# Resolving riddles and presenting new puzzles in Chonorinidae Phylogenetics

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# EVOLUTIONARY INEQUALITY IN *CHONDRINA* AND *ARIANTA* (GASTROPODA: PULMONATA): 'PRIME' AND 'REMNANT' SPECIES

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## INTRODUCTION

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 inequal 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 species is reported

## PRIME AND REMNANT SPECIES

### PRIME SPECIES

In the helicid genus *Arianta* Turton, 1831, *A. arbustorum* is exceptional because of its very large range. It is not restricted to mountainous areas, where the far more locally distributed, congeneric taxa are found. *A. arbustorum* occurs with several subspecies in the Alps, the Pyrenees and central Europe, including southern Scandinavia, Britain and Iceland (Gittenberger et al., 2004). In *Theba* Risso, 1826, another genus of the Helicidae, 17 extant species or subspecies are presently known, all of which restricted to Morocco, southernmost Spain and the eastern Canary islands (Gittenberger & Ripken, 1987). Only a single species, in fact a subspecies, i.e. *Theba pisana pisana* (L., 1758), occurs in the entire Mediterranean region and along the Atlantic coasts from Morocco to Belgium, SW. England and E. Ireland (Falkner, 1990: 234). By their common occurrence and very wide distributional areas, *Arianta arbustorum* and *Theba pisana* exemplify the concept of prime species. Similarly, *Abida secale secale* (Draparnaud, 1801) is the prime taxon in *Abida* Turton, 1831, because of its exceptionally large range, extending from the British isles to Austria, with a single locality in Slovakia (Kerney et al., 1983: 332, map 86; Ložek, 1964: 212). The ten other *Abida* species occupy much smaller ranges in the Pyrenees and the Cantabrian mountains, with only *A. polyodon* (Draparnaud, 1801) extending from the Pyrenees into the Mediterranean zone of southern France and southwards into eastern Spain (Gittenberger, 1973). In *Orcula* Held, 1838, the prime species is *O. dolium* (Draparnaud, 1801), occurring in the Alps and the Carpathians, in contrast to the c. ten congeneric species, which have much smaller ranges in southeastern Europe (Falkner, 1990: 146; Gittenberger, 1978). In *Chondrina* Reichenbach, 1828, it is *C. avenacea* (Bruguière, 1792), occurring in eastern Spain, central Europe, Italy, and the

NW. Balkans (Kerney et al., 1983: 333, map 92; Nordsieck, 1970: 254), with *C. arcadica* (Reinhardt, 1881) reaching from eastern Switzerland and (isolated) southern Scandinavia into Asia Minor (Nordsieck, 1970).

## REMNANT SPECIES

There are molecular phylogeny reconstructions for *Arianta*, *Chondrina*, and *Abida*, but not for *Theba*, and *Orcula*. In *Arianta*, *A. schmidtii* (Rossmässler, 1836) turned out to be the sister group of the entire *A. arbustorum* complex, which is distributed with several subspecies in the Alps, the Pyrenees and central Europe, including southern Scandinavia and Britain (Gittenberger et al., 2004). It is a poorly known, high-alpine, remnant species, restricted to a few mountain peaks in the extreme southeastern part of the Alps in Austria, where it is most probably extinct now (Klemm, 1973: 448), and Slovenia (Bisenberger, 1993: 337).

A molecular phylogeny reconstruction for *Chondrina* [Chapter 3, p. 52] resulted in the discovery of an even more extreme example of the remnant species concept. *Chondrina* contains about 26 species, occurring throughout the mountainous parts of central and southern Europe, Asia Minor and N. Africa (Gittenberger, 1973). The snails occur nearly exclusively on exposed, vertical limestone cliffs. In that habitat a species is often found in great numbers, whereas no more than two species may coexist. The radiation in *Chondrina* is largely nonadaptive, as defined by Gittenberger (1991, 2004). The genus is most speciose in southwestern Europe, the Iberian peninsula, including the French part of the Pyrenees and Morocco. In the Iberian peninsula, limestone-islands with *Chondrina* are found in the more or less isolated sierra's, where 14 species are currently recognized. Three more species are known from Morocco, so that more than half of all known species of *Chondrina* are concentrated in SW. Europe and Morocco.

