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Resolving riddles and presenting new puzzles in Chonorinidae Phylogenetics

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INTRODUCTION AND SUMMARY

- Every so often, you have to unlearn what you thought you already knew,
and replace it by something more subtle.
This *process* is what science is all about, and it never stops. -

- Terry Pratchett et al., *The Science of Discworld* -

INTRODUCTION AND SUMMARY

Land snails are most suitable creatures to study biogeographical patterns. Their proverbial inertness, implying a lack of active dispersal, results in a relatively high degree of local endemism and thus species diversity. Some species are found in high densities, facilitating their easy collecting, at least as empty shells. Gastropod shells fossilize relatively easily, so that their morphological evolution can be followed during geological time. Therefore, land snails are ideal model organisms for a holistic approach to macro-evolutionary studies. Fossils may open a window to the evolutionary past, and shell-morphometrical, molecular, ecological and detailed distributional data, which become readily available for a growing number of species, can be used for phylogeny reconstructions.

The diverse land snail family Chondrinidae, with ca. 70 extant species, is particularly well suited to serve as a model for evolutionary studies. All species are obligatory associated with limestone. The strict connection with calcareous soils and rocks results in island-like distributional patterns and contributes to the high levels of endemism found in this family. The snails usually occur in high densities. Many fossils are known that can unambiguously be assigned to the Chondrinidae. However, since the species occurring on bare rockfaces do not fossilize as easily as the ground dwelling ones, there is an over-representation of the latter group in the fossil record (Chapter 2).

The Chondrinidae show interesting distributional patterns and an intriguing shell morphology. A better understanding of these phenomena may improve our understanding of the historical biogeography and evolutionary history of the western mediterranean fauna and evolutionary processes in general.

CHAPTER 2

This chapter deals with the genus level relations within the Chondrinidae. The family is restricted to the (western) Palaearctic. Contrary to a long held opinion, it does not include the Gastrocoptinae, Hypselostomatinae and Aulacospirinae. There are six genera in the family, viz. *Granopupa*, *Granaria*, *Solatopupa*, *Chondrina*, *Abida* and *Rupestrella*, which can be classified in two subgroups of three genera each. These two taxa are given the status of subfamily, i.e. the Chondrininae with *Chondrina*, *Abida* and *Rupestrella*, and the Granariinae, including *Granopupa*, *Granaria* and *Solatopupa*. The genetic distances suggest that the diversification of the genera occurred in about the same time-span in both subfamilies. However, the results of the molecular clock analyses cannot easily be translated into a biogeographical scenario. Neither of the two scenario's that are discussed can objectively be preferred.

Three different cladograms for the genus *Solatopupa* are tested after data in the literature. The deeper nodes in the genus are poorly supported in either scenario

and no significant difference between the three alternative possibilities was found. Obviously, additional data on the deeper phylogeny of the Chondrinidae are needed. This applies especially to the Granariinae, for which a more robust phylogeny reconstruction is needed. The genus *Granaria* shows up as paraphyletic.

The Chondrininae are the most diverse group, with 82% of the entire species diversity in the Chondrinidae. Partly because of this fact, the main focus of this thesis is on the Chondrininae.

CHAPTER 3

This chapter contributes to a better understanding of the historical biogeography of the genus *Chondrina* Reichenbach, 1828. Representatives of this genus occur on calcareous rocks, in particular on vertical, exposed rockfaces. Currently 37 species are recognized, with about 25 subspecific taxa. They are widely distributed in the western and central Palaearctic, from Portugal and Morocco in the southwest to Iran in the east. The genus shows high levels of narrow-range endemics, most notably in the Pyrenees and the Iberian peninsula and to a lesser extent in the southern Alps.

On the basis of a molecular phylogeny reconstruction, it may be concluded that only vicariance events cannot explain the actual situation. Apparently, several waves of dispersal and subsequent speciation occurred, starting from the southwestern part of the present generic range. Until recently, this was obscured by repetitive cases of parallel or convergent evolution in shell characters, which became clear with the use of molecular data. These data also revealed that *Chondrina farine-sii*, as defined by Gittenberger (1973), is not even a species complex, but a combination of more or less closely related taxa, united on the basis of similarities in shell characters, that have originated by convergent evolution.

