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Resolving riddles and presenting new puzzles in Chonorinidae Phylogenetics

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CHONDRINIDAE TAXONOMY REVISITED:
NEW SYNONYMIES, NEW TAXA,
AND A CHECKLIST OF SPECIES AND SUBSPECIES
(MOLLUSCA: GASTROPODA: PULMONATA)

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DISCLAIMER

This work is not issued for purposes of zoological nomenclature
and is not published within the meaning
of the International Code of Zoological Nomenclature (1999)
(see article 8.2)

*“Chaos is found in the greatest abundance wherever order is being sought.
It always defeats order, because it is better organized.”*

- Ly Tin Wheedle -

INTRODUCTION

The subdivision of the land snail family Chondrinidae into four subfamilies, viz. Chondrininae, Gastrocoptinae, Hypselostomatinae and Aulacospirinae, by Zilch (1959), does not reflect the phylogenetic relationships of these taxa. For that and other reasons these four taxa have currently been raised to family status (Wade et al., 2006; Tongkerd et al., 2004). Here we accept that classification. As a consequence, the family Chondrinidae is restricted to the six (western) Palaearctic genera *Granaria* Held, 1837, *Granopupa* Boettger, 1889, *Solatopupa* Pilsbry, 1917, *Chondrina* Reichenbach, 1828, *Abida* Turton, 1831, and *Rupestrella* Monterosato, 1894. These genera are quite different in speciosity and biogeographically.

The widely accepted nomenclature of the mainly European representatives of the Chondrinidae is largely based on the monograph by Gittenberger (1973). However, since its publication several new taxa have been described, and some partial revisions were published. The monograph is also incomplete, especially since the genus *Rupestrella*, and the polytypic species *Granaria frumentum* (Draparnaud, 1801) sensu lato, and *Chondrina farinesii* (Des Moulins, 1835) and conchologically similar species, are not or only unsatisfactorily dealt with.

The following account should be seen as mainly corrective and complementary to the data and conclusions presented by Gittenberger (1973). Several taxa are described as new, especially in the genera *Abida* and *Chondrina*. Some taxa are redescribed in English. Many illustrations, showing intra- and interspecific variation supplement the verbal characterizations. For many species we also refer to the descriptions by Kerney & Cameron (1979).

MATERIALS AND METHODS

The material used in this study was mainly obtained from the collection of the National Museum of Natural History, Leiden, The Netherlands. This institute also keeps the extensive collection of Mr. Altimira Aleu and many samples donated by Mr. Vilella Tejedó, with a vast number of chondrinids from the Iberian peninsula. A major collecting effort by two students from Leiden University, Ms. M. van Schoor and Ms. I. Erkelens, who collected *Chondrina* species on the Iberian peninsula, greatly improved our knowledge on the morphology and distribution of these taxa. Their collection was donated to the Leiden Museum. Additional chondrinid material from Italy, France, Spain and Portugal was collected during fieldwork by the authors during the period 2004-2007. The collection of the Zoological Museum, Amsterdam, was used to extent our knowledge of the distribution of the Chondrinidae species.

Two private collections were also studied. They were kindly put at our disposal by their owners, viz. Messrs. J.C.A. Eikenboom (Hellevoetsluis, The Netherlands) and Ir. H.P.M.G. Menkhorst (Capelle aan de IJssel, The Netherlands).

The following abbreviations are used: MNHN (Museum National d'Histoire Naturelle, Paris, France), MHNG (Museum d'Histoire Naturelle, Geneva,

Switzerland), MCNB (= Museu de Ciències Naturales, Barcelona, Spain), MVHN (= Museu Valencià d'Història Natural, Valencia, Spain), RMNH (= National Museum of Natural History (formerly 'Rijksmuseum van Natuurlijke Historie', Leiden, The Netherlands), SMF (= Natur-Museum Senckenberg, Frankfurt am Main, Germany) and ZMA (= Zoological Museum, Amsterdam, The Netherlands).

The systematic part of this study deals with the morphology, mainly conchology, and the distributional data of the Chondrinidae. The distributional data were derived from the collections, as well as from detailed literature references (Alonso, 1974; Alonso, 1977; Arrébola Burgos & Gittenberger, 1993; Arrébola Burgos & Gómez, 1998; Bech, 1993; Beckmann, 2002; Gittenberger, 1973; Montoya et al., 2001; Pilsbry, 1918 [march]; Pilsbry, 1918 [november]; Verdcourt, 1963; Altimira, 1959; Altimira, 1960; Martínez-Ortí et al., 2004).

Whenever possible, we add a reference to the Cytochrome Oxidase subunit 1 (COI), which has been selected as the preferential 'genetic barcode' by the 'Consortium for the Barcode Of Life' (CBOL: <http://barcoding.si.edu>). The codes have been submitted to NCBI's online GenBank database (<http://www.ncbi.nlm.nih.gov/>) Accession numbers are provided with the taxa.

Photographs of shells were made with an Olympus motorized stereomicroscope SZX12 with AnalySIS Extended Focal Imaging Software.

SYSTEMATICS

CHONDRINIDAE C.-M. STEENBERG, 1925

Molecular studies (Wade et al., 2001, 2006; Kokshoorn & Gittenberger, [chapter 2, pp. 21-40]) have shown that there exists a deep phylogenetic split within the Chondrinidae (fig. 1). There is a clade containing *Granaria*, *Granopupa* and *Solatopupa*, with as its sister-group a clade of *Chondrina*, *Abida* and *Rupestrella*. Whereas *Granaria*, *Granopupa* and *Abida* are genera with ground dwelling snails, *Solatopupa*, *Chondrina* and *Rupestrella* species occur on vertical, exposed rock faces. Thus in both clades species with the contrasting habitat preferences occur. The clades might have evolved because of, or in conjunction with, a shift in habitat choice. If so, then we have to accept a reversal and parallelism in both clades. Because of these results, we restrict the subfamily Chondrininae for the clade with *Chondrina*, *Abida* and *Rupestrella*, and introduce the subfamily Granariinae for the sister-clade with *Granaria*, *Granopupa* and *Solatopupa*.

It is hypothesized that the plesiomorphic bauplan of the apertural teeth, with the palatalis inferior as the most prominent palatal tooth, is still present in both the *Granaria* species and *Granopupa granum* (see Gittenberger, 1973: 26). In *Abida* there is a modification implying that the two main palatals are equally prominent. In *Solatopupa*, *Chondrina* and *Rupestrella* species with reduced apertural teeth occur. This parallel reduction is restricted to species occurring on large limestone cliffs. It is likely that in this habitat there is an absence of selection in favour of a complete set of apertural teeth.

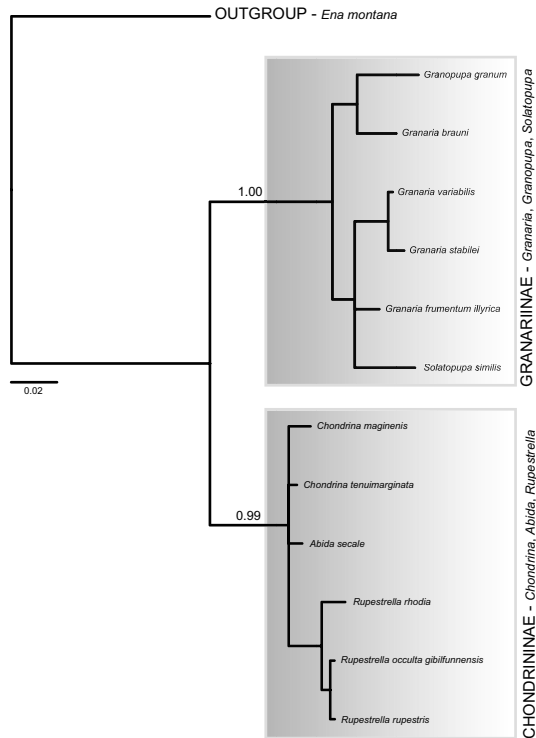


Figure 1. Phylogenetic reconstruction of the Chondrinidae showing the split between the Chondrininae and Granariinae (Kokshoorn & Gittenberger, [chapter 2, p. 33]).

Granariinae subfam. nov.

Type genus: *Granaria* F. Held, 1837.

Additional genera: *Granopupa* O. Boettger, 1889, and *Solatopupa* H.A. Pilsbry, 1917.

Notes. — This subfamily is rather poor in terminal taxa as compared to the Chondrininae. A mere 18 species and subspecies are currently recognized, versus over 100 in the Chondrininae. The oldest fossils known for the Chondrinidae have the *Granaria* bauplan, as is exemplified by *Granaria bythiniformis* (Miller, 1907) and *Granaria multicostulata* (Gutzwiller, 1905), both from the Eocene. In fact, all presently known fossils of pre-Pleistocene age are classified with *Granaria*. This is in striking contrast with what is known for the Chondrininae, where the oldest fossils are from the late Pleistocene (Kokshoorn & Gittenberger, [chapter 2]).

See also the notes with *Granopupa*.

Granopupa O. Boettger, 1889

Type species (by monotypy): *Pupa granum* Draparnaud, 1801.

Notes. – Only a single *Granopupa* species is actually recognized. According to the molecular analysis it takes a basal position in the Granariinae. See also the notes with *Granaria*.

Granopupa granum (Draparnaud, 1801)

Type locality: France.

Notes. – This species has by far the widest distribution of all chondrinids. It has even been reported from Ascension island, in the middle of the Atlantic ocean (7.94W 14.36S) (Ashmole & Ashmole, 1997). The species is found in Portugal and Spain, in the Mediterranean zone and eastwards to Iran and Afghanistan (Gittenberger, 1973: 40) and the Arabian peninsula (Neubert, 1998: 365, fig. 51; 367, fig. 52). The record from northern Somalia (Verdcourt, 1963: 408-409; Gittenberger, 1973) is based on the description of *Granopupa somalensis* Verdcourt, 1963. However, that species should be classified with *Rupestrella*. Hence the southernmost distribution of *Granopupa* is found in Tunisia, Algeria and Morocco.

Granaria F. Held, 1837

Type species (design. Herrmannsen, 1847: 488): *Pupa frumentum* Draparnaud, 1801.

Notes. – The genus *Granaria* is disjunctly represented by 7 extant species, in a very large area, reaching from western Europe in the West towards Iran in the East. Two species groups can be distinguished on the basis of distributional data, i.e. a western group, represented from the Iberian peninsula to the Balkans and a poorly known eastern group, known after few samples from Iran, Pakistan, Oman and Yemen. The phylogenetic relationships of the latter group of conchologically similar species, probably forming a clade, is uncertain. Maybe the eastern group of alleged *Granaria* species is more closely related to *Granopupa*. Because conchological, autapomorphic character states are unknown, their classification will remain problematic as long as both anatomical and molecular data are not available.

Granaria frumentum (Draparnaud, 1801)

Type locality: France.

Notes. – Sólymos & Domokos (1999) found a positive correlation between shell height and mean annual temperature, and a negative correlation between shell height and precipitation.

Granaria frumentum illyrica (Rossmässler, 1835)

Type locality: the Balkans.

Notes. – Several authors (e.g. Klemm, 1973; Kerney & Cameron, 1979; Falkner et al., 2002) deal with *G. illyrica* as a separate species next to *G. frumentum*. However, in the absence of new information, we follow Gittenberger (1973) in considering *G. f. illyrica* and *G. f. apennina* (Küster, 1850) subspecific taxa. We are not convinced that *G. f. frumentum* and *G. f. illyrica* may occur sympatrically without being connected by intermediate populations in a hybrid zone. *Granaria f. illyrica* varies considerably in conchological characters and may be considered polytypic, as is suggested by our preliminary molecular data. It reaches from SE Austria and Hungary far south into the Balkans.

Granaria variabilis (Draparnaud, 1801)

Type locality: France.

Granaria stabilei (Von Martens, 1865).

Type locality: Italy, Torino, Susa in the Dora Riparia valley; 500-600 m altitude.

Notes. – Next to the nominal subspecies, *G. stabilei anceyi* (Fagot, 1881) is recognized as a separate taxon by some authors (Falkner et al., 2002: 108; Pavon, 2005). According to Falkner et al. (2002: 108), *G. s. stabilei* is restricted to the Italian-French main alpine chain, where it is hardly ever found below altitudes of 1800 m, whereas *G. s. anceyi* occurs in the Mediterranean coastal mountains of the French departments of Bouches-du-Rhône and Var, at medium to low altitudes. Shells of the latter subspecies are said to be more slender, with more prominent apertural teeth and radial sculpture.

Although usually found in sheltered habitats, the species may co-occur with *Chondrina avenacea* on SW exposed vertical rockfaces. This was observed in the Italian part of the Alpes-Maritimes (BK, personal observation).

Granaria braunii (Rossmässler, 1842)

Type locality: France, Aude, Carcassone. According to Moquin-Tandon (1856: 379) this locality is incorrect (see Gittenberger, 1973: 57), but this has no consequences for the current interpretation of this species.

Granaria braunii marcusii Gittenberger & Ripken, 1993

Type locality: Spain, Alicante, slope of a barranco E of urbanización Verde Pino, 2 km S of Benitachell (UTM BC58).

Granaria arabica (Dohrn, 1860)

Type locality: Arabia.

Granaria lapidaria (Hutton, 1849)

Type locality: Pakistan, Quetta, NW of the Bolan pass.

Granaria persica Gittenberger, 1973

Type locality: Iran, Seauch, in the mountains SE of Kermān; 2290 m altitude.

Notes. — Recently, the species was recorded in Oman (RMNH 97627: H. Dekker & F.G. de Ceuninck van Capelle leg. 2004)

Solatopupa H.A. Pilsbry, 1917

Type species (by original designation): *Bulimus similis* Bruguière, 1792.

Boata (1988, 1991) has reconstructed a phylogeny for the genus using karyological data, and molecular (allozymes) and morphological characters. Her work revealed the existence of a cryptic species, for which the name *S. juliana* (Issel, 1866) was available. Ketmaier et al. (2006) provided a phylogeny reconstruction for the genus on the basis of DNA sequencing data. In that reconstruction *S. cianensis* takes a basal position among the *Solatopupa* species, which is not congruent with the findings of Boata (1988, 1991). Kokshoorn & Gittenberger [chapter 2] demonstrated that the position of *S. cianensis* is ambiguous, as is the deeper phylogeny of the genus.

Microsatellite markers for all species have been developed by Matamoro Vidal et al. GenBank accession numbers: EF450054 – EF450062).

Solatopupa cianensis (Caziot, 1910)

Type locality: France, Alpes-Maritimes, Gorges du Cians, south of Beuil, right side of the river; 1200 m altitude.

Notes. – This species occurs solely on red porphyre rocks in two gorges, du Cians and de Daluis, in the Alpes-Maritimes. According to Ketmaier et al. (2006) it shows several plesiomorphic character states, but this is not convincingly substantiated. Anyway, *S. cianensis* differs markedly from the other *Solatopupa* species.

See also Gittenberger (1973: 62-81) for data on the other taxa in *Solatopupa*.

CHONDRININAE STEENBERG, 1925

Abida W. Turton, 1831

Type species (by monotypy): *Pupa secale* Draparnaud, 1801.

All the *Abida* species occur in the mountain chain formed by the Pyrenees and the Cantabrian Mts. Only *A. polyodon* and especially *A. secale* additionally occur elsewhere. This genus has been the subject of a phylogenetic study by Kokshoorn & Gittenberger [chapter 6, pp. 73-98].

POLYTYPIC *ABIDA SECALE*

Abida secale (Draparnaud, 1801)

Type locality: France.

Notes. – Since the last comprehensive study on this species (Gittenberger, 1973), two subspecies have been added to this extremely polytypic species. Four more are added here. The molecular data support the monophyly of *A. secale* s.l. as interpreted by Gittenberger (1973). These data also suggest that relatively recently there has been a hybridization between *A. attenuata* (Fagot, 1886) and *A. secale* (Kokshoorn & Gittenberger, [chapter 6]), resulting in introgression of the *A. attenuata* mitochondrion into *A. secale*. This obscured the phylogenetic relations between the populations and subspecies in *A. secale*.

Gittenberger (1973) postulated that *A. secale* forms a ring species complex. On the basis of samples of shells kept in museum collections, he suggested that the extreme morphological variation in the Sierra del Cadí, with a complex system of clines, locally resulted in intraspecific reproductive isolation. Using newly collected material with more precise locality data for biogeographical, morphological and molecular studies, we could neither confirm nor convincingly falsify the ring species model. For the moment being, we still prefer to unite a large group of subspecific taxa under the heading of a single species, i.e. *A. secale* s.l. The intra- and intersubspecific morphological variation does not prevent the delimitation of subspecies that are geographically coherent (but see Bech & Viader, 1996) and more or less clearly interconnected.

The results generated by DNA sequencing show that *A. secale secale* dispersed into its present range across Europe from its origin in or near the Segre valley in northern Spain. Morphologically the nominate subspecies is most closely linked to the subspecies found in southern France, i.e. *A. s. boileausiana*, *A. s. saxicola* and *A. s. andorrensis*. Based on extensive collections in that area, we concluded that there is a differentiation between subspecies with a more northerly and those with a more southerly distribution in northern Spain. *Abida s. andorrensis* (with *A. s. ionicae*) and

A. s. brongersmai are linked by intermediates in the west and north of the Segre valley. The molecular data suggest that *A. s. brongersmai* and *A. s. brauniopsis* are linked by the high-altitude taxa *A. s. cadiensis* and *A. s. cadica* across the Cadí and Moixeró mountain ranges, although shell forms intermediate between *A. s. cadiensis* and *A. s. cadica* are not known. South of the Cadí-Moixeró mountain ranges *A. s. tuxensis* and *A. s. liliensis* are found, linked by intermediates. Further eastwards, *A. s. liliensis* gradually changes into *A. s. affinis*, which is linked by intermediates to *A. s. margaridae*, with *A. s. merijni* across the Moixeró range. Because of their shell morphology and distribution, and not contradicted by the molecular data, the taxa occurring further south, i.e. *A. s. bofilli* and *A. s. meridionalis*, are classified with the southern group. Since specimens intermediate between *A. s. andorrensis* and *A. s. tuxensis* are also known (Gittenberger, 1973; personal observations), this series of taxa cannot be separated from *A. secale*.

Based on these observations, we suggest a scenario with temporary isolation between a northern and a southern group of populations, resulting in a morphological differentiation with the unique development of a protruding aperture in the '*andorrensis-brongersmai-brauniopsis-cadica*' group. There are minor climatic differences throughout the area, but we were not able to correlate any of these with potentially adaptive conchological characteristics. The scenario presented here would explain the absence of intermediates between geographical neighbouring taxa like *A. s. brongersmai* and *A. s. margaridae*, and *A. s. tuxensis* – *A. s. brauniopsis* – *A. s. liliensis*. Unfortunately, there is no fossil record for *Abida*; this makes it impossible to verify these hypothesized events or to suggest a timeframe.

The distribution of the subspecies in the Cadí area is shown in figure 2. The distributional patterns in NE Spain outside this area are shown in figure 3. These maps are based on records from three major Dutch collections of Chondrinidae, viz. the National Museum of Natural History (Leiden), the Zoological Museum (Amsterdam) and the private collection of Mr. J. Eikenboom (Hellevoetsluis). Only those samples were included that contained 1 km UTM or other comparably accurate geographical data. A few records from the literature (Gittenberger, 1973; Bech, 1993; Martínez-Ortí et al., 2004) were added if these data were sufficiently accurate.

Abida secale secale (Draparnaud, 1801) (pl. 1 figs A-J)

Pupa secale Draparnaud, 1801: 59. Type locality: France. Lectotype: Museum of Natural History, Vienna 77709.

Description (after Gittenberger, 1973). – Shell more or less slender, cylindro-conical, with 8 1/4-9 5/8 weakly to moderately inflated whorls, sculptured with irregularly placed, weak to rather prominent axial ribs. Body whorl obliquely flattened, not or only slightly narrowed, with an indistinct keel and an indistinct indentation at the position of both the infrapalatalis and the palatalis superior. The palatal side of the aperture slightly leaning forward (in lateral view). Umbilicus open, partly

obscured by the last part of the body whorl. Shell height, 6.0-9.5 mm; width, 2.0-2.9 mm. The parietal edges of the aperture are connected by a faint to barely visible callus. Angularis mostly connected with spiralis. Subangularis partly fused with angularis. Parietalis present. Columellaris reaching further than the columella in front, but not to the edge of the aperture. Infracolumellaris as prominent as the columellaris or somewhat smaller. A third, much less developed columellar fold, the basalis, is often present. Infrapalatalis, palatalis inferior and palatalis superior are hardly to clearly indented or interrupted, reaching in front to the edge of the aperture. At the anterodorsal palatal centre a suprapalatalis and a suturalis are present.

Genetic barcode. – GenBank accession numbers EU395399 - EU395415, EU395427.

Notes. – *Abida secale secale* is somewhat variable in size across its range (see pl. 1 figs G, H). However, the apertural dentition is very uniform. This also accounts for samples from high altitudes in the Alps (i.e. pl. 1 fig. I). This is strikingly different from the situation in the Pyrenees, where shell morphology varies conspicuously with the altitude (Kokshoorn & Bos, [chapter 7]).

Abida secale saxicola (Moquin-Tandon, 1843) (pl. 1 figs K-L)

Pupa saxicola A. Moquin-Tandon, 1843: 174 [9]. Type locality (after Moquin-Tandon, 1856: 366; see also Gittenberger, 1973: 94): France, Pyrénées-Orientales, Villefranche-de-Conflent.

Abida secale petrophila (Fagot, 1888). Gittenberger, 1973: 94.

Description (after Gittenberger, 1973). – Shell slender to very slender, cylindro-conical, with 8 3/4-10 weakly inflated whorls, sculptured with regularly placed axial ribs. Body whorl obliquely flattened, not narrowed, with an indistinct keel. A slight external indentation accompanies the palatalis superior, a stronger one corresponds with the infraparietalis. The palatal side of the aperture slightly leaning forward (in lateral view). Umbilicus open. Shell height, 6.8-8.8 mm; width, 2.2-2.7 mm.

Apertural lip moderately to strongly thickened, sometimes with some minor plicae; parietal edges connected by a faint callus. Angularis connected with spiralis. Subangularis lamelliform, prominent. A more or less well developed infraparietalis is present. Columellaris longer than infracolumellaris, reaching the edge of the aperture. Infrapalatalis, palatalis inferior and palatalis superior clearly indented and reaching up to the edge of the aperture. A suprapalatalis and a weak suturalis are present at the dorsal anterodorsal palatal centre.

Genetic barcode. – GenBank accession number EU395398.

Abida secale boileausiana (Küster, 1845) (Pl. 1 figs M-N)

Pupa boileausiana Küster, 1845: pl. 13 figs 21-23. Type locality: France, Ariège, Vicdessos.

