. nov.), considering these populations as belonging to the type form of *Siciliaria tiberii* and, more precisely, “to the southern and eastern form with less strong dorsal keel”. Nordsieck (2013b, supplemented 2021) justifies his identification stating that “There is no doubt that

Clausilia tiberii A. Schmidt (1868: 42–43) belongs to the southern form” despite not justifying or explaining why “there is no doubt”, considering also that no locality is provided in Schmidt’s description.

Nordsieck (2013b, supplemented 2021) stated that “Originals from Benoit (SMF 67544, 96458, see also Benoit 1859: pl. 6, fig. 7) do not differ from the form from Monte Kumeta”. Following the caption of fig. 10 “M. della Scala” was wrongly identified by Nordsieck as Monte Kumeta. Information provided by locals during field collections allowed us to ascertain that Monte della Scala is an old, almost forgotten toponym for Monte Maganoce. Monte Maganoce was once named “Monte della Scala” because of the church called “Madonna della Scala” was located along its slopes.

Moreover, in the text Nordsieck cited samples SMF 67544, 96458, while in fig. 10 the caption indicated the sample as “N 10008”. Thus, it is not clear if the depicted specimen originated from Benoit or from a different source and kept in Nordsieck’s collection.

Monte Kumeta was also deemed by Nordsieck as a spelling mistake for Monte della Fiera (pers. comm., April 2021) and stating that “form from Monte della Fiera belongs to the northern subspecies (of *S. tiberii*), based on SMF samples”. Monte della Fiera (37°59'47.90"N, 13°8'48.22"E) is 10 km distant from Monte Kumeta and represents the eastern continuation of Monte Belliemi. It is not clear what the “northern subspecies” may be, but probably it is referred as the northern form of the nominate subspecies.

In the COI and combined tree (Fig. 4) *S. calcarae jatinensis* ssp. nov. is well embedded into *Siciliaria calcarae* subclade A2. The morphologically similar *S. calcarae parajatinensis* ssp. nov. is also well embedded into *S. calcarae* clade in the COI tree.

We agree that the sample depicted in Fig. 10 is similar to *S. calcarae jatinensis* ssp. nov., but it is not clearly explained by Nordsieck (2013b; supplemented 2021) why it is supposed to belong to *S. tiberii*. To check this hypothesis, we included in our molecular genetic analysis two specimens of *S. tiberii tiberii* from Capo Rama (Terrasini) representing the “northern” form in both COI and concatenated trees, they fall well embedded within the subclade that comprises all (and exclusively) the remaining *S. tiberii* subspecific taxa.

Regarding shell morphology, we carefully browsed Schmidt’s description (1868: 41–43). Few important details better fit with the shell morphology of the “northern” type form of *Siciliaria tiberii* (Figs 26.1, 26.3) rather than with the specimen depicted by Nordsieck (2013b, supplemented 2021, fig. 10) and the specimen we depicted in Figs 19.9–19.11. Schmidt refers to the more expanded peristome (“mehr umgeschlagene Mündung”), the deep dorsal keel (“sendet nach unten eine stark entwickelte Gaumenfalte ab, welche auf der, durch die tiefe, breite Nackenfurche gebildeten, inneren Wölbung steht”) and the deep palatal hollow. Other shell differences are detectable comparing Figs 19.9–19.11 and Figs 26.1, 26.3, the number and shape of the ribs of the neck and along the whorls, strength and visibility of the AUPP, the length of the PRI, the presence of a second lower AUPP in *S. calcarae parajatinensis* ssp. nov.,

the strength and visibility of the sutural papillae, the depth of the sutures and the more convex whorls of *S. tiberii tiberii*. Thus, phylogenetic and morphological evidence prevent us from considering the Monte Jato and Monte Kumeta populations as belonging to *S. tiberii*.

Distribution. *Siciliaria calcarae jatinensis* ssp. nov. is known only from the type locality: the abandoned quarry north of the town of San Giuseppe Jato. Its actual distribution range must be further investigated as it is probably present along the north-western cliffs of the Monte Jato, E of the town of San Giuseppe Jato.

Ecology. The new subspecies is an obliged limestone rock-dweller, exclusively collected on walls and cliffs, both natural or resulting from the previous quarrying activity.

Etymology. *Siciliaria calcarae jatinensis* ssp. nov. is named after Monte Jato (San Giuseppe Jato), where the new subspecies was discovered.

***Siciliaria calcarae parajatinensis* ssp. nov.**

<http://zoobank.org/BF415C49-9548-4ECB-8E6E-6236F8789AD4>

Figs 1.F, 18.8–18.9, 19.9–19.12, 24.9–24.10

Type locality. Italy, Sicily, Monreale, W part of Monte Kumeta toward Jato Antica, 630 m asl, 37°57'8.18"N, 13°13'14.57"E.

Type material. 1 *Holotype* (NHMW 113617) and 4 *Paratypes* (NHMW 113618): ITALY, Sicily, Monreale, W part of Monte Kumeta toward Jato Antica, 630 m asl, 37°57'8.18"N, 13°13'14.57"E, W. De Mattia and J. Macor leg., 22.iv.2017. 3 dissected spm. (CWDM 18225): same locality.

Shell diagnosis. Shell not decollate; whorls ribbed; dorsal keel weak but distinguishable; inferior lamella high or very high; anterior upper palatal plicae present and detached from the lunella; parietalis long; palatal edge of clausilium plate distally receding, plate gutter-like narrowed, palatal edge against distal end bent upwards and more or less pointed.

Shell description (Figs 19.9–19.12, 24.9, 24.10). The shell is elongated, fusiform, sinistral, not decollate but sometimes decollate. It is light brown in colour. The external surface is regularly ribbed. The spire is slowly and regularly growing with (decollate) $9\frac{1}{2}$ – $10\frac{3}{4}$ slightly convex whorls. The sutures are shallow with whitish papillae present all along the teleoconch, moderately denser along the last whorls. The basal and the cervical keels are distinguishable. The umbilicus is closed. The aperture is $\sim\frac{1}{5}$ of shell height and roundish to subovoid in shape. The PRI is short and its length slightly exceeds the L. It is not fused with the L. The PRI is not visible from a frontal view of the aperture. The L is dorsal. The PUPP is absent or vestigial. The AUPP is thin, detached from the L and barely visible from the aperture. The BAS starts directly from the L and it is long and strong, well visible from the aperture. The SCL is absent. The IL is high to very high. The SUL is tooth-like, very long and remarkably overlapping with the SPL. The SCOL is sometimes visible. The peristome is continuous, markedly thickened and reflected. It is not superiorly fused to the wall of the first

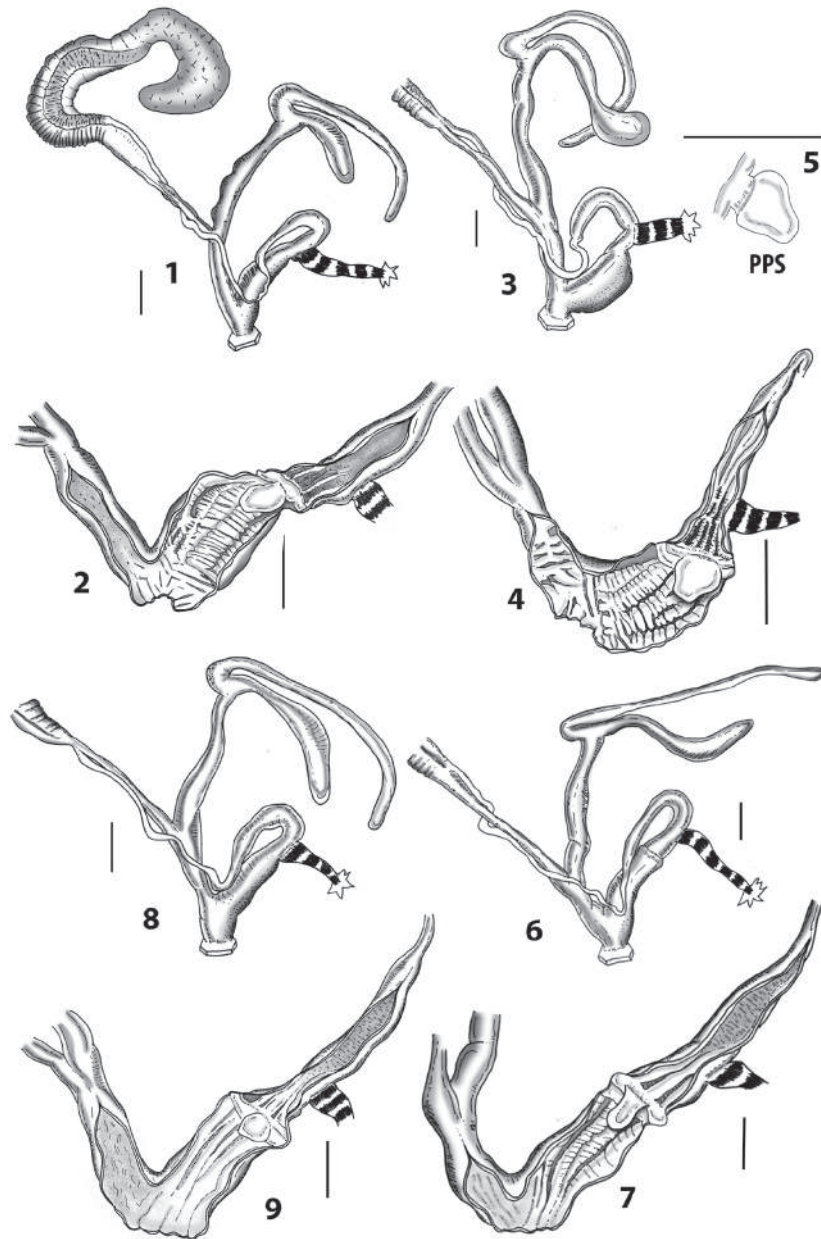


Figure 18. *Siciliaria calcarae borgettensis* ssp. nov., road to Romitello, Borghetto **18.1** whole distal genital organs **18.2** internal distal part of genital organs. *Siciliaria calcarae jatinensis* ssp. nov. San Giuseppe Jato **18.3** whole distal genital organs **18.4** internal distal part of genital organs **18.5** detail of the pseudopapilla **18.6** whole distal genital organs **18.7** internal distal part of genital organs. *Siciliaria calcarae parajatinensis* ssp. nov., west side Monte Kumeta **18.8** whole distal genital organs **18.9** internal distal part of genital organs.

whorl. The palatal edge of the clausilium is distally receding and bent upwards. The plate is narrow and gutter-like. The palatal edge against distal end is bent upwards and more or less blunt.

Measurements. *Holotype*: not decollate shell height 21.7, whorl width 4.2, aperture height 4.1, aperture width 3.3. *Paratypes* (n = 30, not decollate): shell height 21.7 ± 1.4 , whorl width 4.4 ± 0.2 , aperture height 4.2 ± 0.2 , aperture width 3.1 ± 0.4 .

External morphology of the genital organs (Fig. 18.8). The FO is longer than the V (FO/V ratio 2.0–2.2). The VD is thin along its whole course. The FDBC is slightly longer than the BC+SDBC (FDBC/BC+SDBC ratio 1.0–1.2). The BC+SDBC is club-like and longer than the V (BC+SDBC/V ratio 1.4–1.6), with a clear distinction between the SDBC and the BC. The apex is very big and rounded. The D is slightly longer than the V (D/V ratio 2.1–2.2) and slightly longer than the BC+SDBC (D/BC+SDBC ratio 1.0–1.2), thinner than the BC+SDBC and with a small and round apex. The V is big and cylindrical. The A is large. The PC is longer than the V (P+E/V ratio 2.7–3.0). The PR is very short and robust. The ET is well visible. The E is longer than the P (E/P ratio 1.2–1.4) and gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Fig. 18.9). The A shows weak longitudinal pleats entering directly from the P. The P presents 4 to 6 smooth and weak longitudinal pleats. These pleats become irregular and weaker as approaching their distal sections. The PP is big, rounded to rhomboid, smooth with a round apex. The P-E transition presents a first distal ER, while the PP and ELP originate from the second proximal ER. The epiphallar formula is: 1ER+2ER(PP+ELP). The E distally presents a variable set of irregular smooth small pleats that abruptly vanish. The remaining E shows a coarse pattern of finely granulated wall. The V shows a smooth and fine granulation, with no pleats or folds.

Comparative and taxonomical remarks. *Siciliaria calcarae parajatinensis* ssp. nov. in the COI tree is well embedded within the *calcarae* subclade and closely related to the nominate subspecies (Fig. 4). For a further differential comparative analysis see the comparative and taxonomical remarks of *Siciliaria calcarae jatinensis* ssp. nov.

Distribution. *Siciliaria calcarae parajatinensis* ssp. nov. is exclusively known from the type locality, the western slopes of the Monte Kumeta. Further field research could extend its distributional range to the whole western side of the Monte Kumeta (Monreale) and surrounding mountains. Following Nordsieck (2013b, supplemented 2021, Fig. 10) the range of *Siciliaria calcarae parajatinensis* ssp. nov. can be extended also for Monte Maganoce (also known as Monte della Scala), W of Piana degli Albanesi. In the central-eastern part of Monte Kumeta massif the type form of *S. calcarae calcarae* is known to occur.

Ecology. *Siciliaria calcarae parajatinensis* ssp. nov. is an obligate rock-dweller and inhabits limestone walls and boulders. The type locality, that is not included in any protected area, comprises a rich population.

Etymology. *Para* = next to, considering strong morphological, genetic and distribution affinities with the newly described *Siciliaria calcarae jatinensis* ssp. nov.



Figure 19. *Siciliaria calcarae borgettensis* ssp. nov., road to Romitello, Borghetto **19.1** shell **19.2** detail of the aperture **19.3** clausiliar plate double side **19.4** shell **19.5** detail of the aperture. *Siciliaria calcarae jatinensis* ssp. nov. San Giuseppe Jato **19.6** shell **19.7** detail of the aperture **19.8** clausiliar plate double side. *Siciliaria calcarae parajatinensis* ssp. nov., west side Monte Kumeta **19.9** shell **19.10** detail of the aperture **19.11** detail of the columellar side of last whorl **19.12** clausiliar plate double side.

***Siciliaria calcarae orlandoi* Liberto, Reitano, Giglio, Colomba & Sparacio, 2016**
Figs 1.F, 20.1–20.4, 21.1–21.5, 24.11

Siciliaria (Siciliaria) calcarae orlandoi Liberto, Reitano, Giglio Colomba and Sparacio
2016: 371.

Specimens examined. ITALY, Sicily, Monreale, Bosco Ficuzza, Ponte Arcere, 470 m asl, 37°55'46.42"N, 13°23'5.22"E, [Lab ID 36_1, COI: MW758921, ITS2: MW757132 MW757133], W. De Mattia and J. Macor leg., 25.iv.2017. 4 dissected spm.

Shell (Figs 21.1–21.5, 24.11). Shell not decollate; whorls striated, with sutural papillae; dorsal keel little distinct; lateral lunella; principal plica not fused with lunella; inferior lamella moderately high; anterior upper palatal plica reduced, separated from a very short upper palatal plica; palatal edge of clausilium plate distally not receding, palatal edge distally more or less strongly bent upwards.

Measurements (n = 12, not decollate). shell height 18.0 ± 0.7 , whorl width 4.1 ± 0.1 , aperture height 3.8 ± 0.2 , aperture width 2.7 ± 0.1 .

External morphology of the genital organs (Fig. 20.1). The FO is longer than the V (FO/V range 1.9–2.3). The VD is thin along its whole course. The FDBC is slightly shorter or as long as the BC+SDBC (FDBC/BC+SDBC range 0.9–1.0). The BC+SDBC is cylindrical to club-like and longer than the V (BC+SDBC/V range 3.3–3.6), with no distinction between the SDBC and the BC. The apex is big and round. The D is much longer than the V (D/V range 3.8–4.2) and longer than the BC+SDBC (D/BC+SDBC range 1.3–1.5), slightly thinner than the BC+SDBC and with a small rounded apex. The V is very short and cylindrical. The A is very large. The PC is longer than the V (PC/V range 3.0–3.3). The PR is long and robust. The ET is well visible. The E is slightly longer than the P (E/P range 1.2–1.3), almost abruptly shrinking and turning into the VD.

Internal morphology of the genital organs (Fig. 20.2). The A shows a set of transverse fleshy folds as they represent the continuation of the penial sculpture. The P presents a set of transverse, interrupted fleshy smooth pleats. These pleats are laterally surrounded by two longitudinal small smooth pleats. The fine structure of the wall is smooth. The PP is oval, smooth and with a round apex. The P-E transition presents a first distal ER, while both PP and ELP originate from the second proximal ER. The epiphallar formula is: 1ER+2ER(PP+ELP). The E shows two main longitudinal fringed pleats that fade before the VD. The wall of the E is finely granulated. The V is almost totally smooth but the wall is also finely granulated.

Ecology. Following Liberto et al. (2016: 372): "*Siciliaria calcarae orlandoi* lives under the bark of dead trees and in the leaf litter of woods vegetating both in sandstone (Bosco del Cappelliere, Diga Scanzano) and calcareous (Alpe Cucco, Rocca Busambra) soils; in these two last localities *S. calcarae orlandoi* is found also on calcareous rocks into the woods". We collected this subspecies on *Quercus* sp. barks close to a small creek.

Distribution. *Siciliaria calcarae orlandoi* is known to occur in the Nature Reserve of the Bosco della Ficuzza, Rocca della Busambra, Bosco del Cappelliere e Gorgo del Drago that is included in the wider Sicani Mountains Regional Nature Park (Liberto et al. 2016: 372).

***Siciliaria calcarae cruenta* ssp. nov.**

<http://zoobank.org/BA270C4D-6DCE-46C0-BB8F-2CC3C55DE703>

Figs 1.F, 20.3–20.4, 21.6–21.10, 24.12–24.14

Type locality. Italy, Sicily, Monreale, N side of Monte Gibilmesì, 890 m asl, 38°03'37.03"N, 13°12'38.53"E.

Type material. 1 *Holotype* (NHMW 113619) [Lab ID 47_1, COI: MW758933, ITS2: MW757078, MW757079] and two *Paratypes* (NHMW 113620): ITALY, Sicily, Monreale, N side of Monte Gibilmesì, 890 m asl, 38°03'37.03"N, 13°12'38.53"E, [Lab ID 47_2, COI: MW758934, ITS2: MW757077, MW757087, MW757088; Lab ID 47_3, MW758935; Lab ID 47_4, MW758936], W. De Mattia and J. Macor leg., 22.vi.2015. 4 dissected spm. 4 *Paratypes* (CWDM 18226): same locality.

Shell diagnosis. Shell not decollate; whorls finely striated; dorsal keel absent or barely distinguishable; inferior lamella high or very high; anterior upper palatal plicae present but weak, detached from the lunella; parietalis very long; palatal edge of clausilium plate distally receding, plate somehow cylindrical, palatal edge against distal end bent upwards and more or less pointed.

Shell description (Figs 21.6–21.10, 24.12–24.14). The shell is elongated but somehow compressed, markedly fusiform to slightly pyriform, sinistral and not decollate. It is very dark reddish-brown in colour. The external surface is irregularly finely striated to almost completely smooth in some part of the teleoconch. The spire is slowly and regularly growing, with (decollate) $9 \frac{1}{4}$ to $10 \frac{3}{4}$ slightly convex whorls. The sutures are moderately deep with white papillae all along the teleoconch, definitely denser along the last whorls. The basal and the cervical keels are only barely distinguishable. The umbilicus is closed. The aperture is $\sim \frac{1}{5}$ of shell height and roundish to subovoid in shape. The PRI is short and it ends at the level of the L. It is not fused with the L but presents a thickening along its posterior part in correspondence with the L. The PRI is not visible from a frontal view of the aperture. The L is dorsal to dorso-lateral. The PUPP is very short or knob-like and connected to the L. The AUPP is thin or rarely absent, detached from the L and not visible from the aperture. The BAS starts directly from the L and it is long and strong, well visible from the aperture. The SCL is absent or very short, connected with the L and resembling an irregular thickening. The IL is high to very high. The SUL is tooth-like, extremely long and remarkably overlapping with the SPL. The SPL is short and it ends at half of the last whorl. The SCOL is not visible. The peristome is continuous, markedly thickened and reflected. It is not superiorly fused to the wall of the first whorl. The palatal edge of the clausilium

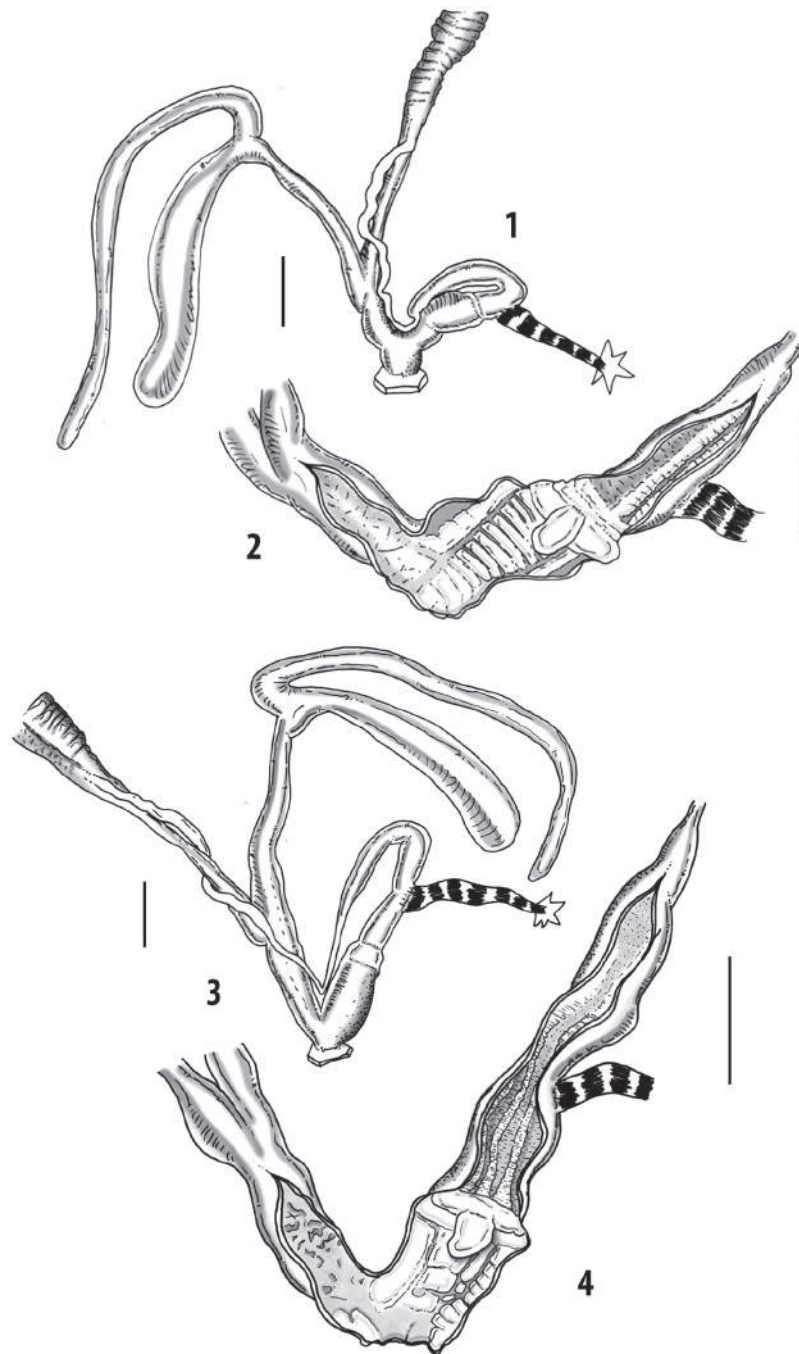


Figure 20. *Siciliaria calcarae orlandoii* Liberto, Reitano, Giglio, Colomba & Sparacio, 2016, Bosco Ficuzza **20.1** whole distal genital organs **20.2** internal distal part of genital organs. *Siciliaria calcarae cruenta* ssp. nov., Monte Gibilmesì **20.3** whole distal genital organs **20.4** internal distal part of genital organs.



Figure 21. *Siciliaria calcarae orlandoii* Liberto, Reitano, Giglio, Colomba & Sparacio, 2016, Bosco Ficuzza **21.1** shell **21.2** detail of the aperture **21.3** clausiliar plate double side **21.4** shell **21.5** detail of the aperture. *Siciliaria calcarae cruenta* ssp. nov., Monte Gibilmesì **21.6** shell **21.7** detail of the aperture **21.8** shell **21.9** detail of the aperture **21.10** view of the clausiliar plate.

is distally receding and bent upwards. The plate is somehow cylindrical and gutter-like. The palatal edge against distal end bent upwards and more or less blunt.

Measurements. *Holotype*: not decollate shell height 19.2, whorl width 4.4, aperture height 4.3, aperture width 3.2. *Paratypes* (n = 11, not decollate): shell height 19.4 ± 1.0 , whorl width 4.5 ± 0.3 , aperture height 4.3 ± 0.3 , aperture width 3.1 ± 0.2 .

External morphology of the genital organs (Fig. 20.3). The FO is longer than the V (FO/V range 1.8–2.1). The VD is thin along its whole course. The FDBC is slightly shorter than the BC+SDBC (FDBC/BC+SDBC range 0.8–0.9). The BC+SDBC is club-like to cylindrical and longer than the V (BC+SDBC/V range 2.1–2.3), with no clear distinction between the SDBC and the BC. The apex is big and rounded. The D is longer than the V (D/V range 3.5–3.8) and longer than the BC+SDBC (D/BC+SDBC range 1.3–1.4), slightly thinner than the BC+SDBC and with a small and round apex. The V is cylindrical. The A is large. The PC is longer than the V (P+E/V range 2.9–3.1). The PR is long and robust. The E is longer than the P (E/P range 2.1–2.3) and gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Fig. 20.4). The A is smooth or with few weak fleshy folds. The P presents a large longitudinal fleshy scarcely segmented pleat. Accessory pleats are also present, heavily segmented or smooth, running from the proximal part of the P as far as the A. The fine structure of the penial wall is smooth. The penial pseudopapilla is big, rhombus-shaped and smooth. The P-E transition presents a first distal ER, the PP originates from the second proximal ER. The ELP are not connected to the second proximal ER. The epiphallar formula is: 1ER+2ER(PP)+ELP. The E shows a pattern of 3 to 4 irregular longitudinal extremely fringed pleats. These pleats merge one into another forming two main fringed pleats that run as far as the VD. The V shows a weak irregular pattern of smooth pleats.

Comparative and taxonomical remarks. The morphologically most similar taxon to *Siciliaria calcarae cruenta* ssp. nov. is *Siciliaria calcarae borgettensis* ssp. nov., but it differs from the latter by its very dark and remarkably smoother shell and the AUPP is not sharp but always suffused and almost not visible from the aperture. As regards the genital organs, contrary to *Siciliaria calcarae borgettensis* ssp. nov., *Siciliaria calcarae cruenta* ssp. nov. presents a very long SDBC+BC and FO. The sculpturing of the internal penis differs by the less fringed longitudinal pleats and the EPLs that reach proximally back as far as the beginning of the VD. *Siciliaria calcarae cruenta* ssp. nov. is similar to *Siciliaria calcarae orlandoi*, anyhow the latter presents a more finely striated shell, its AUPP is stronger and usually closer to the lunella. It was found in haplogroup 1, while *Siciliaria calcarae cruenta* ssp. nov. is in the haplogroup 2.

Distribution. *Siciliaria calcarae cruenta* ssp. nov. is known only from the type locality: northern slopes of Monte Gibilmesì near Sagana (Montelepre). Further field investigation is needed in order to determine the actual distribution of the taxon.

Ecology. This subspecies was found climbing on limestone cliffs hiding among moss and rocks crevices.

Etymology. *Siciliaria calcarae cruenta* ssp. nov. was named after its intense dark red colour of the shell (*cruentus* = *bloody*).

***Siciliaria ferrox* Brandt, 1961**

Figs 1.F, 22.1–22.6, 23.1–23.4, 24.15–24.16

(?) Clausilia confinata commeata – Westerlund 1892: 47.*Siciliaria ferrox* Brandt 1961: 6.*Siciliaria (Siciliaria) ferrox* – Manganelli et al. 1995: 25.*Siciliaria ferrox* – Reitano et al. 2007: 328.*Siciliaria ferrox* – Welter-Schultes 2012: 339.*Siciliaria ferrox* – Liberto et al. 2015: 2015: 489.*Charpentieria ferrox* – De Mattia 2017e.

Remarks. In the COI tree (Fig. 4) *Siciliaria ferrox* forms a separate subclade, which is separated by ~17% p distance from the other *Siciliaria* species. This species is restricted to the easternmost area of *Siciliaria* distribution, in the environs of Trabia, Altavilla Milicia and Termini Imerese. It is allotopic, isolated from all other *Siciliaria* species, except for the area of Montagna Grande, where also *S. calcarae* was reported (Nordsieck 2013b: 8). The species presents a distinctive shell as stated by Brandt (1961: 6): “(...) die sich durch den doppelten Nackenkiel und die zwei falschen oberen Gaumenfalten unterscheidet.” Following our genital anatomical investigations, the internal structure of the genital organs revealed to be unique among the *Siciliaria* species, namely an extremely modified ER that becomes finely longitudinally fringed (Fig. 22.2). Moreover, the penial papilla is uncommonly long and irregular (Fig. 22.2–22.3) and the ELP are extremely fringed as well.

The status of *Clausilia confinata commeata* Westerlund, 1892 (Westerlund 1892: 47) is not clear as its original description is poor, lacking the description of essential shell characters (AUPP) and unavailability of the type material (Reitano et al. 2007: 328).

Specimens examined. ITALY, Sicily, Trabia, Contrada Sant’Onofrio, 170 m asl, 37°59'17.62"N, 13°36'51.11"E, [Lab ID Sf_1, COI: MW758922, ITS2: MW757115; Lab ID Sf_2, COI: MW758917], W. De Mattia and J. Macor leg., 21.xii.2007. 3 dissected spm.

Shell (Figs 23.1–23.4, 24.15, 24.16). Shell mostly not decollate; whorls ribbed, sutural papillae recognisable; dorsal keel distinct or indistinct; inferior lamella moderately high or high; two anterior upper palatal plicae present, upper one mostly separated from upper palatal plica; palatal edge of clausilium plate distally less or not receding, palatal edge distally not bent upwards (as in Nordsieck 2013b).

Measurements (n = 32, decollate). shell height 17.7 ± 0.7 , whorl width 3.8 ± 0.1 , aperture height 3.6 ± 0.2 , aperture width 2.4 ± 0.2 .

External morphology of the genital organs (Fig. 21.1). The FO is longer than the V (FO/V range 1.4–1.9). The VD is thin along its whole course except for its proximal section where it is wider. The FDDB is longer than the BC+SDDB (FDDB/BC+SDDB range 1.6–2.1). The BC+SDDB is club-like and slightly shorter than the V (BC+SDDB/V range 0.8–0.9), with no clear distinction between the SDDB and

the BC. The apex is wide and round. The D is longer than the V (D/V range 1.8–2.0) and longer than the BC+SDBC (D/BC+SDBC range 1.9–2.2), thinner than the BC+SDBC and with a pointed apex. The V is short, wide and cylindrical. The A is small. The PC is longer than the V (P+E/V range 2.0.7–2.2). The PR is long and thin. The E is slightly thinner and shorter than the P (E/P range 0.8–0.9), almost abruptly shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 22.3–22.6). The A shows small irregular pleats. These pleats are the direct continuation of the irregular sculpture of both the distal P and V. Proximally, the P presents three or four fleshy pads.

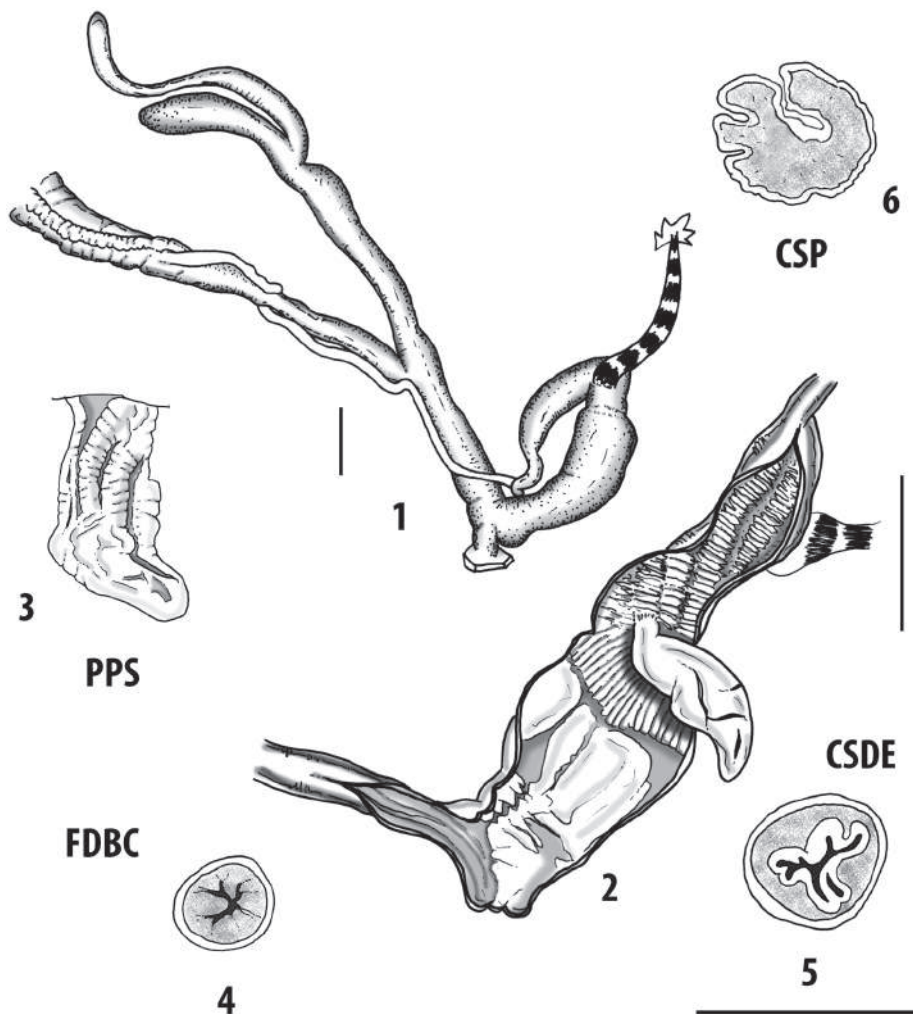


Figure 22 *Siciliaria ferrox* (Brandt, 1961). Trabria Sant’Onofrio **22.1** whole distal genital organs **22.2** internal distal part of genital organs **22.3** detail of the pseudopapilla **22.4** cross section of the FDBC **22.5** cross section of the distal epiphallus **22.6** cross section of the pseudopapilla.

These pleats turn into an irregular-wrinkly pattern towards the distal part. The PP is always big, irregular and wrinkly. It is tapered towards the apex that is elongated and irregular. In cross section a clear folding is visible. It originates almost directly from the epiphallar transition wall. The transition wall shows an extremely irregular surface with a set of longitudinal papillated “pleats”. The transition area presents a particular structure, namely an extremely longitudinally fringed ring. It is not clear if the characteristic epiphallar ring becomes this fringed ring or it is missing and replaced by this unique structure. The epiphallus shows two main longitudinal extremely fringed pleats. The V shows a smooth irregular pattern of fine longitudinal pleats.

Ecology. *Siciliaria ferrox* inhabits limestone walls, hiding in rocks cracks and crevices. According to De Mattia (2017e) *Siciliaria ferrox* is considered as Critically Endangered following the IUCN criteria B1ab(iii)+2ab(iii).

Distribution. *Siciliaria ferrox* occupies the easternmost part of the distribution range of the northwestern Sicilian *Siciliaria*. It is found from Altavilla Milicia, Sant’Onofrio to Termini Imerese.

***Siciliaria tiberii* (A. Schmidt, 1868), s. l.**

Remarks. *Siciliaria tiberii* s. l. forms an independent subclade in the COI tree and is separated from the other *Siciliaria* species by 14.3–17.8% (Fig. 4, Table 3).



Figure 23. *Siciliaria ferrox* (Brandt, 1961). Trabia Sant’Onofrio **23.1** shell **23.2** detail of the aperture **23.3** shell **23.4** detail of the aperture.

***Siciliaria tiberii tiberii* (A. Schmidt, 1868)**

Figs 1.F, 25.1–25.2, 26.1–26.5, 29.1–29.3

Clausilia tiberii Schmidt 1868: 40.*Clausilia tiberiana* Benoit 1876: 152.*Siciliaria tiberii* – Boettger 1877: 33.*Siciliaria (Siciliaria) tiberii* – Nordsieck 1979: 259.*Charpentieria tiberii* – Beckmann 2004: 188.*Charpentieria (Siciliaria) tiberii tiberii* – Nordsieck 2007: 54.*Siciliaria tiberii* – Welter-Schultes 2012: 343.*Siciliaria tiberii* – Nordsieck 2013b: 8.*Charpentieria tiberii* – De Mattia 2017f.

Specimens examined. ITALY, Sicily, Terrasini, Capo Rama, 30 m asl, 38°08'19.06"N, 13°03'14.01"E, [Lab ID 19_1, COI: MW758919, ITS2: MW757116, MW757117; Lab ID 19_2, COI: MW758920], W. De Mattia and J. Macor leg., 16.xii.2007. 3 dissected spm.

Shell (Figs 26.1–26.5, 29.1–29.3). Shell decollate; whorls ribbed; dorsal keel prominent; inferior lamella high to very high; anterior upper palatal plica strong and long, separated from the lunella; sometimes the anterior upper palatal plica presents a distal knob, sometimes another lower weak upper palatal plica is present close to the ALPP; anterior lower upper palatal plica strong and long; palatal edge of clausilium plate distally not receding, palatal edge distally more or less strongly bent upwards.

Measurements (n = 40, decollate): shell height 16.3 ± 1.2 , whorl width 4.0 ± 0.1 , aperture height 3.1 ± 0.2 , aperture width 2.3 ± 0.2 .

External morphology of the genital organs (Fig. 25.1). The FO is longer than the V (FO/V range 2.0–2.3). The VD is thin along its whole course except for the proximal part where it is larger in diameter. The FDBC is longer than the BC+SDBC (FDBC/BC+SDBC range 1.5–1.7). The BC+SDBC is club-like to cylindrical and slightly longer than the V (BC+SDBC/V range 1.2–1.5), with no clear distinction between the SDBC and the BC. The apex is big and rounded. The D is slightly longer than the V (D/V range 1.7–1.9) and slightly longer than the BC+SDBC (D/BC+SDBC range 1.1–1.5), thinner than the BC+SDBC and with a small and round apex. The V is big and cylindrical. The A is large and long. The PC is longer than the V (P+E/V range 2.9–3.4). The PR is very short and robust. The ET is clearly visible. The E is longer than the P (E/P range 1.1–1.7) and gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Fig. 25.2). The A shows few fleshy weak irregular folds. The P presents a set of transverse smooth pleats. The pleats are slightly irregular and tend to fade towards the A. The penial wall is smooth. The PP is big, elongated and markedly wrinkled with a pointed apex. It originates from one transverse epiphallar ring. The E shows two main fringed pleats that run as far as the VD. The V shows a weak irregular pattern of smooth pleats.

Ecology. *Siciliaria tiberii tiberii* is found under stones, among scree, rocky debris and on dry stonewalls along the coastline, on a limestone plateau. According to De Mattia (2017f), the taxon is Near Threatened.

Distribution. Beckmann (2004: 188), following Nordsieck's personal communications cites *Siciliaria tiberii tiberii* from a southern area surrounding San Cipirello

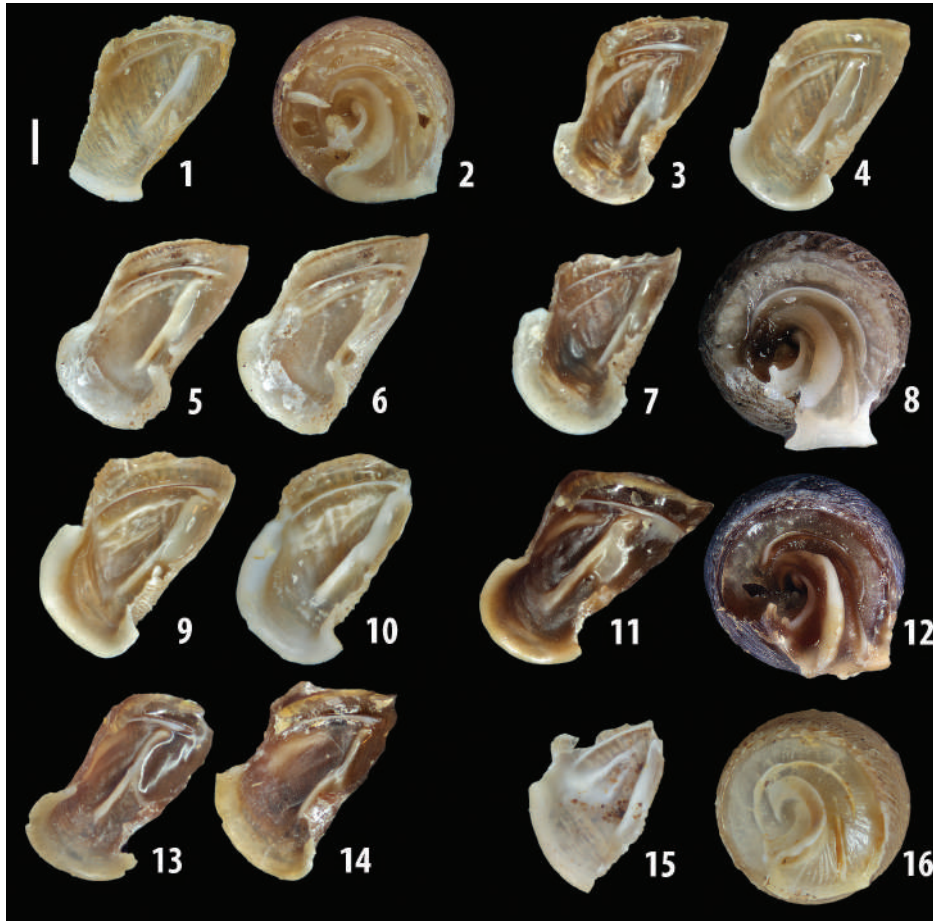


Figure 24. *Siciliaria calcarae calcarae* (Philippi, 1844), Visicari, Castellammare del Golfo **24.1** palatal plicae **24.2** parietal lamellae. *Siciliaria calcarae belliemi* (Brandt, 1961), Monte Belliemi, Partinico **24.3** palatal plicae. *Siciliaria calcarae belliemi* (Brandt, 1961), Castello di Calatubo, Alcamo **24.4** palatal plicae. *Siciliaria calcarae borgettensis* ssp. nov., road to Romitello, Borghetto **24.5–24.6** palatal plicae. *Siciliaria calcarae jatinensis* ssp. nov., San Giuseppe Jato **24.7** palatal plicae **24.8** parietal lamellae. *Siciliaria calcarae parajatensis* ssp. nov., west side Monte Kumeta **24.9–24.10** palatal plicae. *Siciliaria calcarae orlando* Liberto, Reitano, Giglio, Colomba & Sparacio, 2016, Bosco Ficuzza **24.11** palatal plicae **24.12** parietal lamellae. *Siciliaria calcarae cruenta* ssp. nov., Monte Gibilmesì **24.13–24.14** palatal plicae. *Siciliaria ferrox* (Brandt, 1961). Trabia Sant'Onofrio **24.15** palatal plicae **24.16** parietal lamellae.

(Madonna dei Furi, Monte Palmeto, Monte della Fiera, San Giuseppe Jato and Monte della Scala). As previously stated, this identification revealed to be wrong.

As a result, the actual distributional range of *Siciliaria tiberii tiberii* seems to be limited to the area from San Cataldo (Partinico) in the south to Monte Palmeto and Capo Rama (Terrasini) in the north to the northern slopes of Monte Pecoraro. Further field research is needed in order to define its actual distribution. Recent findings of Diego Viola (Trieste, Italy) from a locality between San Giuseppe Jato and Piana degli Albanesi revealed the presence of a population of *Siciliaria* cfr. *tiberii* that clearly differ, as a shell, from *S. calcarae jatinensis* ssp. nov. and *S. calcarae parajatinensis* ssp. nov. (personal communication). The poor samples available (few damaged shells) did not allow us a thorough investigation.

Remarks. Monte San Calogero in the east (cited by Nordsieck as also included in the *S. tiberii* distribution), is an isolate limestone massif 10 km SE of Termini Imerese, 50 km east of San Cipirello and 65 km SSE of Capo Rama. The presence of *S. tiberii tiberii* in this locality, due to its remarkable distance, should be confirmed by further field research and not only inferred from museum samples. Mislabelling or wrong locality assignments could have played a role in this regard (as for *Siciliaria septemPLICATA alcamoensis*, see below). The diagnosis provided by Nordsieck (2013b: 8) “Shell not or only in part decollate; dorsal keel less strong” imply that it might represent another population of *S. calcarae* s. l., yet more field and taxonomical research is needed. *Clausilia tiberiana* Paulucci 1878 is deemed as junior synonym of *Siciliaria tiberii tiberii* by Nordsieck (2013b: 8). The authorship is probably wrong as Paulucci (1878: 13) cites *Clausilia tiberiana* Benoit: Benoit (1875: 152) introduced the name *Clausilia tiberiana* as a “Elegante e bella specie de’ dintorni di S. Giuseppe delle Mortelle contrada non lungi da Palermo” and depicted this taxon in 1876 (Table VI, fig. 7). Benoit (1881: 107) stated that again that “Questa bellissima e grande conchiglia, non conosciuta dagli autori siciliani vive nella contrada detta S. Giuseppe delle Mortelle, non lungi da Palermo”. Despite intensive collecting in the surrounding of Palermo by one of the authors (WDM), we were unable to identify the position of this old toponym (also by asking locals).

***Siciliaria tiberii alcamoensis* Brandt, 1961, comb. nov.**

Figs 1.F, 25.3–25.5, 26.6–26.9, 29.4, 29.5

Siciliaria (Siciliaria) alcamoensis Brandt 1961: 9.

Siciliaria (Siciliaria) septemPLICATA alcamoensis – Manganelli et al. 1995: 25.

Siciliaria septemPLICATA hemmeni Beckmann 2004: 190.

Charpentieria (Siciliaria) septemPLICATA alcamoensis – Nordsieck 2007: 54.

Siciliaria septemPLICATA alcamoensis – Nordsieck 2013b: 10.

Examined specimens. ITALY, Sicily, Cinisi, Piano Margi, 670 m asl, 38°08'58.56"N, 13°09'25.83"E, [Lab ID 37_1, COI: MW758928, ITS2: MW757102, MW757101], W. De Mattia and J. Macor leg., 14.iv.2017. 2 dissected spm.

Shell (Figs 26.6–26.9, 29.4–29.5). Shell decollate; whorls striated to rib-striated; dorsal keel very prominent; inferior lamella high; anterior upper palatal plica present, mostly separated from upper palatal plica, sometimes a second or also third upper palatal plica present; anterior lower palatal plica strong; palatal edge of clausilium plate distally not receding, palatal edge distally more or less strongly bent upwards.

Measurements (n = 18, decollate): shell height 21.5 ± 1.3 , whorl width 5.2 ± 0.3 , aperture height 4.6 ± 0.2 , aperture width 3.4 ± 0.4 .

External morphology of the genital organs (Fig. 25.3). The FO is longer than the V (FO/V range 1.4–1.6). The VD is thin along its whole course. The FDBC is as long as the BC+SDBC (DBC/BC+SDBC = 1.0). The BC+SDBC is spindle-like to cylindrical and longer than the V (BC+SDBC/V range 1.4–1.5), with no distinction between the SDBC and the BC. The apex is pointed. The D is longer than the V (D/V range 2.5–2.6) and longer than the BC+SDBC (D/BC+SDBC range 1.6–1.8), thinner than the BC+SDBC and with a pointed apex. The V is long, cylindrical and small in diameter. The A is large. The PC is much longer than the V (P+E/V range 2.4–2.6). The PR is long and thin. The ET is clearly visible. There is a clear distinction between P and E, there is a visible ER, and a proximal narrowing. The E is longer than the P (E/P range 2.0–2.1), gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 25.4–25.5). The A shows a set of irregular fleshy folds. The P presents two or three main large longitudinal pleats. These pleats are heavily transversely segmented, getting a comb-like shape. The fine structure of the wall is smooth.

The PP is large, elongated, and heavily wrinkled. The P-E transition presents one ER with both the PP and ELP originating from the ER. The epiphallar formula is: 1ER(PP+ELP). The E shows a set of three or four smooth longitudinal pleats. The V is almost completely smooth. The wall shows a fine granulation.

Ecology. *Siciliaria tiberii alcamoensis* comb. nov. inhabits scattered isolated limestone boulders, and is hiding in rock cracks and crevices. After careful field research in a wide area around Piano Margi, the taxon revealed to be remarkably rare and scattered.

Distribution. *Siciliaria tiberii alcamoensis* comb. nov. is known only from a small area of less than 1 km² in the surrounding of the type locality: Piano Margi south of Cinisi on the Montagna Longa. Further field research is needed to define its actual distribution range.

Remarks. Brandt (1961: 9) described *Siciliaria* (*Siciliaria*) *alcamoensis* based on material from the Senckenberg Museum (SMF163949), provided by Monterosato and labelled as *Clausilia difficilis* from “Alcama in NW-Sizilien, ohne nähere Fundortangabe”. Brandt (1961: 9) introduced the name *alcamoensis* as *Clausilia difficilis* sensu Monterosato [non *Clausilia difficilis* Retowski, 1889, currently *Roseniella difficilis* (Retowski, 1889)] is a nomen nudum. Brandt (1961: 10) stated that he was not able to find this species again during field collecting nearby Alcama, but he also lists in the type material: “Paratypoides Coll. Brandt Cl. 2365/2 leg. Belluci”. He did not provide the collecting site of the paratype material so its origin is unknown, but it is conceivable that their shell morphology matches with what he described as *Siciliaria* (*Siciliaria*) *alcamoensis* indeed. Undoubtedly, the locality indication provided by Monterosato

on the original SMF label is wrong. Despite intensive field research (WDM) all over the Alcamo area and Bosco d'Alcamo/Monte Bonifato, no specimens/population was found that matches Brandt's description of *Siciliaria alcamoensis*. Beckmann (2004: 190) described *Siciliaria septemPLICATA hemmeni* from Piano Margi (Cinisi, Palermo). Its description and the pictures (Beckmann 2004: 189 and 190) match with Brandt's *Siciliaria* (*Siciliaria*) *alcamoensis*, as stated by Nordsieck (2013b: 7) and therefore, it is reasonable to assume that the Monterosato material (SMF163949) was collected from the same area of Beckmann's species.

Siciliaria tiberii alcamoensis comb. nov. (Figs 26.6–26.9) was treated as a subspecies of *S. septemPLICATA* (MolluscaBase 2021). This is due to the fact that the typical form of *S. septemPLICATA* (e.g., Monte Gallo populations, Figs 10.1–10.7), is quite similar regarding the morphology of the clausiliar apparatus, (Nordsieck 2013b), despite they greatly differ in the shell surface, sutures ornamentation, colouration, thickness and dimensions. The genital morphology (Figs 25.3–25.4) of *S. tiberii alcamoensis* greatly differs from that of *S. s. septemPLICATA* (Figs 9.1–9.2). In the COI and concatenated trees,

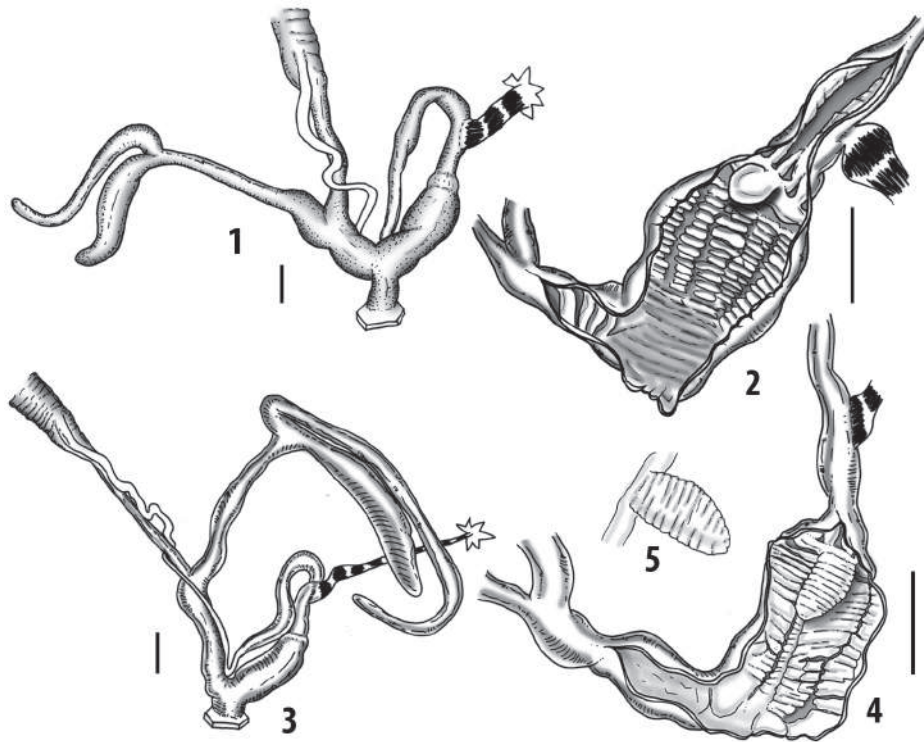


Figure 25. *Siciliaria tiberii tiberii* (A. Schmidt, 1868), Capo Rama, Terrasini **25.1** whole distal genital organs **25.2** internal distal part of genital organs. *Siciliaria tiberii alcamoensis* Brandt, 1961 comb. nov., Piano Margi, Carini **25.3** whole distal genital organs **25.4** internal distal part of genital organs **25.5** detail of the pseudopapilla.

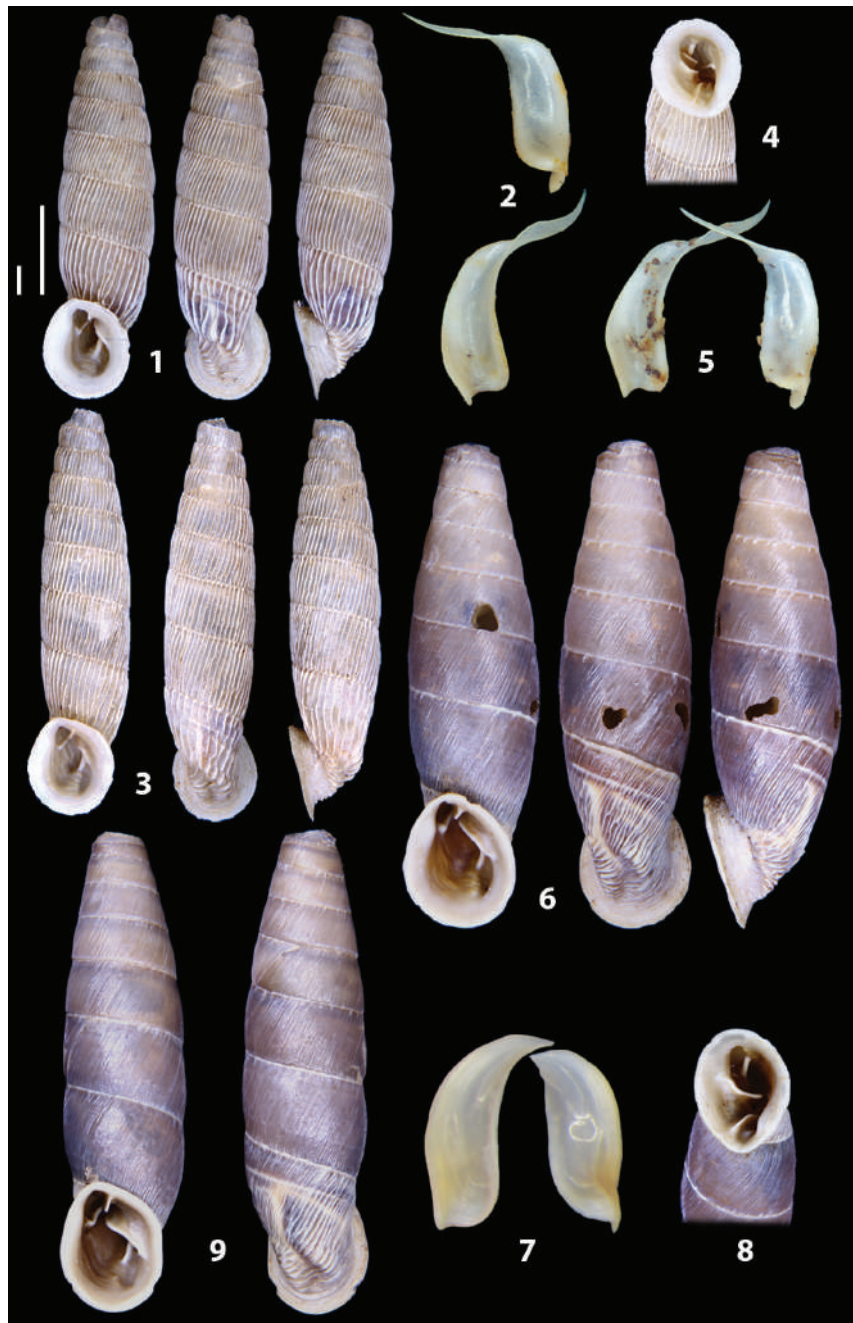


Figure 26. *Siciliaria tiberii tiberii* (A. Schmidt, 1868), Capo Rama, Terrasini **26.1** shell **26.2** clausiliar plate double side **26.3** shell **26.4** detail of the aperture **26.5** clausiliar plate double side. *Siciliaria tiberii alcamoensis* Brandt, 1961 comb. nov., Piano Margi, Carini **26.6** shell **26.7** clausiliar plate double side **26.8** detail of the aperture **26.9** shell.

S. t. alcamoensis is well embedded within the *Siciliaria tiberii* clade. Since it is found well within the distribution range of *S. tiberii* s. l., introgression due to hybridisation appears as an unlikely explanation. It might be better explained by incomplete lineage sorting. Possible interspecies hybridisation should be tested on a larger sample size with additional nuclear markers. There is no argument for considering *S. s. alcamoensis* as a subspecies of *S. septemplicata*, we here consider it a subspecies *S. tiberii*.

***Siciliaria tiberii armettensis* ssp. nov.**

<http://zoobank.org/BF64153C-F65F-4EA2-8794-269213F5A345>

Figs 1.F, 27.1–27.3, 28.1–28.3, 29.6–29.8

Type locality. ITALY, Sicily, Carini, Grotta dei Puntali o dell'Armetta, 90 m asl, 38°8'58.56"N, 13°9'25.83"E.

Type material. 1 *Holotype* (NHMW 113621) [Lab ID 38_1, COI: MW758880, ITS2: MW757098, MW757099, MW757100] and 4 *Paratypes* (NHMW 113622): Italy, Sicily, Carini, Grotta dei Puntali o dell'Armetta, 90 m asl, 38°08'58.56"N, 13°09'25.83"E, [Lab ID 38_2, COI: MW758881], W. De Mattia and J. Macor leg., 16.iv.2017. 3 dissected spm. 8 *Paratypes* (CMWDM 18227): same locality.

Shell diagnosis. Shell decollate; whorls moderately ribbed; dorsal keel prominent; inferior lamella high; anterior upper palatal plica present, knob present at distal end of the upper palatal plica, detached from the lunella; lower anterior palatal plica (ALPP) present; palatal edge of clausilium plate distally not receding, palatal edge distally strongly bent upwards.

Shell description (Figs 28.1–28.3, 29.6–29.8). The shell is elongated, fusiform, sinistral, decollate and robust. It is brown to dark reddish in colour. The shell surface has small ribs, more densely packed towards the decollate tip and gradually spreading towards the aperture. There are whitish papillae along the moderately deep sutures throughout the whole teleoconch. The spire is slowly and regularly growing, with $7\frac{1}{2}$ (after decollation) slightly convex whorls. The basal and cervical keels are well distinct. The umbilicus is closed. The aperture is roundish to subovoid and its height is $\sim \frac{1}{4}$ to $\frac{1}{5}$ of shell height. The PRI is short and it ends at the level of the L. It is not fused with the L and presents a slight thickening along its posterior end. The PRI is not visible from a frontal view of the aperture. The L is dorso-lateral to lateral. The PUPP is short or obsolete, knob-like and connected to the L. The AUPP is strong and long, detached from the L and clearly visible from the aperture. The distal end of the AUPP has a well-developed knob. The BAS starts directly from the L and it is long and strong, well visible from the aperture. The SCL is absent or resembling an irregular small thickening, connected with the lunella. The IL is very high to extremely high. The SUL is tooth-like, long and overlapping with the SPL. The SPL is long and it ends at $\frac{4}{5}$ of the last whorl. The SCOL is not visible. The peristome is continuous, markedly thickened and reflected. It is not superiorly fused to the wall of the first whorl. The palatal edge of the clausilium is distally receding and bent upwards. The

plate is cylindrical in shape. The palatal edge against the distal end is bent upwards and more or less blunt.

Measurements. *Holotype*: decollate shell height 20.1, whorl width 4.8, aperture height 4.6, aperture width 3.1. *Paratypes* (n = 35, decollate): shell height 19.7 ± 1.6 , whorl width 4.6 ± 0.2 , aperture height 4.2 ± 0.3 , aperture width 2.8 ± 0.3 .

