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Genera, subgenera and species of the Cochlostomatidae (Gastropoda, Caenogastropoda, Cochlostomatidae)

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The generic taxonomy of the family Cochlostomatidae (Gastropoda, Caenogastropoda) is revised on the basis of shell and genital tract morphology, and molecular data. Five genera are distinguished, viz. *Imerezia* gen. nov., *Toffolettia* Giusti, 1971, *Rhabdotakra* A.J. Wagner, 1897, *Obscurella* Clessin, 1889, and *Cochlostoma* Jan, 1830. These taxa differ in details of the genitalia and the shells. They are well separated clades according to the DNA analyses of the nuclear *H3* and mitochondrial *16S* ribosomal markers. *Imerezia* gen. nov. and *Toffolettia* are monotypic. *Obscurella* has radiated in SW Europe, mainly in the Pyrenees and the Cantabrian mountains. *Cochlostoma* shows a vicariant radiation in central and eastern Europe, mainly in the Alps, the Appennines, the Dinarids and the Greek mountains. *Cochlostoma* is by far the most speciose genus. It is subdivided here into 8 subgenera, viz. *Cochlostoma* s. str., *Turritus* Westerlund, 1883, *Auritus* Westerlund, 1883, *Eupomatias* Wagner, 1897, *Lovcenia* subgen. nov., *Dalfreddia* subgen. nov., *Wagneriola* subgen. nov., and *Clessiniella* subgen. nov., corresponding with clades resulting from the DNA analysis. Most of these subgenera can also be diagnosed on the basis of a combination of features of the female genital tract and shell morphology.

Some European and most of the African species could not be investigated because of lack of material for dissection and sequencing. The genus *Obscurella* especially needs to be studied in more detail.

Key words: Gastropoda, Caenogastropoda, Cochlostomatidae, taxonomy, nomenclature, genital tract, molecular phylogeny, *16S* mtDNA, histone *H3* nDNA.

INTRODUCTION

The family Cochlostomatidae Kobelt, 1902 (Gastropoda, Caenogastropoda) comprises gonochoric, terrestrial, mainly rock-dwelling snails, inhabiting the calcareous mountain ranges surrounding the Mediterranean Basin. It was considered a monotypic family until Giusti (1971) introduced the genus *Toffolettia* for the species that was known before as *Cochlostoma striolatum* (Porro, 1840). Later on, Raven (1990) proposed to rise *Obscurella* to the genus level but his opinion was not accepted and recent checklists (AnimalBase Project Group, 2005; Bank, 2013) still mention only two genera, viz. the speciose *Cochlostoma* Jan, 1830, and the monotypic *Toffolettia* Giusti, 1971 (considered a junior synonym of *Striolata* Wagner, 1897, by some authors). This family has been judged as ''A modern revision .. is needed ..'' by Manganelli & Giusti (1997: 202) and as ''problematic'' by Gofas (2001: 1277). Maybe the generic taxonomy of the Cochlostomatidae species has hitherto been neglected because of their homogeneous, poorly diagnosable shell morphology, together with vague original descriptions, undefined type localities, often unavailable type material and nomenclatorial issues.

We have now analysed sufficient material to present our opinion regarding the general taxonomy of the Cochlostomatidae on the basis of the structure of the genitalia, the shell morphology and molecular data. We provide a new generic and subgeneric framework for the family, with a preliminary overview of the species. To keep this paper in an acceptable size, synonyms of species names will not be listed, while in general we refer only to the nomenclature that is used in the Fauna Europea checklist (Bank, 2013) (apart from the African species). In following articles, we will specifically deal with the taxonomy and nomenclature at the species and subspecies level.

MATERIALS AND METHODS

In Table 1 (see supplementary information at www.basteria.nl/publicaties/e_basteria_supplements.htm) the populations that could be studied are listed. Samples are deposited in the molluscan collections of Naturalis Biodiversity Center (Leiden, The Netherlands: RMNH), and the Hungarian Natural History Museum (Budapest, Hungary: HNHM).

For each sample several conchological characters were studied (see Fig. 1), not all of which were already used in this article, however. The features of the protoconch (number of whorls, smooth versus ribbed part), the structure of the umbilical region (umbilicus visible versus hidden by a columellar lobe) and the shape of the operculum were analysed with a stereoscope LEICA MZ6. Using its micrometric eyepiece, the total height of the shell was measured. High definition pictures of 5 (if possible) undamaged female specimens were taken in both frontal and lateral view by a Canon EOS 600D with a macro lens EF-S 60mm 1:2.8 and an additional NL-5 close up lens, mounted on a tripod with a micrometric slide. For each specimen, several photographs were made, at different focal planes, and combined as a single picture using the software Helicon Focus. With the software GIMP 2.6.11 - GNU, several potentially diagnostic distances and angles were established. The distances were measured in pixels and then translated into metric measures on the basis of the number of pixels per millimeter. This ratio was determined by comparing the height in pixels on the picture and the height in millimeters that was measured directly.

The number of whorls was determined in an unusual but practical way, i.e. after the photographs in frontal view. The whorls are numbered from the basal body whorl as the first one upwards. The apical whorls are counted as usual in apical view and indicated in tenths of a whorl. To measure the shell height, the tip of the protoconch is aligned with the internal side of the columella, which is visible at the left side of the aperture. In addition to the total shell height, the heights of the first, the second, the third, and the fourth whorl, the height of the aperture between the highest point of the parietal lobe and the basis, the height of the aperture along the main axis, and the height of the parietal lobe were measured (Fig. 1).

Along a plane rectangular to the main axis, the widths of the whorls, the widths of the sutures, the width of the most basal, fully visible protoconch whorl, the width of the aperture, and the maximal widths of the lips at the columellar side were determined. The convexity of a whorl was quantified by the ratio between the width of that whorls and the mean

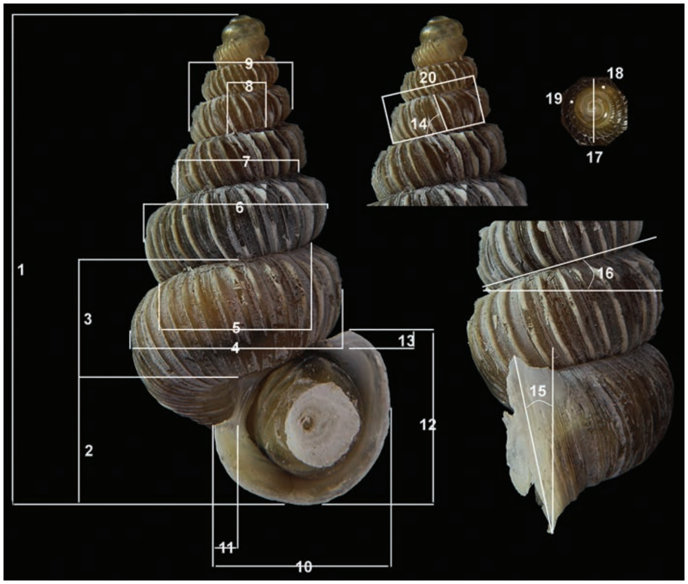


Fig. **1.** Shell morphology. Height: **2**, aperture at the columellar side; **3**, first whorl; **12**, aperture at the parietal side; **13**, parietal lobe. Width: **4**, first whorl; **5**, first suture; **6**, second whorl; **7**, second suture; **9**, fourth whorl; **10**, aperture; **11**, lip at the columellar side. **8**, distance between the five most central ribs on the fourth whorl. Inclination: **14**, of the ribs; **15**, of the aperture; **16**, of the first suture, in lateral view. **17**, axis for the count of the protoconch whorls. **18,** end of the smooth part. **19**, end of the protoconch. **20,** diameter of the basal suture of the fourth whorl.

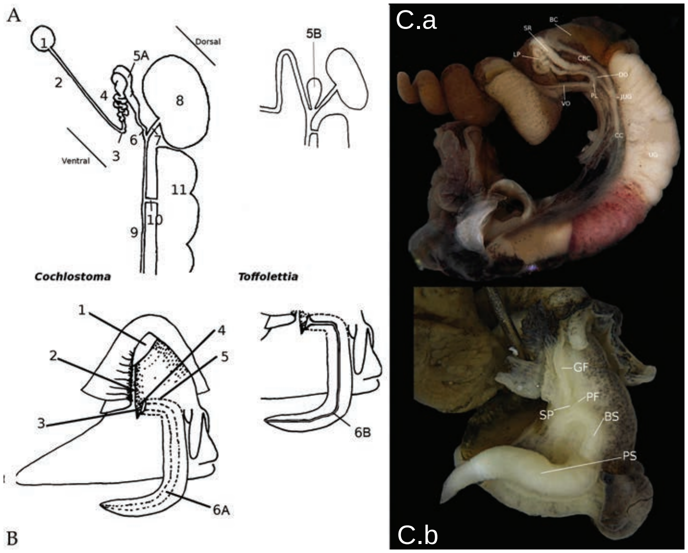


Fig. **2.** Genitalia, terminology. **A**, Female genitalia in *Cochlostoma* and *Toffolettia*. **1**, ovary; **2**, visceral oviduct (VO); **3**, proximal loop (PL); **4**, loops of the visceral oviduct (LP); **5**, seminal receptacle (SR) as an enlargement of the oviduct (**5a**) or as a separate diverticulum (**5b**); **6**, distal oviduct (DO); **7**, pedunculus of the bursa (CBC); **8**, bursa copulatrix (BC); **9**, copulatory duct (CC); **10**, channel of the uterine gland (JUG); **11**, uterine gland. **B**. Male genitalia: **1**, anus; **2**, groove fold (GF); **3**, sperm pocket (SP); **4**, penial funnel (PF); **5**, body spermiduct (BS); **6**, penial spermiduct (PS) (**6a**) or penial groove (**6b**). **C.a.** Female of *Cochlostoma* (*Clessiniella*) *tergestinum*. **C.b.** Male of *Cochlostoma* (*Dalfreddia*) *subalpinum*.

value for its upper and lower suture ('6'/(['5'+'7']/2) in Fig. 1). The ratio between the widths of the first and that of the fourth suture is used as a value for the slenderness of the shell.

The number of ribs per mm is calculated by measuring the distance between the first and the last of the most central five ribs of a whorl, in frontal view. This is done on the first (measuring the distance along the upper suture) and on the fourth whorl (using the distance at the lower suture).

The ribbing may be regular or irregular, whereas the ribs may be sharp or rounded and straight or sinuous. The inclination of the ribs is calculated by taking the average of the inclination of the three most central ribs of the fourth whorl up and the most central rib of the third whorl. The angle between the main axis and the lower suture of the fourth whorl is also determined. By doing so, the inclination of the ribs was related to either the main axis or the suture. To determine the inclination of the aperture, the shell was studied in lateral view with the basal point of the aperture aligned with the tip of the protoconch. In that position, the angle between the lip of the aperture and the main axis was measured. The inclination of the sutures was also measured.

To investigate the female genital morphology, the shell was carefully removed; the body was fixed in absolute ethanol and positioned so that the ventral side is visible at the level of the bursa copulatrix, between the second and the third whorl. In contrast to the approach of Giusti (1971), Varga (1984), and Colomba et al. (2014), in which the genitalia are separated from the body, we analysed these structures ’in situ’, so that the relative position of the different organs can be studied (Zallot, 2001; De Mattia et al., 2011). The genitalia are described starting from the ovary or the testis, which are always situated in the apical part of the body. For a schematic overview of the main types, see Fig 2. The anatomical details of individual specimens are figured with the help of a camera lucida and a stereoscope. For the nomenclature we follow Zallot (2002: 95-96).

The following characters were investigated: absence or presence of a separate seminal receptacle; the angle between the pedunculus of the bursa copulatrix and the seminal receptacle or the distal oviduct; the course of the pedunculus of the bursa copulatrix; the shape of the seminal receptacle; the location of the insertion of the pedunculus at the bursa copulatrix; the position of the seminal receptacle; the location of the junction of the uterine gland with regard to the connection between the distal oviduct and the pedunculus.

To study the male genital morphology, the lower whorls of the shell are removed in order to expose the right side of the foot. The mantle is then cut vertically from the front up to the anus and, behind it, the tip of the prostatic gland. Because of the absence of a specific nomenclature for some parts of the male genitalia, new terms had to be defined (see Fig. 2).

For 106 populations, representing most of the known species and all genera/subgenera (after Zilch, 1958) apart from *Apolloniana* (only dry shells available), DNA analyses were performed (see Table 1). The samples cover 47 nominal taxa, representing the three hitherto accepted genera *Cochlostoma*, *Obscurella*, and *Toffolettia*, and *Rhabdotakra* and *Imerezia* gen. nov., which are added in this article. Within *Cochlostoma*, 39 samples represent the various subgenera.