Description (after Gittenberger, 1973). – Shell rather fragile as compared to other *A. secale* forms, less slender and more conical, with 7 3/4-9 1/2 whorls, which are

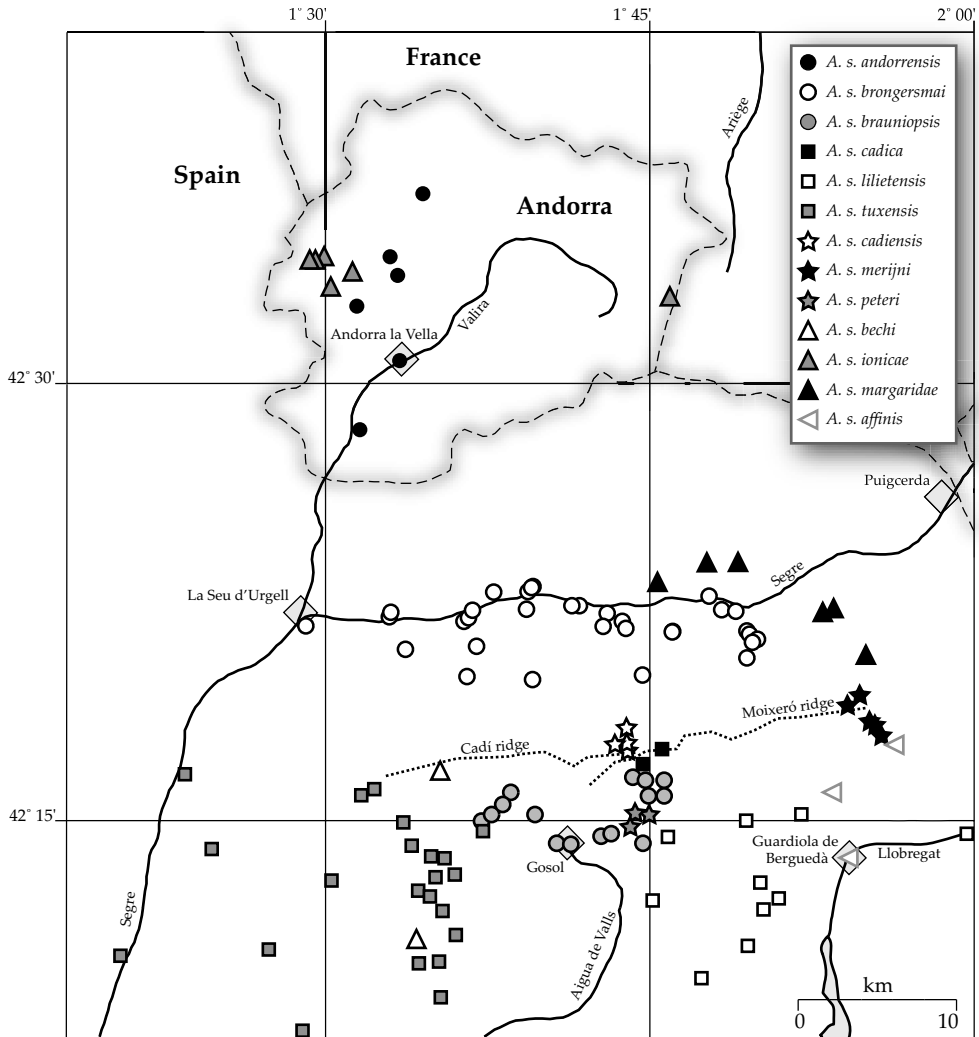


Figure 2. Distribution of *Abida secale* subspecies in NE Spain and Andorra.

weakly to moderately inflated and sculptured with regularly placed, axial ribs. Body whorl obliquely flattened, not or only slightly narrowed and without keel. A slight external indentation accompanies the palatalis superior, just behind the apertural edge. The palatal side of the aperture slightly leaning forward (in lateral view). Umbilicus open. Shell height, 5.4-7.4 mm; width, 2.2-2.5 mm.

Apertural lip moderately to strongly thickened; its parietal edges connected by

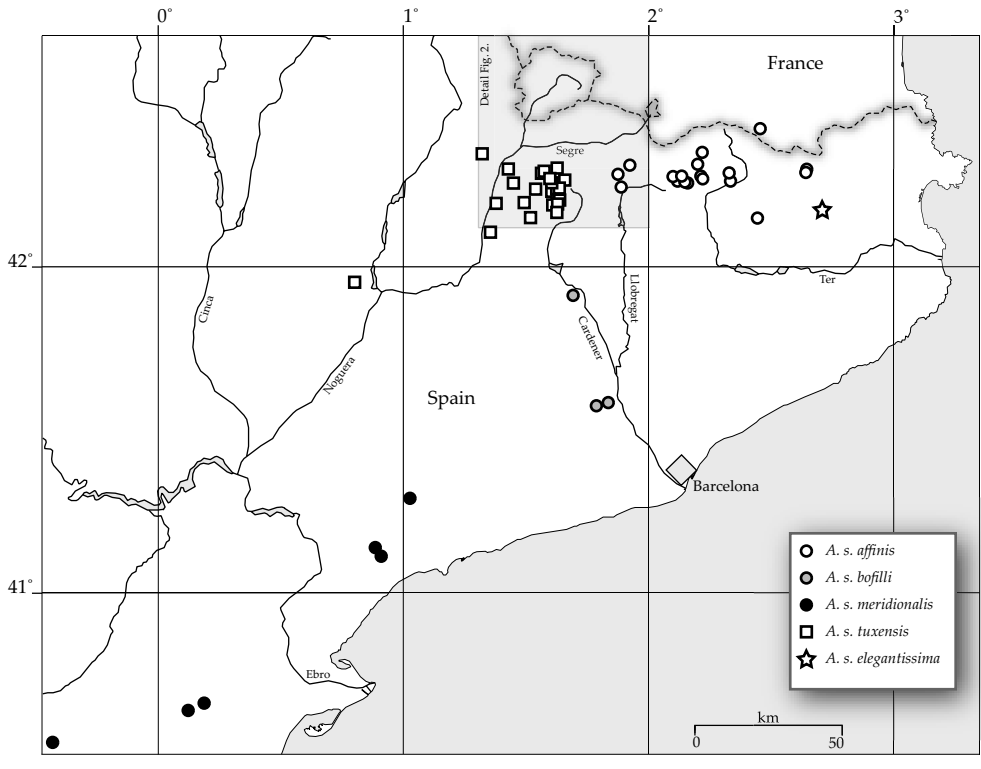


Figure 3. Distribution of *Abida secale* subspecies in NE Spain.

a faint callus.

Angularis connected with spiralis. Subangularis more or less prominent. Infraparietalis present. Columellaris clearly stronger and longer than infracolumellaris, gently curving upward to the edge of the aperture. Infrapalatalis, palatalis inferior and palatalis superior clearly indented and reaching up to the edge of the aperture. At the anterodorsal palatal centre, a suprapalatalis and a weak suturalis are present. Aperture narrowed by the strongly developed columellar and parietal folds; distances between those folds smaller than their own height.

Genetic barcode. – GenBank accession number EU395344.

Abida secale andorrensis (Bourguignat, 1863) (pl. 2 figs A-F)

Pupa andorrensis Bourguignat, 1863: 153. (Or: Mollusques de San-Julia de Loria: 24). Type locality: Andorra, Santa Juliá de Lória. Lectotype: Colln Bourguignat, Museum of Natural History, Geneva.

Description (after Gittenberger, 1973). – Shell slender, cylindro-conical to fusiform, with $8\frac{5}{8}$ - $10\frac{3}{4}$ weakly inflated whorls, sculptured with regularly placed, moderate to strong axial ribs. The sculpture is often partially obsolete. Body whorl obliquely flattened and more or less clearly narrowed, with a strong keel. A slight external indentation accompanies the palatalis superior, at the position of the infraparietalis the apertural lip is mostly slightly indented. The palatal side of the aperture appears vertical (in lateral view). Umbilicus open. Shell height, 7.3-11.8 mm; width, 2.4-3.5 mm.

Apertural lip strongly thickened, continuing along the parietal side or aperture with a more or less prominent parietal callus. Rarely the aperture protrudes up to 0.2 mm. Angularis connected with spiralis. Subangularis lamelliform, more or less prominent. Infraparietalis well developed. Columellaris reaching only slightly further than the columella in front, conspicuously broader than the other lamellae there and ending abruptly, or sometimes connected with an indistinct fold on the apertural lip. Infracolumellaris longer, often reaching the apertural edge. Infrapalatalis, palatalis inferior and palatalis superior clearly indented and reaching up to the edge of the aperture. At the weak anterodorsal palatal center, a suprapalatalis and often a suturalis are present. At the apertural edge several more or less indistinct or more prominent folds may be present.

Genetic barcode. – GenBank accession numbers EU395339 - EU395342.

Notes. – *Abida s. andorrensis* was reported from the northeastern part of the Segre valley, between Martinet and Prullans (Gittenberger, 1973). We consider this a dubious record, since this subspecies has not been found there during surveys in 2004-2006. Maybe atypical specimens of *A. s. brongersmai* (see for instance pl. 4 figs B-C) have been misidentified. However, *A. s. andorrensis* does occur in Spain. It has been recorded from the area around Nargó, west of the Segre river, as well as from the Parque Nacional Aigües Tortes, 5 km NE of Bohi (Boi) (Lerida). South of Nargó forms that are intermediate between *A. s. andorrensis* and *A. s. tuxensis* (pl. 2 figs D-F) are found.

Abida secale tuxensis (Westerlund, 1902) (pl. 2 figs G-K)

Pupa (Torquilla) tuxensis Westerlund, 1902: 40. Type locality: Tuxent, Lérida, Spain. Lectotype: Museum of Natural History, Göteborg 2252.

Description. – Shell slender or very slender, more or less cylindro-conical, with $7\frac{7}{8}$ to $10\frac{1}{2}$ whorls, sculptured with regularly placed axial ribs. Body whorl obliquely flattened, slightly narrowed, with a very indistinct keel. Palatalis superior accompanied by a clear external indentation of the apertural lip. Palatal side of the aperture very slightly leaning forward (in lateral view). Shell height, 10.2-13.8 mm; width, 3.1-3.7 mm. The greatest width is found approximately halfway the height of the shell. Umbilicus open.

Apertural lip moderately to strongly thickened; parietal edges connected by very faint callus. Angularis and spiralis connected, with a slight indentation or a weak callus. Subangularis present, partly attached to angularis. Parietalis present, infra-parietalis only when more undefined folds are present on the apertural lip. Columellaris reaching more or less far beyond the columella in front; not truncated. Infracolumellaris and columellaris about equally well developed. The infrapalatalis, the palatalis inferior and the palatalis superior are hardly to clearly incised or interrupted. They reach up to the edge of the aperture. At the anterodorsal palatal center a suprapalatalis and often a suturalis are present.

Genetic barcode. — GenBank accession numbers EU395416 - EU395426.

Notes. — This subspecies has not been distinguished from *A. s. lilietensis* by Gittenberger (1973). However, in *A. s. tuxensis* the shell is generally larger and more cylindrical than in *A. s. lilietensis*, which is characterized by more spindle-shaped, often smaller shells. The two subspecies occur allopatrically (fig. 2).

Abida secale lilietensis (Bofill, 1886) (pl. 3 figs A-H)

Pupa lilietensis Bofill, 1886: 155. Type locality: La Pobla de Lillet, Barcelona, Spain. Lectotype: Museo de Zoologia, Barcelona.

Description. — Shell slender, more or less cylindro-conical to fusiform, with 1 1/4-1 3/4 protoconch whorls and an additional 7 7/8 to 8 5/8 whorls, sculptured with fine, regularly placed axial ribs. Body whorl obliquely flattened, slightly narrowed, with a very indistinct keel. Palatalis superior accompanied by a clear external indentation of the apertural lip. Palatal side of the aperture slightly leaning forward (in lateral view). Height, 8.2-10.9 mm; width, 2.4-3.1 mm. Greatest width at approximately half the height of the shell. Umbilicus narrowly open.

Apertural lip moderately to strongly thickened; its parietal edges connected by a very faint callus. Angularis and spiralis connected by a faint callus or not at all. Subangularis present, partly attached to angularis. Parietalis and often a faint to strong infraparietalis are present. Columellaris reaching slightly to clearly beyond the columella in front, front end not truncated. Infracolumellaris and columellaris equally well developed. Infrapalatalis, palatalis inferior and palatalis superior hardly to clearly incised or interrupted, reaching up to the edge of the aperture. At the anterodorsal palatal center, a suprapalatalis and often a suturalis are present.

Genetic barcode. — GenBank accession numbers EU395385 - EU395393.

Notes. — *Abida s. lilietensis* is somewhat variable across its range, with forms that are intermediate to *A. s. affinis*. There can be variation in apertural shape and shell shape within a single population (i.e. pl. 3 figs E-F)

Abida secale affinis (Rossmässler, 1839) (pl. 3 figs I-M)

Pupa affinis Rossmässler, 1839: 26. Type locality: France, Pyrénées-Orientales, La Preste. Holotype: Natur-Museum Senckenberg, Frankfurt 3890.

Description (after Gittenberger, 1973). – Shell very slender, fusiform or somewhat cylindro-conical, with $8\frac{1}{4}$ - $9\frac{5}{8}$ weakly to moderately inflated whorls, sculptured with more or less regularly placed, weak to strong axial ribs. Body whorl obliquely flattened, not or only slightly narrowed, with a very indistinct keel and a very short basis. Palatalis superior accompanied by an external indentation in the apertural lip. Palatal side of the aperture slightly leaning forward (in lateral view). Umbilicus narrowly open. Shell height, 6.0-11.3 mm; width, 2.0-2.9 mm.

Apertural lip moderately thickened; its parietal edges connected by a very faint callus. Angularis not connected with spiralis, a short subangularis is present. Parietalis well developed, situated deep inside body whorl and not visible in frontal view. Infraparietalis only present when there are more weak folds on the apertural lip. Columellar lamellae weakly developed, reaching hardly beyond the columella. Infrapalatalis, palatalis inferior and palatalis superior are more or less indented or interrupted, reaching up to the edge of the aperture. Suprapalatalis and weak suturalis present at dorsal to posterodorsal palatal center.

Genetic barcode. – GenBank accession numbers EU395329 - EU395338.

Abida secale elegantissima Gittenberger, 1973 (pl. 3 fig. N)

Abida secale elegantissima Gittenberger, 1973: 108. Type locality: Coll de Sta. Maria de Finestras, Sierra de Finestras, Girona, Spain. Holotype: Museo de Zoologia, Barcelona.

Description (after Gittenberger, 1973). — Shell fusiform, more slender than any other *Abida* species or subspecies, with $9\frac{3}{4}$ -11 moderately inflated whorls, sculptured with more or less regularly placed, weak axial ribs. Body whorl obliquely flattened, narrowed with an indistinct keel and a very short basis. Palatal side of aperture slightly leaning forward (in lateral view). Umbilicus very narrowly open. Shell height, 8.9-10.9 mm; width, 2.3-2.7 mm. The maximum width is reached approximately halfway the total shell height.

Apertural lip strongly thickened; its parietal edges connected by a thin callus. Angularis weakly connected with spiralis or separated. Subangularis inconspicuous. Parietalis inconspicuous in frontal view, but increasingly higher deeper inside the body whorl. Infraparietalis often present, as well as several weak folds on the apertural lip. Columellaris longer than infracolumellaris, reaching up to the edge of the aperture. A basalis is also present. Infrapalatalis, palatalis inferior and palatalis superior are more or less clearly indented or interrupted, reaching up to the edge of the aperture. Suprapalatalis and sometimes a weak suturalis present at posterodorsal palatal center.

Notes. – Extensive fieldwork in the area, with repeated visits to the supposed type locality, did not yield any specimens of this subspecies. This very characteris-

tic form has either gone extinct in the recent past, or the locality data added to the sample are incorrect.

Abida secale brongersmai Gittenberger, 1973 (pl. 4 figs A-E)

Abida secale brongersmai Gittenberger, 1973: 115. Type locality: Spain, Lérida, road to Alás, near Torres, right side of the river Segre, east of La Seu d'Urgell. Holotype: National Museum of Natural History (RMNH), Leiden 54778.

Description (after Gittenberger, 1973). – Shell slender cylindro-conical to fusiform, with 9 1/4-11 1/4 weakly to moderately inflated whorls, sculptured with regularly placed, fine axial ribs. Initial teleoconch whorls often without sculpture. Body whorl obliquely flattened, slightly narrowed, with a distinct keel. Palatalis superior accompanied by a slight to moderately prominent indentation, infrapalatalis with conspicuous external indentation just behind apertural lip. Palatal side of the aperture vertical or slightly leaning backwards (in lateral view). Umbilicus moderately wide, circular. Shell height, 8.0-11.2 mm; width, 2.8-3.3 mm.

Aperture roundish. Apertural lip strongly thickened, continuous across the parietal side, often protruding up to 1 mm. Angularis relatively high near the aperture but quickly decreasing in prominence, reaching past the front end of the parietalis, not or more or less clearly connected with spiralis. Subangularis well developed, not connected to angularis. Parietalis and infraparietalis well developed. Several weak to strong folds may be present on the apertural lip. Columellaris ending abruptly on the columella, clearly broader than the other lamellae there. Infracolumellaris, reaching further beyond the columella, often connected with a lamella on the apertural lip. Infrapalatalis, palatalis inferior and palatalis superior indented, reaching up to the edge of the aperture. At the anterodorsal palatal center a suturalis, an equally long or longer suprapalatalis and often a short basalis are present.

Genetic barcode. GenBank accession numbers EU395348, EU395357 - EU395367.

Notes. – Both shell sculpture and apertural protrusion vary in this conspicuous subspecies. This variation is partly correlated with altitude (Kokshoorn & Bos, [chapter 7; pl. 4 figs A-C]). In the easternmost part of its present range *A. s. brongersmai* occurs close to *A. s. margaridae*, but intermediate populations are not known (Kokshoorn & Gittenberger, [chapter 6]). This might be due to the introduction of *A. s. brongersmai* in the area north of Pedra (SE of Bellver de Cerdanya). In that area, limestone rocks have been used for the construction of walls, creating an artificial habitat for *A. secale* (Kokshoorn & Gittenberger, [chapter 6: 88, fig. 3]). Maybe the rocks originated from the region where *A. s. brongersmai* occurs.

Abida secale margaridae Bech, 1993 (pl. 4 figs F-K)

Abida secale margaridae Bech, 1993: 50-51. Type locality: Spain, Lérida, road to Collado de Toses, between Das and Urús. Holotype: Museo de Zoología, Barcelona.

Material. – The following description of this subspecies is based on material collected near (or at) the

type locality (RMNH 100613); Spain, Gerona, road from Das to Masella (GI-404), 1 km SE of Das (= 1.5 km S of Alp), 1,325 m alt., 42.36127°N / 1.87672°E.

Description (n=13). – Shell slender, elongated cylindro-conical, with 9 1/4-10 6/8 weakly inflated whorls, sculptured with regularly placed axial ribs. Body whorl obliquely flattened, slightly narrowed, with a distinct keel. Palatalis superior accompanied by a clear external indentation of the apertural lip, usually resulting in a slightly concave palatal apertural border. Palatal side of aperture slightly leaning forward (in lateral view). Shell height, 10.2-12.3 mm; width (of body whorl), 3.0-3.5 mm. The maximum shell width is reached in the upper half of the shell. Umbilicus widely open.

Apertural lip strongly reflected, moderately to strongly thickened. Parietal edges usually connected by a thin callus. Angularis and spiralis connected, with a slight indentation or a weak callus. Subangularis present, partly attached to angularis. Parietalis present, infraparietalis usually present, and if so, accompanied by several minor folds on the parietal and columellar side. Columellaris reaching more or less clearly beyond the columella, occasionally up to the apertural lip. Infracolumellaris weakly developed, not or hardly reaching beyond the columella. Palatalis inferior and palatalis superior reaching the edge of the aperture. In frontal view, no more palatal folds are visible inside the aperture, but there are a suturalis, a suprapalatalis and an infrapalatalis near the inner end of the two more prominent palatals, as far as 1/2-3/4 whorl from the aperture.

Genetic barcode. – GenBank accession numbers EU395394 - EU395396.

Notes. – *Abida s. margaridae* is very variable in shell characters, even within populations (pl. 4 figs F-H).

Abida secale brauniopsis Altimira, 1963 (pl. 5 figs A-G)

Abida secale brauniopsis Altimira, 1963: 19. Type locality: Spain, Lérida, Gosol, Sierra del Cadí. Lectotype: National Museum of Natural History (RMNH), Leiden 54780.

Description (after Gittenberger, 1973). – Shell slender, fusiform to cylindro-conical, with 8 3/4-9 3/4 weakly inflated whorls, sculptured with regularly placed, fine axial ribs. Body whorl obliquely flattened, narrowed, with a very distinct keel. Palatalis superior accompanied by a slight external indentation. Infrapalatalis with a prominent external indentation just behind apertural lip. Palatal side of aperture vertical (in lateral view). Umbilicus widely open. Shell height, 7.5-10.8 mm; width, 2.5-2.8 mm.

Aperture narrowed, with only slightly curved columellar and palatal sides and basally a sharp angle. Apertural lip strongly thickened, continuous across parietal side, broadly reflected and often protruding up to 1 mm. Angularis relatively high near the aperture but quickly decreasing in prominence, reaching beyond the front end of the parietalis, not or only weakly connected with the spiralis. Subangularis connected with angularis. Infraparietalis obsolete or lacking. Columellaris not

reaching beyond the columella, clearly broader than the other lamellae at its frontal, abrupt ending. Infracolumellaris reaching further beyond the columella but never up to the apertural lip. Infrapalatalis, palatalis inferior and palatalis superior indented, reaching up to the edge of the aperture; some additional minor lamellae are occasionally present on the palatal apertural lip. At the anterodorsal palatal center a suturalis, a somewhat stronger, but equally long suprapalatalis and a shorter basalis are present.

Genetic barcode. – GenBank accession numbers EU395345 - EU395347, EU395349 - EU395356.

Notes. – In the Sierra del Cadí, south of the Comabona, populations of *Abida secale* are found that are intermediate between *A. s. brauniopsis* and *A. s. brongersmai*. In these populations the shells share the multitude of folds on the apertural lip with *A. s. brongersmai*, but the aperture is still narrowed, not roundish (pl. 5 figs C-E).

Abida secale meridionalis Martínez-Ortí, Faci & Gómez, 2004 (Pl. 8 figs A-D)

Abida secale meridionalis Martínez-Ortí, Faci & Gómez, 2004: 63. Type locality: Spain, Teruel, Cantavieja, 4 km W of Cantavieja along 800P road at rkm 93,5, UTM YK1588; 1,460 m alt.

Description (after Martínez-Ortí et al., 2004). – Shell slender, elongated cylindrical, with 9 1/2-12 3/4 moderately inflated whorls, sculptured with regularly placed axial ribs, that are often worn. Body whorl slightly obliquely flattened, somewhat narrowed, with an indistinct keel. Palatalis superior accompanied by a clear external indentation of the apertural lip, usually causing the palatal side of the aperture to appear somewhat concave. Shell height, 5.4-12.5 mm, width, 2.8-3.1 mm. The greatest width of the shell is reached in its upper half. Umbilicus narrowly open.