External morphology of the genital organs (Fig. 27.1). The FO is longer than the V (FO/V range 1.5–1.8). The VD is thin along its whole course. The FDBC is slightly longer than the BC+SDBC (FDBC/BC+SDBC range 1.0–1.3). The BC+SDBC is irregularly spindle-like and longer than the V (BC+SDBC/V range 1.6–1.9), with no distinction between the SDBC and the BC. The apex is pointed. The D is longer than the V (D/V range 3.0–3.2) and longer than the BC+SDBC (D/BC+SDBC range 2.1–2.3), much thinner than the BC+SDBC and with a small but round apex. The V is short, cylindrical and large in diameter. The A is large. The PC is much longer than the V (P+E/V range 2.6–2.8). The PR is short and robust. The ET is not clearly visible. The E is longer than the P (E/P range 1.7–1.9), gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 27.2, 27.3). The A shows a set of irregular fleshy folds. The P presents a main longitudinal fleshy fold that goes from the PP as far as the A. This fold is heavily segmented in an oblique way. Additionally, the P also shows a set of small longitudinal and irregular small pleats that reach the A. The fine structure of the wall is smooth. The PP is small, elongated and smooth. The P-E transition presents a first distal and a second median ER while both the PP and ELP originates from a third proximal ER. The epiphallar formula is: 1ER+2ER+3ER(PP+ELP). The E shows five to seven smooth longitudinal pleats that proximally turn into a pattern of coarse small weak pleats that gradually fade away towards the VD. The V shows a set of heavy and robust transverse smooth pleats that proximally begin somehow irregularly. The wall is smooth.

Comparative analysis. *Siciliaria tiberii armettensis* ssp. nov., like the nominate subspecies, has a ribbed shell and it is clearly distinguishable from all the remaining subspecies that present a more or less striated but ribless shell surface. Nonetheless, the nominate subspecies shows a stronger ribbing, with elevated and robust ribs. The distal end of the AUPP always presents a knob that is well visible from the frontal view (Figs 28.1–28.2). This feature is shared also by the nominate subspecies (Fig. 26.1) but only by the $\approx 25\%$ of the investigated specimens (n = 40).

Ecology. *Siciliaria tiberii armettensis* ssp. nov. inhabits east-exposed limestone walls and cliffs, hiding among tuft of vegetation, rocks cracks and crevices.

Distribution. *Siciliaria tiberii armettensis* ssp. nov. is exclusively known from the type locality, the surroundings of the Grotta dei Puntali o dell'Armetta. Further field investigation along the Monte Pecoraro eastern slopes is needed in order to determine the actual distribution of the taxon. Grotta dei Puntali o dell'Armetta are included in the protected area Riserva Naturale Grotta dei Puntali.

Etymology. The taxon is named after the Grotte dell'Armetta, a complex of natural caves where wall engravings and stone handcrafted tools, dated from the Paleolithic to the Bronze Age, were discovered (Mannino 1978).

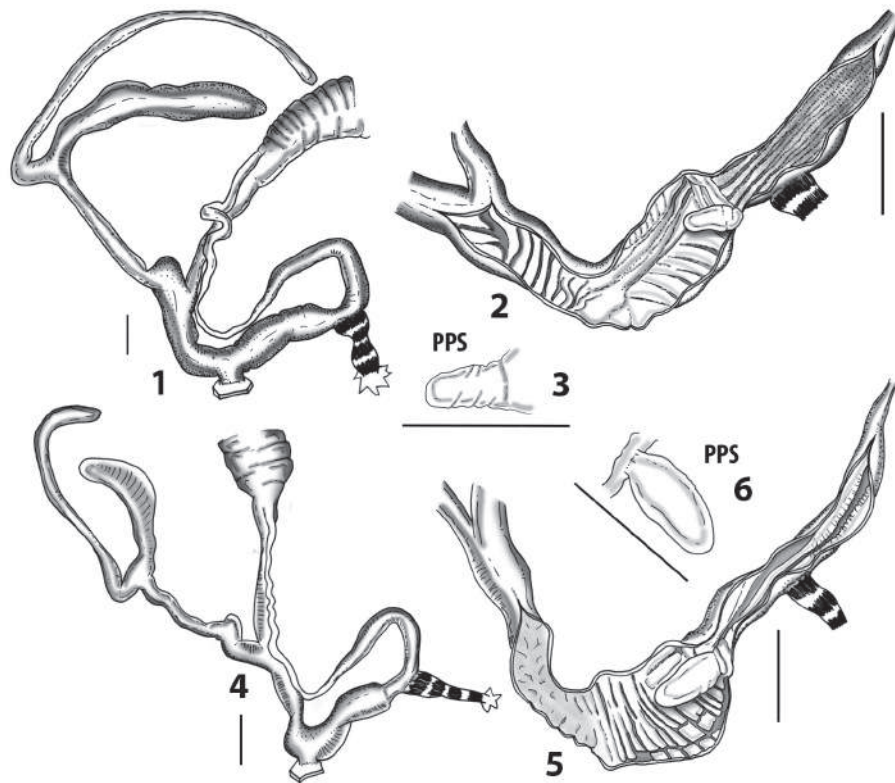


Figure 27. *Siciliaria tiberii armettensis* ssp. nov., Grotta dei Puntali, Carini **27.1** whole distal genital organs **27.2** internal distal part of genital organs **27.3** detail of the pseudopapilla. *Siciliaria tiberii scalettensis* Beckmann, 2004 Portella Scaletta, Villagrazia **27.4** whole distal genital organs **27.5** internal distal part of genital organs **27.6** detail of the pseudopapilla.

***Siciliaria tiberii scalettensis* Beckmann, 2004**

Figs 1.F, 27.4–27.6, 28.5–28.9, 29.9–29.11

Charpentieria (Siciliaria) tiberii scalettensis Beckmann 2004: 188.

Siciliaria tiberii scalettensis – Nordsieck 2007: 54.

Siciliaria tiberii scalettensis – Nordsieck 2013b: 10.

Specimens examined. ITALY, Sicily, Cinisi, Portella Scaletta, 90 m asl, 38°10'35.53"N, 13°07'27.22"E, [Lab ID 17_2, COI: MW758923, ITS2: MW757108, MW757109, MW757110], W. De Mattia and J. Macor leg., 18.iv.2017. 3 dissected spm. Italy, Sicily, Cinisi, along the SS113 road from Villagrazia di Carini to Cinisi, 70 m asl, 38°10'42.45"N, 13°07'34.50"E, [Lab ID 39_1, COI: MW758882, ITS2: MW757095, MW757096, MW757097], W. De Mattia and J. Macor leg., 18.iv.2017. 2 dissected spm.

Shell (Figs 28.5–28.9, 29.9–29.11). Shell mostly decollate; whorls striated; dorsal keel mostly prominent; inferior lamella high to very high; anterior upper palatal



Figure 28. *Siciliaria tiberii armettensis* ssp. nov., Grotta dei Puntali, Carini **28.1** shell **28.2** shell clausiliar plate double side **28.3** detail of the aperture **28.4** clausiliar plate double side. *Siciliaria tiberii scalettensis* Beckmann, 2004 Portella Scaletta, Villagrazia **28.5** shell **28.6** detail of the aperture **28.7** shell **28.8** detail of the aperture **28.9** clausiliar plate double side.

plica present, separated or connected with upper palatal plica; a second lower separate upper palatal present, anterior lower palatal plica strong; palatal edge of clausilium plate distally not receding, palatal edge distally more or less strongly bent upwards.

Measurements (n = 45, decollate). shell height 18.5 ± 1.3 , whorl width 4.6 ± 0.2 , aperture height 4.0 ± 0.2 , aperture width 2.9 ± 0.2 .

External morphology of the genital organs (Fig. 27.4). The FO is as long as the V (FO/V = 1.0). The VD is thin along its whole course. The FDBC is slightly longer than the BC+SDBC (FDBC/BC+SDBC range 1.2–1.3). The BC+SDBC is club-like to cylindrical and slightly shorter than the V (BC+SDBC/V range 0.8–0.9), with no clear distinction between the SDBC and the BC. The apex is big and rounded. The D is longer than the V (D/V range 1.3–1.7) and longer than the BC+SDBC (D/BC+SDBC range 1.6–1.8), thinner than the BC+SDBC and with a small and round apex. The V is cylindrical. The A is large. The PC is longer than the V (P+E/V range 1.5–1.9). The PR is short and robust. The ET is visible. The E is longer than the P (E/P range 2.0–2.2) and gradually shrinking and turning into the VD.



Figure 29. *Siciliaria tiberii tiberii* (A. Schmidt, 1868), Capo Rama, Terrasini **29.1–29.2** palatal plicae **29.3** parietal lamellae. *Siciliaria tiberii alcamoensis* Brandt, 1961 comb. nov., Piano Margi, Carini **29.4** parietal lamellae **29.5** palatal plicae. *Siciliaria tiberii armettensis* ssp. nov., Grotta dei Puntali, Carini **29.6** parietal lamellae **29.7–29.8** palatal plicae. *Siciliaria tiberii scalettensis* Beckmann, 2004 Portella Scaletta, Villagrazia **29.9–29.10** palatal plicae **29.11** parietal lamellae.

Internal morphology of the genital organs (Figs 27.5, 27.6). The A is smooth or with few fleshy weak, oblique folds. The P presents a set of transverse, often interrupted smooth pleats. The penial wall is smooth. The PP is big, elongated and smooth. The P-E transition presents one ER. The PP doesn't originate from an ER and is connected to ELP. The epiphallar formula is: 1ER+PP(ELP).

The P of the population from the road to Cinisi (300 from NNE of the type locality), proximally shows pleats that are longitudinal and progressively turn into a transverse pattern as proceeding towards the A. The PP is also markedly different, being heavily wrinkled but the epiphallar formula is the same as the LT. The E shows a pattern of three or four smooth longitudinal pleats. These pleats merge one into another forming two main fringed pleats that run as far as the VD. The V is almost smooth with a very fine granulation.

Ecology. *Siciliaria tiberii scalettensis* inhabits limestone walls and cliffs, hiding among tuft of vegetation, rocks cracks and crevices. The taxon is common at the type locality (Villa Paradiso) with a rich population and few more scattered, smaller populations among the limestone spur.

Distribution. *Siciliaria tiberii scalettensis* is known only from a small area of less than 0.5 km² around the of the type locality: Portella Scaletta along the SS113 road, from Villagrazia di Carini to Cinisi (Palermo). It was collected along a limestone spur heading NNE.

Remarks. 90% of the specimens (n = 45) of *Siciliaria tiberii scalettensis* present a second, lower AUPP, shorter than the superior AUPP and detached both from the AUPP and the L. This feature is shared only with the nominate subspecies.

Sicania taxonomic part

In Table 7 the main differences among the *Sicania* taxa regarding both shell and genital main taxonomical characters are summarised.

Order Stylommatophora

Infraordo Clausilioidei Gray, 1855

Superfamilia Clausilioidea Gray, 1855

Familia Clausiliidae Gray, 1855

Subfamilia Alopiinae A.J. Wagner, 1913

Tribus Delimini R.A. Brandt, 1956

Genus *Sicania* Tomlin, 1929

Sicania crassicostata (L. Pfeiffer, 1856), **comb. nov.**

Figs 1.F, 30.1–30.4, 31.1–31.7, 39.1–39.2

Clausilia crassicostata L. Pfeiffer 1856: 184.

Clausilia crassicostata – Schmidt 1868: 40.

Siciliaria crassicostata – Boettger 1877: 33.

Clausilia crassicostata – Westerlund 1884: 45.

Siciliaria (Siciliaria) crassicosata – Manganelli et al. 1995: 25.

Charpentieria crassicosata – Beckmann 2004: 188.

Charpentieria crassicosata – Nordsieck 2007: 54.

Siciliaria crassicosata – Welter-Schultes 2012: 339.

Charpentieria crassicosata – De Mattia 2017g.

Remarks. The morphology of the genital organs of *Sicania crassicosata* comb. nov. revealed to be very stable in both of the investigated populations (Fig. 30.1–30.4). The internal sculpturing of P is made of large longitudinal pleats that it is a common genital trait, with very few exceptions, for all the taxa belonging to *Sicania*.

The shell is remarkably ribbed to percostated. It shares few characters with *Sicania nobilis spezialensis* comb. nov. stat. nov., e.g., the (mostly) missing AUPP, both the very short (or missing) ALPP and the spiralis (mostly) not overlapping the parietalis (Fig. 39.1–39.2).

Although *Sicania eminens* comb. nov. was initially introduced by Schmidt (1868: 40) as a variety of *Sicania crassicosata* comb. nov. due to shell similarities (and distribution proximity), the mt tree based on COI sequences reveals *Sicania crassicosata* comb. nov. as a distinct clade which is the sister group of *Sicania nobilis* s. l. (Figs 4–6). Considering the ITS2 tree and the combined tree (COI plus ITS2), the relationships among the three taxa are not well resolved. Notably, the distances between the three taxa are in the same range (~ 13%; see Table 2). The form of *Sicania crassicosata* comb. nov. from the surroundings of Tonnara di Monte Cofano is remarkably percostate, whereas the population we investigated from Mangiapane is ribbed (as stated also in Nordsieck 2013b: 9).

Specimens examined. ITALY, Sicily, Castelluzzo, cliffs W of the Tonnara di Monte Cofano, 50 m asl, 38°06'44.89"N, 12°40'34.27"E, [Lab ID 33_1, COI: MW758876; Lab ID 33_2, COI: MW758877, ITS2: MW757103, MW757104, MW757105 MW757131], W. De Mattia and J. Macor leg., 21.xii.2007. 3 dissected spm. Italy, Sicily, Custonaci, cliffs N of the Mangiapane cave, 63 m asl, 38°05'40.91"N, 12°40'10.98"E, [Lab ID 1_1, COI: MW758912, ITS2: MW757114, MW757113; Lab ID 1_4, COI: MW758924] W. De Mattia and J. Macor leg., 21.xii.2007. 2 dissected spm.

Shell (Figs 31.1–31.8, 39.1–39.2).: Shell decollate; whorls markedly ribbed, in part percostate; dorsal keel weak; inferior lamella moderately high or high; anterior upper palatal plica missing, ALPP very short or mostly missing; palatal edge of clausilium plate distally not receding, palatal edge distally somewhat or not bent upwards (Nordsieck 2013b).

Measurements (n = 24, decollate). shell height 24.6 ± 1.2 , whorl width 4.9 ± 0.1 , aperture height 4.8 ± 0.3 , aperture width 3.0 ± 0.1 .

External morphology of the genital organs (Figs 30.1, 30.3). The FO is much longer than the V (FO/V range 2.8–3.0). The VD is thin along its whole course except for its proximal section that becomes wider. The FDBC is longer than the BC+SDBC (FDBC/BC+SDBC range 1.7–1.9). The BC+SDBC is club-like and longer than the V (BC+SDBC/V = 2.0), with clear distinction between the SDBC and the BC. The apex is wide and rounded. The D is much longer than the V (D/V range 3.0–3.1) and longer than the BC+SDBC (D/BC+SDBC range 1.6–1.9), thinner than the BC+SDBC,

Table 7. Main morphological differences (shell and genital organs) among the *Sicania* taxa.

	<i>Sicania crassicosata</i> comb. nov.	<i>Sicania eminens</i> comb. nov.	<i>Sicania nobilis nobilis</i> comb. nov.	<i>Sicania nobilis spezialensis</i> comb. nov., stat. nov.
Whorls	ribbed, percostate	ribbed	weakly rib-striated	densely ribbed
Surface	opaque	opaque	white surface layer	white surface layer
Dorsal keel	weak	weak or missing	missing	missing
AUPP	missing	present, visible from outside	present, mostly not visible from outside	mostly missing
ALPP	very short or mostly missing	present, visible from outside	present, visible from outside	very short to knob-like, not visible from outside
Spiralis	not overlapping parietalis	overlapping parietalis	slightly overlapping parietalis	mostly not overlapping parietalis
Sculpturing of atrium	fleshy pleats	large fleshy pleats	irregular folds	irregular fleshy folds.
Sculpturing of vagina	smooth to an irregular	smooth to an irregular	smooth to an irregular	distally irregular pleats, proximally oblique pleats
Sculpturing of penis	longitudinal fleshy smooth pleats	longitudinal fleshy pleats	smooth, tubercles, longitudinal, segmented pleats	longitudinal fleshy smooth pleats
Pseudopapilla	short and conical	small and rounded	big and elongate to small and round	little, rhombus-shaped and smooth
Epiphallar ring	single	single	two or three	two
Sculpturing of epiphallus	two main longitudinal pleats	two main longitudinal pleats	two main longitudinal pleats	three or four irregular longitudinal fringed pleats

slim and with a pointed apex. The V is wide and cylindrical. The A is large. The PC is much longer than the V (P+E/V range 3.2–3.4). The PR is short and robust. The ET is missing. The E is thinner and slightly longer than the P (E/P range 1.0–1.3), gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 30.2, 30.4). The A shows few large fleshy pleats that are the direct continuation of the penial pleats. The P presents 3–6 longitudinal heavy fleshy smooth pleats that can sometimes become wrinkly and segmented. The fine structure of the wall is smooth. The V shows an irregular pattern of fine pleats. Distally, the V shows a large fleshy continuous cushion that abruptly turns proximally into a dense and irregular net-like pattern of small smooth pleats. The PP is big, short and conical with a pointed apex. The PP is big, elongated and smooth. The P-E transition presents two slightly different structures in the two dissected population. The population from Tonnara Cofano presents one ER. The PP does not originate from an ER and is connected to ELP. The epiphallar formula is: 1ER+PP(ELP). The Mangiapane population presents one ER with the PP originating from it. The ELP are not connected with the ER. The epiphallar formula is: 1ER(PP)+ELP. The E has two main longitudinal pleats, heavily segmented towards the VD, that proximally fade or can also show three smooth longitudinal pleats that almost abruptly turn into an irregular pattern of dense, small, transversely-oriented papillae.

Ecology. *Sicania crassicosata* comb. nov. was collected on limestone cliffs or under rocks and boulders. According to De Mattia (2017g) *Sicania crassicosata* comb. nov. is considered Critically Endangered, following the IUCN criteria B1ab(i,ii,iv,v); C2a(ii) mainly due its very restricted geographic range and the severe population fragmentation.

Distribution. This species has a very limited distribution range, restricted to the western part of Monte Cofano north of Custonaci (Tonnara di Cofano and Cornino). A (probably) introduced population is known to occur on the Island of Favignana (Trapani) (Nordsieck 2013b), but we did not have the opportunity to check this record in the field, in order to assess whether or not the population is still extant.

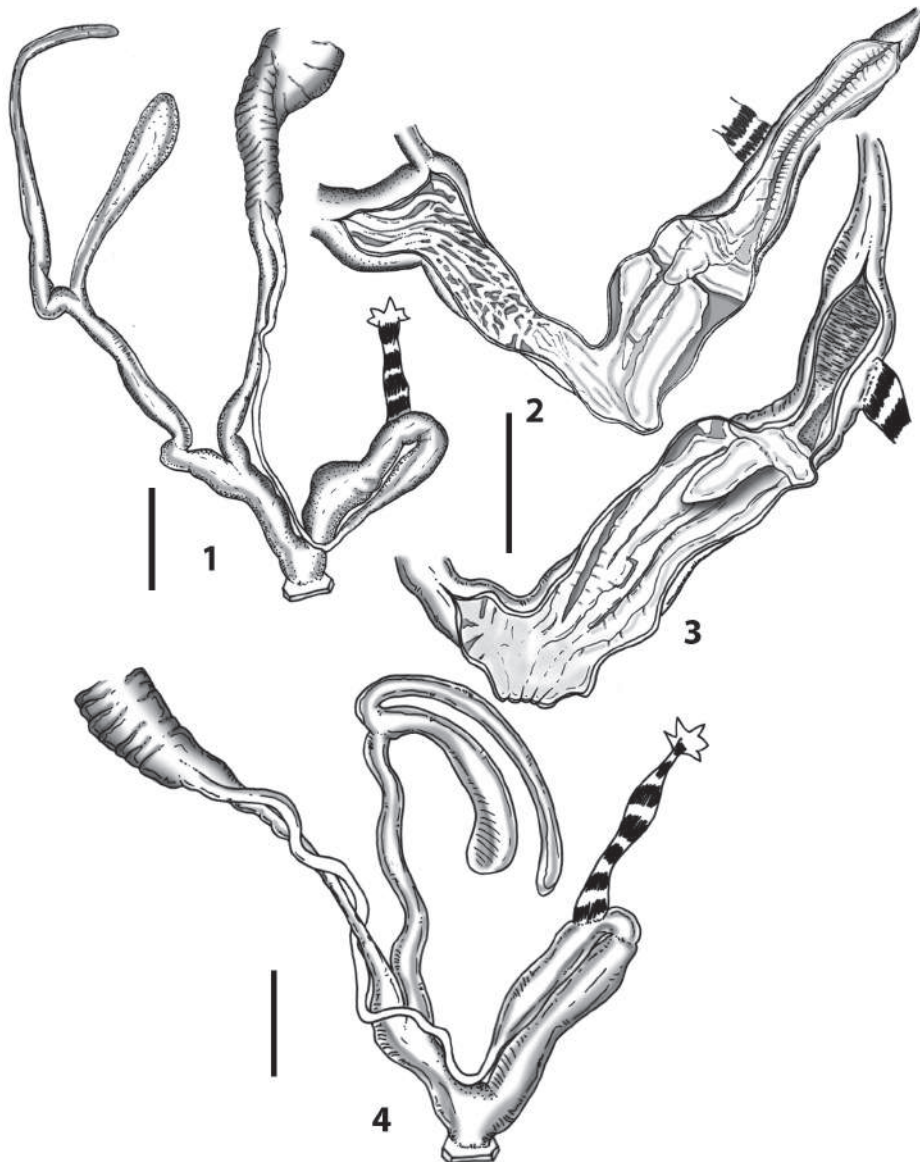


Figure 30. *Sicania crassicostata* (L. Pfeiffer, 1856), comb. nov., Monte Cofano **30.1** whole distal genital organs **30.2** internal distal part of genital organs **30.3** whole distal genital organs **30.4** internal distal part of genital organs.



Figure 31. *Sicilia crassicostata* (L. Pfeiffer, 1856), comb. nov., Monte Cofano **31.1** shell **31.2** detail of the aperture **31.3** clausiliar plate double side **31.4** detail of the columellar side of last whorl **31.5** shell **31.6** detail of the aperture **31.7** clausiliar plate double side. Custonaci **31.8** shell.

***Sicania eminens* (A. Schmidt, 1868), comb. nov.**

Figs 1.F, 32.1–32.9, 33.1–33.12, 39.3, 39.4

Clausilia crassicosata var. *eminens* Schmidt 1868: 40.*Clausilia crassicosata* var. *eminens* – Westerlund 1884: 45.*Siciliaria crassicosata eminens* – Alzona 1971: 92.*Charpentieria eminens* – Beckmann 2004: 188.*Charpentieria eminens* – Nordsieck 2007: 53.*Siciliaria crassicosata* var. *eminens* – Welter-Schultes 2012: 339.*Siciliaria eminens* – Nordsieck 2013b: 9.*Charpentieria eminens* – De Mattia 2017h.

Remarks. *Sicania eminens* comb. nov. inhabits a restricted range that approximately includes the surroundings of Custonaci and the S slopes of Monte Cofano in the east as far as Castellammare del Golfo in the west.

The general genital outline is stable for all the dissected populations. The internal sculpturing of the penis reveals a basic pattern of one to four longitudinal pleats. The remaining main genital internal parts (penial pseudopapilla, epiphallus and atrium) show good stability despite slight variations, which will be described below. Only the internal wall of the vagina could be either smooth or with a strong sculpturing.

The shell is remarkably ribbed although the number of the ribs (density) progressively decreases along a geographical S-N axis, whereby simultaneously the thickness of the ribs increases. Southern populations, e.g., from Dolina Buffara and Baglio Messina, present a dense ribbing (with an average of 70 ribs along the first whorl) whereby the northernmost populations from the environs of Mangiapane Caves and Scurati show much less rib density (with an average of 32 ribs along the first whorl). The northern populations are found a few hundred meters from the southernmost population of *Sicania crassicosata* comb. nov. and could be, by inexperienced eyes, easily confused with it. Probably this is the reason why the taxon was for long time considered as a subspecies of *Sicania crassicosata* comb. nov. (Alzona, 1971: 92). Nevertheless, *Sicania eminens* comb. nov. can be distinguished by the markedly pyriform shape of its shell and the presence of a strong anterior upper palatal plica and the ALPP, both of them clearly visible from outside of the shell's aperture and missing in *Sicania crassicosata* comb. nov. (Figs 31.1–31.7, 39.1, 39.2).

Sicania eminens comb. nov. is monophyletic in both the COI and in the ITS2 tree (both well supported). The ITS2 sequences were almost identical (Fig. 5). The distribution of the samples within the subclade, in spite of their low number, approximately reflects the S-N gradient in the rib density of the shells. The upper part includes the southern high-rib-density populations of Dolina Buffara and Baglio Messina, whereas the lower part includes the low-rib-density populations of Custonaci and Contrada Scurati. The results of the molecular genetic analysis, the morphology of the genital organs, conchological and biogeographic investigations confirm the status of *Sicania eminens* comb. nov. as a valid species, clearly distinguished from *Sicania crassicosata* comb. nov.

Specimens examined. ITALY, Sicily, Custonaci, contrada Scurati, crossing with Strada Provinciale 19, 60 m asl, 38°4'55.97"N, 12°40'9.91"E, [Lab ID 51_1, COI: MW758896, ITS2 MW757072; Lab ID 51_2, COI: MW758897], W. De Mattia and J. Macor leg., 12.iv.2017. 2 dissected specimens. Italy, Sicily, Custonaci, contrada Scurati, 60 m asl, 38°05'18.10"N, 12°40'17.18"E, [Lab ID 52_1, COI: MW758898; Lab ID 52_2, COI: MW758899, ITS2 MW757071, MW757085, MW757086], W. De Mattia and J. Macor leg., 12.iv.2017. 2 dissected spm. ITALY, Sicily, Custonaci, contrada Scurati, crossing with Strada Provinciale 18, 65 m asl, 38°4'56.04"N, 12°40'9.86"E, W. De Mattia and J. Macor leg., 12.iv.2017. 2 dissected spm. ITALY, Sicily, Custonaci, contrada Scurati, limestone cliffs S of the village, 60 m asl, 38°06'44.89"N, 12°40'34.27"E, W. De Mattia and J. Macor leg., 12.iv.2017. 2 dissected spm. Italy, Sicily, Custonaci, Buffara, NE side of the hollow, 150 m asl, 38°04'0.52"N, 12°41'1.34"E, [Lab ID 49_1, COI: MW758892; Lab ID 49_2, COI: MW758893], W. De Mattia and J. Macor leg., 12.iv.2017. 2 dissected spm. ITALY, Sicily, Custonaci, Baglio Messina, 340 m asl, 38°04'6.38"N, 12°41'48.68"E, [Lab ID 50_1, COI: MW758894, ITS2 MW757073, MW757074, MW757075, MW757076; Lab ID 50_2, COI: MW758895], W. De Mattia and J. Macor leg., 12.iv.2017. 2 dissected spm.

Shell (Figs 33.1–33.12, 39.3, 39.4). shell decollate; whorls ribbed; dorsal keel weak or missing; inferior lamella mostly high; anterior upper palatal plica strong, mostly separated from upper palatal plica, ALPP tending to be shortened but visible; palatal edge of clausilium plate distally not receding, palatal edge distally somewhat or not bent upwards (Nordsieck 2013b).

Measurements (n = 45, decollate): shell height 20.1 ± 0.7 , whorl width 4.7 ± 0.3 , aperture height 4.7 ± 0.4 , aperture width 3.1 ± 0.1 .

External morphology of the genital organs (Figs 32.1, 32.4, 32.6, 32.8). The FO is remarkably longer than the V (FO/V range 4.1–4.7). The VD is thin along its whole course. The FDBC is longer than the BC+SDBC (FDBC/BC+SDBC range 1.6–1.9). The BC+SDBC is club-like and longer than the V (BC+SDBC/V range 2.1–2.5), with distinction between the SDBC and the BC. The apex is wide and round. The D is much longer than the V (D/V range 4.4–4.9) and longer than the BC+SDBC (D/BC+SDBC range 2.4–2.7), thinner than the BC+SDBC, slim and with a pointed apex. The V is short, wide and cylindrical. The A is very large. The PC is much longer than the V (P+E/V range 3.7–4.2). The PR is short and robust. The ET is not present in all the dissected samples. The E is thinner and shorter than the P (E/P range 0.8–0.9), almost abruptly shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 32.2, 32.3, 32.5, 32.7, 32.9). The A shows few large fleshy pleats that are the direct continuation of the penial pleats. The P presents 1–4 longitudinal fleshy pleats. These pleats can be totally smooth (Contrada Scurati), only one or few of them are segmented (metameric) (Contrada Scurati, Dolina Buffara) or the only pleat is proximally segmented and distally irregular (Baglio Messina). The fine structure of the wall is smooth. The PP is

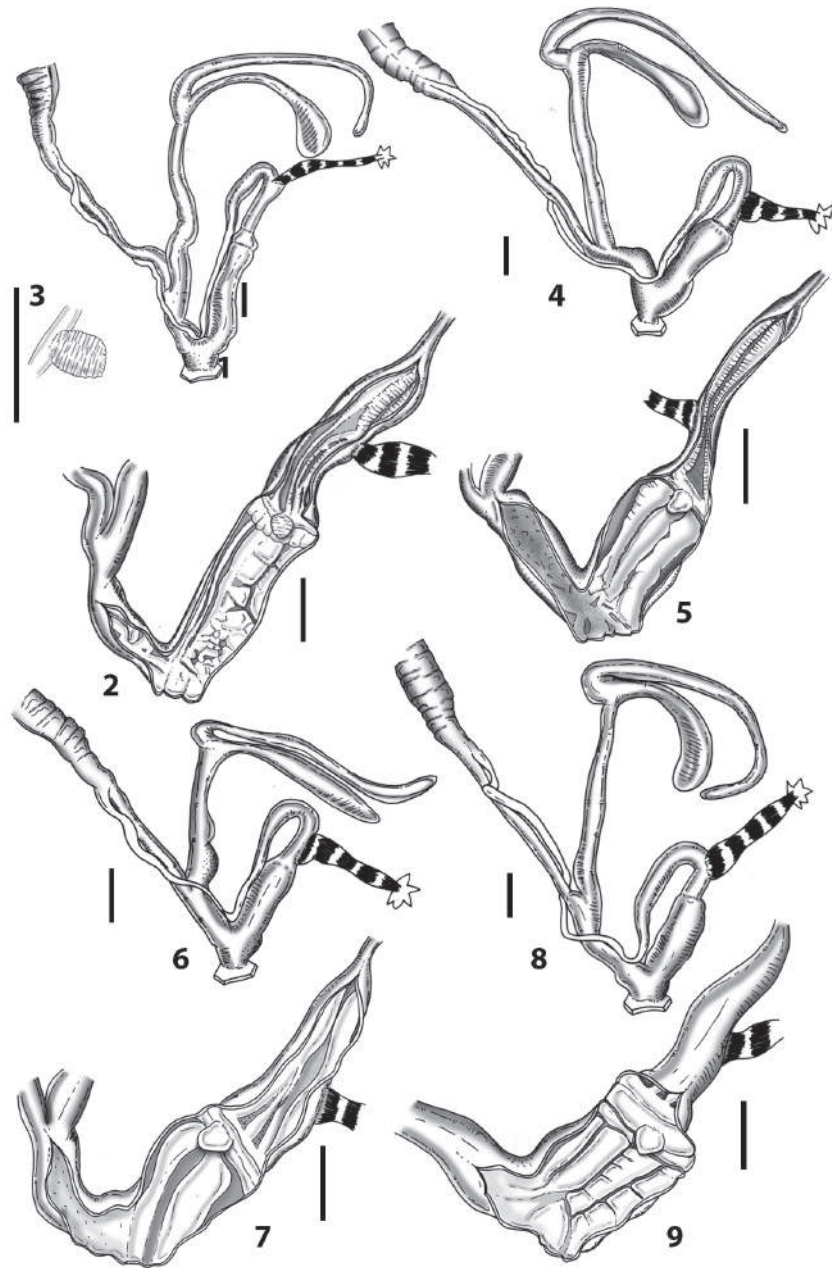


Figure 32. *Sicania eminens* (A. Schmidt, 1868), comb. nov., Custonaci, Baglio Messina **32.1** whole distal genital organs **32.2** internal distal part of genital organs **32.3** detail of the pseudopapilla. Dolina Buffara **32.4** whole distal genital organs **32.5** internal distal part of genital organs. Contrada Scurati, Custonaci **32.6** whole distal genital organs **32.7** internal distal part of genital organs. Contrada Scurati toward Mangiapane **32.8** whole distal genital organs **32.9** internal distal part of genital organs.

always very small and rounded. It is smooth but in Baglio Messina where it is remarkably wrinkly. The P-E transition presents three slightly different structures in the dissected populations. The samples from Dolina Buffara present one ER with the PP and ELP originating from the ER. Its epiphallar formula is: 1ER(PP+ELP). The samples from Scurati show a common structure, namely a first distal ER where the PP originates and the ELP originate from the second proximal ER. The epiphallar formula is: 1ER(PP)+2ER(ELP). The population from Baglio Messina present a slight difference with a first distal ER, whereas the PP and the ELP originate from the second proximal ER. The epiphallar formula is: 1ER+2ER(PP+ELP). The E shows two main longitudinal pleats that can be either smooth or fringed. These two pleats distally originate from a set of smaller irregular pleats. The V can be either completely smooth or with a set of irregular smooth pleats.

Ecology. *Sicania eminens* comb. nov. inhabits limestone cliffs and boulders, hiding in rock cracks and crevices. It is also found climbing on tree barks and decaying woods (Custonaci, Baglio Messina). This taxon has never been found syntopic with other *Sicania* or *Siciliaria* taxa. Along its eastern distributional range, it is sympatric with *Siciliaria calcarae calcarae*. According to De Mattia (2017h) *Sicania eminens* comb. nov. is considered Endangered following the IUCN criteria B1ab(iv,v)+2ab(iv,v). Approximately 20% of its distribution range (mainly in the southern part) is currently under a heavy quarrying activity. This results in a complete habitat destruction. Only a very small part of its distributional range falls under a protected area: Riserva Naturale Orientata di Monte Cofano, between Monte Cofano and Monte Palatimone. The subpopulations are fragmented and localised over very small areas. This species is assessed as Endangered since it has a very restricted geographic range, it occurs at less than five locations and there is a continuing decline in the quality of the habitat and in the number of mature individuals due to extended periods of drought in the summer. In addition, this species is an extremely sought-after item for shell collectors and traders (De Mattia 2017h).

Distribution. The distribution range of *Sicania eminens* comb. nov. includes the southern slopes of Monte Cofano and Monte Palatimone in the north and, in the south, the line from Monte Sparagio-Castellammare del Golfo (east) and Monte Buffara (west). Nordsieck (2013b) includes the surroundings of Calatafimi and Monte Bonifato near Alcamo but recent field research failed to find this taxon in these localities.

***Sicania nobilis* (L. Pfeiffer, 1848), s. l., comb. nov.**

Remarks. *Sicania nobilis* comb. nov. s. l. has a big, weakly striated shell, mostly decoliate and whitish in colour. *Sicania nobilis* comb. nov. forms a well-supported clade in the COI tree. Even in the ITS2 tree almost all sequences cluster, except those of population 14 (SanVito Lo Capo, Torazza, 3 clones), which are found within the *S. eminens* + *S. nobilis* cluster. This might point towards hybridisation between those taxa. Such an assumption would deserve further investigation.

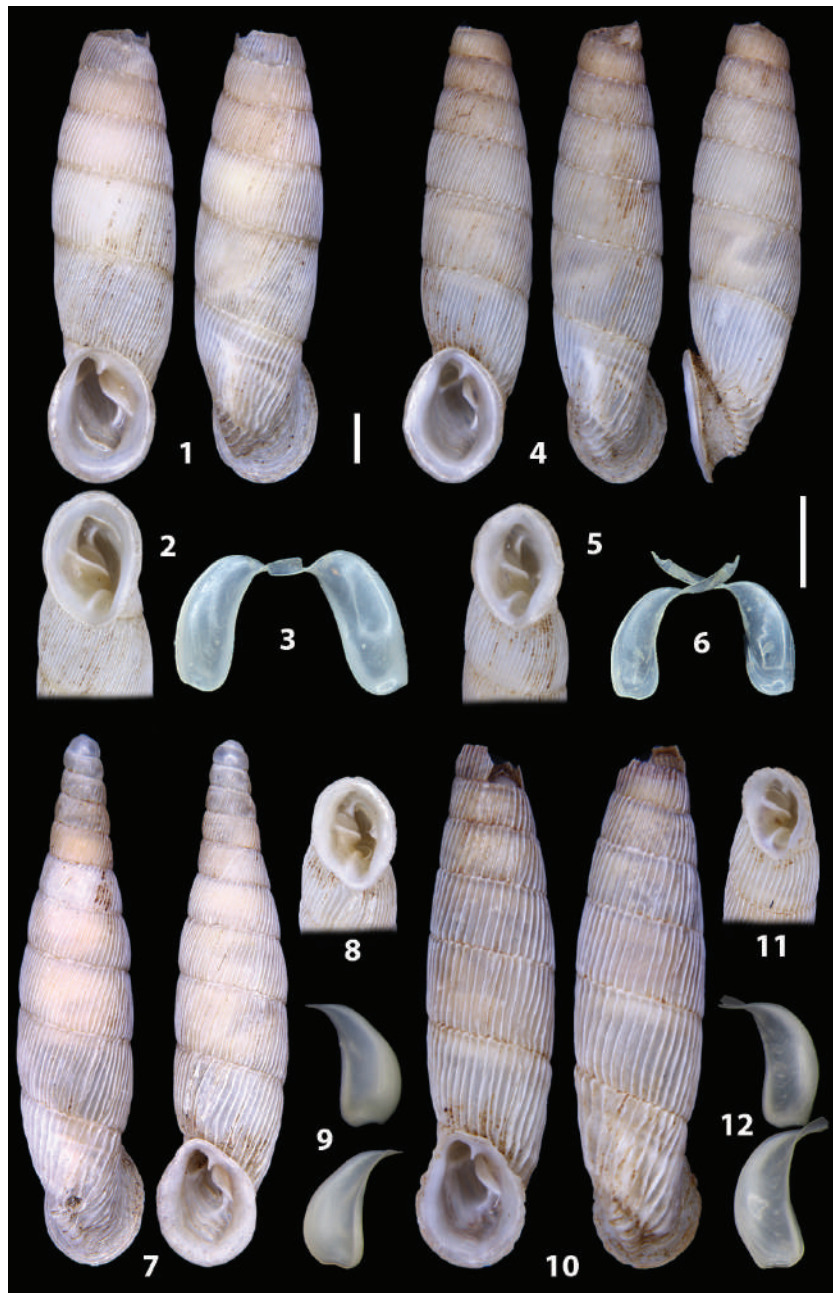


Figure 33. *Sicania eminens* (A. Schmidt, 1868), comb. nov., Custonaci, Baglio Messina **33.1** shell. **33.2** detail of the aperture **33.3** clausiliar plate double side. Dolina Buffara **33.4** shell **33.5** detail of the aperture **33.6** clausiliar plate double side. Contrada Scurati, Custonaci **33.7** shell **33.8** detail of the aperture **33.9** clausiliar plate double side. Contrada Scurati toward Mangiapane **33.10** shell **33.11** detail of the aperture **33.12** clausiliar plate double side.

Sicania nobilis comb. nov. cannot be framed within a precise genital morphological outline. The anatomy of the genital organs of *Sicania nobilis* comb. nov. exhibits significant differences among the populations (albeit stable within a population), especially concerning the features of the internal sculpturing of V (smooth to transversal pleats), penis (smooth, with tubercles of fringed longitudinal pleats) and the shape of the penial pseudopapilla (small and roundish to big and elongate). As seen in the genital descriptions, also ratios among principal genital parts show great variability. *Sicania nobilis spezialensis* stat. nov. comb. nov. shows a further different genital outline (Fig. 35.1–35.7) (e.g., the internal penis with robust smooth longitudinal pleats) that differs from all the *Sicania nobilis* s. l. dissected populations. Therefore, the morphology of the genital organs cannot serve as a specific diagnostic set of characters, except for *Sicania spezialensis* comb. nov., yet, from this taxon only one population was available.

Sicania nobilis comb. nov. s. l. is clearly differentiated from the remaining *Sicanial/Siciliaria* taxa by shell morphology, especially the waxy whitish surface of the whorls and the arrangement of the plicae and lamellae, as repeatedly reported in literature with detailed descriptions and differential diagnoses (Nordsieck 1984, 2002, 2013b; Beckmann 2004).

***Sicania nobilis nobilis* (L. Pfeiffer, 1848), comb. nov.**

Figs 1.F, 34.1–34.8, 36.1–36.13, 39.5–39.7

Clausilia nobilis L. Pfeiffer 1848: 434.

Clausilia sicula Benoit 1876: 151.

Siciliaria (Siciliaria) nobilis episoma Brandt 1961: 7.

Siciliaria (Siciliaria) nobilis – Manganelli et al. 1995: 25.

Siciliaria (Siciliaria) nobilis (= *episoma*) – Manganelli et al. 1995: 25.

Charpentieria nobilis – Beckmann 2004: 188.

Siciliaria nobilis – Welter-Schultes 2012: 341.

Siciliaria nobilis – Nordsieck 2013b: 8.

Charpentieria nobilis – De Mattia 2017i.

Specimens examined. ITALY, Sicily, Castelluzzo, Monte Cofano E of Tonnara di Monte Cofano, 80 m asl, 38°06'22.04"N, 12°40'59.77"E, W. De Mattia and J. Macor leg., 19.xii.2007. 2 dissected spm. I.D. 7. ITALY, Sicily, San Vito lo Capo, Castelluzzo, west cliffs E of town, 120 m asl, 38°06'25.71"N, 12°44'33.37"E, [Lab ID 60_1, COI: MW758906, ITS2: MW757065, MW757066, MW757067, MW757139; Lab ID 60_2, COI: MW758907; Lab ID 60_4, COI: MW758938; Lab ID 60_5, COI: MW758939], W. De Mattia and J. Macor leg., 14.iv.2017. 2 dissected spm. ITALY, Sicily, San Vito lo Capo, cliffs S of “El-Bahira” camping, 60 m asl, 38°08'48.81"N, 12°44'6.61"E, [Lab ID 62_2, COI: MW758914; Lab ID 62_3, COI: MW758940], W. De Mattia and J. Macor leg., 14.iv.2017. 2 dissected spm. ITALY, Sicily, San Vito lo Capo, Torre delle Usciére, 5 m asl, 38°10'30.07"N, 12°46'14.09"E, [Lab ID 18_1,

COI: MW758918, ITS2: MW757106, MW757107], W. De Mattia and J. Macor leg., 19.xii.2007. 2 dissected spm. “*episoma*” ITALY, Sicily, San Vito lo Capo, boulders W of the town, 50 m asl, 38°10'51.85"N, 12°43'37.70"E, [Lab ID 14_1, COI: MW758875, ITS2: MW757128, MW757129, MW757130], W. De Mattia and J. Macor leg., 19.xii.2007. 2 dissected spm.

Shell (Figs 36.1–36.13, 39.5–39.7). Shell decollate; with well-developed whitish surface layer; whorls mostly weakly rib-striated, with sutural papillae; dorsal keel missing; inferior lamella moderately high or high; anterior upper palatal plica present, mostly separated from the lunella; ALPP tending to be shortened, posterior lower palatal plica more or less reduced; palatal edge of clausilium plate distally not receding, palatal edge distally somewhat or not bent upwards.

Measurements (n = 45, decollate). shell height 22.9 ± 1.6 , whorl width 5.0 ± 0.2 , aperture height 4.8 ± 0.3 , aperture width 3.6 ± 0.4 .

External morphology of the genital organs (Figs 34.1, 34.3, 34.5, 34.7). The FO is much longer than the V (FO/V range 1.9–3.4). The VD is thin along its whole course. The FDBC is slightly shorter or longer than the BC+SDBC (FDBC/BC+SDBC range 0.9–2.1). The BC+SDBC is club-like to cylindrical and longer than the V (BC+SDBC/V range 1.4–3.1), with no distinction between the SDBC and the BC. The apex is big and round. The D is longer than the V (D/V range 2.1–3.3) and longer than the BC+SDBC (D/BC+SDBC range 1.3–2.0), thinner than the BC+SDBC and with a small but round apex. The V is short, cylindrical and large in diameter. The A is very large. The PC is much longer than the V (P+E/V range 1.8–3.7). The PR is very short and robust. The ET is always present. The E is slightly longer than the P (E/P range 1.2–1.6), very gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 34.2, 34.4, 34.6, 34.8). The A is smooth or shows weak large longitudinal pleats. The V shows a variable pattern of sculpturing: from smooth to an irregular pattern of small pleats. The P also presents a variable pattern of sculpturing: totally smooth or with coarse and irregular big tubercles, or one or two longitudinal remarkably segmented pleats. The PP can be either big, elongated with a rounded or pointed apex or small, short, round and totally smooth. The P-E transition presents two different structures. The samples from Cofano (7), San Vito (14) and Torre Usciè (18) present a first distal and a second median ER while both the PP and ELP originates from a third proximal ER. The ephiphallar formula is: 1ER+2ER+3ER(PP+ELP). The samples from Castelluzzo (60) and San Vito cliffs (62) present a simpler ephiphallar thickening structure, namely a first distal ER and the PP originates from the second proximal ER. The ELP are not connected to the second proximal ER. The ephiphallar formula is: 1ER+2ER(PP)+ELP. The E shows two main longitudinal smooth or fringed pleats that distally fades out or abruptly ends before the VD. These pleats originate from the merging of 3–7 minor distal pleats. The V is smooth.

Ecology. *Sicania nobilis nobilis* comb. nov. is a strictly limestone dweller and inhabits cliffs and big isolated boulders, hiding among rock cracks and crevices. It is found both in dry, sun exposed cliffs (i.e., San Vito lo Capo, cliffs S of “El-Bahira“

camping) or shady walls under dense tree cover (San Vito lo Capo, Castelluzzo, west cliffs E of town). According to De Mattia (2017i) *Sicania nobilis nobilis* comb. nov. is considered Endangered following the IUCN criteria B1ab(iii,v)+2ab(iii,v).

Distribution. *Sicania nobilis nobilis* comb. nov. is known to occur in two limestone massifs: Monte Cofano and in San Vito lo Capo Peninsula, from Monte Acci to Monte Monaco.

Remarks. *Siciliaria nobilis episoma* hwas described by Brandt (1961: 7) from "Barbello bei San Vito" by its smaller dimensions, opaque (glanzlose) and markedly striated (scharf rippenstreifigen) shell. Although we were unable to find the locality named Barbello, the description of this taxon corresponds to a population known to inhabit the area east of San Vito lo Capo at Torre dell'Usciére, on limestone cliffs few meters from the shoreline. In the mt tree, this population is positioned within the *Sicania nobilis* clade (Figs 4–6) its COI sequence almost identical to that of an individual from San Vito (ID 14_1). The distinctive shell characters provided by Brandt (1961) reveal to be weak and not reliable to justify the introduction of a new subspecific name. The "opaque" and the "markedly striated" shell surface seems to be a common character of *Sicania nobilis* comb. nov. (see Figs 36.1, 36.4, 36.7 and 36.10, 36.13), as well as the shell's dimensions that fall inside the variability of *Sicania nobilis nobilis* comb. nov. Moreover, also regarding the morphology of its genital organs, *Sicania nobilis episoma* does not show any substantial difference from the nominate subspecies. We therefore support the opinion of Nordsieck (2007: 54) that the name "*episoma*" should be deemed as a junior synonym of *S. nobilis nobilis* comb. nov.

***Sicania nobilis spezialensis* (Nordsieck, 1984), stat. nov., comb. nov.**

Figs 1.F, 35.1–35.7, 36.14–36.16

Siciliaria (Siciliaria) spezialensis Nordsieck 1984: 202.

Siciliaria (Siciliaria) spezialensis – Manganelli et al. 1995: 25.

Charpentieria spezialensis – Beckmann 2004: 188.

Siciliaria spezialensis – Welter-Schultes 2012: 343.

Siciliaria spezialensis – Nordsieck 2013b: 9.

Charpentieria spezialensis – De Mattia 2017j.

Specimens examined. ITALY, Sicily, San Vito Lo Capo, Macari, E side of Monte Speziale, 75 m asl, 38°07'41.78"N, 12°44'9.24"E, [Lab ID 63_1, COI: MW758910, ITS2: MW757039, MW757040; Lab ID 63_2, COI: MW758911], W. De Mattia and J. Macor leg., 14.iv.2017. 4 dissected spm.

Shell (Figs 36.14–36.16). Shell decollate; whorls densely ribbed, without or with very weak sutural papillae; dorsal keel absent; inferior lamella moderately high; anterior upper palatal plica absent, posterior upper palatal plica very short; ALPP very short to knob-like, posterior lower reduced; palatal edge of clausilium plate distally not receding, palatal edge distally not bent upwards (see Nordsieck, 1984: 202).

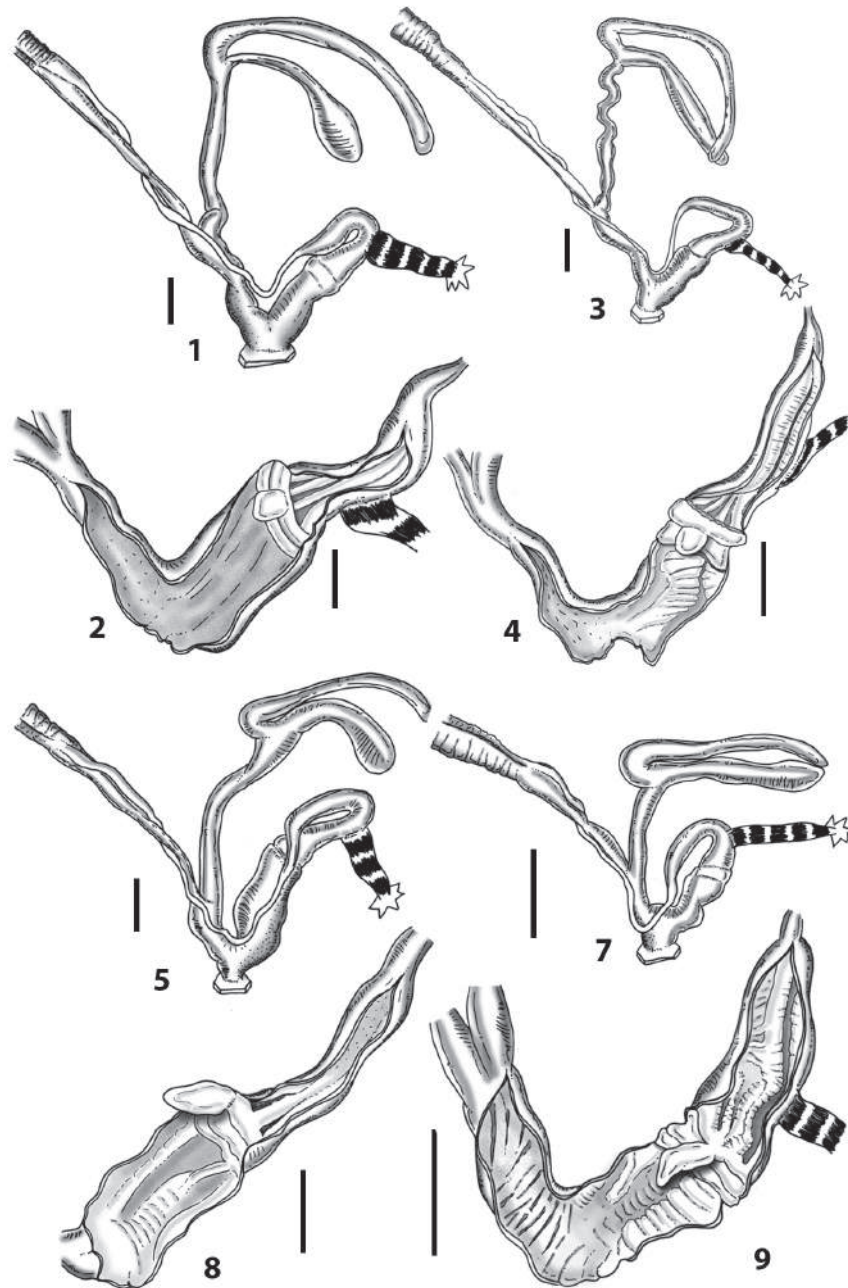


Figure 34. *Sicania nobilis nobilis* (A. Schmidt, 1868), comb. nov., Castelluzzo **34.1** whole distal genital organs **34.2** internal distal part of genital organs. San Vito Lo capo, camping **34.3** whole distal genital organs **34.4** internal distal part of genital organs. San Vito Lo Capo, boulders **34.5** whole distal genital organs **34.6** internal distal part of genital organs. Torre delle Usciere (ex. forma *episoma*) **34.7** whole distal genital organs **34.8** internal distal part of genital organs.

Measurements (n = 24, decollate). shell height 22.2 ± 1.3 , whorl width 5.1 ± 0.2 , aperture height 4.1 ± 0.3 , aperture width 2.8 ± 0.3 .

External morphology of the genital organs (Figs 35.1, 35.3). The FO is longer than the V (FO/V range 1.9–2.2). The VD is thin along its whole course. The FD/BC is slightly longer than the BC+SDBC (FD/BC/BC+SDBC range 1.1–1.2). The BC+SDBC is club-like and longer than the V (BC+SDBC/V range 1.7–1.8), with no clear distinction between the SDBC and the BC. The apex is big and rounded. The D is longer than the V (D/V range 2.1–2.3) and longer than the BC+SDBC (D/BC+SDBC range 1.3–1.7), thinner than the BC+SDBC and with a small and round apex. The V is cylindrical. The A is very large. The PC is longer than the V (P+E/V range 1.8–2.0). The PR is short and robust. The E is almost as long as the P (E/P range 0.8–0.9), gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 35.2, 35.4–35.7). The V distally presents a set of irregular, weak, and fleshy folds that proximally become a set of oblique smooth pleats. The A shows a set of irregular fleshy folds. The P presents 4–to 6 longitudinal fleshy smooth pleats, slightly depressed in the middle forming a sort of longitudinal hollow. These pleats distally become weak and irregular entering in the A. The fine structure of the wall is smooth. The PP is little, rhombus-shaped and smooth. The P-E transition presents a first distal ER, whereas the PP and the ELP originate from the second proximal ER. The epiphallar formula is: 1ER+2ER(PP+ELP). The E shows a pattern of three or four irregular longitudinal fringed pleats. The wall of the E is smooth.

Ecology. *Sicania nobilis spezialensis* stat. nov., comb. nov. is a strictly limestone dweller and inhabits cliffs, hiding among rock cracks and crevices. As previously deemed as a species, according to De Mattia (2017j) the taxon is Critically Endangered.

Distribution. *Sicania nobilis spezialensis* stat. nov., comb. nov. is known only from the type locality: along the western cliffs of Monte Speziale in the surroundings of Macari (San Vito lo Capo). No overlapping zone with *Sicania nobilis nobilis* stat. nov., comb. nov. is known until now. Although, in its original description, the taxon was reported for one locality only (Nordsieck 1984: 202 “Monte Speziale bei San Vito”), the same author reported later and extended area of distribution (Nordsieck 2013b: “from Macari and Castelluzzo to Monte Speziale and Monte Acci”).

Remarks. *Sicania nobilis spezialensis* stat. nov., comb. nov. is now considered as a subspecies of *S. nobilis*. It is well embedded within the clade of *Sicania nobilis* in both COI and combined trees. *Sicania nobilis spezialensis* stat. nov., comb. nov. is a local isolated, spatially restricted ribbed form of the more widespread *Sicania nobilis* comb. nov. with few different features of the shell, viz. the lack of the anterior upper palatal plica and a clausilium plate that fits into a frame of the palatal plicae.

Mauritanica taxonomic part

The genus *Mauritanica* comprises four species that are distributed over northeastern Algeria and central-northern Tunisia (Nordsieck 2002; Sparacio et al. 2020). It is currently considered as a subgenus of *Charpentieria* (MolluscaBase 2021). Only the Tunisian taxa were recently reviewed (Sparacio et al. 2020), mainly by means of shell

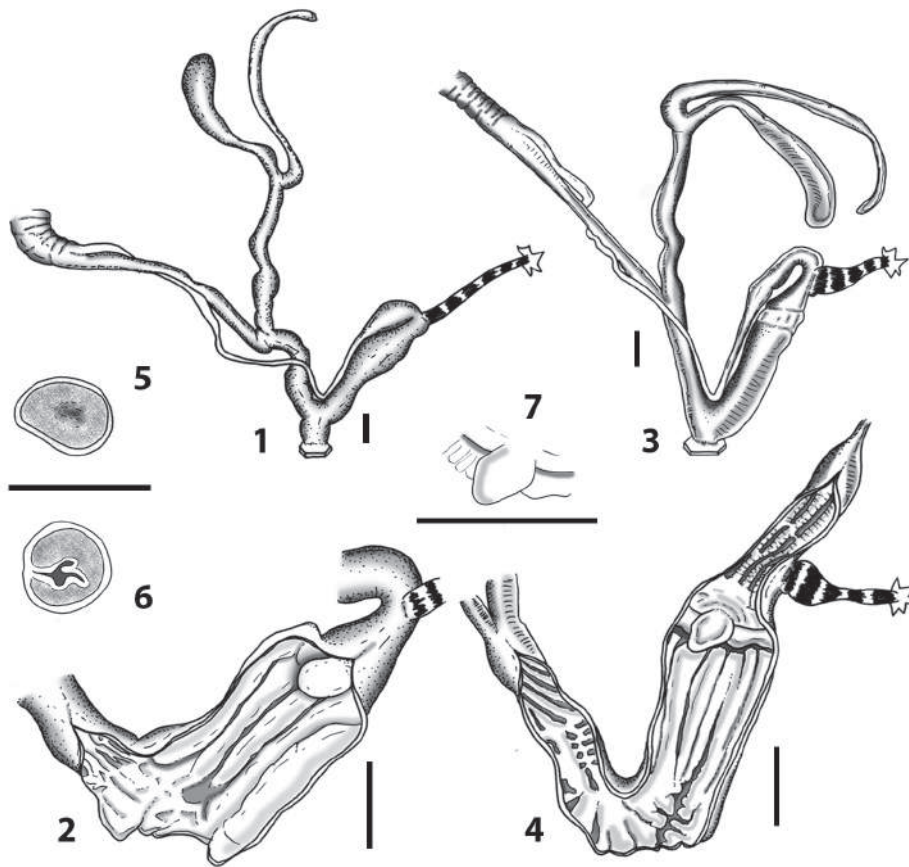


Figure 35. *Sicania nobilis spezialensis* (Nordsieck 1984), stat. nov., comb. nov. Macari **35.1** whole distal genital organs **35.2** internal distal part of genital organs **35.3** whole distal genital organs. **35.4** internal distal part of genital organs **35.5** cross section of the pseudopapilla **35.6** cross section of the epiphallus **35.7** detail of the pseudopapilla.

morphology and a brief analysis of the anatomy of the genital organs, discussing the position of the genus and separating it from *Charpentieria* without involving additional morphological and molecular genetic data.

In our molecular genetic analysis (Figs 4–6) we only had *Mauritanica perinni polygyra* available. In the COI, ITS2 and combined trees, this species falls outside the *Siciliaria/Sicania* clades, forming a separate independent clade together with *Siciliaria scarificata*, endemic to Marettimo. In the COI tree, this clade represents the “sister” clade of *Sicania* (average p distance 17%) and the same is found in the ITS2 tree (Fig. 5), yet with lower support. Despite low sample number, no association with any of the other *Charpentieria* lineages was observed.

