

A new species of *Chondrina* (Gastropoda, Pulmonata, Chondrinidae) from Piedmont (Northern Italy)

MARCO BODON

Dipartimento di Scienze Fisiche, della Terra e dell'Ambiente, Università di Siena, Via P.A. Mattioli 4, I-53100 Siena, Italy;
mabodon@tin.it [corresponding author]

GIANBATTISTA NARDI

Via Boschette 8/A, I-25064 Gussago, Brescia, Italy; gbnardi@libero.it

SIMONE CIANFANELLI

Museo di Storia Naturale, Sezione Zoologica de "La Specola", Università di Firenze, Via Romana 17, I-50125 Firenze, Italy;
simone.cianfanelli@unifi.it

BAS KOKSHOORN

Naturalis Biodiversity Center, P.O. Box 9517, NL-2300RA Leiden, The Netherlands;
bas.kokshoorn@naturalis.nl

65

A narrow range endemic species is described from NW Italy as *Chondrina feneriensis* spec. nov. The new species is classified with other centre-East Alpine taxa on the basis of a molecular phylogenetic analysis. It is closely related to *C. generosensis* Nordsieck, 1962. The two taxa differ morphologically in some characters of the shell and the genital tract, and in mitochondrial DNA sequence data. These differences, and the absence of intermediate forms, support its taxonomic status as a separate species, rather than a subspecies of *C. generosensis*.

Chondrina feneriensis spec. nov. is restricted to a small area in the Fenera massif in Piedmont, at the boundary between the Vercelli and the Novara districts, where it inhabits dry limestone cliffs.

Key words: Chondrinidae, taxonomy, ecology, distribution, Piedmont, Italy.

INTRODUCTION

The genus *Chondrina* Reichenbach, 1828, includes molluscs that are obligatorily associated with calcareous rocks. The genus is distributed in the Turanic-European-Mediterranean region. There are three areas with high species diversity in the genus, viz. the Iberian Peninsula with Morocco, the Alps, and the Balkans. The genus consists of more than 40 currently known species and several subspecies, but the number is slightly variable according to the different authors (Nordsieck, 1962, 1970; Gittenberger, 1973; Kerney et al., 1983; Gittenberger, 1984; Falkner, 1990; Schileyko, 1998; Gittenberger, 2002; Kokshoorn & Gittenberger, 2010; Schütt, 2010; Welter-Schultes, 2012; Bank, 2013).

The taxonomy of the genus has historically been based on morphological characteristics of the shell, because the genital tract is rather simple and generally devoid of important diagnostic characteristics. Only recently, revisions in the taxonomy of the genus have

been made based on DNA analyses (Kokshoorn et al., 2010).

Many of the Alpine species with a limited distribution are represented at the Italian side of the Alps. *Chondrina bergomensis* (Kuster, 1850) is an endemic species of the Bergamo province, in the central Prealps of Lombardy (Nordsieck, 1962; Graack, 1985; Manganelli et al., 1995; Eikenboom, 1996; Kokshoorn & Gittenberger, 2010; Welter-Schultes, 2012). *Chondrina generosensis* Nordsieck, 1962, is limited to the NW Lombardy and the neighbouring areas of Ticino (Switzerland) (Nordsieck, 1962; Gittenberger, 1973; Groh, 1990; Manganelli et al., 1995; Wüthrich, 1996; Proschwitz & Johannesson, 1996; Turner et al., 1998; Kokshoorn & Gittenberger, 2010; Boschi, 2011; Welter-Schultes, 2012; Rüetschi, 2013). *Chondrina megacheilos* (De Cristofori & Jan, 1832) is a polytypic species living in Italy (Alps and Prealps of Lombardy, Trentino-Alto Adige and western Venetia), in areas bordering Switzerland and in the southern Alps, between France and Liguria. Its subspecies are *C. m. megacheilos*, occurring in Lombardy and Ticino, *C. m. avenoides* (Westerlund, 1874) and *C. m. toscolana* (Schröder, 1913), present in more or less restricted areas along the central Alps, *C. m. frassiniana* Nardi, 2009, an endemic species of the Prealps of the Brescia province, *C. m. caziotana* Pilsbry, 1918, known from the western Alps, in a small area between the Alpes Maritimes in France and western Liguria (Nordsieck, 1962; Gittenberger, 1973; Kerney et al., 1983; Maassen, 1987; Manganelli et al., 1995; Eikenboom, 1996; Falkner & Stummer 1996; Nardi, 2009; Manganelli et al., 1995; Turner et al., 1998; Gerber, 2002; Kokshoorn & Gittenberger, 2010; Kokshoorn et al. 2010; Boschi, 2011; Gargominy et al., 2013; Welter-Schultes, 2012; Bank, 2013). *Chondrina multidentata* (Strobel, 1851), another polytypic species with three subspecies, i.e. *C. m. gredleriana* (Clessin, 1887), *C. m. multidentata* (Strobel, 1851) and *C. m. schista* (Westerlund, 1887), is distributed in the central-eastern Alps and Prealps, roughly between Lombardy and Friuli (Nordsieck, 1962; Gittenberger, 1973; Maassen, 1987; Boato et al., 1989; Manganelli et al., 1995; Eikenboom, 1996; Nardi, 2009; Kokshoorn et al. 2010; Kokshoorn & Gittenberger, 2010; Welter-Schultes, 2012; Bank, 2013). *Chondrina arcadica* (Reinhardt, 1881), another polytypic species with a large distribution in SE Europe, is represented in the NE Alps (Italy, Switzerland, Austria and Slovenia) with *C. a. clienta* (Westerlund, 1883) (Nordsieck, 1962; Gittenberger, 1973; Manganelli et al., 1995; Eikenboom, 1996; Boato et al., 1989; Nardi, 2009; Welter-Schultes, 2012). *Chondrina burtscheri* Falkner & Stummer, 1996, was described from the northern Alps of Austria, and has also doubtfully been reported from an isolated locality in Trentino-Alto Adige (Gerber, 2002; Nardi, 2009;

Kokshoorn & Gittenberger, 2010). Two other taxa are restricted to the French Alps, viz. *C. falkneri* Gittenberger, 2002, living in the departments Drôme and Isère, and *C. gerhardi* Gittenberger, 2002, known for a single locality in the department Hautes-Alpes (Gittenberger, 1973; Falkner et al., 2002; Gittenberger, 2002).

Chondrina avenacea (Bruguière, 1792), the polytypic type-species of the genus, is widespread in Italy in the Alps, in peninsular Italy, Sicily and Sardinia, as well as in many other European countries, from Spain to Croatia. Next to the nominotypical subspecies, which has a large range in southern Europe, there are many other subspecies, which are distributed in the eastern Prealps and the northern Balkans: *C. a. istriana* Ehrmann, 1931, *C. a. latilabris* (Stossich, 1895), *C. a. lepta* (Westerlund, 1887), *C. a. lessinica* (Adami, 1885) and *C. a. veneta* Nordsieck, 1962 (Nordsieck, 1962, 1970; Gittenberger, 1973; Boato et al., 1985; Wolf & Rähle, 1987; Boato et al., 1989; Manganelli et al., 1995; Falkner & Stummer, 1996; Turner et al., 1998; Gavetti et al., 2008; Liberto et al., 2010; Welter-Schultes, 2012; Bank, 2013; Pall-Gergely, 2013).

Rarity and fragmentation of limestone areas in the NW Italian Alps are responsible for the scarce occurrence of the genus *Chondrina* in northern Piedmont and Valle d'Aosta. The only records concern *C. a. avenacea*, historically collected in some localities of the Aosta province (Stabile, 1864; Lessona, 1880; Boettger, 1883; Pegorari, 1883; Pollonera, 1885). More recently the subspecies has also been found in NE Piedmont (province of Verbano-Cusio-Ossola) at two localities, viz. the Val Formazza (Nordsieck, 1962) and the NW slope of Agaro Lake (unpublished personal data). It has also been recorded in Val Divedro, on the southern slope of the Swiss Alps (Turner et al., 1998; Boschi, 2011). During searches carried out in the period 1986-2014 on the limestone massif of M. Fenera in NE Piedmont (at the boundary between the provinces of Vercelli and Novara) some populations of *Chondrina* have been sampled. These samples represent a single taxon, which is morphologically and genetically different from all other known taxa. It is considered a new species, which is described in this paper.

MATERIAL AND METHODS

Specimens were collected by hand from limestone cliffs. Dry shells were prepared to study shell morphology. A part of the samples was fixed in 80% ethanol to study the genitalia. Few specimens were fixed in 95% ethanol for DNA analysis.

Bodies were isolated by crushing the shells and were dissected using very fine, pointed watchmaker's forceps under a light stereo microscope. The genitalia



Fig. 1. Shells of *Chondrina feneriensis* spec. nov. (A-L) and *Chondrina generosensis* Nordsieck, 1962 (M-Q). A, holotype collected at Colma, M. Fenera (Valduggia, Vercelli), S. Cianfanelli, E. Talenti & M. Calcagno leg. 14/X/1990 (MZUFC GC/46039); B-F, paratypes (B-F) collected in the same locality, S. Cianfanelli, E. Talenti & M. Calcagno leg. 14/X/1990 (MZUFC GC/46040); G-I, paratypes collected near the Buco della Bondaccia, M. Fenera (Borgosesia, Vercelli), M. Bodon, F. Stoch & T. Pascutto leg. 13/VIII/1997 (MZUFC GC/46347); J-L, paratypes collected near the Grotte di Magiaiga, Ara, M. Fenera (Grignasco, Novara), M. Bodon leg. 20/V/1990 (MZUFC GC/46346); M-Q, shells collected at NE of the top of M. Generoso (San Fedele Intelvi, Como), G. Nardi, A. Braccia & R. Frassine leg. 13/VIII/2013 (MZUFC GC/45790).

were drawn using a camera lucida. All the parameters (shells height, shell diameter, aperture height and aperture diameter) were measured using a precision calliper, a millimetric lens, or a software installed on the light microscope. Radulae were obtained by dissecting out buccal bulbs. These were washed in distilled water, mounted on copper blocks, sputter-coated with gold and photographed using a

scanning electron microscope. Shells were photographed using a digital camera mounted on a light stereo microscope and processed with software for merging multiple focal planes.