DNA was extracted with a Qiagen DNA tissue kit following the manufacturers instructions. Lysis was done overnight (up to 16 hrs). Generally PCRs were carried out with a 1:100 dilution of the DNA extracts in order to prevent inhibition of the PCR. In case of PCR failure it occasionally helped to treat the DNA extracts with DNAzol (Invitrogen), again following the manufacturers guidelines. Two markers were selected for phylogenetic reconstructions: *histone H3 nDNA*, using the primers H3F and H3R of Colgan et al. (2000) and *16S mtDNA*, using the primers of Palumbi et al. (1991). This resulted in 75 *16S* and 79 *H3* DNA sequences. PCRs were carried out in 25 µl volumes using 1.25 units of Taq DNA polymerase (Qiagen), 0.4 mM of each primer and 0.2 mM dNTPs. For *16S,* 5 µl Q-solution (Qiagen) was added per reaction to obtain a final concentration of 1X. The PCR thermoprofile for both markers was initial denaturation 2 min. @ 94°C, denature 15 sec. @ 94°C, anneal 30 sec. @ AT°C, extend 40 sec. @ 72°C (repeat from 2nd step 39X), final extension 5 min. @ 72°C. Where AT is the annealing temperature; 57°C for *H3* and 50°C for *16S*. PCR products were cleaned with a Montage purification kit (Millipore) at Macrgoen Inc. Europe (Amsterdam) and Sanger sequenced in both directions on an ABI3730XL with the same primers used for PCR. Sequences were assembled and edited using Sequencher v.4.10.1 (Gene Codes Corporation). For phylogenetic analyses of the Cochlostomatidae outgroup sequences for both markers were downloaded from GenBank (Table 1). For *H3* these were manually aligned in Geneious v.7.1.5 (Biomatters Ltd.) and MAFFT (Katoh & Standley, 2013) was used for the alignment of *16S*. Of the latter alignment conserved regions were selected with GBLOCKS (http://molevol.cmima.csic.es/castresana/Gblocks_server.html) using the default options (i.e. neither the 'more relaxed' nor the 'more stringent' option was selected). This resulted in a dataset consisting of 298 characters (= 54% of the original 549 positions).

For each alignment a best-fit nucleotide substitution model was selected with MrModeltest v.2.3 (Nylander, 2004). Phylogenetic analyses were done in MrBayes 3.2.2. (Ronquist & Huelsenbeck, 2003) hosted by the CIPRES Science Gateway (Miller et al., 2010). For each marker two simultaneous MCMC runs (four chains each) were executed for 10 M generations. Trees were sampled every 1000 generations and the first 2500 trees were discarded as burnin. FigTree v.1.4.0 (Rambaut, 2009) was used to collapse the species trees to the subgenus level. To focus on the Cochlostomatidae, the genus *Cochlostoma* in particular, the above procedure was repeated without the non-Cochlostomatidae outgroup sequences. Based on the result of the first analyses, *Imerezia lederi* and *Rhabdotakra canestrinii* were selected as outgroup for respectively *16S* and *H3*.

The distribution maps (Fig. 11) have been plotted by using the geographical coordinates of only our sampling localities. As a consequence, the range of a genus or a subgenus may be wider than it is presented here.

Guided by the results of our molecular analyses, the morphological and distributional data were newly interpreted to achieve a phylogeny reconstruction that can be used as the basis of a revised nomenclature. Our classification is not always unequivocally supported by morphological apomorphies, establishing *Cochlostoma* once more as a difficult group.

Because only the positions of the type species in particular clades determine the use of the generic and subgeneric names, original descriptions were neglected as being potentially misleading while the type species were studied and characterized anew. These names, often introduced under the heading "Sectio", are valid according to the ICZN, Art. 10.4. For all the nominal taxa of the genus group the type species are indicated, with a reference to their designation.

Referring to ICZN Article 10.4, the 19 'Formenkreis' names that were introduced by Wagner (1897) are not accepted as valid because, in accordance with the historical basics of systematic zoology, we consider Formenkreis "a term such as superspecies", if not a synonym. Wagner hardly ever referred to those names after 1897 (Wagner, 1906: 133), and if so, he did not use italics, emphasizing the special status: " .. gehört zum Formenkreis des *Auritus dalmatinus* L. Pfr. (Dalmatina m.) ..". See the notes with *Toffolettia* for more details. Despite the views expressed by Graf (2010), we also do not accept as valid, the dozens of names ending with "iana" or "ana" that were introduced by French and Spanish authors during a short period, ending in the beginning of the 20th century. These authors never combined those names with an epithet. The names should be interpreted "as modifications of available names [species-group names] throughout a taxonomic group by addition of a standard prefix or suffix [*iana* or *ana*] in order to indicate that the taxa named are members of that group." (ICZN, Article 1.3.7) and not considered valid. A more detailed argumentation against the unnecessary, disturbing alteration of interpretations in nomenclatorial matters is beyond the scope of this article.

THE GENUS *COCHLOSTOMA* AND ITS SUBGENERA: A HISTORICAL REVIEW

The generic name *Cochlostoma* was introduced by Jan (1830) for a subgenus of *Cyclostoma* Lamarck, 1799, without giving any description. Later on Wenz (1923: 1773) designated *Cyclostoma maculatum* Draparnaud, 1805, currently *Cochlostoma septemspirale* (Razoumowsky, 1789), as its type species. Most of the subsequent authors, primarily Westerlund (1883, 1885), Clessin (1889) and Wagner (1897), overlooked or ignored *Cochlostoma* and used *Pomatias* Studer, 1789 [type species *Nerita elegans* Müller, 1774, currently *Pomatias elegans* (Müller, 1774)], following Hartmann (1821). Eventually Kobelt (1902) assigned to *Pomatias* only a small number of palaearctic terrestrial operculate snails and reintroduced *Cochlostoma* as a valid generic name. Kobelt's view was accepted by Zilch (1958), the first author who published an almost complete checklist of the genus after Wagner (1897) and Kobelt (1902). The most recent checklists, largely confined to the European species, i.e. of the AnimalBase Project Group (2005) and Bank (2013), use *Cochlostoma*, while listing 64 species (without subgenera) and 56 species (with subgenera), respectively. This striking contrast illustrates the poor actual knowledge of the Cochlostomatidae.

Westerlund (1883, 1885) is the first author who defined subgroups in *Cochlostoma*. On the basis of only the characters of the umbilicus and the aperture, four new 'Sectio', viz. *Anotus*, *Personatus*, *Auritus,* and *Turritus,* were introduced. Few years later, Clessin (1889) described the new 'Sectio' *Pomatiella*, *Strobelia, Obscurella* and *Scalarinella*, without considering Westerlund's previous nomenclature. His division was restricted to few species however, since he considered only a limited part of the range of the genus. A major monograph on '*Pomatias'* (= *Cochlostoma*) was published by Wagner (1897). Hardly considering the available nomenclature, he introduced many new 'Sectio' names that have subgeneric status. His classification was based on a more detailed analysis of shell features than that of the previous authors. He introduced, again as 'Sectio', the following new names: *Rhabdotakra*, *Stereopoma*, *Pleuropoma* and *Titanopoma***.** Neglecting nearly all the already available nominal subgeneric taxa, only Westerlund's *Auritus* was used but with a totally different meaning. Kobelt & Möllendorff (1898, 1899) published two checklists, accepting Wagner's subgeneric taxa while introducing the enigmatic subgenus *Macaropoma* (1898: 143) (see Incertae sedis) and *Holcopoma* (1899: 139) as a new name for *Pleuropoma*.

Zilch (1958), in a useful article, but incomplete from the perspective of general taxonomy, published an annotated list of the type and typoid (= specimens cited in the literature) shells in the Senckenberg collection. He largely followed Kobelt's latest checklist (1902) and adopted 7 subgenera, viz. *Cochlostoma* s. str., *Obscurella, Personatus, Turritus, Holcopoma, Auritus*, and *Apolloniana* Brandt, 1958. Confusingly, Kobelt (1902) and Zilch (1958) sometimes classified the same species in different subgenera. Alzona (1971), Bank (1988) and Schütt (1977) followed Zilch (1958) as regards the subgeneric division of *Cochlostoma*. Giusti (1971), while emphasizing the lack of diagnostic conchological and anatomical characters, refrained from a subgeneric classification.

Raven (1990) proposed to rise *Obscurella* to genus rank, with the subgenera *Cantabrica* and *Canestrinia*. Gofas & Bakkeljau (1994) noted that the latter name was preoccupied and had to be replaced by *Rhabdotakra* Wagner, 1897.

RESULTS

DNA analyses. — We obtained both the *16S* and the *H3* sequence, for 33 of the 47 analysed taxa. Of the remaining 14, we have at least one of the two sequences for 11 taxa. For 3 of the 47 taxa (*C. bicostulatum, C. macei, C. simrothi*), molecular data could not be acquired. The phylogenetic trees resulting from the analysis of the *H3* and the *16S* marker are presented in Fig. 3. The Cochlostomatidae are shown as a monophyletic group. The analyses of both molecular markers resulted in the same main clades, which correspond to the genera *Imerezia* gen. nov., *Toffolettia*, *Rhabdotakra*, *Obscurella* and *Cochlostoma* s. str.

Within the genus *Cochlostoma*, both the *H3* and the *16S* analysis indicate the same main clades which we here define as subgenera.

Morphological analyses. — The analysis of the female genitalia proved to be very useful, but only so if studied in situ. Among the taxa of the Cochlostomatidae the morphology of the female genitalia varies at different levels (see Figs 4, 5). The structure of the male genitalia varies as well, but here the condition of the body, which may be more or less strongly retracted due to different ways of preservation, may hamper a comparative analysis. Males may also be dimorphic, having either a normal or a micro penis (see Varga, 1984).

The female genitalia differ between the main phylogenetic lineages (genera), which were recognized by the DNA analyses. At a lower taxonomic level, i.e. for the subgenera of *Cochlostoma*, this is not always the case.

In Figs 6 and 7 the shells of the type species of all the genera and subgenera are illustrated. Most authors agree that the taxa of the Cochlostomatidae can hardly be characterized by shell characters alone. We here propose a new start for cochlostomatid conchology, adding some features that have never been used before in taxonomy, or have never been noticed altogether, while devaluing other characters that proved to be potentially misleading. The sculpture of the protoconch and the structure of the columella are more relevant than hitherto accepted, whereas the DNA analysis definitively proves that the shape of the umbilicus, being either open or closed, what has formerly been considered of the utmost importance to define subgenera of *Cochlostoma*, can only be diagnostic at the species level, and has to be considered a homoplasious character at that level.

A clear transformation series may only be seen in the operculum, starting from a simple, thin and transparent operculum to a thick, more robust one, and eventually an operculum with a calcareous extra layer in some species of *Cochlostoma* (*Auritus)* (Fig. 8.4). Other characters, like the hollow versus a solid columella (Figs 9, 10) and the features of the protoconch (Fig. 14), are clearly related to different phylogenetic lineages, but should be used with care because of obvious convergences and difficulties in distinguishing synapomorphy from symplesiomorphy.

SYSTEMATIC PART

Family Cochlostomatidae Kobelt, 1902

Type genus: *Cochlostoma* Jan, 1830

Type species (design. Wenz, 1923: 1773): *Cyclostoma maculatum* Draparnaud, 1805 [= *Cochlostoma septemspirale* (Razoumowsky, 1789)].