The separation of *Mauritanica* from *Siciliaria/Sicania* is consistent through all the trees, thus we provisionally keep *Mauritanica* as a distinct genus, although the type

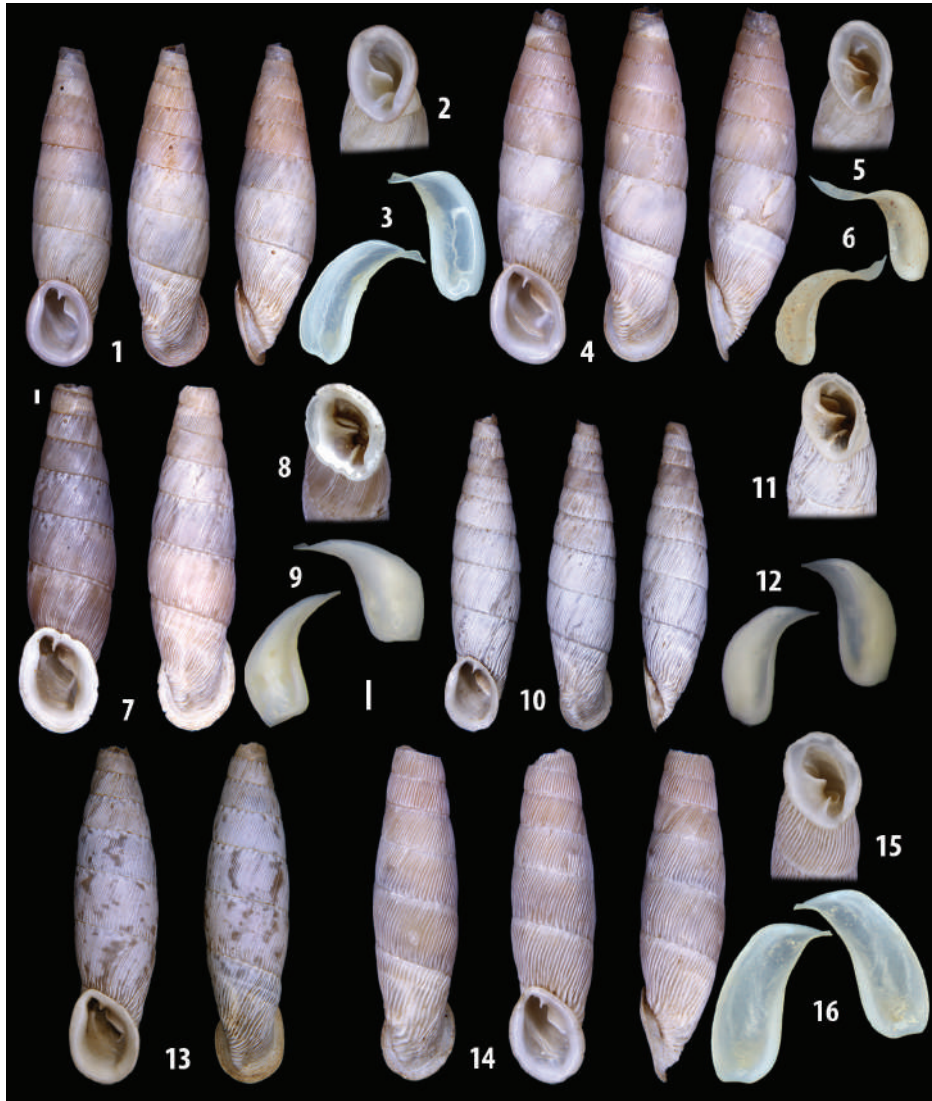


Figure 36. *Sicania nobilis nobilis* (A. Schmidt, 1868), comb. nov., Castelluzzo **36.1** shell **36.2** detail of the aperture **36.3** clausiliar plate double side. San Vito Lo capo, camping **36.4** shell **36.5** detail of the aperture **36.6** clausiliar plate double side. San Vito Lo Capo, boulders **36.7** shell **36.8** detail of the aperture **36.9** clausiliar plate double side. Torre delle Usciere (ex. forma *episoma*) **36.10** shell **36.11** detail of the aperture **36.12** clausiliar plate double side. Monte Cofano, Tonnara Cofano **36.13** shell. *Sicania nobilis spezialensis* (Nordsieck 1984), stat. nov., comb. nov. Macari **36.14** shell **36.15** detail of the aperture **36.16** clausiliar plate double side.

species *Mauritanica tristrami* (L. Pfeiffer, 1861) was not available to us. In order to fully understand the phylogenetic relationships of *Mauritanica* with *Siciliaria*/ *Sicania* more genetic markers and specimens are essential.

Both *M. perinni polygyra* and *M. scarificata* underwent anatomical investigation. A similar external genital morphology was detected. The only noticeable difference is the relative length of the FO, with a V/FO ratio of 1.1 for *M. scarificata* and 0.6 for *M. perinni polygyra*. Remarkable differences were detected regarding the internal details of the penial complex. *Mauritanica scarificata* presents 3 ERs with a very short and globose PP that makes it fall into the general *Siciliaria/Sicania* genital anatomical arrangement. *Mauritanica perinni polygyra* lacks any ER and the PP is irregular with a convolute surface pattern. It is directly connected to the OELP. Unfortunately, the genital descriptions and the pictures provided by Sparacio et al. (2020) do not include fine details of the internal genital organs (ER, PP structure and origin, ELP etc) so that any comparison to our results is impossible.

Following our genital anatomical investigations, the common genital anatomical traits deemed by Nordsieck (2013a, 2013b) to justify his proposal to consider *Mauritanica* as a subgenus of *Siciliaria*, namely, "the presence of a thickening in the passage from the penis to the epiphallus and the indistinct delimitation between proximal and distal penis" revealed that it is probably not a reliable feature. The thickening was not found in *Mauritanica perinni polygyra* (Fig. 37). Moreover, the delimitation between proximal and distal penis revealed to be an extremely subtle and variable character also in *Siciliaria*, *Charpentieria* and *Stigmatica*. Only few taxa of *Charpentieria* show a detectable, constant and distinct delimitation between proximal and distal penis [e.g., *Charpentieria itala lorinae* (Fig. 46.7) and *Charpentieria itala trepida* (Fig. 49.1)].

***Mauritanica scarificata* (L. Pfeiffer, 1856), comb. nov.**

Figs 1.F, 37.1–37.5, 38.1–38.4, 39.8, 39.9

- Clausilia scarificata* L. Pfeiffer 1856: 185.
- Clausilia scarificata* – L. Pfeiffer 1859: 765.
- Clausilia sacrificata* – Benoit 1876: 152.
- Clausilia confinata* – Benoit 1881: 105.
- Clausilia (Siciliaria) confinata* Monterosato 1892: 28.
- Siciliaria scarificata* – Manganelli et al. 1995: 25.
- Charpentieria scarificata* – Beckmann 2004: 188.
- Siciliaria scarificata* – Welter-Schultes 2012: 342.
- Siciliaria scarificata* – Nordsieck 2013b: 7.
- Siciliaria scarificata* – Liberto et al. 2015: 482.
- Charpentieria scarificata* – De Mattia 2017k.
- Charpentieria scarificata* – MolluscaBase eds 2021.

Specimens examined. ITALY, Sicily, Marettimo, W of the town, path to Pizzo Falcone. 80 m asl, 37°58'11.08"N, 12°03'59.36"E, [Lab ID 2_1, COI: MW758915, ITS2: MW757112, MW757111; Lab ID 2_2, COI: MW758916], leg. WDM, JM, 12.vi.2015. 29 live spm, 4 dissected spm.

Shell (Figs 38.1–38.4, 39.8–39.9). Shell mostly decollate; whorls ribbed, sutural papillae visible; dorsal keel indistinct ore missing; inferior lamella high; anterior upper palatal plica present, separated from or connected with upper palatal plica; palatal edge of clausilium plate distally receding, palatal edge distally somewhat or not bent upwards (as in Nordsieck, 2013b).

Measurements (n = 35, decollate): shell height 18.5 ± 1.0 , whorl width 4.6 ± 0.2 , aperture height 4.0 ± 0.3 , aperture width 2.9 ± 0.2 .

External morphology of the genital organs (Fig. 37.1, 37.3). The FO is longer than the V (FO/V range 1.8–2.1). The VD is thin along its whole course. The FDBC is slightly longer than the BC+SDBC (FDBC/BC+SDBC range 1.1–1.2). The BC+SDBC is cylindrical to club-like and longer than the V (BC+SDBC/V range 1.3–1.4), with no clear distinction between the SDBC and the BC. The apex is big and round. The D is much longer than the V (D/V range 4.1–4.5) and longer than the BC+SDBC (D/BC+SDBC range 1.4–1.5), thinner than the BC+SDBC and with a small and round apex. The V is V-shaped with a narrow distal part next to the A. The A is large. The PC is longer than the V (P+E/V range 3.0–3.3). The PR is short and robust. The E is longer than the P (E/P range 1.2–1.3), gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Figs 37.2, 37.4–37.5). The A is smooth. The P presents two or three big smooth longitudinal pleats that originate directly from the rings of the pseudopapilla. The fine structure of the wall is smooth. The PP is small, smooth and with a pointed apex. It originates from the first proximal ER. The E shows two to four main but smooth ELP that fade before the VD. The wall of the E is smooth. The V is from almost smooth to very finely granulated. The epiphallar formula is: 1ER+ 2ER+3ER(PP)+ELP.

Ecology. *Mauritanica scarificata* comb. nov. is found in a variety of habitats: limestone walls and cliffs, isolated boulders, under rocks and among scree and rocky debris. The species is common and abundant throughout the Island of Marettimo. According to De Mattia (2017k) *Mauritanica scarificata* comb. nov. is considered Least Concern.

Distribution. *Mauritanica scarificata* comb. nov. is endemic of the island of Marettimo.

***Mauritanica perinni polygyra* (O. Boettger, 1879)**

Figs 37.6–37.10, 38.5, 38.6

Clausilia (Mauritanica) polygyra Boettger in Kobelt 1879: 153.

Charpenteria (Mauritanica) perinni polygyra – Nordsieck 2002: 27, 29, 35, 36.

Charpenteria (Mauritanica) perinni polygyra – Nordsieck 2007: 54.

Mauritanica perinni polygyra – Sparacio et al. 2020: 318.

Remarks. *Mauritanica perinni polygyra* was recently revised by Sparacio et al. (2020: 318). Based on differences of the shell morphology alone, Sparacio et al. (2020: 319)

proposed species status for *Mauritanica perinni polygyra*, independent from *Mauritanica perinni perinni* (Bourguignat, 1876). A genital comparison with the nominate subspecies was not possible since the genital organs of this taxon were not provided by Sparacio et al. (2020). Moreover, a comparison between our anatomical results and

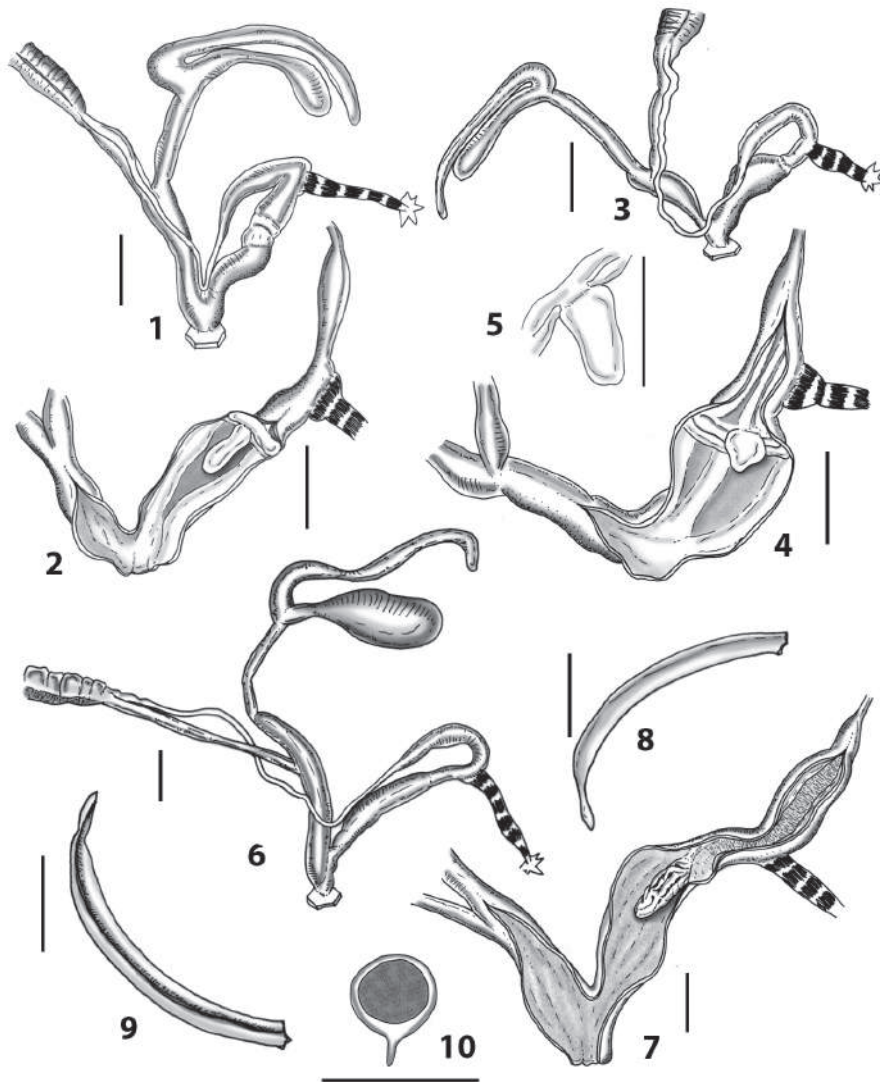


Figure 37. *Mauritanica scarificata* (L. Pfeiffer, 1856), comb. nov., Marettimo **37.1** whole distal genital organs **37.2** internal distal part of genital organs **37.3** whole distal genital organs **37.4** internal distal part of genital organs **37.5** detail of the pseudopapilla. *Mauritanica perinni polygyra* (O. Boettger, 1879), Tunisia, Zaghuan **37.6** whole distal genital organs **37.7** internal distal part of genital organs **37.8–37.9** spermatophore **37.10** cross section of the spermatophore.

those provided by Sparacio et al. (2020: 337, figs 60–61) for *Mauritanica perinni polygyra* was rather difficult: Essential details, as the internal structure of the epiphallus and the presence/absence of the ER and ELP are not detectable. The fine structure of the internal penis is not clear and, contrary to our results that show a smooth internal wall, the vagina seems to have a smooth longitudinal pleat (2020: 337, fig. 61). The presence of the ET is not clear as well (2020: 337, fig. 60).

Specimens examined. TUNISIA, above Zaghouan (road to summit), 789 m asl, 36°22'2.45"N, 10°07'11.81"E, [Lab ID SMF335011_1, COI: MW758966, ITS2: MW757044, MW757045], ex Nordsieck coll. (11639), currently SMF 335011/1, 1 dissected spm.

Shell (Figs 38.5, 38.6). Shell decollate or not decollate; whorls finely and irregularly striated, flat, with dense papillae along the sutures; dorsal keel indistinct; inferior lamella high; anterior upper palatal plicae absent; posterior upper palatal plica present; lunella dorso-lateral; little subclaustralis, clausilium plough-like with subrectangular plate (Sparacio et al. 2020: 318).

Measurements (n = 1, decollate). shell height 22.4, whorl width 4.1, aperture height 3.3, aperture width 2.4.

External morphology of the genital organs (Fig. 37.6). The FO is longer than the V ($FO/V = 2.1$). The VD is thin along its whole course. The FDBC is slightly shorter than the BC+SDBC ($FDBC/BC+SDBC = 0.9$). The BC+SDBC is club-like and longer than the V ($BC+SDBC/V = 1.4$), with clear distinction between the SDBC and the BC. The SDBC is very short. The apex is big and round. The D is much longer than the V ($D/V = 1.9$) and longer than the BC+SDBC ($D/BC+SDBC = 2.2$), thinner than the BC+SDBC and with a small and round apex. The V is cylindrical but the presence of the spermatophore may modify its normal shape. The A is small. The PC is longer than the V ($P+E/V = 2.8$). The PR is long and robust. The ET is not clearly visible. The E is shorter than the P ($E/P = 0.9$), gradually shrinking and turning into the VD.

Internal morphology of the genital organs (Fig. 37.7). The A, V and the P show a very finely granulated surface. The PP is small, elongated. Its surface is very irregular, folded and its internal texture is spongy. The P-E transition is simple, with no ER. The origin of the PP is connected with one of the two ELP. The epiphallar formula is: PP(ELP). The E shows two smooth longitudinal pleats that fade before the VD. Between the ELP an irregular transverse small, interrupted pattern gives an overall coarse appearance.

Spermatophore (Figs 37.8–37.10). The spermatophore is thin, elongated. It is 4.7 mm long and 0.8 mm wide at its widest point. The tail is pointed and sharp. The head is missing, probably already digested. The upper keel is simple and goes from the tip of the tail as far as the broken head part. The lower keel is missing.

Ecology. *Mauritanica perinni polygyra* is a limestone dweller, on cliffs, crevices and under stones (Sparacio et al. 2020: 319).

Distribution. *Mauritanica perinni polygyra* is known only from Djebel Zaghouan area (Sparacio et al. 2020: 319).



Figure 38. *Mauritanica scarificata* (L. Pfeiffer, 1856), comb. nov., Marettimo **38.1** shell **38.2** shell **38.3** detail of the aperture **38.4** clausiliar plate double side. *Mauritanica perinni polygyra* (O. Boettger, 1879), Tunisia, Zaghouan **38.5** shell **38.6** shell (picture courtesy of Claude and Amandine Evanno).

An overview of *Siciliaria* related genera *Charpentieria*, *Gibbularia*, and *Stigmatica*

The separation of *Siciliaria* and *Sicania* (and provisionally *Mauritanica*) from the other genera is well supported, but the relationships among *Charpentieria*, *Stigmatica* and *Gibbularia* remain unresolved and appear as polytomy in the trees. *Charpentieria* (four species included) forms one (poorly supported) clade but, the relationships within this clade received no considerable support. The genera *Stigmatica* and *Gibbularia* are not monophyletic and populations from distant areas show high genetic distances



Figure 39. *Sicilia crassicostata* (L. Pfeiffer, 1856), comb. nov., Monte Cofano **39.1** palatal plicae **39.2** parietal lamellae. *Sicilia eminens* (A. Schmidt, 1868), comb. nov., Custonaci, Baglio Messina **39.3–39.4** palatal plicae. *Sicilia nobilis nobilis* (L. Pfeiffer, 1848), comb. nov., Castelluzzo **39.5–39.6** palatal plicae **39.7** parietal lamellae. *Mauritanica scarificata* (L. Pfeiffer, 1856), comb. nov., Marettimo **39.8** palatal plicae **39.9** parietal lamellae.

(Table 2). *Stigmatica* is based on *Clausilia stigmatica* by tautonymy and, in our trees (Figs 4–6), only this clade with the type species *Stigmatica stigmatica* can be deemed as a representative of this genus. Despite emerging from a polytomy, additional taxa included in our trees and currently considered as belonging to *Stigmatica* (namely *Stigmatica vulcanica* and *Stigmatica pantocratoris*) are clearly separated from the type species. We thus only conventionally keep them as *Stigmatica* species. A focused approach with more genetic markers and specimens is needed to identify the phylogenetic relationships among the species currently included into *Stigmatica* (following MolluscaBase 2021). A similar approach is used for *Gibbularia*, which needs to be excluded from *Siciliaria/Sicilia* (Figs 4–6). Its phylogenetic relationship with the other genera is far from being resolved.

Papillifera, which was used as outgroup, appeared monophyletic in our trees, even though the distances within this genus are in the same range as among different genera.

Southern alpine *Charpentieria*

The taxa included in the alpine *Charpentieria itala–ornata–dyodon* clade show a pan-Southern Alpine distribution, with *C. dyodon* isolated in Piemonte and Ticino, *C. itala* along central and eastern Southern Alps whereas *C. ornata* is present along the easternmost Southern Alps and northwestern Balkans. The taxa included in the *C. stenzii*

subclade occupy the eastern Southern Alps, from eastern Trentino-Alto Adige, Friuli-Venezia Giulia, W Slovenia and SE Austria.

Despite the low support values, the COI and the ITS2 phylogenetic trees (Figs 4, 5) show a general picture where *Charpentieria dyodon dyodon* (S. Studer, 1820) appears as the sister species of *Charpentieria itala* (with *C. itala itala*, *C. itala baldensis* and *C. itala lorinae*). *Charpentieria stenzii* (with *C. stenzii cincta* and *C. stenzii letochana*) represents a separate clade.

The results presented by Scheel and Hausdorf (2012: 3799, 3801) and Xu and Hausdorf (2021: 8) showed that *C. dyodon* is the sister species of the *C. itala* complex whereas *C. stenzii* is sister to *C. ornata*. These results are difficult to compare with our trees, but at least not in contrast.

The stenzioid subspecies of *C. itala* included in our genital anatomical investigations (*clavata*, *variscoi*, *balsamoi*, and *lorinae*) were first assigned to *C. stenzii* (Käufel, 1928) but later transferred to *C. itala* by Nordsieck (1963a, b). In 2007, Nordsieck (2007) transferred these taxa to *C. clavata*. Scheel and Hausdorf (2012), following their molecular genetic results considered the stenzioid *C. clavata* as subspecies of *C. itala*, and thus, its subspecies obtained a new combination with *C. itala*. Scheel and Hausdorf (2012: fig. 3) and Xu and Hausdorf (2021: 6, fig. 5, supplementary table S1) revealed gene flow between *C. stenzii* and the stenzioid subspecies of *C. itala* across the contact zone and also highlighted several mixture events within the *C. itala* complex.

The list of the dissected material (at least two specimens per population) is found in the Table 8.

The present anatomical investigation indeed generated consistent results that are congruent with the molecular genetic outcomes.

Charpentieria itala-ornata-dyodon and *C. stenzii* groups of taxa show the same external overall shape of the distal genital organs (Figs 40, 41, 43–46, 48, 49, 51–55). No major difference can be observed regarding the main genital parts as, e.g., the shape and relative dimensions of the OSD, FO, A and penial complex (P+E). Only the V is shorter in *C. stenzii*, with an average P/V ratio of 1.4 for *C. itala* and 2.3 for *C. stenzii*. Moreover, this general external genital arrangement of *Charpentieria* is not distinguishable by any means from *Siciliaria*, *Sicania*, and *Mauritanica*.

The genus *Charpentieria* was introduced by Stabile (1864: 80) [type species: *Charpentieria dyodon* (S. Studer, 1820)]. The type species was subsequently designated by Kennard and Woodward (1923: 306). Boettger (1877: 53) listed only *C. dyodon* and its subspecies for the genus *Charpentieria*.

Boettger (1877: 35) introduced the name *Tirolica* as "Gruppe der Stentzi" (type species: *Delima stenzii* = *Charpentieria stenzii*), that included most of the stenzioid southern alpine taxa known in 1877. This genus included taxa currently belonging to both *Charpentieria itala* (*C. i. balsamoi* and *C. i. lorinae*) and *C. stenzii* (*C. s. stenzii* and its synonym *Clausilia saccata* Küster, 1848, *C. stenzii cincta* and its synonyms: *Clausilia rosmaessleri* L. Pfeiffer, 1841, *Clausilia cincta* var. *maior* Rossmässler, 1842 and *Clausilia cincta* var. *minor* Westerlund, 1878 and finally *C. s. letochana* and its synonym *Clausilia funki* Gredler, 1874). Inexplicably, Boettger (1877:35) did not in-

clude the stenzioid *C. stenzii paroliniana* (De Betta & Martinati, 1855) and *C. itala clavata*. Xu and Hausdorf (2021: 6), after sequencing 843 loci, found that *C. stenzii* is well embedded in *Charpentieria*. Although our anatomical investigations revealed a peculiar internal structure of the P–E transition and the penial pseudopapilla is found exclusively in *C. stenzii* (we named it hemipapilla, see point 6.6 for a detailed description), we follow Xu and Hausdorf (2021) in not separating this group on generic level. The hemipapilla was not found in the stenzioid subspecies despite the notable gene flow with *C. stenzii*, as proven by Xu and Hausdorf (2021: 7).

Table 8. Examined taxa of *Charpentieria* with information on shell type (stenzioid/nonstenzioid), availability of genetic data (DNA) and epiphallar formula.

Taxon	Specimens examined	Shell stenzioid/ nonstenzioid	DNA	Epiphallar formula
<i>Charpentieria dyodon dyodon</i> (S. Studer, 1820)	Trasquera di Iselle, Verbano, Piedmont, Italy. 750 m asl. 46°12'29.53"N, 08°12'46.18"E, I. Niero leg. and det.	-	Y	PP(ELP)
<i>Charpentieria dyodon alpina</i> (Stabile, 1859)	Margone, Val di Lanzo, Usseglio, Torino, Piedmont, Italy. 1500 m asl, 45°14'04.89"N, 07°12'18.90"E, leg. and det.	-	N	PP(ELP)
<i>Charpentieria dyodon thomasiana</i> (Küster, 1850)	Sentiero per Prà del Vecia, Piedicavallo, Biella, Piedmont, Italy. 1200 m asl. 45°41'32.37"N, 07°58'02.37"E, leg. and det.	-	N	PP(ELP)
<i>Charpentieria dyodon thomasiana</i> (Küster, 1850)	Santuario di Oropa, Biella, Piedmont, Italy. 1100 m asl 45°37'49.01"N, 07°58'42.07"E, W. De Mattia and J. Macor leg. and det.	-	N	PP(ELP)
<i>Charpentieria ornata</i> (Rossmässler, 1836)	Ogulin city centre, Croatia. 320 m asl. 45°16'2.55"N, 15°13'33.34"E, W. De Mattia and J. Macor leg. and det.	-	N	PP+ELP
<i>Charpentieria itala itala</i> (G. von Martens, 1824)	San Donato, Barbarano Vicentino, Vicenza, Veneto, Italy. 300 m asl. 45°24'22.30"N, 11°31'11.93"E, W. De Mattia and J. Macor leg. and det.	nonstenzioid	Y	PP(ELP)
<i>Charpentieria itala albopustolata</i> (De Cristofori & Jan, 1832)	Brescia, city castle walls, Lombardia, Italy. 200 m asl. 45°32'29.87"N, 10°13'28.37"E, W. De Mattia and J. Macor leg. and det.	nonstenzioid	N	PP(ER+ELP)
<i>Charpentieria itala allatollae</i> (Käufel, 1928)	Albergo alla Tolla, Val Ampola, Storo, Trentino-Alto Adige, Italy. 720 m asl. 45°51'7.62"N, 10°38'04.51"E, W. De Mattia and J. Macor leg. and det.	nonstenzioid	N	PP(ELP)
<i>Charpentieria itala baldensis</i> (Strobel, 1851)	Naole, San Zeno di Montagna, Verona, Veneto, Italy. 900 m asl. 45°38'43.67"N, 10°44'15.86"E, I. Niero leg. and det.	nonstenzioid	Y	ER+PP+ELP
<i>Charpentieria itala balsamoi</i> (Strobel, 1850)	Loc. Galleria, Bracca, Val Serina, Bergamo, Lombardia, Italy. 45°49'24.49"N, 09°43'06.73"E, W. De Mattia and J. Macor leg. and det.	stenzioid	N	PP(ER(ELP))
<i>Charpentieria itala clavata</i> (Rossmässler, 1836)	Ballabio, Lecco, Lombardia, Italy. 710 m asl. 45°54'25.96"N, 09°25'55.16"E, W. De Mattia and J. Macor leg. and det.	stenzioid	N	PP(ELP)
<i>Charpentieria itala latestriata</i> (Küster, 1850)	Bedulita, Bergamo, Lombardia, Italy. 625 m asl. 45°47'16.15"N, 09°32'42.26"E, W. De Mattia and J. Macor leg. and det.	nonstenzioid	N	PP(ER+ELP)
<i>Charpentieria itala lorinae</i> (Gredler, 1869)	Val di Lorina, Storo, Brescia, Lombardia, Italy. 600 m asl. 45°50'35.28"N, 10°37'12.47"E, W. De Mattia and J. Macor leg. and det.	stenzioid	Y	ER+PP(ELP)
<i>Charpentieria itala zalloti</i> nom. nov.	Udine, Friuli-Venezia Giulia, Italy. 140 m asl. 46°03'53.37"N, 13°14'12.35"E, L. Anzil leg., W. De Mattia det.	nonstenzioid	N	PP(ER(ELP))

Taxon	Specimens examined	Shell stenzioid/ nonstenzioid	DNA	Epiphallar formula
<i>Charpentieria itala zalloti</i> nom. nov.	Udine, Friuli-Venezia Giulia, Italy. 140 m asl. 46°03'53.37"N, 13°14'12.35"E, L. Anzil leg., W. De Mattia det.	nonstenzioid	N	PP(ER(ELP))
<i>Charpentieria itala serravalensis</i> (Nordsieck, 1963)	Serravalle near Vittorio Veneto, Veneto, Italy. 500 m asl. 46°00'04.46"N, 12°17'11.13"E, W. De Mattia and J. Macor leg. and det.	nonstenzioid	non- sten- zioid	PP(ER(ELP))
<i>Charpentieria itala trepida</i> (Käufel, 1928)	Forte Cima Ora, Anfo, Brescia, Lombardia, Italy. 1500 m asl. 45°47'50.57"N, 10°28'03.60"E, W. De Mattia and J. Macor leg. and det.	stenzioid	N	PP(ELP)
<i>Charpentieria itala triumphinae</i> Nardi, 2011	Cima Caldoline, Lavenone, Brescia, Lombardia, Italy. 1700 m asl. 45°48'03.54"N, 10°24'20.12"E, G. Nardi leg. and det.	stenzioid	N	PP(ER(ELP))
<i>Charpentieria itala variscoi</i> (Pini, 1883)	Lavina, Val Taleggio, Bergamo, Lombardia, Italy. 650 m asl. 45°53'11.73"N, 09°33'55.46"E, W. De Mattia and J. Macor leg. and det.	stenzioid	N	PP(ER+ELP)
<i>Charpentieria stenzii stenzii</i> (Rossmässler, 1836)	San Romedio, Trento, Italy. 730 m asl. 46°22'03.83"N, 11°06'31.84"E, W. De Mattia and J. Macor leg. and det.	stenzioid	N	EP(ELP)
<i>Charpentieria stenzii butoti</i> (Bank, 1987)	Fai della Paganella, Trento, Trentino-Alto Adige, Italy. 600 m asl. 46°12'57.04"N, 11°04'22.88"E, W. De Mattia and J. Macor leg. and det.	stenzioid	N	EP(ELP)
<i>Charpentieria stenzii cincta</i> (Brumati, 1838)	Bosplans, Pordenone, Friuli-Venezia Giulia, Italy. 500 m asl. 46°11'58.11"N, 12°38'5.24"E, W. De Mattia and J. Macor leg. and det.	stenzioid	Y	EP(ELP)
<i>Charpentieria stenzii cincta</i> (Brumati, 1838)	Val Resia, sella di Carnizza, Tarvisio, Friuli-Venezia Giulia, Italy. 400 m asl. 46°20'15.55"N, 13°19'17.11"E, W. De Mattia and J. Macor leg. and det. Mattia leg. and det.	stenzioid	N	EP(ELP)
<i>Charpentieria stenzii faueri</i> (Bank, 1987)	Grotte di Oliero Valstagna, Vicenza, Veneto, Italy. 800 m asl. 45°50'47.79"N, 11°40'04.24"E, W. De Mattia and J. Macor leg. and det.	stenzioid	N	EP(ELP)
<i>Charpentieria stenzii letochana</i> (Gredler, 1874)	Val Fonda, Misurina, Belluno, Veneto, Italy. 1500 m asl. 46°36'27.42"N, 12°12'20.01"E, W. De Mattia and J. Macor leg. and det.	stenzioid	Y	EP(ELP)
<i>Charpentieria stenzii nordsiecki</i> Fauer, 1991	Cison di Val Marino, Treviso, Veneto, Italy. 250 m asl. 45°58'05.53"N, 12°08'52.60"E, W. De Mattia and J. Macor leg. and det.	stenzioid	N	no pseudopapilla
<i>Charpentieria stenzii paroliniana</i> (De Betta & Martinati, 1855)	Loc. La Goccia, Foza, Valstagna, Vicenza, Veneto, Italy. 800 m asl. 45°52'29.20"N, 11°38'59.73"E, W. De Mattia and J. Macor leg. and det.	stenzioid	N	EP(ELP)
<i>Charpentieria stenzii westerlundi</i> (Nordsieck, 1993)	Val Fiscalina, Croda Rossa, Sesto, Bolzano, Trentino-Alto Adige, Italy. 1500 m asl. 46°38'02.83"N, 12°21'42.79"E, I. Niero leg. and det.	stenzioid	N	EP(ELP)

Boettger, 1877, introduced the genus *Itala* as “Gruppe der *itala*” (type species: *Delima itala* = *Charpentieria itala*), including all the alpine non-stenzioid taxa, excluding *C. dyodon* but including two stenzioid taxa: *C. stenzii paroliniana* and *C. itala clavata*. He also included two taxa from the Balkans: *Delima conspersa* [= *Strigilodelima conspersa* (L. Pfeiffer, 1848)] and its synonym *Delima platystoma* Küster, 1850. As for *Tirolica*, the recent results by Xu and Hausdorf (2021: 6–8) indicated that the *Charpentieria itala* complex should not be separated on a (sub)generic level (i.e., *Itala*).

Wagner (1925: 17) introduced the genus subgenus *Alpidelima* [type species *Clausilia itala* Martens, 1824, by subsequent designation by Schileyko (2000: 664)] that must be deemed as a junior synonym of *Charpentieria*.

Nordsieck (1963a: 95, figs 9–10; 97, fig. 11; 1963b: 185, 189, 193, 197) depicted the genital organs of some taxa currently belonging to the genus *Charpentieria* from the Alps. The sketchy drawings lacked important details, both concerning internal and external features. Except for fig. 11a of Nordsieck (1963a), the exact position of the insertion of the proximal vas deferens into the beginning of the free oviduct was not clear. The internal structure of the penis-epiphallus transition was not investigated. The pseudopapilla was shown, but its origin was missing as well as its connection to (and the presence/absence of) the epiphallar ring(s) and the epiphallar longitudinal pleats. Only in Nordsieck (1963a: fig. 11b) the origin of the pseudopapilla and the epiphallar ring seem to be roughly depicted. Nordsieck (1963a) reported the presence of the penial flagellum for all the four taxa, which is in contrast to our results, based on 63 specimens, where this particular anatomical structure was never detected despite careful check.

He introduced a new subspecific taxon, *C. itala serravalensis* (1963a: 175), but depicted its external anatomy of the genital organs [Nordsieck, 1963b: 184–185, Abb. 47 *itala serravalensis*, Serravalle (präp. 109)] with the same genital drawing provided for *C. itala itala* in Nordsieck, (1963a: 97, fig. 11a, b). The shell description, genital organs and measures provided for *C. itala serravalensis* (Nordsieck 1963b: 175) match with the morphology of the specimens from Colli Euganei (San Donato, Barbarano Vicentino, Padova, Italy) (Fig. 44.1–44.4) studied in the present paper.

Nordsieck cites *C. itala itala* (1963a) but unexpectedly, Nordsieck (1963b) neither cited the nominate subspecies, nor did he provide information about the type locality of the species

Charpentieria itala was described by G. von Martens (1824: 442), but he did not provide any indication about the collecting site. L. Pfeiffer (1853: 606) reports the description of the species given by Martens. In his "Reisebemerkungen über einige Binnenschnecken Italiens", E. von Martens (1857: 129), the son of G. von Martens, finally gives precise indications where his father collected the first series of specimens of *C. itala* (between Mira and Dolo): "Zwischen Mira und Dolo hatte mein Vater auch früher seine *Clausilia itala*". Dolo and Mira are located in the province of Venice, between Venice and Padova, along the river Brenta in the Pianura Padana. Being it a quaternary alluvial plain area, the specimens were probably collected on walls and houses. Eduard von Martens (1857: 129) collected more samples of *C. itala* from the walls of the Botanic Garden of Padova. These alluvial plain populations probably originate from downstream transport by creeks, deriving from the Colli Euganei and Colli Berici, which flow into the Brenta River.

Brief genital anatomical description of *Charpentieria dyodon* subspecific taxa: the parapseudopapilla

Charpentieria dyodon is the name-bearing species of the genus *Charpentieria*. It comprises five subspecies [*C. dyodon dyodon* (Studer, 1820; *C. dyodon alpina* (Stabile, 1859); *C. dyodon paulucciana* (Pollonera, 1885); *C. dyodon studeri* (Pini, 1885) and *C. dyodon thomasiana* (Küster, 1850)]. These taxa are distributed over an area that includes the western Southern Alps of Piemonte, Italy (from Dora Riparia River to Lago Maggiore)

and the South Switzerland (Ticino and Valais). This species is not sympatric with any other *Charpentieria* species.

In our COI tree only the nominate subspecies *Charpentieria d. dyodon* was included (Figs 4–6). It emerged as the sister species of *C. itala*, yet with only low node support.

Three out of five subspecies of *C. dyodon* were anatomically investigated (Table 8). They revealed a common overall genital arrangement (Figs 40, 41), including a stable presence of the penial pseudopapilla. The pseudopapilla can be either simple or rooted. The internal wall of the penis is smooth, the epiphallus shows two fringed longitudinal pleats and the internal wall of V presents many smooth longitudinal pleats. *Charpentieria dyodon* has a distribution detached from *C. itala* with no overlapping areas. *Charpentieria dyodon* shows substantial differences of the shell characters (smooth or weakly striated surface, lunella mostly absent and no palatal folds, sutural papillae very scarce or absent) and epiphallar structure (see the following chapter).

The four populations of *Charpentieria dyodon* included for dissection, revealed a very stable morphology of the genital organs (Figs 40, 41). The internal surface of the P is smooth and the V presents many smooth longitudinal pleats that stop before entering the atrium. The external transition between P and E is always visible. *Charpentieria dyodon* revealed a peculiar morphology of the pseudopapilla and the internal transition area between penis and epiphallus (Figs 40, 41). The parapseudopapilla involves the pseudopapilla and the epiphallar longitudinal pleats: the pseudopapilla has its origin at the distal end of one epiphallar longitudinal pleat (“occupied” epiphallar longitudinal pleat) and the opposite wall is delimited and narrowed by the other epiphallar longitudinal pleat (“free” epiphallar longitudinal pleat) and connected by a ER, creating a funnel-like structure. The PPP, at a first glance, resembles a true penial papilla, but it remarkably lacks the seminal channel. The extremely large ER of the PPP completely obstructs the lumen of the transition area. The connection between the penis and epiphallus is represented by a short, narrow passage, named “epiphallar funnel” (EF), that is found at the base of the PPP and it is quite difficult to detect.

This parapseudopapilla represents an intermediate form between the simple structure of *Charpentieria itala* and the hemipapilla (HP) of *Charpentieria stenzii*. In the normal PP the transition stretch E is relatively wide and the counter wall opposite of the PP is represented by the simple P-E transition wall.

***Charpentieria dyodon dyodon* (S. Studer, 1820)**

Figs 40.1, 40.2, 42.1

Distribution. *Charpentieria dyodon* s. l. has a limited distribution, restricted to northern Piedmont and adjacent Swiss territories. The nominate subspecies is restricted to the surroundings of Iselle (Piedmont) and adjacent Swiss localities.

Specimens examined. ITALY, Piedmont, Trasquera di Iselle, Verbano. 750 m asl, 46°12'29.53"N, 8°12'46.18"E, [Lab ID 44_1, COI: MW758956. ITS2: MW757051, MW757052; Lab ID C44_3, COI: MW758951], I. Niero leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 40.1). The FO is slightly longer than the V. The FDDB is shorter than the BC+SDBC (SDBC+BC). The BC+SDBC is club-like and longer than the V with no distinction between the SDBC and the BC. The apex is round. The D is slightly longer than the BC+SDBC, thinner with a small but round apex. The V is short, cylindrical and large in diameter. The PC is much longer than the V. The PR is short and robust. The E is shorter than the P and very thin.

Internal morphology of the genital organs (Fig. 40.2). The A and the P are smooth, with a very fine granulated sculpturing. The V shows many smooth longitudinal pleats. The smooth PP is simple, big, conical with a pointed apex. Its base is partially connected to the ELP and transversally extends along the transition wall, narrowing the transition passage. The epiphallar formula is: PP(ELP). The E shows two main longitudinal moderately fringed pleats that proximally fade before the VD.

***Charpentieria dyodon alpina* (Stabile, 1859)**

Figs 40.3–40.4, 42.2

Distribution. *Charpentieria dyodon alpina* is found in scattered populations along the Val di Lanzo, NW of Torino (Piedmont).

Specimens examined. ITALY, Piedmont, Torino, Margone, Val di Lanzo, Usseglio. 1500 m asl, 45°14'4.89"N, 07°12'18.90"E, leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 40.3). The FO is almost as long as the V. The FDDB is slightly shorter than the BC+SDBC (SDBC+BC). The BC+SDBC is cylindrical and longer than the V with no clear distinction between the SDBC and the BC. The apex is round. The D is shorter than the BC+SDBC, thinner with a round apex. The V is as long as the first duct of the BC+SDBC. The PC is 2 × as long as the V. The PR is long and robust. The E is slightly longer than the P and thin.

Internal morphology of the genital organs (Fig. 40.4). The A and the P are smooth, with a very fine granulated sculpturing. The V shows many smooth longitudinal pleats. The smooth simple PP is simple, big, club-like with a round apex. Its base is partially connected to the ELP and transversally extends along the transition wall, narrowing the transition passage. The epiphallar formula is: PP(ELP). The E shows two main longitudinal moderately fringed pleats that proximally fade before the VD.

***Charpentieria dyodon thomasiana* (Küster, 1850)**

Figs 41.1–41.4, 42.3, 42.4

Specimens examined. ITALY, Piedmont, Biella, Santuario di Oropa. 1100 m asl 45°37'49.01"N, 07°58'42.07"E, W. De Mattia and J. Macor leg. and det., 3 dissected spm. ITALY, Piedmont, Biella, Sentiero per Prà del Vecia, Piedicavallo. 1200 m asl, 45°41'32.37"N, 07°58'2.37"E, leg. and det., 2 dissected spm.

Distribution. *Charpentieria dyodon thomasiana* is found in the surroundings of Oropa and Piedicavallo, surroundings of Biella (Piedmont).

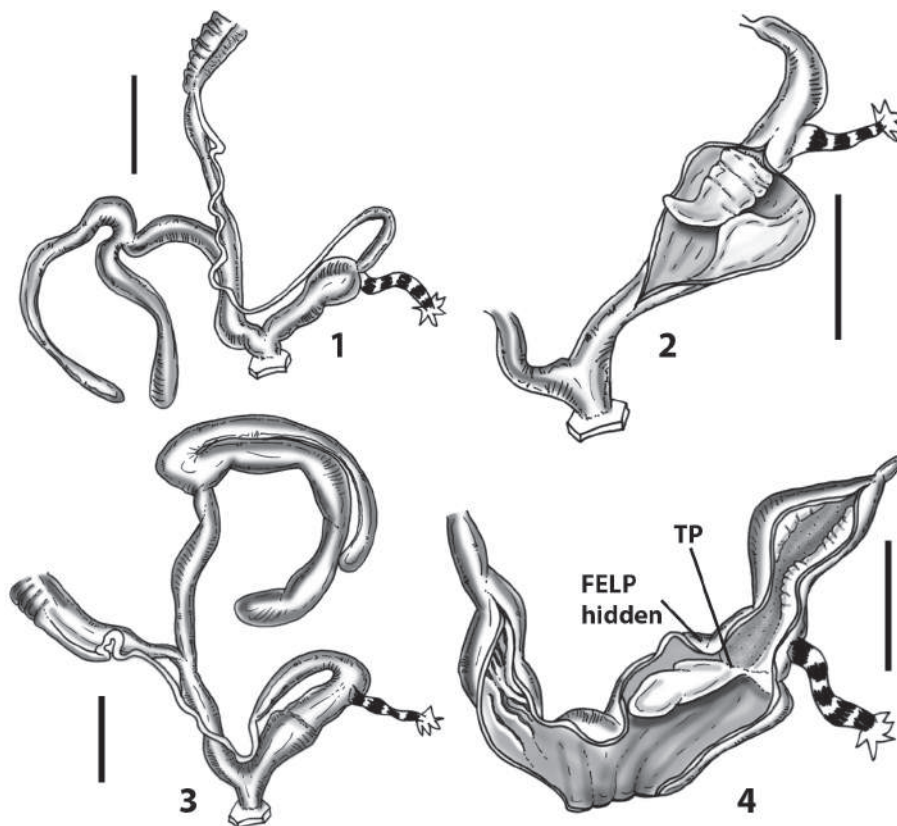


Figure 40. *Charpentieria dyodon dyodon* (S. Studer, 1820), Verbano **40.1** whole distal genital organs **40.2** internal distal part of genital organs. *Charpentieria dyodon alpina* (Stabile, 1859). Val di Lanzo, Usseglio **40.3** whole distal genital organs **40.4** internal distal part of genital organs.

External morphology of the genital organs (Fig. 41.1, 41.3). The FO is half as long as the V. The FDBC is shorter than the BC+SDBC (SDBC+BC). The BC+SDBC is club-like and longer than the V with slight distinction between the SDBC and the BC. The apex is pointed. The D is slightly longer than the BC+SDBC, thinner with a round apex. The V is long and cylindrical. The PC is longer than the V. The PR is long and robust. The E is slightly shorter than the P and thin.

Internal morphology of the genital organs (Fig. 41.2, 41.4). The A and the P are smooth, with a very fine granulated sculpturing. The V shows many smooth longitudinal pleats. The smooth simple PP is simple, elongated with a pointed apex. Its base is partially connected to the ELP and transversally extends along the transition wall, narrowing the transition passage. The epiphallar formula is: PP(ELP). The E shows two main longitudinal moderately fringed pleats that proximally fade before the VD.

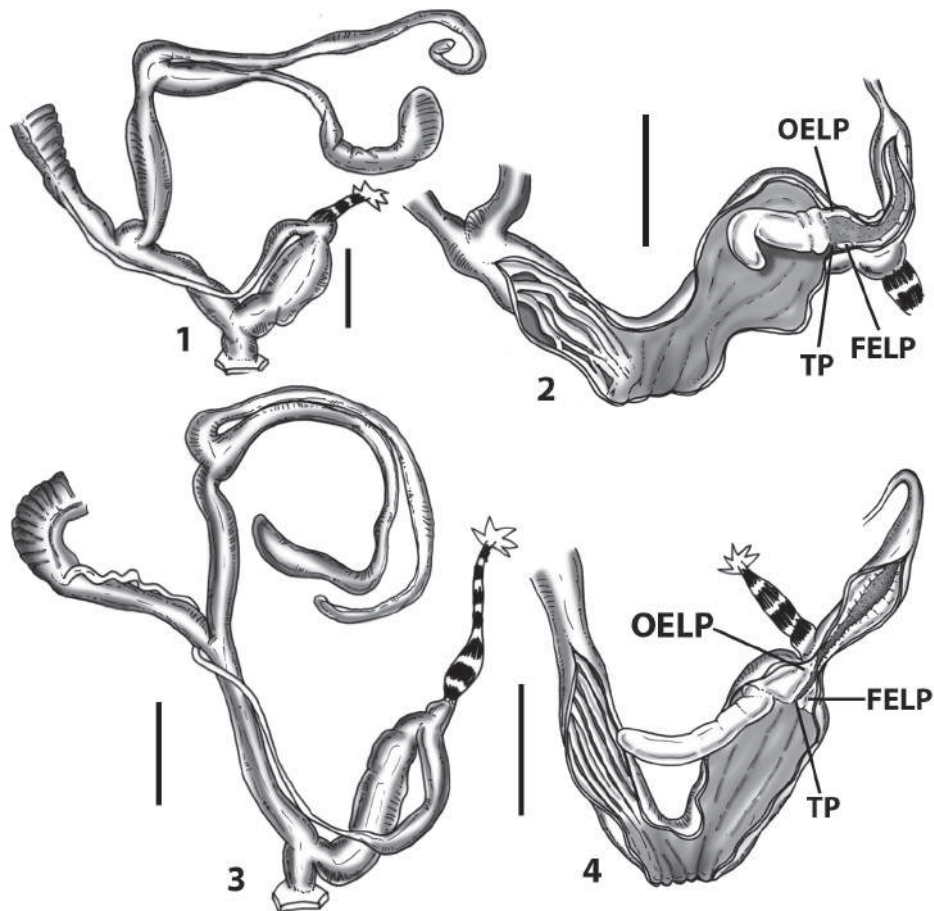


Figure 41. *Charpentieria dyodon thomasiana* (Küster, 1850), Piedicavallo **41.1** whole distal genital organs **41.2** internal distal part of genital organs. Oropa, Biella **41.3** whole distal genital organs **41.4** internal distal part of genital organs.

Brief genital anatomical description of the subspecific taxa of *Charpentieria ornata* and *Charpentieria itala*

The Southern Alpine *C. itala* is distributed from Como Lake to the Garda Lake, Trentino, Veneto (including Colli Berici and Colli Euganei) and the Pre-Alps of Friuli. Nordsieck (1963b) provided, for the eastern border of its distribution, the axis Pordenone-Ampezzo. Recent collecting extended its eastern distribution as far Udine and Cividale in Friuli (WDM, personal unpublished data). Its eastern distribution range overlaps with *C. stenzii* and in few localities they are found syntopic (e.g., San Romedio, Trento, where *C. stenzii stenzii* and *C. itala serravalensis* are found syntopic). Concerning the nomenclature of *C. itala*, we adopted the system by Scheel and Hausdorf (2012) that considered *C. clavata* as a subspecies of *C. itala*.



Figure 42. *Charpentieria dyodon dyodon* (S. Studer, 1820), Verbano **42.1** shell. *Charpentieria dyodon alpina* (Stabile, 1859). Val di Lanzo, Usseglio **42.2** shell. *Charpentieria dyodon thomasiana* (Küster, 1850), Piedicavallo **42.3** shell. Oropa, Biella **42.4** shell.

Its shell is weakly striated to frankly ribbed, with evident sutural papillae and a strong lunella, which is remarkably curved. Twelve out of the seventeen currently valid subspecies of *C. itala* were anatomically investigated, revealing a common overall arrangement of the genital organs. The pseudopapilla can be either smooth or markedly wrinkled and occupies almost the whole penial volume.

***Charpentieria ornata* (Rossmässler, 1836)**

Figs 43.1, 43.2, 47.1

Distribution and remarks. *Charpentieria ornata* has a wide distribution that includes Sudetes, southeastern Alps (Slovenia) and the western Dinarids (Welter-Schultes 2012). This species has a detached distribution which is not overlapping with *C. itala* and it is also frequently found (as the latter species) in disturbed habitats (walls, artificial limestone cliffs etc), revealing a good degree of anthropophily. *Charpentieria ornata* presents, for the subgenus, an unusually short pseudopapilla. Moreover, contrary to *C. itala*, the peristome is never detached from the body whorl.

Specimens examined. CROATIA, Ogulin city centre, 320 m asl, 45°16'2.55"N, 15°13'33.34"E, W. De Mattia and J. Macor leg. and det. 3 dissected spm.

External morphology of the genital organs (Fig. 43.1). The FO is almost as long as the V. The FDBC is as long as the BC+SDBC. The BC+SDBC is club-like to cylindrical in shape, with slight distinction between the SDBC and the BC. The apex is wide and rounded. The D is slightly longer than the BC+SDBC with a round apex. The V is long and slim. The PC is only 1.5 × longer than the V. The P is swollen. The PR is short and robust. The P-E transition is clearly visible. The E is as long as the P and much thinner in diameter.

Internal morphology of the genital organs (Fig. 43.2). The V is smooth. The P presents big irregular longitudinal pleats that reach the A. The pleats are smooth and discon-

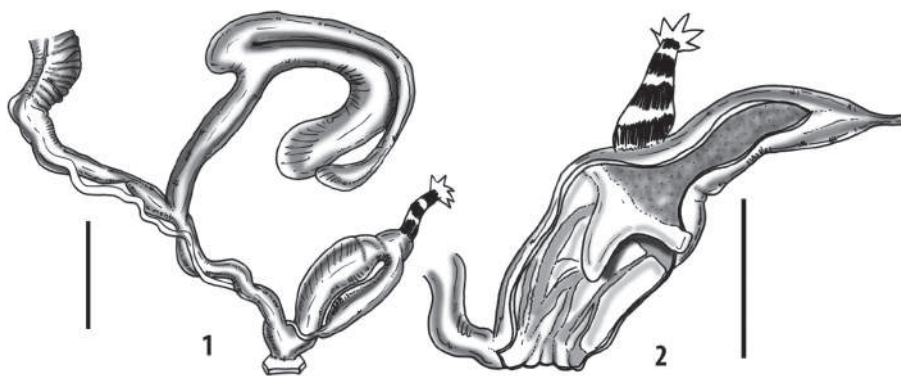


Figure 43. *Charpentieria ornata* (Rossmässler, 1836), Ogulin, HR **43.1** whole distal genital organs **43.2** internal distal part of genital organs.

tinuous, irregularly splitting and merging one into another. The PP is smooth and short, almost triangular and doesn't reach the A. It is detached from the ELP. The epiphallar formula is: PP+ELP. The ELP are small and smooth. They proximally fade before the VD.

***Charpentieria itala itala* (G. von Martens, 1824)**

Figs 44.1–44.4, 47.2–47.4

Distribution and remarks. The actual distribution of *C. itala itala* depends on the status and validity of other subspecific taxa with similar shell morphology, especially *C. itala serravalensis* or other available names of uncertain validity as *Clausilia itala vicentina* Schmidt, 1868 or *Clausilia alboguttulata* var. a, *major* Pirona, 1865. Following the original descriptions (Pirona 1865: 693; Schmidt 1868: 47), both taxa probably have “overlapping” distribution with the nominate subspecies, being cited for the surroundings of Vicenza and the western Friuli plain. According to the current systematics, *C. itala itala* is distributed in the Pianura Veneta (Venetian Plain), Colli Euganei and Berici, including the Prealpine hills of Vicenza.

Specimens examined. ITALY, Veneto, Vicenza, San Donato, Barbarano Vicentino. 300 m asl, 45°24'22.30"N, 11°31'11.93"E, [Lab ID C1_1, COI: MW758952], W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 44.1). The FO is almost as long as the V. The FDBC is longer than the BC+SDBC. The BC+SDBC is club-like, with visible distinction between the SDBC and the BC. The apex is rounded. The D is slightly longer than the BC+SDBC with a round apex. The V is long and partially swollen. The PC is only slightly longer than the V. The P is short and remarkably swollen. The PR is long and robust. The E is slightly longer than the P and thinner in diameter.

Internal morphology of the genital organs (Fig. 44.2). The A and the P present big transversal pleats. The pleats are smooth and discontinuous along the distal part of the P and in the A. The V is smooth. The PP is smooth, elongated with a round apex and directly connected to the ELP. The epiphallar formula is: PP(ELP). The E shows two ELP, fringed at their distal ends. They proximally fade before the VD.

***Charpentieria itala albopustolata* (De Cristofori & Jan, 1832)**

Figs 44.5, 44.6, 47.5

Distribution. *Charpentieria itala albopustolata* is widely distributed throughout the Central Alps of Lombardia (Nardi 2011: 101) and a small area of southwestern Veneto, next to the southern part of Garda Lake (F. Scarlassara pers. comm.) and Verona.

Specimens examined. ITALY, Lombardia, Brescia, city castle walls. 200 m asl, 45°32'29.87"N, 10°13'28.37"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 44.5). The FO is almost $2 \times$ as long as the V. The FDBC is much longer than the BC+SDBC. The BC+SDBC is club-like, with visible distinction between the SDBC and the BC. The apex is rounded. The D is slightly longer than the BC+SDBC, thin and with a round apex. The V is long and thin. The PC is double as long as the V. The P is long and swollen at its proximal part. The PR is long and thin. The E is very short and thin in diameter. The overall appearance of the external morphology of the genital organs is slim and elongated.

Internal morphology of the genital organs (Fig. 44.6). The A and the P are smooth, with very loose and barely visible longitudinal elevations. The V is smooth. The PP is folded, elongated with a pointed apex. The ER is present and it is connected with the ELP by means of 5 or 6 small longitudinal pleats. The PP originates from the ER. The epiphallar formula is: PP(ER+ELP). The E shows two fringed ELP. They proximally fade before the VD.

***Charpentieria itala allatollae* (Käufel, 1928)**

Figs 44.7, 44.8, 47.6

Distribution. This taxon is known to occur in Val Ampola and Val Lorina (Province of Trento, Trentino-Alto Adige, Italy). It is also reported by Gredler (1891) for Monte Tombea as *Clausilia tombeana* Gredler, 1891 and from other localities in eastern Lombardia by Nardi (2011: 101).

Specimens examined. ITALY, Trentino-Alto Adige, Trento, Storo, Albergo alla Tolla, Val Ampola. 720 m asl, 45°51'7.62"N, 10°38'4.51"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 44.7). The FO is $1.5 \times$ longer than the V. The FDBC is longer than the BC+SDBC. The BC+SDBC is club-like, with visible distinction between the SDBC and the BC. The apex is rounded. The D is slightly longer than the BC+SDBC, thin and with a round apex. The V is short but wide in diameter. The PC is double as long as the V. The P is swollen along its whole length. The PR is short and robust. The E is longer than the P but thinner in diameter.

Internal morphology of the genital organs (Fig. 44.8). The A, the V and the P are smooth, with few, very loose and barely visible longitudinal elevations. The PP is almost smooth, elongated with a pointed apex. The PP originates from the distal end of the ELP. The ER is not present. The epiphallar formula is: PP(ELP). The E shows two ELP that proximally fade before the VD.

Remarks. This taxon, previously considered as a junior synonym of *C. itala lorinae* (Nordsieck 1963b: 184) was recently elevated (with no explanation) as a valid subspecies by the same author (Nordsieck 2007: 54). It was long considered as a transitional hybrid form between *C. clavata* and *C. itala* but this assumption was based exclusively upon shell characters (Nardi 2011: 101). Scheel and Hausdorf (2012: 3799) proved this is not correct as the taxa previously belonging to one or the other species appear deeply intermingled in the phylograms they provided.

***Charpentieria itala baldensis* (Strobel, 1851)**

Figs 45.1–45.3, 47.7

Distribution. *Charpentieria itala baldensis* is exclusively known from Monte Baldo and Monte Altissimo (Verona, Veneto, Italy), restricted to the peak areas.

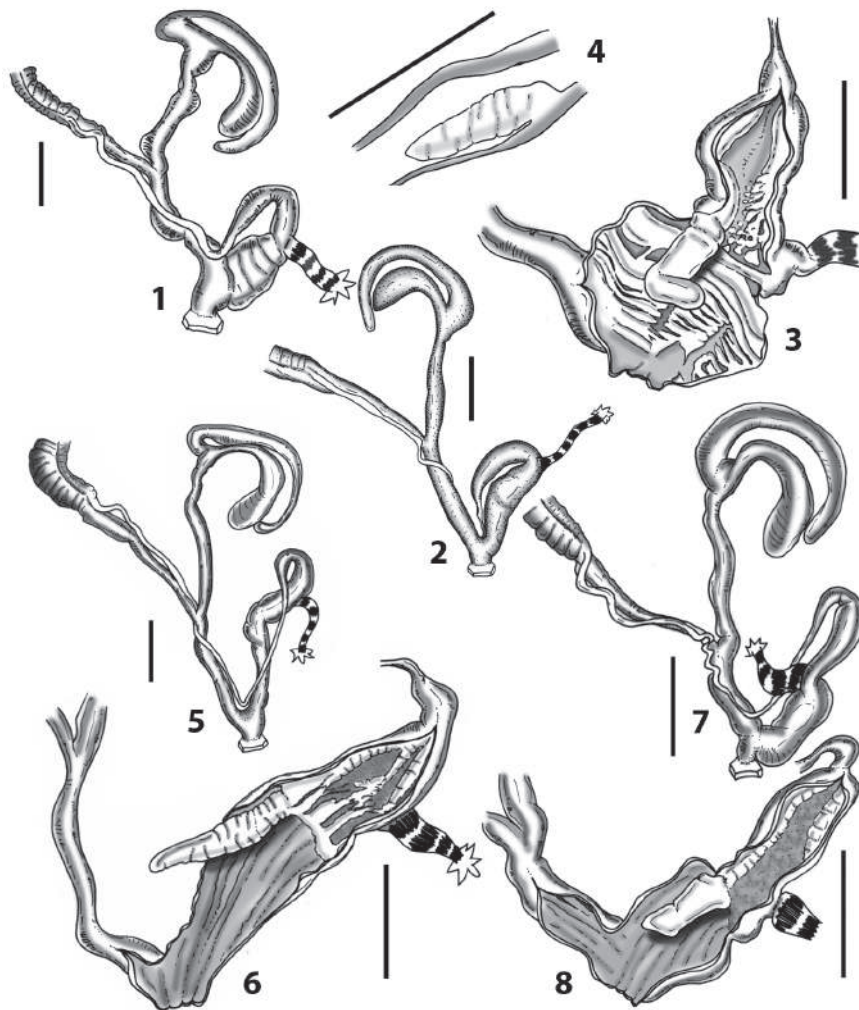


Figure 44. *Charpentieria itala itala* (G. von Martens, 1824), Barbarano Vicentino **44.1**, **44.2** whole distal genital organs **44.3** internal distal part of genital organs **44.4** detail of the pseudopapilla. *Charpentieria itala albopustolata* (De Cristofori & Jan, 1832), Brescia **44.5** whole distal genital organs **44.6** internal distal part of genital organs. *Charpentieria itala allatollae* (Käufel, 1928), Val Ampola, Storo **44.7** whole distal genital organs **44.8** internal distal part of genital organs.

Specimens examined. ITALY, Veneto, Verona, Naole, San Zeno di Montagna. 900 m asl, 45°44'25.95"N, 10°51'13.69"E, [Lab ID C2_2, COI: MW758955], I. Niero leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 45.1). The FO is as long as the V. The FDDB is longer than the BC+SDBC (SDBC+BC). The BC+SDBC presents a very distinguishable second duct as the BC abruptly inflates. The apex is rounded. The D is slightly longer than the BC+SDBC, with a thin proximal part and a swollen distal part. The V is long and thin in diameter. The PC is double as long as the V. The P is slightly swollen at its proximal part. The transition area P-E is clearly detectable from outside. The PR is short and robust. The E is slightly longer than the P but thinner in diameter.

Internal morphology of the genital organs (Figs 45.2, 45.3). The A and the V show smooth few, very loose and barely visible longitudinal elevations. The P shows five to six smooth longitudinal plates that proximally directly start from the ER. The PP is smooth, very elongated with a pointed apex and it occupies almost the whole penial internal volume. Its basis is slightly swollen. The PP originates independently, not connecting neither with the ER or the ELP. The epiphallar formula is: ER+PP+ELP. The E shows two remarkably fringed ELP. They proximally fade before the VD.