For details on the acquisition of the molecular data, see Kokshoorn et al. (2010). Four individuals, representing each of the three sampling locations of *Chondrina* spec. nov., were used for DNA analysis.

Species	Locality	H	D	h	d	N
<i>C. feneriensis</i>	Hamlet Colma (Valduggia, VC)	5.19 ± 0.28	2.18 ± 0.09	1.65 ± 0.10	1.37 ± 0.07	30
		(4.60-5.71)	(1.98-2.37)	(1.44-1.78)	(1.19-1.50)	
	Near the cave "Buco della Bondaccia" (Borgosesia, VC)	5.63 ± 0.35	2.27 ± 0.08	1.89 ± 0.16	1.58 ± 0.11	30
		(5.01-6.30)	(2.11-2.41)	(1.62-2.28)	(1.43-1.83)	
	The "Belvedere" (Borgosesia, VC)	5.98 ± 0.30	2.41 ± 0.10	1.91 ± 0.08	1.59 ± 0.10	4
		(5.79-6.43)	(2.33-2.51)	(1.80-2.00)	(1.50-1.72)	
	Near the cave "Grotta della Finestra" (Borgosesia, VC)	5.70 ± 0.22	2.28 ± 0.11	1.88 ± 0.07	1.55 ± 0.08	15
		(5.40-6.33)	(2.15-2.51)	(1.74-1.97)	(1.41-1.71)	
	Near the "Grotte di Magiaiga" (Grignasco, NO)	5.80 ± 0.25	2.32 ± 0.11	1.80 ± 0.05	1.52 ± 0.05	14
		(5.30-6.18)	(2.15-2.53)	(1.74-1.90)	(1.43-1.62)	
	Below the "Rifugio Belvedere" (Borgosesia, VC); shell deposit	5.90 ± 0.21	2.40 ± 0.06	1.87 ± 0.08	1.60 ± 0.06	5
		(5.64-6.21)	(2.31-2.48)	(1.74-1.96)	(1.51-1.66)	
<i>C. generosensis</i>	NE of the top of M. Generoso, 1525 m a.s.l. (San Fedele Intelvi, CO), NR0186, G. Nardi, A. Braccia & R. Frassine leg. 13/08/2013	6.29 ± 0.60	2.59 ± 0.14	2.23 ± 0.28	1.65 ± 0.12	14
		(5.42-7.36)	(2.36-2.82)	(1.93-2.80)	(1.45-1.91)	
	Poncione di Ganna, 800 m a.s.l. (Valganna, VA), MR8782, M. Bodon & E. Bodon leg. 14/04/2013	5.32	2.24	1.8	1.44	1
	Forra di Valle Fredda, 450 a.s.l. (Induno Olona, VA), MR8678, M. Bodon & E. Bodon leg. 30/09/2012	5.42	2.27	1.67	1.44	1
	Near the beer factory, 400 m a.s.l. (Induno Olona, VA), MR8677, M. Bodon & E. Bodon leg. 26/05/2013	6.33 ± 0.28	2.39 ± 0.10	1.89 ± 0.04	1.56 ± 0.02	3
(6.01-6.50)		(2.29-2.48)	(1.84-1.93)	(1.54-1.58)		

Table 1. Shell parameters of five living populations and one shell deposit of *Chondrina feneriensis* spec. nov. from M. Fenera (Piedmont) and four living populations of *Chondrina generosensis* Nordsieck, 1962, from Lombardy. Acronyms: H = shell height, D = shell diameter, h = mouth height, d = mouth diameter (aperture minor diameter), N = number of shells. Mean ± standard deviation; min and max value in parenthesis.

Some presumably (based on morphological and biogeographical data) closely related taxa were included in the DNA analyses for comparison (see Table 3). *Chondrina avenacea* (Bruguière, 1792) was selected as an outgroup. A section of the mitochondrial Cytochrome Oxidase subunit I gene was sequenced (forward and reverse sequence) for each individual. The obtained DNA sequences were edited manually and aligned using ClustalW (Thompson et al., 1994). Neighbour-Joining analysis was performed using uncorrected pairwise distances. Branch support analyses

were performed using a bootstrap algorithm under both maximum likelihood (100 replicates) and parsimony (1,000 replicates) optimality criterion (Paup v4.0a146; Swofford, 2002). The maximum likelihood analysis was performed under the General Time Reversible model including a gamma distribution (shape 1.1818) and the proportion of invariable sites (0.5694). The resulting phenetic tree, including branch support, is shown in Figure 6.

The material examined is preserved in the following collections: Museo di Storia Naturale dell'Uni-

Species	Locality	vd	e	pp	dp	bc	dbc	fo	v
<i>C. feneriensis</i>	Hamlet Colma (Valduggia, VC)	1,89	1,18	1,25	0,79	1,54	2,11	0,50	0,71
		2,11	1,64	1,21	0,79	1,18	1,64	0,46	0,93
	Near the cave "Buco della Bondaccia" (Borgosesia, VC)	1,89	1,82	1,21	0,71	1,68	2,14	0,36	0,68
	Near the cave "Grotta della Finestra" (Borgosesia, VC)	1,57	1,21	1,21	0,75	1,61	1,14	0,39	0,61
	Near the "Grotte di Magiaiga" (Grignasco, NO)	1,89	1,39	1,18	0,86	1,32	1,93	0,43	1,00
		2,25	1,32	1,36	0,89	1,43	1,39	0,36	0,82
<i>C. generosensis</i>	NE of the top of M. Generoso, 1525 m a.s.l. (San Fedele Intelvi, CO), NR0186, G. Nardi, A. Braccia & R. Frassine leg. 13/08/2013	2,79	2,07	1,43	1,04	1,82	3,25	0,32	0,71
		2,61	1,71	1,36	1,07	2,29	3,32	0,46	1,14
	Poncione di Ganna, 800 m a.s.l. (Valganna, VA), MR8782, M. Bodon & E. Bodon leg. 14/04/2013	2,21	1,61	1,32	1,14	1,79	2,14	0,39	0,71

Table 2. Anatomical parameters of six specimens from four populations of *Chondrina feneriensis* spec. nov. from M. Fenera (Piedmont) and three specimens from two populations of *Chondrina generosensis* Nordsieck, 1962, from Lombardy. Acronyms in section Material and Methods.

versità di Firenze, sezione di Zoologia de "La Specola", Via Romana 17, I-50125 Florence, Italy (MZUFC); Naturalis Biodiversity Center, P.O. Box 9517, NL-2300RA Leiden, The Netherlands (RMNH); M. Bodon, Via delle Eliche 100/8, I-16148 Genoa, Italy (MBC); S. Cianfanelli, Via Monferrato, 3, I-50142 Florence, Italy (SCC); G. Nardi, Via Boschette 8/A, I-25064 Gussago (BS), Italy (GNC); E. Talenti, Piazza Ferruccio Parri 4, I-50066 Incisa Valdarno (FI), Italy (ETC); Gruppo Speleologico Biellese C.A.I., Via Malvezzi 3, I-13051 Biella, Italy (GSBC); Soprintendenza archeologica del Piemonte, Piazza San Giovanni 2, I-10122 Turin, Italy (SAPC).

Anatomical acronyms (Figs 2, 6; Table 2): ag = albumen gland; bc = bursa copulatrix; dbc = duct of the bursa copulatrix; dp = distal penis; e = epiphallus; f = flagellum; fhd = first hermafrodite duct; fo = free oviduct; ga = genital atrium; o = ovotestis or gonad; p = papillae; pos = prostatic ovispermiduct; pp = proximal penis; prm = penial retractor muscle; uos = uterine ovispermiduct; v = vagina; vd = vas deferens.

The collection data are listed as follows: locality name, mountain slopes, altitude, municipality and province in parentheses, UTM ED50 coordinates, collector(s) and date, number of specimens (preserved in ethanol or analysed for DNA) and/or number of shells (dry specimens or shells).

SYSTEMATIC PART

Family Chondrinidae Steenberg, 1925
Subfamily Chondrininae Steenberg, 1925

Chondrina Reichenbach, 1828

Chondrina feneriensis spec. nov. (Figs 1-3)

Type material. – Holotype: Italy, Piedmont, Vercelli, Valduggia, hamlet Colma, eastern slope of M. Fenera, 730 m a.s.l. UTM 32T MR4762, S. Cianfanelli, E. Talenti & M. Calcagno leg. 14.x.1990 (shell, MZUFC GC/46039). Paratypes: from type locality, M. Bodon, E. Pezzoli leg. 05.iv.1986 (2 dissected specimens, MZUFC GC/45672; 1 shell, MBC; 2 radulae, MZUFC GC/45672 stub SEM MB/90); S. Cianfanelli, E. Talenti & M. Calcagno leg. 14.x.1990 (2 specimens, 6 shells, MZUFC GC/46040, stub SEM MZ/254, 255 (2 radulae), 256 (shells)); 10 specimens, RMNH; 13 specimens, 19 shells, SCC 1893/105; 3 shells, ETC); M. Bodon, E. Bodon & G. Nardi leg. 21/X/2012 (3 specimens processed for DNA, RMNH; 2 shells, MBC).

Entrance of the cave "Buco della Bondaccia" (n. 2505 Pi), western slope of M. Fenera, 690 m a.s.l. (Borgosesia, Vercelli), 32T MR4662, M. Bodon, E. Bodon & G. Nardi leg. 21.x.2012 (7 shells, MBC).

Near the cave "Buco della Bondaccia", western slope of M. Fenera, 690 m a.s.l. (Borgosesia, Vercelli), 32T MR4662, M.