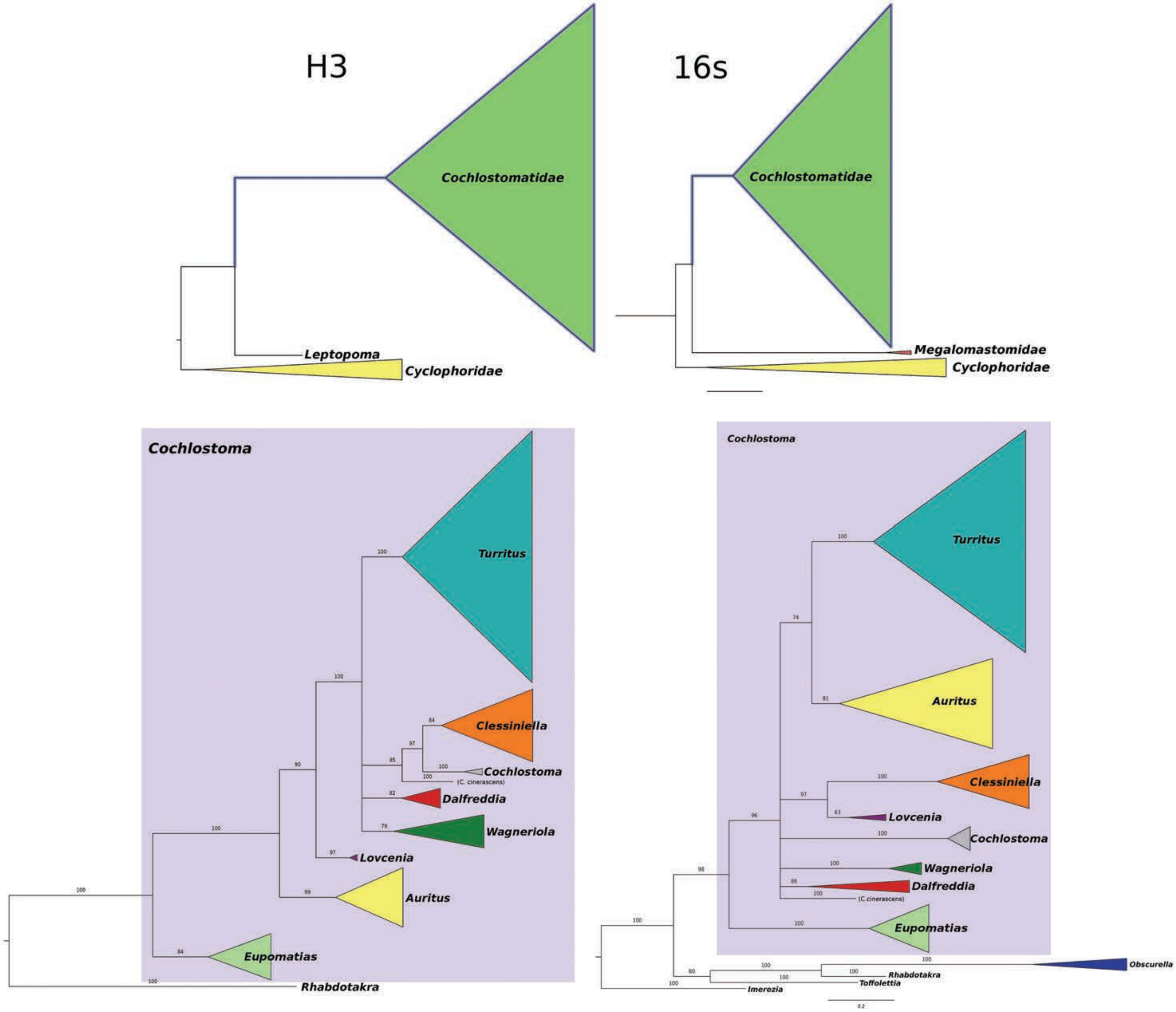


Fig. **3.** Phylogenetic trees based on histone *H3* and *16S* sequences, the length along the abscissa represents the genetic distance within the group and the width along the ordinate indicates the number of analysed samples.

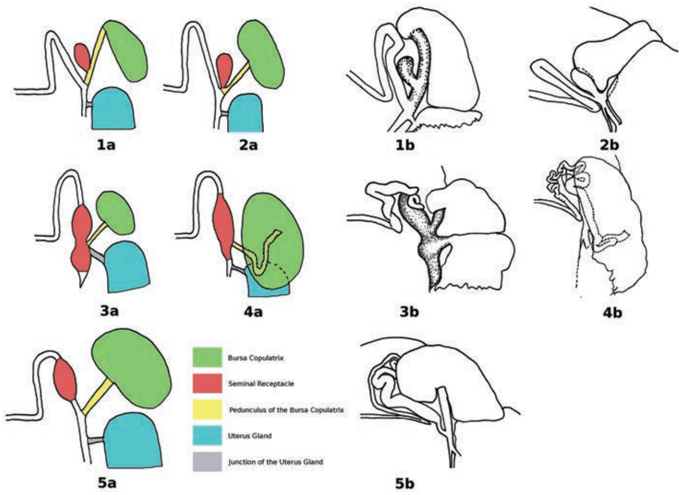


Fig. **4.** Schematic views (a) and drawings (b) made with a camera lucida for the characteristic parts of the female genitalia. **1a**, *Imerezia* gen. nov., **1b**, *I. lederi*; **2a**, *Toffolettia*, **2b**, *T. striolata*; **3a**, *Rhabdotakra*, **3b**, *R. canestrinii*; **4a**, *Obscurella*, **4b**, *O. obscura*; **5a**, *Cochlostoma*, **5b**, *C. (Eupomatias) henricae*.

The family Cochlostomatidae is classified in the superfamily Cyclophoroidea Gray, 1847 (Bouchet et al., 2005), which belongs to the Caenogastropoda, a clade that has not yet been ranked taxonomically (Bouchet et al., 2005; Ponder & Lindberg, 2008). Bouchet et al. (2005) assigned 9 families to the Cyclophoroidea, without accepting a family Cochlostomatidae, however; these authors consider that taxon a subfamily, i.e. Cochlostomatinae, of the family Diplommatinidae. Other authors (Manganelli & Giusti, 1997; Fehér, 2004) accept its ranking as a family. Manganelli & Giusti (1997) report as autapomorphies of the Cochlostomatidae the radular teeth formula, the stomach with a distinct caecum, and the presence of a penis. Using analyses with several molecular markers (*16S*, *18S*, *28S*, *COI*, *H3*), Webster et al. (2012) showed that the Cochlostomatidae form a monophyletic group indeed. Our study additionally shows that *Imerezia* gen. nov. and *Toffolettia* Giusti, 1971, also belong to this family.

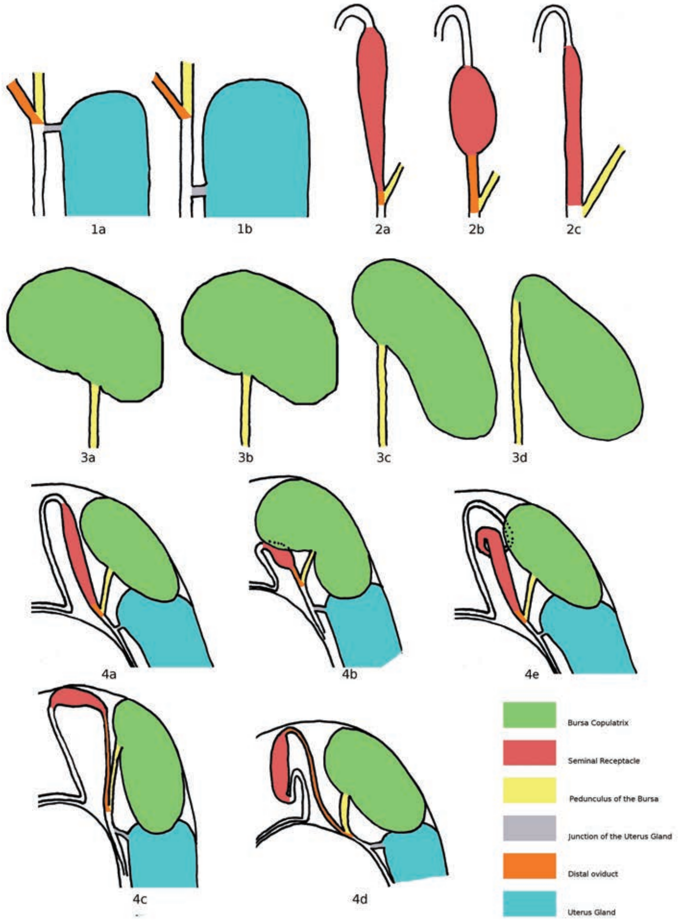


Fig. **5.** Schematic views of characteristic parts of the female genitalia, showing taxonomically relevant details within the genus *Cochlostoma*. **1**, variation in the position of the channel of the uterine gland with regard to the connection between the distal oviduct and the pedunculus of the bursa: **a**, close; **b**, far. **2**, various shapes of the seminal receptacle: **a**, club-shaped; **b**, oval; **c**, tubular. **3**, variation in the position of the pedunculus of the bursa: **a**, anterior; **b**, ventral; **c**, posterior; **d**, apical. **4**, variation in the position of the seminal receptacle and the length of the distal oviduct: **a**, elongated tubular seminal receptacle with short distal oviduct; **b**, oval seminal receptacle, situated in the ventral part of the body, with a short distal oviduct; **c**, seminal receptacle situated at the dorsal side of the body, with a long distal oviduct; **d**, reversed seminal receptacle; **e**, twist of the proximal oviduct in *Cochlostoma (Eupomatias).*

Identification key for the genera

1a The seminal receptacle is a separate diverticulum (Fig. 4.1, 4.2)........ 2
1b The seminal receptacle is an enlarged part of the oviduct (Fig. 4.3, 4.4, 4.5)........ 3
2a Diverticulum situated on the pedunculus of the bursa copulatrix (Fig. 4.1): .... *Imerezia* gen. nov.
2b Diverticulum situated in between the distal oviduct and the pedunculus of the bursa copulatrix (Fig. 4.2): *Toffolettia.*
3a The angle between the seminal receptacle and the distal oviduct and the pedunculus of the bursa copulatrix is much more than 45 degrees (Fig. 4.4): .... *Obscurella.*
3b The angle between the seminal receptacle and the distal oviduct and the pedunculus of the bursa copulatrix is 45 degrees or less (Fig. 4.3, 4.5)........ 4.
4a Bursa copulatrix small, of the same magnitude as the seminal receptacle (see Fig. 4.3): .... *Rhabdotakra.*
4b Bursa copulatrix much larger than the seminal receptacle (see Fig. 4.5): .... *Cochlostoma.*

Imerezia **gen. nov.**

Type species: *Pomatias lederi* Boettger, 1881.

Diagnosis.— The seminal receptacle is a separate diverticulum, inserting on the lower half of the pedunculus of the bursa copulatrix at ¼ of its total length (Fig. 4.1a). Pedunculus connected apically to the bursa (Fig. 5.3d). Penis with a superficial sperm groove. The initial 1.4 whorls of the protoconch are smooth. The columella is tubular.

Description. — Shell conical, relatively tumid, 10-12 mm high, with 8-9 whorls, which are gradually increasing in width. Protoconch with 2.0-2.5 whorls; its initial 1.3-1.4 whorls smooth, further on they are finely ribbed. The entire teleoconch is provided with sinuous, narrowly spaced, relatively thin ribs. Our specimens are bleached, but according to Boettger (1881: 244) the shells are greyish brown, with three series of reddish spots [probably on the body whorl only] and whitish ribs. Aperture roughly oval-circular, inclined relative to the main axis and ending with a prominent lip. At the columellar side the lip gradually narrows adapically, leaving the umbilicus fully visible. In lateral view, the body whorl slightly enlarges, forming a parietal lobe. There is a slightly protruding internal callus narrowing the aperture. The columella is tubular, i.e. with an internal cavity, over its entire length; in the penultimate whorl, it has a barely visible muscle scar, where the retractor muscle is attached. The operculum is thin and without any sculpture.

From the ovary in the apical whorls the oviduct runs, clearly visible, on the ventral side of the body, just below the surface. At a certain point its direction changes abruptly, from ventrally to dorsally (proximal loop). Further on its direction changes again, descending towards the ventral conjunction with the pedunculus of the bursa copulatrix. On the pedunculus, at ¼ of its length towards the bursa, the seminal receptacle inserts as a separate diverticulum. The pedunculus connects to the bursa apically (Fig. 4.1a-b). The uterine gland discharges into the copulatory duct close to the connection between the distal oviduct and the pedunculus. The gonopore is situated at the distal tip of the uterine gland.

From the testis, the internal spermiduct runs at the ventral side of the body, ending near the apex of the prostatic gland. The internal part ends at the proximal edge of the mantle, at the right side of the body, where the prostatic gland and the anus open. From that place on, there is a more or less clearly defined groove, bordered by a fold of the mantle. This groove continues at the surface of the body, from close to the posterior edge of the mantle to the basis of the penis and further on towards its tip. The penis is situated far away from the right eye.

Taxa: *lederi* Boettger, 1881.

Range. — The only known species of the genus *Imerezia* occurs in the Caucasus Mts (Fig. 11.1.; see also Kantor et al., 2010), where it is the only representative of the Cochlostomatidae.

Remarks. — The *16S* genetic distance between *Toffolettia striolata* and *Imerezia lederi* is of the same magnitude as the distance between *Toffolettia striolata* and all *Cochlostoma* species (Table 2; see supplementary information at www.basteria.nl/publicaties/e_basteria_supplements.htm).

Derivatio nominis: The epithet *Imerezia* refers to the Georgian region where the only species of this genus lives.