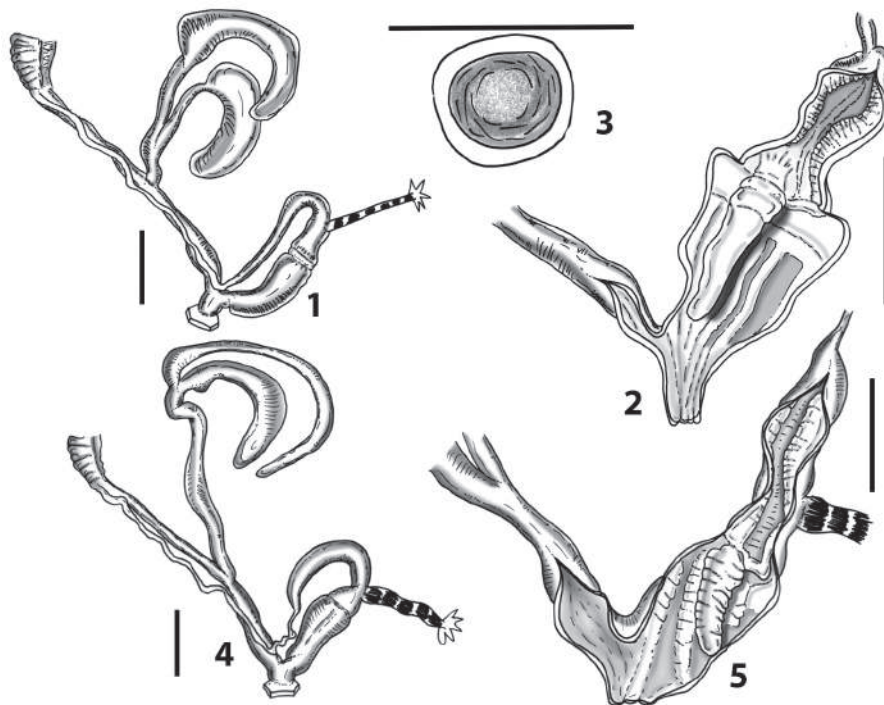


Figure 45. *Charpentieria itala baldensis* (Strobel, 1851), San Zeno, Verona **45.1** whole distal genital organs **45.2** internal distal part of genital organs **45.3** cross section of the pseudopapilla. *Charpentieria itala balsamoi* (Strobel, 1850), Val Serina, Bracca **45.4** whole distal genital organs **45.5** internal distal part of genital organs.

Remarks. This small subspecies, found exclusively at higher altitudes, was previously considered as a transitional form between *C. itala albopustolata* and *C. itala rubiginea* (Nordsieck 1963b: 176–177). The same author (Nordsieck 2007: 54) recently elevated it (with no taxonomic explanation) as a valid subspecies. The taxon was described by Strobel (1851: 25) and not by Charpentier (1852: 384) as stated in MolluscaBase (2021).

***Charpentieria itala balsamoi* (Strobel, 1850)**

Figs 45.4, 45.5, 47.8

Distribution. This subspecies is known from Val Serina (province of Bergamo, Lombardia), Italy (Nardi 2011: 101).

Specimens examined. ITALY, Lombardia, Bergamo, Val Serina, Loc. Galleria, Bracca. 45°49'24.49"N, 09°43'6.73"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 45.4). The FO is 1.5 × longer than the V. The FDBC is extremely short. The BC+SDBC is club-like, with no distinction between the SDBC and the BC. The D is longer than the BC+SDBC. The V is cylindrical. The PC is double as long as the V. The P is slightly swollen at its proximal part with a clearly visible transition between P and EP. The PR is long and robust. The E is slightly longer than the P but thinner in diameter.

Internal morphology of the genital organs (Fig. 45.5). The A and the V are almost smooth, with fine and barely visible longitudinal elevations. The P shows 3 oblique fringed pleats that proximally are not connected to the ER. The PP is fringed and occupies almost the whole penial internal volume. The PP originates from the ER that is connected with the ELP. The epiphallar formula is: PP(ER(ELP)). The E shows two remarkably fringed ELP. They proximally fade before the VD.

***Charpentieria itala clavata* (Rossmässler, 1836)**

Figs 46.1–46.3, 47.9

Distribution. This subspecies is known to occur in central-western Lombardia, in the provinces of Bergamo and Lecco (Nordsieck 1963b; Nardi 2011).

Specimens examined. ITALY, Lombardia, Lecco, Ballabio. 710 m asl, 45°54'25.96"N, 09°25'55.16"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 46.1). The V is slightly longer than the FO. The FDBC is longer than the SDBC+BC. The BC+SDBC is cylindrical, with no clear distinction between the SDBC and the BC. The D is longer than the BC+SDBC. The V is cylindrical and long. The PC is ~ 1.5 × longer than the V. The P is conical and the transition between P and EP is not clearly visible. The PR is short and robust. The E is shorter than the P but shows almost the same diameter.

Internal morphology of the genital organs (Figs 46.2, 46.3). The A and the V show irregular smooth folds that continue proximally inside the P. The P, as the V and

A, does not present a regular pattern of pleats but a combination of irregular smooth folds. The PP is very big, folded with a wide base. It occupies the whole penial volume and reaches the A. The PP originates from the epiphallar wall and it is connected with the ELP. The epiphallar formula is: PP(ELP). The E shows two moderately fringed ELP. They proximally fade before the VD.

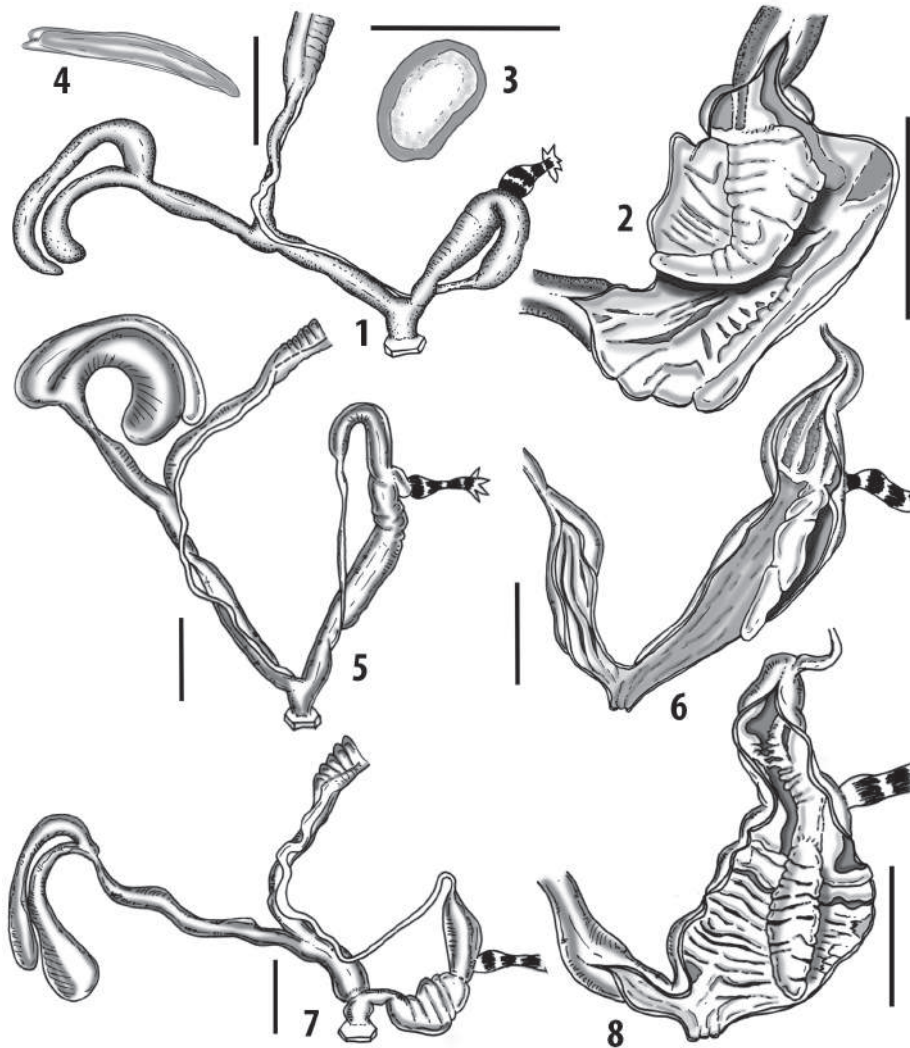


Figure 46. *Charpentieria itala clavata* (Rossmässler, 1836), Ballabio, Lecco **46.1** whole distal genital organs **46.2** internal distal part of genital organs **46.3** cross section of the pseudopapilla **46.3** spermaphore. *Charpentieria itala latestriata* (Küster, 1850), Bedulita, Bergamo **46.5** whole distal genital organs **46.6** internal distal part of genital organs. *Charpentieria itala lorinae* (Gredler, 1869), Val Lorina, Storo **46.7** whole distal genital organs **46.8** internal distal part of genital organs.

***Charpentieria itala latestriata* (Küster, 1850)**

Figs 46.4, 46.5, 47.10

Distribution. Known to occur in central Lombardia, Italy (Nardi 2011: 101).

Specimens examined. ITALY, Lombardia, Bergamo, Bedulita. 625 m asl, 45°47'16.15"N, 09°32'42.26"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 46.5). The V is almost 2 × longer than the FO. The FDBC is as long as the SDBC+BC. The BC+SDBC is club-like, with a more or less clear distinction between the SDBC and the BC. The D is longer than the BC+SDBC and slender. The V is cylindrical and long, slightly tapered along its proximal part. The PC is ~ 1.5 × longer than the V. The P is conical and the transition between P and EP is not clearly visible. The PR is short and robust. The E is shorter than the P but shows almost the same diameter. The whole genital organs show a slender appearance [recalling the ectomorph genital organs as in De Mattia et al. (2020)].

Internal morphology of the genital organs (Fig. 46.6). The V presents irregular longitudinal pleats that stop just before the A. The A the P are mainly smooth with barely visible longitudinal elevations. The PP is smooth, slender, elongated and slightly irregular in shape. It occupies half of the internal penial volume. The PP originates from the ER that is connected with the ELP by means of four minor smooth longitudinal pleats. The epiphallar formula is: PP(ER+ELP). The E shows two moderately fringed ELP. They proximally fade before the VD.

***Charpentieria itala lorinae* (Gredler, 1869)**

Figs 46.6, 46.7, 47.11

Distribution. The distribution of this subspecies is limited to Val Lorina and surrounding peaks, across the border of Trento and Brescia provinces (Lombardia and Trentino-Alto Adige), Italy (Nardi 2011:101).

Specimens examined. ITALY, Lombardia, Brescia, Val di Lorina, Storo. 600 m asl, 45°50'23.18"N, 10°36'49.06"E, [Lab ID C3_2, COI: MW758954], W. De Mattia and J. Macor leg. and det., 3 dissected spm.

External morphology of the genital organs (Fig. 46.7). The V is half as long as the FO. The FDBC is very long, at least 2 × the SDBC+BC. The BC+SDBC is club-like, with a more or less clear distinction between the SDBC and the BC. The D is slightly shorter than the BC+SDBC. The V is cylindrical and very short, wide in diameter. The PC is ~ 2 × longer than the V. The P is short, folded and wide in diameter and the transition between P and EP is clearly visible. The PR is short and robust. The E is almost as long as P and wide in diameter. The genital organs show a slender appearance [recalling the ectomorph genital organs as in De Mattia et al. (2020)].

Internal morphology of the genital organs (Fig. 46.8). The A the V are mainly smooth with weak longitudinal elevations. The P presents strong irregular transversal smooth pleats. The PP is folded, irregular and elongated. It occupies almost the whole internal penial volume. The ER is found distally of the PP and not connected with it.



Figure 47. *Charpentieria ornata* (Rossmässler, 1836), Ogulin, HR **47.1** shell. *Charpentieria itala itala* (G. von Martens, 1824), Barbarano Vicentino **47.2–47.3** shell **47.4** clausiliar plate double side. *Charpentieria itala albopustolata* (De Cristofori & Jan, 1832), Brescia **47.5** shell. *Charpentieria itala allatollae* (Käufel, 1928), Val Ampola, Storo **47.6** shell. *Charpentieria itala baldensis* (Strobel, 1851), San Zeno, Verona **47.7** shell. *Charpentieria itala balsamoi* (Strobel, 1850), Val Serina, Bracca **47.8** shell. *Charpentieria itala clavata* (Rossmässler, 1836), Ballabio, Lecco **47.9** shell. *Charpentieria itala latestriata* (Küster, 1850), Bedulita, Bergamo **47.10** shell. *Charpentieria itala lorinae* (Gredler, 1869), Val Lorina, Storo **47.11** shell.

The PP is directly connected with the ELP. The epiphallar formula is: ER+PP(ELP). The E shows two irregularly fringed ELP. They proximally fade before the VD.

***Charpentieria itala zalloti* nom. nov.**

Figs 48.1–48.2, 50.1–50.2

Remarks. During field collecting (WDM), five populations belonging to *C. itala* ssp. were found in the surrounding of Udine and Cividale (Friuli, Italy). These populations show a remarkably reduced size of the shell comparing to the nominate subspecies or *C. itala serravalensis*, that are the closest *C. itala* subspecies in the west (Figs 44, 48). Moreover, the sutures are almost colourless, the shell is translucent and the peristome is continuous (Figs 50.1, 50.2). Nordsieck (1963b) stated that the eastern distributional limit for *C. itala* is represented by the axis Pordenone-Ampezzo. Thus, these Friulian populations were neglected or simply not known by him. Nevertheless, these populations of *C. itala* were not unknown to past authors. Pirona (1865: 692) cited "*Clausilia alboguttata* Wagn. [= *C. itala*]. Nei muri vecchi muscosi (On old mossy walls); Udine, Tricesimo, Dolegna, Sacile, Portogruaro". He listed two morphotypes: var. a, *major* for the western part (Caneva and Portogruaro) and var. b, *minor* for Udine and Dolegna. In his description, for var. b, *minor* Pirona (1865) pointed out the translucent shell (*cornea*) and the continuous peristome (*peristomate continuo*) and these details, as previously stated, are regularly found also in the easternmost populations recently collected. Concerning the anatomy of the genital organs, these populations present the absence of the (2) longitudinal epiphallar pleats (Figs 48.1–48.2). As regards the identity of the var. a, *major*, following Pirona's description (*saturate rubiginea, peristomate soluto*) it can be postulated that he dealt with the nominate subspecies.

The type locality of the nominate subspecies is less than 50 km west of Portogruaro. Thus, following Pirona (1865) and recent research, the distributional area of *C. itala* is further extended eastward as far as the Friuli plain and Cividale/Dolegna in the east.

Despite Pirona's (1865) thorough description, *Clausilia minor* Pirona, 1865 is several times preoccupied by: *Clausilia minor* Küster, 1850, currently a synonym of *Medora contracta contracta* (Rossmässler, 1842); *Clausilia minor* Küster, 1850, currently a synonym of *Medora almissana almissana* (Küster, 1847); *Clausilia minor* Charpentier, 1852, currently a synonym of *Albinaria profuga* (Charpentier, 1852); *Clausilia minor* A. Schmidt, 1856, currently a synonym of *Clausilia rugosa provincialis* Coutagne, 1886; *Clausilia minor* Walderdorff, 1864, currently a synonym of *Delima montenegrina semilabiata* (Walderdorff, 1864).

The Friulian populations with translucent shell and reduced shell dimensions are here named *C. itala zalloti* nom. nov.

Nordsieck (2011, supplemented May 2021) in chapter 4 clearly referred to our data and manuscript when he felt the need to supplement his web article. He cited Pirona (1865) stating that "The form from Udine, Friuli (...) is strikingly similar to that from Verona. (...) Because of this similarity it is deemed to have been introduced." We

disagree with his rushed conclusion, as the presence of this taxon also in many natural spots along the low Prealps makes an introduction quite unlikely or, at least, deserving additional research.

Distribution and habitat. *Charpentieria itala zalloti* nom. nov. is found on limestone stonewalls (Cividale) or natural limestone small cliffs (Udine castle hill, Tricesimo and Julian Prealps), usually in shady spots. The taxon is found in the Friuli plain and in natural habitats along the low Prealps. Pirona (1865: 692) provides a wider distribution including territories in the west, as far as Sacile, and in the east as far as Dolegna.

Specimens examined. ITALY, Friuli-Venezia Giulia, Udine, castle hill. 140 m asl, 46°03'53.37"N, 13°14'12.35"E, L. Anzil leg., W. De Mattia det., 3 dissected spm. ITALY, Friuli-Venezia Giulia, Udine, Tribil Superiore. 600 m asl, 46°08'26.55"N, 13°37'3.22"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm. ITALY, Friuli-Venezia Giulia, Udine, Lesizza. 340 m asl, 46°7'55.33"N, 13°33'57.00"E, W. De Mattia and J. Macor leg. and det. ITALY, Friuli-Venezia Giulia, Udine, Stermizza. 730 m asl, 46°11'15.09"N, 13°31'31.28"E, W. De Mattia and J. Macor leg. and det. ITALY, Friuli-Venezia Giulia, Udine, Rucchin. 670 m asl, 46°9'12.62"N, 13°38'12.23"E, W. De Mattia and J. Macor leg. and det.

External morphology of the genital organs (Fig. 48.1). The V is slightly shorter than the FO. The FDBC is as long as the SDBC+BC. The BC+SDBC is club-like, with a more or less clear distinction between the SDBC and the BC. The D is slightly shorter than the BC+SDBC. The V is cylindrical and wide in diameter. The PC is only slightly longer than the V. The P is short but wide in diameter and the transition between P and EP is clearly visible. The PR is short and robust. The E is almost as long as the P but small in diameter.

Internal morphology of the genital organs (Fig. 48.2). The V is smooth. The P presents two strong irregular longitudinal folded pleats that reach the A. The PP is folded and elongated with a pointed tip. It occupies almost the whole penial volume. The PP originates from the ER which is connected to the ELP. The two ELP are weak. The epiphallar formula is: PP(ER(ELP)).

Etymology. *Charpentieria itala zalloti* nom. nov. was named after Enrico Zallot (Feltre, Italy-Monster, The Netherlands), skilled malacologist, as a token of friendship and esteem.

Charpentieria itala serravalensis (Nordsieck, 1963)

Figs 48.3, 48.4, 50.3

Distribution. This taxon is widespread throughout the southeastern Alps, from Val Sugana in the west, Alpi Venete, Alps of Belluno and the axis Ampezzo-Pordenone in the east (Italy) (Nordsieck 1963b: 175).

Specimens examined. ITALY, Veneto, Serravalle (L.T.) near Vittorio Veneto. 500 m asl, 46°00'4.46"N, 12°17'11.13"E, W. De Mattia and J. Macor leg. and det., 3 dissected spm.; ITALY, Trentino-Alto Adige, Trento, San Romedio. 730 m asl, 46°22'3.83"N, 11°06'31.84"E, W. De Mattia and J. Macor leg. and det.

External morphology of the genital organs (Fig. 48.3). The V is as long as the FO. The FDBC is as long as the SDBC+BC. The BC+SDBC is cylindrical, short, with no distinction between the SDBC and the BC. The D is slightly shorter than the SDBC+BC. The V is cylindrical and long, thin in diameter. The PC is approximately as long as the V. The P is swollen and wide in diameter and the transition between P and EP is clearly visible. The PR is short and robust. The E is almost as long as the P but thinner in diameter.

Internal morphology of the genital organs (Fig. 48.4). The A and the V are smooth, with of almost undetectable longitudinal elevations. The P presents weak tubercles longitudinally arranged along irregular lines. The PP is smooth and elongated. It is small comparing to the whole penial volume. The PP originates from the ER, which is connected with the ELP. The epiphallar formula is: PP(ER(ELP)). The E shows two fringed ELP. They proximally fade before the VD.

Remarks. The actual status and validity of *C. itala serravalensis*, especially in relation to the nominate subspecies, must be further assessed with more field research and morphological/genetic molecular studies.

***Charpentieria itala trepida* (Käufel, 1928)**

Figs 48.5, 48.6, 50.4

Distribution: The taxon is known for several stations around the Idro Lake, at the boundary between the provinces of Brescia and Trento (Nardi 2011: 98).

Examined material: Forte Cima Ora, Anfo, Brescia, Lombardia, Italy. 1500 m asl, 45°47'50.57"N, 10°28'3.60"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 48.5): The V is 3 × longer than the FO. The FDBC is 2 × longer than the SDBC+BC. The BC+SDBC is markedly club-like, short, with clear distinction between the SDBC and the BC. The D is slightly longer than the SDBC+BC and thinner in diameter. The V is cylindrical and long, slightly swollen in its mid part. The PC is ~ 2 × as long as the V. The P is distally pedunculate and abruptly swollen and widens in diameter along its proximal part. The transition between P and EP is not clearly visible. The PR is long and robust. The E is much shorter than the P but wide in diameter.

Internal morphology of the genital organs (Fig. 48.6): The A is smooth. The V presents smooth longitudinal pleats. The P is completely smooth. The PP is folded and elongated. It occupies half of the internal penial volume. The ER is missing. The PP is directly connected with the ELP. The epiphallar formula is: PP(ELP). The E shows two moderately fringed ELP. They proximally fade before the VD.

Remarks: In the surroundings of Forte Cima Ora (Anfo) we collected this costate form that was wrongly identified as *Charpentieria itala tiesenhauseni* (Gredler, 1855) by Nardi (2011: 98, Fig. 6). *Charpentieria itala tiesenhauseni* seems to be restricted to the type locality (Bocca di Valle) and few additional localities E of the Lago d'Idro (Nordsieck pers. comm.). The population from Forte Cima Ora is here considered as a costate form of *C. itala trepida* (see Nordsieck 2007: 54).

***Charpentieria itala triumphinae* Nardi, 2011**

Figs 48.5–48.6, 49.1–49.2, 50.4, 50.5

Distribution. This subspecific taxon of *C. itala* is endemic to the Central Alps. It is known from the type locality and few scattered localities in the Val Trompia area: Corna Blacca, Passo delle Portole, Cima Caldoline, Passo della Berga and other localities in the municipalities of Lavenone and Collio (Brescia, Lombardia, Italy), from 1500 m asl up (Nardi 2011: 99–100).

Specimens examined. ITALY, Lombardia, Brescia, Lavenone, Cima Caldoline. 1700 m asl, 45°48'3.54"N, 10°24'20.12"E, G. Nardi leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 49.1). The V is half as long as the FO. The FDBC is 2 × longer than the SDBC+BC. The BC+SDBC is club-like, short, with no clear distinction between the SDBC and the BC. The D is slightly longer than the SDBC+BC. The V is short and cylindrical. The PC is ~ 2 × as long as the V. The P is swollen. The transition between P and EP is clearly visible. The PR is short and robust. The E is much shorter than the P but wide in diameter.

Internal morphology of the genital organs (Fig. 49.2). The A is smooth. The V presents irregular pleats. The P is completely smooth. The PP is folded and elongated. It occupies $\frac{3}{4}$ of the internal penial volume. The PP originates from the ER that is directly connected with the ELP. The epiphallar formula is: PP(ER(ELP)). The E shows two moderately fringed ELP. They proximally fade before the VD.

Remarks. Nardi (2011: 99) roughly described the anatomy of the genital organs providing a sketch of a specimen from the same locality we had available as well. His description and depiction differ from our anatomical results by a remarkably shorter FO and a longer V, whereas the remaining genital external details seem to be similar (e.g., the penial complex). Nardi (2011: 99) did not provide any detail of the internal sculpturing of the genital organs, depicting only the pseudopapilla (named "papilla penis"). Moreover, the pseudopapilla appears slightly different according to our results, being it smooth instead of folded. However, its general conical shape and dimensions (in comparison with the volume of the penis) match with our results. The folding of its surface could be due to a reproductive/seasonal/physiological moment of the specimen at the time of collecting/fixation.

***Charpentieria itala variscoi* (Pini, 1883)**

Figs 49.3, 49.4, 50.6

Distribution. This taxon is known only from the Val Brembana and Val Taleggio (Bergamo, Lombardia, Italy) (Nordsieck 1963b).

Specimens examined. ITALY, Lombardia, Bergamo, Lavina, Val Taleggio. 650 m asl, 45°53'11.73"N, 09°33'55.46"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 49.3). The V is slightly shorter than the FO. The FDBC is as long as the SDBC+BC. The BC+SDBC is club-like in

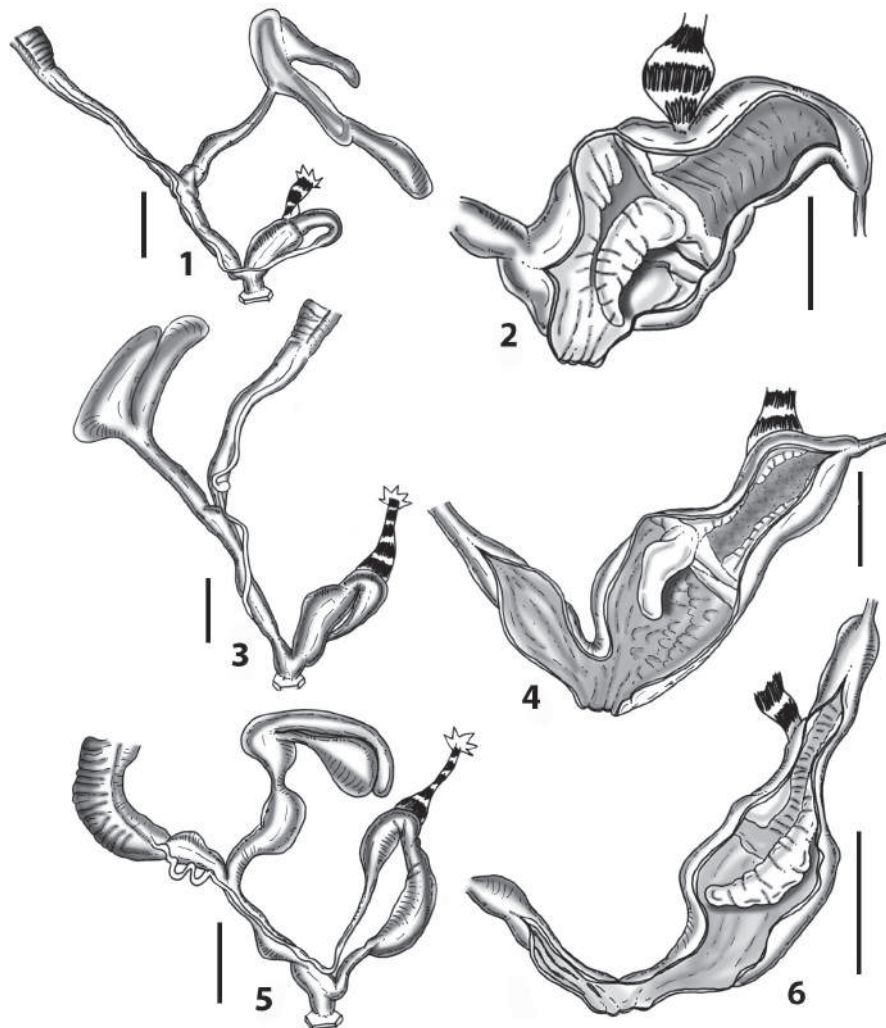


Figure 48. *Charpentieria itala zalloti* nom. nov., Udine **48.1** whole distal genital organs **48.2** internal distal part of genital organs. *Charpentieria itala serravalensis* (Nordsieck, 1963), Serravalle, Vittorio Veneto **48.3** whole distal genital organs **48.4** internal distal part of genital organs. *Charpentieria itala trepida* (Käufel, 1928), Cima Ora, Anfo **48.5** whole distal genital organs **48.6** internal distal part of genital organs.

shape with clear distinction between the SDBC and the BC. The D is longer than the SDBC+BC. The V is short and slightly swollen. The PC is $\sim 3 \times$ as long as the V. The P is fusiform. The transition between P and EP is not clearly visible. The PR is long and thin. The E is slightly shorter than the P and thinner in diameter.

Internal morphology of the genital organs (Fig. 49.4). The A and the V are smooth. The P is distally smooth, with transversal irregular weak pleats along its proxi-

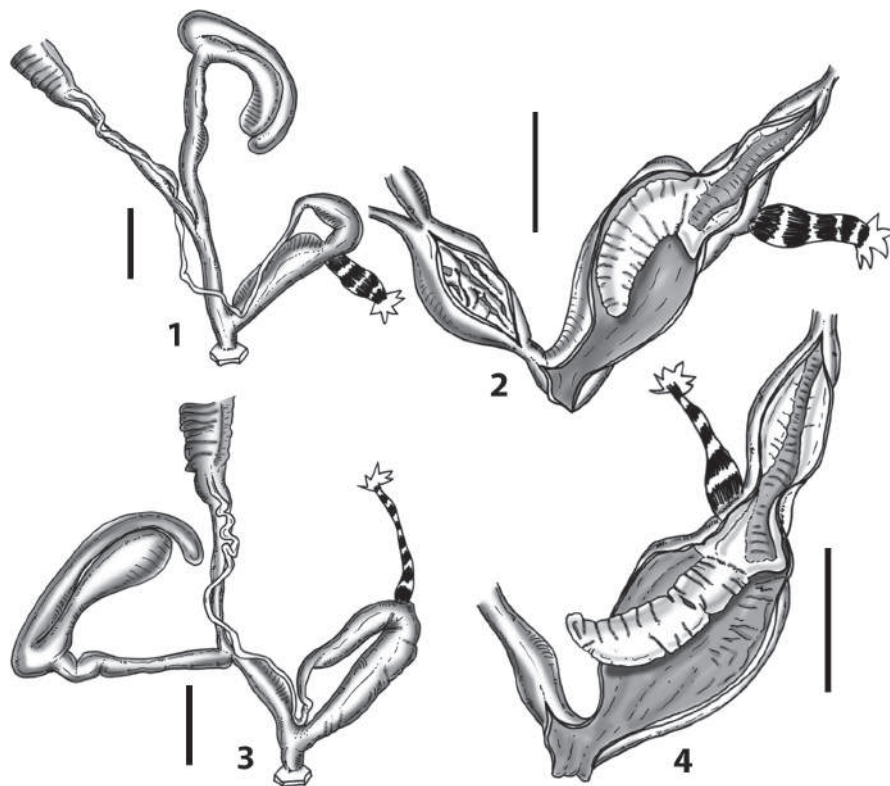


Figure 49. *Charpentieria itala triumplinae* Nardi, 2011, Lavenone, Brescia **49.1** whole distal genital organs **49.2** internal distal part of genital organs. *Charpentieria itala variscoi* (Pini, 1883), Val Taleggio, Bergamo **49.3** whole distal genital organs **49.4** internal distal part of genital organs.

mal part. The PP is folded and very elongated. It occupies the whole penial volume. The PP originates from the ER that is connected with the ELP by means of few minor longitudinal pleats. The epiphallar formula is: PP(ER+ELP). The E shows two moderately fringed ELP. They proximally fade before the VD.

Brief genital anatomical description of *Charpentieria stenzii* subspecific taxa

Charpentieria stenzii is present along the Eastern Alps, from the Val di Non in Trentino and Pre-Alps of Veneto in the West to the Alpi Giulie in the East (Zallot 2001; Welter-Schultes 2012). Currently nine subspecific taxa are considered valid (Zallot 2001: 137–138; MolluscaBase 2021). *Charpentieria stenzii* shows a remarkable variability as regards the shell features. This is well depicted and described in Zallot (2001: 143–155). As for *C. itala* the subspecies were traditionally based on shell morphological characters, e.g., the sculpturing of the shell surface (smooth, striated to ribbed) or the development and variability of the internal plicae and lamellae. The shell is almost



Figure 50. *Charpentieria itala zalloti* nom. nov., Udine **50.1–50.2** shell. *Charpentieria itala serravalensis* (Nordsieck, 1963), Serravalle, Vittorio Veneto **50.3** shell. *Charpentieria itala trepida* (Käufel, 1928), Cima Ora, Anfo **50.4** shell. *Charpentieria itala triumphinae* Nardi, 2011, Lavenone, Brescia **50.5** shell. *Charpentieria itala variscoi* (Pini, 1883), Val Taleggio, Bergamo **50.6** shell.

smooth or weakly striated to striated or frankly ribbed (as in *C. stenzii letochana*). The suture is always remarkably whitish. Compared to *C. dyodon*, *C. itala* and *C. ornata*, the species, presents a reduction of the buccal armature, with both, columellaris and parietalis generally small to almost absent. The lunella is usually weak to almost undetectable (Zallot 2001).

Eight of nine subspecies of *C. stenzii* were anatomically investigated (Table 8). A new anatomical feature, namely the hemipapilla, was discovered and revealed to be typical and exclusive of this species. The hemipapilla consists of an uninterrupted, circular and fleshy elevated ring that almost entirely obliterates the lumen along the penis and epiphallus transition area, slightly distally to the PR. The base of the pseudopapilla is fused with almost the entire ring, making it difficult to distinguish it from a real penial papilla. The sperm channel is anyway present, it is not just a narrow section as in the epiphallar ring of *Sicania/Siciliaria* or the rooted pseudopapilla. Its outlet is found at the base of the pseudopapilla (Figs 51–54). The pseudopapilla is channel-less and filled-up of spongy tissue. The inner atrial pad depicted and deemed by Nordsieck (1963b) as a characteristic of the species, in our genital anatomical investigations was found only in *C. stenzii letochana*. The other subspecies of *C. stenzii* showed a variable inner sculpturing of the atrium, from irregular smooth pleats (as *C. stenzii faueri*) to almost smooth (as *C. stenzii westerlundii*) with different degrees of complexity in between.

***Charpentieria stenzii stenzii* (Rossmässler, 1836)**

Figs 51.1–51.3, 56.1

Distribution. Italy, Trentino-Alto Adige, including westernmost Dolomites in the surroundings of Schlern mountain, Val di Non and Passo della Mendola (Nordsieck 1963b: 191; Zallot 2001: 154).

Specimens examined. ITALY, Trentino-Alto Adige, Trento, San Romedio. 730 m asl, 46°22'3.83"N, 11°06'31.84"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 51.1). The V is slightly longer than the FO. The FDBC is as long as the SDBC+BC. The BC+SDBC is cylindrical in shape without clear distinction between the SDBC and the BC. The D is longer than the SDBC+BC and thinner. The V is short and wide in diameter. The PC is ~ 3 × longer than the V. The P is cylindrical. The transition between P and EP is not clearly visible. The PR is short and thin. The E is slightly shorter than the P and thinner in diameter.

Internal morphology of the genital organs (Figs 51.2–51.3). The A and the V are smooth or with weak irregular convolute pleats. The P presents irregular and wide longitudinal pleats. The hemipapilla is smooth and very short. The outlet of the hemipapilla is roundish. The E shows two moderately fringed ELP. They proximally fade before the VD.

***Charpentieria stenzii butoti* (Bank, 1987)**

Figs 51.4–51.8, 56.2

Specimens examined. ITALY, Trentino-Alto Adige, Trento, Fai della Paganella. 600 m asl, 46°12'57.04"N, 11°04'22.88"E, W. De Mattia and J. Macor leg. and det., 3 dissected spm.

Distribution. Massif of Mount Paganella, Trentino-Alto Adige, Italy (Zallot 2001: 154).

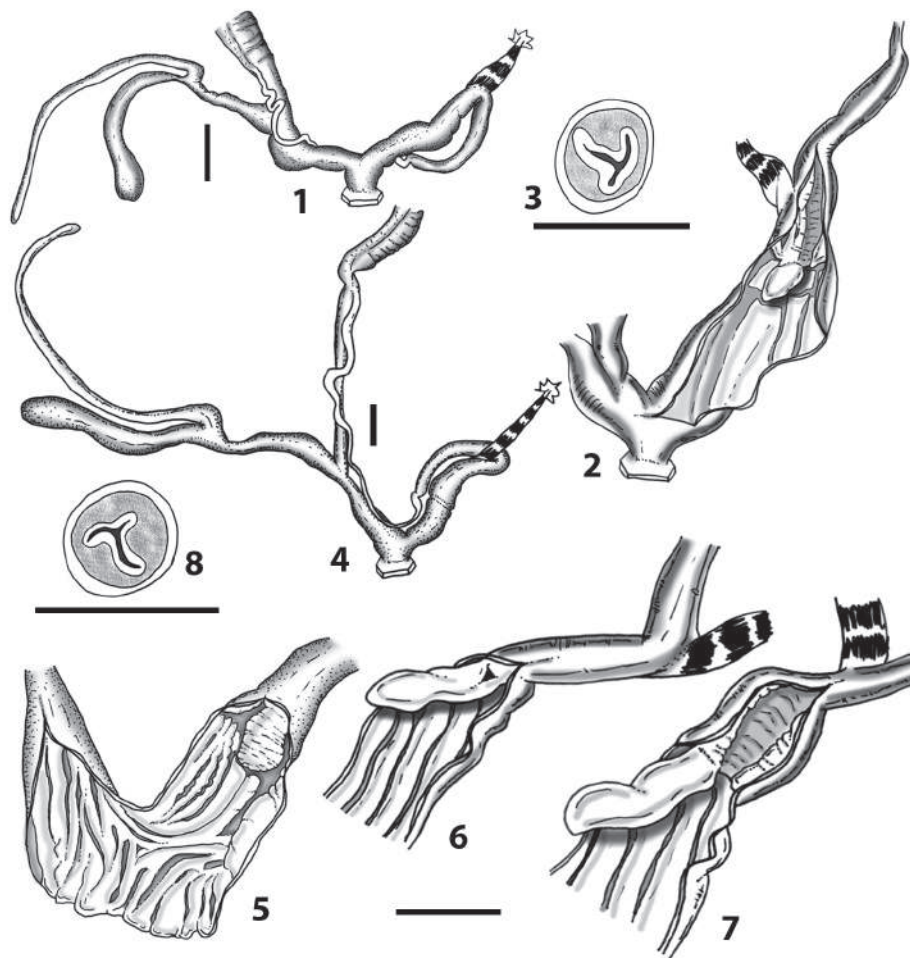


Figure 51. *Charpentieria stenzii stenzii* (Rossmässler, 1836), San Romedio, Trento **51.1** whole distal genital organs **51.2** internal distal part of genital organs **51.3** cross section of the epiphallus. *Charpentieria stenzii butoti* (Bank, 1987), Fai della Paganella **51.4** whole distal genital organs **51.5** internal distal part of genital organs **51.6** detail of the hemipapilla: uncut **51.7** detail of the hemipapilla: cut funnel **51.8** cross section of the epiphallus.

External morphology of the genital organs (Fig. 51.4). The V is shorter than the FO. The FDBC is slightly shorter than the SDBC+BC. The BC+SDBC is cylindrical in shape without clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and thinner. The V is short and wider in diameter along its distal part. The PC is $\sim 3 \times$ longer than the V. The P is cylindrical. The transition between P and EP is clearly visible. The PR is long and thin. The E is longer than the P but thinner in diameter along its proximal part.

Internal morphology of the genital organs (Figs 51.5–51.8). The A, the V and the P show many more or less irregular, mostly smooth longitudinal pleats. The hemipapilla is smooth and short. The outlet of the hemipapilla is triangular. The E shows two fringed ELP. They proximally fade before the VD.

***Charpentieria stenzii cincta* (Brumati, 1838)**

Figs 52.1–52.6, 56.3

Specimens examined. ITALY, Friuli-Venezia Giulia, Pordenone, Bosplans. 500 m asl, 46°11'40.51"N, 12°38'14.26"E, [Lab ID C2_2, COI: MW758953, ITS2: MW757049, MW757050], W. De Mattia and J. Macor leg. and det., 2 dissected spm; ITALY, Friuli-Venezia Giulia, Tarvisio, Val Resia, sella di Carnizza. 400 m asl, 46°20'15.55"N, 13°19'17.11"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.

Distribution. *Charpentieria stenzii cincta* presents a wide distribution, approximately including in Italy the Alpi and Prealpi Carniche and Giulie, Dolomiti, Cansiglio and Monti Lessini (Zallot 2001: 154), Stubai Alps (Tribulaun) and farther to the East: Alps of Carinthia and westernmost Slovenia.

External morphology of the genital organs (Fig. 52.1). The V is much shorter than the FO. The FDBC is slightly shorter than the SDBC+BC. The BC+SDBC is cylindrical to club-like in shape, without clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and thinner. The V is very short and wide in diameter. The PC is $\sim 3 \times$ longer than the V. The P is cylindrical and swollen along its proximal part. The transition between P and EP is clearly visible. The PR is short and thin. The E is longer than the P but thinner in diameter.

Internal morphology of the genital organs (Figs 52.2–52.6). The A, the V and the P show many more or less irregular (longitudinal to oblique) smooth pleats. The hemipapilla is smooth to moderately folded and usually short. The outlet of the hemipapilla is slit-like. The E shows two fringed ELP. They proximally fade before the VD.

***Charpentieria stenzii faueri* (Bank, 1987)**

Figs 53.1–53.4, 56.4

Specimens examined. ITALY, Veneto, Vicenza, Grotte di Oliero near Valstagna. 800 m asl, 45°50'47.79"N, 11°40'4.24"E, W. De Mattia and J. Macor leg. and det., 3 dissected spm.

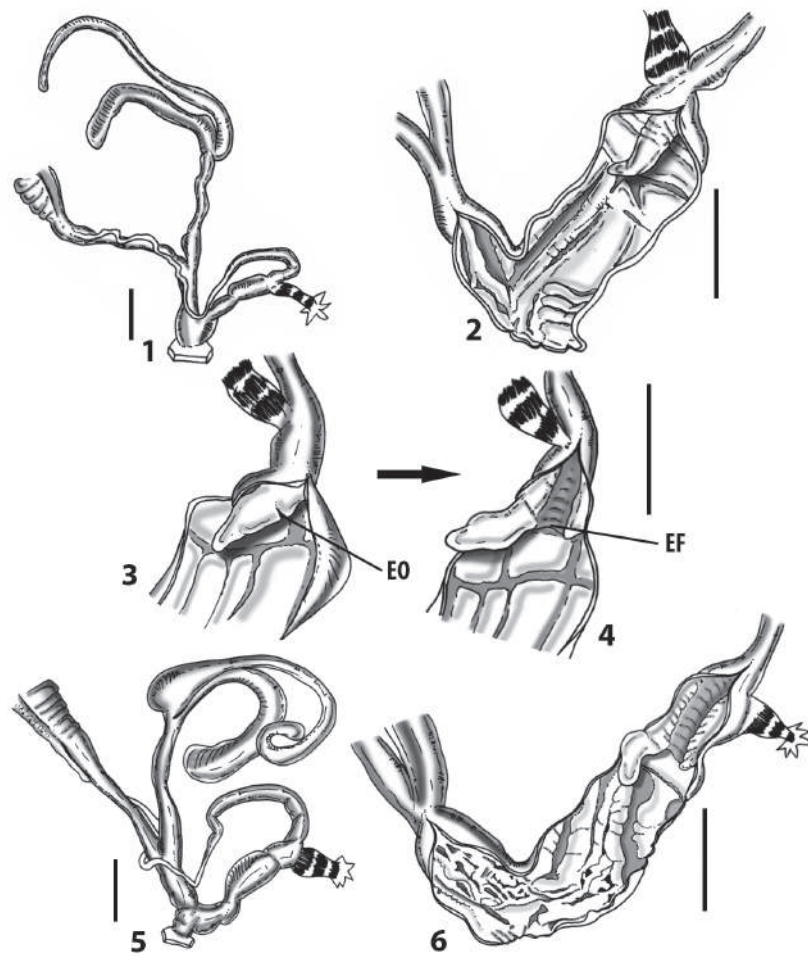


Figure 52. *Charpentieria stenzii cincta* (Brumati, 1842), Bosplans, Pordenone **52.1** whole distal genital organs **52.2** internal distal part of genital organs **52.3** detail of the hemipapilla: uncut **52.4** detail of the hemipapilla: cut funnel. *Charpentieria stenzii cincta* (Brumati, 1842), Val Resia, Udine **52.5** whole distal genital organs **52.6** internal distal part of genital organs with cut funnel.

Distribution. *Charpentieria stenzii faueri* is exclusively known from Col del Vento and Grigno (Trento, Trentino-Alto Adige) and Oliero (Vicenza, Veneto), Italy (Bank 1987: 139).

External morphology of the genital organs (Fig. 53.1). The V is much shorter than the FO. The FDBC is as long as the SDBC+BC. The BC+SDBC is cylindrical to club-like in shape, without clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and thinner. The V is very short and wide in

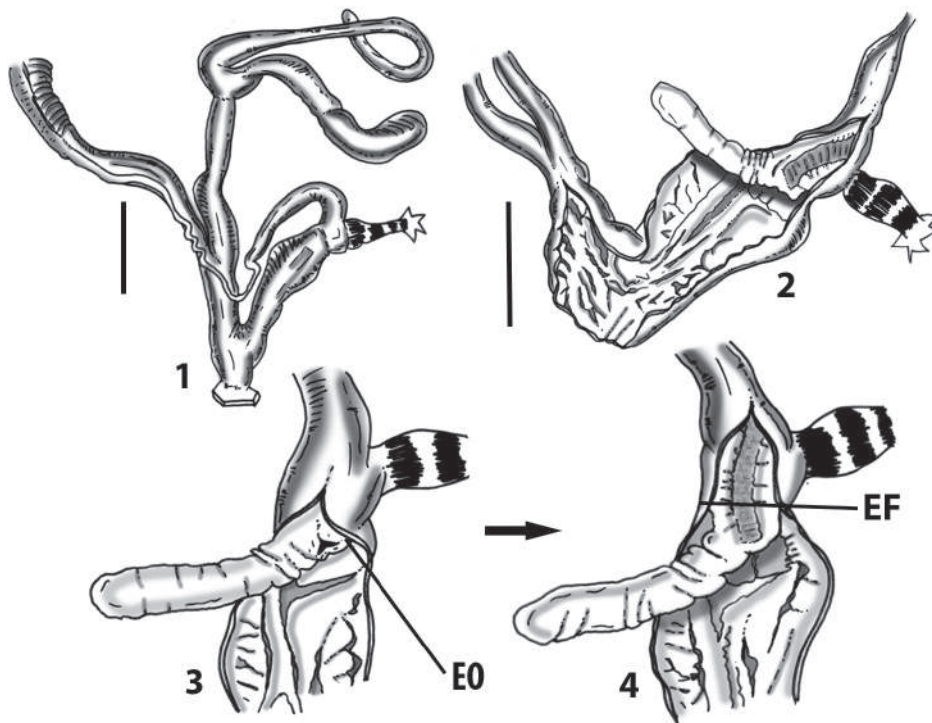


Figure 53. *Charpentieria stenzii faueri* (Bank, 1987), Oliero, Vicenza **53.1** whole distal genital organs. **53.2** internal distal part of genital organs with cut funnel **53.3** detail of the hemipapilla: uncut **53.4** detail of the hemipapilla: cut funnel.

diameter. The PC is $\sim 3 \times$ longer than the V. The P is cylindrical and swollen along its proximal part. The transition between P and EP is clearly visible. The PR is short and robust. The E is as long as the P but much thinner in diameter.

Internal morphology of the genital organs (Figs 53.2–53.4). The A, the V and the P show many more or less irregular smooth pleats. The hemipapilla is long, smooth to moderately folded. The outlet of the hemipapilla is triangular. The E shows two fringed ELP. They proximally fade before the VD.

***Charpentieria stenzii letochana* (Gredler, 1874)**

Figs 54.1–54.6, 56.5

Specimens examined. ITALY, Veneto, Belluno, Misurina, Val Fonda. 1500 m asl, 46°36'27.42"N, 12°12'20.01"E, [Lab ID C19_1, COI: MW758957], W. De Mattia and J. Macor leg. and det., 2 dissected spm.

Distribution. *Charpentieria stenzii letochana* is exclusively known from Val Fonda (Belluno, Veneto) and Val Pusteria (Schönleiental) (Bolzano, Trentino-Alto Adige), Italy (Nordsieck 1963b: 198).

External morphology of the genital organs (Fig. 54.1). The V is shorter than the FO. The FDBC is as long as the SDBC+BC. The BC+SDBC is slim, club-like in shape, with a clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and thinner. The V is short and thin in diameter. The PC is $\sim 2 \times$ longer than the V. The P is cylindrical and slightly swollen along its proximal part. The transition between P and EP is clearly visible. The PR is long and robust. The E is as long as the P but much thinner in diameter.

Internal morphology of the genital organs (Figs 54.2–54.6). The V presents irregular smooth pleats. The A has a fleshy, mushroom-like fold. The P shows many irregular smooth to fringed pleats. The hemipapilla is short, smooth to moderately folded. The outlet of the hemipapilla is slit-like. The E shows two moderately fringed ELP. They proximally fade before the VD.

***Charpentieria stenzii nordsiecki* (Fauer, 1991)**

Figs 55.1, 55.2, 56.6

Specimens examined. ITALY, Veneto, Treviso, Cison di Val Marino. 250 m asl, 45°58'5.53"N, 12°08'52.60"E, W. De Mattia and J. Macor leg. and det., 4 dissected spm.

Distribution. *Charpentieria stenzii nordsiecki* is exclusively known from the pre-alpine area of Cison di Valmarino, Valmareno and Passo San Boldo (Treviso, Veneto), Italy (Fauer 1991: 164).

External morphology of the genital organs (Fig. 55.1). The V is shorter than the FO. The FDBC is longer than the SDBC+BC. The BC+SDBC is slim, fusiform in shape, without a clear distinction between the SDBC and the BC. The D is longer than the SDBC+BC and thinner. The V is moderately long and thin in diameter. The PC is $\sim 3.5 \times$ longer than the V. The P is slim and cylindrical. The transition between P and EP is clearly visible. The PR is long and robust. The E is longer than the P and slightly thinner in diameter. The genital organs show an extremely slender appearance [recalling the ectomorph genital organs as described in De Mattia et al. (2020)].

Internal morphology of the genital organs (Figs 55.1–55.2). The V and the A are smooth. The P shows 3 to 4 smooth pleats. The pleats proximally fade toward the transition with the E. The hemipapilla is missing. The E shows two moderately fringed ELP. They proximally fade before the VD.

Remarks. *Charpentieria stenzii nordsiecki* lacks the pseudopapilla and presents an extremely ectomorphic genital organs type. This morphotype of genital organs was already found in the genus *Montenegrina* [e.g., *Montenegrina lillae* Fehér & Szekeres, 2016 and *Montenegrina skipetarica* (Soós, 1924)] (De Mattia et al. 2020). It seems that there is not direct correlation between ectomorphic state of genital organs and lack of the papilla/pseudopapilla as other *Montenegrina* taxa [e.g., *Montenegrina ja-*

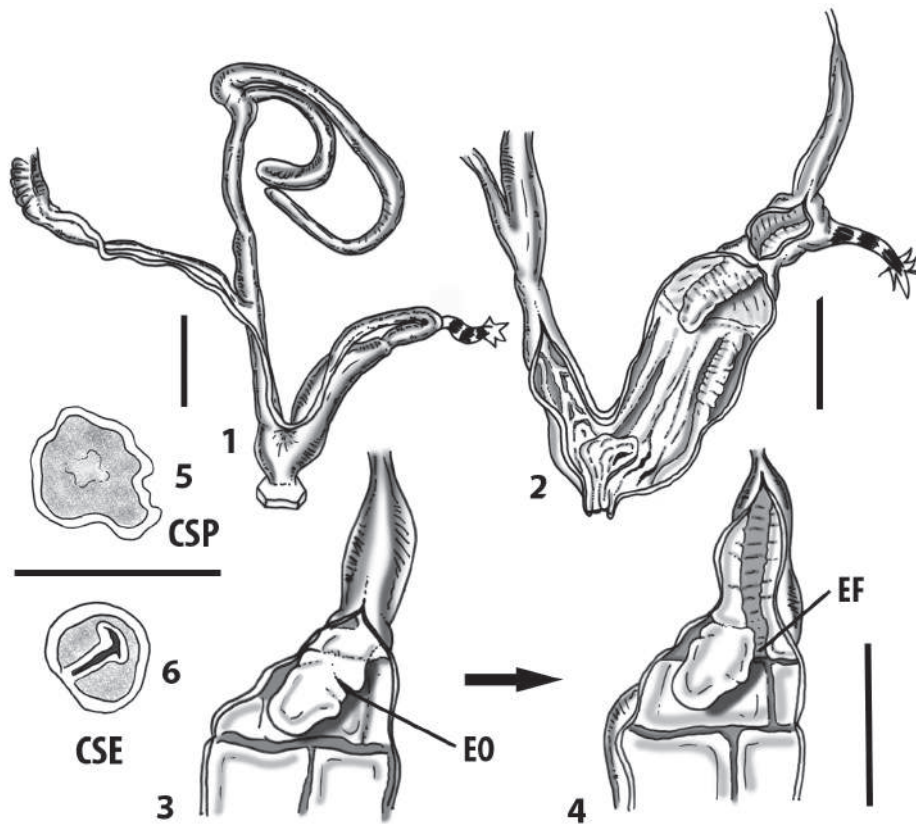


Figure 54. *Charpentieria stenzii letochana* (Gredler, 1874), Val Fonda, Belluno **54.1** whole distal genital organs **54.2** internal distal part of genital organs **54.3** detail of the hemipapilla: uncut **54.4** detail of the hemipapilla: cut funnel **54.5** cross section of the pseudopapilla **54.6** cross section of the epiphallus.

ninensis (Mousson, 1859) or *Montenegrina okolensis okolensis* Szekeres, 2006] or also in *Stigmatica* [e.g., *Stigmatica splendens* (Nordsieck, 1996), see below]) that despite showing the lack of the papilla/pseudopapilla, present a mesomorphic state of genital organs (De Mattia et al. 2020). The complete absence of the papilla/pseudopapilla could probably represent an apomorphic character state due to isolation and lack of gene flow among populations.

***Charpentieria stenzii paroliniana* (De Betta & Martinati, 1855)**

Figs 55.3–55.5, 56.7

Distribution. *Charpentieria stenzii paroliniana* is known from the lower Valle del Brenta from Carpanè, Cison del Grappa to Primolano, and surrounding mountains on the right bank of the Brenta River (Foza, Vicenza, Veneto), Italy (Nordsieck 1963b: 196).

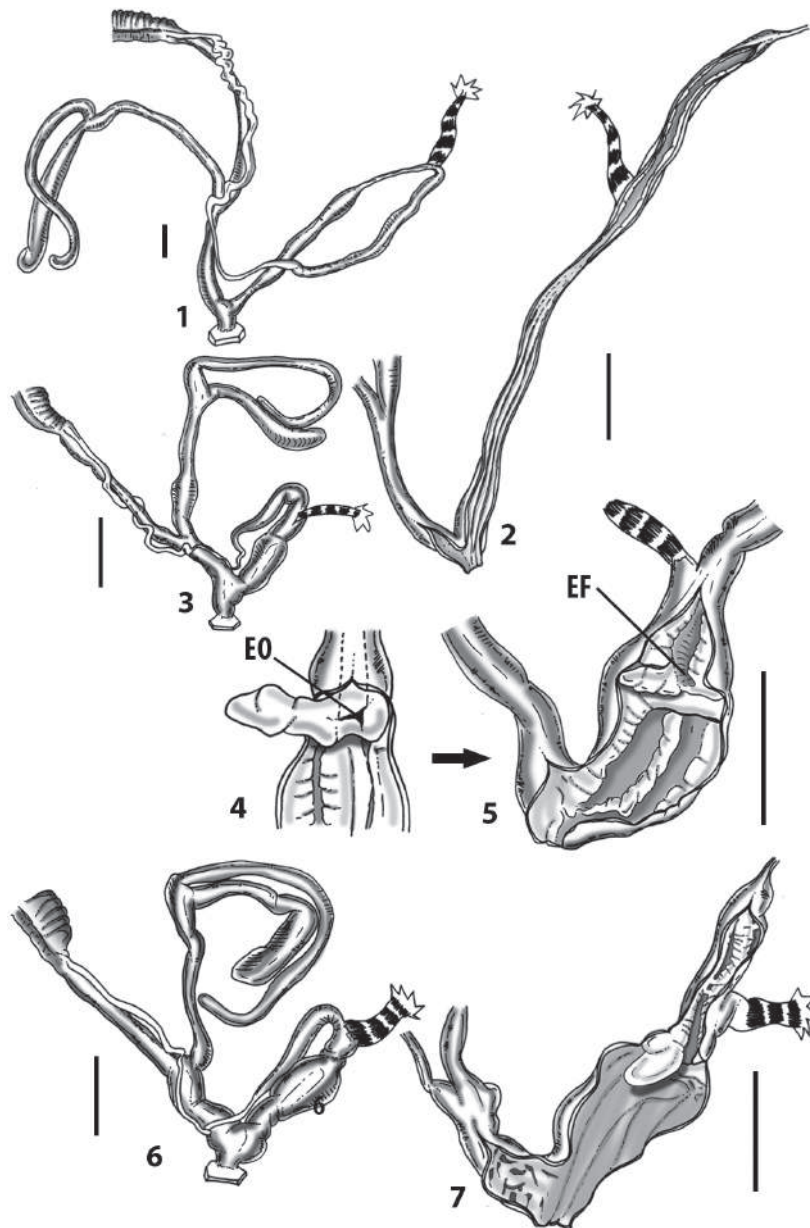


Figure 55. *Charpentieria stenzii nordsiecki* Fauer, 1991, Cison di Valmarino, Treviso **55.1** whole distal genital organs **55.2** internal distal part of genital organs. *Charpentieria stenzii paroliniana* (De Betta & Martinati, 1855), Valstagna, Vicenza **55.3** whole distal genital organs **55.4** detail of the hemipapilla: uncut **55.5** internal distal part of genital organs with cut funnel. *Charpentieria stenzii westerlundi* Nordsieck, 1993, Val Fiscalina, Bolzano **55.6** whole distal genital organs **55.7** internal distal part of genital organs with cut funnel.



Figure 56. *Charpentieria stenzii stenzii* (Rossmässler, 1836), San Romedio, Trento **56.1** shell. *Charpentieria stenzii butoti* (Bank, 1987), Fai della Paganella **56.2** shell. *Charpentieria stenzii cincta* (Brumati, 1842), Bosplans, Pordenone **56.3** shell. *Charpentieria stenzii faueri* (Bank, 1987), Oliero, Vicenza **56.4** shell. *Charpentieria stenzii letochana* (Gredler, 1874), Val Fonda, Belluno **56.5** shell. *Charpentieria stenzii nordsiecki* Fauer, 1991, Cison di Valmarino, Treviso **56.6** shell. *Charpentieria stenzii paroliniana* (De Betta & Martinati, 1855), Valstagna, Vicenza **56.7** shell. *Charpentieria stenzii westerlundi* Nordsieck, 1993, Val Fiscalina, Bolzano **56.8** shell.

Specimens examined. ITALY, Veneto, Vicenza, Valstagna, Foza, Loc. La Goccia. 800 m asl, 45°52'29.20"N, 11°38'59.73"E, W. De Mattia and J. Macor leg. and det., 3 dissected spm.

External morphology of the genital organs (Fig. 55.3). The V is much shorter than the FO. The FDBC is as long as the SDBC+BC. The BC+SDBC is club-like in shape, with a more or less clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and slightly thinner. The V is short but wide in diameter. The PC is $\sim 2.5 \times$ longer than the V. The P is cylindrical and slightly swollen. The transition between P and EP is clearly visible. The PR is long and robust. The E is longer than the P but thinner in diameter.

Internal morphology of the genital organs (Figs 55.4–55.5). The V is smooth. The P shows three to four irregularly fringed pleats that continue as far as the A. The hemipapilla is very short, conical and moderately folded. The outlet of the hemipapilla is triangular. The E shows two fringed ELP. They proximally fade out before the VD.

Charpentieria stenzii westerlundi Nordsieck, 1993

Figs 55.6, 55.7, 56.8

Distribution. *Charpentieria stenzii westerlundi* is known only from Val Fiscalina (Fischleintal) in the surrounding of Sesto (Bolzano, Trentino-Alto Adige), Italy (Nordsieck 1963b: 196).

Specimens examined. ITALY, Trentino-Alto Adige, Bolzano, Sesto, Val Fiscalina (Fischleintal), Croda Rossa. 1500 m asl, 46°38'2.83"N, 12°021'42.79"E, I. Niero leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 55.6). The V is much shorter than the FO. The FDBC is as long as the SDBC+BC. The BC+SDBC is club-like in shape, with a more or less clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and slightly thinner. The V is short but wide in diameter. The PC is $\sim 2.5 \times$ longer than the V. The P is cylindrical and slightly swollen. The transition between P and EP is clearly visible. The PR is long and robust. The E is longer than the P but thinner in diameter.

Internal morphology of the genital organs (Fig. 55.7). The V is smooth. The P shows three to four irregularly fringed pleats that continue as far as the A. The hemipapilla is very short, conical and moderately folded. The outlet of the hemipapilla is triangular. The E shows two fringed ELP. They proximally fade out before the VD.

Remarks. The original name of this “Form vom Fischleintal in Südtirol” (Nordsieck 1993: 36) namely *Clausilia cincta* var. *disjuncta* Westerlund, 1878, is pre-occupied by *Clausilia disjuncta* Mortillet, 1854 [= *Armenica disjuncta* (Mortillet, 1854)]. The new name *Charpentieria stenzii westerlundi* nom. nov. was provided by Nordsieck (1993: 36).

Brief genital anatomical description of three *Gibbularia gibbula* subspecific taxa

Gibbularia is a monotypic genus, currently considered both as a subgenus of *Siciliaria* (Nordsieck 2007; Nordsieck 2013a) or a subgenus of *Charpentieria* (MolluscaBase 2021).

MolluscaBase eds. (2021) citation is based on Nordsieck (2002: 29) and the information provided by Nordsieck's papers of 2007 and 2013a have never been subsequently adopted. The (sub)genus was briefly reviewed by Nordsieck (2013a: 6). The diagnosis is shell-based and the genus is subdivided into two main groups of species as seen in Table 9. *Charpentieria (Gibbularia) gibbula honii* (O. Boettger, 1879) differs from the *Charpentieria (Gibbularia) gibbula gibbula* (Rossmässler, 1836) by virtue of a few details of the buccal armature and shape of the clausilium (Nordsieck 2013a: 6). Although considered as a subgenus of *Siciliaria* by Nordsieck (2013a: 4) highlighted the lack of the epiphallar thickening in *Gibbularia*.

Table 9. *Siciliaria (Gibbularia) gibbula* taxa as grouped by Nordsieck (2013a: 6).