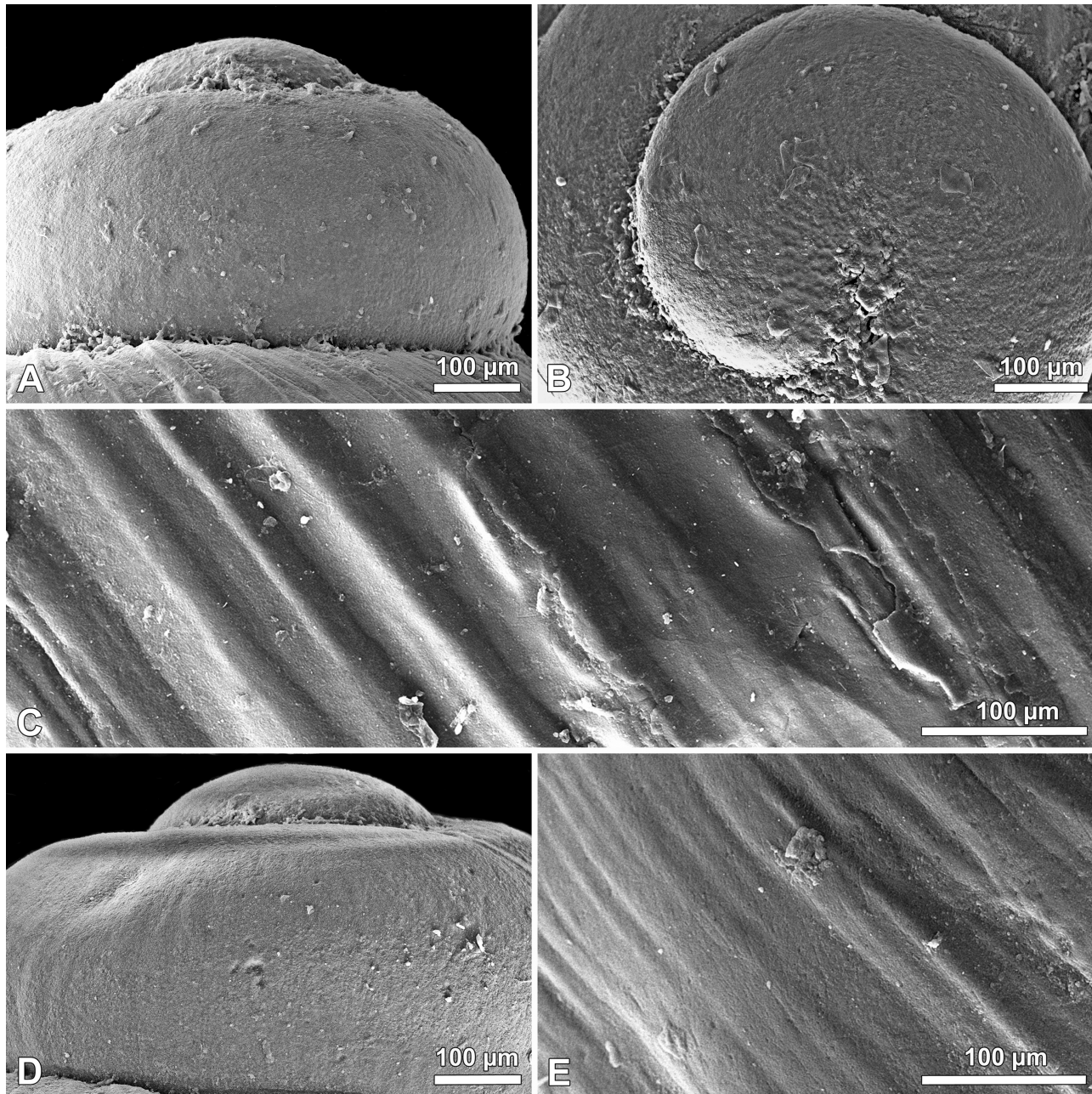


Fig. 2. High magnification of protoconch (first whorl), lateral view (**A, D**), apical view (**B**) and teleoconch on penultimate whorl (**C, E**) of *Chondrina feneriensis* spec. nov. (**A-C**) and *Chondrina generosensis* (**D-E**). Shells collected at Colma, M. Fenera (Valduggia, Vercelli), S. Cianfanelli, E. Talenti & M. Calcagno leg. 14/X/1990 (A-B, MZUFC GC/ 46040 stub SEM 256) and at NE of the top of M. Generoso (San Fedele Intelvi, Como), G. Nardi, A. Braccia & R. Frassine leg. 13/VIII/2013 (C-D, MZUFC GC/ 45790 stub SEM 256).

Bodon, F. Stoch & T. Pascutto leg. 13.viii.1997 (6 specimens, 10 shells, RMNH; 3 shells, MZUFC GC/46347); M. Bodon, E. Bodon & G. Nardi leg. 21.x.2012 (1 dissected specimen, 2 specimens, MZUFC GC/46936; 4 shells, MBC; 7 specimens, 10 shells, GNC; 3 specimens processed for DNA and 2 specimens, RMNH).

"Il Belvedere", western slope of M. Fenera, 690 m a.s.l. (Borgosesia, Vercelli), 32T MR4662, M. Bodon, F. Stoch & T. Pascutto leg. 13.viii.1997 (4 shells, MBC; 1 shell, GSBC).

Near the cave "Grotta della Finestra", below the "Belvedere", western slope of M. Fenera, 675 m a.s.l. (Borgosesia, Vercelli), 32T MR4662, M. Bodon, E. Bodon & G. Nardi leg.

21.x.2012 (1 dissected specimen, 1 specimen, MZUFC GC/46934; 6 shells, MBC; 3 specimens, 7 shells GNC; 3 specimens processed for DNA and 2 specimens, RMNH).

Near the caves "Grotte di Magiaiga", Ara, southern slope of M. Fenera, 400 m a.s.l. (Grignasco, Novara), 32T MR4760, M. Bodon & E. Pezzoli leg. 05.iv.1986 (2 dissected specimens, 3 specimens, MZUFC GC/46935; 5 shells, MBC); M. Bodon & G. Vezzani leg. 20.v.1990 (3 shells, MZUFC GC/46346, 7 shells, RMNH).

Other material examined. – Shells collected during archaeological excavations in 1966-1978 near the caves, western slope of M. Fenera (Borgosesia, Vercelli), 32T MR4760: Riparo del

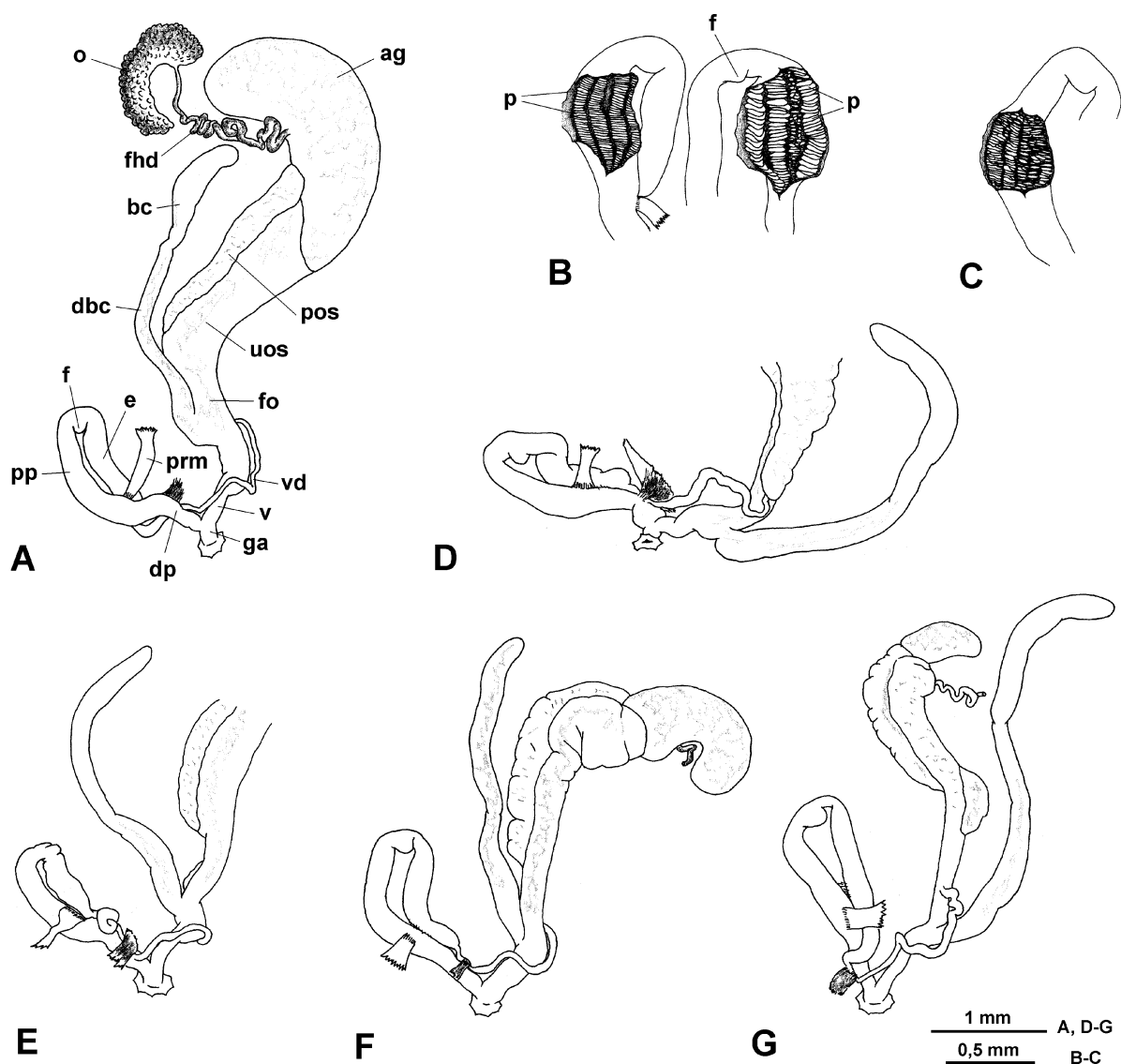


Fig. 3. Genitalia of *Chondrina feneriensis* spec. nov. Whole genitalia (A); inner structure of the proximal penis (B, left; C) and of the ephiphallus (B, right); distal genitalia (D, E); whole genitalia (gonad excluded; F-G). Specimens collected at Colma, M. Fenera (Valduggia, Vercelli), M. Bodon & E. Pezzoli leg. 05/IV/1986 (A-B, D, MZUFC GC/45672); near the Grotta della Finestra, below the Belvedere, M. Fenera (Borgosesia, Vercelli), M. Bodon, E. Bodon & G. Nardi leg. 21/X/2012 (C, F, MZUFC GC/46934); near the Grotte di Magiaiga, Ara, M. Fenera (Grignasco, Novara), M. Bodon & E. Pezzoli leg. 05/IV/1986 (E, MZUFC GC/46935); near the Buco della Bondaccia, M. Fenera (Borgosesia, Vercelli), M. Bodon, E. Bodon & G. Nardi leg. 21/X/2012 (G, MZUFC GC/46936). Acronyms in section Material and Methods.