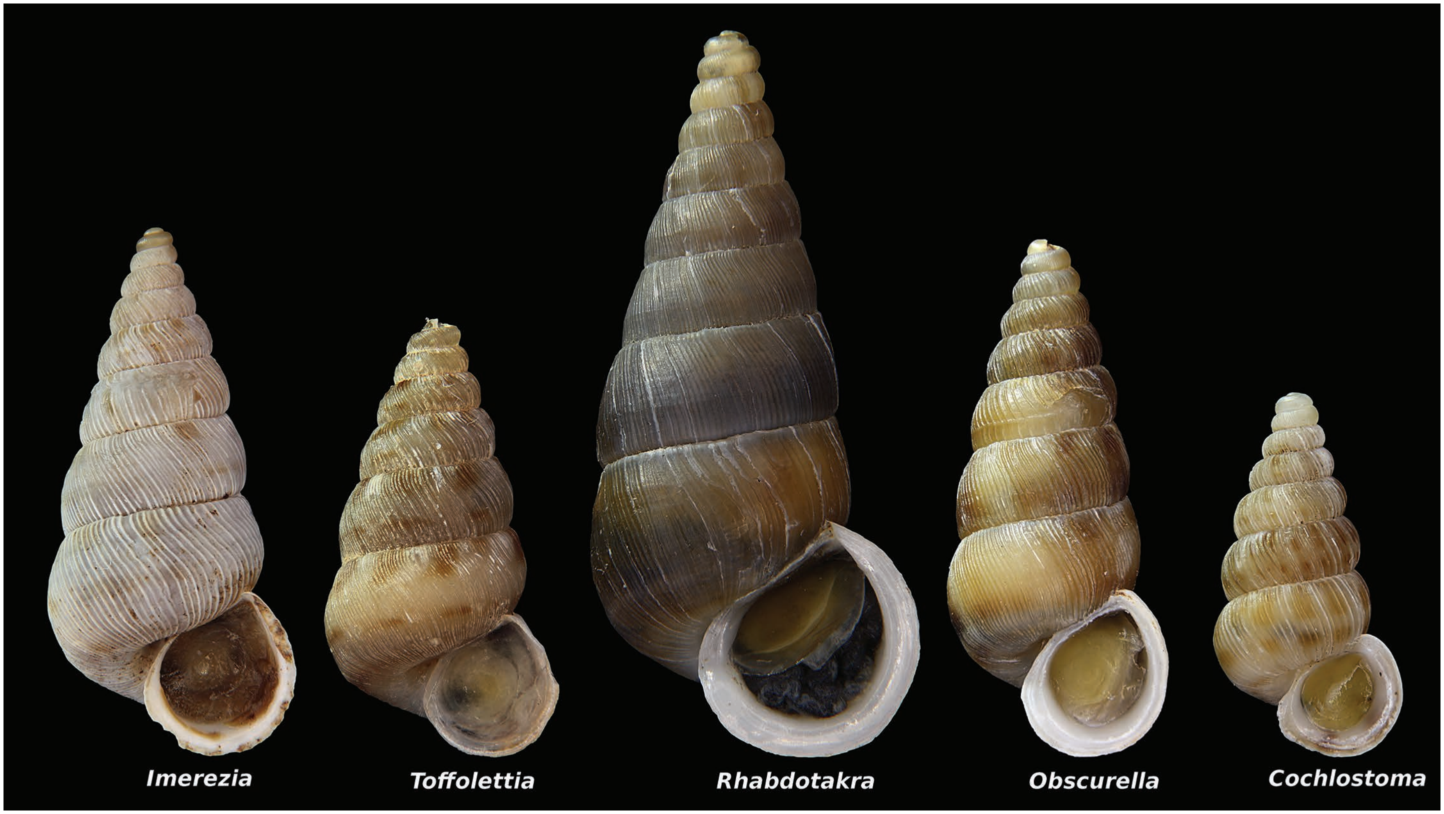


Fig. **6.** Shells of the type species of the genera of Cochlostomatidae: *Imerezia lederi* (height 11.1 mm); *Toffolettia striolata* (height 9.2 mm); *Rhabdotakra canestrinii* (height 15.2 mm); *Obscurella aprica* (height 10.9 mm); *Cochlostoma (C.) septemspirale* (height 7.7 mm).

Genus *Toffolettia* Giusti, 1971

Toffolettia Giusti, 1971: 367**.** Type species (monotypy): *Pomatias striolatum* Porro, 1840.

Striolata G. Falkner, Ripken & M. Falkner, 2002: 69. Type species (monotypy): *Striolata striolata* (Porro, 1840).

Diagnosis.— The seminal receptacle is a separate diverticulum inserting near the junction of the distal oviduct and the pedunculus of the bursa copulatrix (Fig. 4.2a-b). The pedunculus connects about halfway with the bursa. Penis with a superficial sperm groove. The initial 0.3 whorls of the fragile protoconch are smooth. The columella is tubular.

Description.— Shell conical, relatively tumid for the family, 8-10 mm high, with 7-8 whorls, which are gradually increasing in width. Protoconch thin and fragile, not occupied by the body in adult snails, with 2.0-2.5 whorls; the initial 0.3-0.5 whorls are smooth, further on they become finely ribbed. The entire teleoconch is provided with sinuous, narrowly spaced, thin ribs. The colour varies from a light yellow to dark brown, usually with 2 band-like series of reddish spots, one on the upper part of the whorls and another one close to the lower suture; on the body whorl there is a third row more basally. Aperture roughly oval-circular, inclined relative to the main axis and ending with a poorly developed lip, which leaves in frontal view the umbilicus fully visible. In lateral view, the body whorl is not at all inflated near the apertural lip. The columella is tubular over its entire length; it has a barely visible muscle scar where the retractor muscle is attached.

The operculum is thin, transparent, and flexible.

From the ovary in the apical whorls the oviduct runs, clearly visible, on the ventral side of the body just under the surface. At a certain point its direction changes abruptly, from ventrally to dorsally (proximal loop), reaching the dorsal side of the body, from where it changes its course once again while descending towards the ventral connection with the pedunculus of the bursa copulatrix. The seminal receptacle inserts as a separate diverticulum near the junction of the distal oviduct and the pedunculus. The pedunculus connects ventrally to about the middle of the bursa. The uterine gland discharges into the copulatory duct close to the connection between the distal oviduct and the pedunculus. The gonopore is situated at the distal tip of the uterine gland.

From the testis, the internal spermiduct runs at the ventral side of the body, ending near the apex of the prostatic gland. The closed spermiduct ends at the proximal edge of the mantle, at the right side of the body, where the prostatic gland and the anus open. From that place on there is a sperm groove, bordered by a more or less clearly discernible fold. The groove continues, clearly visible, towards the penial tip. The penis is situated far away from the right eye.

Taxa: *striolata* (Porro, 1840).

Range.— NW Italy (Liguria) and nearby SE France (Fig. 10.1).

Remarks.— Giusti (1971) introduced the generic name *Toffolettia* for *Pomatias striolatum* Porro, 1840, when he recognized its conspicuous anatomical differences from *Cochlostoma*. More recently, Falkner et al. (2002) used *Striolata* A.J. Wagner, 1897, as a valid, senior, generic name, introduced by Wagner (1897) while referring to the "Formenkreis *Striolata*". According to Falkner et al. (2002: 69) "A.J.Wagner (1897: 583 [19], 590 [26]) a introduit pour le "Formenkreis" de *Pomatias (Rhabdotakra) striolatus* le nom du nouveau genre *Striolata*. Ce nom est disponible (ICZN, Art. 10.4) et a priorité sur *Toffolettia*, que Giusti (1971) avait séparé comme genre indépendant de *Cochlostoma*" [has introduced for the 'Formenkreis' of *Pomatias (Rhabdotakra) striolatus* the name of the new genus *Striolata*. This name is valid (ICZN, Art. 10.4) and has priority over *Toffolettia*, which Giusti (1971) had separated as an independent genus from *Cochlostoma*]. Several authors accepted this view (Gargominy & Ripken 2011; Welter-Schultes et al., 2011; Welter-Schultes, 2012). Indeed, the ICZN, Art. 10.4, on the availability of names for divisions of genera, states on the one hand that "A uninominal name proposed for a genus-group division of a genus, even if proposed for a secondary (or further) subdivision, is deemed to be a subgeneric name even if the division is denoted by a term such as 'section' or 'division'", but the article continues, saying on the other hand: "but a name used for an aggregate of species which is denoted by a term such as 'superspecies' is not deemed to be a genus-group name [Art. 6.2]". The rather confusing indeed, second part of Art. 10.4 has been neglected by the authors, none of which have discussed the meaning of superspecies versus Formenkreis. Mayr & Ashlock (1991) in their fundamental 'Principles of Systematic Zoology [2^{nd} ed.]' cite (p. 53) 'Artenkreis' as a synonym for superspecies. Mallet (2001, 2007) explains that Bernhard Rensch replaced the term 'Formenkreis' by two new terms, viz. 'Rassenkreis' (circle of races) and 'Artenkreis' (circle of species). Because Wagner (1897) sometimes lists more than one species as belonging to a single 'Formenkreis', we consider his use of the term in congruence with the term 'Artenkreis' and, as a consequence as synonymous with superspecies. These views regarding the meaning of Formenkreis, Artenkreis and superspecies are shared with other authors (e.g. Stresemann, 1936; Stöcker & Dietrich, 1986; Mallet, 2001, 2004, 2007). It could be argued that Wagner sometimes refers to a 'Formenkreis' for only a single species, not an 'aggregate of species'. The use of the German plural 'Formen' [= forms] combined with 'Kreis' [= circle] indicates however, that he had a variety of forms in mind. Apart from this, we prefer to keep to the ICZN without exploring the mind of a 19th century author, and consider 'Formenkreis' if not a synonym, at least 'a term such as' superspecies. As a consequence, we feel forced to regard the 19 Formenkreis names published by Wagner (1897) as invalid. By doing so, we follow Wagner who only once (see above) used the 'Formenkreis' names in his later papers (Wagner, 1906, 1907, 1914; Sturany & Wagner, 1914). Kobelt (1902) and Zilch (1958) also neglected them.

Genus *Rhabdotakra* A.J. Wagner, 1897

Rhabdotakra A.J. Wagner, 1897: 568 [4]. Type species (design. Westerlund, 1903: 123**):** *Pomatias insubricum* Pini, 1877 (= *P. canestrinii* Adami, 1876).

Canestrinia Raven, 1990: 55. Type species (monotypy): *Pomatias canestrinii* Adami, 1876. Not *Canestrinia* Berlese, 1881.

Diagnosis.— The seminal receptacle is an enlarged part of the oviduct. The angle between the pedunculus and the seminal receptacle is about 45°. The pedunculus connects more or less eccentrically, but not apically, to the bursa, which is relatively small as compared with the size of the other organs. The seminal receptacle has a characteristic, bipartite shape (Fig. 4.3a, 4.3b), caused by a constriction about halfway. Penis with an internal spermiduct.

Description. — Shell conical, rather elongated, somewhat flattened in profile, 15-16 mm high, with 9-10 whorls, which are gradually increasing in width. Protoconch fragile and transparent, not occupied by the body in adult snails, with 2.0-2.5 whorls; the initial 1.0-1.3 ones smooth, after that developing fine ribs. The entire teleoconch with fine, weak, narrowly spaced ribs. The shell is light yellow-brown, without spots, with a grayish hue in live animals due to the dark body inside. Aperture oval-circular, slightly inclined relative to the main axis, with a flattened lip. At the left side (frontal view) the peristome ends with a flat, gradually narrowing columellar lobe, leaving the umbilicus fully visible. The body whorl slightly increases in size near the aperture (lateral view). The entire columella is tubular with a wide internal cavity; it has no muscle scar.

The operculum is thin, transparent and flexible.

From the ovary in the apical whorls, the oviduct runs, clearly visible, at the ventral side of the body, just under the surface. At a certain point its direction changes abruptly, from ventrally to dorsally (proximal loop). After some curves and twists, the oviduct then widens to become the seminal receptacle, which starts narrowing shortly before the junction with the pedunculus. There is no proper distal oviduct. The uterine gland discharges close to the connection between the seminal receptacle and the pedunculus. The bursa copulatrix is small, with a more or less eccentrical, but not apical, insertion of the pedunculus. The seminal receptacle seems to be bipartite because after the connection with the uterine gland it widens again over a short distance before the very short and narrow copulatory channel starts. The uterine gland is subdivided in three parts. The gonopore is situated at the distal tip of the uterine gland.

From the testis, an internal spermiduct runs at the ventral side of the body, ending near the apex of the prostatic gland. The internal part ends at the proximal edge of the mantle, at the right side of the body, where the prostatic gland and the anus open. From that place on, a more or less clearly defined sperm groove, bordered by a fold of the mantle, runs towards the penial funnel, where the short, internal, body spermiduct begins. The penis is situated close to the right eye. It is longer than the body, its proximal third is cylindrical, further on it is slightly flattened.

Taxa: *canestrinii* (Adami, 1876).

Range. — *Rhabdotakra canestrinii* lives in a restricted area on the southern side of the Central Alps in northern Italy, at high altitudes in the Mt. Presolana range (Fig. 11.1, cyan triangle). It may be considered a relic species, which has survived the Pleistocene glaciations under nunatak conditions together with species like for example the sympatric endemic helicid snail *Chilostoma frigidum* (Cristofori & Jan, 1832).

Remarks. — The *16S* genetic distance between *Rhabdotakra canestrinii* and *Obscurella aprica* is of the same magnitude as the difference between *Rhabdotakra* and *Toffolettia* (Table 2*)*.

Genus *Obscurella* Clessin, 1889

Anotus Westerlund, 1883. Type species (design. nov.): *Cyclostoma obscurum* Draparnaud, 1805. Not *Anotus* Agassiz, 1846.