<i>Siciliaria (Gibbularia) gibbula</i> (Rossmässler, 1836)	
<i>Siciliaria (Gibbularia) gibbula gibbula</i> (Rossmässler, 1836) GROUP	<i>Siciliaria (Gibbularia) gibbula honii</i> (O. Boettger, 1879) GROUP
<i>Siciliaria (Gibbularia) gibbula gibbula</i> (Rossmässler, 1836)	<i>Siciliaria (Gibbularia) gibbula honii</i> (O. Boettger, 1879)
<i>Siciliaria (Gibbularia) gibbula multiplex</i> (Westerlund, 1884)	
<i>Siciliaria (Gibbularia) gibbula niethammeri</i> (Rensch, 1934)	
<i>Siciliaria (Gibbularia) gibbula pelagosana</i> (O. Boettger, 1877)	
<i>Siciliaria (Gibbularia) gibbula cf. sanctangeli</i> (A. J. Wagner, 1925)	
<i>Siciliaria (Gibbularia) gibbula selecta</i> (Monterosato in Cecconi, 1908)	

Table 10. Examined taxa of *Gibbularia* and *Stigmatica* with information on availability of genetic data (DNA; Yes/No) and epiphallar formula.

Taxon	Examined specimens	Epiphallar formula	DNA
<i>Gibbularia gibbula gibbula</i> (Rossmässler, 1836)	Muggia, Europa Gardens, Trieste, Friuli-Venezia Giulia, Italy. 30 m asl. 45°36'17.64"N, 13°45'59.24"E. W. De Mattia and J. Macor leg. and det.	PP	Y
<i>Gibbularia gibbula gibbula</i> (Rossmässler, 1836)	Apricena, Foggia, Puglia, Italy. 75 m asl. 41°47'01.22"N, 15°26'39.92"E, H. Nordsieck leg and det.	ER(ELP)+PP	Y
<i>Gibbularia gibbula cf. sanctangeli</i> (A.J. Wagner, 1925)	Mattinata close to Vieste, Puglia, Italy. 500 m asl. 41°45'15.61"N, 16°04'56.31"E, W. De Mattia and J. Macor leg. and det.	ER(PP+ELP)	N
<i>Stigmatica stigmatica stigmatica</i> (Rossmässler, 1836)	Reka Dubrovačka, Sustjepan, Dubrovnik, Croatia. 5 m asl. 42°40'12.26"N, 18°05'38.24"E, W. De Mattia and J. Macor leg. and det.	ER(PP+ELP)	N
<i>Stigmatica stigmatica cf. stigmatica</i> (Rossmässler, 1836)	Rijeka Reževići, on the Budva–Petrovac road, 100 m asl. 42°13'33.84"N, 18°54'40.70"E, Deli, Eröss, Fehér leg. W. De Mattia det.	ER(PP+ELP)	N
<i>Stigmatica stigmatica cf. stigmatica</i> (Rossmässler, 1836)	Orjen Mts, Podi and Kamenno, Herceg Novi-Trebinje Road, Montenegro. 325 m asl. 42°28'08.05"N, 18°32'29.17"E. Deli, Eröss, Fehér leg. W. De Mattia det.	ER(PP+ELP)	N
<i>Stigmatica stigmatica sturmii</i> (L. Pfeiffer, 1848)	Punta Penne next to the Airport, Brindisi, Puglia, Italy. 5 m asl. 40°40'31.60"N, 17°56'40.44"E, H. Nordsieck leg. and det.	PP	Y

Taxon	Examined specimens	Epiphallar formula	DNA
<i>Stigmatica ernae</i> Fauer, 1978	San Rufo, Passo della Sentinella, Salerno, Campania, Italy. 850 m asl. 40°25'27.06"N, 15°26'17.44"E. W. De Mattia and J. Macor leg. and det.	PP+ELP	N
<i>Stigmatica incerta</i> (Küster, 1861)	Serra San Bruno, Vibo Valentia, Calabria, Italy. 945 m asl. 38°32'42.36"N, 16°19'09.42"E, W. De Mattia and J. Macor leg. and det.	PP(ER)+ELP	N
<i>Stigmatica kobeltiana</i> (Küster, 1876)	Altília, Cosenza, Calabria, Italy. 460 m asl. 39°07'58.01"N, 16°15'01.92"E, W. De Mattia and J. Macor leg. and det.	PP(ER)+ELP	N
<i>Stigmatica kobeltiana</i> (Küster, 1876)	Gerace, Strada Provinciale 1, 3.5 km NW of the town, Reggio Calabria, Calabria, Italy. 400 m asl. 38°16'53.42"N, 16°11'49.3" E, W. De Mattia and J. Macor leg. and det.	PP(ER)+ELP	N
<i>Stigmatica lamellata</i> (Rossmässler, 1836)	Gardiki fortress, Corfu, Greece. 40 m asl. 39°28'37.39"N, 19°53'05.74"E, W. De Mattia and J. Macor leg. and det.	PP+ELP	N
<i>Stigmatica paestana paestana</i> (Philippi, 1836) (= <i>S. p. semisculpta</i> Paulucci, 1878)	Monte Telegrafo, Argentario, Toscana, Italy. 600 m asl. 42°23'13.90"N, 11°10'03.98"E, A. Margelli leg. and det.	PP(ER)+ELP	N
<i>Stigmatica paestana inustructa</i> (Westerlund, 1883)	Balvano, Potenza, Basilicata; Italy. 450 m asl. 40°38'40.44"N, 15°30'39.09"E, I. Niero leg. and det.	PP(ELP)	N
<i>Stigmatica paestana inustructa</i> (Westerlund, 1883)	Balvano, near the castle, Potenza, Basilicata; Italy. 450 m asl. 40°39'01.23"N, 15°30'38.91"E, W. De Mattia and J. Macor leg. and det.	PP(ELP)	N
<i>Stigmatica pantocratoris pantocratoris</i> (O. Boettger, 1889)	Lafki, Corfu, Greece. 420 m asl. 39°46'18.23"N, 19°50'47.23"E, W. De Mattia and J. Macor leg. and det.	PP+ELP	N
<i>Stigmatica splendens</i> (Nordsieck, 1996)	Vlorë district, Qeparo, macchia with tree spurses W of the village, 20 m, 50 m asl. 40°03'25.07"N, 19°49'47.06"E, Juhász, Kovács, Murányi, Puskás leg. W. De Mattia det.	ELP	N
<i>Stigmatica pantocratoris margaritifera</i> (Nordsieck, 1996)	Delvinë District, Krongj, rocky grassland at the peak region of Mt Kojino-lithar, Albania. 890 m asl. 39°54'12.34"N, 20°10'11.39"E, Barina, Pifkó, Puskás leg. W. De Mattia det.	PP(ER)+ELP	N
<i>Stigmatica vulcanica vulcanica</i> (Benoit, 1860)	Cosenza, Via Porta Piana, Calabria, Italy. 300 m asl. 39°17'02.08"N, 16°15'30.22"E, H. Nordsieck leg. and det.	PP+ER(ELP)	Y
<i>Stigmatica vulcanica vulcanica</i> (Benoit, 1860)	Castello di San Lucido, Paola, Calabria, Italy. 120 m asl. 39°21'33.06"N, 16°02'39.97"E, I. Niero leg. and det.	PP+ER(ELP)	Y
<i>Stigmatica vulcanica vulcanica</i> (Benoit, 1860)	Amantea, Cosenza, Calabria, Italy. 30 m asl. 39°08'24.65"N, 16°04'18.13"E, I. Niero leg. and W. De Mattia det.	PP(ER)+ELP	N
<i>Stigmatica vulcanica vulcanica</i> (Benoit, 1860)	Contrada Piscitello, Belpasso, Catania, Sicily, Italy. 650 m asl. 37°36'13.96"N, 14°59'25.42"E, W. De Mattia and J. Macor leg. and det.	PP+ELP	N
<i>Stigmatica vulcanica sigridae</i> (Nordsieck, 2013)	Contrada Rizzuto, Cosenza, Calabria, Italy. 770 m asl. 39°14' 51.24"N, 16°10'30.51"E, W. De Mattia and J. Macor leg. and det.	PP(ER)+ELP	N
<i>Stigmatica vulcanica sigridae</i> (Nordsieck, 2013)	Contrada Rizzuto road to San Bartolo, Cosenza, Calabria, Italy. 740 m asl. 39°15'20.65"N, 16°11'09.16"E, W. De Mattia and J. Macor leg. and det.	PP(ER)+ELP	N

In our study, two populations of *Gibbularia gibbula gibbula* underwent molecular genetic analysis and genital anatomical investigations, one from northern Italy: Muggia (Trieste) and one from Southern Italy: Apricena (Foggia) (Table 10). Their genital morphology is similar, with only slight differences such as the sculpturing of the internal penis (finely granulated vs. finely granulated + 1 weak smooth longitudinal pleats) and the presence of a weak epiphallar ring in the Apricena's population. Both populations show a pseudopapilla directly originating from the epiphallar wall. *Gibbularia gibbula* cf. *sanctangeli* (not in the phylogenetic trees) from Gargano was also dissected and shows a remarkable different anatomy of the genital organs compared to the previ-

ous taxon. It shows an epiphallar ring that is connected to the ELP and also represents the origin of the pseudopapilla. In the mt tree, phylogenetic relationships among *Gibbularia* and the other genera, appear as a polytomy and low support values prevent us to provide any reliable statement. In the ITS2 tree, its distance from *Charpentieria* appears clear, preventing us to consider *Gibbularia* as a subgenus of *Charpentieria* as once listed by Nordsieck (2007).

Gibbularia until now was considered as a subgenus of *Siciliaria* (MolluscaBase 2021; Nordsieck, 2013a). Our results indicate that no *Gibbularia* sample falls inside *Siciliarial*/*Sicania* subclades, suggesting a meaningful phylogenetic distance. Its position inside *Siciliaria* cannot be maintained, albeit its relationships with the other genera (mainly with *Stigmatica*), are still not clear. For this reason, we currently consider *Gibbularia* a valid genus until further results will be available.

***Gibbularia gibbula gibbula* (Rossmässler, 1836)**

Figs 57.1–57.4, 58.1–58.4

Distribution. The actual distribution of the genus *Gibbularia* is far from being completely understood. This is mainly due to the passive anthropocorous dispersion and the absence of clear data about its centre of dispersion. Only a wide range was provided, that includes eastern peninsular and northeastern Italy as far as Istria to central Dalmatia (Alzona 1971: 89; Welter-Schultes 2012: 340; Nordsieck 2013a: 3). The subspecific taxa, except for the nominotypic one, present restricted to very restricted distribution ranges, e.g., *Gibbularia gibbula pelagosana* from Pelagosa or *Gibbularia gibbula selecta* from Tremiti Islands (Alzona 1971: 89–90).

Specimens examined. ITALY, Friuli-Venezia Giulia, Muggia, Trieste, Europa Gardens. 20 m asl, 45°36'8.91"N, 13°46'0.72"E, [Lab ID G64_1, COI: MW758958, ITS2: MW757048, MW757082, MW757083; Lab ID G64_2, COI: MW758959], W. De Mattia and J. Macor leg. and det., 3 dissected spm.

External morphology of the genital organs (Fig. 57.3). The V is slightly longer than the FO. The FDDB is slightly longer than the SDDB+BC. The BC+SDDB is club-like in shape, with a clear distinction between the SDDB and the BC. The D is much longer than the SDDB+BC and slightly thinner. The V is short but wide in diameter. The PC is ~ 2 × longer than the V. The P is cylindrical. The transition between P and EP is visible. The PR is very short and robust. The E is much shorter than the P and thin in diameter.

Internal morphology of the genital organs (Fig. 57.4). The V, the A and the P show a smooth with a fine granulation that becomes coarser along the proximal P. The pseudopapilla is short, roundish and originates directly from the P-E transition wall. The epiphallar formula is: PP. The E shows a particular sculpturing made of extremely tiny transverse, interrupted micro-pleats.

Additional specimens examined. ITALY, Puglia, Foggia, Apricena. 75 m asl, 41°47'1.22"N, 15°26'39.92"E, [Lab ID 12167_1, COI: MW758947; Lab ID

12167_2, COI: MW758948, ITS2: MW757055, MW757056, MW757057], H. Nordsieck leg and det., 2 dissected spm.

External morphology of the genital organs (Fig. 57.1). The V is half as long as the FO. The FDBC is 3 × longer than the SDBC+BC. The BC+SDBC is club-like in shape, with a clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and slightly thinner. The V is moderately long but small in diameter. The PC is ~ 2 × longer than the V. The P is cylindrical. The transition between P and EP is not clearly visible. The PR is long and robust. The E is much shorter than the P and thin in diameter.

Internal morphology of the genital organs (Fig. 57.2). The V and the A are smooth. The P presents four to five smooth longitudinal, little elevated pleats. The PP is short, roundish and originates directly from the P-E transition wall. The epiphallar formula is: ER(ELP)+PP. The weak distal ELP soon disappear revealing a smooth internal E.

***Gibbularia gibbula* cf. *sanctangeli* (A. J. Wagner, 1925)**

Figs 57.5, 57.6, 58.6

Distribution. The taxon is exclusively known from the southern slopes of Monte Sant'Angelo, Gargano Peninsula (Puglia, Italy) (Wagner 1925: 57).

Specimens examined. ITALY, Puglia, Mattinata close to Vieste, southern slopes of the Gargano Peninsula. 500 m asl, 41°45'15.61"N, 16°04'56.31"E, W. De Mattia and J. Macor leg. and det., 3 dissected spm.

External morphology of the genital organs (Fig. 57.5). The V is 4 × shorter than the FO. The FDBC is much longer (2 ×) than the SDBC+BC. The BC+SDBC is club-like in shape, with a more or less clear distinction between the SDBC and the BC. The D is remarkably longer than the SDBC+BC. The V is extremely short but wide in diameter. The PC is ~ 3.5 × longer than the V. The P is spindle-like and slightly swollen. The transition between P and EP is clearly visible. The PR is short and robust. The E is almost as long as the P but slightly thinner in diameter.

Internal morphology of the genital organs (Fig. 57.6). The V is smooth. The P shows four to five main vast smooth pleats. These pleats are mainly longitudinally arranged but tend to become smaller and irregular to transversal along the proximal P. The pseudopapilla originates from the epiphallar thickening. The ER is connected with the ELP. The epiphallar formula is: ER(PP+ELP). The E shows four to five small longitudinal pleats that merge into two smooth ELP. They proximally fade before the VD.

Remarks. As a shell, *Gibbularia gibbula* cf. *sanctangeli* shows reliable differences with the nominate subspecies, e.g., the bigger dimensions, the slender shape with flatter whorls, the suture without the darker band and the more prominent cervical keels. The principalis and the anterior upper palatal plicae are usually not visible from frontal view (Fig. 58.5). We cite this population as cf. *sanctangeli*, since the typical form is known from the type locality only and this one may represent a transitional form.

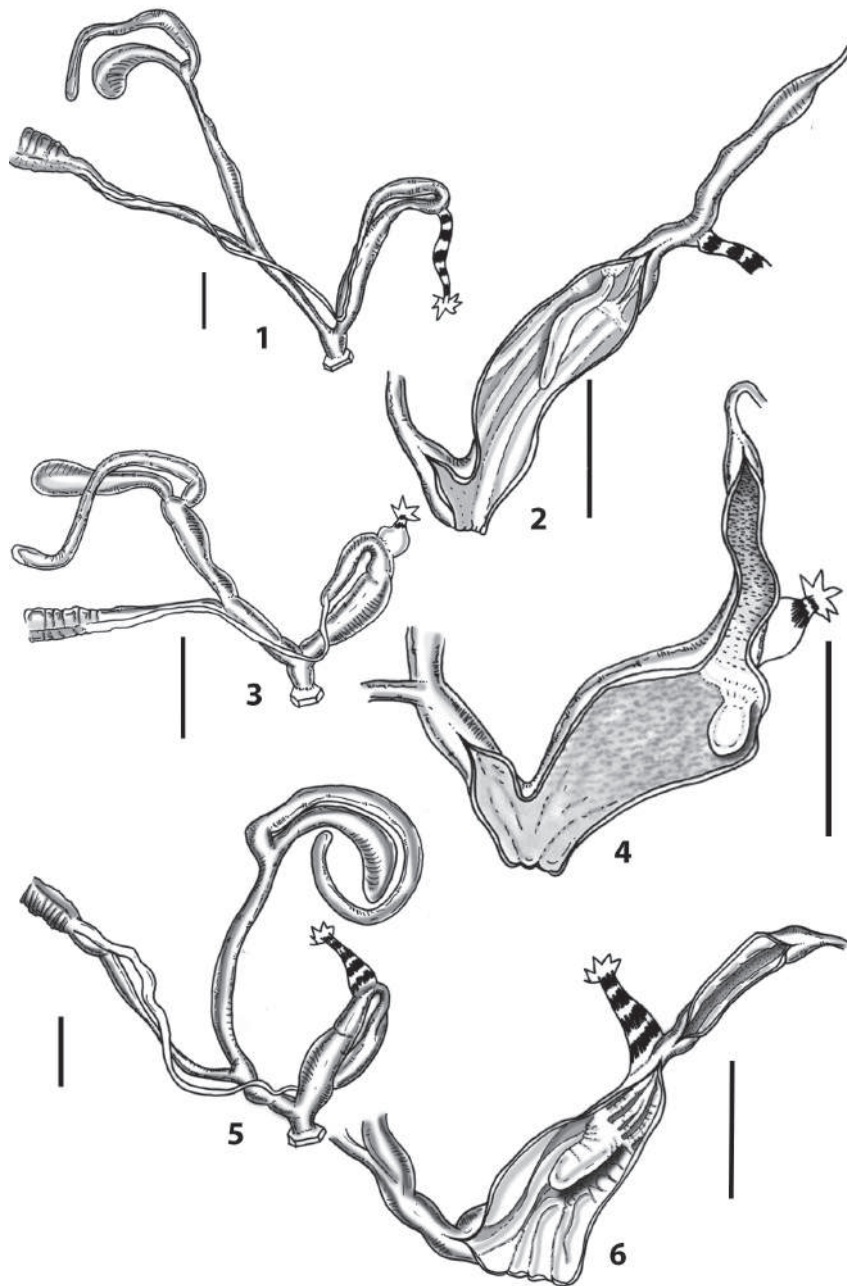


Figure 57. *Gibbularia gibbula gibbula* (Rossmässler, 1836). Apricena, Foggia **57.1** whole distal genital organs **57.2** internal distal part of genital organs. Muggia, Trieste **57.3** whole distal genital organs **57.4** internal distal part of genital organs. *Gibbularia gibbula* cf. *sanctangeli* (A. J. Wagner, 1925), Mattinana, Vieste **57.5** whole distal genital organs **57.6** internal distal part of genital organs.

Brief genital anatomical description of ten *Stigmatica* taxa

Stigmatica (type species *Clausilia stigmatica* Rossmässler, 1836 = *Siciliaria (Stigmatica) stigmatica*) is currently considered as a subgenus of *Charpentieria* (MolluscaBase 2021) probably based on Nordsieck (2002: 29). Nordsieck's decision (2007, 2013a) where *Stigmatica* is again deemed as a subgenus of *Siciliaria* wasn't adopted. *Stigmat-*



Figure 58. *Gibbularia gibbula gibbula* (Rossmässler, 1836). Apricena, Foggia **58.1** shell **57.2** clausiliar plate double side. Muggia, Trieste **58.3–58.4** shell **58.5** detail of the aperture. *Gibbularia gibbula* cf. *sanctangeli* (A. J. Wagner, 1925), Mattinata, Vieste **58.6** shell.

ica includes 16 taxa among species and subspecies and presents a wide distribution, including taxa from the SW Balkans (S Dalmatia, NW Greece and Ionian Islands, Montenegro and Albania) and Peninsular Italy from Tuscany southward and E Sicily (Welter-Schultes 2012; MolluscaBase 2021), in a typical pattern of trans-Adriatic distribution as already known for, e.g., *Medora* (Nordsieck 1970; 2012). In order to assess the relationships between *Stigmatica* and *Siciliaria*, four taxa of *Stigmatica* have undergone both molecular and genital anatomical investigations. Three additional populations were exclusively anatomically investigated (Table 10). In both the COI and ITS2 trees, *Stigmatica* forms three independent lineages, distant from *Siciliaria/Sicania* (Figs 4–6). In the ITS2 tree the few available clones confirmed its polyphyly, as *Stigmatica pantocratoris pantocratoris* from Corfu and *Stigmatica stigmatica sturmii* from Brindisi fall in different distant subclades. As a genital anatomical peculiarity, *Stigmatica* shows, even though rarely, the presence of a vestigial epiphallar flagellum, which has never been found in *Siciliaria/Sicania*. This structure, when present, is very difficult to be identified as extremely small and almost transparent. It was recorded in one specimen of *Stigmatica incerta* and *Stigmatica vulcanica sigridae*.

***Stigmatica stigmatica stigmatica* (Rossmässler, 1836)**

Figs 59.1–59.6, 61.1–61.3

Distribution. The nominate subspecies is distributed from southern Dalmatia (from the Neretva River southward), Herzegovina, Montenegro to northern Albania.

Specimens examined. CROATIA, Dubrovnik, Sustjepan, Reka Dubrovačka. 5 m asl, 42°40'12.26"N, 18°05'38.24"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm; MONTENEGRO, Rijeka Reževići, on the Budva–Petrovac road, 100 m asl, 42°13'33.84"N, 18°54'40.70"E, Deli, Eröss, Fehér leg. W. De Mattia det., 2 dissected spm.; MONTENEGRO, Orjen Mts, Podi and Kameno, Herceg Novi-Trebinije Road. 325 m asl, 42°28'8.05"N, 18°32'29.17"E Deli, Eröss, Fehér leg. W. De Mattia det., 2 dissected spm.

External morphology of the genital organs (Figs 59.1, 59.3, 59.5). The V is much shorter than the FO. The FD BC is longer than the SD BC+BC. The BC+SD BC is club-like in shape, with a more or less clear distinction between the SD BC and the BC. The D is extremely longer than the SD BC+BC but remarkably thinner. The V is very short but wide in diameter. The PC is ~ 4–5 × longer than the V. The P is cylindrical or slightly swollen. The transition between P and EP is clearly visible. The PR is short but very robust. The E is usually as long as the P and thinner in diameter.

Internal morphology of the genital organs (Figs 59.2, 59.4, 59.6). The V is smooth. The P shows a pattern of irregularly fringed or smooth pleats, sometimes forming an irregular net-like pattern, usually disappearing toward the A that is smooth. The pseudopapilla is small and roundish. It originates from the E wall, which is connected with the ELP. The epiphallar formula is ER(PP+ELP). The E shows two fringed ELP, sometimes remarkably irregular and connected with small fleshy transversal bridges. They proximally fade before the VD.

***Stigmatica stigmatica sturmii* (L. Pfeiffer, 1848)**

Figs 60.1, 60.2, 61.4

Distribution. This taxon is restricted to the Salento (Puglia, Italy) and central Albania with the type form (Nordsieck 2013a: 6).

Specimens examined: ITALY, Puglia, Brindisi, Punta Penne next to the Airport. 5 m asl, 40°40'31.60"N, 17°56'40.44"E, [Lab ID 12194_1, COI: MW758949, ITS2: MW757053, MW757054; Lab ID 12194_2, COI: MW758950], H. Nordsieck leg. and det. 2 dissected spm.

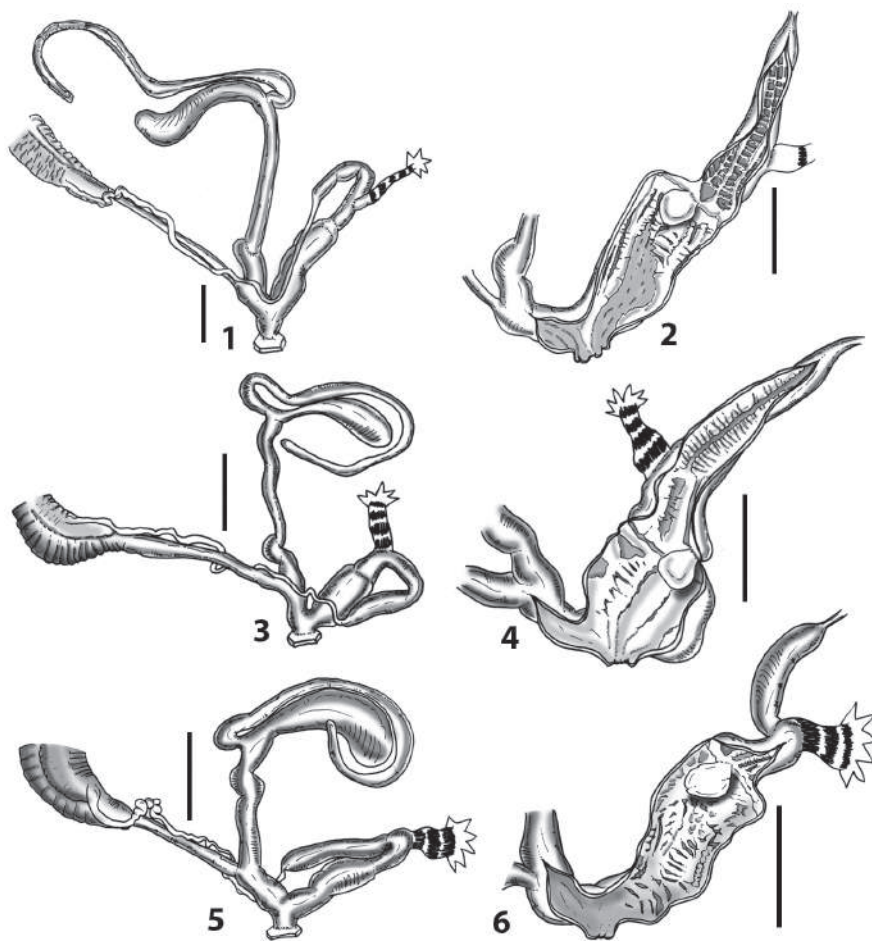


Figure 59. *Stigmatica stigmatica stigmatica* (Rossmässler, 1836), Dubrovnik, HR **59.1** whole distal genital organs **59.2** internal distal part of genitalia. *Stigmatica stigmatica* cf. *stigmatica* (Rossmässler, 1836). Budva, Montenegro **59.3** whole distal genital organs **59.4** internal distal part of genitalia. Orjen Mountains, Montenegro **59.5** whole distal genital organs **59.6** internal distal part of genitalia.

External morphology of the genital organs (Fig. 60.1). The V is shorter than the FO. The FDBC is longer than the SDBC+BC. The BC+SDBC is club-like in shape, with a more or less clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and slightly thinner. The V is moderately long and thin in diameter. The PC is $\sim 2 \times$ longer than the V. The P is slim and cylindrical. The transition between P and EP is not visible. The PR is long and robust. The E is shorter than the P and thinner in diameter.

Internal morphology of the genital organs (Fig. 60.2). The V is smooth. The P shows a single smooth longitudinal pleat that reaches the atrium. The pseudopapilla is elongated with an irregular surface. It originates from the E wall. The epiphallar formula is PP+ELP. The E shows two smooth ELP. They proximally fade before the VD.

Remarks. The morphology of the genital organs of this population is remarkably different from all other *Stigmatica*, and it shows high affinity with the genus *Gibbularia*. This is also suggested by the ITS2 tree, where *G. gibbula gibbula* from Apricena and this population cluster together implying that this population might be misidentified and belongs to the genus *Gibbularia*. However, in the COI tree, *S. s. sturmi* forms a very distant lineage. Thus, this taxon certainly deserves thorough investigation with a larger sample size.

Stigmatica ernae (Fauer, 1978)

Figs 60.3, 60.4, 61.5, 61.6

Distribution. This species is restricted to the eastern side of the Monti Alburni, Campania, Italy.

Specimens examined. ITALY, Campania, Salerno, San Rufo, Passo della Sentinella. 850 m asl, 40°25'27.06"N, 15°26'17.44"E. W. De Mattia and J. Macor leg. and det., 3 dissected spm.

External morphology of the genital organs (Fig. 60.3). The FO is 4–5 \times longer than the V. The FDBC is 2 \times as long as the SDBC+BC. The BC+SDBC is slightly club-like in shape, with a more or less clear distinction between the SDBC and the BC. The D is longer than the SDBC+BC. The V is short. The PC is $\sim 3 \times$ longer than the V. The P is irregular and folded in shape. The transition between P and E is slightly visible. The PR is very long and slim. The E is half as long as the P and thinner in diameter.

Internal morphology of the genital organs (Fig. 60.4). The V is smooth. The P shows five to six irregular transverse smooth pleats that stop before entering in the atrium. The pseudopapilla is moderately short with a smooth surface. It originates from the E wall. The epiphallar formula is PP+ELP. The E shows two smooth ELP. They proximally fade before the VD.

Remarks. *Stigmatica ernae* shows an extremely long FO and, as a whole, the female part of the distal genital organs shows an ectomorphic type (except as regards the vagina) whereas the PC is relatively short.

***Stigmatica incerta* (Küster, 1861)**

Figs 60.5, 60.6, 61.7

Distribution. *Stigmatica incerta* is found in the Madonie and Nebrodi mountains in Sicily and in southern Calabria.

Specimens examined. ITALY, Calabria, Vibo Valentia, Serra San Bruno. 945 m asl, 38°32'42.36"N, 16°19'09.42"E, W. De Mattia and J. Macor leg. and det., 3 dissected spm.

External morphology of the genital organs (Fig. 60.5). The FO is 2.5 × as long as the V. The FDBC is remarkably longer than the SDBC+BC. The BC+SDBC is short, bulky, club-like in shape, with a more or less clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and thinner. The PC is ~ 4 × longer than the V. The P is moderately wide in diameter and swollen. The transition between P and EP is clearly visible. The PR is long and robust. The E is longer than the P but thinner in diameter.

Internal morphology of the genital organs (Fig. 60.6). The V presents few smooth longitudinal pleats, distally merging one into another, that stop immediately before entering the A. The P shows three or four slightly fringed pleats that continue almost as far as the A. These penial pleats tend to distally merge one into the other. The pseudopapilla is moderately long and smooth. It originates directly from the E wall, which is connected with the ELP by thin smooth longitudinal pleats. The two ELP are moderately fringed. The epiphallar formula is: PP(ER)+ELP.

Remarks. This species is restricted to higher altitudes from 800 m asl up. It is found in mixed *Fagus* and *Picea* forests on barks and moss in humid habitats. Benoit (1876: 152) reports this taxon also on barks of *Acer campestre* (maple) from the Madonie and *Quercus* sp. (oak) from Gibilmanna (Palermo).

***Stigmatica kobeltiana* (Küster, 1876)**

Figs 60.7–60.12, 61.8–61.11

Distribution. Calabria, Italy (Nordsieck 2013a: 7).

Specimens examined. ITALY, Calabria, Cosenza, Altìlia. 460 m asl, 39°07'58.01"N, 16°15'01.92"E, [Lab ID St11_1, COI: MW758965], W. De Mattia and J. Macor leg. and det., 2 dissected spm; ITALY, Calabria, Reggio Calabria, Gerace, Strada Provinciale 1, 3.5 km NW of the town. 400 m asl, 38°16'53.42"N, 16°11'49.3"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm; ITALY, Calabria, Cosenza, Amantea. 30 m asl, 39°08'24.65"N, 16°04'18.13"E, W. I. Niero leg., W. De Mattia det., 1 dissected spm.

External morphology of the genital organs (Figs 60.7, 60.9, 60.11). The V is as long as the FO. The FDBC is longer than the SDBC+BC. The BC+SDBC is club-like in shape, with a more or less clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and slightly thinner. The V is long but thin in diameter. The PC is ~ 2 × longer than the V. The P is wide in diameter and swollen. The transition between P and EP is clearly visible. The PR is long and robust. The E is slightly longer than the P but thinner in diameter.

Internal morphology of the genital organs (Figs 60.8, 60.10, 60.12). The V presents many smooth longitudinal pleats that stop immediately before entering the A. The P shows five to seven longitudinal to irregularly fringed pleats that continue as far as the A where they become smooth. These penial pleats are irregular and randomly split and merge again one into the other and irregularly split or merge one into another. The pseudopapilla is smooth, short to moderately long. It originates from the ER which is connected to the ELP by means of three or four smooth longitudinal pleats. The two ELP are slightly fringed and fade before entering the VD. The epiphallar formula is PP(ER)+ELP.

***Stigmatica lamellata* (Rossmässler, 1836)**

Figs 60.13–60.15, 61.12

Distribution. The species is distributed in southwestern Albania and Corfu, Greece (Welter-Schultes 2012).

Specimens examined. GREECE, Corfu, Gardiki fortress. 40 m asl, 39°28'37.39"N, 19°53'5.74"E, W. De Mattia and J. Macor leg. and det., 3 dissected spm.

External morphology of the genital organs (Fig. 60.13). The V is much longer than the FO. The FDDB is shorter than the SDBC+BC. The BC+SDBC is club-like in shape, with a clear distinction between the SDBC and the BC. The SDBC appears very thin. The D is shorter than the SDBC+BC and slightly thinner. The V is very long, cylindrical and thin in diameter. The PC is $\sim 2 \times$ longer than the V. The P is cylindrical spindle-like. The transition between P and EP is only slightly visible and an ER is not clearly detectable. The PR is long and robust. The E is longer than the P but thinner in diameter.

Internal morphology of the genital organs (Figs 60.14–60.15). The V is smooth. The P shows transversal, huge smooth pleats that stop before the A. The pseudopapilla is elongated, subquadrangular and smooth. The pseudopapilla originated directly from the epiphallar wall and its base is connected to one EPL. The ER is missing. The epiphallar formula is: PP+ELP. The E shows two smooth ELP. They proximally fade before the VD.

***Stigmatica paestana paestana* (Philippi, 1836)**

Figs 62.1–62.3, 64.1

Distribution. The nominate subspecies is widespread in central and southern peninsular Italy [from Tuscany (Monte Argentario) and S. Abruzzo to N. Calabria] (Nordsieck 2013a: 7).

Specimens examined. ITALY, Toscana, Grosseto, Porto Ercole, Monte Telegrafo. 600 m asl, 42°23'13.90"N, 11°10'3.98"E, A. Margelli leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 62.1). The V is much shorter than the FO. The FDDB is as long as the SDBC+BC. The BC+SDBC is club-like in shape, with a more or less clear distinction between the SDBC and the BC. The D extremely long, much longer than the SDBC+BC and much thinner. The V is very short

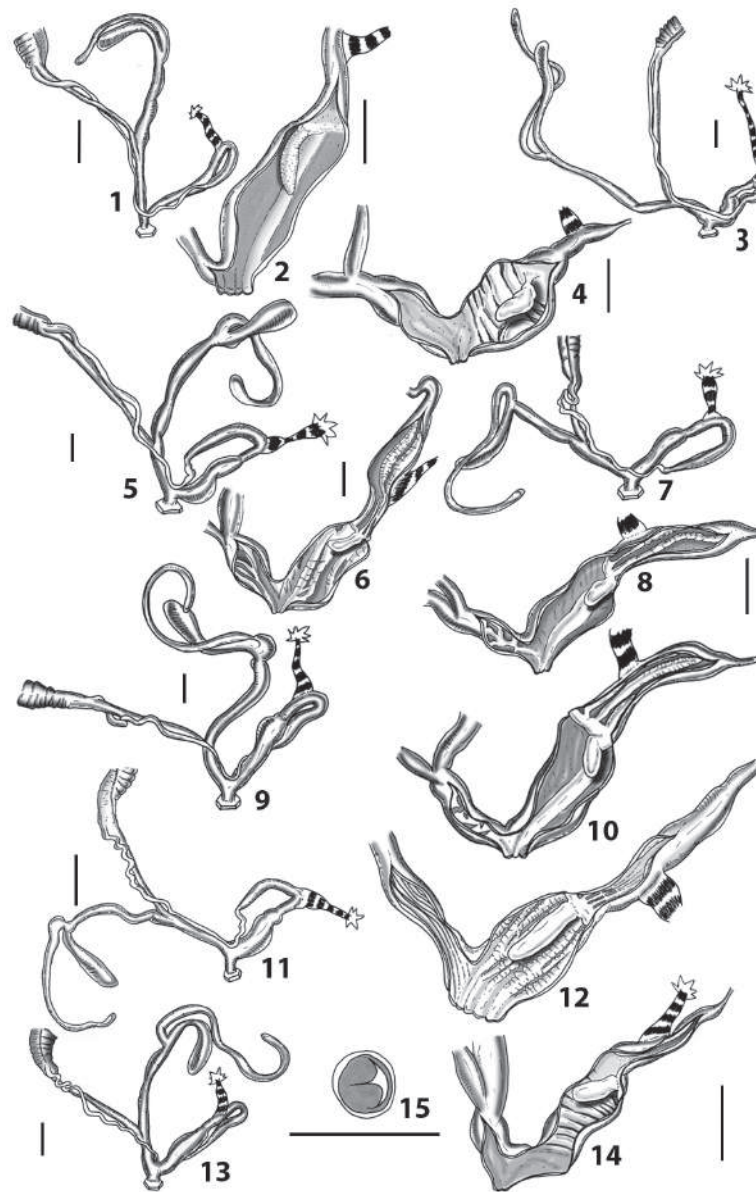


Figure 60. *Stigmatica stigmatica sturmii* (L. Pfeiffer, 1844), Punta Penne, Brindisi **60.1** whole distal genital organs **60.2** internal distal part of genital organs. *Stigmatica ernae* Fauer, 1978, San Rufo, Passo Sentinella **60.3** whole distal genital organs **60.4** internal distal part of genital organs. *Stigmatica incerta* (Küster, 1861), Serra San Bruno, Vibo Valentia **60.5** whole distal genital organs **60.6** internal distal part of genital organs. *Stigmatica kobeltiana* (Küster, 1876). Altilia, Cosenza **60.7** whole distal genital organs. **60.8** internal distal part of genital organs; Gerace **60.9** whole distal genital organs **60.10** internal distal part of genital organs; Amantea, Cosenza **60.11** whole distal genital organs **60.12** internal distal part of genital organs. *Stigmatica lamellata* (Rossmässler, 1836), Corfu, Greece **60.13** whole distal genital organs. **60.14** internal distal part of genital organs **60.15** cross section of the epiphallus.



Figure 61. *Stigmatica stigmatica stigmatica* (Rossmässler, 1836), Dubrovnik, HR **61.1** shell. *Stigmatica stigmatica* cf. *stigmatica* (Rossmässler, 1836), Budva, MONT **61.2** shell. *Stigmatica stigmatica* cf. *stigmatica* (Rossmässler, 1836), Orjen Mountains, MONT **61.3** shell. *Stigmatica stigmatica sturmii* (L. Pfeiffer, 1844), Punta Penne, Brindisi **61.4** shell. *Stigmatica ernae* Fauer, 1978, San Rufo, Passo Sentinella **61.5–61.6** shell. *Stigmatica incerta* (Küster, 1861), Serra San Bruno, Vibo Valentia **61.7** shell. *Stigmatica kobeltiana* (Küster, 1876). Altìlia, Cosenza **61.8** shell. Gerace, Reggio Calabria **61.9** shell **61.10** detail of the aperture; Aman-tea, Cosenza **61.11** shell. *Stigmatica lamellata* (Rossmässler, 1836), Corfu, Greece. 61.12. shell.

but wide in diameter. The PC is $\sim 5 \times$ longer than the V. The P is cylindrical. The transition between P and EP is clearly visible with a narrowing and the presence of the ER. The PR is long and robust. The E is slightly longer than the P and similar in diameter.

Internal morphology of the genital organs (Figs 62.2, 62.3). The V, the A and the P lack any macro-sculpturing. The internal surface shows a coarse fine granulation. The pseudopapilla is cylindrical with a smooth surface. The pseudopapilla originates from a weak ER that is not connected with the ELP. The E shows two moderately fringed ELP. They proximally fade before the VD. The epiphallar formula is PP(ER)+ELP.

***Stigmatica paestana intusstructa* (Westerlund, 1883)**

Figs 62.4, 62.5, 64.2

Distribution. This taxon is present in Basilicata, known from the area surrounding Balvano (Italy) (Nordsieck 2013b: 7).

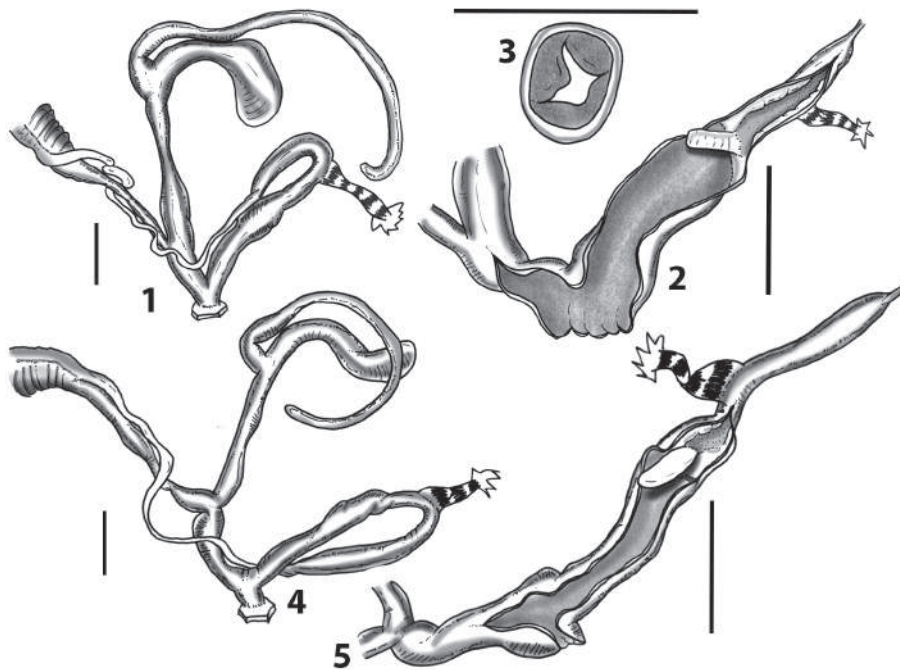


Figure 62. *Stigmatica paestana paestana* (Philippi, 1836), Monte Argentario, Grosseto **62.1** whole distal genital organs **62.2** internal distal part of genital organs **62.3** cross section of the epiphallus. *Stigmatica paestana intusstructa* (Westerlund, 1883), Balvano, Potenza **62.4** whole distal genital organs **62.5** internal distal part of genital organs.

Specimens examined. ITALY, Basilicata, Potenza, Balvano, near the castle. 450 m asl, 40°39'01.23"N, 15°30'38.91"E, W. De Mattia and J. Macor leg. and det., 3 dissected spm; ITALY, Basilicata, Potenza, Balvano. 450 m asl, 40°38'40.44"N, 15°30'39.09"E, I. Niero leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 62.4). The V is much shorter than the FO. The FDBC is longer than the SDBC+BC. The BC+SDBC is slightly club-like in shape, with a more or less clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and much thinner. The V is short but wide in diameter. The PC is $\sim 4 \times$ longer than the V. The P is cylindrical and slightly swollen. The transition between P and EP is clearly visible with a narrowing and the presence of the ER. The PR is short and robust. The E is longer than the P.

Internal morphology of the genital organs (Fig. 62.5). The V, the A and the P lack any macro-sculpturing. The internal surface shows a coarse fine granulation. The pseudopapilla is elongated and with a smooth surface. It originates directly from the wall of the E. Its basis is connected with one ELP. The E shows two moderately fringed ELP. They proximally fade before the VD. The epiphallar formula is PP(ELP).

Remarks. *Stigmatica paestana intusstructa* shows an anatomy of the genital organs very similar to the nominate subspecies.

***Stigmatica pantocratoris pantocratoris* (O. Boettger, 1889)**

Figs 63.1, 63.2, 64.3

Distribution. The nominate subspecies is restricted to the Island of Corfu, Greece.

Specimens examined. GREECE, Corfu, Lafki. 420 m asl, 39°46'18.23"N, 19°50'47.23"E, [Lab ID St9_2, COI: MW758964, ITS2: MW757041, MW757042, MW757043], W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Fig. 63.1). The V is much shorter than the FO. The FDBC is longer than the SDBC+BC. The BC+SDBC is spindle-like in shape, with a clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and much thinner. The V is short but wide in diameter. The PC is $\sim 2.5 \times$ longer than the V. The P is cylindrical and slightly swollen. The transition between P and EP is not clearly visible and ER is difficult to detect. The PR is short and robust. The E is longer than the P but thinner in diameter.

Internal morphology of the genital organs (Fig. 63.2). The V presents many smooth longitudinal pleats that stop before entering the A. The A and the P are smooth. The pseudopapilla is smooth, long and occupies almost the whole penial volume. It originates directly from the wall of the E and it is not connected with the ELP. The E shows two moderately fringed ELP. They proximally fade before the VD. The epiphallar formula is PP+ELP.

***Stigmatica pantocratoris margaritifera* (Nordsieck, 1996)**

Figs 63.5, 63.6, 64.4

Distribution. *Stigmatica pantocratoris margaritifera* is known from northern Greece up to Kozani and Veria, SW Albania (Gjirokaštër, Delvinë and Sarandë districts), and the Greek-Albanian border region of Epirus near Konitsa (Nordsieck 1996: 11).

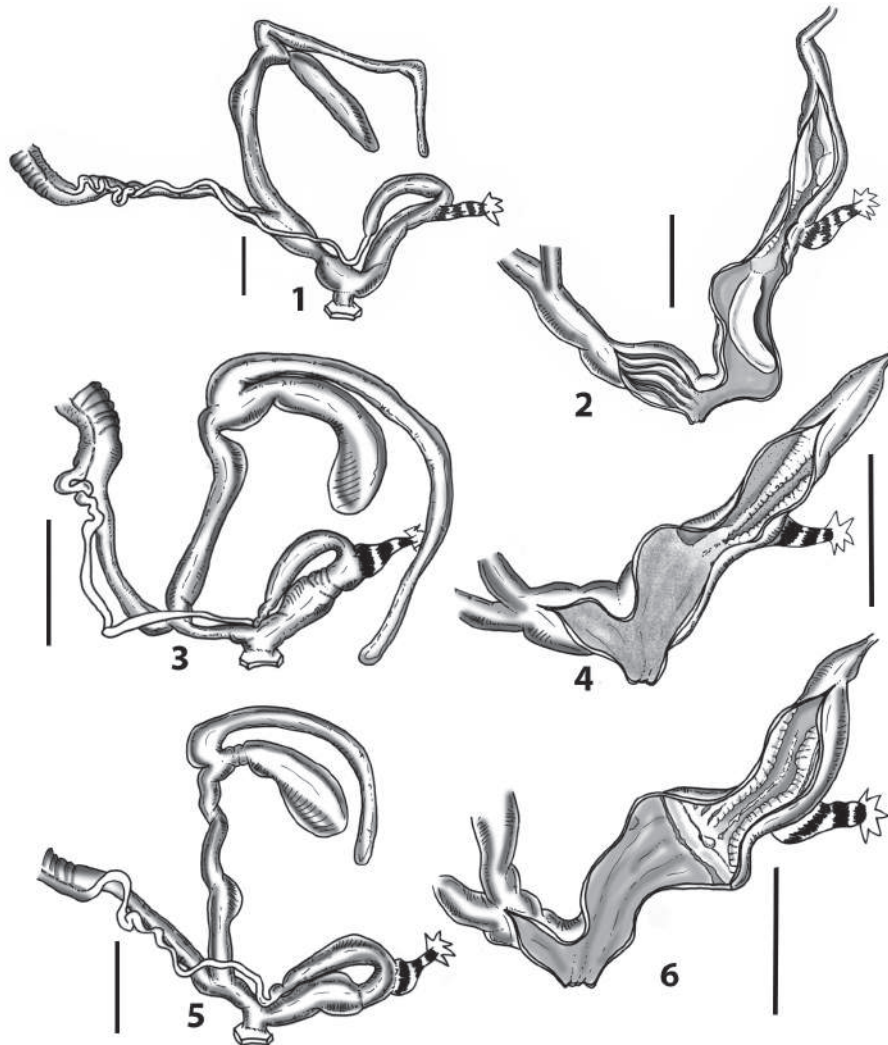


Figure 63. *Stigmatica pantocratoris pantocratoris* (O. Boettger, 1889), Pantocrator, Corfu **63.1** whole distal genital organs **63.2** internal distal part of genital organs. *Stigmatica splendens* (Nordsieck, 1996), Qeparo, AL **63.3** whole distal genital organs **63.4** internal distal part of genital organs. *Stigmatica pantocratoris margaritifera* (Nordsieck, 1996), Krongj, AL **63.5** whole distal genital organs **63.6** internal distal part of genital organs.

Specimens examined. ALBANIA, Delvinë District, Krongj, rocky grassland at the peak region of Mt Koqinolithar. 890 m asl, 39°54'12.34"N, 20°10'11.39"E, Barina, Pifkó, Puskás leg. W. De Mattia det., 2 dissected spm.

External morphology of the genital organs (Fig. 63.5). The V is much shorter than the FO. The FDBC is longer than the SDBC+BC. The BC+SDBC is large, club-like in shape, with a more or less clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and thinner in diameter. The V is very short but large in diameter. The PC is $\sim 5 \times$ longer than the V. The P is large and proximally folded. The transition between P and EP is clearly visible with an evident epiphallar narrowing is not evident. The ER is visible. The PR is short and robust. The E is longer than the P and not much thinner in diameter.

Internal morphology of the genital organs (Fig. 63.6). The V, the A and the P lack any macro-sculpturing. The internal surface shows a very fine granulation. The pseudopapilla is extremely reduced, almost vestigial. It originates from a well-developed ER that seems not to be connected with the ELP. The E shows two fringed ELP. They proximally fade before the VD. The epiphallar formula is PP(ER)+ELP.

Remarks. Mainland populations of *Stigmatica pantocratoris* revealed a reduction or the complete lack of the pseudopapilla, whereas it is well developed in the nominate subspecies on the island of Corfu. More anatomical research would be necessary to improve the knowledge about the character states of the pseudopapilla, in order to properly assess, together with genetic molecular data, the status of these taxa.

Stigmatica splendens (Nordsieck, 1996)

Figs 63.3, 63.4, 64.4

Distribution. This taxon is restricted to southern Albania from Tepelenë area near Lum i Bençës (Nordsieck 1996: 12).

Specimens examined. ALBANIA, Vlorë district, Qeparo, macchia with tree spurges W of the village, 20 m, 50 m asl, 40°03'25.07"N, 19°49'47.06"E, Juhász, Kovács, Murányi, Puskás leg. W. De Mattia det., 2 dissected spm.

External morphology of the genital organs (Fig. 63.3). The V is much shorter than the FO. The FDBC is shorter than the SDBC+BC. The BC+SDBC is club-like in shape, large, with a more or less clear distinction between the SDBC and the BC. The D is extremely long, much longer than the SDBC+BC and slightly thinner. The V is short and very thin in diameter. The PC is $\sim 3 \times$ longer than the V. The P is large and proximally folded. The transition between P and EP is clearly visible even if the epiphallar narrowing is not evident. The ER is visible. The PR is short and robust. The E is longer than the P but thinner in diameter.

Internal morphology of the genital organs (Fig. 63.4). The V, the A and the P lack any macro-sculpturing. The internal surface shows a coarse fine granulation. The pseudopapilla is missing. The transition between P and E is visible. The E shows two fringed ELP that start with two smooth longitudinal pleats. They proximally fade before the VD. The epiphallar formula is: ELP.



Figure 64. *Stigmatica paestana paestana* (Philippi, 1836), Monte Argentario, Grosseto **64.1** shell. *Stigmatica paestana intusstructa* (Westerlund, 1883), Balvano, Potenza **64.2** shell. *Stigmatica pantocratoris pantocratoris* (O. Boettger, 1889), Pantocrator, Corfu **64.3** shell. *Stigmatica splendens* (Nordsieck, 1996), Qeparo, AL **64.4** shell. *Stigmatica pantocratoris margaritifera* (Nordsieck, 1996), Krongj, AL **64.5** shell.

Remarks. The lack of the pseudopapilla represents a possible apomorphic state of the epiphallus as already seen in other genera (e.g., *Montenegrina*, De Mattia 2020).

***Stigmatica vulcanica vulcanica* (Benoit, 1860)**

Figs 65.1–65.6, 66.1–66.3

Distribution. *Stigmatica vulcanica vulcanica* is found in northeastern Sicily, Eolian Islands and Calabria (Nordsieck 2013a: 7).

Specimens examined. ITALY, Calabria, Cosenza, Via Porta Piana. 300 m asl, 39°17'2.08"N, 16°15'30.22"E, [Lab ID 12068_2, COI: MW758943, ITS2: MW757060, MW757061], H. Nordsieck leg. and det., 2 dissected spm; ITALY, Calabria, Paola, Castello di San Lucido, Via Porta Piana. 120 m asl, 39°21'33.06"N, 16°02'39.97"E, I. Niero leg. and det., 1 dissected spm; ITALY, Calabria, Cosenza, Amantea. 30 m asl, 39°08'24.65"N, 16°04'18.13"E, W. I. Niero leg., W. De Mattia det., 1 dissected spm; ITALY, Sicily, Catania, Belpasso, Contrada Piscitello. 650 m asl, 37°36'13.96"N, 14°59'25.42"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.

External morphology of the genital organs (Figs 65.1, 65.3, 65.5, 65.7). The V can be as long as or shorter or longer than the FO. The FDBC is longer than the SDBC+BC. The BC+SDBC is club-like to slightly elongated in shape, with a more or less clear distinction between the SDBC and the BC. The D is as long as or much longer than the SDBC+BC and thinner. The PC is $\sim 2 \times$ longer than the V. The P is cylindrical and slightly swollen. The transition between P and EP is clearly visible and two samples out of nine showed a strong ET. The PR is long and robust. The E is longer than the P but thinner in diameter.

Internal morphology of the genital organs (Figs 65.2, 65.4, 65.6, 65.8). Belpasso, Catania, Sicily (Fig. 65.2): The V is smooth. The P shows a chevron-like pattern that gradually disappears as approaching the A. The proximal penis presents an irregular pattern of smooth small pleats. The pseudopapilla is very long and reaches the A. It is smooth and slightly irregularly folded at its base. The ER is not present. The E distally shows many small irregular pleats that proximally merge into two smooth ELP. They proximally fade before the VD. The epiphallar formula is: PP(ELP).

Cosenza and Paola, Calabria (Figs 65.4, 65.6): The V is smooth. The P shows many fine smooth longitudinal pleats that tend to fade towards the A. The pseudopapilla is very long and almost reaches the A. It is smooth and blade-shaped. A strong ER is present. The pseudopapilla originates from the E wall, independent from the ER and it is connected to the ELP by means of 3 to 8 smooth longitudinal pleats. The epiphallar formula is: PP+ER(ELP). The two ELP are smooth and fade before entering the VD.

Remarks. *Stigmatica vulcanica vulcanica* showed a variable morphology of the genital organs. The Sicilian samples present an anatomy of the genital organs that greatly differs from those from Calabria. The internal penis of two populations from Cosenza shows longitudinal pleats vs. the chevron pattern of the Sicilian samples. Moreover, the pseudopapilla and the transition between P and E are different (presence of the ER vs. absence of ER).

Unfortunately, genetic molecular data are not yet available from topotypic populations from the Mongibello-Etna (Sicily) thus, although the anatomical investigations highlight reliable differences, the relationships with and the status of the Calabrian populations still have to be properly assessed.

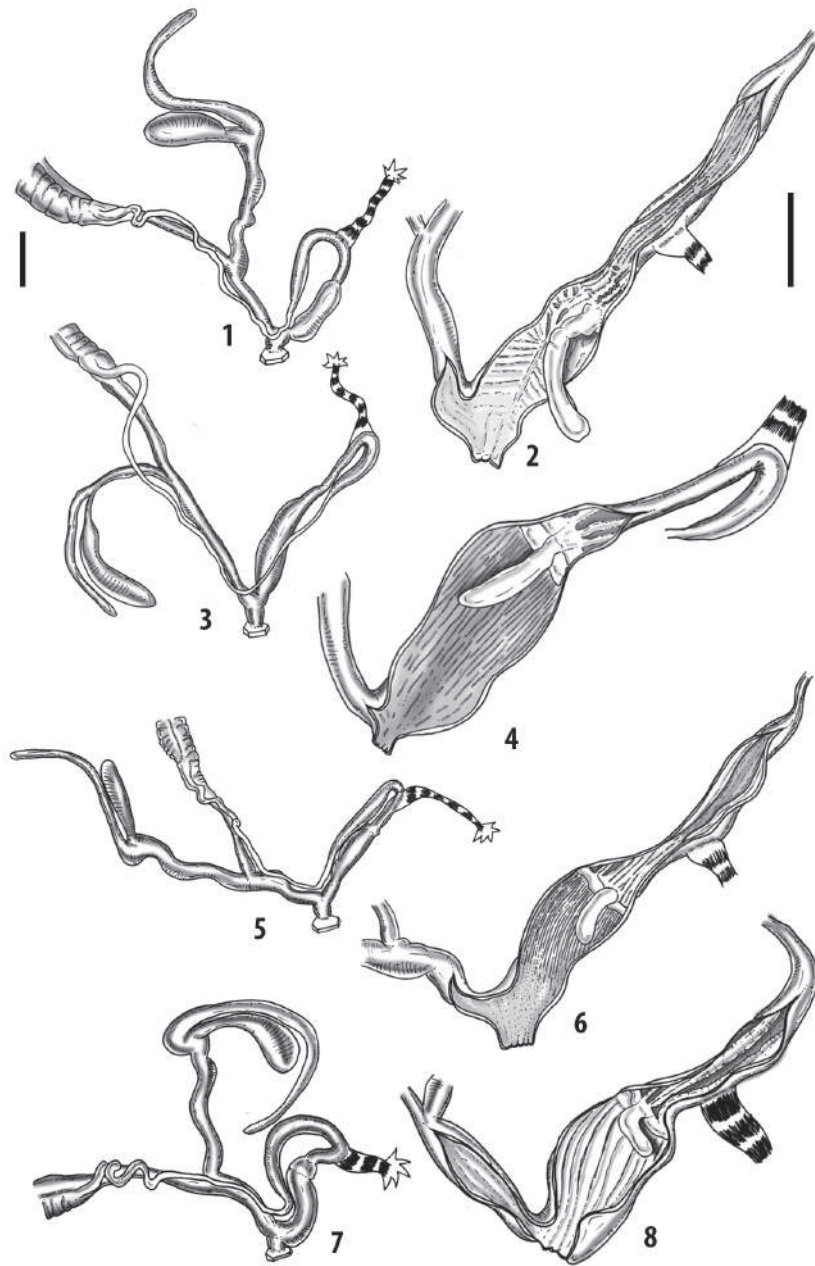


Figure 65. *Stigmaticea vulcanica vulcanica* (Benoit, 1860), Belpasso, Catania **65.1** whole distal genital organs **65.2** internal distal part of genital organs. Cosenza **65.3** whole distal genital organs **65.4** internal distal part of genital organs. Paola **65.5** whole distal genital organs **65.6** internal distal part of genital organs. *Stigmaticea vulcanica sigridae* Nordsieck, 2013, Mendicino, Cosenza **65.7** whole distal genital organs **65.8** internal distal part of genital organs.

***Stigmatica vulcanica sigridae* Nordsieck, 2013**

Figs 65.7, 65.8, 66.4, 66.5

Distribution. *Stigmatica vulcanica sigridae* is restricted to a small range east of Cosenza in central Calabria (Nordsieck 2013a: 10).

Specimens examined. ITALY, Calabria, Cosenza, Contrada Rizzuto. 770 m asl, 39°14'51.24"N, 16°10'30.51"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm; ITALY, Calabria, Cosenza, Contrada Rizzuto road to San Bartolo, Cosenza, Calabria, Italy. 740 m asl, 39°15'20.65"N, 16°11'09.16"E, W. De Mattia and J. Macor leg. and det., 2 dissected spm.



Figure 66. *Stigmatica vulcanica vulcanica* (Benoit, 1860), Belpasso, Catania **66.1** shell. Cosenza **66.2** shell; Paola **66.3** shell. *Stigmatica vulcanica sigridae* Nordsieck, 2013, Mendicino, Cosenza **66.4–66.5** shells.

External morphology of the genital organs (Fig. 65.9). The V as long as the FO. The FDBC is $1.5 \times$ longer than the SDBC+BC. The BC+SDBC is club-like in shape, with a clear distinction between the SDBC and the BC. The D is much longer than the SDBC+BC and remarkably thinner. The V is wide in diameter. The PC is $\sim 2.5 \times$ longer than the V. The P is cylindrical and slightly swollen. The transition between P and EP is clearly visible with a strong ET. The PR is short and robust. The E is longer than the P but thinner in diameter.

Internal morphology of the genital organs (Fig. 65.10). The V shows a weak longitudinal sculpturing. The P shows 6 to 8 smooth longitudinal pleats that fade as entering into the A. The pseudopapilla is smooth and short. It originates from the ER which is connected to the ELP by means of three or four smooth longitudinal pleats. The two ELP are slightly fringed and fade before entering the VD. The epiphallar formula is PP(ER)+ELP.

Remarks. *Stigmatica vulcanica sigridae* was described based on shell characters that slightly differ from the nominate subspecies (Nordsieck 2013a: 10). Its anatomy of the genital organs, except for the smooth (instead of fringed) longitudinal penial pleats, matches with the nominate subspecies populations from Calabria but nevertheless keeps reliable differences with the Sicilian samples.

***Papillifera* Hartmann, 1842**

Remarks. The genus *Papillifera* was used as the outgroup genus in the molecular genetic analysis (Figs 4–6). The general features of the genus *Papillifera* were summarised by Nordsieck (2013a: 8) who provided two lists of synonyms without any explanation or justification. *Papillifera* includes two species: *P. papillaris* and *P. solida* (Margelli 2014; MolluscaBase 2021). The current known distribution and status of its (sub) specific taxa is far of being satisfactorily assessed, due to the unknown or inadequately evaluated validity of many old names.