Apertural lip strongly reflected, moderately to strongly thickened. Parietal edges usually connected by a more or less prominent callus. Angularis and spiralis connected with a slight indentation or a weak callus. Subangularis present, partly attached to angularis. Strong parietalis and weak infraparietalis regularly present. Columellaris reaches, with an upward curve, up to the apertural lip. Infracolumellaris weakly developed, never extending far beyond the columella. A third, indistinct columellar fold may be present. The infrapalatalis, palatalis inferior and palatalis superior reach up to the edge of the aperture. The palatalis superior regularly forms a swelling on the apertural lip. If so, then this is accompanied by indistinct folds. At the anterodorsal palatal center a suprapalatalis may be present.

Genetic barcode. – GenBank accession number EU395397.

Abida secale bofilli (Fagot, 1884) (pl. 8 fig. E)

Pupa bofilli Fagot, 1884: 189. Type locality: Spain, barcelona, Montserrat. Lectotype: Westerlund, Naturhistoriska Museet, Göteborg.

Description (after Gittenberger, 1973). – Shell slender to very slender, shortly

cylindrical, becoming conical towards the apex, with 9-10 3/4 weakly inflated whorls, sculptured with regularly placed axial striae.

Body whorl obliquely flattened, not or only slightly narrowed, with a distinct keel. Infrapalatalis accompanied by a very prominent external indentation in the apertural lip. Palatal side of aperture leaning slightly forward (in lateral view). Umbilicus very narrowly open. Shell height, 6.9-8.6 mm; width, 2.1-2.5 mm.

Apertural lip weakly to moderately thickened, connected across the parietal side by faint callus. Angularis connected with spiralis, subangularis present. No infra- parietalis but several minor folds may be present on the apertural lip. Columellaris somewhat more prominent than infracolumellaris, both equally strongly decreasing in prominence towards the aperture, but reaching well beyond the columella. Infrapalatalis, palatalis inferior and palatalis superior indented to interrupted, reaching up to the edge of the aperture. Suprapalatalis and often a weak suturalis present at the dorsal palatal center.

Genetic barcode. – GenBank accession number EU395343.

ABIDA SECALE AT HIGH ALTITUDES

Populations classified with the following six subspecies, i.e. *A. s. cadica*, *A. s. cadicensis*, *A. s. vilellai* subsp. nov., *A. s. peteri* subsp. nov., *A. s. ionicae* subsp. nov. and *A. s. merijni* subsp. nov., are restricted to relatively high elevations in Spain and Andorra. In the Alps, *A. secale* populations occur at equally high localities but there the snails are not or hardly differentiated conchologically.

The more or less clearly clinal, altitudinal variation that may be observed in a small part of the total range of *Abida secale* does not allow for an objective, sharp delimitation of the subspecies that are distinguished here from the valleys and the mountain summits, respectively. Consequently, the interpretation of 'intermediate' forms may be somewhat subjective. A morphometric study, assessing altitudinal variation in *A. secale*, revealed convergent similarities next to obvious differences between these forms (Kokshoorn & Bos, [chapter 7]). Those results enable the following description of four new subspecies of *A. secale*. These forms from high altitudes cannot simply be considered illustrative for ecophenotypical variation, since they are restricted geographically to a minor part of the large range of *A. secale*. They are independent evolutionary lineages with their own diagnostic character states, and are connected to different subspecies occurring at lower altitudes.

KEY TO THE HIGH-ALTITUDE FORMS OF *A. SECALE* [WITH THEIR RANGES]

1. a. Shell with protruding aperture [Sierra del Cadí] *A. s. cadica*
- b. Shell without protruding aperture 2
2. a. Angularis connected to spiralis 3
- b. Angularis not connected to spiralis 4
3. a. Shell slender cylindrical, aperture continuous and slightly protruded or with strong parietal callus. Infraparietalis well developed [Andorra and Pico Mainera, Spain] *A. s. ionicae*
- b. Shell more fusiform, aperture discontinued at parietal side or with weak callus. No infraparietalis present [Sierra Moixero] *A. s. merijni*
4. a. Aperture continuous at parietal side 5
- b. Aperture not continuous or with only a weak callus 6
5. a. Infraparietalis present. [Andorra and Pico Mainera, Spain] *A. s. ionicae*
- b. Infraparietalis absent, angularis reaching past front end of parietalis [Sierra del Cadí] *A. s. cadica*
- c. Infraparietalis absent, angularis reaching approximately to the front end of the parietalis. [Sierra del Cadí] *A. s. cadiensis*
6. a. Columellar folds reaching beyond columella in front, both about equally prominent 7
- b. Columellar folds not reaching beyond columella, columellaris clearly more prominent than subcolumellaris and parietalis [Pedraforca mtn, Spain] *A. s. peteri*
7. a. Palatalis superior with strong callous bulb at apertural lip [Sierra Moixero] *A. s. merijni*
- b. Additional indistinct folds may be present on apertural lip [Sierra del Cadí and Port del Comte] *A. s. vilellai*

Abida secale cadica (Westerlund, 1902) (pl. 6 figs A-C)

Pupa (Torquilla) cadica Westerlund, 1902: 39. Type locality: Spain, Lérida, Collado de Tancalaporra, Sierra del Cadí. Lectotype: Naturhistoriska Museet Göteborg 2261.

Description (after Gittenberger, 1973). — Shell fusiform, relatively short, with 7 3/4-8 1/2 weakly inflated whorls, sculptured with regularly placed, weak axial ribs. Body whorl obliquely flattened, slightly narrowed, with a very distinct keel. Infrapalatalis accompanied by a very clear external indentation just behind apertural lip. Palatal side of the aperture slightly leaning forward (in lateral view). Umbilicus very narrowly open. Shell height, 6.1-7.5 mm; width, 2.2-2.5 mm.

Apertural lip strongly thickened, continuous across the parietal side, broadly reflexed and protruding up to c. 0.2 mm. Angularis relatively wide near the aper-

ture but rapidly decreasing in prominence inside, reaching beyond the frontal end of the parietalis, hardly separated from the spiralis. Subangularis and infraparietalis missing. Columellaris somewhat more prominent than infracolumellaris, but both not reaching beyond columella. Infrapalatalis, palatalis inferior and palatalis superior interrupted, reaching up to the edge of the aperture. Suprapalatalis and a weak suturalis present at anterodorsal palatal center.

Genetic barcode. — GenBank accession number EU395368.

Notes. — Additional material of this species collected by the authors (RMNH 104126/15) fits the original description by Gittenberger (1973), which was based on 3 specimens only. However, the size range (shell height and width) has been updated. *Abida s. cadica* may be considered 'derived' from *A. s. brauniopsis*.

Abida secale cadiensis Gittenberger, 1973 (pl. 6 figs D-L)

Abida secale cadiensis Gittenberger, 1973: 110. Type locality: Spain, Lérida, Martinet. Holotype: National Museum of Natural History (RMNH), Leiden 54782.

Description (after Gittenberger, 1973). — Shell cylindro-conical, with 7 3/4-8 1/2 weakly to moderately inflated whorls, sculptured with irregularly placed, weak axial striae, rather glossy. Body whorl obliquely flattened, not or only slightly narrowed, with a more or less distinct keel. Infrapalatalis accompanied by more or less prominent external indentation. Palatal side of the aperture slightly leaning forward (in lateral view). Umbilicus very narrowly open. Shell height, 5.2-7.5 mm; width, 2.2-2.8 mm.

Apertural lip weakly thickened, continuous across the parietal side by a very strong callus at least. Angularis not connected with spiralis, ending approximately where a prominent parietalis begins. Subangularis obsolete, a minor knob attached to the angularis, or missing. Infraparietalis absent. Columellaris somewhat more prominent than infracolumellaris, both not reaching beyond the columella. Palatalis inferior and palatalis superior interrupted, reaching up to the edge of the aperture. Infrapalatalis short but prominent at the anterodorsal palatal center, not or only very weakly developed in the frontal part of the palatal folds. Suprapalatalis and occasionally a weak suturalis are present at the anterodorsal palatal center.

Genetic barcode. — GenBank accession numbers EU395374 - EU395377, EU395383 - EU395384.

Notes. — *Abida s. cadiensis* is clearly a high-altitude form, 'derived' from *A. s. brongersmai*, which looks very different at first sight. However, a series of intermediates is known from the northern side of the Sierra del Cadí, especially from the Comabona mtn (pl. 6 figs I-K).

Abida secale vilellai subsp. nov. (pl. 6 figs M-P)

Type series. – Spain, Lérida. Holotype (RMNH 109892): Sierra del Comte, Port del Comte, S of Tossa Pelada mtn, 2,100 m alt., Escola leg. Paratypes: type locality (RMNH 54960/3); Sierra del Cadí, Torre del Cadí mtn, 2,400 m alt., 42.28387°N / 1.56363°E, 04-viii-2004 (RMNH 99118/6).

Description (n=10). – Shell slender to broadly fusiform, with 8 1/8-8 3/4 moderately inflated whorls, sculptured with regularly placed, moderately strong axial ribs. Body whorl slightly flattened obliquely and more or less narrowed, without a distinct keel. Palatal side of the aperture slightly protruding. A vague external indentation may accompany the palatalis superior; at the position of the infraparietalis the apertural lip is usually slightly indented. The palatal side of the aperture appears vertical (in lateral view). Umbilicus narrowly open. Shell height, 6.8-7.7 mm; width, 2.6-2.8 mm.

Apertural lip reflected, thickened, discontinued at parietal side or connected by a faint callus. Angularis not connected to spiralis. Subangularis obsolete or absent. Columellaris slightly more prominent than the infracolumellaris and reaching shortly beyond columella. Both lamellae do not extend to the apertural lip. Palatalis inferior and palatalis superior clearly indented, reaching the edge of the aperture. At the inconspicuous, anterodorsal palatal center a vague suprapalatalis and infrapalatalis may be present.

Differentiation. – The shells are on average larger than those in populations of the other high-altitude taxa occurring at comparable altitudes, i.e. *A. s. cadiensis*, *A. s. cadica*, *A. s. ionicae*, *A. s. peteri* and *A. s. merijni*. *Abida s. vilellai* is most similar to *A. s. tuxensis*, differing in size and by a reduction of the number of the apertural teeth and their prominence. Intermediates between *A. s. tuxensis* and *A. s. vilellai* are known from the W-flank of the Torre del Cadí mtn. The specimens from the type locality possess a more strongly reduced apertural dentition than those from the Torre del Cadí. Specimens from the latter locality have a prominent infrapalatalis and sometimes a suturalis.

Etymology. – With great pleasure we have named this subspecies in honour of the Spanish malacologist Manuel Vilella Tejado, President of the Associació Catalana de Malacologia, to acknowledge his long-lasting stimulating work on the Catalan malacofauna.

Genetic barcode. – GenBank accession number EU395372.

Abida secale peteri subsp. nov. (pl. 7 figs A-C)

Type series. – Spain, Lérida, Sierra del Cadí, Pedraforca mtn. Holotype (RMNH 109890): 2,300 m alt., B. Kokshoorn & P. Lindenburg leg., 06-viii-2004. Paratypes: type locality (RMNH 99135/23); 2,250 m alt., B. Kokshoorn & P. Lindenburg leg., 06-viii-2004 (RMNH 54961/6); E-side, c. 50 m below the coll, 2,250 m alt., B. Kokshoorn & P. Lindenburg leg., 06-viii-2004 (RMNH 99136/5).

Description (n=35). – Shell slender spindle-shaped, with 7 3/8-8 1/8 slightly inflated whorls, sculptured with regularly placed, vague axial ribs. The sculpture is often partially faded. Body whorl slightly flattened and more or less narrowed, without apparent keel. Palatal side of the aperture slightly protruding in the middle (in lateral view). Umbilicus widely open. Shell height, 5.1-7.3 mm; width, 2.0-2.2 mm

Apertural lip thickened, strongly reflected and discontinuous at the parietal side or connected by a thin callus. Angularis not connected with spiralis. Subangularis absent. Columellaris not reaching beyond columella, clearly broader than subcolumellaris and parietalis. Infracolumellaris like columellaris but less prominent. Palatalis inferior and palatalis superior clearly indented and almost reaching the edge of the aperture. At the anterodorsal palatal center a weak suprapalatalis and infrapalatalis are present. A suturalis is usually absent.

Differentiation. – This subspecies shares character states with both *A. s. liliensis* and *A. s. brauniopsis*. These two subspecies occur at the foot and along the flanks of the mountain, i.e. *A. s. brauniopsis* on the south- and westside, and *A. s. liliensis* on the NE-flank. The pronounced columellaris, widely open umbilicus and the strongly reflected apertural lip point to a relation with *A. s. brauniopsis*. However, along the eastflank of the mountain, at altitudes from 1,650 to 2,100 m, shells that are clearly intermediate between *A. s. peteri* and *A. s. liliensis* are found. These specimens have a discontinuous apertural lip and the more slender shape that links these two taxa. *A. s. peteri* resembles *A. s. cadiensis* and *A. s. merijni*, but differs in that it is somewhat smaller and less conical and by its very fine striae that are more pronounced in both *A. s. cadiensis* and *A. s. merijni*.

Etymology. – This subspecies is named after Mr. Peter Lindenburg. Without his help and support, the first fieldwork period of the first author would not have been possible. Together collecting trips to the peaks of the Pedraforca mtn and the Torre del Cadí mtn were made, where material of this new subspecies was collected.

Genetic barcode. – GenBank accession numbers EU395369 - EU395370, EU395373, EU395378.

Abida secale ionicae subsp. nov. (pl. 7 figs D-K)

Type series. – Andorra. Holotype (RMNH 109059): Arinsal (= 8 km NNW of Andorra la Vella), Alt de la Capa mtn (= 2.8 km WSW of Arinsal), 2,500 m alt., 42.56203°N / 1.45567°E, B. Kokshoorn leg., 16-ix-2007 (fig. 10). Paratypes: type locality (RMNH 109060/20); Alt de la Capa mtn, 2,350 m alt., 42.56180°N / 1.45981°E, B. Kokshoorn leg., 16-ix-2007 (RMNH 109061/16); Alt de la Capa mtn, 2,100 m alt. 42.56355°N / 1.46659°E, B. Kokshoorn leg., 16-ix-2007 (RMNH 109062/31); Pal (= 5.6 km NW of Andorra la Vella), N-side above town, 42.54618°N / 1.47136°E, B. Kokshoorn leg., 15-ix-2007 (RMNH 109063/30); Pas de la Casa, 2,100 m alt., “Wageningse Studenten leg.”, vi-2002 (RMNH 109064/3); Pico Mainera mtn, M. Vilella leg. (RMNH 111881/1 paratype).

Description (n=58). – Shell slender cylindrical to slightly fusiform, with 7-8 3/4 weakly inflated whorls, sculptured with regularly placed, moderate to strong axial

ribs. The sculpture is often partially obsolete. Body whorl obliquely flattened and more or less narrowed, with a prominent keel. A slight external indentation accompanies the palatalis superior; at the position of the infraparietalis the apertural lip is mostly slightly indented. The palatal side of the aperture appears vertical (in lateral view). Umbilicus open. Shell height, 5.1-7.1 mm, width, 2.0-2.7 mm

Apertural lip thickened, continuous at parietal side or connected by a more or less prominent callus. Occasionally the aperture slightly protrudes. Angularis connected with spiralis. Subangularis lamelliform and more or less strongly developed. Infraparietalis prominent. Columellaris reaching only slightly beyond the columella, at its front end clearly thicker than the other lamellae; ending abruptly and sometimes connected with an indistinct fold on the apertural lip. Infracolumellaris longer, often reaching the apertural edge. Infrapalatalis, palatalis inferior and palatalis superior clearly indented and reaching the edge of the aperture. At the weak anterodorsal palatal center a suprapalatalis and often a suturalis are present. At the apertural edge several more or less indistinct folds may be present.

Differentiation. – *Abida s. ionicae* differs clearly from *A. s. andorrensis*. Although these subspecies are connected by a series of intermediates, the extremes are easily distinguishable. Shells of *Abida s. ionicae* are smaller than *A. s. andorrensis* (5.1–7.1 mm versus 9.6–11.8 mm in height) and much more slender. The former subspecies is found at c. 1,600 m altitude and higher, whereas *A. s. andorrensis* is known from c. 900–1,500 m altitude. *Abida s. ionicae* differs from the other high-altitude forms by its slightly more cylindrical shape and the very prominent axial ribbing. A single shell is known from the province of Lérida, Spain: Pico Mainera mtn, NW of Sort (pl. 7 fig. K).

Ecology. – The subspecies is known from altitudes between 1,600 and ~2,700 m, where it occurs in Andorra on calcareous schist with limonitized pyrite crystals.

Etymology. – This subspecies is named after Ms. Ionica Smeets, a good friend of the first author, to celebrate 15 years of friendship.

Genetic barcode. – GenBank accession number EU395371.

Abida secale merijni subsp. nov. (pl. 7 figs L-Q)

Type series. – Spain, Barcelona, Sierra Moixeró. Holotype (RMNH 109891): summit of Pedro dels Quatre Batlles mtn (Tossa d'Alp) (= 15 km N of Bagà), 2,530 m alt., 42.31637°N / 1.88965°E, B. Kokshoorn & M.M. Bos leg., 07-v-2006. Paratypes: type locality (RMNH 104103/30); Cap del Serrat Gran mtn (15 km NE of Bagà), 2,400 m alt., 42.30759°N / 1.91407°E, 07-v-2006 (RMNH 104101/48); ditto, 2,366 m alt., 42.30759°N / 1.91407°E, 07-v-2006 (RMNH 104083/72); ditto, 2,326 m alt., 42.32549°N / 1.90163°E, 07-v-2006 (RMNH 104105/33); ditto, 2,163 m alt., 42.29859°N / 1.91423°E, 04-v-2006 (RMNH 104081/108).

Description (n=258). – Shell slender fusiform, with 6 7/8–9 slightly inflated whorls, sculptured with regularly placed, moderate to strong axial ribs. The sculpture is often partially worn off. Body whorl slightly flattened obliquely and more or less narrowed, without a distinct keel. Palatal side of the aperture slightly protruding, appears vertical (in lateral view). Umbilicus narrowed but open. Shell height,

5.3-7.4 mm, width, 2.3-2.7 mm

Apertural lip usually strongly thickened, discontinuous at parietal side or connected by a thin callus. Some very weak folds may be present on the lip. Angularis either connected or not with spiralis. Subangularis present, more or less prominent. Columellaris reaching well beyond columella, somewhat more prominent than infracolumellaris. Both lamellae occasionally extend to the apertural lip. Infrapalatalis, palatalis inferior and palatalis superior clearly indented and reaching the edge of the aperture. At the weak anterodorsal palatal center a suprapalatalis and often a suturalis are present. The palatalis superior often forms a strong callous bulb at the apertural lip.

Notes. – In the sample from the peak of the Pedro dels Quatre Battles mtn the apertural dentition is most strongly reduced. The infracolumellaris is hardly visible and does not reach the columella (in frontal view). The subangularis is lacking in this sample. The apertural lip is less strongly thickened than in other (fully grown) specimens in *A. secale*. In this sample angularis and spiralis are not connected, but that differs in other populations of this subspecies.

Differentiation. – *Abida s. merijni* is most closely related to the two lowland forms that occur at the foot and along the flanks of the mountain, i.e. *A. s. margaridae* and *A. s. liliensis*. In *A. s. margaridae* the angularis is always connected to the spiralis, but this is not so in *A. s. liliensis* (and *A. s. affinis*). This might account for the variability of this character state, as observed in *A. s. merijni*.

The strongly thickened apertural lip and the bulbous callus associated with the palatalis superior in *A. s. merijni* can be traced back to *A. s. margaridae*. A similarly thickened apertural lip is observed in *A. s. cadica*. However, *A. s. merijni* differs from the latter subspecies by the absence of a protruding aperture, which is characteristic for *A. s. cadica*. See also the differentiation sections for the other high-altitude forms.

Etymology. – This subspecies is named after Dr. Merijn M. Bos, a good friend of the first author, who accompanied him on collecting trips to the summits of the Sierra's Moixeró and Cadí (and back). His help and support were invaluable.

Genetic barcode. – GenBank accession numbers EU395379 - EU395382.

THE REMAINING *ABIDA* SPECIES

Abida ateni Gittenberger, 1973 (pl. 8 figs F-G)

Abida secale ateni Gittenberger, 1973: 122. Type locality: France, Basses-Pyrénées, Défilé d'Escot, right side of Vallée d'Aspe. Holotype: RMNH 54882.

Description (after Gittenberger, 1973). – Shell moderately slender fusiform, recalling a *Chondrina* species in general shape, with 7 1/4-8 weakly to moderately inflated whorls, sculptured with regularly placed, weak axial ribs. Body whorl obliquely flattened, not or only slightly narrowed, with an indistinct keel. No apparent indentation behind apertural lip. The palatal side of the aperture slightly lean-

ing forward (in lateral view). Umbilicus obscured by the last part of the body whorl. Shell height, 5.8-6.9 mm, width, 2.2-2.6 mm.

Apertural lip moderately to strongly thickened. The parietal edges of the aperture are connected by a thin callus. Angularis connected with spiralis. Subangularis weak. Often with an infraparietalis. Columellar lamellae reaching clearly beyond the columella, without reaching the edge of the aperture. Infracolumellaris slightly less prominent than columellaris. A basalis is often present, which can be as prominent as the infracolumellaris. Infrapalatalis and palatalis inferior neither indented nor interrupted; in some specimens the palatalis superior is weakly indented. All palatal folds reaching the edge of the aperture. Suprapalatalis present at the anterodorsal palatal centre.

Genetic barcode. – GenBank accession numbers EU395325 - EU395326.

Notes. -- On the basis of shell characters this species was regarded as a subspecies of *A. secale* by Gittenberger (1973). Molecular studies indicate that it should be considered the sister species of *A. vergniesiana*, despite the fact that the shells of both species are very different (Kokshoorn & Gittenberger, [chapter 6]). Additional research should make clear whether this result can be confirmed.

Abida attenuata (Fagot, 1886)

Type locality: France, Aude, Défilé de Pierre-Lys (valley of the river Aude).

Description. – This species can be distinguished from all other chondrinid species by the subangularis, which is continuous with the slightly erect, parietal border of the aperture.

See Gittenberger (1973: 125).

Genetic barcode. – GenBank accession numbers EU395322 - EU395324.

Notes. – *Abida attenuata* has a very disjunct distribution, with two small ranges, in SE France and N Spain, respectively. Molecular studies (Kokshoorn & Gittenberger, [chapter 6]) show that we deal with a single species indeed. *Abida attenuata* has apparently hybridized with *Abida secale* in southern France, resulting in introgression of its mitochondrial genome into *Abida secale* (Kokshoorn & Gittenberger, [chapter 6]).

Abida pyrenaearia (Michaud, 1831)

Type locality: France, Hautes-Pyrénées, Pic de Lhyéris SE of Bagères-de-Bigorre.

See Kerney & Cameron (1979: 85).

Genetic barcode. – GenBank accession number EU395304.