CHAPTER 4

Inequality is a basic characteristic of the evolutionary process. The common ancestor of the chordates, for instance, has developed into sea squirts (ascidians) in one lineage and hominids in another, showing that differentiation may take place at quite different rates. Comparably unequal may be the amount of speciation and/or extinction in sister-groups, which may additionally show extreme differences in the size of their ranges. All this became increasingly obvious with the rise of phylogenetic systematics. Among species of gastropod molluscs there are conspicuous examples of both 'remnant' species, representing single lineages, with speciose sister-groups, and 'prime' species, which largely and sometimes misleadingly determine the image of a higher taxon. Some molluscan examples of both kinds of species are mentioned and a striking, newly discovered, remnant *Chondrina* species is reported.

CHAPTER 5

Chapters 6 and 7, and partly chapter 8, deal with the genus *Abida*, and more particularly with the strikingly polytypic species *Abida secale*. The center of morphological diversity in this species is situated in northeastern Spain. This chapter presents some general information on the geology, climate and topography of NE Spain, Andorra and S France. This background information should be helpful in understanding the patterns and processes described in the following chapters.

CHAPTER 6

Abida secale occurs throughout Europe, from England in the west, Belgium and southern Germany in the north and Slovakia in the east. The southern part of its distribution includes N. Italy, France and NE. Spain. The morphological differentiation is small over the largest part of its range. An intriguing exception to this uniformity is found in the extreme southwestern part of the species' range. In SE. France and NE. Spain *A. secale* shows an extreme morphological differentiation, which is consistent with the detailed geography of the area. This has led to the description of three subspecies from the French side of the Pyrenees, one from Andorra and an astonishing eleven from the province of Catalonia, Spain.

DNA studies using both nuclear (ITS-1) and mitochondrial DNA (COI) do not simply support the current classification, based on shell morphology and distribution. The molecular data suggest a recent hybridization event between *A. attenuata* and *A. secale*. The assumed '*attenuata*' mitochondrial COI shows a pattern of introgression into *A. secale*, which is consistent with the geographical structure of the area. The distribution of the hypothesized original '*secale*' mitochondrial DNA is associated with other valleys in northern Spain. This pattern differs from that of the ranges of the subspecies of *A. secale*. Without being identical, both geographical patterns make sense when the position of limestone, mountains and valleys is taken into account.

CHAPTER 7

Adaptation to high-altitude habitats is well known to cause morphological changes in many kinds of organisms, from bacteria to plants and humans. The extreme morphological diversity in *Abida secale* in NE Spain is partly caused by altitudinal variation in shell morphology, which is restricted to only this small part of the eastern Pyrenees, however. Nowhere else in its vast range *A. secale* shows a comparably conspicuous altitudinal variation.

Abida secale offers an interesting case study about the subspecies concept and the corresponding nomenclature. Two subspecies have been described from the Sierra del Cadí, viz. *A. s. cadiensis* and *A. s. cadica*, clearly representing high-altitude forms. Material collected during this project showed that additional high-altitude forms

occur in at least five different mountain ranges in the area. These forms differ from each other in several characters. Since they are derived from populations of different subspecies at the foot of these mountains, they have an independent evolutionary history. We describe the unique high-altitude populations of *A. secale* as separate subspecies instead of relegating these remarkable local forms to oblivion in synonymy.

CHAPTER 8

Based on newly acquired molecular as well as morphometric and distributional data, some cryptic species were revealed. These new taxa are described in this chapter. Some revisions in the currently accepted nomenclature of the Chondrinidae are also made and an annotated checklist is provided for the genus *Rupestrella*. The variation in shell morphology in *Chondrina* and the intraspecific variation in *Abida secale* are illustrated with 14 plates.

Gittenberger (1973) has suggested that *Abida secale* forms a ring species around the Sierra del Cadí. The high-altitude *Abida s. cadiensis* at one end was supposed to be connected via *A. s. brongermai*, *A. s. andorrensis*, *A. s. tuxensis* and *A. s. brauniopsis* to *A. s. cadica* at the other end. Both *A. s. cadiensis* and *A. s. cadica* were supposed to occur sympatrically on the Coll de Tancalaporta, high up in the Sierra del Cadí. During fieldwork we could not find a truly sympatric occurrence of the two taxa, however, but their ranges are only hundreds of meters apart at the Coll de Tancalaporta. Intermediate specimens were not found, but genetically *A. s. cadica* and *A. s. cadiensis* are very close. On the one hand we have to conclude that there is no gradual increase in genetic distance in the series of subspecies from *A. s. cadiensis* to *A. s. cadica*, whereas, on the other hand, intermediate specimens indicative of hybridization were not found.