Papillifera is clearly distinguishable from *Siciliaria* s. s., *Sicania* and *Stigmatica* by its G-type clausiliar apparatus and the general shell features (e.g., the sutural dark band, see Fig. 68.1–68.7). In our study, we dissected the *Papillifera* samples that underwent molecular genetic investigations, which are shown in Fig. 67.1–67.12. The genital anatomical drawings of *Papillifera papillaris papillaris* (O. F. Müller, 1774) (Fig. 67.1–67.2), *Papillifera papillaris affinis* (Philippi, 1836) (Fig. 67.3–67.8), *Papillifera papillaris transitans* (Paulucci, 1878) (Figs 67.9–67.10), and *Papillifera solida solida* (Draparnaud, 1805) (Fig. 67.11–67.12) show a stable genital structure in dimensions, ratios among the main genital parts and internal features.

Nordsieck (2013a: 8) highlights that the anatomy of the genital organs of *Papillifera* is the same as *Siciliaria* s. l. Following our anatomical investigations, this statement must be rejected, as the general internal architecture of the PC (P+E and transition) revealed to be substantially different from *Siciliarial/Sicania* and *Stigmatica*. In detail, *Papillifera* lacks the ET and the connecting longitudinal pleats between PP and the

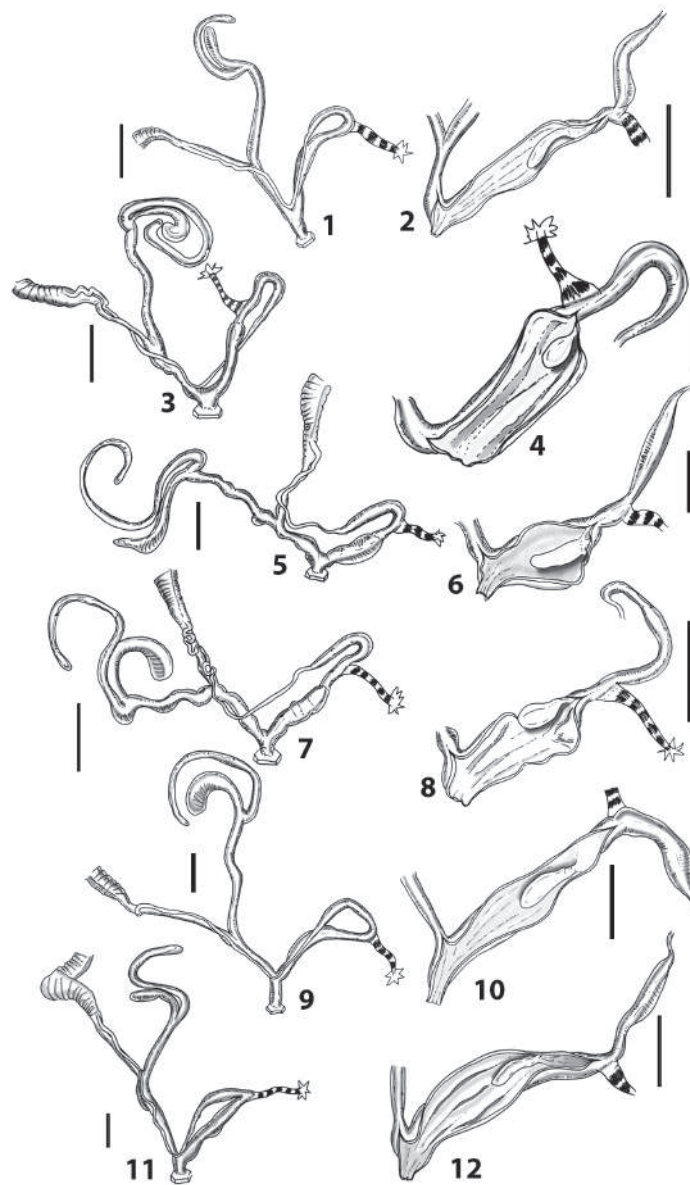


Figure 67. *Papillifera papillaris papillaris* (O.F. Müller, 1774). Vicovaro, Latina **67.1** whole distal genital organs **67.2** internal distal part of genital organs. *Papillifera papillaris affinis* (Philippi, 1836). Jato Antica, San Giuseppe Jato **67.3** whole distal genital organs **67.4** internal distal part of genital organs. Monte Bonifato, Alcamo **67.5** whole distal genital organs **67.6** internal distal part of genital organs.-Western slopes Monte Kumeta, Monreale **67.7** whole distal genital organs **67.8** internal distal part of genital organs. *Papillifera papillaris transitans* (Paulucci, 1878). Road to the Norman Castle, Stilo **67.9** whole distal genital organs **67.10** internal distal part of genital organs. *Papillifera solida solida* (Draparnaud, 1805), Matera **67.11** whole distal genital organs **67.12** internal distal part of genital organs.



Figure 68. *Papillifera papillaris papillaris* (O.F. Müller, 1774). Vicovaro, Latina **68.1** shell **68.2** clausiliar plate. *Papillifera papillaris affinis* (Philippi, 1836). Jato Antica, San Giuseppe Jato **68.3** shell. Monte Bonifato, Alcamo **68.4** shell. -Western slopes Monte Kumeta, Monreale **68.5** shell. *Papillifera papillaris transitans* (Paulucci, 1878). Road to the Norman Castle, Stilo **68.6** shell. *Papillifera solida solida* (Draparnaud, 1805), Matera **68.7** shell.



Figure 69. **69.1** *Siciliaria grohmanniana grohmanniana* (Rossmässler, 1836), Monte Pellegrino, Palermo **69.2** *Siciliaria grohmanniana addaurae* ssp. nov. Grotta dell'Addaura, Punta Priola **69.3** Limestone walls at Grotta dell'Addaura, Punta Priola **69.4** *Siciliaria calcarae belliemi* (Brandt, 1961), Castello Calatubo, Alcamo **69.5** *Siciliaria calcarae parajatinensis* ssp. nov., west side Monte Kumeta **69.6** *Siciliaria tiberii armettensis* ssp. nov., Grotta dei Puntali, Carini.



Figure 70. **70.1** *Siciliaria leucophryna* (L. Pfeiffer, 1862), Grotta Conza, Palermo **70.2** *Siciliaria tiberii scalettensis* Beckmann, 2004 Portella Scaletta, Villagrazia **70.3** Limestone walls at Monte Cofano, Custonaci **70.4** *Sicania crassicostata* (L. Pfeiffer, 1856), comb. nov., Monte Cofano, Custonaci **70.5** *Sicania nobilis spezialensis* (Nordsieck 1984), stat. nov., comb. nov. Macari.

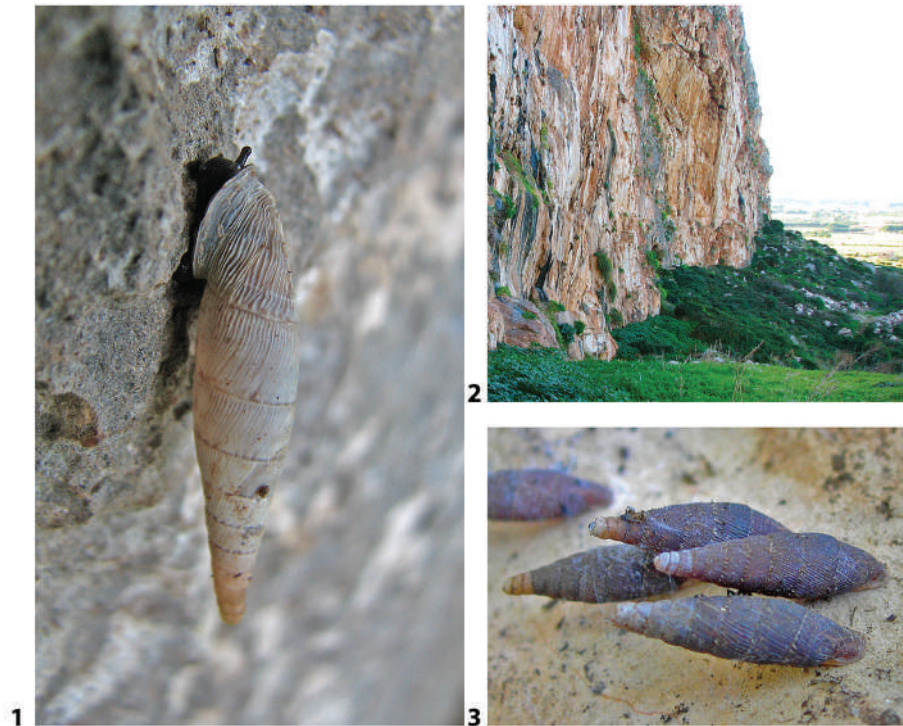


Figure 71. **71.1** *Sicilia nobilis nobilis* (L. Pfeiffer, 1848), comb. nov., Monte Cofano, Tonnara Cofano **71.2** Limestone walls at Monte Cofano, Tonnara Cofano **71.3** *Mauritanica scarificata* (L. Pfeiffer, 1856), comb. nov., Marettimo.

Table 11. Examined taxa of *Papillifera* with information on availability of genetic data (DNA) and description of the variability penis-epiphallus transition (epiphallar formula).

Taxon	Examined specimens	Epiphallar formula	DNA
<i>Papillifera papillaris papillaris</i> (O.F. Müller, 1774)	Vicovaro, Latina, Lazio, Italy. 320 m asl. 42°01'04.58"N, 12°54'19.30"E, H. Nordsieck leg. and det.	PP+ELP	Y
<i>Papillifera papillaris affinis</i> (Philippi, 1836)	Jato Antica, Monreale, Sicily, Italy, 830 m asl, 37°58'2.36"N, 13°11'45.19"E, W. De Mattia and J. Macor leg. and det.	PP+ELP	Y
<i>Papillifera papillaris affinis</i> (Philippi, 1836)	western part of Monte Kumeta toward Jato Antica, Monreale, Sicily, Italy, 630 m asl, 37°57'8.18"N, 13°13'14.57"E, W. De Mattia and J. Macor leg. and det.	PP+ELP	Y
<i>Papillifera papillaris affinis</i> (Philippi, 1836)	Monte Bonifato, west side of the mountain, over the quarry, Alcamo, Sicily, Italy. 550 m asl, 37°57'16.92"N, 12°58'09.06"E, W. De Mattia and J. Macor leg. and det.	PP+ELP	Y
<i>Papillifera papillaris transitans</i> (Paulucci, 1878)	road to the Norman Castle, Stilo, Reggio Calabria, Calabria, Italy. 320 m asl. 38°28'45.91"N, 16°27'48.05"E, H. Nordsieck leg. and det.	PP+ELP	Y

ELP. The epiphallar formula of *Papillifera* is: PP+ELP. The sculpturing of the internal walls of the penis are mainly smooth or with very soft longitudinal pleats. The pseudo-papilla is elongated to rounded, smooth and unrooted, directly emerging from the P-E transition walls. The E shows two smooth ELP.

Table 12. New *Siciliaria/Sicania* checklist and comparison with lists provided by Nordsieck (2013b) and MolluscaBase eds. (2021).

Nordsieck 2013b	MolluscaBase 2021	De Mattia, Reier and Haring 2021
<i>Siciliaria grobmanniana</i> (Rossmässler, 1836)	<i>Charpentieria grobmanniana</i> (Rossmässler, 1836)	<i>Siciliaria grobmanniana grobmanniana</i> (Rossmässler, 1836) <i>Siciliaria grobmanniana addaurae</i> ssp. nov. De Mattia, Reier and Haring
<i>Siciliaria septemPLICATA</i> (Philippi, 1836)	<i>Charpentieria septemPLICATA</i> (Philippi, 1836)	<i>Siciliaria septemPLICATA</i> (Philippi, 1836)
<i>Siciliaria leucophryna</i> (L. Pfeiffer, 1862)	<i>Charpentieria leucophryna</i> (L. Pfeiffer, 1862)	<i>Siciliaria leucophryna</i> (L. Pfeiffer, 1862)
<i>Siciliaria calcarae</i> (Philippi 1844)	<i>Charpentieria calcarae</i> (Philippi, 1844)	<i>Siciliaria calcarae calcarae</i> (Philippi 1844)
<i>Siciliaria calcarae belliemii</i> (Brandt, 1961)	<i>Charpentieria calcarae belliemii</i> (Brandt, 1961)	<i>Siciliaria calcarae belliemii</i> (Brandt, 1961) <i>Siciliaria calcarae boygettensis</i> ssp. nov. De Mattia, Reier and Haring <i>Siciliaria calcarae jatinensis</i> ssp. nov. De Mattia, Reier and Haring <i>Siciliaria calcarae parajatinensis</i> ssp. nov. De Mattia, Reier and Haring
	<i>Charpentieria calcarae orlandoi</i> Liberto, Reitano, Giglio, Colomba & Sparacio, 2016	<i>Siciliaria calcarae orlandoi</i> Liberto, Reitano, Giglio, Colomba & Sparacio, 2016 <i>Siciliaria calcarae cruenta</i> ssp. nov. De Mattia, Reier and Haring
<i>Siciliaria ferrox</i> (Brandt, 1961)	<i>Charpentieria ferrox</i> (Brandt, 1961)	<i>Siciliaria ferrox</i> (Brandt, 1961)
<i>Siciliaria riberothi</i> (Brandt, 1961)	<i>Charpentieria riberothi</i> (Brandt, 1961)	see Nordsieck (2013b)
<i>Siciliaria tiberii tiberii</i> (A. Schmidt, 1868)	<i>Charpentieria tiberii</i> (A. Schmidt, 1868)	<i>Siciliaria tiberii tiberii</i> (A. Schmidt, 1868) <i>Siciliaria tiberii armettensis</i> ssp. nov. De Mattia, Reier and Haring
<i>Siciliaria septemPLICATA alcamoensis</i> Brandt, 1961	<i>Siciliaria septemPLICATA alcamoensis</i> Brandt, 1961	<i>Siciliaria tiberii alcamoensis</i> Brandt, 1961 comb. nov.
	<i>Charpentieria septemPLICATA hemmeni</i> Beckmann, 2004	
<i>Siciliaria tiberii scalettensis</i> Beckmann, 2004	<i>Charpentieria tiberii scalettensis</i> Beckmann, 2004	<i>Siciliaria tiberii scalettensis</i> Beckmann, 2004
<i>Siciliaria crassicosata</i> (L. Pfeiffer, 1856)	<i>Sicilia crassicosata</i> (L. Pfeiffer, 1856)	<i>Sicania crassicosata</i> (L. Pfeiffer, 1856) comb. nov.
<i>Siciliaria eminens</i> (A. Schmidt, 1868)	<i>Charpentieria eminens</i> (A. Schmidt, 1868)	<i>Sicania eminens</i> (A. Schmidt, 1868) comb. nov.
<i>Siciliaria nobilis</i> (L. Pfeiffer, 1848)	<i>Charpentieria nobilis</i> (L. Pfeiffer, 1848)	<i>Sicania nobilis nobilis</i> (L. Pfeiffer, 1848) comb. nov.
<i>Siciliaria spezialensis</i> (Nordsieck, 1984)	<i>Charpentieria spezialensis</i> (Nordsieck, 1984)	<i>Sicania nobilis spezialensis</i> (Nordsieck, 1984) comb. nov.; stat. nov.
<i>Siciliaria scarificata</i> (L. Pfeiffer 1856)	<i>Charpentieria scarificata</i> (L. Pfeiffer 1856)	<i>Mauritanica scarificata</i> (L. Pfeiffer 1856) comb. nov.

Conclusions

The system of *Siciliaria* s. l. that we propose here is based on an integrative approach, as was performed with the recently revised genus *Montenegrina* (De Mattia et al. 2020; Mason et al. 2020). It combines information on genital organs, shell morphology, and DNA sequence data which is a new approach for this genus. A comprehensive and detailed revision of the genus, including related Delimini genera such as *Charpentieria*,

Stigmatica, *Gibbularia*, and *Papillifera* is still missing in the literature on Clausiliidae. We are aware that the proposed system, particularly of related genera, is based on incomplete sampling and thus has to be considered as preliminary. However, we are aware that a single straightforward, universally applicable rationale on how species should be delimited in Delimini (and Clausiliidae in general) is absent and taxonomic decisions remain arbitrary.

For the genus *Montenegrina* (De Mattia et al. 2020), the morphology of the genital characters of *SiciliarialSicania* was remarkably helpful for alpha-taxonomy but gave poor contribution to the phylogenetic reconstruction. At an upper-genus level, the epiphallar thickening(s) failed to represent a discriminatory character among *SiciliarialSicania* and the related genera *Charpentieria*, *Gibbularia*, *Stigmatica*, and *Papillifera*. This study revealed the complexity and variability of the genital characters of a genus thought to display low, if no, morphological variability at all. Finally, the shell-based system (Fig. 2) does not reflect the phylogeny of *SiciliarialSicania* (and *Mauritanica* as regards the Sicilian taxon).

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10. Publication 3

De Mattia, W., Haring, E., Kapun, M., Fehér, Z., Mason, K. & Steiner, G. (2025). Quantitative and qualitative statistical analyses of the shell and the genital traits of the doorsnail genus *Montenegrina* O. Boettger, 1877 (Gastropoda: Clausiliidae). *Archiv für Molluskenkunde* 154(1): 35–57.

Quantitative and qualitative statistical analyses of the shell and the genital traits of the doorsnail genus *Montenegrina* O. Boettger, 1877 (Gastropoda: Clausiliidae)

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Abstract. The importance of genital morphology for alpha- and supraspecific taxonomy of pulmonate land snails has been known since the 19th century. Despite that, the genital anatomy of the family Clausiliidae has been considered of low discriminatory importance at the species level, although it has great potential for discriminating genera. No statistical analyses of fundamental aspects of genital morphology of clausiliids, such as measurements, size ranges, mean values, standard deviation, and trait categorization, are yet found in the literature. Moreover, no data on statistical correlations among the various morphological parts (genitalia and shell) have been reported to date. In the present study we investigate the clausiliid genus *Montenegrina* as a model for such morphometric analyses. Measurements show a high degree of variability and large overlaps among the *Montenegrina* taxa. Correlation tests show positive correlations among some shell characters, while correlations among genital characters prove to be generally weaker. Additionally, we compare quantitative (morphometric measurements) and qualitative (categorization of traits) data with principal component analyses (PCA) to test if genitalia and shell morphological features correspond to the phylogeny based on published previously mitochondrial DNA sequences. The morphometric analyses of shell and genital characters show that, although specimens of the same taxon mostly cluster together, many clades overlap in the PCA scatter plots and/or form intermingled clusters in the neighbour-joining (NJ) trees. Finally, we ask if the taxa studied show character displacement. Among the 4 syntopic pairs of taxa that exist in the genus *Montenegrina*, 3 show a morphological Euclidean distance well above the average for the genus, although the discriminant power is notably weak. Assumptions on how ecological factors should result in differences of shell and/or genital morphology—thus, ecological character displacement (ECD)—remain speculative. Our findings are compatible with both the assumption of reproductive character displacement (RCD) as well as the non-adaptive radiation hypothesis raised by earlier work on this group.

Key words. Shell morphology, genital morphology, measurements, categorisation, bivariate regression model, principal component analysis, multivariate analysis, morphological taxon delimitation, character displacement, character-state frequency, new genus diagnosis

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Introduction

Despite an increasing number of newly described taxa of pulmonate land snails, the shell morphology often has been found to be insufficiently diagnostic (GIUSTI & MANGANELLI 1992). Conversely, the importance of genital morphology as a discriminatory tool for alpha- and

supraspecific taxonomic research of pulmonate land snails has been known since the last decades of the 19th century. For many families (e.g. Oxychilidae, Pristilomatidae, and Hydrobiidae) anatomical investigations combined with morphometrics have granted new insights into morphological variation, which are fundamental for taxonomy and systematics. Comparative studies of genital characters

allow separation of species that show extremely similar shells with poor or no discriminant shell characters. However, within the family Clausiliidae, genital anatomy has always been considered of low diagnostic importance at the species level, despite being discriminant at the genus level. WAGNER (1919, 1924, 1925) was the first to publish genital anatomical drawings of Clausiliidae, but the significance of the genital anatomy at the genus level was only later established by NORDSIECK (e.g. 1963a, b, 1969a, b, 1970) and SZEKERES (1969). Yet, anatomical details of genitals were published for a limited number of taxa represented by a few specimens only. Indeed, no quantitative statistical analyses of genital morphology of clausiliids have been carried out until now. For various parts of the genitalia, fundamental parameters, such as absolute measurements, size ranges, mean values, and standard deviations have been reported but not formally investigated with statistical analyses. Consequently, it remains largely unknown, for example, whether statistical correlations exist among genital traits or between genital and shell traits. For example, we do not yet know if there is any correlation (and if so, to what extent) between the shell size and the size of the genitalia. Other potentially important correlations need to be investigated and evaluated to better understand clausiliid biology and ecology. Evidently, such a statistical approach can be applied at different taxonomical levels: single populations, (sub-) specific levels, groups of species, phylogenetically related groups of taxa, or a whole genus. Sample size plays a key role regarding statistical power as well as capturing phenotypic variation in natural populations (FABER & FONSECA 2014).

In the present study, we used the taxon-rich door-snail genus *Montenegrina* O. Boettger, 1877 (Gastropoda: Clausiliidae) as a model genus to perform extensive morphological analyses. *Montenegrina* is a geographically narrow-ranged genus. Its distribution includes the western parts of the Balkan Peninsula, that is, Montenegro, Kosovo, North Macedonia, Albania, and Greece. Most (sub-)species show extremely patchy distributions, which are limited to limestone substrates (predominantly cliffs and rocky areas) and occur from the southernmost parts of the Dinaric Mountains to the northern part of the Pindos Mountains (FEHÉR & SZEKERES 2016). According to the last revision (DE MATTIA et al. 2020), this genus consists of 69 species with many subspecies. DE MATTIA et al. (2020) presented detailed descriptions of the genital anatomical features and summarized data on shell morphology of various taxa. In parallel, MASON et al. (2020) genetically investigated a comprehensive set of samples covering the whole geographic distribution of the genus and established a phylogeny of the genus based on 3 mitochondrial marker sequences. Altogether, those genetic and morphological data provided a suitable basis to revise the genus. Yet, the large amount of data, both quantitative

(morphometric measurements) and qualitative (categorization) data obtained by DE MATTIA et al. (2020) were used only in a descriptive manner and had not been analyzed in depth using statistical methods.

The present study aims to integrate these data and to provide basic morphometric data and statistical analyses to address the following questions: Are there correlations between the shell height and the overall dimensions of genitalia? Is there any allometric correlation between the sizes of the genital traits? Three genital parts, namely the penis (P), the epiphallus (E), and the vagina (V) are strictly functionally intertwined, so is it reasonable to hypothesize that their sizes are positively correlated? Does a large penial complex also correspond to a large vagina? Does a big epiphallus (where the spermatophore is produced) correspond to a large diverticulum of the bursa copulatrix (where the spermatophore is received after mating and where its lysis process begins)? We additionally analysed shell and genital characters with a multivariate approach (ordination principal component analysis (PCA) and multivariate clustering) to test if, and to what extent, genitalia and shell morphological features reflect the phylogenetic relationships provided by MASON et al. (2020, 2023). Do phylogenetic trees based on DNA sequences and trees based on morphometric data from shell and genitalia provide a comparable phylogenetic signal? Furthermore, the original species descriptions contain only coarse descriptions of shell and genital features, so that the question remains whether morphometric data can be consistently used for the delimitation of taxa.

The genus *Montenegrina* shows extreme plasticity in the morphology of both genitalia and shells. The origin of this surprising diversity may stem from pronounced isolation of populations, as already discussed by DE MATTIA et al. (2020), FEHÉR & SZEKERES (2016), and MASON et al. (2020). All taxa belonging to *Montenegrina* exhibit an autecology that is characterized by extraordinarily specialised interactions between individuals and the environment. They are relegated exclusively to calcareous rocky environments, found only on rock boulders and cliffs, and probably specialised in feeding on endolithic lichens. The discontinuity of ecologically suitable environments throughout the geographic distribution of the genus has therefore created, and continuously creates, a heavy discontinuity in gene flow, resulting in real ecological islands, where genetic drift may lead to speciation. Concerning sympatry, that is the overlapping geographic ranges of *Montenegrina* species, it must be mentioned that for this genus with its usually isolated and small-ranged taxa, the term syntopy (defining co-occurrence in the same place/habitat) is more relevant. Most *Montenegrina* taxa show neither sympatry (defining partial or total overlap of the distribution range) nor syntopy with other congeneric taxa (FEHÉR & SZEKERES 2016, FEHÉR et al. 2018). There are, however, a few cases of co-occurrence,

that is, syntopic pairs of taxa. FEHER & SZEKERES (2016: 129–130) listed 7 cases of syntopy, 4 of which have anatomical and morphological data available for comparisons in this study.

The close interaction between syntopic taxa sharing an ecological niche, especially at the trophic level, can lead to a phenomenon where closely related taxa differ phenotypically more from each other in areas where they co-occur compared to specimens of the same taxa from places where their ranges do not overlap. This phenomenon is known as character displacement, which may manifest as ecological character displacement (ECD) and reproductive character displacement (RCD) (PFENNIG & PFENNIG 2012). The comprehensive amount of available data on genital morphology of *Montenegrina*, now allows us to address the question whether RCD is a phenomenon in this genus: is

the divergence in genital morphology larger among syntopic taxa compared to non-syntopic taxa? It also raises questions on the correlation of morphometric and genetic divergences and geographical distances.

Material and Methods

Table 1 shows the material investigated, namely *Montenegrina* taxa, genetic clades, the number of taxa investigated, number of samples investigated morphologically (shell morphology plus genital morphology) as well as genetically. To give an overview of the phylogenetic relationships among taxa and the various clades, Figure 1 shows the Bayesian-inference (BI) tree based on the concatenated mitochondrial sequence data (*COI*, *12S*, *16S*) (according

Table 1. Clades described within *Montenegrina* and taxa included in the present study. Sample size: First number indicates the number of individuals analyzed morphologically (morph; shell and genital anatomy) and the second the number of individuals analysed genetically (genet.). Colours of clades (corresponding to MASON et al. 2020, 2023) are used in subsequent figures. Symbols in combination with colours define taxa and are also used in subsequent graphical and statistical illustrations.

Clade, taxa examined / total	Samples morph. / genet.	Clade, taxa examined / total	Samples morph. / genet.	Clade, taxa examined / total	Samples morph. / genet.
<i>Montenegrina</i> , 92 / 106	259 / 127	<i>prespaensis prespaensis</i> *	11 / 3	<i>helvola carinata</i> ▲	3 / 1
Clade A, 2 / 2	5 / 5	<i>prespaensis sinosi</i> ◇	3 / 2	<i>helvola magna</i> ▼	2 / 1
<i>attemsi</i> ○	2 / 2	<i>stankovici</i> △	2 / 1	<i>helvola ornata</i> ◆	2 / 1
<i>jakupicensis</i> □	3 / 3	Clade E, 11 / 13	24 / 12	<i>helvola pageti</i> *	2 / 1
Clade B, 6 / 7	15 / 7	<i>atanasiensis</i> ●	2 / 2	<i>nana</i> ◇	2 / 1
<i>pifkoi</i> ●	2 / 1	<i>dennisi dennisi</i> ■	2 / 1	<i>ochridensis ochridensis</i> △	2 / 1
<i>pindica</i> ■	2 / 1	<i>dennisi maasseni</i> ▲	3 / 1	<i>ochridensis callistoma</i> ▽	6 / 5
<i>puskasi puskasi</i> ▲	3 / 1	<i>desaretica</i> ▼	2 / 1	<i>tenebrosa tenebrosa</i> ○	2 / 1
<i>puskasi gurelurensis</i> ▼	4 / 2	<i>fusca</i> ◆	2 / 1	<i>tenebrosa szekeresi</i> ○	2 / 1
<i>remota</i> *	2 / 1	<i>hiltrudae densicostulata</i> *	2 / 1	Clade J, 1 / 2	3 / 1
<i>skipetarica</i> ◇	2 / 1	<i>hiltrudae protruda</i> ◇	3 / 1	<i>minuscula</i> ●	3 / 1
Clade C, 7 / 8	14 / 7	<i>sattmanni sattmanni</i> △	2 / 1	Clade K, 7 / 8	16 / 9
<i>csikii</i> ●	2 / 1	<i>sattmanni costulata</i> ▽	2 / 1	<i>globocica</i> ●	3 / 3
<i>ersekensis</i> ■	2 / 1	<i>selcensis</i> ○	2 / 1	<i>grammica improvisa</i> ■	2 / 1
<i>flava</i> ▲	2 / 1	<i>zilchi</i> ○	2 / 1	<i>radikae radikae</i> ▲	2 / 1
<i>nobilis</i> ▼	2 / 1	Clade F, 5 / 5	32 / 11	<i>radikae paparistoe</i> ▼	3 / 1
<i>voidomatis voidomatis</i> *	2 / 1	<i>cattaroensis</i> ●	4 / 2	<i>tomorosi tomorosi</i> ◆	2 / 1
<i>voidomatis konitsae</i> ◇	2 / 1	<i>haringae</i> ■	2 / 1	<i>tomorosi coeruleus</i> *	2 / 1
<i>voidomatis thysi</i> △	2 / 1	<i>subcristata</i> ▲	22 / 6	<i>tomorosi muranyii</i> ◇	2 / 1
Clade D1, 10 / 11	23 / 11	<i>umbilicata umbilicata</i> ▼	2 / 1	Clade L, 14 / 15	36 / 17
<i>edmundi</i> ●	2 / 1	<i>u. antivarcostata</i> ◆	2 / 1	<i>drimmeri</i> ●	2 / 2
<i>fuchsi fuchsi</i> ■	3 / 1	Clade G, 6 / 6	14 / 7	<i>iba</i> ■	2 / 1
<i>golikutensis</i> ▲	2 / 1	<i>lillae</i> ●	2 / 1	<i>laxa</i> ▲	3 / 1
<i>gregoi</i> ▼	2 / 1	<i>okolensis okolensis</i> ■	2 / 1	<i>miraka miraka</i> ▼	4 / 2
<i>janinensis</i> ◆	4 / 2	<i>okolensis caesia</i> ▲	2 / 1	<i>miraka dedovi</i> ◆	2 / 1
<i>klemmi</i> *	2 / 1	<i>prokletiana prokletiana</i> ▼	4 / 2	<i>miraka delii</i> *	2 / 1
<i>lambd. welterschultesi</i> ◇	2 / 1	<i>prokletiana kovacsorum</i> *	2 / 1	<i>miraka disjuncta</i> ◇	2 / 1
<i>pallida</i> △	2 / 1	<i>tropojana</i> ◇	2 / 1	<i>miraka errans</i> △	2 / 1
<i>rugilabris rugilabris</i> ▽	2 / 1	Clade H, 4 / 8	22 / 10	<i>miraka kontschani</i> ▽	2 / 1
<i>rugilabris irmengardis</i> ○	2 / 1	<i>drimica drimica</i> ●	12 / 6	<i>perstriata perstriata</i> ○	3 / 1
Clade D2, 8 / 10	27 / 12	<i>drimica plenostoma</i> ■	8 / 2	<i>perstriata diminuta</i> ○	4 / 1
<i>dofeini dofeini</i> ●	2 / 1	<i>gropana</i> ▲	2 / 1	<i>perstriata mavrovoensis</i> ×	2 / 1
<i>dofeini fagorum</i> ■	3 / 1	<i>timeae</i> ▼	2 / 1	<i>perstriata subcristatula</i> —	2 / 1
<i>kastoriae kastoriae</i> ▲	2 / 1	Clade I, 11 / 12	28 / 18	<i>soosi</i>	2 / 1
<i>kastoriae robusta</i> ▼	2 / 1	<i>gracilis gracilis</i> ●	3 / 2		
<i>pinteri</i> ◆	2 / 2	<i>gracilis barinai</i> ■	2 / 2		

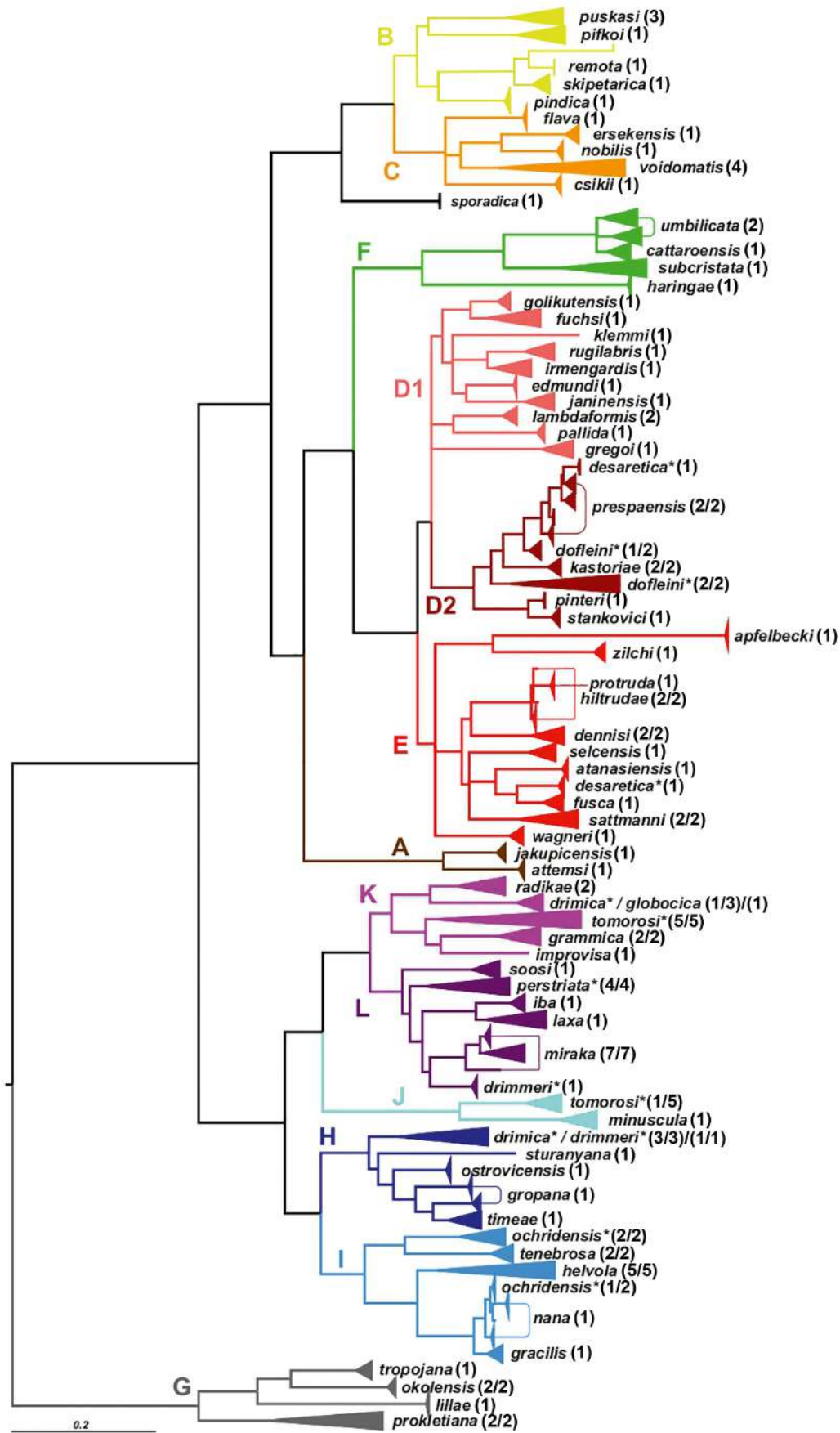


Figure 1. *Montenegro* clades defined by MASON et al. (2020). Bayesian inference tree of concatenated mitochondrial sequences (COI, 12S, 16S) rooted with Clade G, modified by DE MATTIA et al. (2020) and MASON et al. (2023: fig. 1). Numbers of subspecies included (of the total number of subspecies within each species) in parentheses. Thus, monotypic species are indicated by 1 number only. Note that individuals (which are indicated by asterisks) of some taxa were found in more than 1 clade (e.g., *M. ochridensis*, *M. drimmeri*). The colour code of clades corresponds to that given in Table 1.

to MASON et al. 2020), but with the updated taxonomy according to the latest revision (DE MATTIA et al. 2020, MASON et al. 2023). So far none of the nuclear markers analysed has yielded a robust phylogeny of the genus. Therefore, the present tree is the best phylogenetic framework for *Montenegrina* at present (MASON et al. 2020, 2023), and we refer to the clades established in these earlier works.

Shell and genitalia—trait measurements and categorization

Nomenclature of genital anatomy follows DE MATTIA et al. (2020: 696, fig. 3), and nomenclature of shell traits follows FEHÉR & SZEKERES (2016: 9, fig. 2). Figure 2 shows the main genital and shell parameters that were analysed. Concerning genital measurements, since the ducts of the genital apparatus of most representatives of the genus *Montenegrina* have very large diameters in relation to the general size of the genitalia, defining clear boundaries is difficult. In the area of intersection among FO, DBC, and V, a triangular transition zone has been left out of the measurements, and this is because the large thickness/circumference of the ducts creates a space of uncertainty. This standard was strictly applied to all specimens.

The shell traits that were measured are: shell height (SH), number of complete whorls (W: protoconch plus teleoconch), shell maximum width (SMW), aperture height (AH), aperture width (AW), body whorl height (BWH), striae/ribs angle (OA), and lunella angle (LA). For OA, the angles were measured at the third whorl, as counted from the peristome (Fig. 2), which represents the same growth stage for all shells. For the male distal genitalia, the sum length of the penial complex ($P + E = PC$), PC was also considered, because the correlation between P and E is not yet clearly known. Moreover, the relative length of the penial complex as a percentage of SH was calculated ($PCRL = PC / SH * 100$).

For a qualitative approach, several anatomical parts of the shell and the genitals were described and categorised. The following 6 features were analysed for the shell: neck inflection (NI, 2 types), peristome position (PPOS, 3 types), lamella superior vs spiralis (LSS, 3 types), subclaustralis bending (SB, 3 types), lunella position (LP 3 types), and the plica basalis (PB, 3 types). Since inner structures and the sculpturing of the inner walls provide the key characters for the genital anatomical parts (DE MATTIA et al. 2020), the following traits were considered: the atrium type (AT, 4 types), the penis type (PT, 7 types), the epiphallus type (ET, 4 types), the penial papilla type (PPT, 6 types), and the distal vagina type (IDVT, 5 types). These parts revealed the highest variability. Other parts showed comparably little variability and thus were not deemed suitable for taxonomic characterisation. Table 2 summarises the description of qualitative characters and their categories.

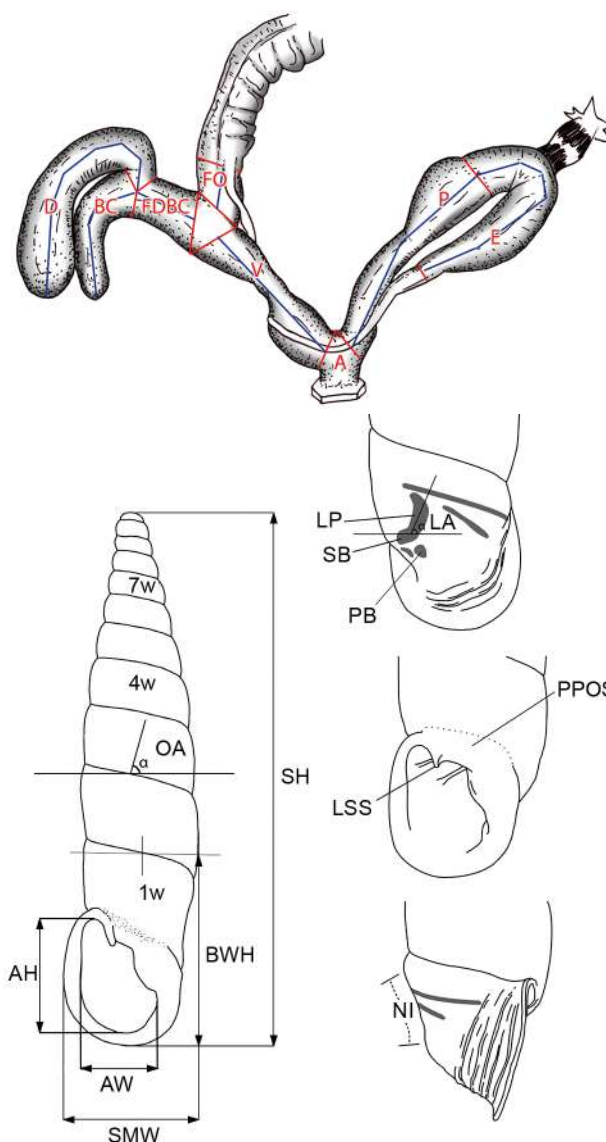


Figure 2. Relevant characters of genitalia and shell with representation of measurements. Genital tract: atrium (A), bursa copulatrix (BC), diverticulum (D), epiphallus (E), primary duct of bursa copulatrix (DBC), free oviduct (FO), penis (P), vagina (V). Shell characters: aperture height (AH), aperture width (AW), body whorl height (BWH), lunella (L), lunella angle (LA), lunella position (LP), lamella superior vs spiralis (LSS), neck inflection (NI), ornamentation (striae/ribs) angle (OA), plica basalis (PB), peristome position (PPOS), subclaustralis bending (SB), SDBC second duct of bursa copulatrix, shell height (SH), shell maximum width (SMW), number of whorls (W).

Statistical analyses

First, we collected descriptive statistics of the main morphometric measurements (of both shell and genitalia) to compare dimensions and trait variability within and among clades and taxa. Size ranges, arithmetic means, and standard deviations were calculated from a data matrix using Microsoft Excel v. 16.51. Tests for normality of the data (following SHAPIRO & WILK 1965), plotted visualisations of means, the bivariate regression model, and multivariate analyses (principal components analysis PCA

Table 2. Qualitative traits of shell and genitalia with character states and coding.

	1	2	3	4	5	6	7
NI Neck inflection	Strong	Weak or absent					
PPOS Peristome position	Projected	Detached or mostly detached	Attached				
LSS Lamella superior vs spiralis	Always overlapping	Intermediate	Always not overlapping				
SB Subclaustralis bending	Broad	Medium	Weak				
LP Lunella position	Dorsal to dorso-lateral	Intermediate	Weak or absent				
PB Plica basalis	Fused	Separate or mostly separate	Residual or absent				
AT Atrium type	Totally smooth	One unilobated/polylobated fold	Three or more folds	Three different sculpturings			
PT Penis type	Completely smooth	Smooth longitudinal pleats	Chevron-like pleats	Fringed longitudinal pleats	Radial pleats	Irregular pleats, no pattern visible	Both longitudinal and radial pleats
ET Epiphallus type	Smooth pleats, background smooth	Smooth pleats, coarse background	Smooth pleats	Fringed pleats			
PPT Penial papilla type	No PP	Globose PP	Conical PP	Bilobated or handlike PP	Big PP, occupying whole penial lumen	Small, slim elongated PP	
IDVT Inner distal vagina type	Smooth vagina	Irregular pleats	Radial pleats	Chevron-like pleats	Longitudinal/slanting pleats		

using all principal component axes, NJ trees performed by means of Euclidean distances) were performed using Past v. 4.02 (HAMMER et al. 2001). The penial complex length (PC) was not used in the multivariate analyses, as this measure is the sum of 2 already individually treated characters (P + E). In contrast, PC is used in basic statistical analyses as a measurement used by DE MATTIA et al. (2020) as a comparison parameter between genitalia size and shell height (SH). PCA was calculated using z-score transformed data. Linear bivariate regression was calculated to determine the significance of correlations between the measurements of the characters. All possible pairs of traits were tested for correlations. Coefficient of determination values $R^2 \geq 75\%$, i.e. that >75% of the variability can be explained by the target variable, were considered to indicate highly supported correlations. Following PUTH et al. (2014), a correlation is considered very strong when the *t*-score value, approaches 8 or higher. The *t*-score is defined as the mean difference of the values scaled by the standard error and is equivalent to the number of standard deviations away from the mean of the *t*-distribution. We adjusted the significance threshold ($\alpha = 0.05$) for the *p* values for multiple testing using the Bonferroni method, which resulted in an

adjusted significance threshold (according to the number of tests). Normal distribution tests were performed on the data pooled at the genus level using Shapiro–Wilk and Lilliefors normality tests (SHAPIRO & WILK 1975, LILLIEFORS 1967), to examine whether the measurements of the main shell characters (SH, W, SMW, BWH, AH, AW, OA, and LA) and genital characters (P, E, V, BC, and D) follow a normal distribution for the genus as a whole ($n = 259$).

Mantel test

We further tested for correlations between genetic, morphological, and geographical distances (of the coordinates of the collecting sites; assessed with Google Earth) by comparing distance matrices based on data from taxa belonging to the Clades D1 and D2 by means of Mantel tests. The first distance matrix included all pairwise geographical Euclidean distances between the collecting sites of all specimens in Clades D1 and D2 that were anatomically investigated. The second matrix was based on the pairwise Euclidean distances of quantitative genital characters among specimens, that is, the points of the PCA (principal component analysis, PC1–PC2). The third

dataset was based on pairwise genetic distances (Kimura 2-parameter distances as implemented in MEGA v. 11.0.10; TAMURA et al. 2021) of *COI* sequences among the above-mentioned specimens (calculated from the data of MASON et al. 2020). Since pairwise distance values are not independent from each other, we tested for significant associations between the 3 different distance measures in R by employing 2-tailed mantel tests with 1 million permutations as implemented in the R package “*ecodist*” (GOSLEE et al. 2007). The analysis pipeline and raw data can be found at https://github.com/capoony/Montenegrina_2023.

Tree inference

The tree from quantitative parameters was based on a pairwise Euclidian distance matrix that was calculated from the first 2 axes of a principal component analysis (PCA). For all quantitative measurements we calculated a distance matrix based on Euclidean distances among all individuals using the *dist* function in the R base package (R CORE TEAM 2021). For the qualitative data, we calculated pairwise Hamming distances, which are defined as the number of positions that differ among 2 strings of equal length, among individuals by counting differences in state across all qualitative traits using the package *culvevo* (Stadler 2018) in R. Since individuals of a given taxon did not differ in qualitative traits when collected at the same sampling site, we restricted the dataset to 1 individual per sampling site and taxon for this analysis to avoid redundancies due to identical quality scores of conspecific individuals from the same sampling location.

For each of the distance matrices (Hamming for qualitative data and Euclidean for quantitative data) we constructed NJ trees using the *nj*-function in R and performed 100 rounds of bootstrapping using the function *boot.phylo* of the *ape* package (PARADIS & SCHLIEP 2019) to test for the statistical support of each node and plotted the tree using the *ggtree* package (XU et al. 2022). Due to the extremely low support of all nodes, support values are not shown in the trees.

Furthermore, maximum parsimony (MP) trees were constructed based on 11 qualitative characters using the dataset with unique individuals as described above with the following parameters: starting tree(s) obtained via stepwise addition; addition sequence: random; number of replicates = 10; starting seed = generated automatically; number of trees held at each step = 1; branch-swapping algorithm: tree-bisection-reconnection (TBR) with reconnection limit = 8. From each population, 1 individual was included, since in all populations there was no variation of qualitative traits (in contrast to measurements, which varied among individuals). Similar to above, we plotted the tree in R using the *ggtree* package (XU et al. 2022).

The full bioinformatic documentation of the tree reconstructions can be found at https://github.com/capoony/Montenegrina_2023.

Abbreviations

Genitalia. A = atrium, AT = atrium type, BC = bursa copulatrix, D = diverticulum, DBC = (first) duct of bursa copulatrix, DV = distal vagina, DVT = distal vagina type, E = epiphallus, ET = epiphallus type, primary (first or only) duct of bursa copulatrix (DBC), FO = free oviduct, IDVT = inner distal vagina type, P = penis, PC = P + E = penial complex, PT = penis type, PP = penial papilla; PPT = penial papilla type, PV = proximal vagina, SDBC = second duct of bursa copulatrix, V = vagina.

Shell. AH = aperture height, AW = aperture width, BWH = body whorl height, L = lunella, LA = lunella angle, LP = lunella position, LSS = lamella superior vs spiralis, NI = neck inflection, OA = ornamentation (striae/ribs) angle, PB = plica basalis, PPOS = peristome position, SB = subclaustralis bending, SH = shell height, SMW = shell maximum width, W = number of whorls.

Statistics. \bar{x} = arithmetic mean, R = range, SD = standard deviation.

Colour code of phylogenetic clades. Following MASON et al. (2020, 2023). Clade A = brown, Clade B = greenish yellow, Clade C = light orange, Clade D1 = salmon, Clade D2 = dark red, Clade E = red, Clade F = green, Clade G = grey, Clade H = dark blue, Clade I = blue, Clade J = light blue, Clade K = violet, Clade L = dark violet.

Results

The results of normality tests for pooled measurements of shell and genital characters at the genus level, are presented in Table S1 (Supplementary Information). Multi-modal distributions would be expected in data pooled across multiple species. Visual inspection of the frequency distribution of measurements shows that some parameters, especially shell height (SH) and aperture height (AH) approached normal distribution at genus level (Fig. S1), and measurements of penis length pooled at the genus level clearly follow a skew distribution (Figs S1, S2).

Shell measurements

Table 3 depicts shell measurements for pooled data for the genus *Montenegrina* and for each clade. Figure 3 shows arithmetic mean \pm standard deviation of shell height (SH) for each taxon studied, while plots of SH, and other shell traits are shown by clade level in Figure S3 (Supplementary Information): shell height (SH), number of whorls (W), shell maximum width (SMW), and body whorl

Table 3. Shell traits measurements: arithmetic mean \pm standard deviation, median and range (minimum–maximum) for each clade and for the genus: shell height (SH), number of whorls (W), shell maximum width (SMW), body whorl height (BWH), aperture height (AH), aperture width (AW), ornamentation angle (OA) and lunella angle (LA). Units are mm (for measurements), counts (for whorls) or degrees (for angles). The colour code of clades is described in detail in Table 1.

Clade	SH	W	SMW	BWH	AH	AW	OA	LA
A	13.0 \pm 0.4	10.5 \pm 0.2	3.3 \pm 0.1	4.3 \pm 0.4	3.1 \pm 0.3	2.4 \pm 0.1	68.2 \pm 71.5	75.7 \pm 1.3
	12.8	10.5	3.3	4.1	2.9	2.4	71.4	76.6
	12.7–13.5	10.2–10.8	3.1–3.4	4.0–4.5	2.9–3.6	2.3–2.6	62.9–61	74.0–76.7
B	19.4 \pm 3.2	10.2 \pm 0.5	4.1 \pm 0.5	5.2 \pm 0.4	3.9 \pm 0.6	3.3 \pm 0.3	68.0 \pm 6.0	78.3 \pm 11.0
	19.1	10.1	4.0	5.2	3.6	3.3	68.8	79.1
	14.8–23.9	9.4–11.0	3.2–4.9	4.7–6.2	3.3–5.0	2.6–3.9	55.5–74.7	59.7–99.3
C	20.2 \pm 2.9	9.4 \pm 0.5	4.8 \pm 0.7	6.6 \pm 0.4	4.7 \pm 0.8	4.4 \pm 0.5	66.3 \pm 3.5	72.0 \pm 7.1
	21.1	9.5	4.6	6.7	4.7	4.3	67.8	69.9
	15.4–25.2	8.7–10.4	3.7–5.9	5.8–7.3	3.7–6.3	3.6–5.2	60.1–70.6	63.9–83.4
D1	16.7 \pm 3.4	9.8 \pm 0.9	4.2 \pm 1.1	5.6 \pm 0.9	3.9 \pm 0.8	3.4 \pm 0.8	68.9 \pm 4.4	75.4 \pm 10.7
	16.3	10.0	4.0	5.3	3.9	3.2	70.1	73.4
	12.1–22.5	8.2–11.2	2.9–7.0	4.2–6.9	2.7–5.8	2.1–5.4	67.3–75.5	54.8–99.0
D2	16.5 \pm 2.4	10.2 \pm 0.6	3.9 \pm 0.4	5.8 \pm 1.2	3.9 \pm 0.5	3.3 \pm 0.4	70.2 \pm 2.6	73.0 \pm 4.5
	16.3	10.1	3.8	5.8	3.8	3.1	70.9	74.0
	11.9–22.4	8.6–11.0	3.4–4.4	3.3–7.1	3.0–4.6	2.5–3.8	63.1–73.2	62.7–81.9
E	17.8 \pm 2.2	9.7 \pm 0.7	4.6 \pm 0.8	6.1 \pm 1.2	4.3 \pm 0.5	3.7 \pm 0.5	68.9 \pm 5.8	64.9 \pm 10.1
	18.3	9.5	4.4	6.3	4.1	3.5	68.6	61.8
	14.0–21.0	8.4–11.4	3.1–6.3	3.8–8.1	3.3–5.5	2.7–4.9	57.1–74.9	55.0–86.2
F	20.8 \pm 2.4	10.3 \pm 0.6	4.8 \pm 0.8	6.7 \pm 1.0	4.8 \pm 0.7	4.0 \pm 0.8	66.1 \pm 4.3	64.8 \pm 8.9
	20.6	10.2	5.1	6.9	5.0	4.3	65.4	67.2
	14.0–25.1	8.9–11.7	3.2–6.5	5.0–8.2	3.0–7.5	2.5–6.1	60.1–75.2	52.1–75.9
G	13.9 \pm 4.1	9.4 \pm 1.0	2.9 \pm 1.0	4.4 \pm 1.4	2.7 \pm 0.7	2.4 \pm 0.6	67.8 \pm 5.2	88.9 \pm 10.4
	13.9	9.1	2.6	4.7	2.7	2.1	67.0	95.7
	10.2–22.6	7.7–11.3	1.8–5.1	2.9–7.0	1.8–3.9	1.9–3.6	59.1–77.5	72.8–99.2
H	18.1 \pm 1.1	9.6 \pm 0.5	4.8 \pm 0.5	6.7 \pm 0.9	4.4 \pm 0.4	3.4 \pm 0.3	70.1 \pm 2.9	75.7 \pm 5.1
	18.3	9.6	4.8	7.0	4.3	3.4	69.9	74.4
	14.9–19.3	8.9–10.6	3.6–5.6	3.9–7.7	3.4–5.1	3.0–3.9	65.1–77.2	67.5–90.2
I	17.1 \pm 1.9	10.8 \pm 0.6	4.3 \pm 0.8	5.7 \pm 0.7	3.6 \pm 0.5	3.3 \pm 0.5	70.9 \pm 3.3	81.0 \pm 7.5
	17.4	11.0	4.1	6.1	3.7	3.4	72.1	81.6
	12.9–21.0	9.4–11.5	2.8–6.2	3.8–6.4	2.2–4.5	2.0–4.0	63.4–75.1	70.0–93.2
J	10.0 \pm 0.1	8.4 \pm 0.1	3.3 \pm 0.1	3.2 \pm 0.1	2.0 \pm 0.1	1.9 \pm 0.1	74.3 \pm 0.3	69.5 \pm 0.4
	10.0	8.4	3.3	3.2	2.0	1.9	74.2	69.5
	9.9–10.1	8.3–8.4	3.2–3.4	3.1–3.3	1.9–2.1	1.8–1.9	74.2–74.6	69.2–69.9
K	17.4 \pm 3.7	10.1 \pm 0.9	4.2 \pm 1.3	5.2 \pm 1.0	3.6 \pm 0.8	3.2 \pm 0.9	69.1 \pm 4.7	70.0 \pm 7.6
	17.6	10.5	3.7	4.9	3.4	2.9	69.9	67.1
	11.9–22.5	8.0–11.2	3.1–6.7	4.1–7.1	3.0–5.2	2.5–5.0	61.4–77.0	61.8–81.6
L	17.5 \pm 2.3	10.4 \pm 0.9	4.3 \pm 1.0	5.3 \pm 1.1	3.8 \pm 0.9	3.5 \pm 0.8	72.7 \pm 4.1	85.6 \pm 11.1
	17.1	10.2	4.2	5.0	3.6	3.4	71.9	88.8
	13.2–21.2	8.5–11.9	2.1–6.1	3.4–7.5	3.2–6.0	2.7–5.5	16.1–80.2	60.9–99.2
Genus	17.6 \pm 3.2	10.1 \pm 0.8	4.3 \pm 1.0	5.7 \pm 1.2	3.9 \pm 0.8	3.4 \pm 0.8	69.5 \pm 4.6	75.9 \pm 11.1
	17.9	10.0	4.2	5.8	3.9	3.4	69.8	74.1
	9.9–25.2	7.7–11.9	1.8–7.0	2.9–8.2	1.8–7.5	1.8–6.1	55.5–80.2	52.1–99.3

height (BWH). Plots of arithmetic mean \pm standard deviation for further shell traits are shown at the clade level in Figure S4: aperture height (AH), aperture width (AW), ornamentation angle (OA), and lunella angle (LA).

Shell height, SH. The highest SH arithmetic mean was found in Clade F (20.8 mm) and the lowest in Clade J (10.0 mm). The largest species-specific SH belongs to *M. voidomatis voidomatis* of Clade C (25.2 mm). The smallest SH is presented by *M. minuscula* (9.9 mm) belonging to Clade J.

Numbers of whorls, W. The highest arithmetic mean of W was found in Clade I (10.8 whorls), whereas the lowest belongs to Clade J with 8.4 whorls. The highest

species-specific W belongs to *M. laxa* of the Clade L (11.9 mm). The smallest W is found in *M. okolensis caesia* (7.7 mm), which is part of Clade G.

Shell maximum width, SMW. The highest clade-specific SMW arithmetic mean was found in Clades F and C (4.8 mm), and the lowest in Clade G with 2.9 mm. The highest SMW of a species was observed in *M. edmundi* of Clade D1 (7.0 mm) and the smallest SMW in *M. prokletiana kovacsorum* (1.8 mm) of Clade G.

Body whorl height, BWH. The highest BWH arithmetic mean was observed in Clades F and H (6.7 mm) and the lowest in Clade J with 3.2 mm. The highest BWH was found in *M. umbilicata umbilicata* (8.2 mm) and the

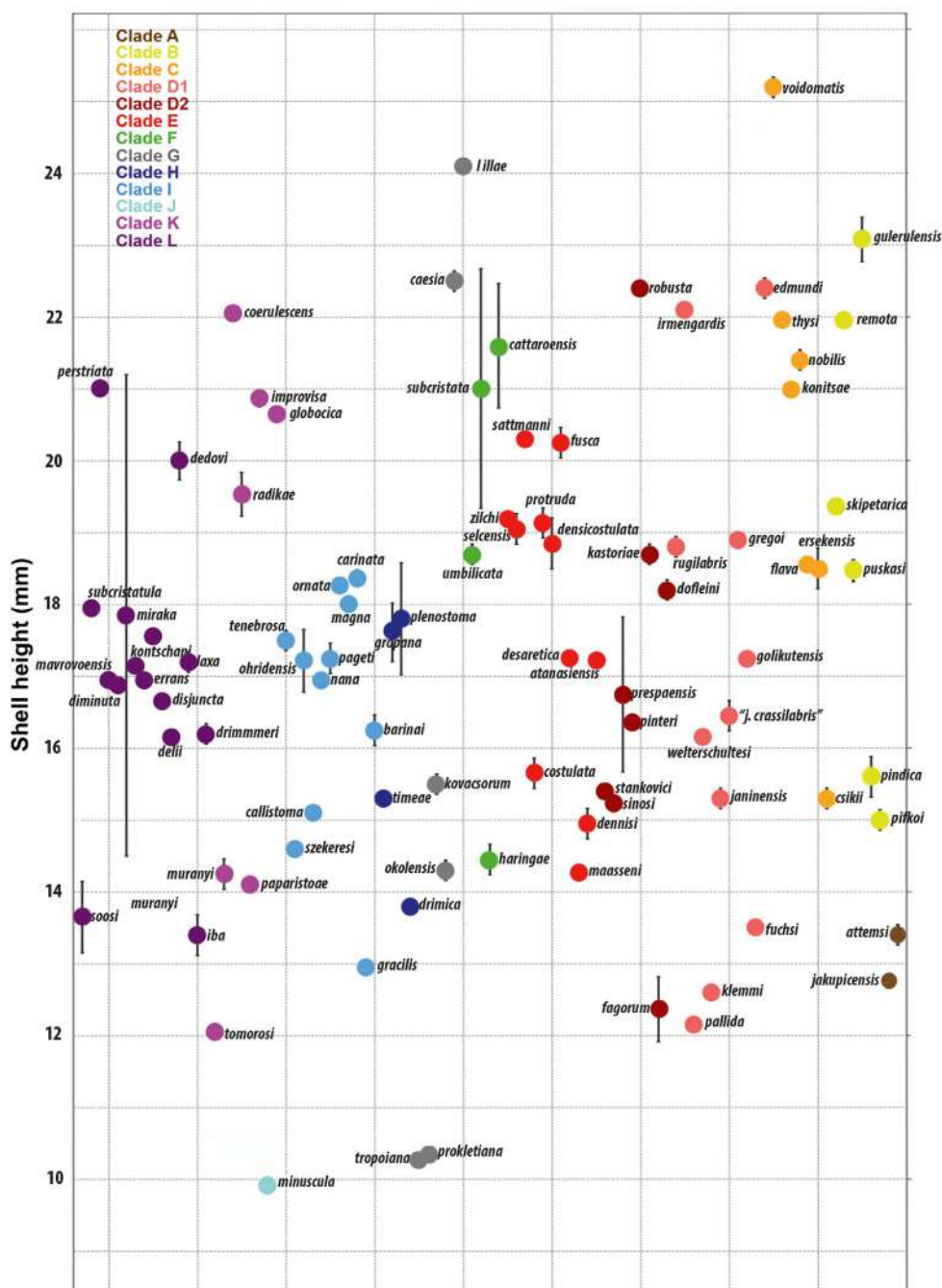


Figure 3. Shell height (mm). Plots of arithmetic mean \pm standard deviation of all taxa. Species are arranged along the x-axis according to clades, starting with Clade A (right) to Clade L (left). The colour code of clades corresponds to Table 1.

lowest in *M. prokletiana kovacsorum* (2.9 mm) of Clade G.