Belvedere, inner deposits, Late Pleistocene (Early-Middle Late Glacial) fossils (layer A2.1: MF4 261, 1 shell, SAPC; MF4 752, 1 shell, SAPC), Holocene (Recent Dryas to Preboreal/Boreal) fossils (layer A1.2: MF4 679, 1 shell, SAPC; layer A1.1: MF4 645, 1 shell, SAPC; MF4 658, 1 shell, SAPC; layer A1: MF4 251, 1 shell, SAPC; MF4 436, 1 shell, SAPC); Riparo del Belvedere, outer deposits, Pleistocene (maybe Early-Middle Late Glacial) fossils (MF4E 825, 1 shell, SAPC), maybe Holocene fossils (MF4E 58, 2 shells, SAPC; MF4E 72, 1 shell, SAPC); limestone cliff located below the "Belvedere", present deposit (MFa 1, 2 shells, SAPC, 5 shells, MBC; MFa 4 G1, 2 shells, SAPC).

Diagnosis. – Shell less than 6.5 mm high, pale brown-yellowish, cylindro-conical to conical, surface finely ribbed-striated. Aperture with angularis, parietalis and columellaris, no or very small spiralis, small infracolumellaris, two short palatal plicae, and sometimes also an obsolete infrapalatal plica. Genitalia with a rudimental, rounded flagellum between ephiphallus and penis.

Shell (165 shells or specimens examined; Figs 1 A-L, 2 A-C). – Shell dextral, rather thin and slender, pale brown-yellowish, slightly translucent, cylindro-coni-

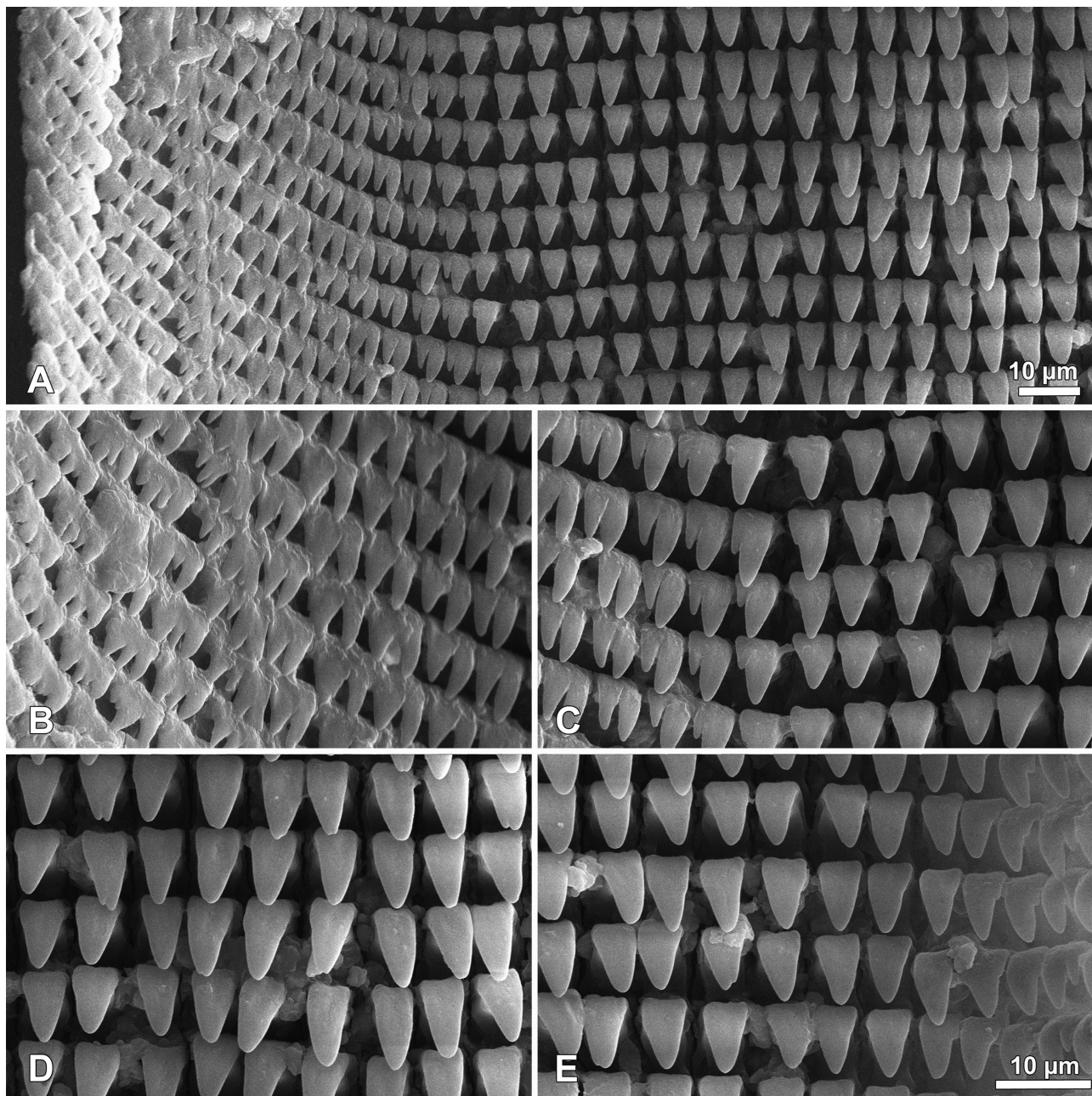


Fig. 4. Radula of *Chondrina feneriensis* spec. nov. Half portion of radula (A); magnification of marginal teeth (B); magnification of marginal and lateral teeth (C); magnification of lateral and central teeth (D); magnification of central and lateral teeth (E). Specimen collected at Colma, M. Fenera (Valduggia, Vercelli), S. Cianfanelli & M. Calcagno leg. 14/X/1990 (MZUFC GC/46040 stub SEM 255).

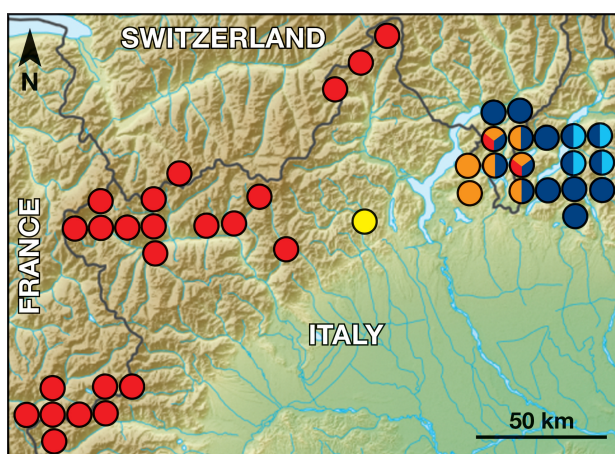


Fig. 5. Distribution of the genus *Chondrina* in southern Alpine NE area (Northern Piedmont, NE Lombardy and boundary areas of France and Switzerland). Red circles: *C. avenacea avenacea*; yellow circle: *C. feneriensis* spec. nov.; orange circles: *C. generosensis*; dark blue circles: *C. megacheilos* (*C. m. megacheilos* and/or *C. m. avenoides*); light blue circles: *C. multidentata multidentata*. Records on the basis of the studied materials, personal unpublished data, literature data and MZUFC data.