Notes. – The two taxa united by Gittenberger (1973) in a polytypic species as *A. p. pyrenaearia* and *A. p. vergniesiana*, should be considered separate species that are not even sister taxa (Kokshoorn & Gittenberger, [chapter 6]).

Abida vergniesiana (Küster, 1850) (pl. 8 figs H-J)

Type locality: France, Ariège, Vicdessos.

Genetic barcode. – GenBank accession numbers EU395327 - EU395328.

Notes. – On the basis of shell characters this species was regarded as a subspecies of *A. pyrenaearia* by Gittenberger (1973). Molecular studies indicate that it should be considered the sister species of *A. ateni*, despite the fact that the shells of both species are very different (Kokshoorn & Gittenberger, [chapter 6]). Additional research should make clear whether this result can be confirmed.

Abida occidentalis (Fagot, 1888)

Type locality: France, Hautes-Pyrénées, St. Sauveur, the valley of the Gave Pau, See Kerney & Cameron (1979: 85).

Notes. – This species has not been found alive since the 1970's. However, some records of empty shells have been published by Dr. M. Bech, who reported the species from both Andorra (Bech, 1983a) and Spain (Bech, 1983b; 1984).

Abida cylindrica (Michaud, 1829)

Type locality: France, Pyrénées-Orientales, Villefranche-de-Conflent.

Description. – This species can be distinguished from all other chondrinid species, except *A. gittenbergeri*, by the conspicuously cylindrical shell, with a short, conical apical part. The apertural lamellae are similar to those in *A. partioti*, which has a very different shell shape, with an elongated, slender conical, apical part. Most characteristic is the prominent infracolumellaris, encircling the columella, descending initially and the ascending again towards the apertural lip.

See also Gittenberger (1973: 125) and the notes on *A. gittenbergeri*.

Genetic barcode. – GenBank accession numbers EU395316 - EU395321.

Abida gittenbergeri Bössneck, 2000

Abida gittenbergeri Bössneck, 2000: 5. Type locality: Spain, Gerona, Albanya, valley of the Rio Muga, c. 1 km above the town, c. 250 m alt., 42°18.54'N / 02°42.25'E. Holotype: Staatliches Museum für Tierkunde Dresden, Nr. 42085.

Description. – This species can be distinguished from all other chondrinid species, except *A. cylindrica*, by the conspicuously cylindrical shell, with a short, conical apical part. The apertural lamellae are remarkably different from those in *A. cylindrica*, and most similar to those in *A. s. secale*, as has been observed also by

Bössneck (2000: 9). The columellar lamellae run parallel in both *A. gittenbergeri* and *A. s. secale*.

See also Gittenberger (1973: 125) and the notes on *A. cylindrica*.

Genetic barcode. – GenBank accession numbers EU395311 - EU395315.

Notes. – This species was originally described from a very small area around Albanya in Spain. Afterwards Bertrand (2003) recorded it from the French side of the border at Coustouges. Tarruella Ruestes (2006) increased its known range considerably westward, into the region where *A. cylindrica* occurs. The two species have never been reported to occur sympatrically, however. Preliminary molecular data indicate their status as sister taxa, as is suggested by their unique shell shape, but not by the apertural lamellae. The molecular data also indicate both taxa as not strictly monophyletic. One sample of *A. gittenbergeri* takes a basal position in the clade containing both taxa (Kokshoorn & Gittenberger, [chapter 6, p. 86]).

Abida partioti (De Saint-Simon, 1848)

Type locality: France, Hautes-Pyrénées, St. Sauveur.

See Kerney & Cameron (1979: 86).

Genetic barcode. – GenBank accession number EU395303.

Notes. – *Abida escudei* Geniez & Bertrand, 2001. According to Gittenberger (2006), *A. escudei* is a junior synonym of *A. partioti*.

Abida bigerrensis (Moquin-Tandon, 1856)

Type locality: France, Hautes-Pyrénées, Bagnères-de-Bigorre.

See Kerney & Cameron (1979: 86).

Genetic barcode. – GenBank accession numbers EU395307-EU395310.

Abida vasconica (Kobelt, 1882)

Type locality: Spain, Burgos, Orduña.

See Gittenberger (1973: 150).

Genetic barcode. – GenBank accession number EU395302.

Abida polyodon (Draparnaud, 1801)

Type locality: France.

See Kerney & Cameron (1979: 86).

Genetic barcode. – GenBank accession numbers EU395305-EU395306.

Chondrina Reichenbach, 1828

Type species (design. Reichenbach, 1836: 152): *Bulimus avenaceus* Bruguière, 1792.

For this genus the results of a preliminary, molecular, phylogenetic analysis are available (Kokshoorn et al., [chapter 3]). This analysis made already clear that in any case, a revision of the classification presented by Gittenberger (1973) is necessary. In particular the nominal taxa united by that author as a single, polytypic species, i.e. *Chondrina farinesii* (Des Moulins, 1835), should not all be lumped. Obviously, there are many more taxa, characterized by shells with more or less obsolete, apertural teeth. In some cases, shell dimensions, shape and sculpture, could be used under the direction of the molecular data, but many questions remain unanswered because of a lack of sufficient information. Since it is unlikely that this situation will improve substantially in the near future, we have already adapted the classification of the *Chondrina* taxa to the new insights. Since the dataset presented in chapter 3 is inconclusive at some points in the tree, we refrain from revising taxa that show ambiguous positions in the tree. New taxa are formally described and named only when they can be recognized on the basis of molecular and (to some extent) conchological characteristics. To promote further research, some taxa are for the time being referred to with numbers only. These taxa can only be defined based on very limited DNA data, so that their geographical distribution and the variation in shell morphology remain unknown. More sequence data are needed to acquire more reliably classified material. Shell morphology should be studied again in search of hitherto unnoticed common characteristics. Inevitably, an additional increase of DNA data will dictate further changes in the following overview. The phylogenetic relationships within *Chondrina* are more complicated than may be assumed at first sight.

The apertural teeth do not vary randomly in *Chondrina*. There is a “bauplan I” with more than two palatals and a spiralis, next to a “bauplan II” with two palatals at most and no spiralis. Toothless forms may be considered derived from the latter bauplan. These two groups are not clades however. Some individual specimens or even species do not belong to one of the alternatives. In *C. aguilarii* there may be an infrapalatalis but never a spiralis, whereas in *C. pseudavenacea* there are three palatals, again without a spiralis. According to Gittenberger (1973: 232) there may be an infrapalatalis, a suprapalatalis and an obsolete spiralis in *C. calpica*. In this species bauplan II is the rule, but rarely specimens with apertural teeth according to bauplan I occur as well. We have to conclude that the apertural teeth became obsolete or were reduced completely several times independently, resulting in shells that misleadingly suggest a close relationship in several cases.

Several authors have contributed to the currently accepted taxonomy of the group (Nordsieck, 1962, 1970; Gittenberger, 1973; Gómez & Angulo, 1982). *Chondrina avenacea* and *C. arcadica clienta* have been used as model organisms in ecological and evolutionary studies (Armbruster et al., 2007; Baur, A. & B. Baur, 1991; Baur, B. & A. Baur, 1990, 1994, 1995; Baur, B. et al., 1993, 1995; Baur, A. et al., 1992,

1994; Fröberg et al., 1993; Hesbacher et al., 1995; Szarowska et al., 2003). However, a study devoted to the phylogeny of the *Chondrina* species was still not available. Gittenberger (1973) divided the genus in four subgroups. He regarded that classification rather artificial, probably reflecting only some morphological and geographical similarities rather than phylogenetic relationships. Since this subdivision does indeed not reflect the evolutionary history of the genus, it is no longer acceptable. Since *C. maginensis* has to be considered the sister-group of all other *Chondrina* taxa combined, that species is dealt with first. The remaining *Chondrina* taxa are provisionally arranged in six species groups, guided by the results of the molecular analysis (Kokshoorn et al., [chapter 3]). Since the taxonomic diversity is much larger than previously expected, the molecular analysis should be considered far from complete. Consequently, the arrangement of species based on it, must be considered hypothetical at most. As a final group, some nominal taxa are listed that have been synonymized or overlooked before, but might represent separate *Chondrina* species or subspecies.

Chondrina maginensis Arrébola & Gómez, 1998 (pl. 13 figs E-G)

Type locality: Sierra Mágina, Andalucía, Spain.

Chondrina maginensis Arrébola & Gómez, 1998: 110-113, fig. 1D (holotype shell), fig. 2B (genital system).

Rupestrella maginensis; Bank, 2003: 15.

Material. – Spain, Jaén, Cuadros (type locality), near Ermita de Cuadros, on limestone rock along an irrigation canal, 579 m alt., UTM VG6482 (RMNH 103205/9, 103207/11); Abánchez de Mágina, on rocks at the base of Castillo de Abánchez, 974 m alt., UTM VG5882 (RMNH 108829/6 in alcohol 70%).

Shell (n=11). – Shell very slender, regularly conical, with c. 8, yellowish brown whorls; height 5.7-6.4 mm, height-width ratio 2.9-3.4.

Protoconch more conspicuous than usual in *Chondrina*, nearly as broad as the adjoining teleoconch whorl, with 1½-1¾ strongly inflated, clearly granular whorls. Teleoconch whorls more or less regularly sculptured with prominent riblets that are separated by wider interspaces. Initial teleoconch whorls convex, separated by a deep suture; final quarter to half of the body whorl obliquely flattened, sometimes with a vague indentation, corresponding with the position of the palatalis superior inside. Apertural lip with a short (half the apertural width) interruption at the parietal side, not or hardly reflexed but slightly thickened by a white callus, regularly rounded basally; palatal side nearly parallel with the columellar axis and columellar side obliquely deviating. Apertural height 1.6-1.7 mm, height/width ratio 1.1-1.4.

Apertural lamellae more or less rudimentary. The columellaris is the most prominent lamella; it does not extend beyond the columella and may be accompanied by a weak subcolumellaris (most clearly seen in oblique view). The angularis may be about as prominent as the parietalis, but is usually more obsolete. Palatal

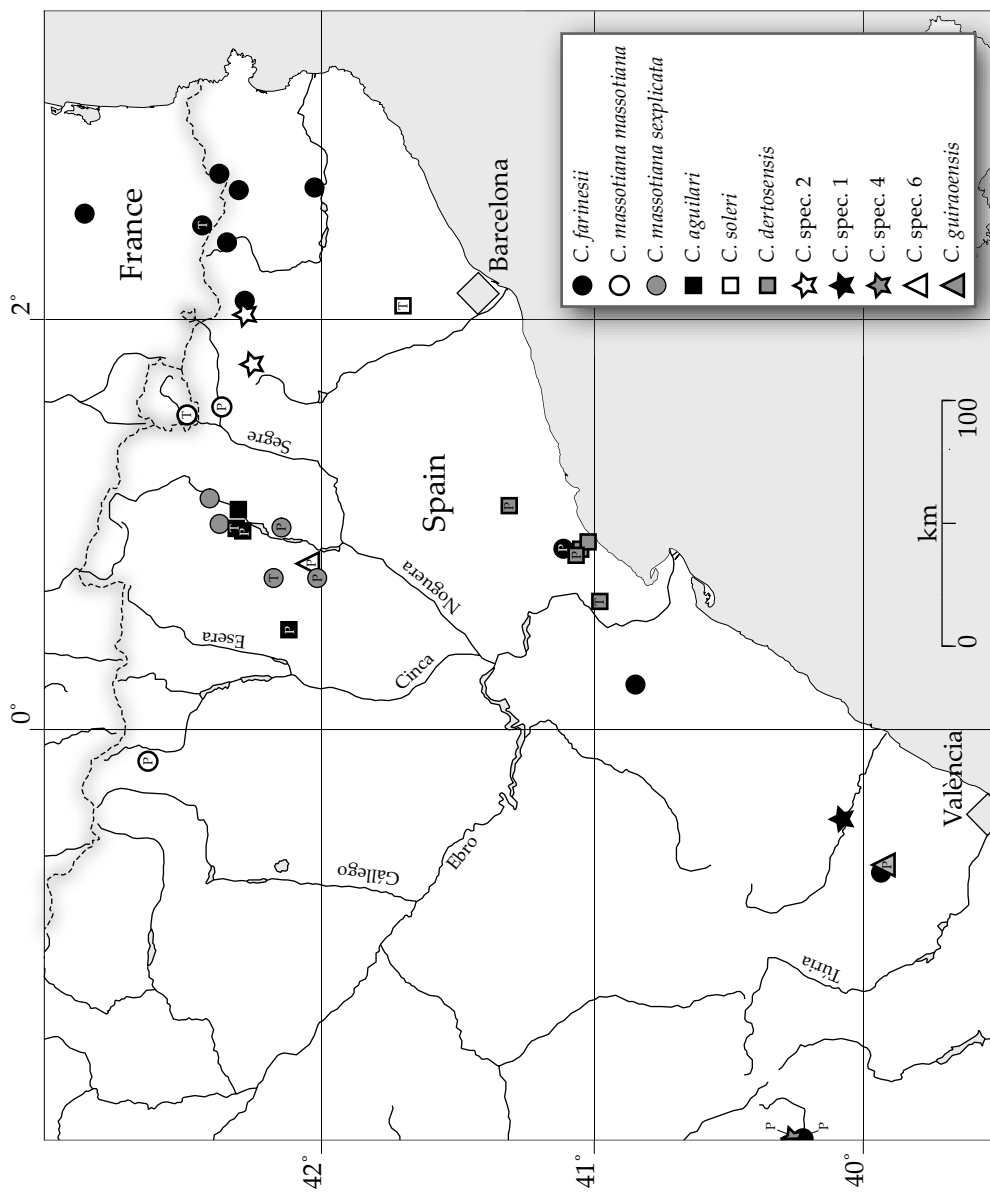


Figure 4. Distribution of *Chondrina* species in northeastern Spain. T = Type locality, P = Photographed, see plates.

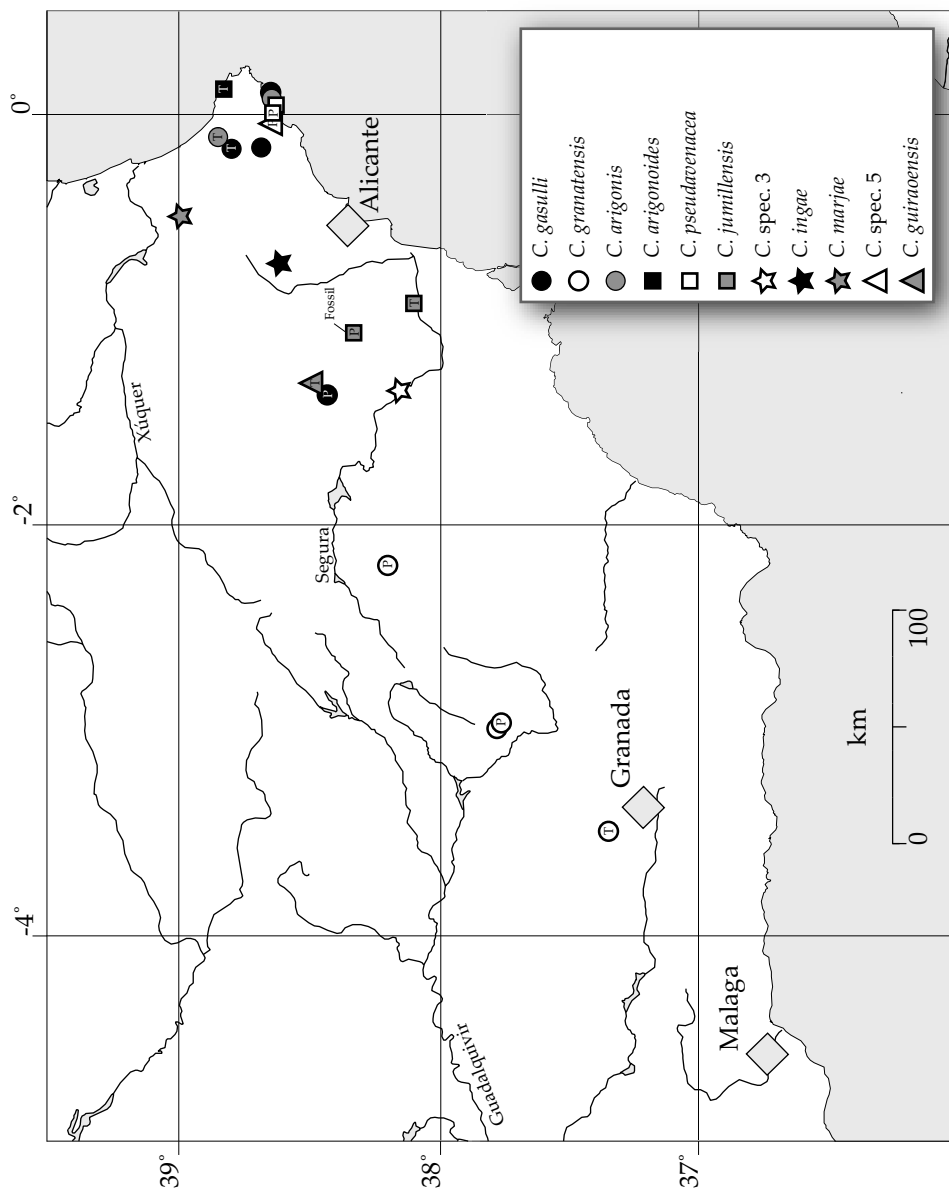


Figure 5. Distribution of *Chondrina* species in southeastern Spain. T = Type locality, P = Photographed, see plates.

lamellae are usually absent, apart from one or even two very weak thickened streaks. According to Arrébola & Gómez (1998) however, the palatal lamellae may be more prominent. The umbilicus is widely open.

Genitalia (n=2) (fig. 6 A, B). – The length of the vagina is about five times its width; it is somewhat longer than the oviduct and about as long as the part of the penis that is situated outside the penial loop. The spermoviduct is about one and a half times longer than the combined vagina and oviduct. The peduculus of the bursa copulatrix is long and slender; the tip of the bursa touches the glandula albuminifera. The male part of the genital tract forms a loop as in other chondrinid species (Gittenberger, 1973). The penis is here defined as the simple, tube-like structure, which reaches from the genital atrium far into the loop, ending with a short, abruptly narrowing segment, after which the epiphallus starts. Inside the most proximal part of the epiphallus there is a vague pattern of some septae. The distal end of the epiphallus is attached to the penis about as far as the length of the vagina from the genital atrium.

Radula (n=2) (fig. 6 C). – The central tooth can be recognized because of its symmetrical basal plate, with a supporting denticle at each side. Next to the unicuspid central tooth there are five or six unicuspid lateral teeth, followed by two or three laterals with a more or less vaguely discernible ectocone. The adjoining marginal teeth, ranging from tooth 9 to 20, are prominently bicuspid and increasingly more irregularly comb-like towards the radular margin, with tooth no. 20 being hardly recognizable as a tooth.

Genetic barcode. – Three partial (598bp) Cytochrome Oxidase subunit I sequences were produced (Kokshoorn et al., [chapter 3]). One specimen from the type locality, GenBank accession no. FJ171596, and two from Abánchez, GenBank accession nos FJ171597 and FJ171598.

Discussion and conclusions. – Because of its shell shape and size, *Chondrina maginensis* has been classified with *Rupestrella* by Bank (2003: 15). However, shell shape in *Rupestrella* is very variable. Species with a slender conical shell, like for example *R. rhodia* (Roth, 1839), are classified in *Rupestrella* indeed, but next to species like *R. philippii* (Cantraine, 1840), with a shell that has a spire with slightly convex sides and a more cylindrical lower part. In *Chondrina*, *C. marmouchana* was considered rather different from the congeneric species by its slender conical shell (Gittenberger, 1973: 251), which reminds of that in *C. maginensis*. Molecular data (Kokshoorn et al., [chapter 3]), however, make clear that the conchological similarity between *C. marmouchana* and *C. maginensis* is due to convergent evolution. In size, *C. maginensis* could be considered either a large *Rupestrella* or a small *Chondrina*. The apertural teeth of the shell cannot be considered diagnostic for either *Chondrina* or *Rupestrella*, since in *Chondrina* these teeth vary from none to several. The structure of the genital tract can also not be used to discriminate between these two genera. According to Gittenberger (1973: 21, 23), only the radula is known to be diagnostic for *Chondrina* versus *Rupestrella* species. In species of the former genus, the central tooth in each row can only be recognized unequivocally by the symmetrical structure of

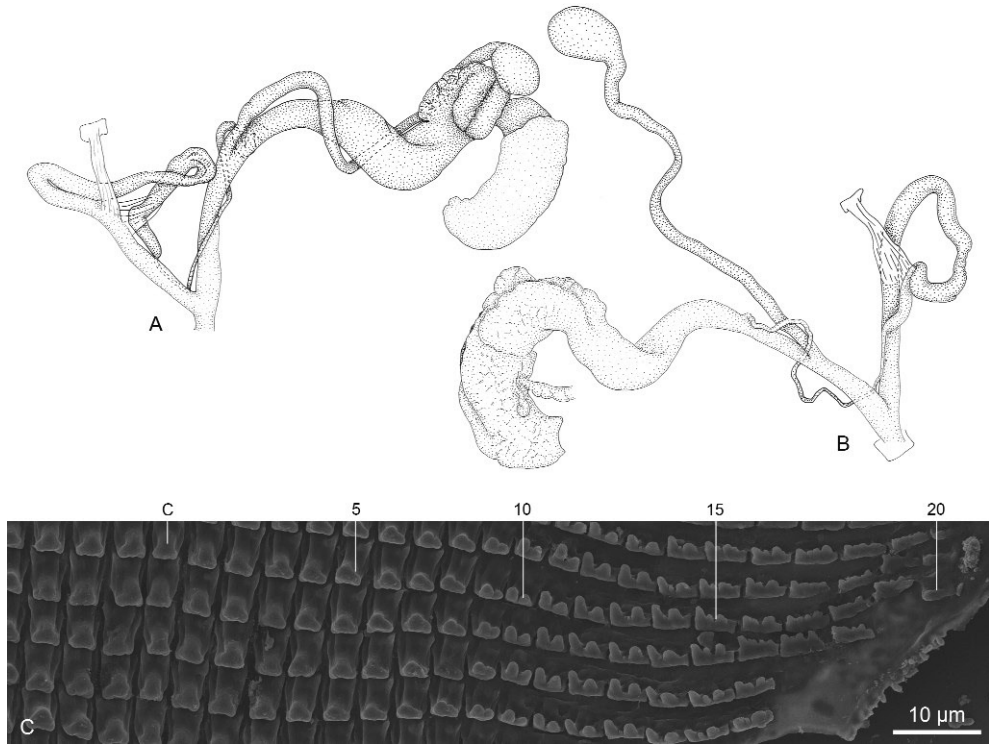


Figure 6. *Chondrina maginensis*, Spain, Jaén, Sierra Mágina, near Ermita de Cuadros. **A-B**, Genitalia (RMNH genital slides 1147a-b); **C**, Radula.

its basal plate, which has a support knob at each side. The central tooth and the adjoining lateral teeth cannot be distinguished at first sight because they all have a single main cusp without any side cusps. This bauplan is found in *C. maginensis* (fig. 6b), which supports its classification in *Chondrina*, not *Rupestrella*.