Aperture height, AH. The largest AH arithmetic mean was found in Clade F (4.8 mm) whereas the lowest one belongs to Clade J with 2.0 mm. The highest AH was specific to *M. umbilicata umbilicata* (7.5 mm). The smallest AH is found in *M. minuscula* (1.8 mm) of Clade J.

Aperture width, AW. The highest AW arithmetic mean was found in Clade C (4.4 mm), whereas the lowest was in Clade J with 1.9 mm. The highest and smallest AW were observed in *M. umbilicata umbilicata* (6.1 mm; Clade C) and *M. minuscula* (1.8 mm; Clade J), respectively.

Ornamentation angle, OA. The highest OA arithmetic

mean was found in Clade J (74.3°), whereas the lowest one belongs to the Clade F with 66.1 degrees.

Lunella angle, LA. The highest LA arithmetic mean was found in Clade G (88.9°), whereas the lowest one belongs to the Clade F with 64.8°.

Species of Clade F have (with *M. subcristata* and *M. umbilicata*) most of the highest mean values of shell measurements, namely SH, SMW, BWH, and AH. Only the highest AW mean value belongs to Clade C, albeit the mean AW of the Clade F is only slightly smaller. Most of the highest and smallest mean values are found in Clades F and J, respectively.

Measurements of genitalia

Arithmetic mean \pm standard deviation of genital parts at the clade level, are summarized in Table 4. The plots of penis length for each taxon are depicted in Figure 4.

Penial complex, PC. The highest PC arithmetic mean was found in Clade B (7.2 mm) and the lowest in Clade J (2.4 mm). The largest PC was found in Clade B as it contains the “ectomorph genitalia” of *M. skipetarica* where the genitalia, in all their parts, present an extremely slender and notably more stretched shape (thus larger size) in

comparison to the genitals of most of the remaining taxa (see DE MATTIA et al. 2020: 802).

Penis, P. The highest P arithmetic mean was found in Clade B (3.6 mm) and the lowest in Clade J (0.8 mm). As for the PC, the largest P was found in Clade B as it contains the “ectomorph genitalia” of *M. skipetarica* (see DE MATTIA et al. 2020: 802).

Epiphallus, E. The highest E arithmetic mean is found in Clade G (4.3 mm), the lowest in Clade J (1.6 mm). *Montenegrina attemsi* presents the smallest epiphallus (1.2 mm), whereas *M. lillae* presents the longest with 9.6 mm.

Table 4. Genitalia traits measurements: arithmetic mean \pm standard deviation, median and range (minimum–maximum) at genus and clade level. $n = 259$. Penial complex (PC), penis (P), epiphallus (E), vagina (V), free oviduct (FO), bursa copulatrix (BC), duct of bursa copulatrix (DBC) and diverticulum (D). Units are mm. The colour code of clades corresponds to Table 1.

Clade	PC	P	E	V	FO	BC	DBC	D
A	3.2 \pm 0.8 3.7 2.4–3.8	1.1 \pm 0.1 1.1 1.0–1.2	2.1 \pm 0.9 2.7 1.2–2.8	1.1 \pm 0.3 1.2 0.8–1.3	0.3 \pm 0.1 0.3 0.2–0.3	1.6 \pm 0.8 2.1 0.8–2.3	0.5 \pm 0.2 0.7 0.3–0.8	1.8 \pm 0.1 1.8 1.8–1.9
B	7.2 \pm 4.7 4.7 3.0–17.0	3.6 \pm 2.9 2.6 1.1–10.0	3.6 \pm 2.1 2.3 1.7–7.8	4.5 \pm 2.6 3.4 2.5–10.7	0.9 \pm 0.4 0.8 0.3–1.3	2.1 \pm 0.2 2.0 1.7–2.4	0.9 \pm 0.2 0.9 0.6–1.3	2.4 \pm 0.9 2.3 1.2–3.6
C	6.8 \pm 2.3 6.6 3.6–10.5	3.0 \pm 1.1 3.1 1.0–4.6	3.8 \pm 1.3 3.1 2.3–6.0	4.3 \pm 2.3 3.4 2.4–10.0	1.1 \pm 0.5 1.0 0.3–2.0	2.9 \pm 1.2 2.8 1.0–4.9	0.9 \pm 0.4 0.8 0.4–1.6	3.3 \pm 1.2 2.9 2.0–5.7
D1	4.5 \pm 1.5 4.4 2.9–8.9	2.0 \pm 1.0 1.8 0.7–5.0	2.5 \pm 0.8 2.5 1.4–3.6	2.8 \pm 1.5 2.8 0.7–6.5	0.8 \pm 0.5 0.6 0.2–2.1	2.2 \pm 1.1 1.8 1.2–5.6	0.7 \pm 0.3 0.7 0.2–1.2	2.8 \pm 1.3 2.8 1.3–5.2
D2	4.1 \pm 0.8 4.3 2.8–5.6	1.6 \pm 0.5 1.6 0.9–2.8	2.6 \pm 0.6 2.7 1.7–3.6	2.8 \pm 1.4 2.4 1.1–5.7	1.0 \pm 0.4 0.9 0.4–2.0	2.1 \pm 0.5 2.2 1.5–3.4	0.7 \pm 0.3 0.6 0.2–1.1	1.7 \pm 0.4 1.6 1.0–2.6
E	4.7 \pm 1.2 4.3 3.5–7.3	1.9 \pm 0.3 1.9 1.5–2.5	2.8 \pm 1.1 2.5 1.7–5.5	2.8 \pm 1.1 2.3 1.5–5.4	1.3 \pm 0.4 1.1 0.7–2.1	2.4 \pm 0.4 2.3 1.8–3.1	0.7 \pm 0.3 0.6 0.2–1.2	2.2 \pm 0.6 2.1 1.5–3.4
F	6.2 \pm 1.9 5.9 3.2–9.0	2.9 \pm 1.1 2.7 1.4–4.9	3.2 \pm 1.1 2.9 1.8–5.3	3.6 \pm 1.5 3.7 1.4–5.8	1.3 \pm 0.8 1.1 0.3–4.0	2.9 \pm 0.9 2.9 1.7–4.5	1.0 \pm 0.7 0.7 0.2–2.6	3.1 \pm 0.9 3.0 1.7–5.2
G	6.5 \pm 3.0 5.0 4.4–13.2	2.4 \pm 1.2 2.0 1.3–4.6	4.3 \pm 2.2 3.4 3.0–9.6	2.8 \pm 1.7 1.6 1.3–9.4	1.3 \pm 1.2 0.9 0.3–3.9	3.1 \pm 0.9 2.9 1.9–5.0	1.2 \pm 0.5 1.0 0.7–2.4	3.4 \pm 2.1 2.8 1.8–8.6
H	4.5 \pm 1.0 4.3 2.1–6.2	2.1 \pm 0.5 2.0 1.3–3.6	2.6 \pm 0.7 2.6 1.6–3.6	2.7 \pm 0.6 2.4 1.8–3.7	1.1 \pm 0.2 1.1 0.6–1.4	2.3 \pm 0.8 2.4 1.0–3.4	0.4 \pm 0.2 0.3 0.1–0.9	2.4 \pm 0.7 2.5 1.5–4.3
I	5.7 \pm 1.6 5.1 4.1–9.0	2.5 \pm 1.2 2.4 1.0–5.1	3.1 \pm 0.8 3.2 1.3–4.3	3.5 \pm 1.9 3.0 1.8–8.3	1.0 \pm 0.5 1.0 0.4–2.0	2.4 \pm 0.8 2.1 1.3–4.6	0.8 \pm 0.8 0.6 0.1–3.0	2.5 \pm 0.9 2.7 1.4–4.4
J	2.4 \pm 0.1 2.4 2.4–2.5	0.8 \pm 0.1 0.8 0.7–0.9	1.6 \pm 0.1 1.6 1.5–1.6	3.5 \pm 0.4 3.3 3.2–3.9	0.4 \pm 0.1 0.4 0.3–0.4	1.6 \pm 0.1 1.6 1.6–1.7	0.6 \pm 0.1 0.6 0.5–0.7	1.3 \pm 0.1 1.3 1.3–1.4
K	4.8 \pm 1.6 4.3 3.0–8.9	2.0 \pm 0.7 2.0 1.1–3.1	2.9 \pm 1.1 2.6 1.5–5.9	2.0 \pm 0.8 1.9 0.7–4.1	1.1 \pm 0.2 1.1 0.6–1.4	2.0 \pm 1.2 2.9 1.6–5.5	0.5 \pm 0.2 0.5 0.4–1.0	2.4 \pm 1.0 2.2 1.1–4.5
L	5.1 \pm 1.6 4.6 2.9–8.6	2.3 \pm 1.1 2.6 1.0–4.5	2.9 \pm 0.8 2.6 1.7–4.5	2.3 \pm 0.8 2.9 1.3–4.6	1.3 \pm 0.5 1.2 0.4–2.5	2.6 \pm 0.9 2.7 1.4–4.8	0.9 \pm 0.3 0.8 0.4–1.4	3.3 \pm 1.3 3.4 1.6–6.6
Genus	5.3 \pm 2.1 4.6 2.1–17.0	2.3 \pm 1.2 2.1 0.7–10	3.0 \pm 1.2 2.7 1.2–9.6	3.0 \pm 1.7 2.8 0.7–10.7	1.1 \pm 0.6 1.1 0.2–4.0	2.4 \pm 0.9 2.2 0.8–5.6	0.8 \pm 0.5 0.8 0.1–3.0	2.7 \pm 1.2 2.9 1.0–8.6

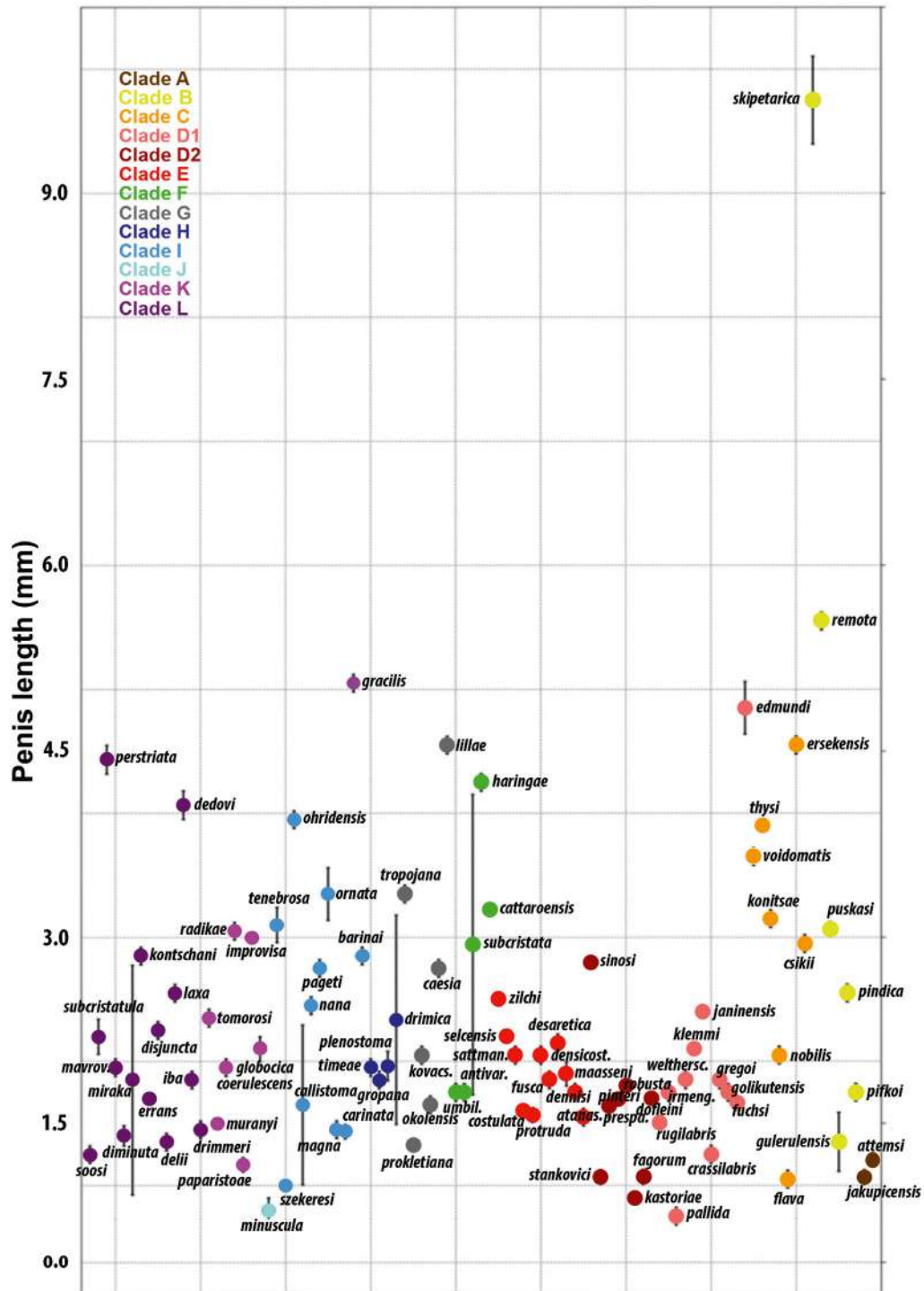


Figure 4. Penis length (mm). Plots of arithmetic mean \pm standard deviation for all taxa analysed. Species are distributed along the x-axis according to clades, starting with Clade A (right) to Clade L (left). The colour code of clades is described in detail in Table 1.

Vagina, V. The highest V arithmetic mean was found in Clade B (4.5 mm) and the lowest in Clade A (1.1 mm). *Montenegrina janinensis* and *M. tomorosi muranyi* present the shortest vagina (0.7 mm), whereas *M. skipetarica* presents the longest: 10.7 mm.

Free oviduct, FO. Clades E, F, G, and L (1.3 mm) had the highest FO arithmetic mean and the lowest was found in Clade A (0.3 mm). *Montenegrina pallida* and *M. golikutensis*

show the shortest vagina (0.2 mm), and *M. haringae* presents the longest with 4.0 mm.

Bursa copulatrix, BC. The highest BC arithmetic mean is found in Clade G (3.1 mm), and the lowest BC was present in Clades A and J (1.6 mm). *Montenegrina attemsi* presents the smallest bursa copulatrix (0.8 mm), whereas *M. gregoi* shows the longest (5.6 mm).

Duct of bursa copulatrix, DBC. The highest DBC

arithmetic mean is found in Clades G (1.2 mm) and the lowest DBC in Clade H (0.4 mm).

Diverticulum, D. The highest D arithmetic mean is found in Clades G (3.4 mm) and the lowest D in Clade J (1.3 mm). *Montenegrina dofleini fagorum* presents the smallest diverticulum (1.0 mm), whereas *M. lillae* shows the longest (8.6 mm).

Correlations among parameters of shell morphology

Table 5 shows the results of linear bivariate regressions of the shell's character pairs that showed significant correlation. Of the 28 possible combinations of 8 shell characters (SH, W, SMW, BWH, AH, AW, OA, LA), only 13 (46.4%) showed a value of $p < 0.05$, and of these only 7 (25%) demonstrated a R^2 value of more than 75%. Figure S5 depicts 3 linear bivariate regression plots among shell characters: SMW vs SH (a), (b) BWH vs SH and AH vs SH (c). Figure S6 depicts 2 linear bivariate regression plots among genital characters: V vs PC (a) and E vs P (b). Notably, W does not correlate with SH or any other shell character. The pair AH and AW shows a strong and significant positive correlation between them and respectively with SH, BWH, and SMW. The LA proved to be a totally independent character from all others.

Correlations among parameters of genital morphology

Table 6 shows the results of linear bivariate regressions of the genitalia characters pairs that showed correlation ($R^2 > 25\%$). Of the 28 possible combinations of the 8 genital characters (PC, P, E, V, FO, BC, DBC, D), 20 (71 %) revealed a value of $p < 0.05$, despite none of these having a R^2 value of more than 75%. Only 10 (36%) combinations revealed a R^2 value between 50% and 75%. With all the remaining combinations the correlation values drop.

Concerning the most important parts of genitalia, P, E, and V, the R^2 values in the linear bivariate regression plots (Supplementary Information Figs S6, S7) show a positive correlation between P and PC, between P vs E (despite not strong), and V vs E, an even weaker correlation between P vs V. The size of the diverticulum D of bursa copulatrix complex proved to be related to E which is depicted in Figure S8. The same was observed for BC vs E and DBC vs E (Table 6). This is plausible as the spermatophore is produced in the E and, after mating, it ends up in the gametolythic gland, which must be of adequate size to encompass it entirely.

In general, the parts of the genitalia seem to be more related to each other (71%) (albeit less strongly) than the parts of the shell (46.4%).

Table 5. Linear bivariate regression (LBR) among the 14 shell characters pairs that showed correlation. All other combinations show non-significant correlation. Degrees of freedom = 7. Asterisks in the last column indicate the level of variance of the dependent variables explained (only regressions with $p < 0.05$ are shown): *** ($R^2 > 75\%$), ** ($R^2 50-75\%$), * ($R^2 25-50\%$).

LBR shell characters	R^2	t	p (corr.)	Correlation
AH vs AW	92.2	11.413	0.0001	***
BWH vs AH	92.2	11.83	0.0001	***
BWH vs AW	86.6	8.450	0.0001	***
SH vs AH	85.3	8.011	0.0002	***
SH vs AW	85.2	7.976	0.0001	***
SH vs BWH	80.5	6.740	0.0001	***
SMW vs AW	80.3	6.713	0.0002	***
SMW vs AH	71.9	5.314	0.0003	**
SMW vs BWH	67.4	4.775	0.0006	**
SH vs SMW	67.2	4.748	0.0009	**
AH vs OA	49.2	-3.267	0.0092	*
SH vs OA	43.1	-2.886	0.0160	*
BWH vs OA	42.9	-2.875	0.0169	*
AW vs OA	40.9	-2.761	0.0193	*

Table 6. Linear bivariate regression (LBR) among the 20 genital character pairs that showed correlation. All other combinations show non-significant correlation. Degrees of freedom = 7. Asterisks in the last column indicate the level of variance of the dependent variables explained (only regressions with $p < 0.05$ are shown): ** ($R^2 50-75\%$), * ($R^2 25-50\%$).

LBR genital characters	R^2 [%]	t	p (corr.)	Correlation
BC vs D	71.9	5.311	0.0005	**
P vs E	66.3	4.657	0.0016	**
E vs V	65.3	4.128	0.0007	**
FO vs BC	62.3	4.266	0.0009	**
E vs DBC	60.1	4.071	0.0022	**
E vs D	58.7	3.96	0.0023	**
E vs BC	57.6	3.869	0.0023	**
PC vs D	56.2	3.762	0.003	**
PC vs DBC	53.0	3.523	0.0049	**
DBC vs BC	52.0	3.453	0.0037	**
E vs FO	47.8	3.177	0.0095	*
P vs D	46.8	3.115	0.010	*
FO vs D	46.5	3.096	0.0088	*
PC vs BC	45.9	3.055	0.010	*
PC vs FO	43.3	2.898	0.012	*
P vs V	41.9	2.820	0.0157	*
P vs DBC	36.9	2.537	0.026	*
P vs FO	35.8	2.481	0.029	*
PC vs V	34.9	2.433	0.034	*
P vs BC	31.1	2.231	0.049	*

Correlations among parameters of genital and shell morphology

Table 7 shows the results of linear bivariate regressions of shell characters vs genitalia characters that showed correlation ($R^2 > 25\%$). Of the 64 possible combinations [(SH, W, SMW, BWH, AH, AW, OA, LA) vs (PC, P, E, V, FO, BC, DBC, D)] only 10 (15.6 %) revealed a value of $p < 0.05$, despite none of these having a R^2 value of more than 75%. Only 2 (3%) combinations have a R^2 value between 50% and 75%. With all the remaining combinations the R^2 values fall markedly below 50%.

Out of 10 combinations of genital and shell characters that showed a p -value > 0.05 , none expressed a R^2 value $> 75\%$. Only 2 have an R^2 between 50% and 75%, which are

Table 7. Linear bivariate regression (LBR) among all genital vs shell characters pairs that show (positive or negative) correlations. Degrees of freedom = 14. Asterisks in the last column indicate the level of variance of the dependent variables explained (only regressions with $p < 0.05$ are shown): ** (R^2 50–75%), * (R^2 25–50%).

LBR shell vs genital characters	R^2 [%]	t	p (corr.)	Correlation
SH vs P	66.9	4.722	0.0002	**
SH vs PC	53.8	3.586	0.0043	**
SH vs FO	45.0	3.002	0.014	*
BWH vs FO	38.9	2.648	0.027	*
AW vs P	38.2	2.609	0.026	*
AW vs FO	34.7	2.417	0.036	*
AH vs P	33.8	2.373	0.039	*
OA vs PC	33.3	-2.343	0.049	*
AW vs PC	31.5	2.253	0.0449	*
SH vs D	31.4	2.246	0.044	*

SH vs P and SH vs PC. Figure S9 shows 2 linear bivariate regression plots between (a) P (penis) vs SH (shell height) and (b) E (epiphallus) vs SH. In general, the size of the genitalia and shell characters appear to be unrelated.

Morphological taxon delimitation

The ordination and the clustering of the morphological data (genitalia and shell quantitative parameters) show the diagnostic value for taxon delimitation (DE MATTIA et al. 2020). For each of the present taxa, 15 parameters were available: 8 shell measurements (SH, W, SMW, BWH, AH, AW, OA, LA), and 7 genital measurements (P, E, V, FO, DBC, BC, D).

The results of the principal component analysis (PCA) are visualized in Figure 5 (shell measurements), Figure 6 (genital measurements), and Figure 7 (combined shell and genital data). The loadings of the principal components are listed in Tables S2, S3, and S4. Each colour represents a clade and the symbols represent taxa within a clade ($n = 259$; compare Table 1). Clades are widely overlapping in all 3 plots, and none of them is clearly separated from the others. This indicates that the phylogenetic signal in the morphometric data is very weak and even diagnosis is not possible using these characters when all taxa of the genus are used.

A clustering analysis (NJ clustering) of the Euclidian distances from the PCA of combined shell and genital characters resulted in a tree that illustrates the homoplasy in morphological characters. Again, representatives of taxa cluster together, while at the (sub-)clade level, morphological features appear to be randomly distributed in the tree (Figs S10, S11).

Finally, an MP analysis was performed based on the qualitative data and a strict consensus tree of 60,625 best

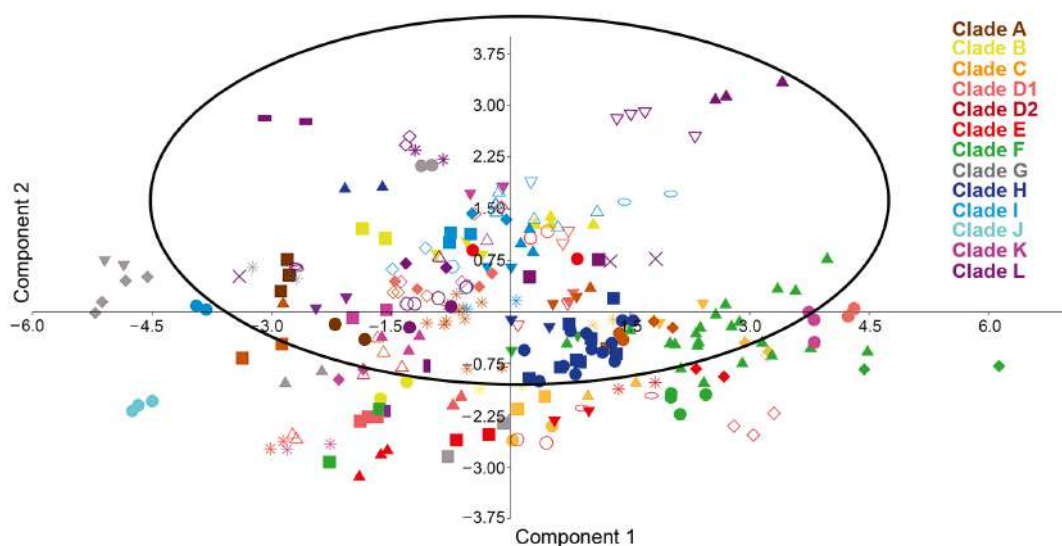


Figure 5. PCA scatter plot based on shell measurements ($n = 259$). Eigenvalue of the PC1 is 4.23991 with 53.056% of the variance explained. Eigenvalue of the PC2 is 1.33485 with 16.704% of the variance explained. Colour code corresponds to Table 1.

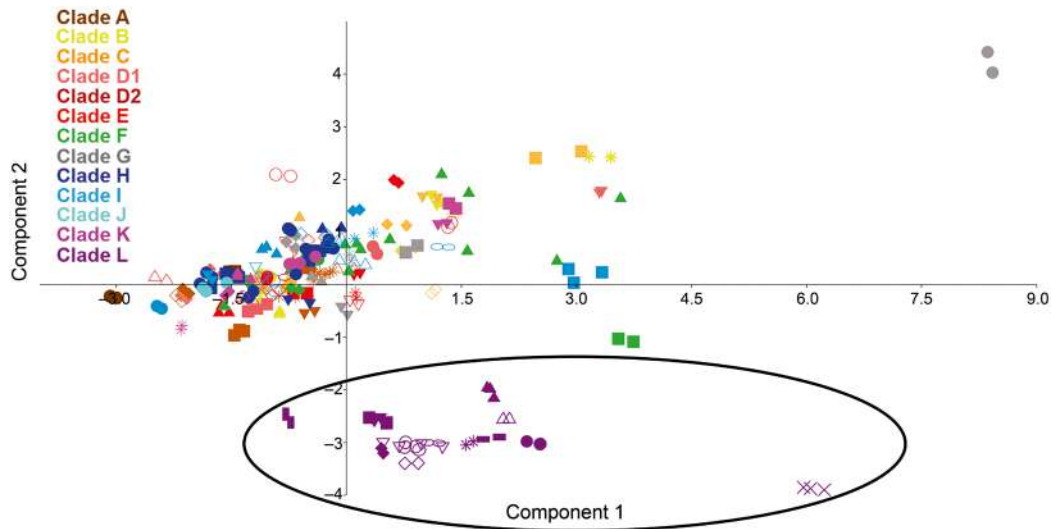


Figure 6. PCA scatter plot based on genital measurements. ($n = 259$). PC1 has an Eigenvalue of 2.8408 and explains 40.571% of the variance explained. PC2 has an Eigenvalue of 1.8775 and explains 26.813% of the variance. Colour code of clades corresponds to Table 1.

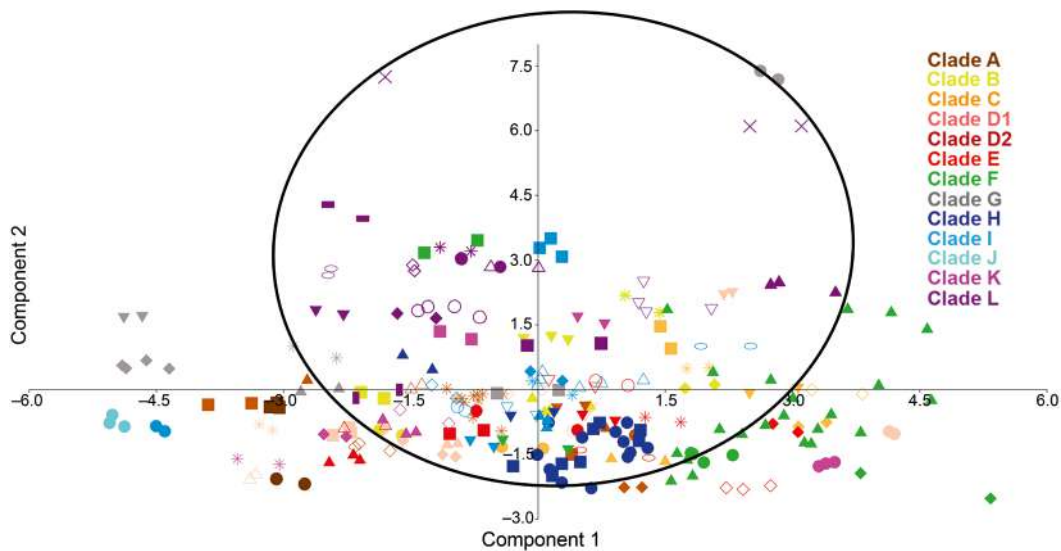


Figure 7. PCA scatter plot based on both shell and genitalia measurements. ($n = 259$). Eigenvalue of the PC1 is 4.9996 with 30.679% of the variance explained. Eigenvalue of the PC2 is 2.9116 with 19.419% of the variance explained. Colour code of clades corresponds to Table 1.

trees is shown in Figure S12. The tree contains a high number of unresolved nodes, while the few clades apparent do not reflect phylogenetic relationships (compared to Fig. 1) at all, except some cases where conspecifics cluster together.

Incongruence between phylogeny and morphological similarities

Due to the high number of taxa included in the genus *Montenegrina*, the PCA plots are quite complex with many overlapping clouds. To present a clearer picture, the ordination and clustering analyses were subsequently focused on members of the sister Clades D1 and D2, due to the

greater phylogenetic proximity between them (compared to other clades) and thus between the taxa they contain (defined by MASON et al. 2020), on the assumption that the closer the phylogenetic relationship the more morphologically similar they might be.

Figures 8 and 9 show PCA scatter plots of shell and genital measurements respectively, where a salmon colour represents Clade D1, dark red represents Clade D2, with each symbol representing a different taxon ($n = 49$). Figure 10 depicts PCA scatter plots based on both shell plus genital measurements of Clades D1 and D2. The specimens belonging to the same taxon are clustering, while the taxa of the clades are widely separated and overlapping with the respective other clade, especially in Figure

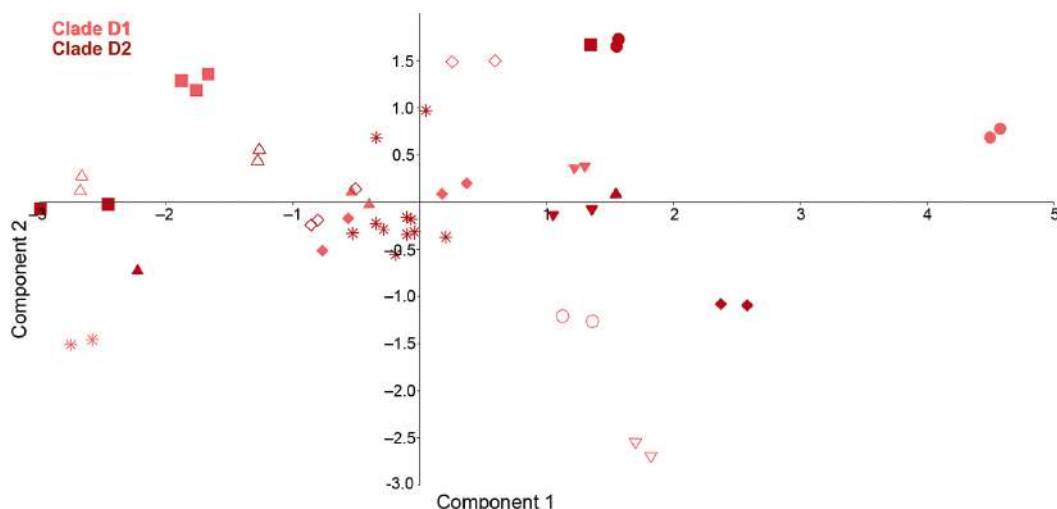


Figure 8. PCA scatter plot of Clades D1 and D2 based on shell measurements ($n = 49$). Eigenvalue of the PC1 is 2.9247 with 54.71% of the variance explained. Eigenvalue of the PC2 is 0.9581 with 17.92% of the variance explained. Colour code of clades and taxa—Clade D1: salmon: full circles *M. edmundi*, full squares *M. fuchsi*, full upward triangles *M. golikutensis*, full downward triangles *M. gregoi*, full diamonds *M. janinensis*, asterisks *M. klemmi*, empty diamonds *M. lambdaformis welterschultesi*, empty upward triangles *M. pallida*, empty circles *M. rugilabris rugilabris*, empty downward triangle *M. rugilabris irmengardis*; Clade D2: dark red: full circles *M. dofleini dofleini*, full squares *M. dofleini fagorum*, full upward triangles *M. kastoriae kastoriae*, full downward triangles *M. kastoriae robusta*, full diamonds *M. pinteri*, asterisks *M. prespaensis prespaensis*, empty diamonds *M. prespaensis sinosi*, empty upward-pointing triangles *M. stankovici*.

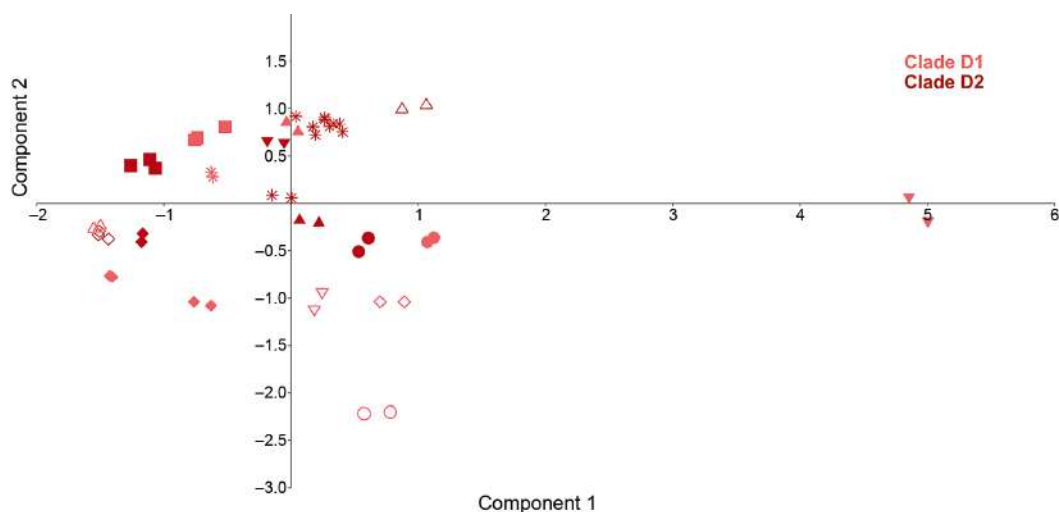


Figure 9. PCA scatter plot of Clades D1 and D2 based on the genital measurements ($n = 49$). Eigenvalue of the PC1 is 1.6698 with 52.4% of the variance explained. Eigenvalue of the PC2 is 0.6516 with 20.449% of the variance explained. Colour code of clades and taxa—Clade D1: salmon: full circles *M. edmundi*, full squares *M. fuchsi*, full upward triangles *M. golikutensis*, full downward triangles *M. gregoi*, full diamonds *M. janinensis*, asterisks *M. klemmi*, empty diamonds *M. lambdaformis welterschultesi*, empty upward triangles *M. pallida*, empty circles *M. rugilabris rugilabris*, empty downward triangle *M. rugilabris irmengardis*; Clade D2: dark red: full circles *M. dofleini dofleini*, full squares *M. dofleini fagorum*, full upward triangles *M. kastoriae kastoriae*, full downward triangles *M. kastoriae robusta*, full diamonds *M. pinteri*, asterisks *M. prespaensis prespaensis*, empty diamonds *M. prespaensis sinosi*, empty upward triangles *M. stankovici*.

8 (genital data). This indicates that taxa belonging to different clades show morphometric convergence in genital measurements. This is the case, for example, in *M. dofleini fagorum* (dark red squares) and *M. pallida* (pinkish empty upward-pointing triangles) as well as in *M. kastoriae robusta* (inverted full, dark-red triangles) and *M. klemmi* (salmon asterisks). These taxa are, however, clearly delimited in the PCA scatter plot of shell measurements. The

loadings of the principal components are listed in Tables S5, S6, and S7.

By removing the “compression effect” caused by a high number of taxa in the same PCA scatter plot, the morphological taxa delimitation is even more effective, as shown in Figure 11 where only the D1 taxa are displayed for shell and genital combined measurements. The loadings of the principal components are listed in Table S8.

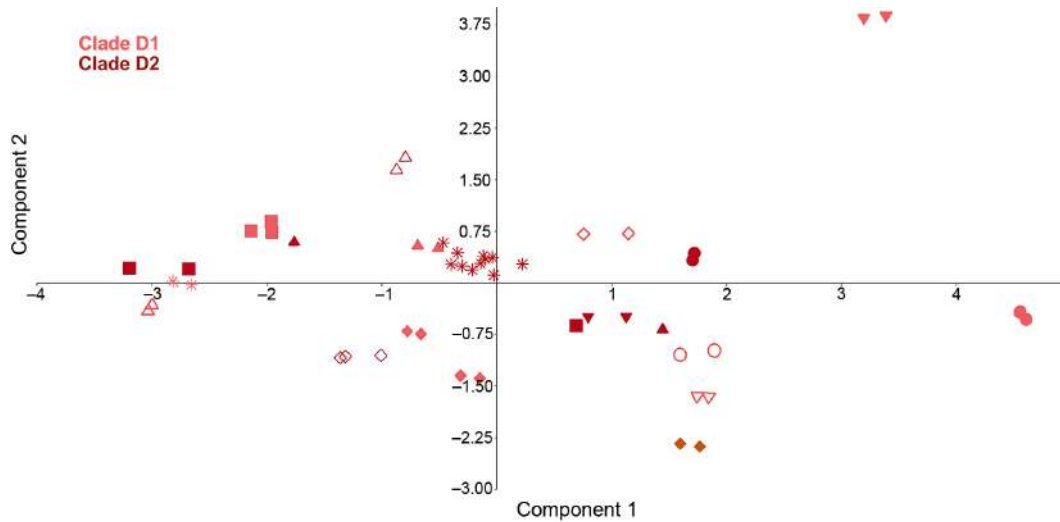


Figure 10. PCA scatter plot of clades based on both shell size and genital measurements D1 and D2 ($n = 49$). Eigenvalue of the PC1 is 3.4402 with 40.321% of the variance explained. Eigenvalue of the PC2 is 1.4313 with 16.776% of the variance explained. Colour code of clades and taxa—Clade D1: salmon: full circles *M. edmundi*, full squares *M. fuchsi*, full upward triangles *M. golikutensis*, full downward triangles *M. gregoi*, full diamonds *M. janinensis*, asterisks *M. klemmi*, empty diamonds *M. lambdaformis welterschultesi*, empty upward triangles *M. pallida*, empty circles *M. rugilabris rugilabris*, empty downward triangle *M. rugilabris irmengardis*; Clade D2: dark red: full circles *M. dofleini dofleini*, full squares *M. dofleini fagorum*, full upward triangles *M. kastoriae kastoriae*, full downward triangles *M. kastoriae robusta*, full diamonds *M. pinteri*, asterisks *M. prespaensis prespaensis*, empty diamonds *M. prespaensis sinosi*, empty upward triangles *M. stankovici*.

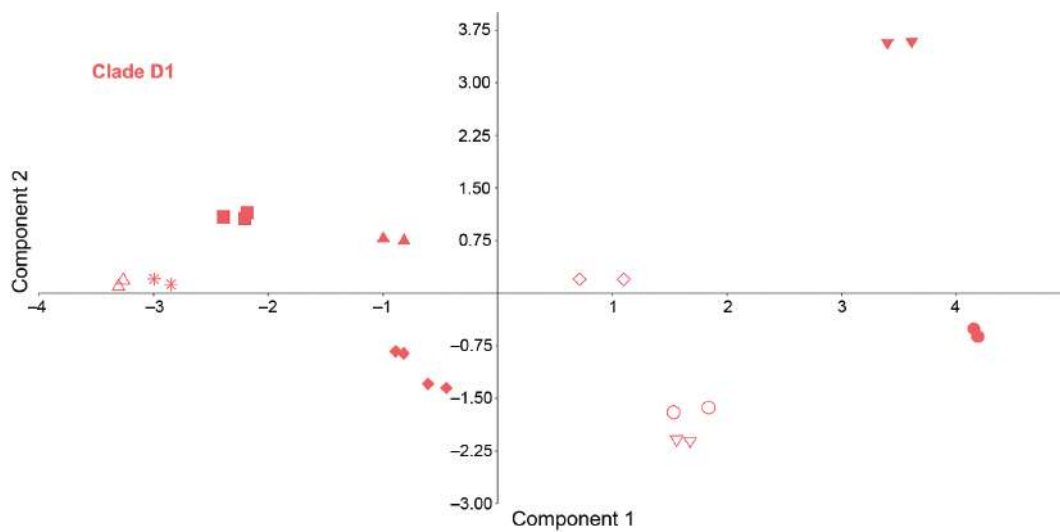


Figure 11. PCA scatter plot depicting both the shell size and the genital parts size group of data of the Clade D1 alone. Each symbol corresponds to a different taxon. ($n = 23$). Eigenvalue of the PC1 is 5.89817 with 47.952% of the variance explained. Eigenvalue of the PC2 is 2.28972 with 18.615% of the variance explained. Colour code of clades and taxa—Clade D1: salmon: full circles *M. edmundi*, full squares *M. fuchsi*, full upward triangles *M. golikutensis*, full downward triangles *M. gregoi*, full diamonds *M. janinensis*, asterisks *M. klemmi*, empty diamonds *M. lambdaformis welterschultesi*, empty upward triangles *M. pallida*, empty circles *M. rugilabris rugilabris*, empty downward triangle *M. rugilabris irmengardis*.

Besides the PCA scatter plots the incongruence between phylogeny and morphology can be visualized by trees. Figures S13 and S14 depict the BI (Bayesian-inference) phylogenetic trees of Clades D1 and D2 from MASON et al. (2020) with the up-to-date nomenclature as presented by MASON et al. (2023); for the nomenclature changes see Supplementary Information Table S9. The dataset matrix of Clades D1 and D2 had a total of 23 (D1) and 26 (D2) specimens, respectively (for detailed infor-

mation on the specimens, see MASON et al. 2020).

Figure 12 depicts the NJ tree (based on Euclidean distances) including both the shell measurements and the genital parts measurements of Clades D1 and D2, while Figure 13 depicts the NJ tree based on Hamming distances from qualitative categorization of traits. Both trees highlight the discrepancy between morphological characters and phylogenetic reconstruction. The topologies of these trees have hardly any branch in common with the

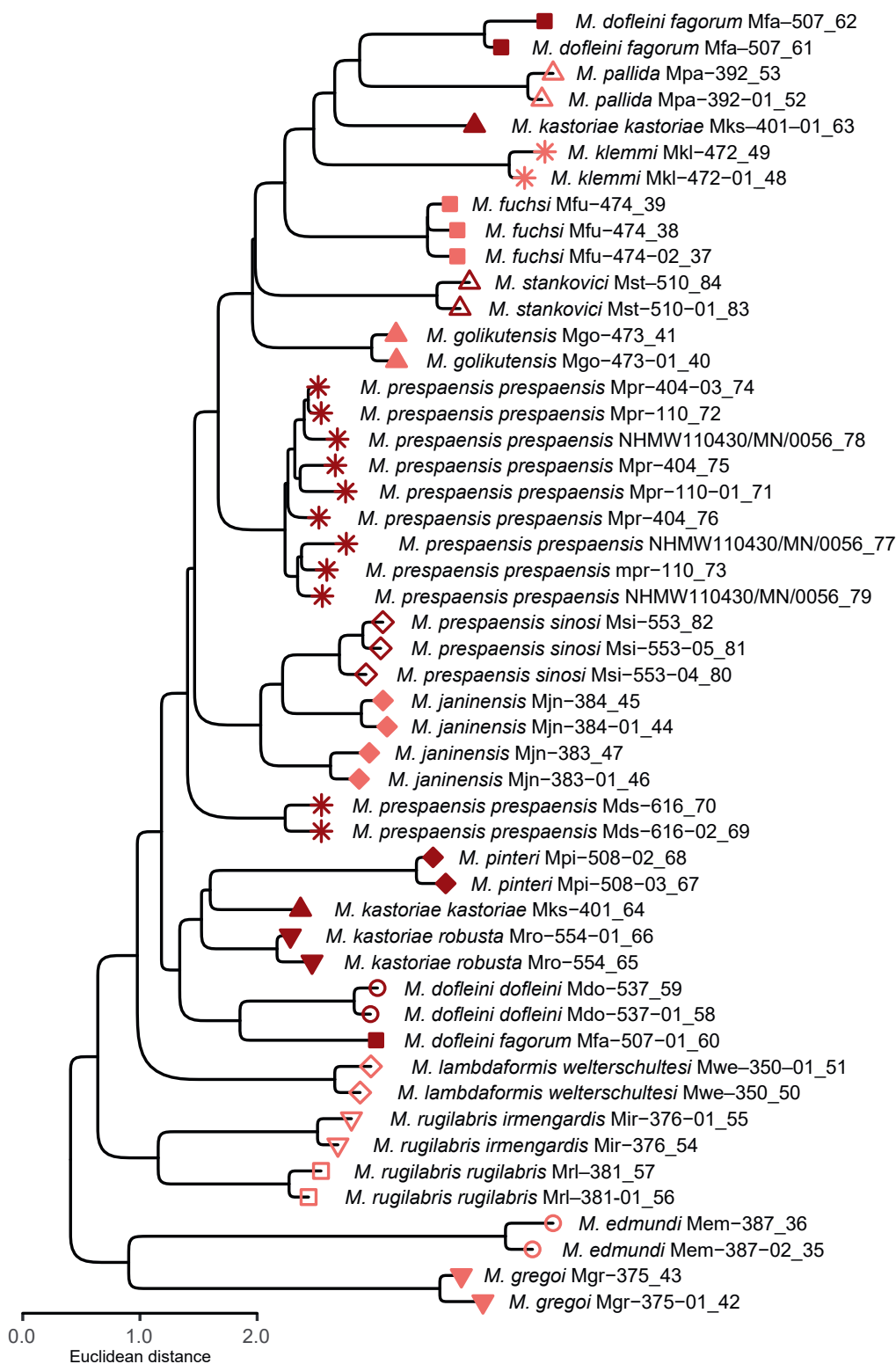


Figure 12. NJ tree based on Euclidean distances from quantitative traits including measurements of both shell and genital parts of Clades D1 (salmon) and D2 (dark red).

molecular tree depicted in Figure 1.

A MP tree delivered similar results (data not shown). There is only 1 character, the peristomal position, with a consistency index of 0.67, while all others are below 0.5. The rescaled CI of the tree was 0.24. This exemplifies that

morphological data of *Montenegrina* gathered in the present study lacks phylogenetic information. On the other hand, the tree based on quantitative morphological characters indicates that they probably are—in combination—a reliable tool for defining taxa

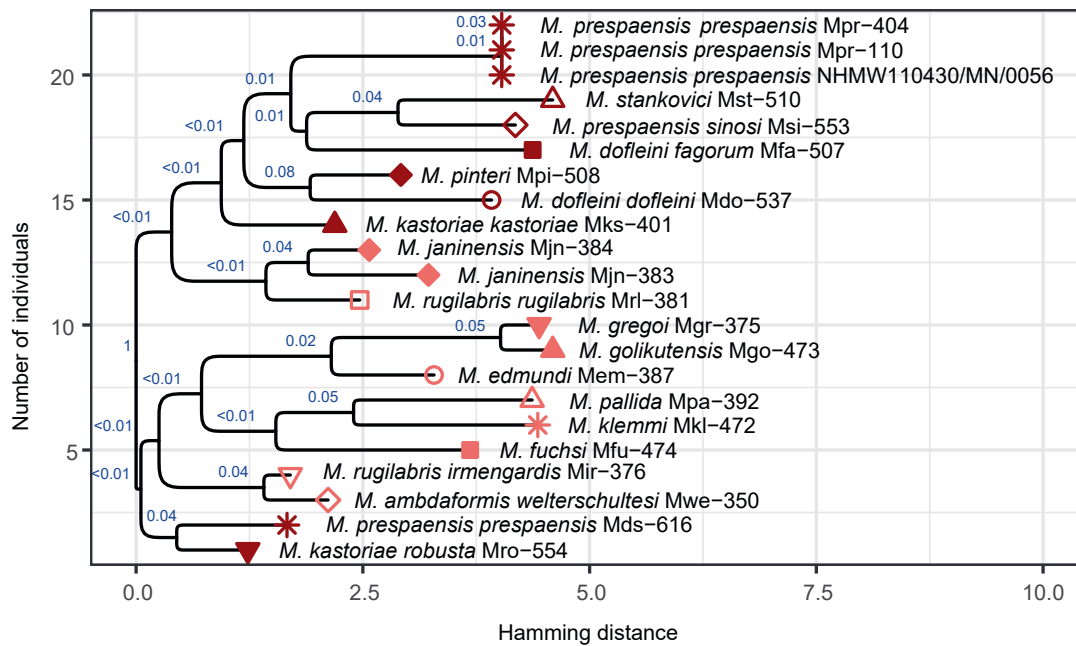


Figure 13. NJ tree based on Hamming distances from qualitative measurements of traits in 22 individuals of 19 taxa from Clades D1 (salmon) and D2 (dark red).

Correlations among geographic, genital morphological, and genetic distances

Having demonstrated the pronounced homoplasy of the qualitative genital characters, we investigated the congruence of quantitative genital data with genetic and geographic distances in Clades D1 and D2. We used pairwise regression analyses of the Euclidian distances derived from the PCA of the genital measurements, maximum-likelihood distances in the molecular phylogenetic tree, and the geographic distances of the coordinates of the collection sites. We therefore asked whether taxa that are geographically or genetically close to each other have more similar genitalia than more distant taxa, due to isolation by distance. In contrast, if geographically closer taxa have different genitalia, this could imply reinforcement of prezygotic isolation as a mating isolation mechanism to avoid interbreeding.

Geographic distances range from 1.3 km between *Montenegrina janinensis* and *M. rugilabris rugilabris* (both from Clade D1) to 173 km between *M. stankovici* and *M. rugilabris irmengardis*. Euclidian distances in genital morphometric space range from 1.35 in the *M. dofleini dofleini* – *M. kastoriae kastoriae* pair (63.4 km apart), to 42.12 in the *M. lambdaformis welterschultesi* – *M. pallida* pair (22 km apart). Conversely, the *M. rugilabris irmengardis* – *M. dofleini fagorum* pair with a Euclidean distance of 6.62 is separated by 158.3 km.

Linear bivariate regression analyses (Fig. 14) show significant correlations among all 3 datasets in terms of p -values (genetic vs geography: $p = 0.000125$, $R^2 = 8.86\%$;

genetic vs morphometry: $p = 0.002647$, $R^2 = 9.04\%$; morphology vs geography: $p = 0.040476$, $R^2 = 1.91\%$). However, the coefficients of determination (R^2) are below 10%, indicating that only 9.704% of the morphological variance is explained by genetic distance and 1.91% by geographic distance. At the same time, only the 8.86% of the genetic distance is explained by geographic distance.

Syntopic *Montenegrina* taxa: is there a signal for genital character displacement?

Using quantitative data of the genital morphology of *Montenegrina*, we addressed the question if and how far the ecological character displacement phenomenon (PFENNIG & PFENNIG 2012) can be detected between the genitalia of syntopic/non-syntopic *Montenegrina* taxa. For 4 pairs of syntopic taxa morphological data was available in the present study. Table 8 provides information about localities of these taxon pairs. Figure 15 shows the PCA scatter plot based on genital measurements of all 259 specimens, with the 4 pairs of syntopic taxa are highlighted by grey shading. The average Euclidean distance of genital morphology among all *Montenegrina* specimens is 10.2. The 4 pairs of syntopic taxa are joined by lines. The Euclidean distances between the syntopic *M. minuscula* and *M. skipetarica skipetarica* (55.60), *M. skipetarica skipetarica* and *M. soosi* (60.20), and *M. selcensis* and *M. miraka errans* (34.90) were found to be quite high. Whereas for the fourth pair, *M. gracilis barinai* and *M. ochridensis ochridensis* (14) it was just a little higher than the average distance of the genus (10.20). Three out of 4 syntopic pairs of taxa analysed showed a

genital morphometric Euclidean distance well above the average for the genus *Montenegrina* suggesting character displacement. The apparent high level of homoplasy, implying that morphological differences mainly occur randomly, is in accordance with both the assumption of RCD as well as the non-adaptive radiation hypothesis of GITTENBERGER (1991).

An extended genital anatomical characterisation of the genus *Montenegrina*

DE MATTIA (2020: 699) provided a new genus diagnosis of the external shape and inner sculpturing of the genitalia of *Montenegrina* but the frequencies of the character states were not available at that time. The new data collected for the current study allow us to provide a newer diagnosis that also includes a more detailed description for the various character states as well as their frequencies. Only for the spermatophore, no additional data are available compared to DE MATTIA et al. (2022: 699).

In the diagnosis, the frequency of the character state is given in parentheses ($n = 259$).

External shape and size of genitalia. The **diverticulum** of the bursa copulatrix can either be shorter (~38%) or longer (~52%) than or sometimes (~10%) equally as long

as the BC + SDBC; the DBC is mainly shorter (~98%), longer than (~1%) or equally as long as (1%) the vagina; **vagina** variable in shape, mainly slim cylindrical (~55%) to short and thick (~45%) with intermediate states, shorter (~21%), longer than (~70%), or equally as long as (~9%) the penis; a **vaginal retractor** is present, inserted on the proximal vagina (~85%) end or on the DBC–vagina transition (~15%), respectively; the **penis** is without flagellum, shorter (~70%), longer than (~21%) or equally as long as (~9%) the vagina without a penial appendix or cecum; the **epiphallus** is shorter (~22%), longer than (~73%), or equally as long as (~5%) the penis; the **penial retractor** is not divided.

Internal features of genitalia. The **vaginal pilaster** is mostly present (~92%); the **vagina** is smooth (~19%) or with an inner sculpturing mainly comprising a combination of pleats of different size and texture, arranged in an irregular (~21%), radial (~48%), chevron-like (~2%), or longitudinal/transversal (~8%) direction; the **penis** is completely smooth without (or extremely suffused) ornamentation (~15%), with smooth longitudinal pleats (~24%), with chevron-like pleats (~11%), with fringed longitudinal pleats (~30%), with radial pleats (~14%), with irregular pleats and no pattern visible (3%), or with both longitudinal and radial pleats (~3%); the

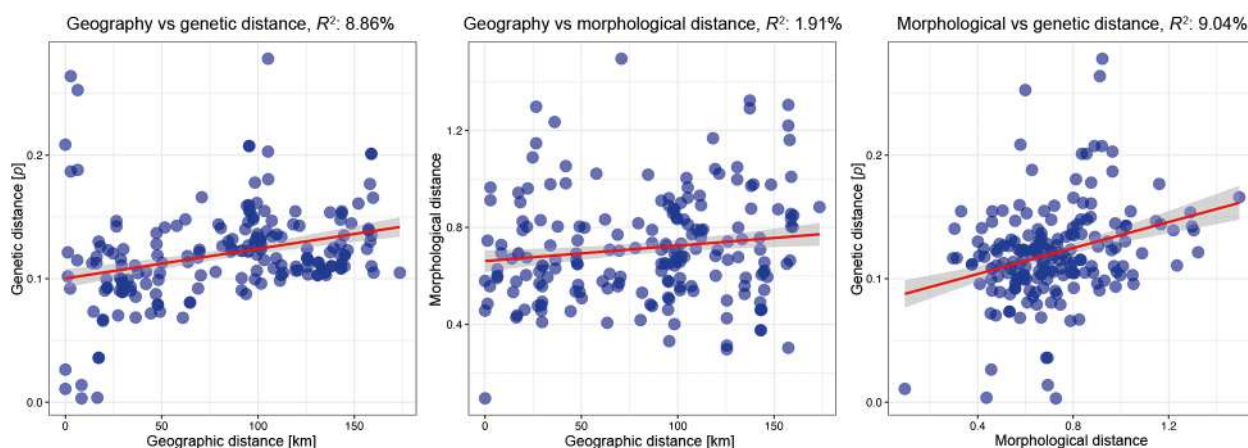


Figure 14. Linear bivariate scatter plots of pairwise distances of the taxa ($n = 23$) belonging to Clades D1 and D2 for each of the 3 distance measures. R^2 values for the linear regressions (red line) and the confidence intervals (grey areas) result from a Mantel test.

Table 8. Four pairs of syntopic taxa within the genus *Montenegrina* analysed in the present study. Modified from FEHER & SZEKERES (2016: 129–130).

	Syntopic taxon pairs	Locality	Habitat
1	<i>M. minuscula</i> / <i>M. skipetarica skipetarica</i>	Albania, Dibër, 3 km W of Qafa Murrë, near Shkëmb i Skenderbeut; 41.6465° N, 020.1898° E	Gorge of river (Lumi i Varoshit), exposed rock surface
2	<i>M. skipetarica skipetarica</i> / <i>M. soosi</i>	Albania, Kukës, 2.5 km N of Bushtricë, Ura e Lapavës (Ura e Lapajve); 41.8949° N, 020.4169° E	Gorge of creek Perroi i Vaut të Cajës (Reka e Caies), exposed rock surface
3	<i>M. gracilis barinai</i> / <i>M. ochridensis ochridensis</i>	Albania, Dibër, Maja e Tremlishit (Maja e Temlës); 41.514° N, 020.316° E	Steep cliffs, exposed rock surface
4	<i>M. selcensis</i> / <i>M. miraka errans</i>	Albania, Shkodër; Shkëmb i Selcës; 40.7480° N, 020.5219° E	Gorge of a river (Lumi i Verbës), exposed rock surface

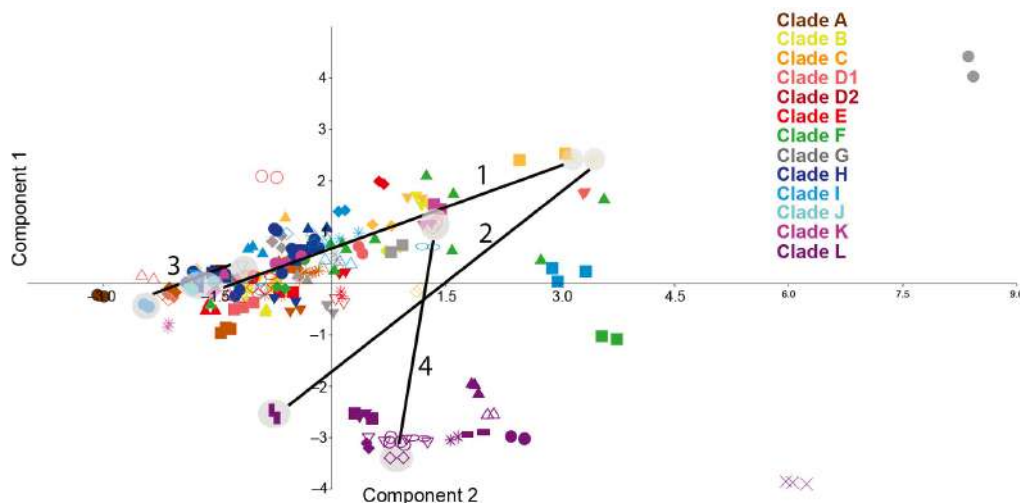


Figure 15. Testing the character displacement by means of the PCA scatter plot (using pairwise Euclidean distances derived from the actual values) of the genital measurements ($n = 259$). Syntenic taxon pairs are highlighted by grey circles and connected by lines (numbers correspond to those in Table 8). *Montenegrina minuscula* and *M. soosi*, despite being both syntopic with *M. skipetarica skipetarica*, they are not reciprocally syntopic, as explained in Table 9. The colour code is described in Table 1.

atrium is simple and totally smooth (~16%), 1 simple or polylobated fold directly originating from the aperture (~39%), 2 or more smooth folds (~43%), or with 3 areas with different sculpturing (1%); the **penial papilla** is mostly present (~89%) but sometimes missing (~11%), globose (~17%), conical (~51%), bilobated or handlike (fringed tip) (~8%), extremely big, occupying almost the whole penial lumen (~1%), or small, slim and elongated (~12%); the **channel of the penial papilla** opens at the tip (~77%) or laterally (~23%); the **epiphallus** has smooth pleats on a smooth background (~68%), smooth pleats on a coarse background (~24%), smooth pleats on a background with a fine chevron-like pattern (~2%), or fringed pleats (~6%).

Discussion

For the first time, this study presents a comprehensive dataset and analysis of both shell and genital traits for almost all species-level taxa of the genus *Montenegrina* in Europe. These data made it possible to obtain the main statistical parameters such as taxon- and clade-specific morphological averages, standard deviations, and value ranges and distributions. These data allow comparing traits among clades (groups of species in the molecular phylogenetic analysis of MASON et al. 2020) as well as among individual taxa.

In addition to quantitative measurements, a qualitative assessment was also carried out by introducing morphological categories for different structural types, both shell and genitalia. This categorization made it possible to provide a new characterizing scheme for genitalia to distinguish taxa of the genus *Montenegrina* which now includes a number of categories of well-defined traits accompanied

by their frequency that will facilitate better description and identification of taxa.

Our quantitative analysis allowed the characterization of taxa, anatomical diagnosis of the genus, insights into character evolution and (in-)dependencies among characters. However, the very time-consuming procedures of measuring the shell and the operations of anatomical investigations of the genitalia precluded a further extension of the sample size. Further studies on selected taxa, using larger sample sizes, should test whether our findings, specifically concerning taxon delimitation and character displacement, can be confirmed. The present morphological approach including genital anatomical traits can be a template for other genera of Clausiliidae to establish common approaches and methodologies to study their taxonomy and systematics.