Obscurella Clessin, 1889. Type species (monotypy**):** *Cyclostoma apricum* Mousson, 1847.

Cantabrica Raven, 1990: 43. Type species (original design.): *Pomatias hidalgoi* Crosse, 1864.

Diagnosis. — The seminal receptacle is an enlargement of the oviduct. The angle between the pedunculus of the bursa copulatrix and the seminal receptacle is at least 90°. The pedunculus connects to the bursa from behind. The kidney is positioned proximally with respect to the bursa (distally in *Cochlostoma*: see Fig. 12). The spermiduct is an internal duct.

Descriptions. — The shell is conical, 13-17 mm high, with 7-9 whorls, which are gradually increasing in width. Protoconch with 2.0-2.5 whorls, fragile, transparent and not occupied by the body in adult snails; its initial 0.3-0.5 whorls smooth, further on they become finely ribbed. The surface of the shell varies from almost smooth to sculptured with prominent, hollow ribs. The pattern is almost the same on the entire teleoconch. Aperture roughly oval-circular and only slightly inclined relative to the columella, ending with a prominent, flattened lip. At the left side (frontal view) the peristome ends with a flat columellar lobe while gradually narrowing and leaving the umbilicus fully visible. At the parietal side (lateral view) the body whorl increases in size close to the aperture, generally forming a prominent parietal lobe. The colour of the shell varies from light yellowish brown to dark brown. In some species there are two rows of spots on the whorls. The entire columella is tubular, with a wide internal cavity, and has a barely visible muscle scar in the penultimate whorl.

The operculum is thin, transparent and flexible.

From the ovary in the apical whorls the visceral oviduct runs, clearly visible, on the ventral side of the body, just below the surface. At a certain point its direction changes abruptly from ventrally to dorsally (proximal loop). From there the oviduct runs with several twists and bends, which can considerably increase its length, towards an inflated segment, i.e. the seminal receptacle. The pedunculus of the bursa copulatrix connects to the seminal receptacle where this is narrowing again. It has a characteristic curve halfway its length and approaches the large bursa from behind; it is ventrally connected to it, roughly in the middle (Fig. 4.4a-b). There is no proper distal oviduct. The uterine gland discharges far from the connection between the seminal receptacle and the pedunculus. Further on, the short copulatory duct narrows abruptly. The uterine gland is subdivided into three clearly distinguishable parts. The gonopore is situated at the distal tip of the uterine gland.

From the testis, an internal spermiduct runs at the ventral side of the body, ending near the apex of the prostatic gland. The internal part ends at the proximal edge of the mantle, at the right side of the body, where the prostatic gland and the anus open. From that place on, a more or less clearly discernible sperm groove, bordered by a fold of the mantle, runs to the sperm pocket in front of the penial funnel, which is situated at the right side of the body, close to the distal edge of the mantle. The body spermiduct runs from close to the posterior edge of the mantle to the basis of the penis, which is situated near the right eye. It is more or less protruding from the body and continues inside the penis as far as its tip. The penis itself may be cylindrical, conical or with a narrow basis and then enlarged.

Taxa: *aprica* (Mousson, 1847); *obscura* (Draparnaud, 1805); *crassilabra* (Dupuy, 1849); *partioti* (Moquin-Tandon, 1848); *martorelli* (Bourguignat, 1880); *gigas* Gofas & Backeljau, 1994, *hidalgoi* (Crosse, 1864), *asturica* (Raven, 1990); *oscitans* Gofas, 1989; *bicostulata* Gofas, 1989; *nouleti* (Dupuy, 1851); *marocana* (Pallary, 1928).

Range. — The most speciose radiation of *Obscurella* is found in the Cantabrian and Pyrenean mountains, but the genus is also represented in an area on the NW-side of the Alps, in Burgundy, and in Morocco (Fig. 11.1, yellow circles).

Remarks. — Our analysis supports Raven's (1990) opinion of raising *Obscurella* to the generic status. The Cantabrian and Pyrenean *Obscurella* species have been revised by Raven (1990) and Gofas (2001). Our *16S* analysis includes three species, viz. the type species and two species that belong to the main clades that resulted from Gofas' allozyme analysis. The other species have been assigned to the genus on the basis of the shell and female genitalia morphology or their obvious close relationships with the analysed species according to Gofas (2001).

Obscurella marocana has been assigned to the genus because of only its shell morphology, viz. the early ribbing of the protoconch, a hollow columella and a simple, thin operculum. It was assigned to *Cochlostoma* (*Apolloniana*) by Zilch (1958).

Genus *Cochlostoma* Jan, 1830

Cochlostoma Jan, 1830: 6**.** Type species (design. Wenz, 1923: 1773): *Cyclostoma maculatum* Draparnaud, 1805 (= *Helix septemspirale* Razoumowsky, 1789).

Maculatus Westerlund, 1883: 68. Type species (monotypy): *Pomatias septemspiralis* (Razoumowsky, 1789).

Pomatiella Clessin, 1889: 590. Type species (design. nov.): *Helix septemspiralis* Razoumowsky, 1789.

Diagnosis. — The seminal receptacle is an enlarged part of the oviduct. The angle between the seminal receptacle/distal oviduct and the pedunculus of the bursa copulatrix is less than 45 degrees. The pedunculus runs close below the skin and its connection with the bursa is not hidden behind the bursa copulatrix; the kidney is situated distally with respect to the bursa (Fig. 12). The bursa is relatively large if compared with the size of the other organs. The spermiduct is an internal channel.

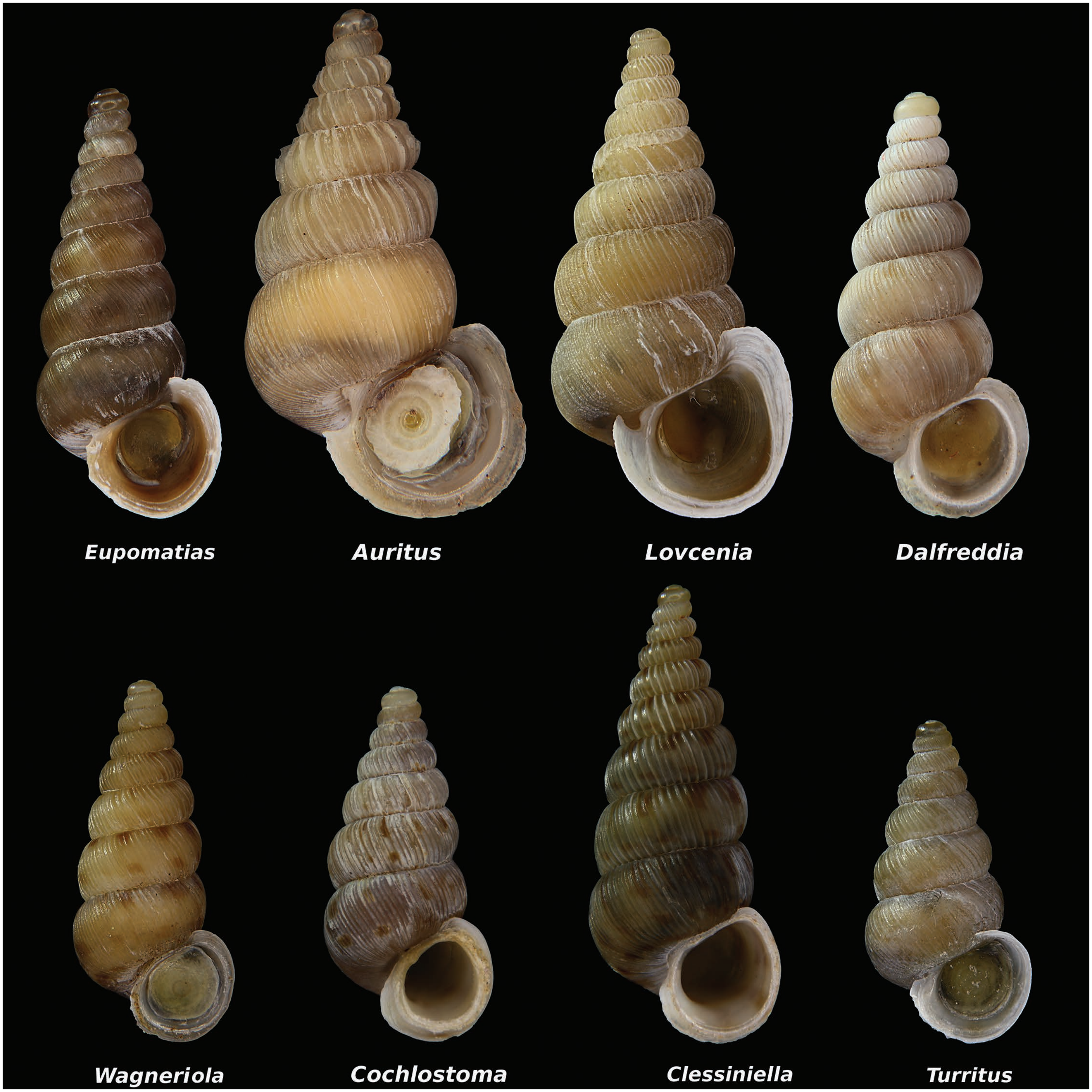
Description. — Shell conical, 6-16 mm high, with 7-11 whorls, which are gradually increasing in width. Protoconch with 2.0-2.5 whorls; the initial 1.2-1.5 whorls smooth (apart from the subgenus *Lovcenia*), after that finely ribbed with more or less widely spaced, prominent ribs. The protoconch is either fragile, transparent and not occupied by the body in adult specimens, or its wall is strong and dull, with the body always reaching the apex. Usually the shell is ribbed but more or less smooth shells (especially the body whorls) may occur as well. The ribs are more or less widely spaced, protruding, sinuous, thickened at the sutures, or taller at the centre of the whorls, They can be thick and rounded, hollow and whitish, or lamellar. The ribbing pattern on the upper teleoconch whorls may differ from that on the body whorl. The aperture is roughly oval-circular, varying from slightly to strongly inclined relative to the main axis, and ends with a more or less broadly developed, flattened lip. In adult specimens, an internal, more or less developed and protruding callus narrows the aperture. At the left side (frontal view) the peristome ends with the columellar lobe which can be curved backwards, covering partly or completely the umbilicus; alternatively the apertural lip may be gradually narrowing in that area, leaving the umbilicus fully visible. In lateral view, the body whorl, may increase in width towards the aperture either gradually or abruptly, or not at all. In the former case it forms a parietal lobe. The colour of the shell varies from light yellow to dark brown, often with two series of reddish spots on the whorls, one above the periphery and another one close to the suture below it. On the basis of the body whorl there may be a third series of spots. The columella is either tubular (with an internal cavity) or solid; on the penultimate whorl there is a more or less prominent muscle scar.

The opercula vary in colour and features of the surface, which may be smooth or provided with a pattern of lines and spirals. It has a double-layer structure, i.e. over a thin, transparent basis there is a second, slightly thicker, yellowish layer. In the subgenus *Auritus* the operculum may have either a granular, calcareous deposit on it, or a super-imposed calcareous structure.

Many species have a pronounced sexual dimorphism, with differences in size and shape of the shell. Usually the males are smaller than the females and have a dark apex of the shell (the initial 3-4 whorls) (see De Mattia et al., 2011; Reichenbach et al., 2012).

From the ovary in the apical whorls the oviduct runs, clearly visible, on the ventral side of the body, just under the surface. At a certain point its direction changes abruptly from ventrally to dorsally (proximal loop). The following part of the oviduct is variable in length, with more or less irregular curves and twists, until it reaches an enlarged part which functions as seminal receptacle (Giusti, 1985). The seminal receptacle is more or less conspicuously elongated and enlarged; narrowing again, it passes into the yellowish, almost transparent distal oviduct. The pedunculus of the bursa copulatrix connects to the distal oviduct at an angle of less than 45°; it may be connected to the large bursa in vari-

Fig. **7.** Shells of the type species of the subgenera of the genus *Cochlostoma*: *C. (Eupomatias) henricae* (height 9.4 mm); *C. (Auritus) auritum* (height 11.1 mm); *C. (Lovcenia) erika* (height 10.6 mm); *C. (Dalfreddia) porroi* (height 9.2 mm); *C. (Wagneriola) scalarinum* (height 7.6 mm); *C. (C.) septemspirale* (height 7.7 mm); *C. (Clessiniella) villae* (height 9.9 mm); *C. (Turritus) stossichi* (height 7.0 mm).