According to the molecular data, *C. maginensis* has to be considered a *Chondrina* species as well. Its resemblance to *Rupestrella* species, like *R. rhodia* might be considered more meaningful, viewed in the light of its phylogenetic position in *Chondrina* as the sistergroup to all other extant *Chondrina* taxa, suggesting that the species retains some plesiomorphic shell characteristics..

Apart from the somewhat unusual shell shape and its surprising phylogenetic relationships as the sister taxon of the combined other *Chondrina* taxa, nothing is known that adds to the oddity of *C. maginensis*.

Distribution. – The species is known only from the north flank of the Sierra Mágina in the province of Jaén, Andalucía, Spain. The original description by

Arrébola & Gómez (1998) lists two localities; the type locality, Cuadros, and the village of Jódar, which lies approx. 6km NE of the type locality. The actual sampling localities have not been mentioned. During fieldwork in 2006 another two localities were added: Torres, ca. 4 km W of Cuadros, and Abánchez de Magina, which lies approximately 5 km W of the type locality. A sample was taken from limestone rocks at the base of Castillo de Abánchez (UTM VG5882), situated at 974 m, which is the highest altitude at which the species has been found sofar.

SPECIES GROUP I

The phylogenetic relationships of the species provisionally united in this group, are unclear (Kokshoorn et al., [chapter 3]).

Chondrina tatrlica Ložek, 1948

This species is endemic to the Tatra mts. We can only conclude that it is not closely related to either *C. avenacea* or *C. arcadica*, which are geographically closest.

Chondrina spelta (Beck, 1837)

The systematic position of this polytypic species from the western Balkans is unclear (Kokshoorn et al., [chapter 3]). We can only conclude that it is not closely related to *C. arcadica*, despite the fact that this species is geographically closest.

Chondrina megacheilos (De Cristofori & Jan, 1832) and *Chondrina multidentata* (Strobel, 1851)

These species are distributed in the southern Alps (Nordsieck, 1962) and might be sister-species according to the DNA data. The shell characters suggest that the northern alpine (Austrian) *C. burtscheri* Falkner & Stummer, 1996, is also closely related to *C. megacheilos*. It was described as a subspecies of that polytypic species. The three individuals that were studied in the molecular analysis gave conflicting results: two specimens came out amidst *C. avenacea* and one clustered with *C. multidentata*. Since *C. burtscheri* occurs in a mixed population with *C. avenacea*, we hypothesize that either contamination, or hybridisation and subsequent mitochondrial introgression might have obscured the factual phylogenetic relationships in this case. Further investigations are necessary here.

SPECIES GROUP II

Chondrina farinesii (Des Moulins, 1835) (pl. 9 figs A-C)

Chondrina (Modicella) jumillensis unidentata Altimira, 1960: 12 (valid after ICZN Article 45.6.4.). Spain, Tarragona, Llaveria (= 6.8 km SSE Falset), entrance to the Cueva del Ramé; UTM CF1850. Type series: RMNH 109859/lectotype (design. nov.) (pl. 9 fig. B), 109860/9 paralectotypes.

Notes. – In a rather unsatisfactory way, on the basis of conchological characters that have shown to be misleading in many cases, but without a better alternative, we provisionally combine a group of populations of snails with similar shells under the heading of *C. farinesii*. In the phylogenetic reconstruction (Kokshoorn et al., [chapter 3]) this is a paraphyletic group.

The type locality of Altimira's *C. unidentata* is situated within the range of *C. dertosensis*, but shells of the former taxon have a less clearly thickened apertural lip and an aperture without any teeth or with an obsolete columellaris and an equally inconspicuous parietalis, and are clearly most similar to regular *C. farinesii* as known from the type locality La Preste and other localities in southern France and NE Spain. Apparently, this nominal taxon was overlooked by Gittenberger (1973).

Chondrina ascendens (Westerlund, 1878)

Notes. – The status of this taxon, considered a separate species by Gittenberger (1973), was confirmed. In the cladogram it is the sister-group of the combined *C. massotiana*, *C. dertosensis*, *C. arigonis* and *C. spec. 3*

Chondrina massotiana (Bourguignat, 1863)

Notes. – *Pupa massotiana* was considered one of many synonyms of *C. farinesii* by Gittenberger (1973). Since it has to be accepted that the latter species is far less variable conchologically than assumed, several nominal taxa have to rise from synonymy.

Acting as First Revisers in the sense of the ICZN (Art. 24.2), we here introduce the following synonymy.

In *C. massotiana* the shell is slender to very slender conical, with growthlines that may be partially arranged as fine riblets. Apertural teeth variable across its range, but nearly always with at least a rather prominent columellaris and a parietalis; never with more than two palatal folds and always without a spiralis. By the more slender shell with a columellaris and a parietalis, *C. massotiana* can be distinguished from *C. farinesii*. Two geographical forms, that are considered subspecies here, can be distinguished more or less clearly.

Chondrina massotiana massotiana (Bourguignat, 1863) (Pl. 9 figs E-J)

Pupa massotiana Bourguignat, 1863: 61. Sant Juliá de Lòria, Andorra. Lectotype (design. Gittenberger, 1973): BG 13160, with 4 paralectotypes (one of which is a fragment of the last whorl and another one lacks the apical whorls); BG 13159/30 paralectotypes.

Pupa penchinatiana Bourguignat, 1863: 62. Sant Juliá de Lòria, Andorra. Lectotype (design. Gittenberger, 1973): BG 13190.

Chondrina farinesii farinesii: Gittenberger, 1973 [part.]: 213, fig. 117. Not Des Moulins, 1835.

Description. – The angularis is a white, linear callus, that varies from prominent to obsolete. There may be two more or less vague palatals, which either are equally long or the palatalis superior is the longer one and reaches the outer lip. The palatals may be obsolete or missing completely, but the parietalis and the columellaris are always present. Shell height 4.3-7.2 mm, width 1.9-2.6 mm.

Notes. – Although Bourguignat (1863: 61, 62) distinguished two species based on the presence of one or two palatal folds, his type series (Colln Bourguignat, Geneva, Nrs 13159, 13160) of *Pupa massotiana* contains shells which vary between two rather prominent palatals and none.

From Linas de Broto in the Spanish province of Huesca, a sample (RMNH 109429) with this species and *C. ascendens* is known.

See also *Rupestrella kabyliana*.

Chondrina massotiana sexplicata (Bofill, 1886) (pl. 9 figs K-N)

Pupa penchinatiana var. *sexplicata* Bofill, 1886: 160. Lectotype (design. Gittenberger, 1973: 222):

Pupa ilerdensis Fagot, 1888: 128. Syntype from type locality: Figuerola de Orcau, Lérida, Spain; SMF 437777.

Chondrina (s.s.) *pulchella bofilliana* Altimira, 1967: 24. Lectotype (design. Gittenberger, 1973: 222): Congost d'Erinyá, Lérida, Spain; RMNH 54874 (pl. 9 fig. M).

Chondrina (s.s.) *pulchella montsiciana* Altimira, 1967: 24. Lectotype (design. Gittenberger, 1973: 222): Port d'Ager, Lérida, Spain; RMNH 54875 (pl. 9 fig. N).

Chondrina (s.s.) *pulchella agerensis* Altimira, 1967: 24. Lectotype (design. Gittenberger, 1973: 222): Port d'Ager, Lérida, Spain; RMNH 54872 (pl. 9 fig. L).

Description. – Shell with six prominent apertural teeth, i.e. columellaris and sub-columellaris, parietalis, a linear, often prominent angularis, and palatales superior and inferior. The palatalis superior may be curved upwards, reaching the whitish apertural lip; otherwise both palatal lamellae are about equally long. Shell height, 4.3-6.8 mm; width, 1.7-2.5 mm.

Chondrina dertosensis (Bofill, 1886) (Pl. 10 figs A-D)

Pupa dertosensis Bofill, 1886: 162. Lectotype (design. Gittenberger, 1973: 222): Sierra de Cardó, Tarragona, Spain; MZB (Pl. 10, fig. B).

Chondrina jumillensis montrealensis Altimira, 1959: 92. Lectotype (design. Gittenberger, 1973: 214): Montreal, Tarragona, Spain; RMNH 54896.

Chondrina farinesii farinesii; Gittenberger, 1973 [part.]: 213, fig. 118. Not Des Moulins, 1835.

Description. – Shell shape varying between slender conical and fusiform with a more or less elongated, conical spire; teleoconch sculptured with regular riblets. Apertural lip not reflexed but internally thickened by a conspicuous white rib. Rarely, the aperture may seem to be toothless in frontal view. The columellaris is than situated as a denticle, deep inside the shell, and both the linear angularis and the parietalis are lacking completely. As the opposite extreme, these teeth can be present, together with one or two, usually low, palatals.

The largest shell, from Prasdip (UTM CF1944), measures 8.5×3.1 mm, with $8\frac{1}{4}$ whorls, whereas the smallest one, from Balneario de Cardó (UTM BF9635), is only 4.6×2.2 mm, with $6\frac{1}{4}$ whorls.

Notes. – The re-evaluation of Bofill's *Pupa dertosensis* as a separate species is mainly based on the results of DNA sequence data. Much more molecular data are necessary, however, to determine the limits of its morphological variation and, consequently, its geographical boundaries. For the time being the combination of riblets and a thickened apertural lip has to be accepted as morphologically diagnostic.

Chondrina spec. 1 (pl. 12 fig. H)

Some specimens from the province of Castellon, along road CV20 from Onda to Montanejos, shortly before Arañuel, 390 m alt., UTM YK1538, with dark brown shells that are very similar to *C. farinesii*, should be considered a separate taxon according to the molecular data (Kokshoorn et al., [chapter 3]).

Chondrina arigonis (Rossmässler, 1859) (pl. 10 fig. F)

Chondrina farinesii arigonis; Gittenberger, 1973: 225.

Notes. – Once classified as a subspecies of *C. farinesii* by Gittenberger (1973), *C. arigonis* is now generally accepted as a species. It occurs sympatrically with other *Chondrina* species, i.e. *C. gasulli*, *C. cf. arigonoides* spec. nov. (see p. 156) and *C. pseudavenacea* spec. nov., but nowhere with *C. farinesii*.

SPECIES GROUP III

This group contains Iberian taxa, from the eastern part of the Spanish Pyrenees to the mountains of southern Spain and, with one species, Morocco.

Chondrina aguilari Altimira, 1967 (pl. 9 fig. D; pl. 10 figs H-J)

Chondrina (s.s.) *pulchella aguilari* Altimira, 1967: 24. Lectotype (design. Gittenberger, 1973: 222): Congost d'Erinyá, Lérida, Spain; RMNH 54873 (pl. 10, fig. I)

Chondrina farinesii farinesii: Gittenberger, 1973 [part.]: 213, fig. 120. Not Des Moulins, 1835.

Description. – Shell slender fusiform with an elongated conical spire, relatively small, dark brown. With 6¼-7 whorls. Teleoconch with more or less obsolete, irregular growthlines. The apertural teeth are characteristic. The angularis is a whitish, dot-like callus, which may be connected to the insertion of the palatal lip, or is lacking completely. In specimens with the most prominently developed teeth, the two palatals are relatively high but short, and do not reach the apertural lip. Usually, the palatalis inferior is somewhat more prominent than the superior. The palatals may be obsolete, but the parietalis and the columellaris are always present. Rarely there is an inconspicuous infracolumellaris and even more rarely a vaguely discernible infrapalatalis (pl. 10, fig. J). Shell height 4.4-5.7 mm, width 1.7-2.1 mm.

Notes. – Some large samples of *Chondrina*'s, collected by C. Altimira, J.L.M. Donders & A.J. de Winter, F.M. Vilella y Tejedó and G.J.M. Visser & J.A. Zoer, made convincingly clear that *C. aguilari* is a separate species that may occur sympatrically, without any intermediate specimens, with *C. massotiana sexplicata*. Shells of the former species are smaller and usually more slender, with a whitish, dot-like instead of linear callus, that may be obsolete or lacking completely, and clearly different palatal folds.

According to the molecular data (Kokshoorn et al., [chapter 3]), this species is closely related to a still poorly known taxon occurring more to the East (*Chondrina* spec. 2; Pl. 12 figs A-D). Another taxon that might be closely related, but for which no molecular data are available has its poorly defined range more to the West (fig. 4).

Chondrina spec. 2 (pl. 12 figs A-D)

Notes. – The shells of two samples that are sister-groups according to the DNA data, are dark brown, with teleoconch whorls that are sculptured with more or less obsolete, irregular growth-lines only. In the aperture there may be a columellar denticle, which is hardly or not visible in frontal view; the apertural lip is moderately thickened inside.

The two samples differ conspicuously in shell size and less so in shape. The shells from Barcelona, 1.5 km N of Saldes (RMNH 102444, UTM CG9677), are 4.1-5.4 mm high and 1.9-2.1 mm broad (n=15) and slender conical to fusiform. Specimens from Lerida, La Pobla de Lillet – Castellar de N'hug (RMNH 103318,

UTM DG1679) are 4.7-5.5 mm high and 2.2-2.3 mm broad (n=9) and generally more fusiform.

According to the DNA data, this taxon is most closely related to *C. aguilari*. Together with that species it has affinities with taxa further south in the eastern part of the Iberian peninsula and Morocco.

Chondrina spec. 3 (pl. 12 fig. E)

Notes. – A sample from Murcia, Sierra de Ricote, c. 2.5 km along the road west of Ricote (UTM XH4123), at 425 m altitude, for which DNA data are available, cannot satisfactorily be identified. The light brown shells have a more or less slender conical spire; the last whorl may be hardly broader than the penultimate one. The teleoconch is sculptured with rather coarse, regular riblets. The aperture is provided with a columellaris, an obsolete infracolumellaris, and a parietalis which are hardly visible in frontal view, there may be an obsolete angularis and an obsolete palatalis superior. The narrow, white, apertural lip is hardly thickened.

The shells are somewhat similar to *C. granatensis* with rudimentary apertural teeth (see the notes with that species).

Chondrina granatensis Alonso, 1974 (Pl. 11 fig. B)

Chondrina farinesii granatensis Alonso, 1974: 87, pls 1, 2; 1977: 271, fig. 1 (lectotype).

Notes. – *Chondrina granatensis* was originally described as a subspecies of *C. farinesii* from the Sierra Harana (= Arana), 18 km NNE Granada centre (UTM VG5432), and two places in the Sierra Elvira, 12 km NW Granada centre (UTM VG3621, 3921) (Alonso, 1974). By the selection of a lectotype (Alonso, 1977), the surroundings of the Cueva del Agua in the Sierra Harana, at 1760 m altitude, became the type locality. Three paralectotypes from there are slender fusiform shells, with rather prominent, more or less regularly arranged riblets. They have five prominent, apertural teeth, without any more obsolete ones.

A sample collected in the province of Jaen, 13 km S of Cazorla (UTM WG0078) may belong to a polytypic *C. granatensis*. The shells are rather similar to the paralectotypes of *C. granatensis* in shape and sculpture, but clearly different in the apertural teeth. Only the columellaris is always present and rather prominent; it is often accompanied by an infracolumellaris denticle. The other teeth are rather obsolete or lacking completely. In the figured shell (Pl. 11, fig. C) the palatal teeth are more conspicuous than usual.

Chondrina marmouchana (Pallary, 1928) (Pl. 11 fig. A)

Notes. – Several large samples of this conchologically somewhat deviant species, which recalls *C. maginensis*, were collected by J. Nienhuis and presented for further study. It is the only species of group III occurring in N. Africa (Morocco).

Chondrina arigonoides spec. nov. (pl. 10 fig. E)

Material. – Spain, Alicante, SW of Marquesa along path into nature reserve; 170 m alt.; UTM BD4600. Type series: RMNH 109861/holotype, 103233/24 paratypes.

Description. – Shell brownish, moderately slender conical, with only the last whorl somewhat narrowed; densely sculptured with relatively coarse riblets, which are increasingly irregular on the lower whorls. Aperture with four prominent teeth, viz. the palatales superior and inferior, parietalis and columellaris, a moderately prominent infracolumellaris, a more or less obsolete angularis, and sometimes a vestigial infrapalatalis. Apertural lip somewhat thickened, not reflexed. Shell height, 5.4–6.4 mm; width 2.5–2.7 mm.

Differentiation. – At some places within the range of *C. arigonis*, *C. arigonoides* is found with shells that are smaller and more conspicuously sculptured, with an apertural lip which is not strongly thickened and flattened.

Notes. – Probably this species, or a closely related one, occurs sympatrically with *C. arigonis* also in the province of Alicante, near the Cascada de El Algar (UTM YH5180), and in the province of Valencia, at Col de Tous, 500 m alt. (UTM YJ0237). Taking the extreme diversity in *Chondrina* into account, we prefer to restrict *C. arigonoides* for the time being to the population for which DNA data are available.

Derivatio nominis. – The epithet refers to the similarity with *C. arigonis* in apertural teeth.

Chondrina marjae spec. nov. (pl. 12 fig.G)

Material. – Spain, Valencia, S-side of Xativa; 160 m alt.; UTM YJ1317. Type series: RMNH 109863/holotype, 103250/25 paratypes.

Description. – Shell brownish, moderately slender conical to rather thickset; with very fine radial striae, which are more obsolete and irregular at the lower whorls. Aperture about as high as broad, with a broadly rounded base, without teeth. Apertural lip somewhat thickened, not reflexed or flattened.

Shell height 5.2–5.7 mm; width 2.4–2.6 mm.

Notes. – Conchologically this species is similar to *C. farinesii*, differing mainly by the more roundish aperture, which is somewhat higher than broad in *C. farinesii*. For the time being we restrict this species to the sample for which DNA data are available. Taking the diversity in *Chondrina* species into account, we refrain from speculations about the actual range of this species on the basis of conchological characters only.

Derivatio nominis. – The epithet *marjae* refers to Ms. Marja van Schoor, who contributed substantially to our knowledge of the Iberian chondrinids by an unpublished report on these snails, written on the basis of material that she collected and analysed together with Ms. I. Erkelens.

Chondrina ingae spec. nov. (pl. 12 fig. F)

Material. – Spain, Alicante, S of Biar, along road into the Sierra de Biar; 960 m alt.; UTM XH9475. Type series: RMNH 109865/holotype, 103221/19 paratypes.

Description. – Shell dark brown, moderately slender conical to rather thickset; sculptured with irregular wrinkles or riblets. Aperture somewhat higher than broad, without teeth. Apertural lip inconspicuously thickened.

Shell height 5.7–6.1 mm; width 2.6–2.8 mm.

Notes. – This species differs conchologically from congeneric ones by the dark brown colour in combination with a toothless aperture, and an irregularly sculptured surface. Taking the diversity in *Chondrina* species into account, we refrain from speculations about the actual range of this species on the basis of conchological characters only.

Derivatio nominis. – The epithet *ingae* refers to Ms. Inge Erkelens, who contributed substantially to our knowledge of the Iberian chondrinids by an unpublished report on these snails, written on the basis of material that she collected and analysed together with Ms. M. van Schoor.

Chondrina pseudavenacea spec. nov. (pl. 13 fig. H)

Type series: Spain, Alicante. – 7 km NE of Altea, Barranco de Mascarat, UTM YH6080, L. Gasull leg. (RMNH 109867/holotype); 7 km NE of Altea, Barranco de Mascarat, UTM YH6080, L. Gasull leg. (RMNH 111888/54 paratypes); Morro de Toix, S-side peninsula, c. 250 m alt., UTM BC4079, BC leg., 6.v.2006 (RMNH 109868/15 paratypes); 2 km ESE Callosa de Ensarria, near cascada El Argar, UTM YH5281, L. Gasull leg. (RMNH 109869/1 paratype); 2 km ESE Callosa de Ensarria, near cascada El Argar, UTM YH5281, H.B. Marcus leg. (RMNH 111887/6 paratypes).

Description. – Shell brownish, conical or somewhat more fusiform, with fine, more or less obsolete growth-lines, which do not give the impression of regular riblets. Aperture with three prominent palatals, of which the infrapalatalis is the weakest, a columellaris and a less conspicuous infracolumellaris, and a very prominent parietalis. An angularis is more or less obsolete or lacking completely and a spiralis is always absent. Shell height 5.8–6.8 mm; width 2.7–3.0 mm.

Notes. – This *Chondrina* species can be recognized relatively easily on the basis of only shell characters. In *C. avenacea*, which is somewhat similar conchologically, the shell is more cylindrical instead of conical, and always has a spiralis in the aperture.

At the three localities from where it is known, this species occurs together with *C. arigonis*, which can easily be distinguished by the presence of only two palatal teeth and a more conspicuously thickened and flattened apertural lip.

Derivatio nominis. – The epithet refers to the similarity with *C. avenacea* in apertural characters.

Chondrina gasulli Gittenberger, 1973 (pl. 11 figs D-F)

Chondrina gasulli Gittenberger, 1973: 246.

Notes. – The species group with *C. arigonoides* spec. nov., *C. marjae* spec. nov., *C. ingae* spec. nov., *C. pseudavenacea* spec. nov. and *C. gasulli* becomes problematic as soon as more than only samples from the type localities are included. Maybe even more species are involved, but the intraspecific variation is still unclear and with it the species boundaries. Molecular data on many more populations are needed to clarify these problems.

SPECIES GROUP IV

Notes. – The subdivisions in the cladogram point to the five species that are currently recognized in this Pyrenean-Cantabrian group, viz. *Chondrina altimirai* Gittenberger, 1973, *C. bigorriensis* (Des Moulins, 1835), *C. centralis* (Fagot, 1891), *C. ripkeni* Gittenberger, 1973, and *C. tenuimarginata* (Des Moulins, 1835). A conchological character state shared by these species is the clearly reflected apertural lip. With the exception of *C. altimirai*, the species have bauplan I for the apertural teeth; only occasionally there is an obsolete infrapalatalis in *C. altimirai*. Except for *C. centralis*, the shells have a more or less conspicuously keeled basis. The widely disjunct *C. centralis* and *C. ripkeni*, both with shells sculptured with coarse riblets, cluster as sister-species. The relatively widespread species *C. bigorriensis* and *C. tenuimarginata* are vicariant along the Pyrenean watershed. The far less common *C. altimirai*, which is conchologically similar to *C. tenuimarginata*, except for the apertural teeth, is known from only a few localities in the Spanish part of the eastern Pyrenees.

SPECIES GROUP V

Notes. – Generally, the species in this group, i.e. *C. calpica*, *C. klemmi* and *C. cliendentata*, have the bauplan II for their apertural teeth, but in *C. calpica* there may occasionally be a spiralis, next to an infrapalatalis and a suprapalatalis. In *C. cliendentata* there may also be an infrapalatalis present.

The problems with the various taxa here are similar to those in group III. More molecular data are needed in the first place. Most taxa are distributed in the southern part of the Iberian peninsula or Morocco. The phylogenetic relationships (Kokshoorn et al., [chapter 3]) that are indicated for *C. cliendentata* Gittenberger, 1973, which is distributed in northern Spain, south of the Picos de Europa, are surprising, also from the perspective of shell morphology.