Correlations among morphological characters

Statistical studies of the relationships among morphological traits allowed us to investigate correlations by means of the linear bivariate regression, either among conchological traits, conchological–genital traits, or among genital traits. Among the different shell parameters, shell height is strongly correlated with several other shell characters. Moreover, SMW shows strong correlation with AH and AW. This implies that these characters are not very suitable for distinguishing species. The other traits, namely the W, OA and the LA, are completely independent of the other shell parameters. For example, the angle of closure of the clausilium with the lunella (LA) shows no correlation with any other shell parameter. In general, the results revealed a high level of homoplasy as specifically evident in the comparisons of syntopic taxa.

Statistically significant correlations were found among the different genital measurements, only between the size of PC and P, E, and V, respectively. The positive PC vs P and PC vs E correlations indicate that both PC components contribute to the increase in PC size and not only one of them. Despite being rather weak, we can deduce the positive correlation between P vs V and P vs E could represent a direct physio-functional relationship between the penial complex and the vagina. It is worth mentioning that the size of empty D, which is a “bladder” with loose, mostly non-muscular walls with a glandular (lytic) function, can greatly change its size when housing the spermatophore. Due to the lack of data, it is impossible to test the hypothesis that a big spermatophore corresponds to a big E.

Tests for correlations of measurements between genital and shell morphology revealed that a large shell, whether in height or in other characters such as SMW or BWH, does not at all correspond to large genitalia or to large size of any of its parts. This lack of correlation between shell and genitalia sizes might suggest that these 2-character complexes are possibly subject to independent selective pressures. The shell, by its very nature and function, could be more influenced by environmental and (micro)climatic factors. At the same time the size (as well as shape and/or structure) of the genitalia could probably be more determined by an evolutionary decoupling as a result of random drift, that is, morphological divergence due to isolation.

Differentiation of taxa and phylogenetic signal

The comprehensive analysis of the whole genus presented here that the many taxa overlapped in the scatter plots using morphometrics, although specimens belonging to the same taxon mostly cluster together in both the PCA scatter plot and the NJ clustering tree. This was not observed at the level of the exemplary Clades D1 and D2, where the taxa were clearly distinguishable based on morphological traits, both of the shell and genitalia, as illustrated in the PCA.

When comparing the phylogenetic signals at the genus-level, the incongruence of the morphometric trees presented here and the molecular phylogenetic tree (MASON et al. 2020) is striking. Moreover, the morphological distances between taxa by no means reflects their distance in molecular phylogenetic reconstruction. Thus, very similar genital morphology (both in shape and internal sculpture) in phylogenetically distant *Montenegrina* taxa may rather be homoplasy than a result of evolutionary constraints.

We analysed in more detail, in the example of Clades D1–D2, the incongruence between phylogenetic reconstruction based on DNA sequences and morpho-clades, indicating that morphology generally lacks phylogenetic signal. These results should, however, be further confirmed

by additional multivariate analysis with a larger number of samples for each taxon. The interesting result that there is only a very weak correlation between geographical and morphological distances (Fig. 14), as shown with clades D1 and D2, where phylogenetically distant taxa show great morphological convergence, is underlined by the low consistency indices. This is supporting the non-adaptive radiation hypothesis proposed for another clausiliid genus (*Albinaria* Vest, 1867, GITTENBERGER 1991) and later confirmed by FEHÉR et al. (2018). Noting the apparent general uniformity of the autecology of *Montenegrina* populations (FEHÉR & SZEKERES 2016: 13), it was already discussed by DE MATTIA et al. (2020: 805) that morphological and genetic differentiation resulting from isolation plus time might be dominated by drift. The ordination and the clustering analyses of morphological characters performed to test this assertion did not reveal any evidence for adaptive character evolution which is also reflected by the high level of homoplasy.

Homoplasy of both shell and genital traits does not invalidate the fundamental importance of morphological characters for the identification of taxa, as demonstrated by the processing of NJ quantitative and qualitative trees shown in Figures 12 and 13, in detail for Clades D1 and D2. In the quantitative and qualitative NJ trees illustrated in Figures S10 and S11, when the entire dataset is used, the few characters used do resolve (apart from very few cases such as *M. drimical/radicale/plenostoma*) the taxa analysed in a satisfactory manner. By adding more characters (both quantitative and qualitative) we expect to see a further refinement of the separation of taxa by morphological means through statistical analysis.

Considering the lack of phylogenetic information of genital and shell characters, the importance of a molecular phylogenetic framework with regard to character changes (i.e. status, character combinations), as well as systematics and nomenclature, becomes apparent.

Character displacement

The incongruence between molecular phylogeny and morphological similarities was observed in other land snails, among them representatives of the subfamily Alopiinae (GIOKAS 2000, UIT DE WEERD & GITTENBERGER 2004). The finding, that even some closely related (and geographically close) taxa are highly different regarding shell and genital morphology, raised the question of character displacement. Unfortunately, only few of the more than 100 taxa of *Montenegrina* live in strict syntopy (sharing the same limestone cliffs and boulders where populations of the 2 taxa intermingle; see FEHÉR & SZEKERES 2016: 128 ff.). Due to the scarcity of available data, it is difficult to test for ecological character displacement (ECD), as reported, for example, by GRANT & GRANT (2014) for Galapagos finches, where exploitation of different food resources is

easily identifiable. It could be hypothesized that 2 syntopic species of *Montenegrina* have specialised on the exploitation of, for example, different species of endolithic lichens; however, it remains unclear why this should result in different shell and/or genital morphology.

Our results rather imply reproductive character displacement (RCD): natural selection acting against interspecific mating of species that got in secondary contact by displacing characters involved in reproduction. Such sympatric reinforcement of prezygotic isolation (DOBZHANSKY 1940, BROWN & WILSON 1996) is a plausible mechanism increasing morphological divergence of the 2 species, but not their genetic distance. Three out of 4 syntopic pairs of taxa analysed showed a genital morphometric Euclidean distance well above the average for the genus *Montenegrina* suggesting character displacement. The apparent high level of homoplasy, implying that morphological differences mainly occur randomly, is in accordance with both the assumption of RCD as well as the non-adaptive radiation hypothesis of GITTENBERGER (1991). Whereas the number of available samples and data are still insufficient for robust conclusions, the discovery of additional syntopic populations of taxa with wider distribution ranges would be helpful to test the RCD in the genus *Montenegrina*.

Acknowledgements

The huge amount of data originated from the huge study material provided by many collectors, all of them listed in FEHÉR & SZEKERES (2016). We are grateful to Miklos Szekeres for the shell traits categorization and useful suggestions. We are grateful to Julia Sigwart for helpful suggestions and corrections. The first author is grateful to Jessica Macor for her continuous help and support. We are greatly indebted to 2 anonymous reviewers, who contributed substantial comments and recommendations to the first version of the manuscript. This study was partly funded by the Austrian Research Fund (FWF project P 26581-B25).

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10.1 Publication 3 supplementary information

Supplementary information

Quantitative and qualitative statistical analyses of the shell and the genital traits of the doorsnail genus *Montenegrina* O. Boettger, 1877 (Gastropoda: Clausiliidae).

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Supporting figures

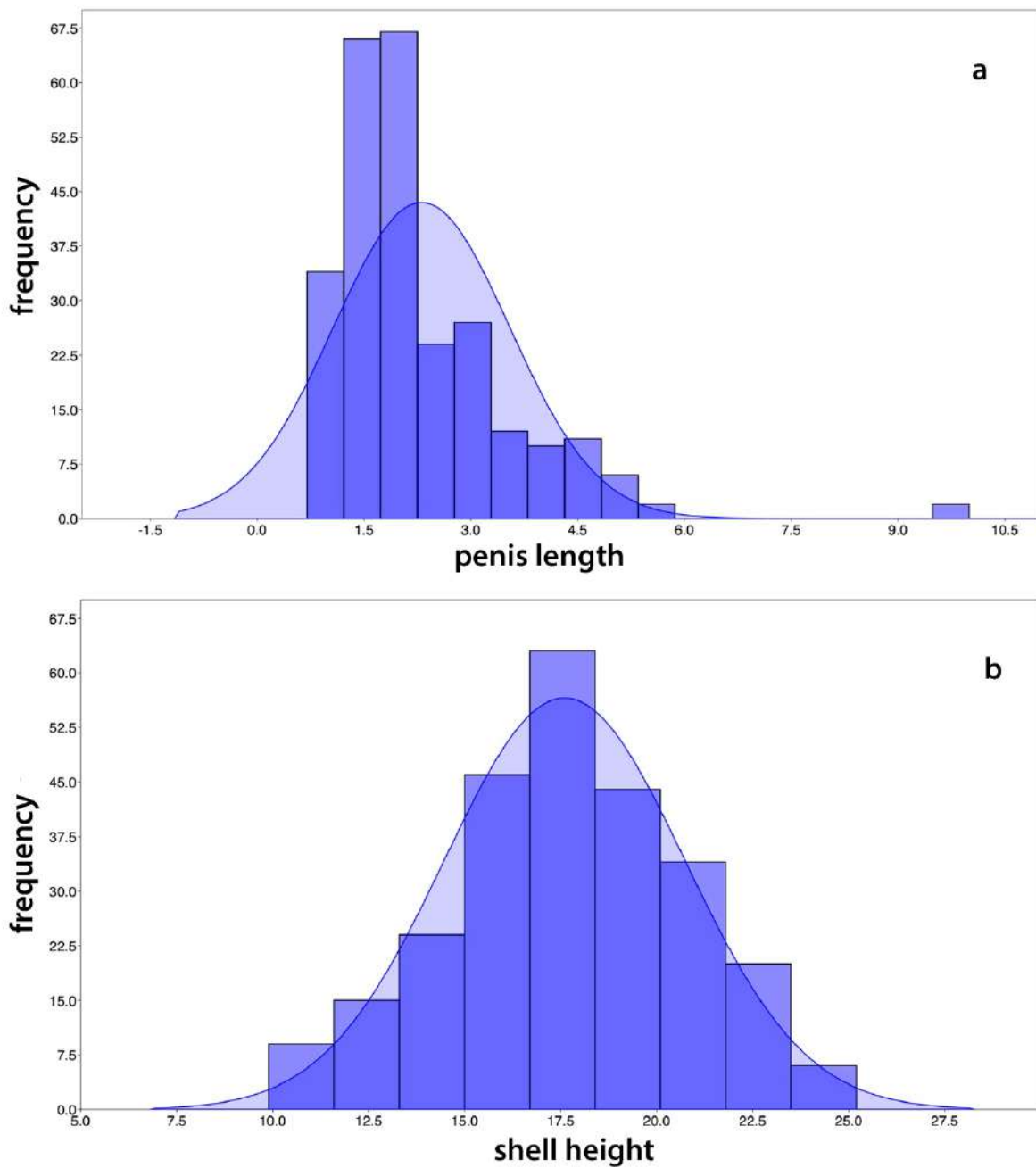


Figure S1. Distributions of the measurements of the shell height SH (a) and the penis length P (b) over the whole genus *Montenegro* ($n = 259$). Neither set of measures has a distribution that satisfies a statistical test of a normal distribution (Table S1).

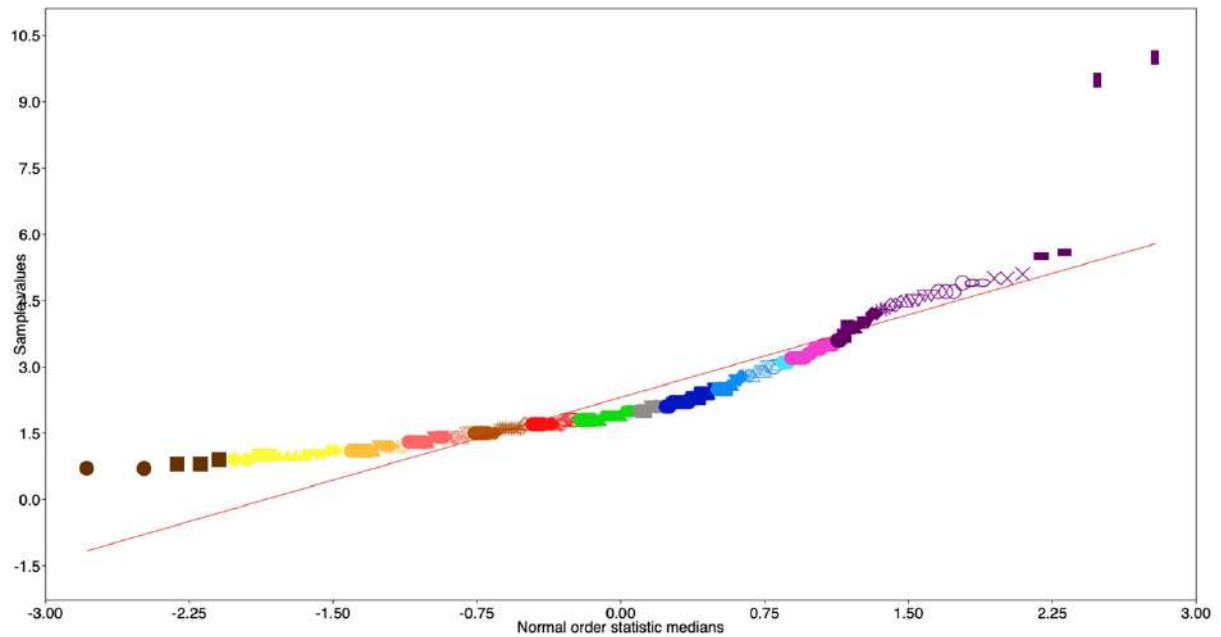


Figure S2. Normal probability plot of the measurements of the penis length P for the whole genus ($n = 259$). The consistent deviation of the distribution of the points from the normality line does not meet the normal distribution criteria of the Chamber test (Chamber et al. 1983). The normal order of statistic medians goes from -2.5463 to 2.5463. To each symbol corresponds a taxon. Colour code of clades: Clade A: brown, Clade B: greenish yellow, Clade C: light orange, Clade D1: salmon, Clade D2: dark red, Clade E: red, Clade F: green, Clade G: grey, Clade H: dark blue, Clade I: blue, Clade J: light blue, Clade K: violet, Clade L: dark violet.

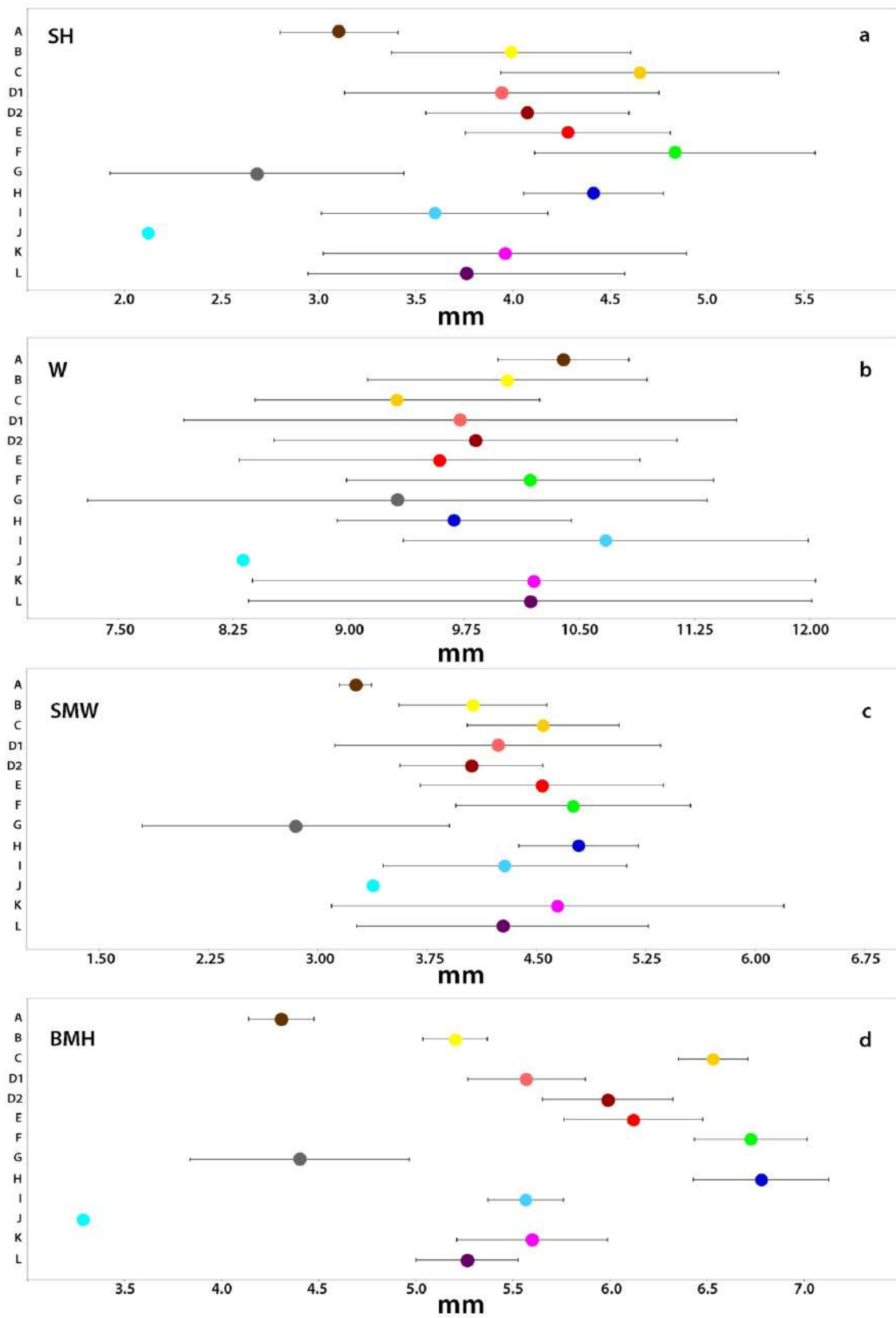


Figure S3. Plots of arithmetic mean \pm standard deviation for (a) shell height (SH), (b) number of whorls (W), (c) shell max width (SMW) and (d) body whorl height (BWH) shell traits, limited to the clade level ($n = 259$)

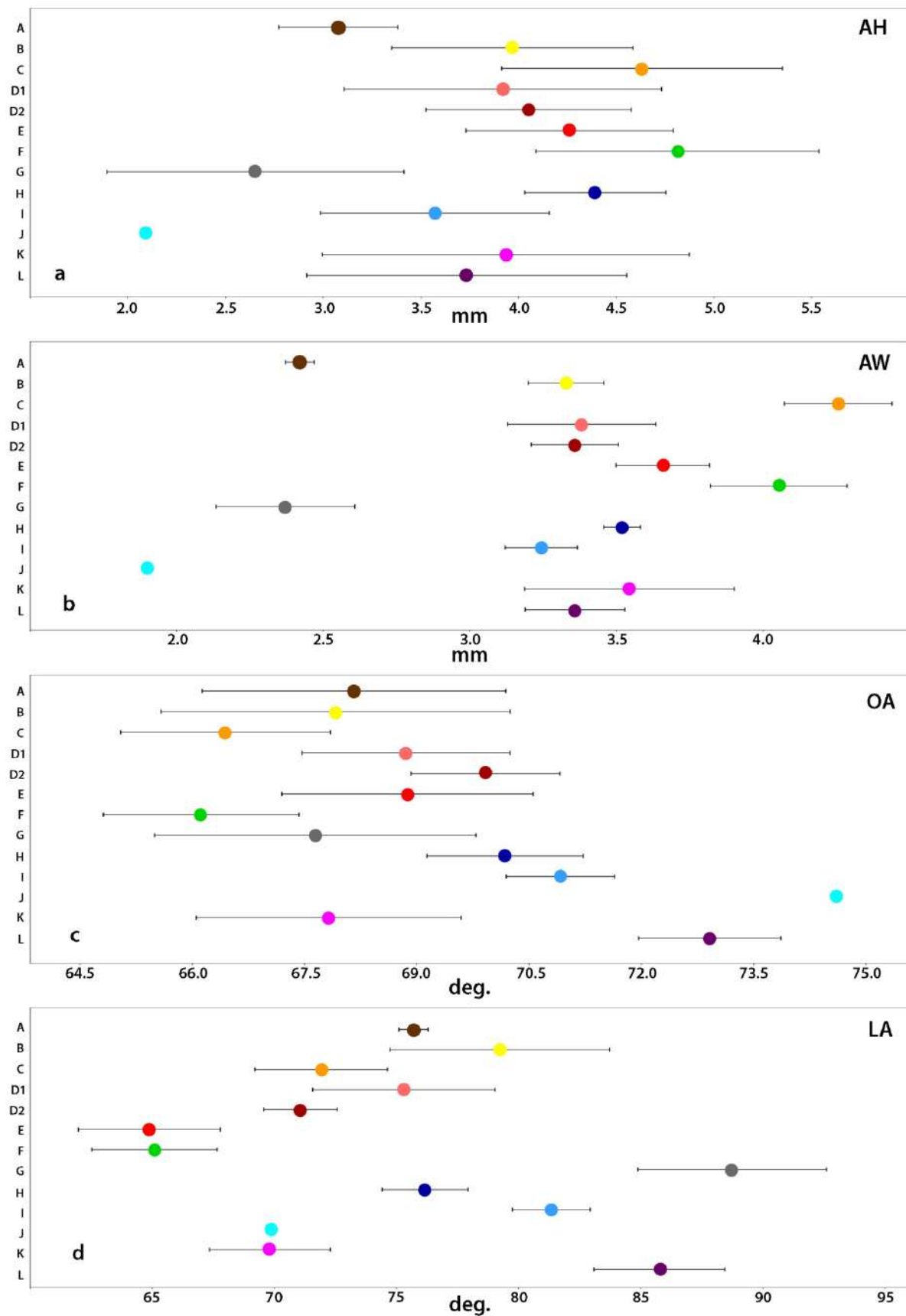


Figure S4. Plots of arithmetic mean \pm standard deviation for shell traits at the clade level ($n = 259$): (a) aperture height (AH), (b) aperture width (AW), (c) ornamentation angle (OA) and (d) lunella angle (LA).

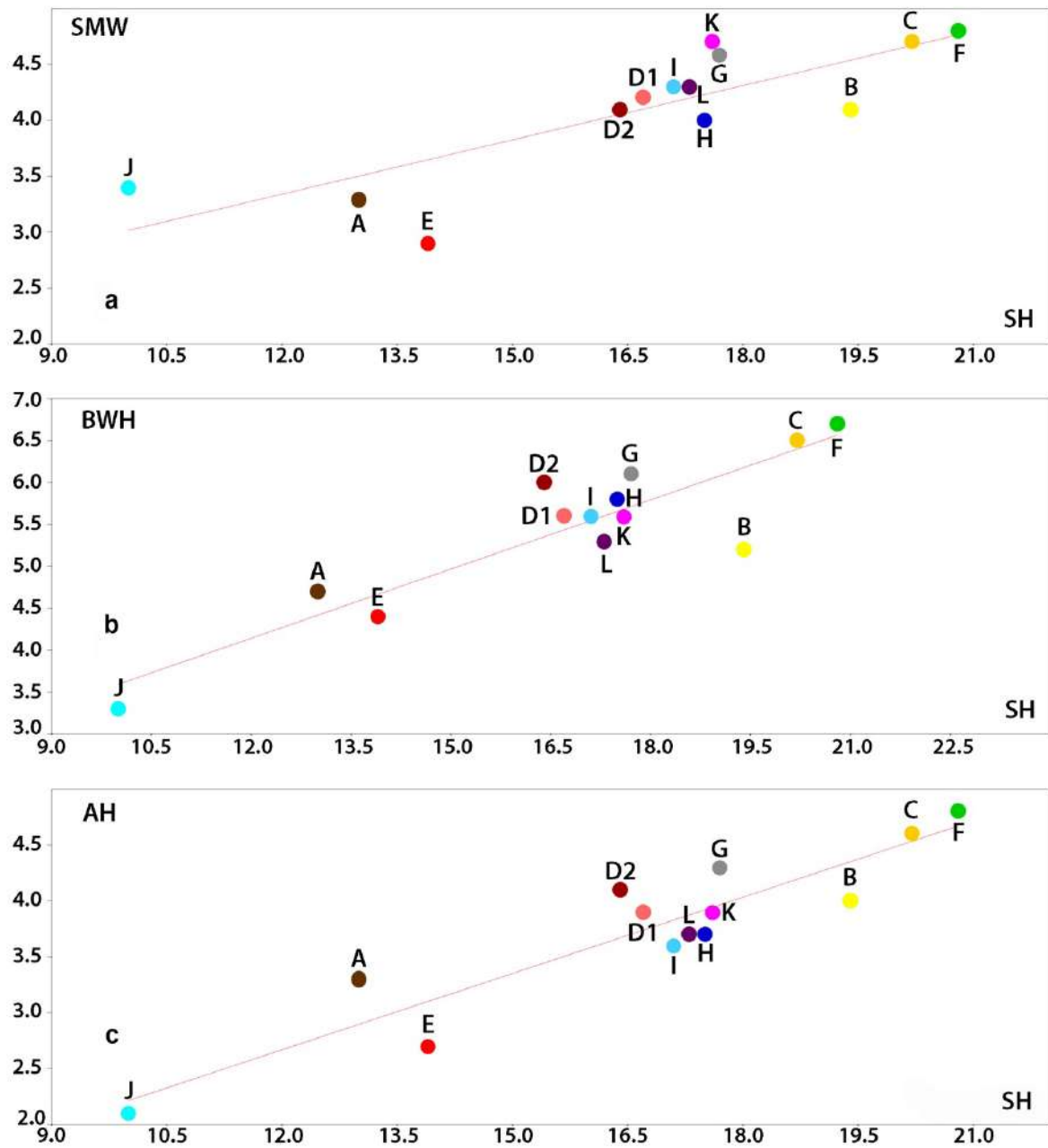


Figure S5. Linear bivariate regression plots at clade level between (a): SH vs SMW (shell maximum width), $R^2=67.2\%$, $t=4.748$, $p(\text{corr})=0.0009$; (b): SH vs BWH (body whorl height), $R^2=36.8\%$, $t=6.740$, $p(\text{corr})=0.0002$; (c): SH vs AH (aperture height), $R^2=85.2\%$, $t=7.796$, $p(\text{corr})=0.0001$.

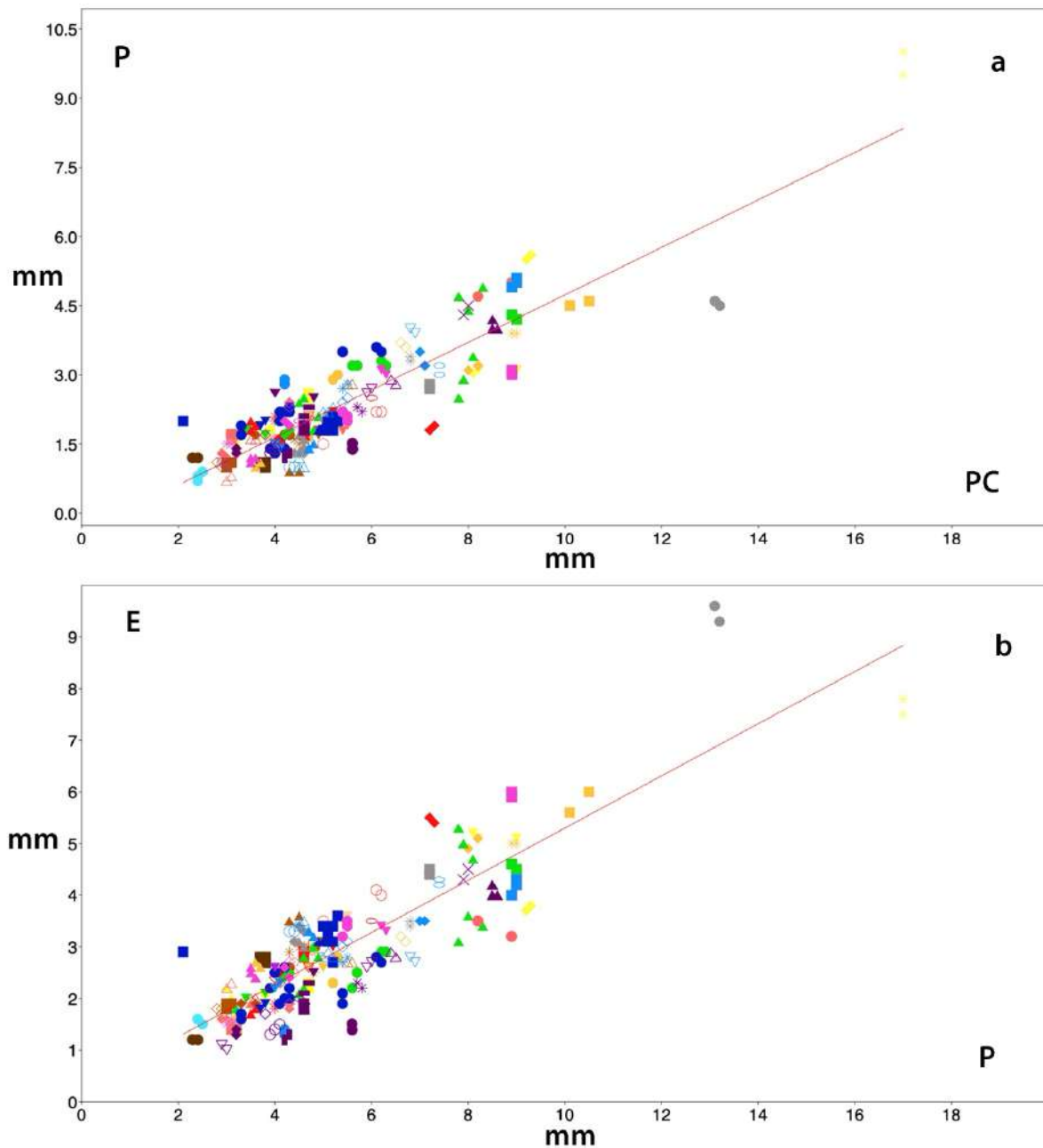


Figure S6. Linear bivariate regression plot testing correlations ($n = 259$) at taxon level between lengths of (a): V (vagina) vs PC (penial complex) $R^2=60.6\%$, $t=13.881$, $p(\text{corr})=0.0001$; (b): E (epiphallus) vs P (penis), $R^2=33.7\%$, $t=7.971$, $p(\text{corr})=0.0001$. To each symbol corresponds a taxon. Colour code of clades: Clade A: brown, Clade B: greenish yellow, Clade C: light orange, Clade D1: salmon, Clade D2: dark red, Clade E: red, Clade F: green, Clade G: grey, Clade H: dark blue, Clade I: blue, Clade J: light blue, Clade K: violet, Clade L: dark violet.

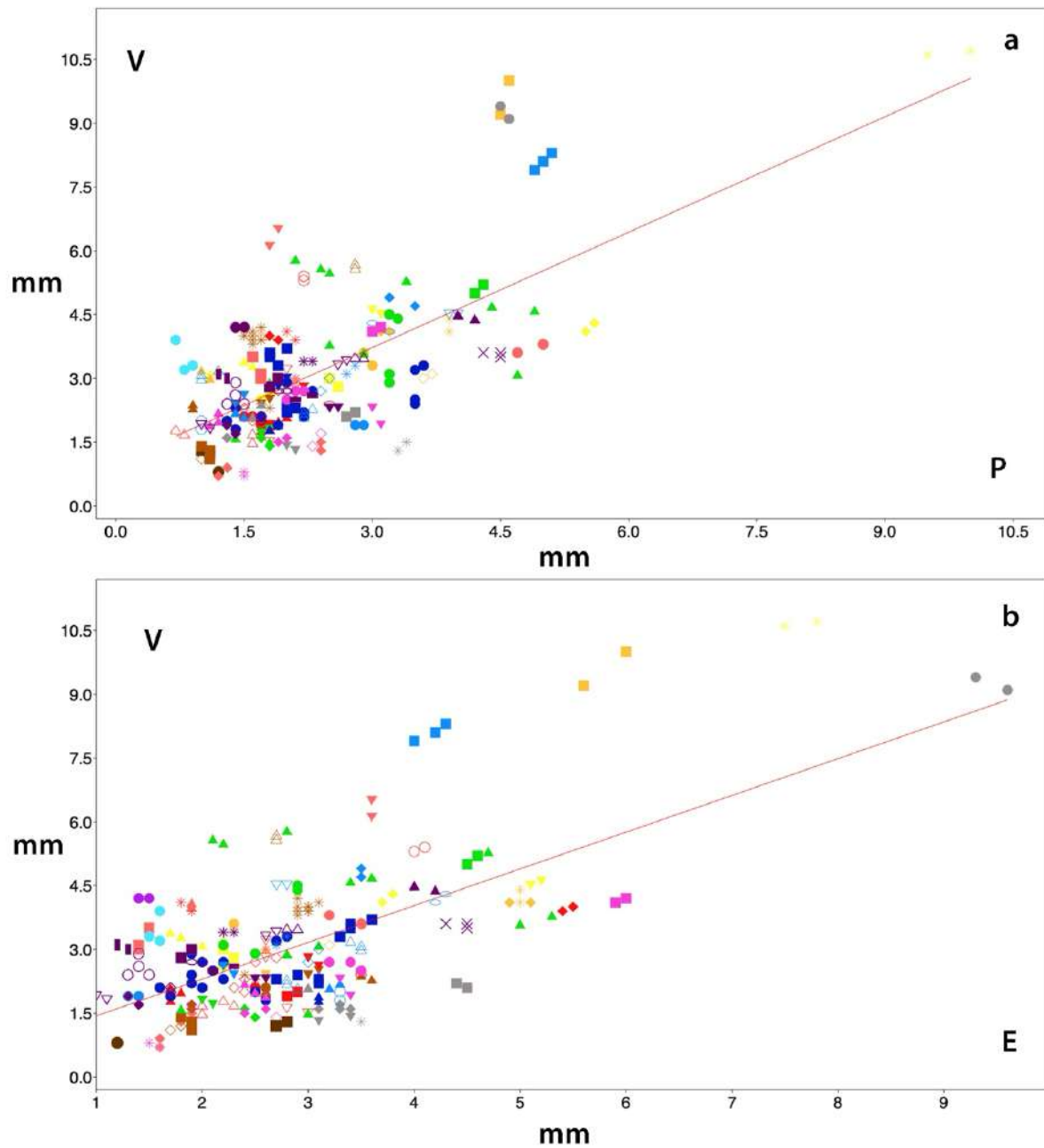


Figure S7. Linear bivariate regression plot testing correlations ($n = 259$) at taxon level between lengths of (a): P (penis) vs V (vagina), $R^2=41.9\%$, $t = 2.82$, $p(\text{corr})=0.0157$; (b): E (epiphallus) vs V, $R^2=65.3\%$, $t = 4.128$, $p(\text{corr})=0.0007$. To each symbol corresponds a taxon. Colour code of clades: Clade A: brown, Clade B: greenish yellow, Clade C: light orange, Clade D1: salmon, Clade D2: dark red, Clade E: red, Clade F: green, Clade G: grey, Clade H: dark blue, Clade I: blue, Clade J: light blue, Clade K: violet, Clade L: dark violet.

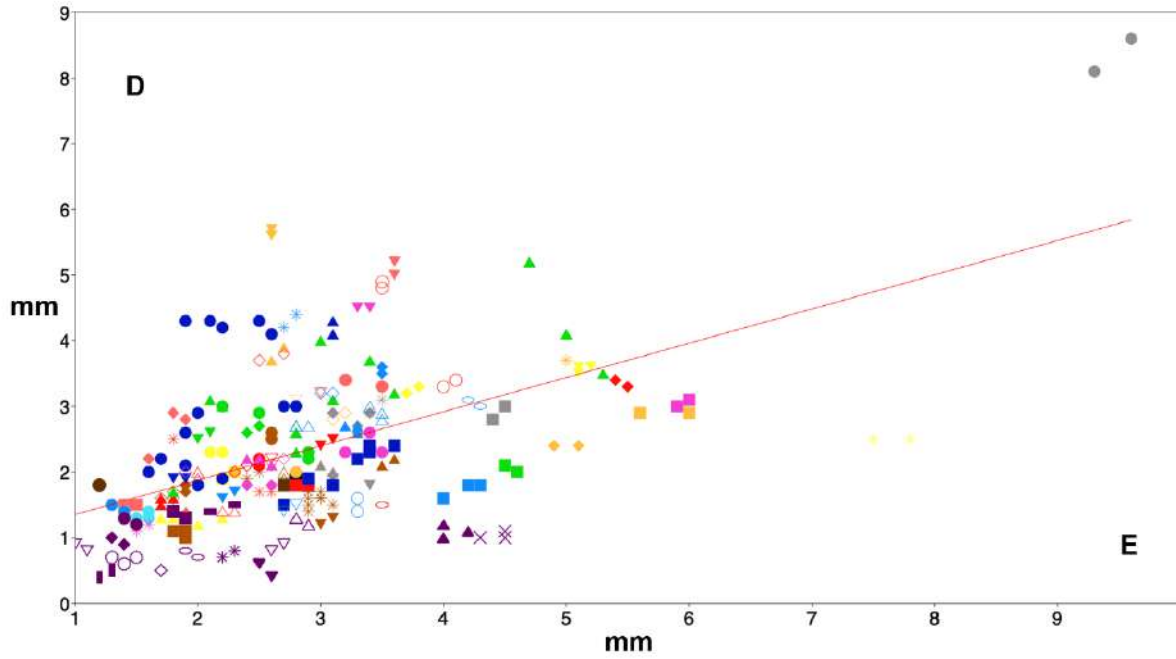


Figure S8. Linear bivariate regression plot testing correlations ($n = 259$) at taxon level between lengths of E (epiphallus) vs D (diverticulum), $R^2=32.1\%$ $t=6.993$ $p(\text{corr})=0.0001$. To each symbol corresponds a taxon. Colour code of clades. Clade A: brown, Clade B: greenish yellow, Clade C: light orange, Clade D1: salmon, Clade D2: dark red, Clade E: red, Clade F: green, Clade G: grey, Clade H: dark blue, Clade I: blue, Clade J: light blue, Clade K: violet, Clade L: dark violet.

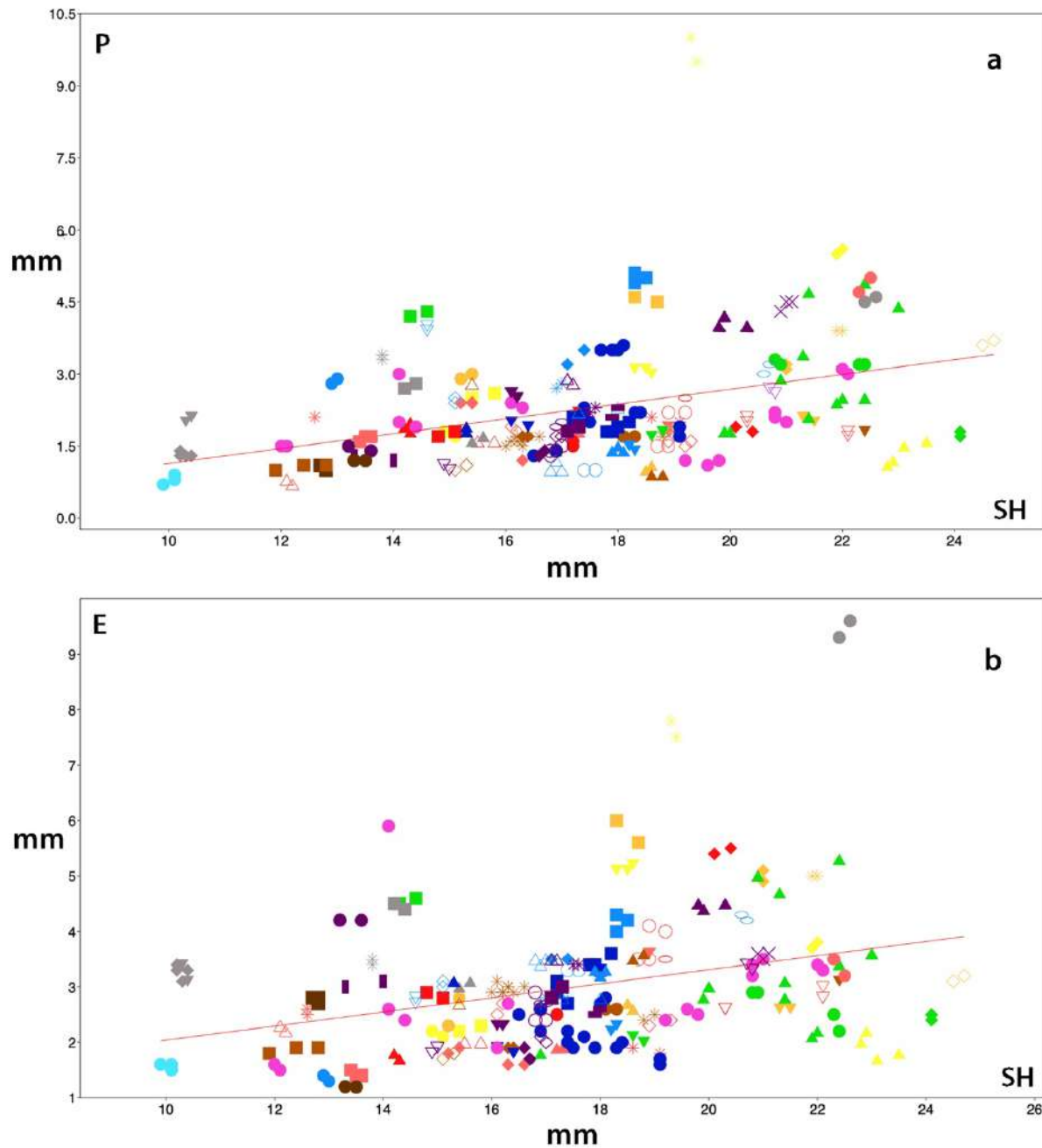
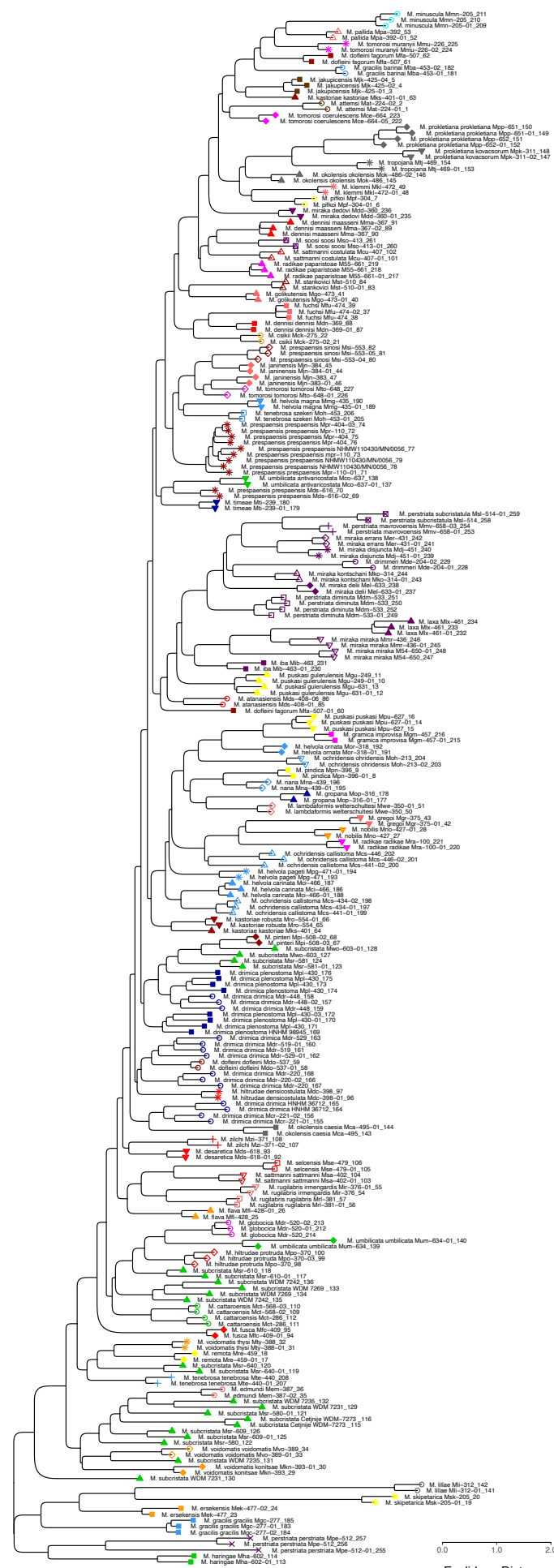


Figure S9. Linear bivariate regression plot testing correlations ($n = 259$) at taxon level between lengths of (a) P (penis) vs SH (shell height), $R^2=66.9\%$, $t=4.722$, $p(\text{corr.})=0.0002$; (b) E (epiphallus) vs SH, $R^2=29.8\%$, $t=2.163$, $p(\text{corr.})=0.0506$. To each symbol corresponds a taxon. Colour code of clades: Clade A: brown, Clade B: greenish yellow, Clade C: light orange, Clade D1: salmon, Clade D2: dark red, Clade E: red, Clade F: green, Clade G: grey, Clade H: dark blue, Clade I: blue, Clade J: light blue, Clade K: violet, Clade L: dark violet.



Euclidean Distance

Figure S10. NJ tree based on Euclidean distances from quantitative traits including measurements of both shell and genital parts of 259 individuals of the clades A, B, C, D1, D2, E, F, G, H, I, J, K, L of the genus *Montenegrina*.

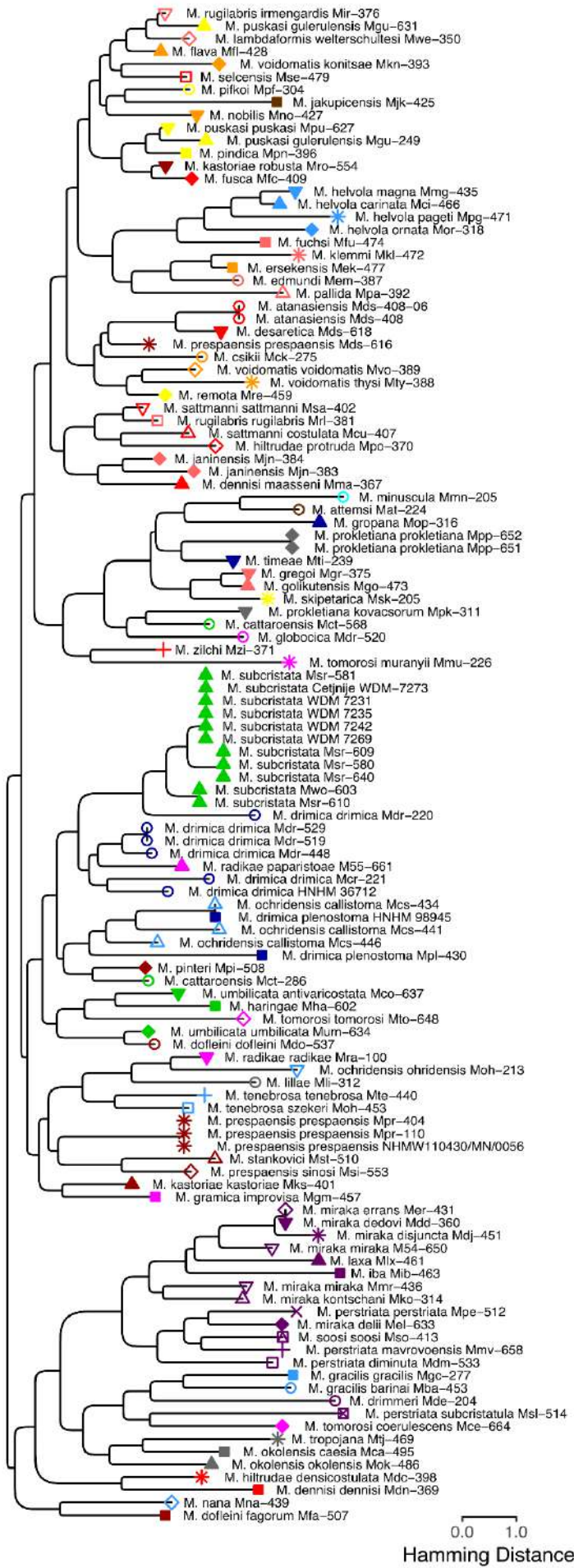


Figure S11. NJ tree using Hamming distances from qualitative measurements of traits in 129 individuals of the clades A, B, C, D1, D2, E, F, G, H, I, J, K, L of the genus *Montenegrina*.

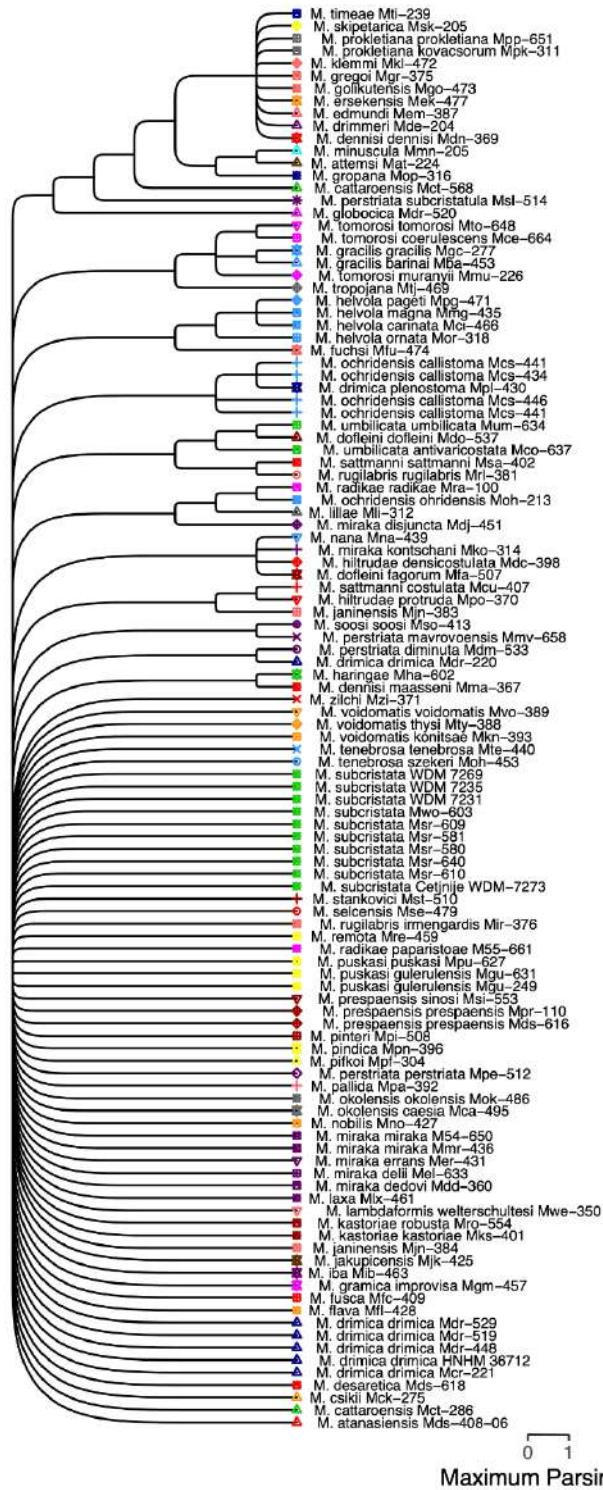


Figure S12. MP strict consensus tree of 60,625 best trees based on qualitative characters. The tree contains a high number of unresolved nodes, while the few clades apparent do not reflect phylogenetic relationships.

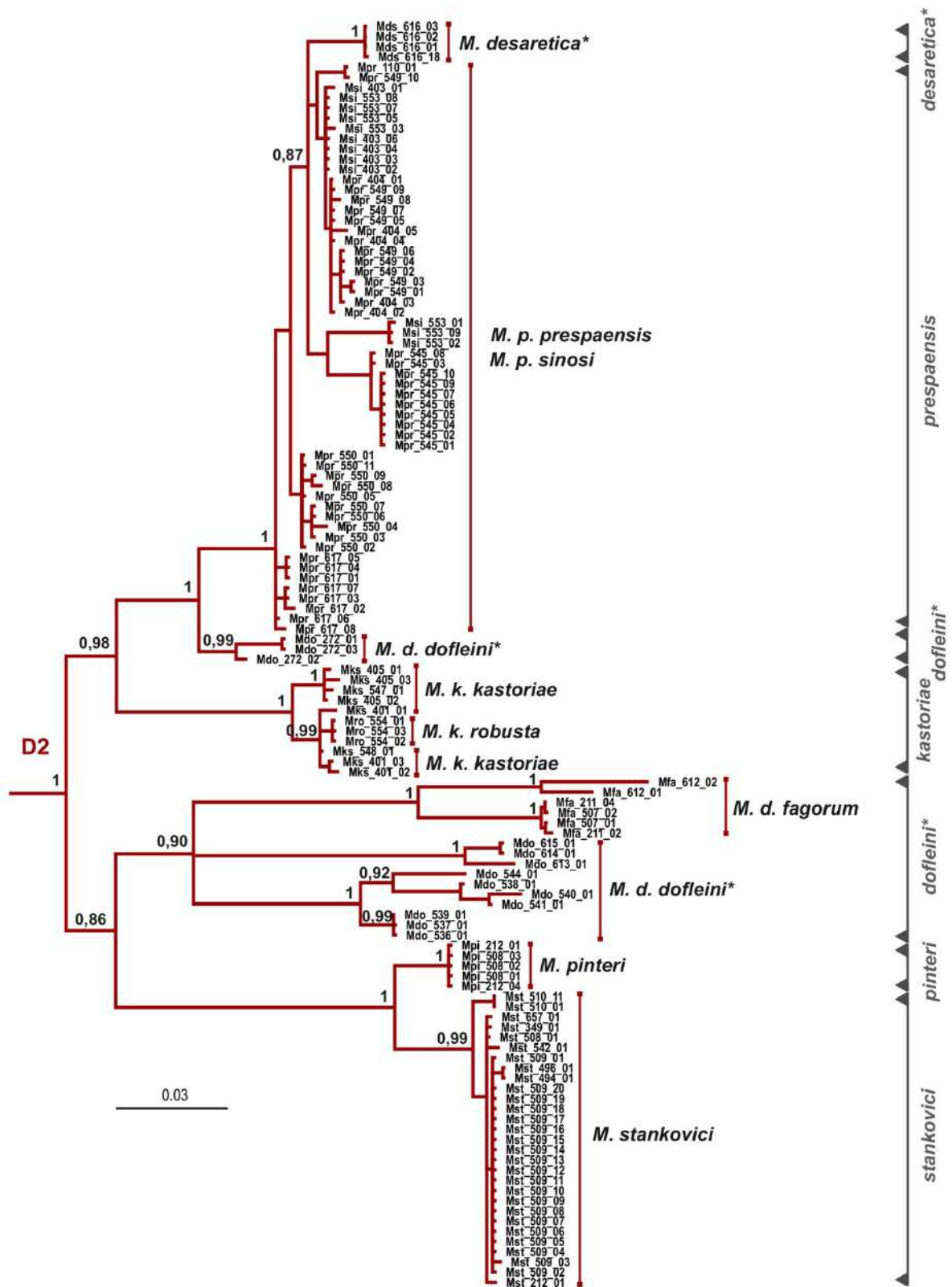


Figure S14. BI (Bayesian Inference) trees of the Clade D2 with the up-to-date nomenclature as reported by MASON et al. (2023).

Supporting tables

Table S1. Normality test of the measurements of data pooled at the genus level for morphometric parameters: shell height (SH), number of whorls (W), shell maximum width (SMW), body whorl height (BWH), aperture height (AH), aperture width (AW), ornamentation angle (OA), lunella angle (LA), penis (P), epiphallus (E), vagina (V), free oviduct (FO), bursa copulatrix (BC) and diverticulum (D) with Shapiro-Wilk (*W*) and Liliefors (*L*) values and *p-values* ($n = 259$). The *W* index, the *p-values* and the *L* index reveal that the measurements are not normally distributed.

	W	L	<i>p-value</i> (normal) cutoff $\alpha=0.05$
SH	0.9876	0.0472	0.0166
W	0.9804	0.0960	0.0001
SMW	0.9902	0.0738	0,0001
BWH	0.9763	0.0908	0.0001
AH	0.9901	0.0565	0.0398
AW	0.9775	0.0817	0.0001
OA	0.9820	0.0865	0.0001
LA	0.9657	0.0763	0.0001
P	0.8150	0.1754	0.0001
E	0.8545	0.1527	0.0001
V	0.8281	0.1329	0.0001
FO	0.8593	0.1478	0.0001
BC	0.8904	0.1629	0.0001
D	0.8858	0.1105	0.0001

Table S2. Loadings of the PCA scatter plot based on shell measurements depicted in Figure 5.

	PC1	PC2
SH	0.41226	0.17638
W	0.17485	0.64348
SMW	0.42613	0.016503
AH	0.46174	-0.03225
AW	0.45096	0.015421
BWH	0.41095	-0.13957
OA	-0.12128	0.33272
LA	-0.13316	0.65045

Table S3. Loadings of the PCA scatter plot PCA scatter plot based on genital measurements depicted in Figure 6.

	PC1	PC2
P	0.29373	-0.55237
E	0.40342	0.41158
V	0.40459	0.24089
FO	0.41564	-0.33585
DBC	0.43966	-0.16459
D	0.21035	0.57188
BC	0.4207	-0.022802

Table S4. Loadings of the PCA scatter plot PCA scatter plot based on both shell and genitalia measurements depicted in Figure 7.

	PC1	PC2
SH	0.40666	0.015786
W	0.19313	0.18403
SMW	0.38454	-0.1237
AH	0.41422	-0.17094
AW	0.41161	-0.11295
BWH	0.37079	-0.17432
OA	-0.10475	0.16262
LA	-0.10679	0.23768
P	0.019123	0.40006
E	0.18592	0.25391
V	0.17653	0.26842
FO	0.10813	0.41708
DBC	0.041025	0.44228
D	0.20843	0.034191
BC	0.16029	0.35775

Table S5. Loadings of the PCA scatter plot based on shell measurements depicted in Figure 8.

	PC1	PC2
SH	0.5069	-0.19213
W	0.37359	-0.49806
SMW	0.39689	0.16818
AH	0.39202	0.14277
AW	0.41092	0.18442
BWH	0.32811	0.48043
OA	-0.11735	0.6327
LA	0.044735	0.035095

Table S6. Loadings of the PCA scatter plot PCA scatter plot based on genital measurements depicted in Figure 9.

	PC1	PC2
P	0.041298	-0.0015511
E	0.28647	-0.054733
V	0.5018	0.5364
FO	0.28234	0.16179
DBC	0.12053	0.22543
D	0.4898	-0.7882
BC	0.5747	0.10403

Table S7. Loadings of the PCA scatter plot PCA scatter plot based on both shell and genitalia measurements depicted in Figure 10.

	PC1	PC2
SH	0.44642	-0.21798
W	0.33053	-0.34114
SMW	0.38348	0.067707
AH	0.3378	-0.13286
AW	0.35372	-0.15282
BWH	0.28093	0.033721
OA	-0.08257	0.25697
LA	0.066198	0.04047
P	0.041542	0.013924
E	0.16057	0.13351
V	0.11031	0.56482
FO	0.12886	0.26595
DBC	0.0055905	0.17739
D	0.32384	0.17245
BC	0.23209	0.50273

Table S8. Loadings of the PCA scatter plot PCA scatter plot based on both shell and genitalia measurements of the Clade D1 only depicted in Figure 11.

	PC1	PC2
SH	0.4012	-0.1913
W	0.34852	-0.35001
SMW	0.40799	0.067386
AH	0.30064	-0.16167
AW	0.32488	-0.21842
BWH	0.14756	0.25201
OA	-0.024407	0.24646
LA	0.13234	-0.18198
P	0.044388	-0.008094
E	0.19336	0.012683
V	0.15041	0.49097
FO	0.17857	0.25061
DBC	0.061773	0.17592
D	0.37938	0.029813
BC	0.27146	0.51887

Table S9. Nomenclature and change of systematics of the taxa belonging to Clades D1 and D2 as reported in DE MATTIA et al. (2020). Taxa in bold are those that changed with regard to FEHÉR & SZEKERES (2016).

FEHÉR & SZEKERES 2016	DE MATTIA, FEHÉR, MASON & HARING 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
<i>Montenegrina fuchsi pallida</i> Fauer, 1993	<i>Montenegrina pallida</i> Fauer, 1993
<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
<i>Montenegrina rugilabris golikutensis</i> Fehér & Szekeres, 2016	<i>Montenegrina golikutensis</i> Fehér & Szekeres, 2016
<i>Montenegrina rugilabris gregoi</i> Fehér & Szekeres, 2016	<i>Montenegrina gregoi</i> Fehér & Szekeres, 2016
<i>Montenegrina rugilabris irmengardis</i> Klemm, 1962	<i>Montenegrina rugilabris irmengardis</i> Klemm, 1962
<i>Montenegrina rugilabris welterschultesi</i> Fehér & Szekeres, 1999	<i>Montenegrina lambdaformis welterschultesi</i> Fehér & Szekeres, 1999
<i>Montenegrina rugilabris lambdaformis</i> Reischütz & Sattmann, 1990	<i>Montenegrina lambdaformis lambdaformis</i> Reischütz & Sattmann, 1990
<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
<i>Montenegrina dofleini pinteri</i> Nordsieck, 1974	<i>Montenegrina pinteri</i> Nordsieck, 1974
<i>Montenegrina dofleini prespaensis</i> Nordsieck, 1988	<i>Montenegrina prespaensis prespaensis</i> Nordsieck, 1988
<i>Montenegrina dofleini sinosi</i> Páll-Gergely, 2010	<i>Montenegrina prespaensis sinosi</i> Páll-Gergely, 2010

<i>Montenegrina dofleini wagneri</i> Szekeres, 2006	<i>Montenegrina wagneri</i> Szekeres, 2006
<i>Montenegrina hiltrudae robusta</i> Nordsieck, 2009	<i>Montenegrina kastoriae robusta</i> Nordsieck, 1972