Sample code	Taxon ID	Locality	District	State	Quota m a.s.l.	UTM ED50	Collection date
BK1408	<i>Chondrina avenacea avenacea</i>	Serravezza, Slope E of Monte Pelato	Tuscany	Italy	1100	32T NP9879	6/16/13
BK1413	<i>Chondrina megacheilos avenoides</i>	S. Anna d'Alfaedo, Km 7.5 of the road 57 between Peri and Fosse, Monti Lessini	Venetia	Italy	800	32T PR4854	9/8/12
BK1414	<i>Chondrina megacheilos avenoides</i>	Breonio, old church of San Marziale, Monti Lessini	Venetia	Italy	850	32T PR5057	9/8/12
BK1425	<i>Chondrina megacheilos megacheilos</i>	Ballabio, Monte Tabor, near Balisio	Lombardy	Italy	900	32T NR3485	7/6/13
BK1426	<i>Chondrina megacheilos megacheilos</i>	Introbio, Cantaliberti, NW Zucco Angelone	Lombardy	Italy	600	32T NR3590	7/6/13
BK1427	<i>Chondrina megacheilos megacheilos</i>	Pasturo, Ponte di Chiuso, near the Rocca di Baiedo	Lombardy	Italy	570	32T NR3490	7/6/13
BK1428	<i>Chondrina megacheilos megacheilos</i>	Cassina Valsassina, a little S of Cascina Fraccia	Lombardy	Italy	1100	32T NR3884	7/6/13
BK1429	<i>Chondrina megacheilos toscolana</i>	Toscolano Maderno, SW of Monte Castello di Gaino, middle Val Toscolano	Lombardy	Italy	280	32T PR2558	5/26/13
BK1430	<i>Chondrina megacheilos toscolana</i>	Valvestino, Km 21 of road 20 of Valvestino, SE of Turano	Lombardy	Italy	580	32T PR2468	7/27/13
BK1431	<i>Chondrina megacheilos frassineiana</i>	Lavenone, slope SW of Cima Caldoline, Valle Sabbia	Lombardy	Italy	1800	32T PR0972	9/16/12
BK1432	<i>Chondrina megacheilos frassineiana</i>	Lavenone, Passo delle Portole, SW Dosso Alto	Lombardy	Italy	1700	32T PR0973	9/16/12
BK1434	<i>Chondrina megacheilos caziotana</i>	Pigna, Monte Pietravecchia, slope ESE along the Sentiero degli Alpini	Liguria	Italy	1300	32T LP9371	6/24/13
BK1435	<i>Chondrina megacheilos caziotana</i>	Saorge, slope SW of Monte Toraggio near the Fontaine Dragurine	Alpes-Maritimes	France	1800	32T LP9270	6/23/13
BK1436	<i>Chondrina multidentata schista</i>	Ospitale di Cadore, near the Fienile Varlonga	Venetia	Italy	820	33T TM9335	6/25/13
BK1437	<i>Chondrina multidentata schista</i>	Castellavazzo, between Codissago and Casso, valley of Torrente Vaioint	Venetia	Italy	755	33T TM9327	6/25/13
BK1438	<i>Chondrina bergomensis</i>	Villa d'Almè, road 470 of Val Brembana, between Villa d'Almè and Sedrina	Lombardy	Italy	290	32T NR4788	9/22/12
BK1439	<i>Chondrina bergomensis</i>	Berbenno, Km 22.5 of the road 17 between Berbenno and Ponte Giurino, Valle Imagna	Lombardy	Italy	550	32T NR4473	9/22/12
BK1440	<i>Chondrina generosensis</i>	Valganna, Poncione di Ganna	Lombardy	Italy	800	32T MR8782	4/14/13
BK1441	<i>Chondrina generosensis</i>	Induno Olona, Fabbrica di Birra, Valganna	Lombardy	Italy	400	32T MR8677	5/27/13
BK1442	<i>Chondrina generosensis</i>	San Fedele Intelvi, NE of the top of Monte Generoso	Lombardy	Italy	1525	32T NR0186	8/13/13
BK1444A	<i>Chondrina feneriensis</i>	Borgosesia, near Buco della Bondaccia, Monte Fenera	Piedmont	Italy	690	32T MR4662	10/21/12
BK1445A, B	<i>Chondrina feneriensis</i>	Borgosesia, near the cave Grotta della Finestra, Monte Fenera	Piedmont	Italy	675	32T MR4662	10/21/12
BK1446	<i>Chondrina feneriensis</i>	Valduggia, Colma, Monte Fenera	Piedmont	Italy	720	32T MR4762	10/21/12
RMNH 72606	<i>Chondrina multidentata gredleriana</i>	Belluno, Peron	Venetia	Italy		33T TM71	1968
RMNH 102859	<i>Chondrina multidentata multidentata</i>	Bergamo, Val Taleggio	Lombardy	Italy		32T NR48	2005
RMNH 102874	<i>Chondrina megacheilos avenoides</i>	Brescia, Toscolano	Lombardy	Italy		32T PR25	2005
BK0714A	<i>Chondrina burtscheri</i>	Bludenz, Montikel mountain	Voralberg	Austria		32T NT62	2007

Table 3. List of the samples subjected to DNA analyses.

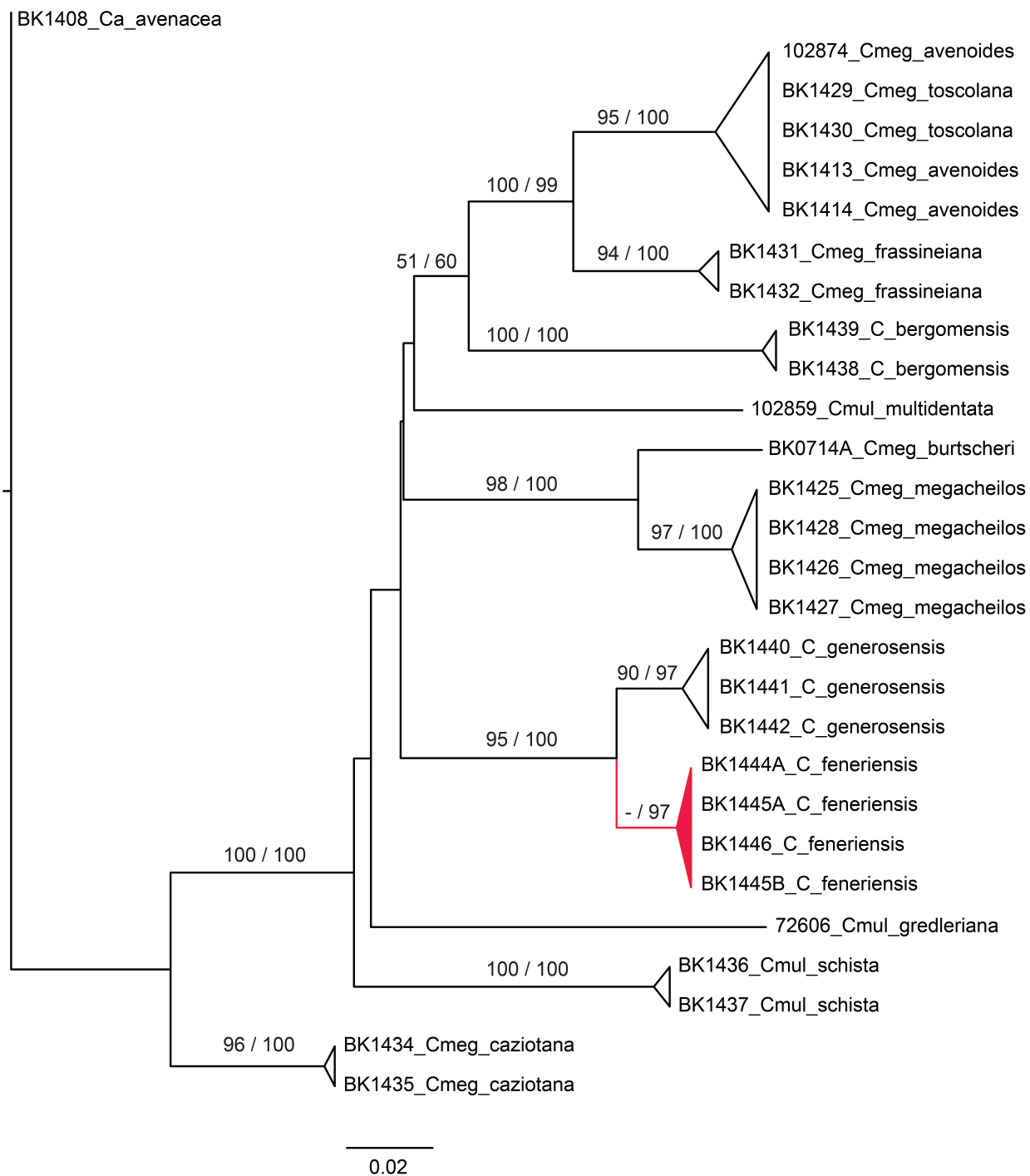


Fig. 6. Neighbour-joining cladogram based on uncorrected pairwise distances between the DNA sequences. The clade containing the DNA sequences of *C. feneriensis* spec. nov. is highlighted in red. Branch lengths indicate uncorrected pairwise distances between taxa. Branch support > 50 % is provided for maximum likelihood and parsimony criterion respectively.

cal to conical with an acute apex, consisting of $6\frac{1}{2}$ - $7\frac{1}{2}$ slightly convex whorls, regularly increasing in size. Last whorl measuring about half the shell height; sutures deep. Protoconch inflated, granular. Surface finely covered by oblique, prominent, and regular longitudinal ribs. Aperture suboval, prosocline, basally rounded; peristome interrupted, thin, whitish, slightly thickened by a reflected white callus, mostly in the

columellar area. Aperture with 4-5 lamellae and 2-3 plicae. Lamellae: well developed angularis, sometimes a very small and deep spiralis, parietalis of the same size as the columellaris, small or very small infracolumellaris; two equally long, rather short palatal plicae, situated centrally, not reaching the peristome, sometimes an onsolete or tubercle-like infrapalatal plica. Umbilicus narrowly open, slit-like.