Eupomatias
Auritus
Lovcenia
Dalfreddia
Wagneriola
Cochlostoma
Clessiniella
Turritus

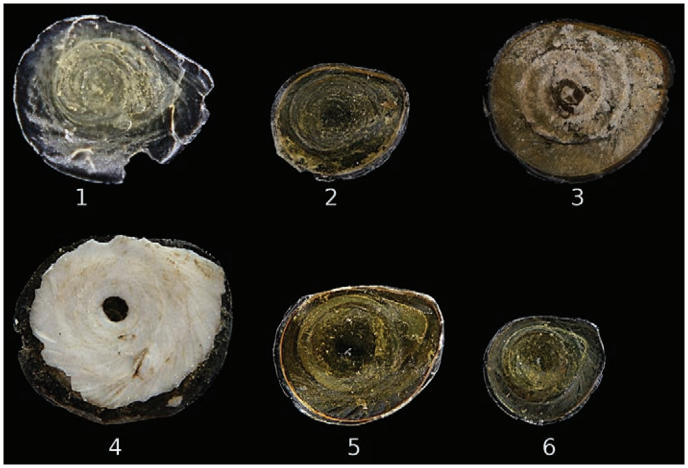


Fig. **8.** Different types of opercula: **1**, *Obscurella aprica*; **2**, *Cochlostoma (Eupomatias) henricae*; **3**, *C. (Auritus) achaicum*; **4**, *C. (Auritus) auritum*; **5**, *C. (Lovcenia) erika*; **6**, *C. (Turritus) sardoum*.

ous ways. More distally the uterine gland discharges into the distal oviduct. The copulatory duct is not always visible. The uterine gland is subdivided into three clearly distinguishable parts. The gonopore is situated at the distal tip of the uterine gland.

From the testis the internal spermiduct runs at the ventral side of the body to the apex of the prostatic gland, which varies in shape. The closed spermiduct ends at the proximal edge of the mantle, at the right side of the body, where the prostatic gland and the anus open. From that place on, a more or less clearly discernible sperm groove, bordered by a fold of the mantle, runs towards the sperm pocket in front of the penial funnel, where the internal body spermiduct begins. This channel runs to the basis of the penis, near the right eye. It is more or less clearly protruding and continues inside the penis as far as its tip. The penis itself can be cylindrical, conical or with a narrow basis and an inflated tip.

Identification key for the *Cochlostoma* subgenera

1a. Only the initial 0.3-0.5 whorls of the protoconch are smooth: .... *Lovcenia*.
1b. A larger part of the protoconch is without riblets: .... 2.
2a. Protoconch fragile and transparent; operculum with calcareous granules or a complex extra layer: *Auritus*.
2b. Protoconch strong and dull; operculum without such additions: .... 3.
3a. The pedunculus inserts apically to the bursa: .... 4.
3b. The pedunculus inserts less eccentrically to the bursa: 5.
4a. The seminal receptacle is reversed as compared to its position in the other subgenera, except *Wagneriola*: .... *Cochlostoma* s. str.
4b. The seminal receptacle is not reversed: .... *Clessiniella*.
5a. The seminal receptacle is reversed as compared to its position in the other subgenera, except *Cochlostoma* s. str.: .... *Wagneriola*.
5b. Position of the seminal receptacle different: .... 6.
6a. The pedunculus connects anterior-ventrally to the bursa; distal oviduct long; uterine gland insertion far from the junction of the distal oviduct and the pedunculus: .... *Wagneriola*.
6b. The pedunculus connects ventrally or posteriorly to the bursa: .... 7.
7a. Seminal receptacle oval in shape: .... 8.
7b. Seminal receptacle different: .... 9.
8a. Proximal oviduct passing over the apex of the seminal receptacle; uterine gland inserting far from the connection between the distal oviduct and the pedunculus: ....*Eupomatias*.
8b. Proximal oviduct not passing over the apex of the seminal receptacle; uterine gland inserting close to the connection between the distal oviduct and the pedunculus: 9.
9a. Seminal receptacle club-shaped, reaching the dorsal side of the body: .... *Dalfreddia*.
9b. Seminal receptacle different: ....*Turritus*.

Subgenus *Cochlostoma* Jan, 1830, s. str.

Diagnosis. — The seminal receptacle is reversed as compared to the arrangement in the other taxa, i.e. its basis is positioned dorsally and the apex ventrally (Fig. 5.4d). The pedunculus is connected apically to the bursa with a characteristic U-shaped path close to the connection with the long distal oviduct (Fig.13.3).

Taxa: *septemspirale* (Razoumowsky, 1789).

Range. — This monotypic subgenus has a wide range, from France to Bosnia. It is the only *Cochlostoma* with a large range also on the northern side of the Alps (Fig. 11.3, red circles).

Remarks. — In the literature up to now *Cochlostoma* s. str. included species with shells with an open, uncovered umbilicus.

Subgenus *Eupomatias* Wagner, 1897

Strobelia Clessin, 1889: 597. Type species (monotypy): *Pomatias henricae* Strobel, 1851. Not *Strobelia* Rondani, 1868.

Eupomatias Wagner, 1897: 568 [4]. Type species (design. Westerlund, 1903: 123): *Pomatias henricae* Strobel, 1851.

Diagnosis. — Seminal receptacle elongated oval. Pedunculus connected ventrally to about the middle of the bursa (Fig. 4.5b); insertion of the uterine gland far from the connection between the pedunculus and the distal oviduct. The proximal oviduct, just before passing into the seminal receptacle, shows a characteristic twist (Fig.5.4e).

Taxa: *henricae* (Strobel, 1851); *philippianum* (Gredler, 1853).

Range . — The subgenus is represented from the southern eastern Alps to the Adige valley in the west (see Bank, 1988). At the northern side of the Alps, in Austria, the subspecies *C. henricae huettneri* (A.J. Wagner, 1897) occurs near Hallstatt and the nominate form near Reutte (Fig. 11.2, yellow squares).

Remarks. — This subgenus is an early branch of the phylogenetic tree, with a high genetic distance from the other *Cochlostoma* taxa.

Subgenus *Auritus* Westerlund, 1883

Auritus Westerlund, 1883: 64. Type species (monotypy): *Cyclostoma auritum* Rossmässler, 1837. *Auritus* is given priority over *Personatus* here.

Personatus Westerlund, 1883: 68. Type species (design. Wenz, 1939: 488): *Pomatias paladilhianus* Saint-Simon, 1869. *Auritus* gets priority over *Personatus*.

Stereopoma A.J. Wagner, 1897: 569 [5]. Type species (design. Westerlund, 1903: 124): *Cyclostoma turriculatum* R.A. Philippi, 1836 (= *Pomatias paladilhianus* Saint-Simon, 1869).

Titanopoma A.J. Wagner, 1897: 570 [6]. Type species (monotypy): *Cyclostoma auritum* Rossmässler, 1837.

Pleuropoma A.J. Wagner, 1897: 570 [6]. Type species (design. Westerlund, 1903: 124): *Cyclostoma tessellatum*. Not *Pleuropoma* Moellendorff, 1893.

Holcopoma Kobelt & Möllendorff, 1899: 139. Nomen novum for *Pleuropoma* A.J. Wagner, 1897. Not *Pleuropoma* Moellendorff, 1893.

Pleuropomatia Tomlin, 1929: 256. Nomen novum for *Pleuropoma* A.J. Wagner, 1897. Not *Pleuropoma* Moellendorff, 1893.

Diagnosis. — The seminal receptacle may have various forms (tubular, oval, or club-shaped) (Fig. 13.1-2).
The operculum has an apomorphic form, with a clear spiral structure and either calcareous granules on its surface or a more or less developed calcareous extra layer. It is the only *Cochlostoma* subgenus with a fragile, transparent protoconch, with 1.3-1.7 smooth whorls, which are not occupied by the body in adult specimens. The columella is solid, with a well developed muscle scar.

Taxa: *achaicum* (Boettger, 1885); *alleryanum* (Paulucci, 1876); *auritum* (Rossmässler, 1837); *fuchsi* Fehér, 2004; *georgi* (A.J. Wagner, 1906*)*; *hellenicum* (Saint-Simon, 1869); *hoyeri* (Polinski, 1922); *paladilhianum* (Saint Simon, 1869); *perseianum* (Kobelt, 1886*)*; *pinteri* Fehér, 2004; *roseoli* (A.J. Wagner, 1901); *tessellatum* (Rossmässler, 1837); *westerlundi* (Paulucci, 1879).

Range. — This is the southeastern clade within *Cochlostoma*, inhabiting the African coastal region east of the Atlas Mts (where an *Obscurella* species occurs), Sicily, Calabria, Apulia in Italy, southern Croatia (Dalmatia), Albania, Montenegro and Greece (Fig. 11.4, purple circles).

Remarks. — The species of this subgenus were formerly assigned to *Holcopoma*, *Auritus,* and *Personatus*. Some Authors have used *Titanopoma* A.J. Wagner, 1897 (see Fehér, 2004), which is a junior synonym of *Auritus,* however.

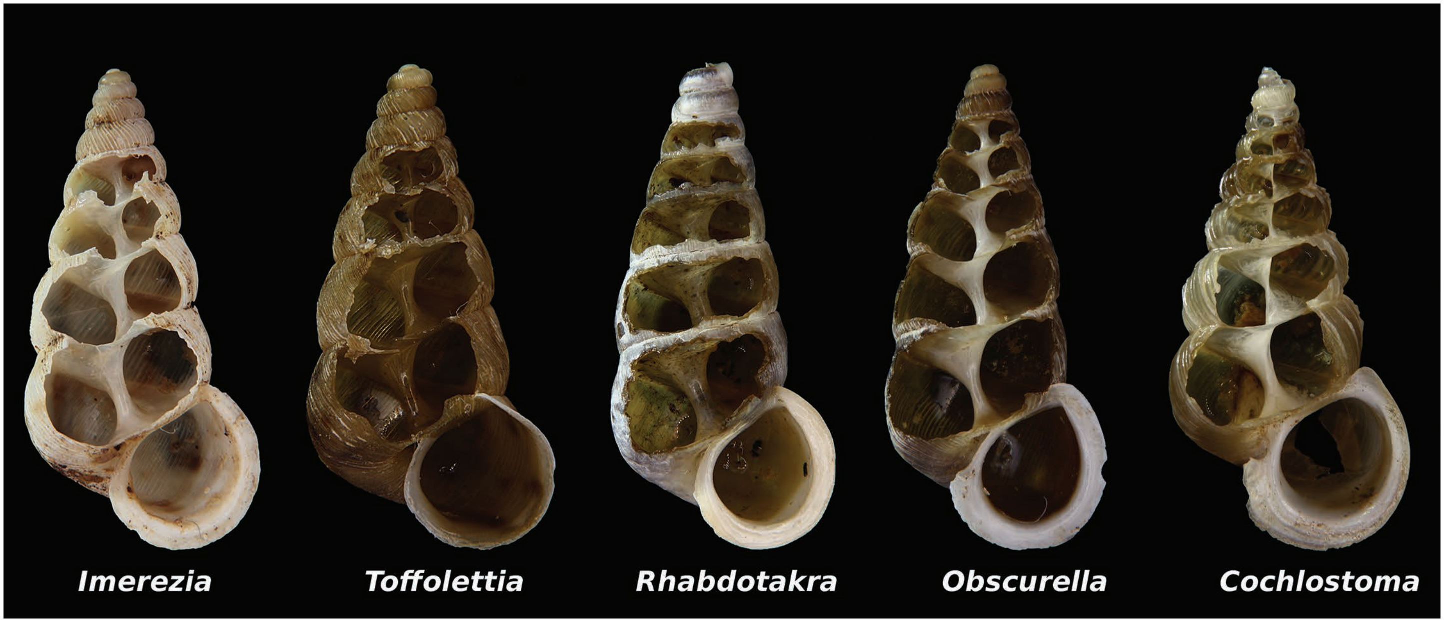


Fig. **9.** Structure of the columella in: *Imerezia lederi*; *Toffolettia striolata*; *Rhabdotakra canestrinii*; *Obscurella martorelli*; *Cochlostoma (Auritus) auritum*.

Lovcenia subgen. nov.

Type species: *Auritus (Auritus) erika* A.J. Wagner, 1906.

Diagnosis. — The seminal receptacle is almost indistinguishable from the oviduct, being only an inconspicuous enlargement; there is no proper distal oviduct (Fig. 13.5). The smooth part of the protoconch is very small, i.e. only 0.3-0.5 whorls (Fig. 14).

Taxa: *erika* (A.J.Wagner, 1906).

Range. — The subgenus is known from a restricted area in Montenegro, northern Albania and likely southern Croatia (Fig. 11.2, red triangles).

Remarks. — The population from the entrance of the cave Shpella e Deleve in northern Albania [E. Gittenberger leg.] is certainly not referable to *C. (Lovcenia) erika* but it is closely related to the latter according to the DNA analysis and the shells have the same early ribbing of the protoconch. Moreover, it shares the habitat with *C. (L.) erika*, being found in the half-dark entrance area of a cave. Unfortunately only male specimens were collected.

Derivatio nominis: The name refers to the Lovćen region in Montenegro, where the type-species of the subgenus is known from.

Subgenus ***Wagneriola*** subgen. nov.