Chondrina cliendentata Gittenberger, 1973

Chondrina kobelti cliendentata Gittenberger, 1973: 173.

Notes. – This species has originally been considered a subspecies of *C. kobelti* by Gittenberger, (1973) and of *C. kobeltoides* by Raven (1986). However, a molecular phylogeny reconstruction (Kokshoorn et al., [chapter 3]) revealed that *C. cliendentata* is most closely related to the combined *C. [calpica] altenai* Gittenberger, 1973, *C. klemmi* Gittenberger, 1973, and *C. calpica* (Westerlund, 1872). Without further speculations, we here give this taxon species status.

SPECIES GROUP VI

Notes. – The species in this group have apertural teeth according to bauplan I.

The similarity of the sympatric species *Chondrina kobelti* (Westerlund, 1887) and *C. kobeltoides* Gittenberger, 1973, which mainly differ in size, can be recognized in the cladogram, where they are sister-species, albeit not strongly supported.

The SW Iberian (Portuguese) *C. lusitanica* (L. Pfeiffer, 1848) is the sister-taxon of the widely disjunct, combined *C. arcadica* (Reinhardt, 1881) and *C. avenacea*. The polytypic *C. arcadica* falls apart in two groups that can also be recognized geographically, i.e. *C. a. clienta* (Westerlund, 1883) versus the combined *C. a. arcadica*, *C. a. bulgarica* and *C. a. caucasica*. (See also the note on *C. burtscheri* in species group I).

Both *C. arcadica clienta* and *C. avenacea* show very high levels of aphillic individuals in populations (up to 99% and 89%, respectively) (Armbruster et al., 2007, Baur & Chen, 1993). The aphillic individuals are still able to outcross as females. The energy that needs not be invested in the development of the male part of the genitalia might enhance their reproductive output (Baur et al., 1993). It is unclear whether this has anything to do with their success, in comparison with other *Chondrina* species, in (re-)colonizing Europe.

SPECIES GROUP VII

The remaining taxa, for now artificially grouped in group VII, no molecular sequence data are presently available.

Chondrina soleri Altimira, 1960 (Pl. 10 fig. G)

Chondrina (Modicella) farinesi soleri Altimira, 1960: 12 (valid after ICZN Article 45.6.4.). Spain, Barcelona, Sant Llorenç del Munt, entrance to the cave Simanya (E-side Montcau mtn), 900 m alt.; UTM DG1814. Type series: RMNH 111877/lectotype (design. nov.) (pl. 10, fig. G), 111878/6 paralectotypes.

Description. – Shell slender fusiform, brown; teleoconch with only irregular growth-lines.

Aperture with an obsolete angularis, which may be lacking completely; columellaris and parietalis developed as small denticles which are hardly or not visible in frontal view. The palatales superior and inferior are short but relatively prominent, white teeth, which are slightly more than their own length away from the apertural lip. Apertural lip white, rib-like thickened inside. Shell measurements (n=7): height 4.6-5.6 mm, width 2.1-2.4 mm; 6-6¼ whorls.

Notes. – This nominal taxon has been overlooked by Gittenberger (1973). In shell shape, sculpture and size, and especially by the short but prominent palatales, this form is somewhat similar to *C. aguilari*. In the latter species however, the parietalis and columellaris are more prominent, and the palatalis inferior is often slightly more prominent than the superior, whereas in *C. soleri* the opposite is the case.

Chondrina jumillensis (L. Pfeiffer, 1853) (Pl. 11 fig. G)

Pupa jumillensis L. Pfeiffer, 1853: 540. Lectotype, design. Haas (1926: 302, 305): Spain, Alicante, Orihuela (Nat. Hist. Museum Stettin). The shell characters enable the conclusion that the lectotype is not from Jumilla, Murcia, which is the second locality mentioned on the original label (Haas, 1926: 304; own observations).

Notes. – Haas (1926: 302, 305) designated a shell of 7 × 3 mm as ‘type’ and illustrated (1926: pl. 27 fig. 8) a ‘cotype with similar dentition’. The figure shows a specimen with an *arigonis*-like apertural lip and dentition. We can only confirm his conclusions about the two forms that received the name *Pupa jumillensis*. Unfortunately, as a consequence of the ICZN, the epithet *jumillensis* is linked to a form that does not occur near Jumilla.

Chondrina guiraoensis Pilsbry, 1918 (Pl. 11 figs H-J)

Pupa jumillensis Rossmässler, 1859: 110. Lectotype, design. Gittenberger (1973: 213) (SMF 43677a): Spain, Murcia, Jumilla. The shell characters enable the conclusion that the lectotype is not from Orihuela, Alicante, which is the second locality mentioned on the original label (Haas, 1926: 304; own observations). Not *Pupa jumillensis* Pfeiffer, 1853.

Chondrina guiraoensis Pilsbry, 1918 [March]: 372, pl. 47 fig. 9. Holotype (ANSP 22790): Spain, Murcia, Jumilla (Pilsbry, 1918 [November]: 51).

Chondrina guiraoensis Pilsbry, 1918 [November]: 51. Unjustified emendation (‘n. n.’) (ICZN Art. 32.5.1).

Chondrina farinesii; Montoya et al., 1999: 131. Not Des Moulins, 1835.

Description. – Shell rather thick-set, with a short conical apical part and a last whorl which is often hardly broader than the penultimate one, light brownish to yellowish brown; teleoconch conspicuously sculptured with rather coarse riblets.

Aperture with a more or less prominent angularis and usually a columellar denticle which is hidden behind the columella in frontal view; and only rarely an obsolete parietalis

Apertural lip neither reflexed nor rib-like thickened inside.

Notes. – In view of the revised interpretation of the eastern Iberian *Chondrina* taxa

with more or less obsolete apertural teeth, *C. guiroensis* is listed here as a species. Quite surprising, the oldest, fossil *Chondrina* shells (Pl. 11 fig. J), collected at the Sierra de Quibas, which is only c. 25 km SE from Jumilla (Montoya et al., 2001), are extremely similar to the Recent *C. guiraoensis*, indicating that there have been no substantial changes in shell morphology in this species during at least 1.3 million years.

Chondrina amphorula Shileyko, 1984 (Pl. 13 figs B-C)

Notes. – According to Shileyko (1984: 231-233) this species resembles *Chondrina arcadica caucasica* (Ehrmann, 1931) (pl. 13 fig. D) but is specifically distinct based on the following characteristics. At first glance *C. amphorula* appears to possess two palatal folds, while in *C. a. caucasica* three are evidently present. This is a clear distinction in localities where both species co-occur, i.e. no intermediates are found. Additionally, the penial loop is consistently longer and thinner in *C. amphorula* than in *C. a. caucasica*.

The species is reported from the following localities: Russia, Kabardino-Balkaria, N-Caucasus, Habaz (44.05°N / 41.77°E), Riykol ravine (= 2 km W of Habaz), Coll. W.J.M. Maassen (leg. Kuznetsov), and from the northern Caucasus (Daghestan) and Armenia. Its affinities with the other species in the genus are unclear. It could either be closely related to the relatively recent radiation of *C. arcadica* (to which it shows some morphological resemblance) or belong to the older radiation which also includes *C. tatica*.

Chondrina generosensis Nordsieck, 1962

Notes. – The specific distinction of this taxon from *C. megacheilos*, of which it was considered a subspecies by Nordsieck (1962), is well supported by both morphological and allozyme data (Proschwitz & Johannesson, 1995). The two species may occur sympatrically in mixed populations, without any intermediates specimens (Wüthrich, 1990: 20; E.G., personal observation)

Chondrina oligodonta (Del Prete, 1879)

Notes. – Because of the worldwide increasing demand for chalk for cement industries or marbles, limestone hills may be threatened by quarrying (Armbruster et al., 2007 and references therein; Clements et al., 2006). *Chondrina oligodonta* (Del Prete, 1879) is currently the only chondrinid species that has been placed on the IUCN red list as Vulnerable (Seddon M.B., 2000), since “This species has a small range and declining quality of habitat, combined with possible competition from other species, therefore making it Vulnerable”. Its occurrence is restricted to the Alpi Apuane in Italy, which are well known for the origin of the Carrera marbles. Quarrying of these marbles presently poses the greatest threat to the species. In Europe, this is exceptional however, so that most *Chondrina* species are not endangered by any direct anthropogenic factor.

Chondrina spec. 4-6 (Pl. 12 figs I-K)

Notes. -- The molecular analyses made clear that there are many more *Chondrina* taxa than were hitherto accepted. Our *Chondrina* spec. 4-6, for which only shells are known, illustrate this view. As long as molecular data are not available for such more or less problematic forms, we refrain from detailed conchological descriptions and speculations about variation and taxonomic relationships.



Plate 1. *Abida secale* subspec. (material in RMNH, unless stated otherwise). **A-J**, *A. s. secale*. **A-B**, Slovakia, N of Bratislava; **C**, Belgium, Dinant; **D**, Switzerland, Basel; **E**, England, Somerset, Cheddar; **F**, Austria, Steiermark, Obersdorf, 800 m alt.; **G**, France, Alpes-de-Haute-Provence, Gorges de St. Pierre, 1,572 m alt. (MNHN GC14); **H**, ditto, 1,561 m alt. (MNHN GC16); **I**, France, Alpes-de-Haute-Provence, peak of Tournon mtn, 2,665 m alt. (MNHN CB16); **J**, Spain, Huesca, Canfranc. **K-L**, *A. s. boileausiana*, France. **K**, Aude, Quillan - Col de Portel; **L**, Ariège, Foix. **M-N**, *A. s. saxicola*, France, Pyrénées-Orientales, Villefranche-de-Conflent (type locality).



Plate 2. *Abida secale* subsp. (material in RMNH). **A-F**, *A. s. andorrensis*. **A**, Andorra, Xixerella, 1,600 m alt.; **B**, Andorra, Santa Julià de Lòria, 950 m alt.; **C**, Spain, Lérida, Nargó – Valldarques; **D**, Spain, Lérida, Coll de Nargó – Orgaña; **E-F**, Spain, Lérida, Coll de Nargó – Valldarques. **G-K**, *A. s. tuxensis*, Spain, Lérida. **G**, Els Castells, 1,300 m alt.; **H-I**, Tuxent (type locality); **J**, Montsech; **K**, Congost d’Orgaña.



Plate 3. *Abida secale* subsp. (material in RMNH). **A-H**, *A. s. liliensis*, Spain, Gerona. **A**, Saldes - Vallcebre, 1,500 m alt.; **B**, E of Vallcebre, 1,025 m alt.; **C**, E of Fumanya, 1,681 m alt.; **D**, N of Bagá (Coll de Pal), 2,000 m alt.; **E-F**, N of Saldes, 1,015 m alt.; **G-H**, La Pobla de Lillet, 934 m alt. (type locality). **I-M**, *A. s. affinis*. **I**, Spain, Gerona, N of Sadernes; **J**, France, Pyrénées Orientales, La Preste (type locality); **K-L**, Spain, Gerona, Campdevanol - Gombren; **M**, Spain, Gerona, Gombren - La Pobla de Lillet. **N**, *A. s. elegantissima*, Spain, Gerona, Coll de Sta. Maria, Finestras mtn (paratype from type locality).



Plate 4. *Abida secale* subsp. nov. (material in RMNH). **A-E**, *A. s. brongersmai*, Spain, Lérida. **A**, Montella, 1,625 m alt.; **B-C**, Montella, 1,300 m alt.; **D**, Torres (RMNH 54778, holotype); **D2**, lateral view bodywhorl and aperture; **E**, Oteró - Vilanova de Banat, 1,200 m alt. **F-K**, *A. s. margaridae*, Spain. **F-H**, Gerona, Pedra, 1,120 m alt.; **I-J**, Gerona, Das - Masella, 1,325 m alt. (type locality); **K**, Lérida, Bellver de Cerdanya - Ordèn, 1,300-1,400 m alt.



Plate 5. *Abida secale brauniopsis*, Spain (material in RMNH). **A**, Lérida, S flank Comabona mtn, 1,972 m alt.; **B1-2**, Lérida, S flank Comabona mtn, 1,820 m alt.; **C-D**, Lérida, S flank Comabona mtn, 1,700 m alt.; **E1-2**, Gerona, N of Saldes, 1,430 m alt.; **F1-2**, Lérida, Gosol (RMNH 54780, lectotype); **G1-2**, Lérida, Gosol, 1,450 m alt. (type locality).



Plate 6. *Abida secale* subsp. nov. (material in RMNH). **A-C**, *A. s. cadica*, Spain, Lérida, Sierra del Cadí, Comabona mtn, S flank, 2,429 m alt. **D-L**, *A. s. cadiensis*, Spain, Lérida, Sierra del Cadí, Comabona mtn, summit and N flank. **D-E**, summit, 2,511 m alt.; **F**, Pas dels Gósolans, 2,430 m alt.; **G-I**, ditto, 2,250 m alt.; **J**, ditto, 2,000 m alt.; **K**, ditto, 2,125 m alt.; **L**, Spain, Lérida, Martinet (RMNH 54782, holotype). **M-P**, *A. s. vilellai* subsp. nov., Spain, Lérida. **M**, Port del Comte, S of Tossa Pelada mtn, 2,100 m alt. (RMNH 54960, paratype [also paratype of *A. s. cadiensis*]); **N1-3**, Port del Comte, S of Tossa Pelada mtn, 2,100 m alt. (RMNH 109892, holotype); **O-P**, Sierra del Cadí, Torre del Cadí mtn, 2,400 m alt. (RMNH 99118, paratype).



Plate 7. *Abida secale* subsp. (material in RMNH). **A-C**, *A. s. peteri* subsp. nov. **A1-3**, Spain, Lérida, Pedraforca mtn, 2,300 m alt., (RMNH 109890, holotype); **B**, ditto (RMNH 99135, paratype, type locality); **C**, ditto, 2,250 m alt. (RMNH 54961, paratype). **D-E**, Andorra, Alt de la Capa mtn, 2,500 m alt (RMNH 109060, paratype, type locality); **F1-3**, ditto (RMNH 109059, holotype); **G-H**, ditto (RMNH 109060, paratypes, type locality); **I**, ditto, 2,100 m alt. (RMNH 109062, paratype); **J**, Andorra, Pas de la Casa, 2,100 m alt. (RMNH 109064, paratype); **K**, Spain, Lérida, Pico Mainera mtn (RMNH 111881). **L-Q**, *A. s. merijni* subsp. nov., Spain, Gerona. **L1-3**, Cap del Serrat Gran mtn, 2,163 m alt. (RMNH104103, paratypes); **M**, ditto, 2,366 m alt. (RMNH 104083, paratype); **N-P**, summit of Pedro dels Quatre Batlles mtn, 2,530 m alt. (RMNH 109891, holotype); **Q**, N flank of Pedro dels Quatre Batlles mtn, 2,326 m alt. (RMNH 104105, paratype).



Plate 8. *Abida* spec. (material in RMNH). **A-E**, *A. s. meridionalis*, Spain. **A**, Tarragona, La Mola de Falset; **B**, Teruel, Cantavieja; **C-D**, Tarragona, La Mola de Colldejou; **C**, 912 m alt.; **D**, 850 m alt.; **E**, Spain, Barcelona, Montserrat. **F-G**, *A. ateni*, France, Basses Pyrénées, Défilé d'Escot (type locality). **F**, (RMNH 54920, paratype); **G**, (RMNH 54882, holotype). **H-J**, *A. vergniesiana*. **H-I**, Andorra, Sornes - Ansalonga; **J1-2**, France, Ariège, Tarascon sur Ariège.

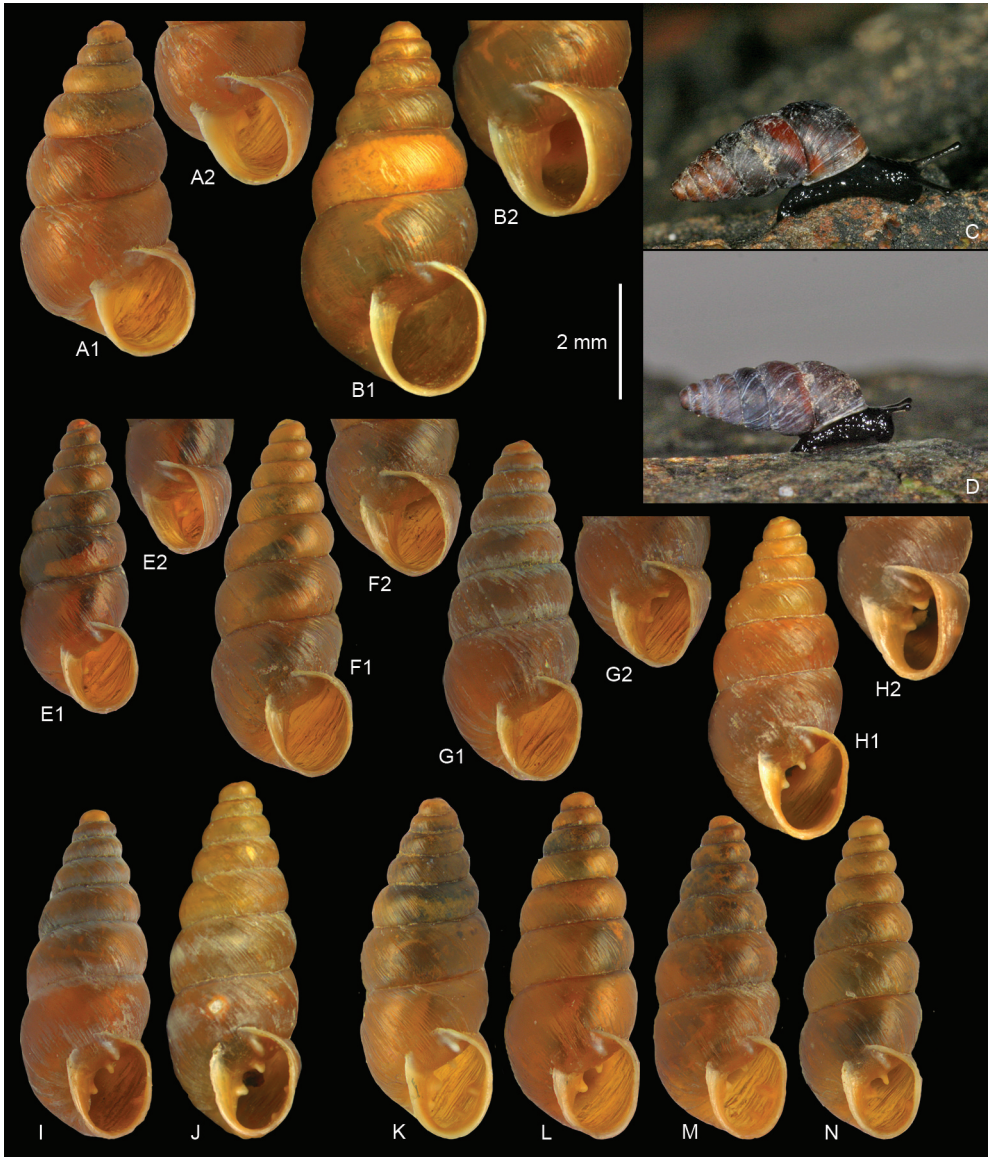


Plate 9. *Chondrina* spec. (material in RMNH, unless stated otherwise). **A-C**, *C. farinesii*. **A1-2**, Spain, Cuenca, Ciudad Encantada, 1000 m alt. (RMNH 109434); **B**, Spain, Tarragona, Llaveria (6.8 km SSE of Falset), entrance cueva del Ramé (RMNH 109859, *C. unidentata* Altimira, lectotype); **C**, France, Pyrénées-Orientales, La Preste (type locality). **D**, *C. aguilari*, Spain, Lérida, Congost de Collegats. **E-J**, *C. m. massotiana*. **E1-2**, Spain, Huesca, Linas de Broto; **F1-2**, Spain, Lérida, Torres; **G1-2**, Andorra, Andorra, Sant Julià de Lòria – Andorra la Vella; **H1-2**, Andorra, Sant Julià de Lòria (MHNG 13160, lectotype); **I**, Spain, Lérida, Garganta de Orgañá; **J**, Andorra, Sant Julià de Lòria (MHNG 13190, lectotype of *Pupa penchinatiana*). **K-N**, *C. massotiana sexplicata*, Spain, Lérida. **K**, Figuerola de Orcau (SMF 43777, syntype of *Pupa ilderensis*, from restricted type locality); **L**, Port d’Ager (RMNH 54872, lectotype of *C. pulchella agerensis*); **M**, Congost d’Erinyá (RMNH 54874, lectotype of *C. pulchella bofilliana*); **N**, Port d’Ager (RMNH 54875, lectotype of *C. pulchella montsiciana*).