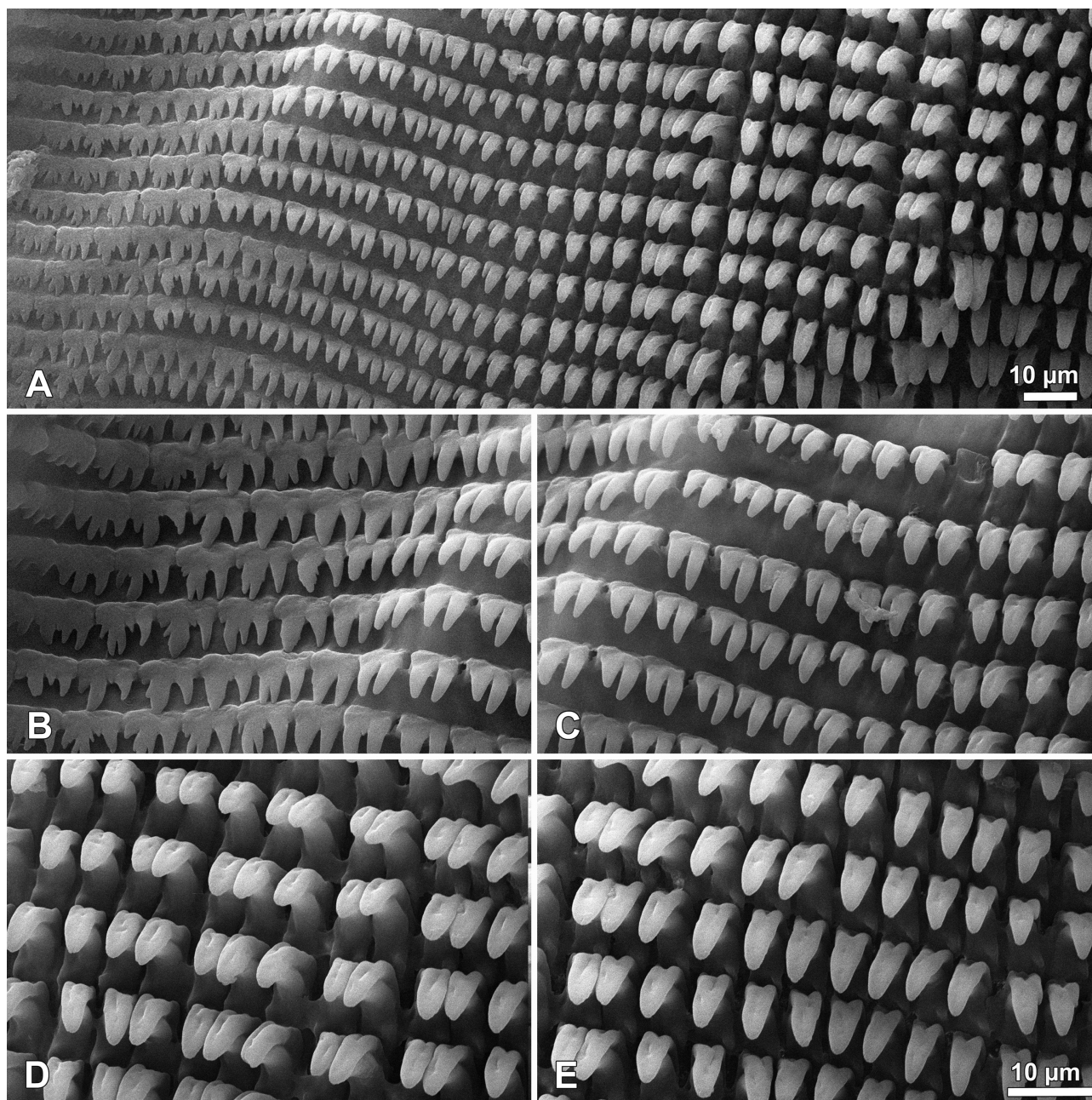


Fig. 7. Radula of *Chondrina generosensis* Nordsieck, 1962. Half portion of radula (A); magnification of marginal teeth (B); magnification of marginal and lateral teeth (C); magnification of lateral and central teeth (D); magnification of central and lateral teeth. Specimen collected at NE of the top of M. Generoso (San Fedele Intelvi, Como), G. Nardi, A. Braccia & R. Frassine leg. 13/VIII/2013 (MZUFC GC/45790 stub SEM MB/91).

Dimensions (Table 1). – Shell height 4.60 - 6.43 mm; diameter 1.98 - 2.53 mm; aperture height 1.44 - 2.28 mm; aperture diameter 1.19 - 1.83 mm.

Body. – Grey; tentacles and sole lightest.

Genitalia (6 specimens examined; Fig. 3). – Small ovotestis and convoluted hermaphrodite duct blackish; albumen gland variable in size; long ovispermiduct, continued in a short free oviduct and, beyond the duct of the bursa copulatrix, in a rather short and thin vagina, ending in a small genital atrium. Duct of the bursa copulatrix very long, without diverticulum;

bursa copulatrix long to very long, cylindrical or banana-like, rounded at the apex and reaching albumen gland. Thin and sinuous vas deferens, ending at the tip of the ephiphallus, where it is followed by a short, rounded, rudimental but clear flagellum and by a cylindrical penis, which is longer than the ephiphallus. A short penial retractor muscle is inserted between the proximal and the distal part of the penis; proximal penis slightly shorter than distal one; small branch of right ommatophore retractor muscle inserting at the distal penis and vas deferens wall, near

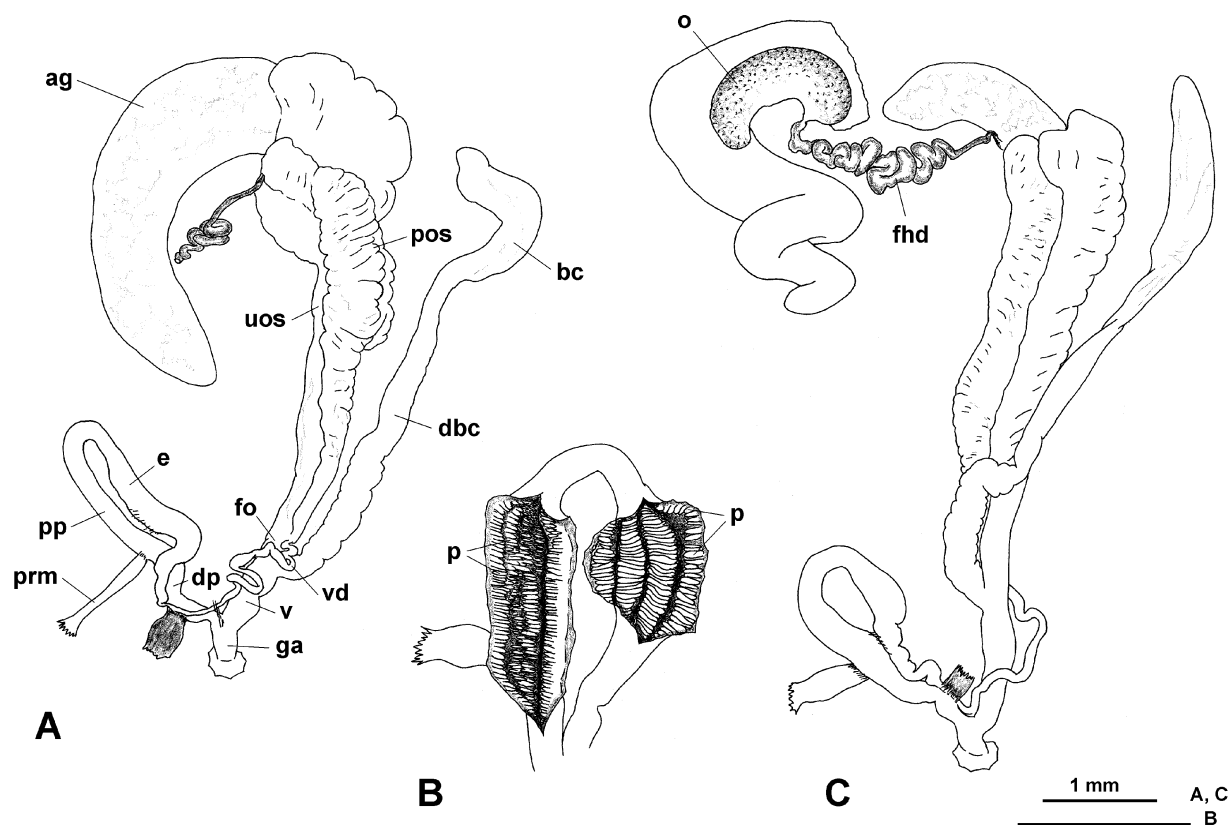


Fig. 8. Genitalia of *Chondrina generosensis* Nordsieck, 1962. Whole genitalia (gonad excluded, **A**); inner structure of the proximal penis (**B**, left), and of the ephiphallus (**B**, right); whole genitalia (**C**). Specimens collected at NE of the top of M. Generoso (San Fedele Intelvi, Como), G. Nardi, A. Braccia & R. Frassinale leg. 13/VIII/2013 (MZUFC GC/45790). Acronyms in section Material and Methods.

genital atrium. Ephiphallus and penis walls with internal longitudinal rows of papillae: 3 rows of papillae in the ephiphallus, 2 elliptical and 1 subtriangular, and a series of secondary, very small papillae between the elliptical ones; 4-6 rows of elliptical or more irregular papillae in the proximal penis.

Radula (4 examined; Fig. 4). – With 90-100 parallel rows of teeth, each of which with c. 63-65 teeth. The central, unicuspid tooth has a prominent mesocone. It is flanked by 14-16 unicuspid lateral teeth at both sides. The following 3-4 bicuspid lateral teeth have a strong mesocone and a small ectocone. The 10-16 marginal teeth gradually change in the number and shapes of the cusps; the initial 4-6 marginal teeth have a mesocone and an equally large ectocone, whereas the following 6-10 marginal teeth change from tri- to irregularly multi-cuspid.

Eymology. – The name of the species refers to the Fenera mountain of the type locality, which encloses the entire currently known distributional range of the species.

Habitat. – Small populations inhabit the rocks, consisting of dolomite or dolomitic limestone, in rather

open environments.

Status and distribution. – The M. Fenera limestone massif (Piedmont, NW Italy) is located in the lower Valsesia, on the right slope of the Sesia valley, at the beginning of the alluvial soils of the Po River Basin. The distribution area of *C. feneriensis* spec. nov. is entirely within the protected SIC Monte Fenera (IT1120003) and Monte Fenera natural park. Because M. Fenera is situated in a preserved area, its protection should be guaranteed. However, excessive collection could represent a serious risk for this endemic species because of its very limited and disjunct distribution area (extended to a few square kilometres). It should be considered an endemic taxon with only five known stations, in one of which it seems to be already extinct. Therefore it should urgently be included in the list of endangered species, the IUCN red list, and in the regional lists of protected species likely to be “vulnerable” according to the criteria of IUCN (IUCN, 2001).

Associated fauna. – No other chondrinids or molluscs typical of calcareous substrate in dry environments coexist in the same habitat. In most humid

environments at the base of cliffs, inside the rocky slits or the entrance of karst caves, other species are present, like *Charpentieria dyodon thomasiana* (Küster, 1850), *Helicodonta obvoluta* (Müller, 1774) and *Chilostoma padanum* (Stabile, 1864) (Pascutto, 1998; personal unpublished data). Other endemic species are already known from M. Fenera (Sindaco et al., 2008), but no other terrestrial snails or slugs. From a taxonomical point of view, *C. feneriensis* spec. nov. is closely related to *C. generosensis*, the distribution area of which is located further east, in the Prealps of Lugano (Fig. 5). No molluscs have their western distributional boundary in M. Fenera, but some species have their eastern boundary here (*Ariunculus speziae* Lessona, 1881), their south-eastern (*Retinella giustii* Riedel, 1998), or north-eastern limit (*Chilostoma padanum* (Stabile, 1864)) (Pascutto, 1998; Sindaco et al., 2008; personal unpublished data).