Scalarinella Clessin, 1889: 600**.** Type species (design. nov.): *Pomatias scalarinum* Villa, 1841. Not *Scalarinella* Dohrn, 1874.

Wagneriola subgen. nov. Type species: *Cochlostoma (Wagneriola) scalarinum* (Villa, 1841).

Diagnosis. — The two species of this subgenus are highly differentiated in the female genitalia. In *C. (W.) scalarinum*

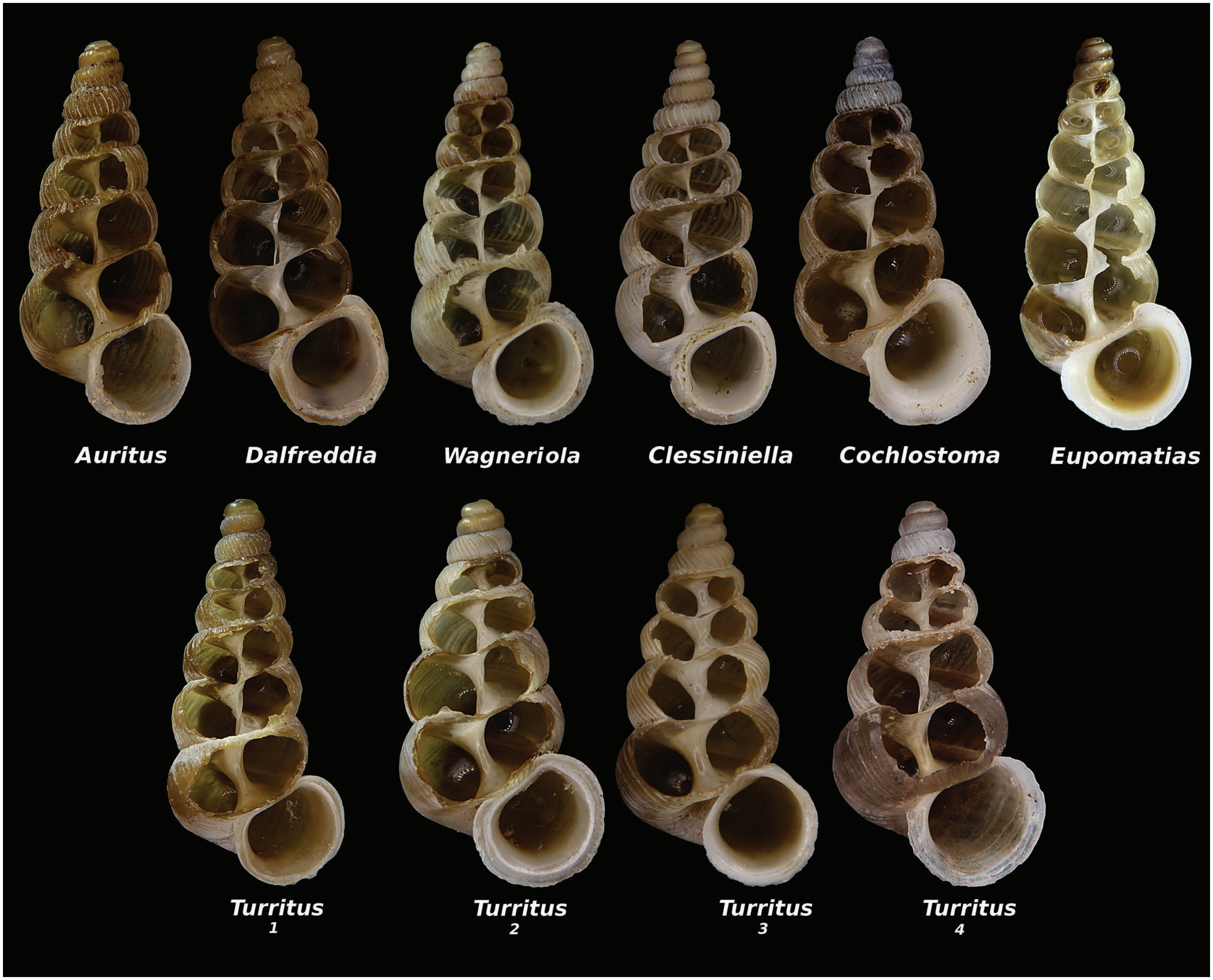


Fig. **10.** Structure of the columella in the subgenera of *Cochlostoma*. Upper row: *C. (Auritus) alleryanum* ; *C. (Dalfreddia) subalpinum*; *C. (Wagneriola) scalarinum*; *C. (Clessiniella) villae*; *C. (C.) septemspirale*; *C. (Eupomatias) henricae*. Lower row, variation among *Turritus* species: **1**, *C. (T.) agriotes*; **2**, *C. (T.) braueri*; **3**, *C. (T.) elegans*; **4**, *C. (T.) stossichi*.

the pedunculus connects anteriorly to the bursa (Fig. 5.3a), the seminal receptacle is situated dorsally, with a long distal oviduct, and the junction of the uterine gland is situated far from the connection between the pedunculus and the distal oviduct (Fig. 13.10). In *C. scalariniformis* the position of the seminal receptacle is reversed (as in *C. septemspirale*) and the pedunculus connects ventrally with the bursa (Fig. 13.9). The shell has a strong and dull protoconch with a relatively large smooth part (1.2-1.5 whorls). The columella is solid. Operculum as in the other subgenera, except for *Auritus*.

Taxa: *scalarinum* (Villa, 1841); *scalariniformis* (A.J.Wagner, 1906).

Range. — *Cochlostoma (Wagneriola) scalarinum* occurs all along Dalmatia, becoming more sporadic in Albania, Macedonia and Greece. It is also found in a restricted area in southern Italy (Cilento, south of the region Campania). *Cochlostoma (W.) scalariniformis* considered a subspecies of *C. sturanii* by Bank (2013), is restricted to the inland Dinarids, from southern Dalmatia as far south as Montenegro and Albania (Fig. 11.3, cyan squares). *Cochlostoma zawinkanum* (A.J. Wagner, 1906), which is also considered a subspecies of *C. sturanii* by Bank (2013), belongs to the subgenus *Turritus* .

Remarks. — The two included species are quite different in their genital morphology. However, they belong to a reasonably supported clade and the *H3* genetic distance between them (the *16S* analysis is missing) is of the same magnitude as is found between species in other subgenera, like *Auritus* and *Clessiniella*.

Cochlostoma (W.) scalariniformis and *C. (C.) septemspirale* are the only known *Cochlostoma* species with a reversed position of the seminal receptacle.

In *C. (W.) scalarinum* the shells have a visible umbilicus, which is hidden in *C. (W.) scalariniformis*.

Derivatio nominis: Named as a tribute to A.J. Wagner for his contribution to the knowledge of this genus.

Dalfreddia subgen. nov.

Type species: *Cochlostoma (Dalfreddia) porroi* (Strobel, 1850).

Diagnosis. — Elongated, club-shaped seminal receptacle. The pedunculus connects about posterior-ventrally to the bursa. The uterine gland is inserted close to the connection between the distal oviduct and the pedunculus (Fig. 13.6). Protoconch strong and dull, with 1.0-1.5 smooth whorls. The umbilicus is covered by the apertural lip.

Taxa: *porroi* (Strobel, 1850); *subalpinum* (Pini, 1884).

Range. — The subgenus is represented in the south-western part of the Alps (Fig. 11.4, orange circles).

Derivatio nominis. — The name is introduced to remember our dear friend Cesare Dal Freddo (Feltre, Italy), a passionate malacologist who passed away prematurely.

Clessiniella subgen. nov.

Type species: *Cochlostoma (Clessiniella) villae* (Strobel, 1851).

Diagnosis. — The pedunculus connects apically, with a conspicuously swollen part, with the bursa. The seminal receptacle is elongated club-shaped. The insertion of the uterine gland is situated close to the connection of the distal oviduct with the pedunculus (Fig. 13.4). Protoconch strong and dull, with riblets starting late. Columella solid. Operculum yellowish, rather thick.

Taxa: *tergestinum* (Westerlund, 1878); *anomphale* (Boeckel, 1939); *waldemari* (A.J. Wagner, 1897); *villae* (Strobel, 1851).

Range. — The subgenus has its main range in the eastern Alps, Istria, and the northern part of the Dinarids. *Cochlostoma (Clessiniella) villae* occurs disjunctly in the western part of the Italian region of Veneto (Fig. 11.4, yellow circles).

Remarks. — We designate *Cochlostoma (Clessiniella) villae* as type species. It is the earliest described species in the subgenus.

Derivatio nominis: *Clessiniella* is named after the German malacologist Stefan Clessin (1833–1911), who contributed substantially to our knowledge of the central European molluscan fauna.

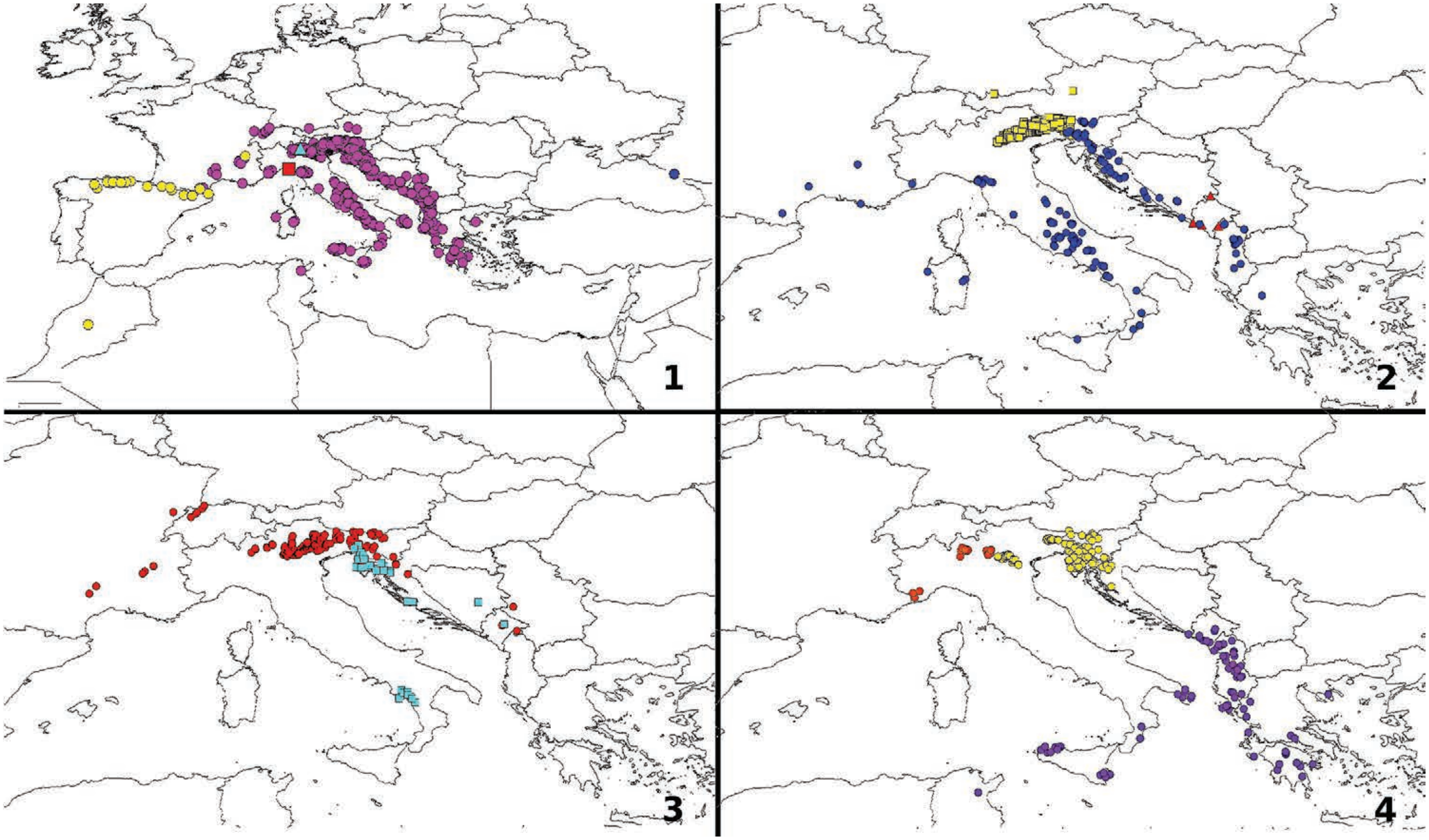


Fig. **11.** Distribution maps of the genera and subgenera, representing the records of material dealt with in this study. Map **1**: yellow circles, *Obscurella*; purple circles, *Cochlostoma*; red square, *Toffolettia*; cyan triangle, *Rhabdotakra*; blue circle, *Imerezia* gen. nov. Map **2**: blue circles, *Turritus*; yellow square, *Eupomatias*; red triangles, *Lovcenia.* Map **3**: red circles, *Cochlostoma*; cyan squares, *Wagneriola.* Map **4**: orange circles, *Dalfreddia*; yellow circles, *Clessiniella*; purple circles, *Auritus.*

Subgenus *Turritus* Westerlund, 1883

Turritus Westerlund, 1883: 72**.** Type species (design. Wenz, 1923: 1781**)**: *Pomatias stossichi* Hirc, 1881.