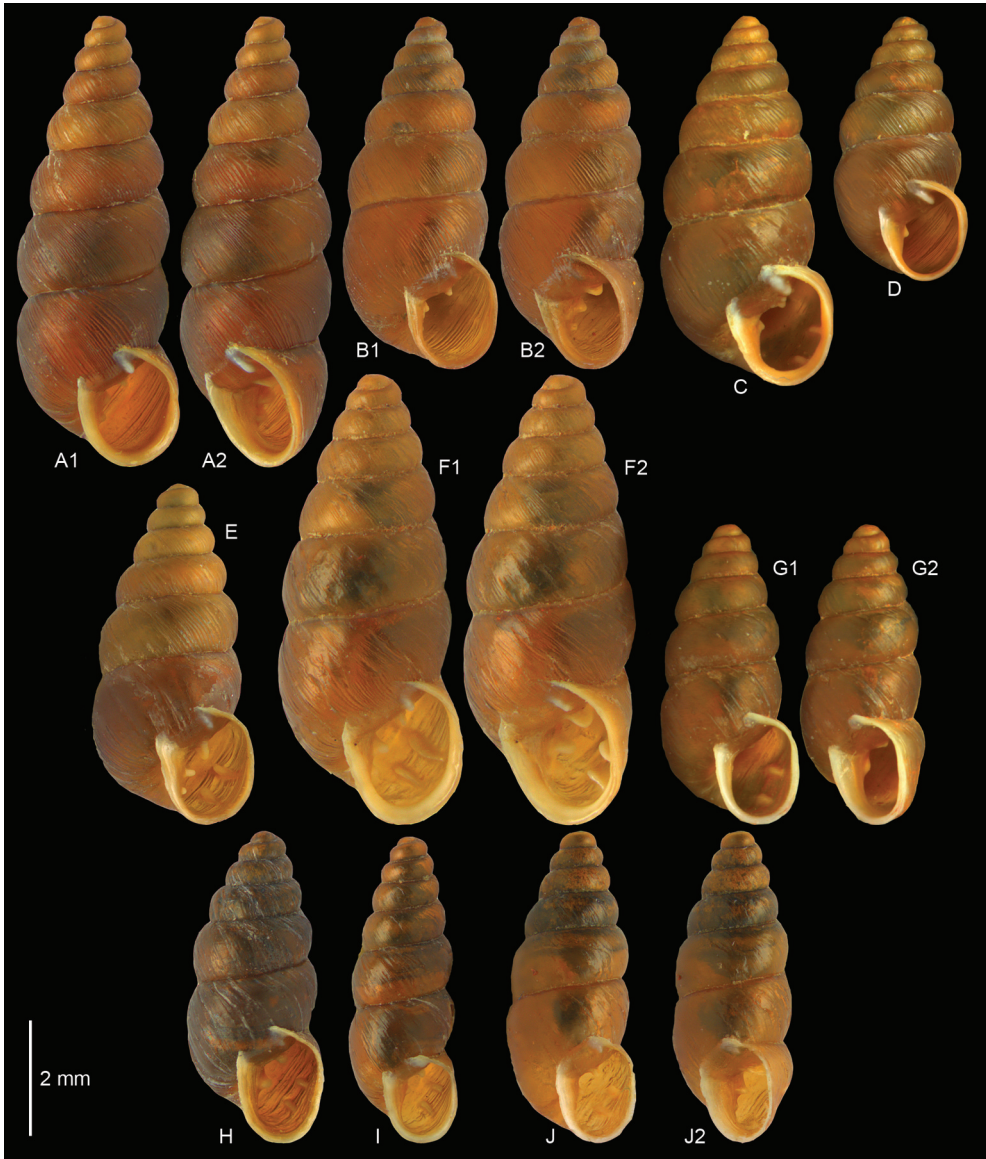


Plate 10. *Chondrina* spec. (material in RMNH, unless stated otherwise). **A-D**, *C. dertosensis*, Spain, Tarragona. **A1-2**, Hospitalet, Prattedip, 340 m alt.; **B1-2**, Sierra de Cardó (MCNB 89-8530, lectotype); **C**, Montreal (RMNH 54896, lectotype of *C. jumillensis montrealensis*); **D**, Cardó. **E**, *C. arigonoides* sp. nov., Spain, Alicante, SW of Denia, Marquesa, 173 m alt. (RMNH 109861, holotype). **F**, *C. arigonis*, Morocco, S of Berkane, Taforhalt (= Taforalt). **G1-2**, *C. soleri*, Spain, Barcelona, Sant Llorenç del Munt, entrance cave Simanya, 900 m alt. (RMNH 111877, lectotype). **H-J**, *C. aguilar*, Spain. **H**, Huesca, 32 km ENE of Basbastro, E Benabarre (RMNH 109437); **I-J**, Lérida, Congost d'Erinyá; **I**, (RMNH 54873, lectotype); **J**, ditto (RMNH54879, paralectotype).

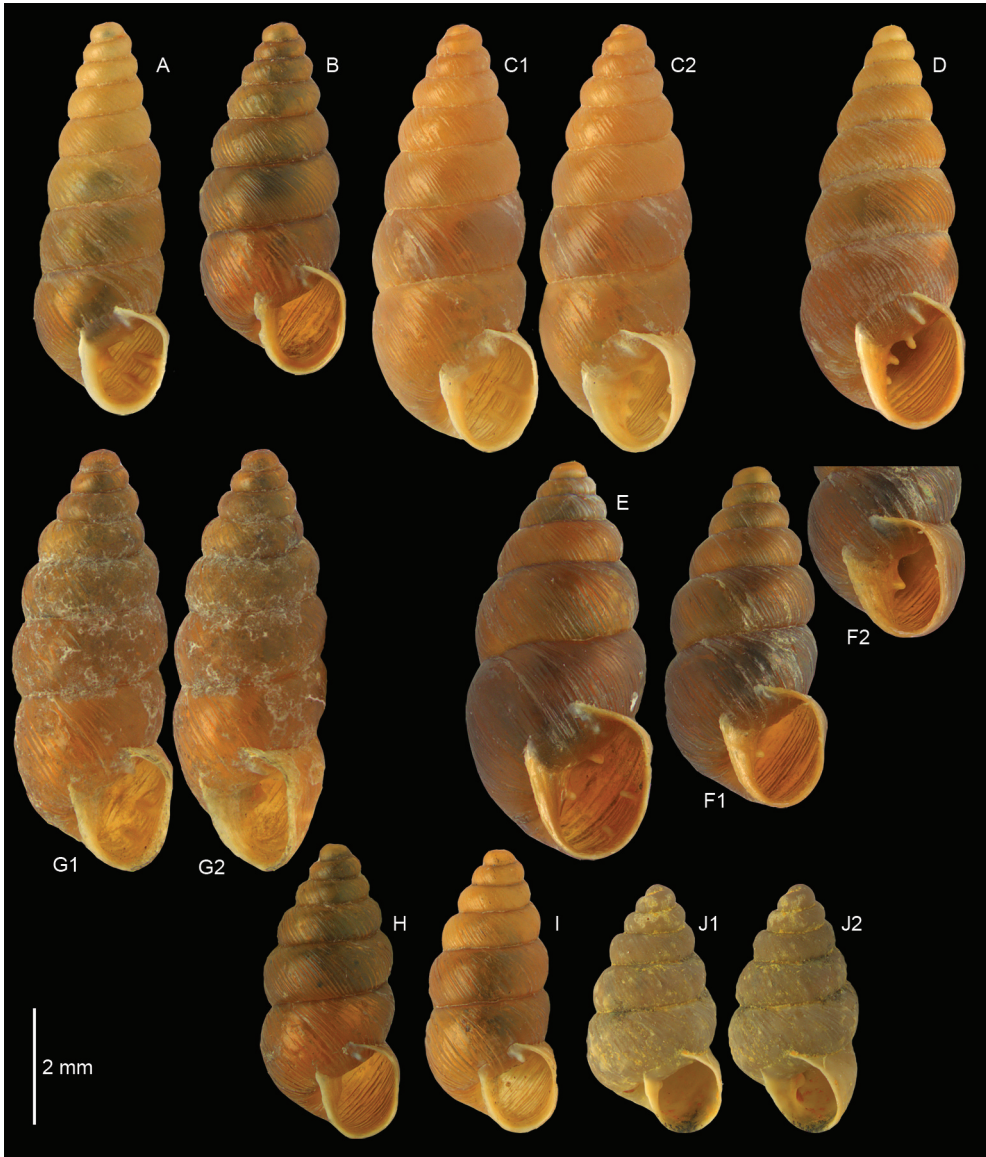


Plate 11. *Chondrina* spec. (material in RMNH, unless stated otherwise). **A**, *C. marmouchana*, Morocco, Moyen Atlas, Talzemt – Tamjilt, Qued Meskedal (RMNH 102334). **B**, *C. granatensis*, Spain, Jaén, Cazorla, Tiscar. **C1-2**, *C. cf. granatensis*, Spain, Jaén/Murcia, Sierra de Taibilla. **D**, *C. gasulli*, Spain, Alicante, Pego – Vall de Ebo (RMNH 54836, holotype). **E-F**, *C. cf. gasulli*, Spain, Alicante. **E**, Altea, Calp, alt. 391 m; **F1-2**, Altea, Guadalest, 509 m alt. **G1-2**, *C. jumillensis*, Spain, Spain, Alicante, Orihuela (SMF 3903, lectotype). **H-J**, *C. guiraoenensis*, Spain. **H**, Murcia, Jumilla, Ermita Sta. Anna (RMNH 109436, type locality); **I**, ditto (SMF 43677a, lectotype); **J1-2**, Murcia, Sierra de Quibas, Pleistocene deposits, 1.3 Ma (MVHN).

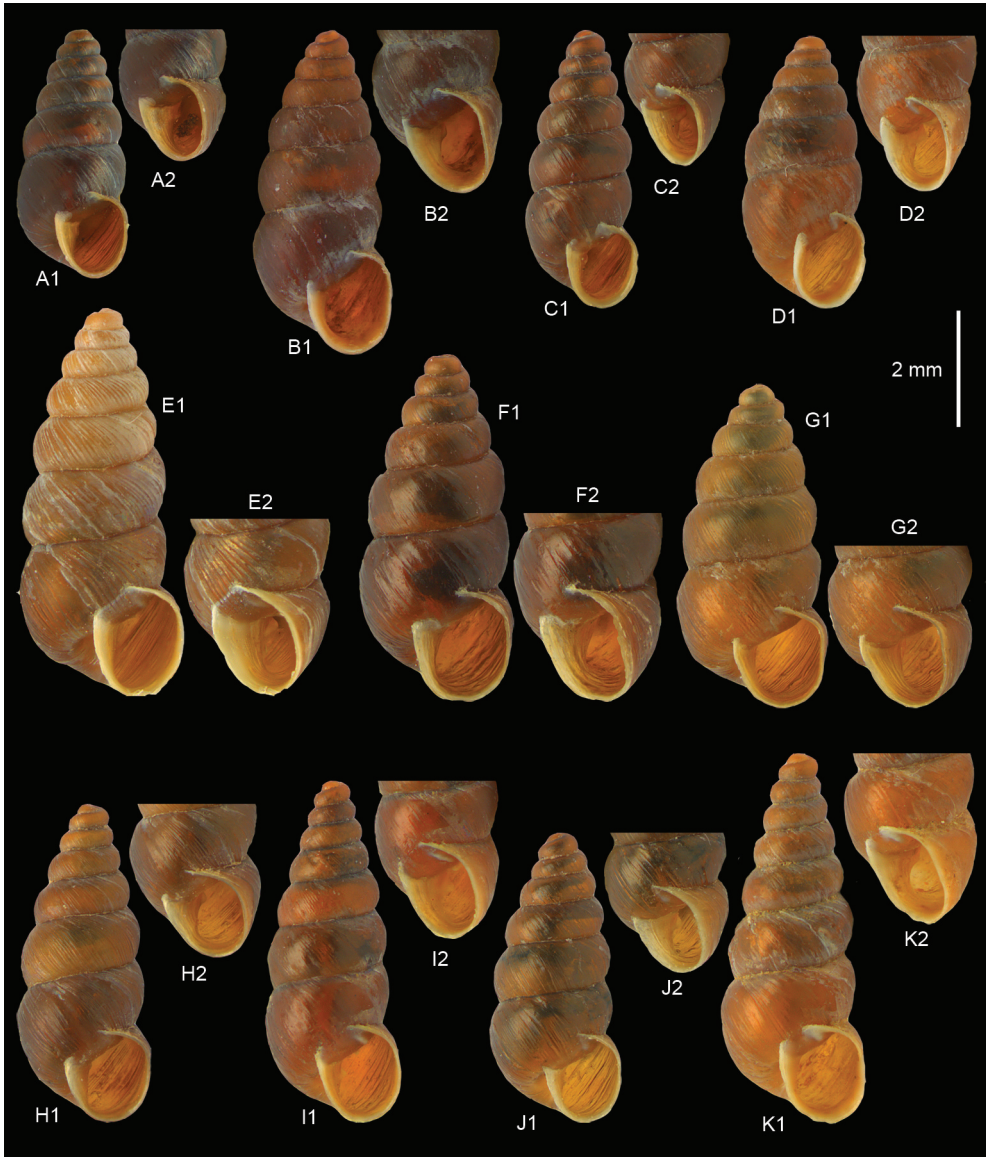


Plate 12. *Chondrina* spec. (material in RMNH). **A-D**, *Chondrina* spec. 2, Spain. **A**, Barcelona, 1.5 km N of Saldes, direction Gresolet, 1015 m alt. (RMNH 102444); **B**, Lérida, La Pobla de Lillet – Castellar de N’hug, 1044 m alt. (RMNH 103318); **C**, Lérida, Oliana, 35 km S of Seo de Urgel (RMNH 109427); **D**, Lérida, Alina, 19 km S of Seo de Urgel, 1611 m alt. (RMNH 109428). **E**, *Chondrina* spec. 3, Spain, Murcica, Ricote (RMNH 103219). **F**, *C. ingae* spec. nov., Spain, Alicante, Alacant, Biar (RMNH 109865). **G**, *C. marjae* spec. nov., Spain, Valencia, Xativa (RMNH 109863). **H**, *Chondrina* spec. 1, Spain, Castellon, Castello, Aranuel, 393 m alt. (RMNH 103260). **I**, *Chondrina* spec. 4, Spain, Cuenca, Ciudad Encantrada, 1000 m alt. (F.M. Vilella y Tejado leg.) (RMNH 109433). **J**, *Chondrina* spec. 5, Spain, Castellon, Begis, Los Cloticos (L. Gasull leg.) (RMNH 109426). **K**, *Chondrina* spec. 6, Spain, Lérida, 28 km NNW of Artesa de Segre, 4 km SSW of Santa Lis (F.M. Vilella y Tejado leg.).

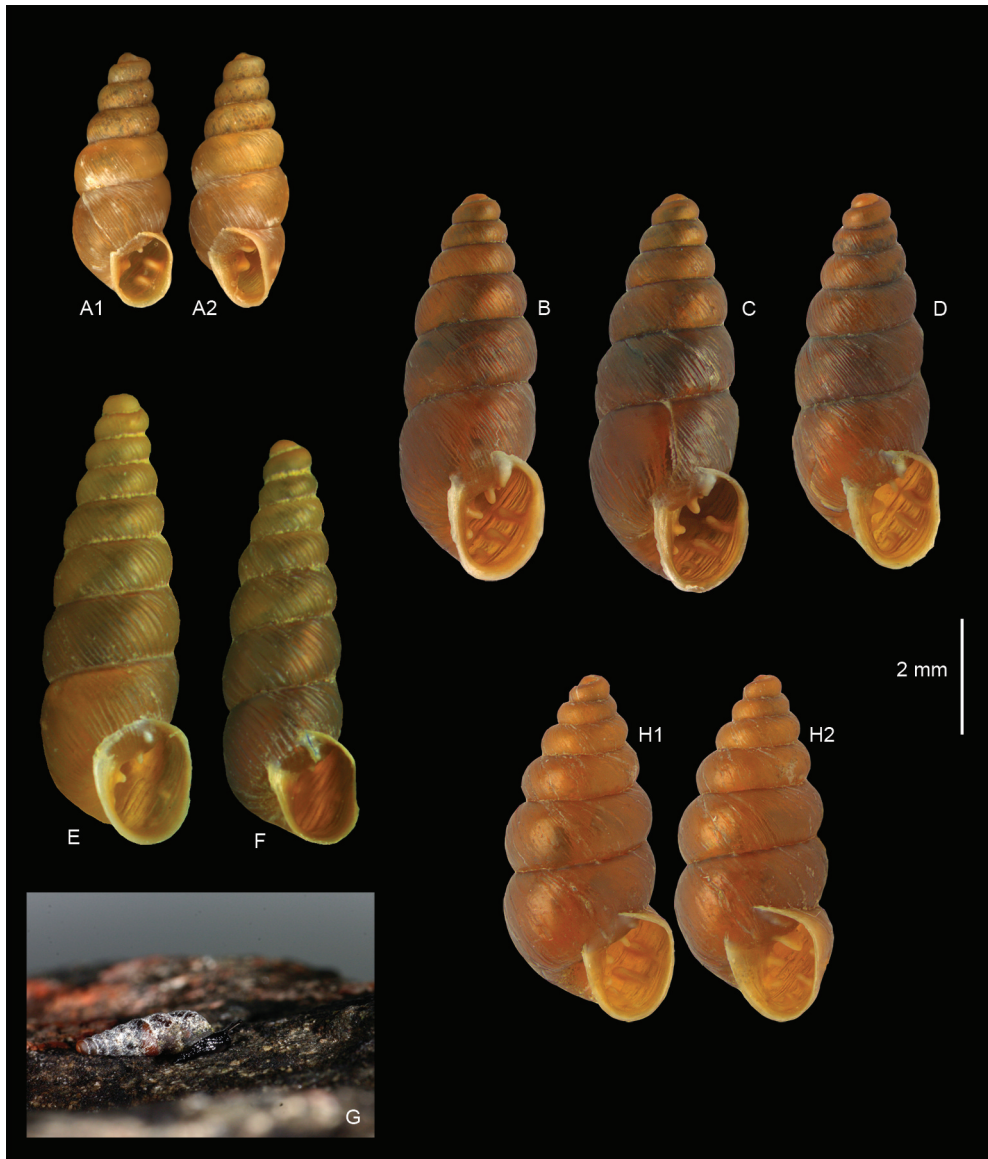


Plate 13. *Rupestrella* and *Chondrina* spec. (material in RMNH, unless stated otherwise). **A1-2**, *R. philippii* (Cantraine, 1840), either Italy, Toscana, Livorno, or Hrvatska, Zadar (= Zara) (RMNH 111874, lectotype, design. nov.). **B-C**, *C. amphorula*, Russia, Daghestan, Riykol gorge, 2 km W of Habaz (Colln W.J.M. Maassen). **D**, *C. arcadica caucasica*, Russia, Daghestan, Riykol gorge, 2 km W of Habaz (sympatric with *C. amphorula*) (Colln W.J.M. Maassen). **E-G**, *C. maginensis*, Spain, Jaén, Sierra de Magina, Abanchez de Magina. **H1-2**, *C. pseudavenacea* spec. nov., Spain, Alicante, Calp, Morro de Toix (RMNH 109867, holotype).

Rupestrella Monterosato, 1894

Type species (by original designation): *Bulinus rupestris* Philippi, 1836.

Rupestrella still is the most poorly known genus in the family. The molecular data place this genus as the sister-group next to *Abida* (see Kokshoorn & Gittenberger, [chapter 2]). Additional morphological and molecular work is necessary but the material to enable such studies is not (yet) available, in particular not for the African taxa. Pilsbry (1918: 332-356) provisionally accepted 16 species, 5 of which as endemic to Sicily and 8 as endemic to northern Africa. Beckmann (2002) recognized 4 species as endemic to Sicily, with 11 subspecific taxa in total.

To stabilize the nomenclature of the two most widespread species, viz. *R. philippii* and *R. rhodia*, a lectotype is here selected for the former species. Additionally we present an uncritical, annotated list of currently recognized *Rupestrella* taxa.

THE TWO MOST WIDESPREAD MEDITERRANEAN SPECIES

Rupestrella philippii (Cantraine, 1840)

Type locality: Sardinia and Sicily, Italy (but see notes).

Diagnosis. – Shell moderately slender fusiform; aperture usually with an angularis.

Notes. – The species generally known as *Rupestrella philippii* (Cantraine, 1840) is a common inhabitant of limestone rockfaces in the central and eastern Mediterranean area, with the exception of northern Africa (Pilsbry, 1918: 341; Schütt, 2005: 80, 81). Throughout its range *R. philippii* may occur together with *R. rhodia* (Roth, 1839). The two species can be distinguished by shell shape and apertural denticles. In *R. philippii* the shell is rather fusiform, i.e. with slightly convex sides in profile, whereas *R. rhodia* is very well characterized by a more slender, always regularly conical shell shape. The apertural teeth are also different. Both species share a columellaris, a parietalis, and two palatales, but with few exceptions there is an additional columellar tooth in *R. rothi* and an angularis only in *R. philippii*.

While describing the species now called *R. philippii*, Cantraine (1840: 140) mentioned the five apertural teeth that are most typical for *R. rothi*. However, his references to the three shells figured by Philippi (1836: pl. 8 fig. 18) as *Bulinus rupestris* and by Rossmässler (1839: pl. 49 figs 637, 638) as *Pupa rupestris* and *P. occulta*, respectively, make clear that he did not judge the variability of his *Pupa philippii* in a modern way. All three shells are regularly conical but only in '*P. occulta*' the aperture is illustrated with teeth, although only three, viz. a single columellaris, only one palatalis and a parietalis. *Rupestrella rupestris* (Philippi, 1836) and *R. occulta* (Rossmässler, 1839) are separate species according to Beckmann (2002: 58, 68). There is no certain Cantraine material of *Rupestrella philippii* in the collection of the

Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussels (Sablon, in litt., 11.02.2008). There are samples collected by Cantraine in the National Museum of Natural History Naturalis, Leiden, but unfortunately, allegedly conspecific specimens collected by Cantraine at different localities have once in the past been put together and identified anew, without any trace left to the names originally given by Cantraine himself. Apparently the shells have once been glued on something and were removed afterwards. In a sample that is now labelled as *Pupa granum*, a name not used for any species listed by Cantraine (1840), four shells of modern *R. philippii* are united with six shells of *R. rhodia*. Their provenance is indicated as Livorno and Zara (= Zadar, Dalmatia, Croatia). Cantraine (1840: 140) reported *Pupa philippii* from “en Dalmatie .. Sicile et en Sardaigne”. On the basis of all data we accept the ten specimens as syntypes and select a shell (RMNH xxx; Pl. 13, fig. A) as lectotype of *Rupestrella philippii*, to stabilize the use of that name. The lectotype is a rather unusual shell without an angularis, corresponding in that character with Cantraine’s original description but still very clearly a *R. philippii* as known in the modern literature.

Our interpretation is supported by a sample with two specimens collected by Cantraine and accompanied by two old labels with different names, viz. *Pupa granum* and *Pupa sardoa*. The locality ‘Livorno’ is written on the label with *P. granum*. *Pupa sardoa* was described by Cantraine (1840: 142) from Sardinia, but he lived for some time in Livorno after he had visited the island. As in the former case, this may have caused confusion. We accept the shells as syntypes of *Pupa sardoa* Cantraine, 1840, which is a junior synonym of *Granopupa granum* (Draparnaud, 1801), as has been suggested before (Pilsbry, 1918: 339).

Rupestrella philippii is known from Italy, the Balkans, and Turkey (Pilsbry, 1918: 341). Its occurrence in Libya is shown here with figure 7b. Remarkable is the record from Tripolitania province, N of Tarhuna, which is the first record west of the Gulf of Sidra (Beckmann, 1977: p. 32). The species has also been reported from Malta (Giusti et al., 1995: 222, figs 177-182). According to material in RMNH, *Rupestrella moraguesi* (Kobelt, 1886), which has often been reported as endemic for the Balearic island of Mallorca (Gasull, 1966: 93), should be considered a junior synonym of *R. philippii*. This makes Mallorca the westernmost known record for *R. philippii*.

Rupestrella rhodia (Roth, 1839)

Type locality: Rhodos island, Greece.

Diagnosis. – Shell slender conical; aperture without an angularis.

Notes. – *R. rhodia* occurs from the Balkans and Turkey to the southern Crimea and Israel (Pilsbry, 1918: 344; material in RMNH).

THE SICILIAN SPECIES OF *RUPESTRELLA* ACCORDING TO BECKMANN (2002)

Rupestrella rupestris (Philippi, 1836)

R. rupestris rupestris (Philippi, 1836)

Type locality: Palermo and Sciacca, Sicily, Italy.

R. rupestris coloba (Pilsbry, 1918)

Type locality: Sicily.

Notes. – According to Beckmann (2002) this subspecies is restricted to the island of Lévanzo off the westcoast of Sicily.

R. rupestris margritae Beckmann, 2002

Type locality: Isola delle Femmine, on rocks of the castle tower in the town, Palermo province, W Sicily, Italy.

R. rupestris carolae Beckmann, 2002

Type locality: Cefalù, castle mountain, Palermo province, Sicily, Italy.