Differentiation. – Among the *Chondrina* species of the Southern Alps, *C. generosensis* is most similar to *C. feneriensis* spec. nov. in shell morphology. It is also geographically closest, known from a restricted area between Lombardy (Italy) and Ticino (Switzerland) (Fig. 5; Nordsieck, 1962; Groh, 1990; Turner et al., 1998; Boschi, 2011). Both species have a yellowish, small shell. *Chondrina feneriensis* spec. nov. is usually smaller (mean values in five populations 5.2–6.0 mm in height and 2.2–2.4 mm in diameter, compared with 6.3 mm in height and 2.4–2.6 mm in diameter in two populations of *C. generosensis*, Tab. 1). It differs also from *C. generosensis* (Fig. 2E) by a more prominently striated shell surface, a more slender spire with a more clearly tapering apex, the spiral lamella missing or extremely reduced (small but always present in *C. generosensis*), and by the constant presence of two short palatal plicae, inside the aperture which do not reach the peristome edge. Sometimes, a third rudimentary plica (infrapalatal) is observed in *C. feneriensis* spec. nov. In *C. generosensis* the superior plica reaches the peristome edge and the inferior and the infrapalatal plicae are shorter but always well developed (Fig. 1 M–Q). These differences are also clear in the fossil shells of *C. feneriensis* spec. nov. The shells date from the Upper Pleistocene to Holocene (Fedele, 1966, 1971, 1972, 1973, 1976, 1988). They do not differ in shell morphology from the extant populations.

Chondrina feneriensis spec. nov. always has a little flagellum, between the ephiphallus and the proximal penis (Fig. 3). This flagellum has not been observed in *C. generosensis*. Specimens that are intermediate between *C. feneriensis* and *C. generosensis*, indicative of a subspecies status, are not known.

Chondrina feneriensis spec. nov. can easily be distinguished from all other closely related taxa living in the Alps, by the morphological characters. It differs

from the geographically also rather close *C. megacheilos* by its thinner, more prominently sculptured shell with a less conspicuously thickened and reflected lip and the plicae and lamellae in the aperture, that recall Bauplan I (Kokshoorn & Gittenberger, 2010), especially by a slimmer angular lamella, a very reduced or missing spiral lamella (spiral lamella elevated or evident in *C. megacheilos*, except in *C. m. avenoides*) and the lower number of palatal plicae (4–6 palatal plicae in *C. m. megacheilos*, only 3–4 in *C. m. avenoides*) (Manganelli et al., 1995; Falkner & Stummer, 1996; Nardi, 2009).

Compared to *C. burtscheri* Falkner & Stummer, 1996, a species that is closely related to *C. megacheilos*, the new species has a more prominent sculpture (dense, irregular, almost imperceptible in *C. burtscheri*), and another apertural armature (always 5 palatal plicae in *C. burtscheri*; Gerber, 2002; Kokshoorn & Gittenberger, 2010).

The differences between *C. feneriensis* spec. nov. and *C. multidentata* are clear: the former has a less slender shell, with more clearly striate surface, the aperture is not laterally compressed, the palatal plicae are not sinuous and not extending deep into the aperture and there are no tubercles on the peristomal margin. The conchological differences between *C. feneriensis* spec. nov. and *C. bergomensis* (Küster, 1850) are less obvious, because both species have a shell yellowish in colour and striated surfaces. However, in *C. feneriensis* spec. nov. the surface of the shell is finely rib-striate, whereas in *C. bergomensis* the ribs are slightly more prominent; a spiral lamella is lacking or obsolete versus always present in *C. bergomensis*, which can also be distinguished by the presence of three longer palatal plicae that are always present (Nordsieck, 1962; Eikenboom, 1996).

The last species belonging to the clade which includes the taxa mentioned above, i.e. *C. latilabris*, has a very different shell because of its reflected and thickened peristome and the plicae/lamellae inside the aperture that remind of *C. megacheilos* (see Nordsieck, 1962).

Among the other Alpine species, that are phylogenetically more distant according to molecular genetic investigations (Kokshoorn & Gittenberger, 2010), *C. avenacea* (Bruguière, 1792) is present, with the nominotypical subspecies, in a wide area of the Piedmont, but west of *C. feneriensis* spec. nov. (Fig. 5), and in many other areas of central and southern Europe (Gittenberger, 1973; Falkner, 1990; Kerney et al., 1983; Welter-Schultes, 2012; Bank, 2013), whereas the two subspecies *C. avenacea leptota* (Westerlund, 1887) and *C. avenacea istriana* Ehrmann, 1931, have an Alpine-eastern distribution (Nordsieck, 1962, 1970; Gittenberger, 1973; De Mattia & Prodan, 2010). By the presence of

two palatal plicae, a short superior palatal plica, not reaching the peristome, and the more prominent sculpture *C. feneriensis* spec. nov. can always be distinguished from these eastern taxa.

The Alpine populations of *Chondrina arcadica* (Reinhardt, 1881), belonging to the subspecies *Chondrina arcadica clienta* (Westerlund, 1883) (Nordsieck, 1962, 1970), differ from *C. feneriensis* spec. nov. by a more prominent sculpture and by the absence of the suprapalatalis. The poorly known species of the western French Alps, i.e. *C. falkneri* Gittenberger, 2002, and *C. gerhardi* Gittenberger, 2002, differ by the lack of clear palatal plicae. The same character allows to distinguish *C. feneriensis* spec. nov. from another Italian endemic taxon, i.e. *Chondrina oligodonta* (Del Prete, 1879), which is devoid of any palatal plicae too, and has a more southern distribution in Tuscany, in the Apuan Alps (Lanza, 1997; Manganelli et al., 2000; Welter-Schultes, 2012; Pall-Gergely, 2013).

The combination of characters of the shell, such as the presence of only two columellar lamellae and two short palatal plicae not reaching the peristome, allows to distinguish *C. feneriensis* spec. nov. from many other taxa from Europe and Morocco, with a few exceptions. These are however distinguishable by other characters (Nordsieck, 1970; Gittenberger, 1973; Kerney et al., 1983; Kokshoorn & Gittenberger, 2010; Welter-Schultes, 2012). Moreover, these other taxa are unrelated as shown by DNA analysis (Kokshoorn & Gittenberger, 2010; Kokshoorn et al., 2010).

DNA analyses. – The Neighbour-Joining analysis (Fig. 6) places *C. feneriensis* as a monophyletic sister group to *C. generosensis*. This placement is strongly supported by the parsimony and maximum likelihood phylogenetic analyses. Uncorrected pairwise distances within *C. feneriensis* range from 0.00146 to 0.00742 (average 0.00464). Between *C. feneriensis* and *C. generosensis* these values range from 0.02928 to 0.04100 (average 0.03648).

Given that the two closely related taxa form monophyletic clades, and that the genetic distance between *C. feneriensis* and *C. generosensis* is approximately an order of magnitude higher than the intraspecific genetic distance within *C. feneriensis*, we feel that the DNA analyses strongly support the differentiation between these taxa as valid species under the biological species concept.

DISCUSSION AND CONCLUSIONS

The taxa belonging to the genus *Chondrina* have always been distinguished on the basis of different combinations of the shell characteristics like dimensions, colouration, sculpture and, especially, apertural teeth (columellar and parietal lamellae, palatal plicae). De-

spite the fact that this last character is sometimes variable, also within the same taxon, it may provide a good basis to recognize interspecific diversity. Instead, the genital tract of *Chondrina* is rather simple and usually without diagnostic characters. The ratio between the length of penis and epiphallus is a rather variable character, therefore it cannot be used as a potentially diagnostic character.

A correct reconstruction of the phylogenetic relationships within the genus *Chondrina*, cannot be based on single characters such as the shell and genitalia; the attempts, mainly based on the number of palatal plicae and on the presence/absence of the spiral lamella (Nordsieck, 1962; Gittenberger, 1973), were not realistic. Only thanks to genetic investigations (DNA analysis) it has been possible to have a reliable phylogenetic reconstruction, although a still preliminary one (Kokshoorn & Gittenberger, 2010).

ACKNOWLEDGEMENTS

We wish to thank Stefano Birindelli (Turin, Italy), Emanuele Bodon (Genoa, Italy), Gabriella Vezzani (Genoa, Italy), Enrico Pezzoli (Bedulita, Bergamo, Italy), Fabio Stoch (Trevigliano Romano, Roma, Italy), Tiziano Pascutto (Biella, Italy), Micaela Calcagno (Florence, Italy) and Enrico Talenti (Florence, Italy), for their help during the researches; Francesco Fedele (Turin, Italy) for allowing the study of the fossil material collected during archaeological excavations in the caves of M. Fenera and for data on excavations, and Maurizio Ulivi (Centro Interdipartimentale di Servizi di Microscopia Elettronica e Microanalisi (MEMA) dell'Università di Firenze, Italy), for technical assistance. We are grateful also to Prof. Dr. Edmund Gittenberger and an anonymous reviewer for the critical revision of the manuscript.

REFERENCES

- BANK, R.A., 2013. Fauna Europaea: Mollusca Gastropoda. Fauna Europaea version 2.6. Last update: April 9th, 2013. – <http://www.faunaeur.org>.
- BOATO, A., BODON, M., GIOVANNELLI, M.M. & MILDNER, P., 1989. Molluschi terrestri delle Alpi sudorientali. – *Biogeographia* 8: 429-528.
- BOATO, A., BODON, M. & GIUSTI, F., 1985. Molluschi terrestri e d'acqua dolce delle Alpi Liguri. – *Lavori della Società Italiana di Biogeografia*, N.S. 9: 237-371.
- BOETTGER, O., 1883. Malakozoologische und palaeontologische Mitteilungen (Schnecken aus Hochsavoyen und Piemont etc.). – *Bericht über die Tätigkeit des Offenbacher Vereins für Naturkunde* 22-23: 157-224, 1 pl.
- BOSCHI C., 2011. Die Schneckenfauna der Schweiz. Ein umfassendes Bild- und Bestimmungsbuch. – Haupt Verlag, 624 pp. Bern.