Hartmannia Newton, 1891: 346. Type species (original design.): *Cyclostoma patulum* Draparnaud, 1801.

Diagnosis. — There are two types of the female genitalia in *Turritus*, viz. (1) the pedunculus connects about ventrally to the bursa, and the seminal receptacle is oval (Fig. 5.4b)**,** with a short but distinct distal oviduct or (2) there is an eccentrical connection (not apical as in *Clessiniella* subgen. nov. or *Cochlostoma* s. str.) with mostly a club-shaped seminal receptacle (Fig. 13.8, 13.11, 13.12). The latter type reminds of that of *Dalfreddia* subgen. nov., a subgenus which is represented in the central Alps only, however. Moreover, in the *Turritus* species with a similar seminal receptacle and pedunculus, the uterine gland inserts far from the connection between the distal oviduct and the pedunculus and much closer in *Dalfreddia* subgen. nov.

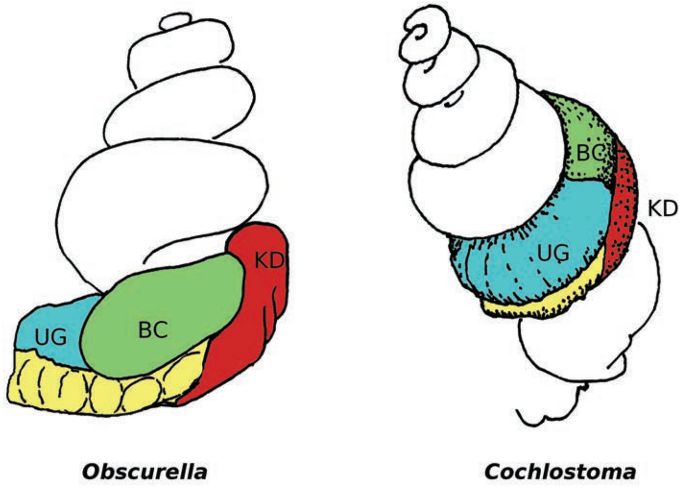


Fig. **12.** Relative position of the kidney in respect to the bursa copulatrix in *Obscurella* and *Cochlostoma*. Abbreviations: BC, bursa copulatrix; KD, kidney; UG, uterine gland.

The columella is either solid or tubular (*C. (T.) elegans* and closely related species: Fig. 10), but there is always a well defined muscle scar. This is the only *Cochlostoma* subgenus with some species with a tubular columella.

Taxa: *adamii* (Paulucci, 1879); *affine* (Benoit, 1876); *braueri* (A.J.Wagner, 1897); *crosseanum* (Paulucci, 1879); *elegans* (Clessin, 1879); *gracile* (Pfeiffer, 1849); *kleciaki* (Braun, 1887); *macei* (Bourguignat, 1869); *mariannae* Nordsieck, 2011; *montanum* (Issel, 1866); *mostarensis* (A.J. Wagner, 1906); *nanum* (Westerlund, 1879); *pageti* Klemm, 1962; *patulum* (Draparnaud, 1801); *sardoum* (Westerlund, 1890); *simrothi* (Caziot, 1908); *stossichi* (Hirc, 1881); *zawinkanum* (A.J. Wagner, 1906).

Range. — The species occur along the Mediterranean coast of Spain and France, the Apennine, Dinarids, Sicily and Sardinia (Fig. 11.2, blue circles).

Remarks. — In this speciose subgenus there are species complexes corresponding to more terminal branches of the phylogenetic tree, which have the same female genitalia type. Despite the lack of molecular data, *C. simrothi* (Caziot, 1908) and *C. macei* (Bourguignat, 1869) have been assigned to this subgenus because of their shells and the structure of the female genitalia.

Incertae sedis

The monotypic, nominal genus *Macaropoma* Kobelt & Moellendorff, 1898, was introduced for the allegedly Macaronesian species *Pomatias barthelemianum* Shuttleworth, 1852, which was described after a single specimen. Kobelt (1902: 536) listed this species as problematic and according to Bank et al. (2002: 205) it ".. is most probably not a Macaronesian taxon.". The holotype was posthumously illustrated by Shuttleworth (1975: pl. 6 fig. 14). Its identity cannot be established. As a consequence, *Macaropoma* cannot be classified at present.

Cochlostoma hueti (Kobelt, 1882) was never found again after 1853, when it was allegedly collected by Alfred Huet du Pavillon on tree trunks near Istanbul, Turkey, and reported as *Pomatias (Ciclostoma) obscurum* by Mortillet (1854: 6). The original description (Kobelt, 1882: 121), in which the author mentions that the species has only the dimensions of *obscurum*, but otherwise recalls *tessellatum*, and the only available picture (Kobelt, 1892: pl. 141 fig. 891) are insufficiently informative. Because of its distribution, the species might be more closely related to *Imerezia* gen. nov. than to *Cochlostoma*. However, Zilch (1958 : 59) listed *Pomatias hueti* as a synonym of *Cochlostoma (Obscurella) obscurum*, while mentioning that the two syntypes of this nominal taxon are lost. Maybe, Zilch was aware of the fact that Alfred Huet du Pavillon collected plants in the Pyrenees in the 1850s, and distrusted the improbable locality data.

Our preliminary molecular data, restricted to *H3* and *16S* sequences, suggest that '*Cochlostoma' cinerascens* (Rossmässler, 1837) occupies an isolated position within *Cochlostoma*. At the moment being we refrain from further conclusions, because our research material is too meagre. Only a single specimen was available for dissection. In the poorly preserved female the pedunculus connects posteriorly to the bursa; the seminal receptacle is club-shaped. The shell has a strong and dull protoconch with riblets starting after 1.2-1.4 whorls; the umbilicus is not covered by a lobe of the peristome. The species is known from the extreme South of

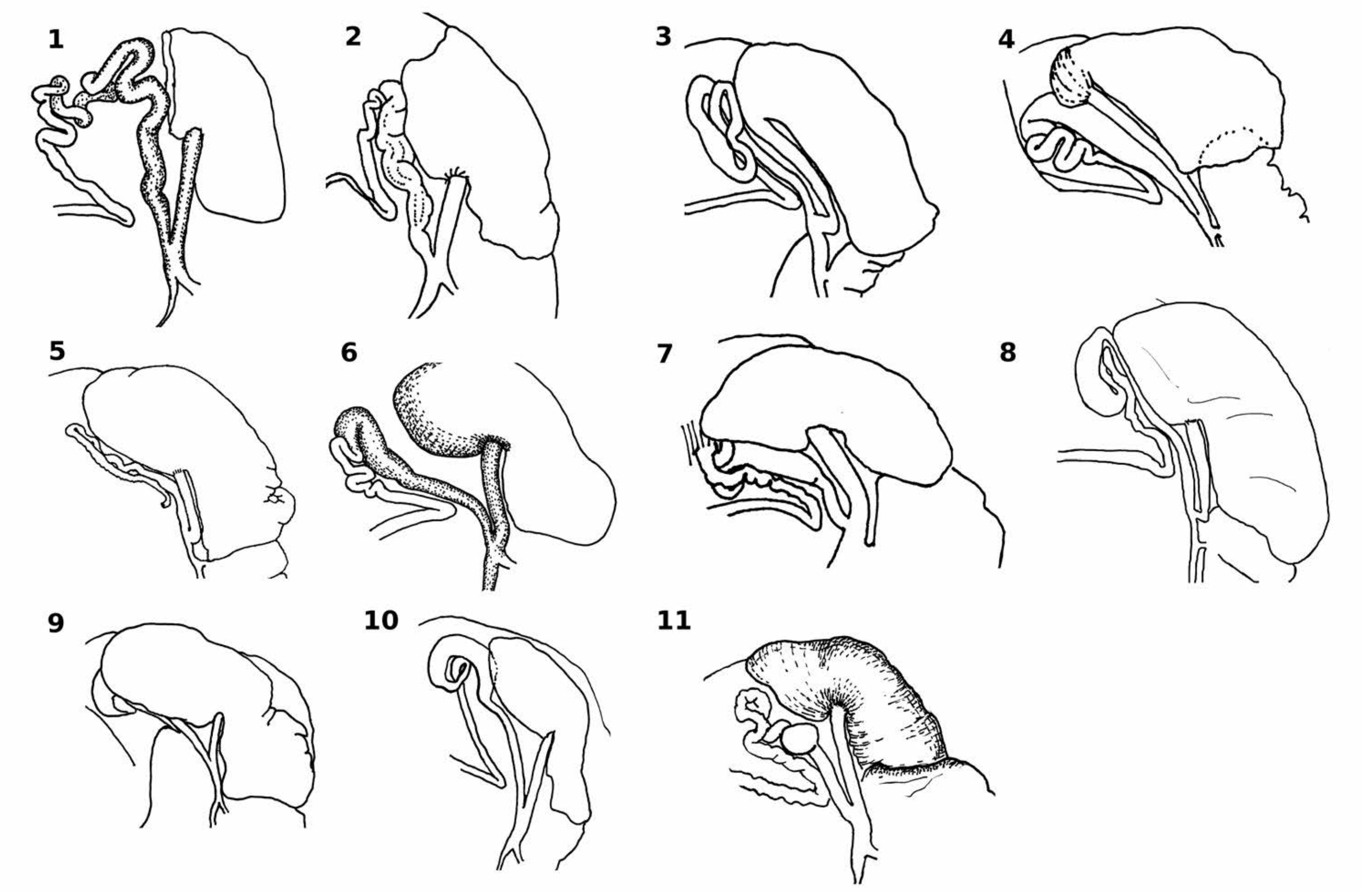


Fig. **13.** Characteristic parts of the female genitalia in the subgenera of *Cochlostoma.* **1**, *C. (Auritus) tessellatum*; **2** , *C. (Auritus) roseoli*; **3**, *C. (C.) septemspirale*; **4**, *C. (Clessiniella) tergestinum*; **5**, *C. (Lovcenia) erika*; **6**, *C. (Dalfreddia) porroi*; **7**, *C. (Turritus) adamii*; **8**, *C. (Wagneriola) (sturanii) scalariniformis*; **9**, *C. (Wagneriola) scalarinum*; **10**, *C. (Turritus) nanum*; **11**, *C. (Turritus) gracile*.

Croatia, close to Montenegro. It was traditionally assigned to *Cochlostoma* s. str. because of the shell with an open umbilicus.

Because of the lack of new material for dissection and DNA sequencing, we could not determine the taxonomic position of: *Cochlostoma atlanticus* (Bourguignat, 1863); *C. cretense* (Maltzan, 1887) [particularly interesting because of its distribution]; *C. barcaense* Brandt, 1958 [assigned by Brandt (1958) to *Cochlostoma* s. str.]; *C. dalmatinum* (Pfeiffer, 1863); *C. euboicum* (Westerlund, 1885) [assigned to *Turritus* by Schütt (1981)]; *C. euconus* (Ancey, 1888) [assigned by Zilch (1958) to the subgenus *Personatus*] ; *C. fontqueri* Haas, 1924 [often considered a subspecies of *C. (Turritus) patulum*] ; *C. mienisi* Schütt, 1978 [originally classified in the subgenus *Holcopoma*]; *C. letourneuxi* (Bourguignat, 1866) [assigned to the subgenus *Personatus* by Zilch (1958)] ; *C. sturanii* (A.J. Wagner, 1897) s. str. [however, two alleged subspecies could

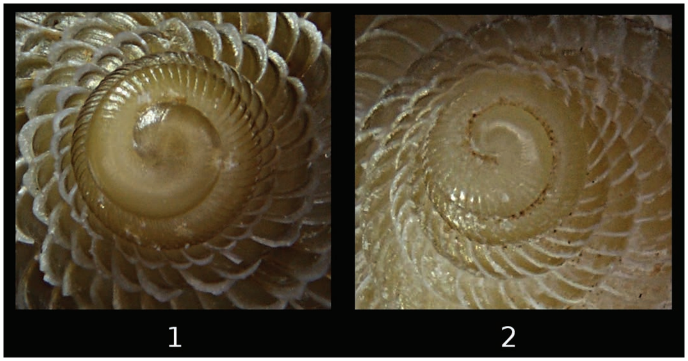


Fig. **14.** Sculpture of the protochonch. **1**, largely smooth in *Cochlostoma* (*Dalfreddia*) *porroi*; **2**, small smooth part in *Cochlostoma* (*Lovcenia*) *erika*.

be studied]; *C. susaense* Brandt, 1958 [originally assigned to the monotypic subgenus *Apolloniana* Brandt, 1958, which cannot be judged properly].

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