R. rupestris lamellosa Beckmann, 2002

Type locality: Sciacca, Agrigento province, Sicily, Italy.

Rupestrella homala (Westerlund, 1892)

R. homala homala (Westerlund, 1892)

Type locality: Galdo mtn, Sicily, Italy.

R. homala massae Beckmann, 2002

Type locality: Cófano mtn, at the castle, Trápani province, Sicily, Italy.

R. homala falkneri Beckmann, 2002

Type locality: Termini, road to Caccamo, Sicily, Italy.

Rupestrella occulta (Rossmässler, 1839)

R. occulta occulta (Rossmässler, 1839)

Type locality: Sicily, Italy.

R. occulta gibilfunnensis (De Gregorio, 1895)

Type locality: Gibilforni mtn near Palermo, Sicily, Italy.

Rupestrella jaeckeli Beckmann, 2002

Type locality: Limestone rock on Biaggio mtn, SE of Agrigent, Sicily, Italy.

THE NORTH AFRICAN TAXA ACCORDING TO PILSBRY (1918) AND VERDCOURT (1963)

The north African taxa according to Pilsbry (1918) and Verdcourt (1963) (*R. somalensis*). The type localities of these north African taxa are shown in fig. 7a.

Rupestrella dupotetii (Terver, 1839)

Type locality: Béjaïa (Bougie), Algeria.

Notes. – Based on differences in shell shape and distributional range, Holyoak & Seddon (1986) recognized two subspecies in *R. dupotetii*, i.e. *R. d. dupotetii* in the eastern part of its African distribution and *R. d. sebouensis* in the west (fig. 7a). Additional material from southern Spain led Arrébola Burgos & Gittenberger (1993) to disagree with this distinction. Pending a revision of all north African taxa, we will here follow the latter authors.

Rupestrella michaudi (Terver, 1839)

R. michaudi michaudi (Terver, 1839)

Type locality: Bougie, on the ridges of Gourayah, a mountain of about 700 m elevation, on rocks exposed to the east, Algeria. (36.772°N / 5.076°E)

R. michaudi isseriana (Pilsbry, 1918)

Type locality: Gorge de Palestro, Kabylia, Algeria. (36.577°N / 3.568°E)

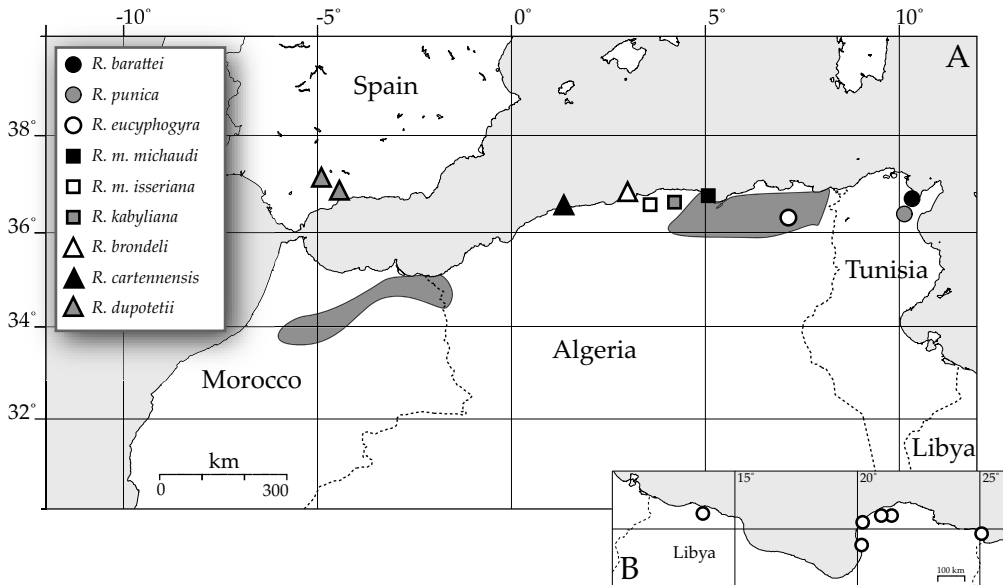


Figure 7. Distribution of *Rupestrella* species in N-Africa. **A**, Type localities of the taxa recognized by Pilsbry (1918) with the approximate distribution of *R. dupotetii* in gray; **B**, Localities of *R. philippi* in N-Africa based on material in the collection of the RMNH.

Rupestrella brondeli (Bourguignat, 1864)

Type locality: Pescade point, Algeria. (36.818°N / 3.010°E)

Rupestrella kabyliana (Letourneux, 1870)

Type locality: Rocks of Tablabalt near Fort Napoleon, Algeria. (36.637°N / 4.201°E)

Notes. — Two samples of '*Pupa penchinatiana*' from Algeria in the Colln Bourguignat (BG12985, 12986), most probably belong to *R. kabyliana*. The shells have (1) more prominent and regular riblets, especially on the spire, (2) the apertural teeth are more prominent, (3) the apertural lip is somewhat reflexed, without being conspicuously thickened, and (4) the apical whorls are in general slightly more slender. The differences are slight indeed, which makes once more clear that the genera *Chondrina* and *Rupestrella* cannot be distinguished unequivocally on the basis of only shell characters.

Rupestrella cartennensis (Letourneux, 1893)

Type locality: Mountain of the Cape of Ténès (Cartenna), in the dép. D'Alger, Algeria. (36.529°N / 1.359°E)

Rupestrella punica (Letourneux & Bourguignat, 1887)

Type locality: On damp rocks near the spring, Djebel Zaghouan, Tunis. (36.397°N / 10.143°E)

Rupestrella barattei (Letourneux & Bourguignat, 1887)

Type locality: In crevices of the rocks, Djebel Bou-Kournein, Tunis. (36.709°N / 10.344°E)

Rupestrella eucyphogyra (Letourneux, 1870)

Type locality: Under rocks of a dolmen of the defile of Mazla, in the region of the Oued-Zenati, Algeria. (36.313°N / 7.166°E)

Rupestrella somalensis (Verdcourt, 1963)

Type locality: Mait-Erigavo Escarpment, 5,900 feet a.s.l., Northern region, Somalia.

Notes. – This species was originally classified with *Granopupa*. Based on the original description and figure, however, it clearly belongs to *Rupestrella*. As already mentioned by Verdcourt (1963) it appears to be affiliated with *R. michaudi*, based on the slender shell shape. Its geographical location is rather isolated. It extends the known distribution of the genus considerably southward.

REFERENCES

- ALONSO, M. DEL R., 1974. Un nuevo chondrinido de la provincia de Granada: *Chondrina farinesii granatensis*, n. sp. (Mollusca, Pulmonata, Chondrininae). – Cuadernos de Ciencias Biológicas 3: 87-89, pls 1, 2.
- ALONSO, M. DEL R., 1977. A description of the lectotype of *Chondrina farinesii granatensis* (Mollusca: Chondrininae). – Archiv für Molluskenkunde 107: 271-272.
- ALTIMIRA, C., 1963. Notas malacológicas. – Miscelánea Zoológica 1 (5): 15-26 [Separate: 1-12. Barcelona].
- ARMBRUSTER, G.F.J., M. HOFER, & B. BAUR, 2007. Effect of cliff connectivity on the genetic population structure of a rock-dwelling land snail species with frequent self-fertilization. – Biochemical Systematics and Ecology 35(6): 325-333.
- ARRÉBOLA BURGOS, J.R., & E. GITTEMBERGER, 1993. New Distributional Data for *Rupestrella Dupotetii* (Terver) (Gastropoda: Chondrinidae) From Southern Spain and Nw Africa, With Notes on

- Allegedly Subspecific Characters. – *Journal of Conchology* 34: 351-355.
- ARRÉBOLA, J.R. & GÓMEZ, B.J., 1998. Nuevas aportaciones al conocimiento del género *Chondrina* (Gastropoda, Pulmonata) en el sur de la Península Ibérica, incluyendo la descripción de *Chondrina maginensis* spec. nov. – *Iberus* 16(2): 109-116.
- ASHMOLE, N.P., & M.J. ASHMOLE, 1997. The Land Fauna of Ascension Island: New Data from Caves and Lava Flows, and a Reconstruction of the Prehistoric Ecosystem. – *Journal of Biogeography* 24(5): 549-589.
- BANK, R.A., 2003. CLECOM-project. Checklist of species-group taxa of continental Mollusca living in Spain. – http://www.faunaeur.org/full_results.php?id=271529.
- BAUR, A., & B. BAUR, 1991. The effect of hibernation position on winter survival in the rock-dwelling land snails *Chondrina clienta* and *Balea perversa* on Öland, Sweden. – *Journal of Molluscan Studies* 57: 331-336.
- BAUR, B., & A. BAUR, 1990. Experimental evidence for intra- and interspecific competition in two species of rock-dwelling land snails. – *Journal of Animal Ecology* 59: 301-315.
- BAUR, B., & A. BAUR, 1994. Dispersal in the land snail *Chondrina avenacea* on vertical rock walls. – *Malacological Review* 27: 53-59.
- BAUR, B., & A. BAUR, 1995. Habitat-related dispersal in the land snail *Chondrina clienta*. – *Ecography* 18: 123-130.
- BAUR, B., X. CHEN, & A. BAUR, 1993. Genital dimorphism in natural populations of the land snail *Chondrina clienta* and the influence of the environment on its expression. – *Journal of Zoology* 231: 275-284.
- BAUR, B., L. FRÖBERG, & A. BAUR, 1995. Species diversity and grazing damage in a calcicolous lichen community on top of stone walls in Öland, Sweden. – *Annales Botanici Fennici* 32: 312-323.
- BAUR, A., B. BAUR, & L. FRÖBERG, 1992. The effect of lichen diet on growth rate in the rock-dwelling land snails *Chondrina clienta* (Westerlund) and *Balea perversa* (Linnaeus). – *Journal of Molluscan Studies* 58: 345-347.
- BAUR, A., B. BAUR, & L. FRÖBERG, 1994. Herbivory on calcicolous lichens: different food preferences and growth rates in two co-existing land snails. – *Oecologia* 98: 313-319.
- BECH, M., 1983a. Presencia de *Abida occidentalis* (Fagot, 1888) em el Pricipat d'Andorra (Mollusca, Pulmonata, Chondrininae). – *Iberus* 3: 107.
- BECH, M., 1983b. Presència a Catalunya d' *Abida occidentalis* (Fagot, 1888) (Mollusca, Pulmonata, Chondrinidae). – *Miscellània Zoològica* 6:151-152.
- BECH, M., 1984. Segunda señalización en Cataluña de *Abida occidentalis* (Fagot, 1888) (Mollusca, Pulmonata, Chondrininae). – *Iberus* 4:135-136.
- BECH, M., 1993. Descripción de *Abida secale margaridae* subsp. nov. y otras aportaciones para la malacofauna de Catalunya. – *Iberus*, 11(1): 49-56.
- BECH, M., & J.M. VIADER, 1996. Àrees de dispersió de les subespècies Catalanes d'*Abida secale secale* (Draparnaud, 1801), (Gastropoda: Pulmonata: Chondrinidae) a la comarca de la Baixa Cerdanya (Catalunya). – *Butll. Centre d'estudis de la Natura del Barcelonès Nord* 3: 289-301.
- BECKMANN, K.-H., 1997. A contribution to the knowledge of the Pupillacea. The *Rupestrella* species of the European-Asiatic Mediterranean area (Gastropoda: Chondrinidae). – *Heldia* 4(5): 31-34.
- BECKMANN, K.-H., 2002. Elemente einer Revision der endemischen Rupestrellen Siziliens. – In: FALKNER, M., K. GROH, & M.C.D. SPEIGHT, eds, *Collectanea Malacologica*: 49-78. Hackenheim.
- BERTRAND, A., 2003. Notes sur la distribution géographique des mollusques continentaux de France et

- de Catalogne. – Documents Malacologiques 4: 33-36.
- BOATA, A., 1988. Microevolution in *Solatopupa* landsnails (Pulmonata Chondrinidae): genetic diversity and founder effects. – Biological Journal of the Linnean Society 34: 327-348.
- BOATA, A., 1991. Allozyme versus discrete morphologic characters in the phylogenetic analysis of the land snail *Solatopupa* (Pulmonata, Chondrinidae). – Bollettino di Zoologia 58: 345-354.
- BOFILL, A., 1886. Contributions à la faune malacologique de la Catalogne. – Bulletins de la Société Malacologique de France 3: 155.
- BOURGUIGNAT, J.R., 1863. Mollusques de San-Julia de Loria. – Revue et Magasin de Zoologie 2 (15): 49-63. (Separate: 1-34. Paris).
- CANTRAINE, F., 1840. Malacologie méditerranéenne et littorale, ou description des mollusques qui vivent dans la Méditerranée ou sur le continent de l'Italie, ainsi des coquilles qui se trouvent dans les terrains tertiaires italiens, avec des observations sur leur anatomie, leur mœurs, leur analogie et leur gisement. Ouvrage servant de faune malacologique italienne et de complément à la Conchiologia fossile subapennina de Brocchi. – Nouveaux Mémoires de l'Académie royale des Sciences et des Belles-Lettres de Bruxelles 13 (VII): 1-173, Pl. I-VI.
- CLEMENTS, R., N.S. SODHI, P.K.L. NG, & M. SCHILTHUIZEN, 2006. Limestone karsts of Southeast Asia: imperiled arks of biodiversity. – BioScience 56: 733-742.
- DRAPARNAUD, J.P.R., 1801. Tableau des mollusques terrestres et fluviatiles de la France: 1-116. Montpellier & Paris.
- FALKNER, G., T.E.J. RIPKEN & M. FALKNER, 2002. Mollusques continentaux de France. Liste de référence annotée et bibliographie. – Patrimoines Naturels 52: 1-350.
- FAGOT, P., 1884. Contribution à la faune malacologique de la Catalogne. – Annales de Malacologie 2: 169-194.
- FALKNER, G., & B. STUMMER, 1996. Isoliertes vorkommen einer südalpinen Kornschnecke in Vorarlberg: *Chondrina megacheilos burtscheri* n.ssp. (Gastropoda: Chondrinidae). – Nachrichtenblatt der Ersten Vorarlberger Malakologischen Gesellschaft 4: 1-8.
- FRÖBERG, L., A. BAUR, & B. BAUR, 1993. Differential herbivore damage to calcicolous lichens by snails. – Lichenologist 25: 83-96.
- GASULL, L., 1966. Algunos moluscos terrestres y de agua dulce de Baleares. – Boletín de la Sociedad de Historia Natural de Baleares 11: 7-161.
- GITTENBERGER, E., 1973. Beiträge zur Kenntnis der Pupillacea III. Chondrininae. – Zoologische Verhandlungen 127: 1-267.
- GITTENBERGER, E., 2006. A new locality and synonym for *Abida partioti* – Basteria 69(1-3): 20.
- GIUSTI, F., G. MANGANELLI & P.J. SCHEMBRI, 1995. The non-marine molluscs of the Maltese islands. – Museo Regionale di Scienze Naturali. Monografia 15: 1-607. Torino.
- GOMEZ, B.J., & E. ANGULO, 1982. El Genero *Chondrina* (Mollusca, Gastropoda) en el Pais Vasco. – Iberus 2: 29-40.
- HAAS, F., 1926. Appendix I. The Abidas and Chondrinas of the Pyrenees and the Iberian peninsula. In: H.A. Pilsbry, ed., Manual of Conchology (Second Series: Pulmonata). Pupillidae (Orculinae, Pagodulinae, Acanthinulinae, etc.) 27 (108 [part.]): 267-315.
- HERRMANNSEN, A.N., 1847. Indicis generum malacozoorum primordia .. 1(2): 233-637.
- HESBACHER, S., B. BAUR, A. BAUR, & P. PROKSCH, 1995. Sequestration of lichen compounds by three species of terrestrial snails. – Journal of Chemical Ecology 21: 233-246.
- HOLYOAK, D.T. & M.B. SEDDON, 1986. Geographical variation in *Rupestrella dupotetii* (Terver)

- (Gastropoda: Chondrinidae) from Morocco and Algeria. – *Journal of Conchology* 32: 185-190.
- KERNEY, M.P., & R.A.D. CAMERON, 1979. A field guide to the land snails of Britain and North-west Europe: 1-288. London.
- KETMAIER, V., GIUSTI, F. & A. CACCONI, 2006. Molecular phylogeny and historical biogeography of the land snail genus *Solatopupa* (Pulmonata) in the peri-Tyrrhenian area – *Molecular Phylogenetics and Evolution* 39: 439-451.
- KÜSTER, H.C., 1845. Fünfte Abtheilung der Heliceen. *Pupa* und *Vertigo*. In: F.H.W. MARTINI & J.H. CHEMNITZ, *Systematisches Conchylien-Cabinet* (2) 1 (15-53): 77-88, pl. 13. [See E.A. Smith & H.W. England, 1937: 92].
- MONTEROSATO, T. Allery di, 1894. Conchiglie terrestri viventi e fossili di Monte Pellegrino. – *Il Naturalista Siciliano* 13: 165-173.
- MONTOYA, P., M.T. ALBERDI, L.J. BARBADILLO, J. VAN DER MADE, J. MORALES, X. MURELAGA, E. PEÑALVER, F. ROBLES, A.R. BUSTOS, A. SÁNCHEZ, B. SANCHIZ, D. SORIA, & Z. SZYNDLAR, 2001. Une faune très diversifiée du Pléistocène inférieur de la Sierra de Quibas (province de Murcia, Espagne). – *Earth and Planetary Sciences* 332: 387-393.
- MOQUIN-TANDON, A., 1843. Mémoire sur quelques mollusques terrestres et fluviatiles nouveaux pour la faune des environs de Toulouse. – *Mémoires de l'Académie des Sciences, Inscriptions et Belles-Lettres de Toulouse* 6: 167-184. [Idem, Toulouse: 1-19].
- MOQUIN-TANDON, A., 1856. Histoire naturelle des mollusques terrestres et fluviatiles de la France 2 (5-6): ?-646. Paris.
- NEUBERT, E., 1998. Annotated checklist of the terrestrial and freshwater molluscs of the Arabian peninsula with descriptions of new species. – *Fauna of Arabia* 17: 333-461.
- NORDSIECK, H., 1962. Die Chondrinen der Südalpen. – *Achiv für Molluskenkunde* 91(1-3): 1-20.
- NORDSIECK, H., 1970. Die *Chondrina*-Arten der dinarischen Länder. – *Archiv für Molluskenkunde* 100(5-6): 243-261.
- PAVON, D., 2005. Occurrence de *Granaria stabilei anceyi* (Fagot, 1881) (Gastropoda, Pulmonata, Chondrinidae) sur le massif de la Sainte-Victoire (Bouches-du-Rhône). – *Malaco* 1: 7.
- PHILIPPI, R. A., 1836. Enumeratio molluscorum Siciliae cum viventium tum in tellure tertiaria fossilium, quae in itinere suo observavit. Vol. 1. – pp. I-XIV, 1-267, Tab. I-XII. Berolini. (Schropp).
- PILSBRY, H.A., 1918 [March]. *Manual of Conchology* (Second Series: Pulmonata). Pupillidae (Gastrocoptinae) 24 (96): 257-380, pls 39-49.
- PILSBRY, H.A., 1918 [Nov. 5]. *Manual of Conchology* (Second Series: Pulmonata). Pupillidae (Gastrocoptinae, Vertigininae) 25 (97): 1-64, pls 1-5.
- PROSCHWITZ, T. VON & JOHANNESSEN, K., 1995. *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.
- RAVEN, J.G.M., 1986. Notes on spanish non-marine molluscs 3. Chondrinidae from the Cantabrian mountains (Gastropoda: Pulmonata). – *Zoologische Mededelingen* 60(2): 27-37.
- REICHENBACH, H.G.L., 1836. Allgemeine Taschenbibliothek der Naturwissenschaften 5. Zoologie oder Naturgeschichte des Thierreichs 2. Zittau und Leipzig. [Not seen].
- ROSSMÄSSLER, E.A., 1839. Iconographie der Land- und Süßwassermollusken, mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten. 2 (3-4): i-iv, 1-46. Dresden, Leipzig.
- TARRUELLA RUESTES, A., 2006. Presencia de *Abida gittenbergeri* Bössneck, 2000 (Gastropoda,

- Pupilloidea, Chondrinidae) en la comarca de la Garrotxa, y nuevas citas de distribución en la comarca de l'Alt Empordà (Cataluña, España). – *Spira* 2(2): 119-123.
- SCHÜTT, H., 2005. Turkish land snails 1758-2005: 1-559. Solingen
- SEDDON, M.B. 2000. *Chondrina oligodonta*. In: IUCN 2007. 2007 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 15 May 2008.
- SHILEYKO, A.A., 1984. Molluscs. Terrestrial mollusks of the suborder Pupillina of the fauna of the USSR (Gastropoda, Pulmonata, Geophila). Fauna SSSR (N.S.) 130: 1-399. [in Russian]
- SMITH, E.A., & H.W. ENGLAND, 1937. Martini and Chemnitz (Kuester's edition) Systematisches Conchylien-Cabinet, 1837-1918. – The Journal of the Society for the Cibliography of natural History 1 (4): 89-99.
- SÓLYMOS, P., & T. DOMOKOS, 1999. A possible connection between macroclimate and shell morphometry of *Granaria frumentum* (Draparnaud, 1801) (Gastropoda: Chondrinidae). – Malakológiai Tájékoztató 17: 75-82.
- SZAROWSKA, M., A. FALNIOWSKI, & K. MAZAN-MAMCZARZ, 2003. Genetic structure of isolated selfers: *Chondrina clienta* (Westerlund, 1888) (Gastropoda: Stylommatophora) in Kraków-Czêstochowa Upland. – Malakologische Abhandlungen 21: 79-89.
- TONGKERD, P., LEE, T., PANHA, S., BURCH, J.B. & D.Ó. FOIGHIL, 2004. Molecular phylogeny of certain Thai Gastrocoptine micro land snails (Stylommatophora: Pupillidae) inferred from mitochondrial and nuclear ribosomal DNA sequences. – Journal of Molluscan Studies 70: 139-147.
- VERDCOURT, B., 1963. A contribution to the Mollusc fauna of Northern Somaliland. – Revue de zoologie et de botanique africaines 68(3-4): 403-420.
- WADE C.M., P.B. MORDAN, & B.C. CLARKE, 2001. A phylogeny of the land snails (Gastropoda: Pulmonata). – Proceedings of the Royal Society of London: Biological Sciences 268: 413-422.
- WADE C.M., P.B. MORDAN, & F. NAGGS, 2006. Evolutionary relationships among the Pulmonate land snails and slugs (Pulmonata, Stylommatophora). – Biological Journal of the Linnean Society 87: 593-610.
- WÜTHRICH, M., 1990. Bericht über das Frühjahrstreffen der DMG in Riva San Vitale (Tessin) vom 25.05-28.05.1989. – Mitteilungen der Deutschen Malakozoologischen Gesellschaft 47: 19-20.
- ZILCH, A., 1959. Gastropoda, 2. Euthyneura. – Handbüch Paläozoologie 6, 2(1): 1-200.