- DE MATTIA, W. & PRODAN, M., 2010. I molluschi (Gastropoda: Architaenioglossa, Pulmonata; Bivalvia) della Val Rosandra (Trieste – Italia). – Atti del Museo Civico di Storia Naturale di Trieste 54: 165-174.
- EIKENBOOM, J.C.A., 1996. Een verslag van 10 jaar landslakken verzamelen in Italië. – De Kreukel 32 (6-8): 61-106, 9 pls.
- FALKNER, G., 1990. Binnenmollusken. – In: Fechter, R. & Falkner G., 1990. – Weichtiere. Europäische Meeres- und Binnenmollusken. Mosaik Verlag, München: 112-273.
- FALKNER, G., RIPKEN, T.E.J., FALKNER, M., 2002. Mollusques continentaux de la France. Liste de référence annotées et bibliographie. – Patrimoines naturels 52: 1-350. Paris.
- FALKNER, G., & STUMMER B., 1996. Isoliertes Vorkommen einer südalpinen Kornschnecke in Vorarlberg: *Chondrina megacheilos burtscheri* n. ssp. (Gastropoda: Chondrinidae). – Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 4: 1-8.
- FEDELE, F., 1966. La stazione paleolitica del Monfenera in Valsesia. – Rivista di Studi Liguri 32 (1-2): 5-105.
- FEDELE, F., 1971. Gli scavi nel riparo del Belvedere sul Monfenera, Valsesia. Campagne 1969 e 1970. – Archivio Antropologia ed Etnografia Università di Torino 101: 231-244.
- FEDELE, F., 1972. Aperçu des recherches dans les gisements du Monfenera (Val Sesia, Alpes Pennines). – Bulletin d'Études Préhistoriques Alpines 4: 5-68.
- FEDELE, F., 1973. Una stazione Vaso a bocca quadrata sul Monfenera, Valsesia (scavi 1969-72). – Preistoria Alpina 9: 151-222.
- FEDELE, F., 1976. Découverte du Paléolithique supérieur en Piémont: les recherches du Monfenera. – Actes Congrès Préhistorique de France, session Provence, 1974, 20: 251-276.
- FEDELE, F., 1988. Paleofauna del Monfenera (Valsesia) e loro correlazioni ecologiche e culturali. 1: insettivori tardiglaciali. – Rivista Piemontese di Storia Naturale 9: 3-42.
- GARGOMINY, O., FALKNER, M., PROSCHWITZ, T. VON & RÜETSCHI, J., 2013. *Chondrina megacheilos*. The IUCN Red List of Threatened Species. Version 2014.2. www.iucnredlist.org. Downloaded on 02 October 2014.
- GAVETTI, E., BIRINDELLI, S., BODON, M. & MANGANELLI, G., 2008. Molluschi terrestri e d'acqua dolce della Valle di Susa. – Museo Regionale di Scienze Naturali, Torino, Monografie 94: 1-274.
- GERBER, J., 2002. Two more northern outposts of the Southern Alpine land snail *Chondrina megacheilos* (Cristofori & Jan 1832) (Gastropoda: Pupilloidea: Chondrinidae). – In Falkner, G., et al., 2002. – Collectanea Malacologica: 33-40, pl. 7.
- GITTENBERGER, E., 1973. Beiträge zur Kenntnis der Pupillacea. III. Chondrinidae. – Brill, 267 pp., 7 pls. Leiden.
- GITTENBERGER, E., 1984. Vicariantists and dispersalists the Chondrininae (Gastropoda, Pulmonata). – In: Solem, A. & van Bruggen, A.C. (eds.), World-wide snails. Biogeographical studies on non-marine Mollusca. – 56-69. Leiden.
- GITTENBERGER, E., 2002. Two more sibling *Chondrina* species, endemic for France (Gastropoda, Pulmonata, Chondrinidae). – In: Falkner, G. et al., 2002. – Collectanea Malacologica: 41-46, 2 pls.
- GIUSTI, F. & MAZZINI, M., 1971. Notulae malacologicae XIV. I molluschi delle Alpi Apuane. Elenco delle specie viventi con descrizione di una nuova specie: *Vitrinobrachium baccettii* n. sp. – Lavori della Società Italiana di Biogeografia, Nuova Serie 1: 202-335, 9 pls.
- GRAACK, W., 1985. Anmerkungen zur *Chondrina bergomensis* (Küster, 1850) (Pulmonata, Chondrinidae). – Basteria 49 (1/3): 28.
- GROH, K., 1990. Systematische Artenliste und Fundortliste der DMG-Exkursion anlässlich der Jahrestagung vom 25. bis 28. Mai 1989 im Tessin. – Mitteilungen der Deutschen Malakozoologischen Gesellschaft 46: 31-39. Frankfurt am Main.
- IUCN, 2001. 2001 IUCN Red List Categories and Criteria version 3.1. – <http://www.iucnredlist.org/technical-documents/categories-and-criteria/2001-categories-criteria>.
- KERNEY, M.P., CAMERON, R.A.D. & JUNGLUTH, J.H., 1983. Die Landschnecken Nord- und Mitteleuropas. – Parey, 384 pp., 24 pls. Hamburg and Berlin.
- KOKSHOORN, B. & GITTENBERGER, E., 2010. Chondrinidae taxonomy revisited: New synonymies, new taxa, and a checklist of species and subspecies (Mollusca: Gastropoda: Pulmonata). – Zootaxa 2539: 1-62.
- KOKSHOORN, B., VAN SCHOOR, M., ERKELENS, I. & GITTENBERGER, E., 2010. Waves of dispersal in island-hopping *Chondrina* species (Gastropoda, Pulmonata, Chondrinidae). – Zoologischer Anzeiger 249: 71-79.
- LANZA B., 1997. La fauna endemica delle Alpi Apuane (Toscana, Italia). – Atti della Società Toscana di Scienze Naturali, serie B 103: 17-34.
- LESSONA, M., 1880. Molluschi viventi del Piemonte. – Memorie dell'Accademia dei Lincei Classe di Scienze Fisiche Matematiche e Naturali, Serie III, 7: 317-380, 4 pls.
- LIBERTO, F., GIGLIO, S., REITANO, A., COLOMBA, M.S. & SPARACIO, I., 2010. Molluschi terrestri e dulciacquicoli di Sicilia della collezione F. Minà Palumbo di Castelbuono. – Danaus ed., Palermo, 135 pp.
- MAASSEN, W.J.M., 1987. Verslag van een verzameltocht door noordoost-Italië. – De Kreukel 23: 141-150, pls 2-3.
- MANGANELLI, G., BODON, M., CIANFANELLI, S., FAVILLI, L. & GIUSTI, F., 2000. Conoscenza e conservazione dei molluschi non marini italiani: lo stato delle ricerche. – Atti del 1° Workshop Internazionale di Malacologia. La Conoscenza della natura e dei Molluschi, Bollettino Malacologico 36 (1-4): 5-42.
- MANGANELLI, G., BODON, M., FAVILLI, L. & GIUSTI, F., 1995. Gastropoda Pulmonata. – In: Minelli, A., Ruffo, S., La Posta, S., 1995, Checklist delle specie della fauna italiana. – 16: 60 pp.
- NARDI, G., 2009. Una nuova sottospecie di *Chondrina megacheilos* (De Cristofori & Jan, 1832) per le Prealpi Bresciane (Gastropoda, Pulmonata, Chondrinidae). – Bollettino Malacologico 45 (2): 83-93.
- NORDSIECK, H., 1962. Die Chondrinen der Südalpen. – Archiv für Molluskenkunde, 91 (1/3): 1-20.
- NORDSIECK, H., 1970. Die *Chondrina*-Arten der dinarischen Länder. – Archiv für Molluskenkunde 100 (5/6): 243-261.
- PALL-GERGELY, B., 2013. *Chondrina oligodonta*. The IUCN Red List of Threatened Species. Version 2014.2. –

- www.iucnredlist.org. Downloaded on 02 October 2014.
- PASCUTTO, T., 1998. Indagini biospeleologiche in cavità del Piemonte settentrionale. Provincie di Biella, Vercelli, Novara e Torino (dal 1992 al 1997). – Club Alpino Italiano, Sezione di Biella, i-vi + 83 pp.
- PEGORARI, L., 1883. Contribuzione alla fauna malacologica della Dora Baltea. – *Bullettino della Società Veneto Trentina di Scienze Naturali*, Padova 2: 148-185.
- POLLONERA, C., 1885. Elenco dei molluschi terrestri viventi in Piemonte. – *Atti Accademia delle Scienze di Torino* 20: 675-703.
- PROSCHWITZ, T. VON & JOHANNESON, K., 1996. *Chondrina megacheilos* (Cristofori & Jan) and *Chondrina generosensis* Nordsieck (Pulmonata: Chondrinidae). Morphological and biochemical evidence for their separation as good species. – *Heldia* 2 (3-4): 60-68.
- RÜETSCHI, J., 2013. *Chondrina generosensis*. The IUCN Red List of Threatened Species. Version 2014.2. – www.iucnredlist.org. Downloaded on 02 October 2014.
- SCHILEYKO, A.A., 1998. Treatise on recent terrestrial pulmonate molluscs. Part 1. Achatinellidae, Amastridae, Orculidae, Strobilopsidae, Spelaeodiscidae, Valloniidae, Cochlicopidae, Pupillidae, Chondrinidae, Pyramidulidae. – *Ruthenica*, Supplement 2: 1-127.
- SCHÜTT, H., 2010. Turkish Land Snails. 5th, revised edition with colour photos. – Verlag Natur & Wissenschaft: 1-560. Solingen.
- SINDACO, R., SAVOLDELLI, P. & SELVAGGI, A., 2009. La Rete Natura 2000 in Piemonte. I Siti di Importanza Comunitaria. – Regione Piemonte, 576 pp.
- STABILE, J., 1864. Mollusques terrestres vivants du Piémont. – *Atti Società Italiana di Scienze Naturali* 7: 1-141, 2 pls.
- SWOFFORD, D.L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- THOMPSON, J.D., HIGGINS, D.G., & GIBSON, T.J., 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. – *Nucleic Acids Research* 22: 4673-4680.
- TURNER, H., KUIPER, J.G.J., THEW, N., BERNASCONI, R., RÜETSCHI, J., WÜTHRICH, M., GOSTELI, M., 1998. – Atlas der Mollusken der Schweiz und Liechtensteins. *Fauna Helvetica* 2: 1-527.
- WELTER-SCHULTES, F.W., 2012. European non-marine molluscs, a guide for species identification. – Planet Poster Edition, 679 pp. + Q1-Q78. Gottingen.
- WOLF, M. & RÄHLE, W., 1987. Ergebnisse einer molluskenexkursion in die westlichen Julischen Alpen. – *Mitteilungen der Deutschen Malakozoologischen Gesellschaft* 41: 31-41.
- WÜTHRICH, M., 1996. Die Chondrinen des Südtessins (Pulmonata: Chondrinidae). – *Heidia* 2 (3/4): 57-59, Taf. 9-10. München.