Surprisingly, the DNA analysis made clear that *Chondrina maginensis* Arrébola & Gómez, 1998, has to be considered the sistergroup of all the other extant *Chondrina* species that could be investigated, i.e. 31 species in total. *Chondrina maginensis* is known from the Spanish department of Jaén, where it occurs at only a few localities in the Sierra Mágina (c. 25 km W. of the city of Jaén) (fig 1). The generic classification of this remnant species, which is somewhat aberrant by its slender conical shell shape, could be confirmed by studying the radula.

For the genus *Abida*, a comparable remnant species cannot be indicated, since none of the species has an extremely small range. In both *Theba* and *Orcula*, species with very small ranges are known, but since there is no phylogeny reconstruction available for these genera, we can only speculate that one or more of these narrowly endemic species could be considered a remnant taxon.

## THE ORIGIN OF PRIME AND REMNANT SPECIES

To enable an in depth discussion about the evolutionary origin of prime and remnant species, data on a much higher number of genera with strongly contrast-

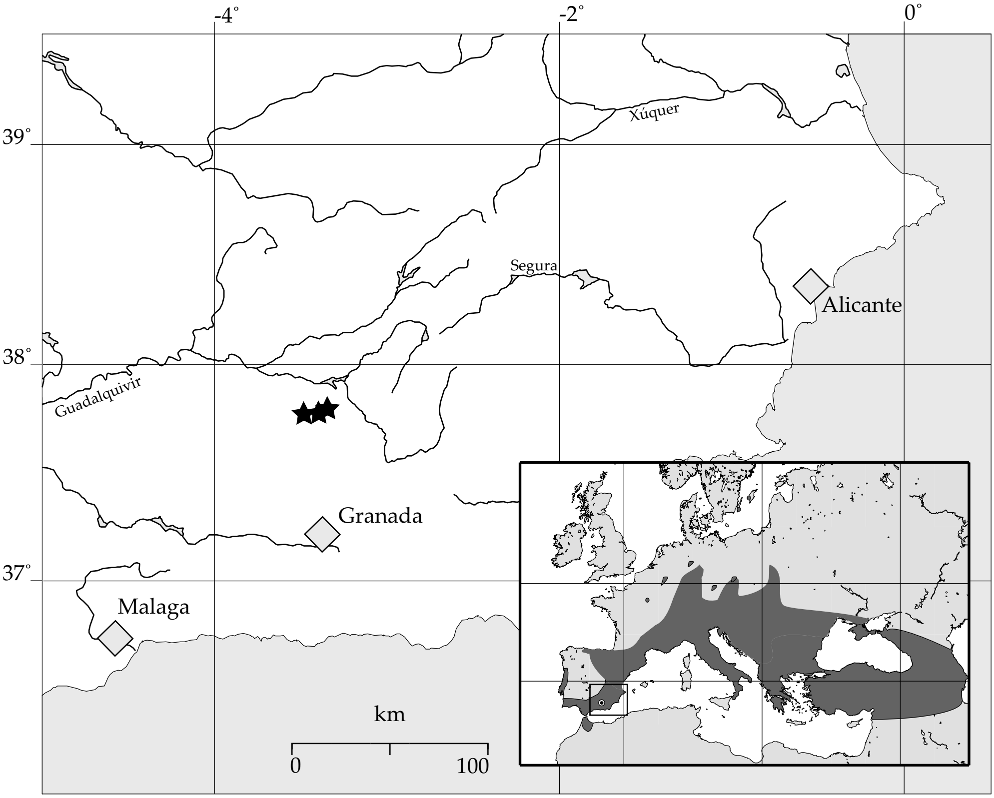

Figure **1**. Distribution of the 'remnant species' *Chondrina maginensis* (black stars) in the Sierra Mágina, Andalucia, Spain. Small map shows the current distributional area of extant *Chondrina* species.

ing species' ranges, are necessary. Here we can only mention that in *Arianta*, *Chondrina* and *Abida*, the prime species evolved relatively recently, whereas the lineages of remnant species are older. *Arianta arbustorum arbustorum* might have reached its actual, large range because of an ecological 'key innovation' which enabled it to occur in the lowlands, in contrast to the congeneric taxa, which remained dependent on an alpine habitat. This might not apply to the *Chondrina* and *Abida* prime species, occurring in habitats similar to those of their congeneric relatives. Maybe, these prime species achieved their status by chance. After an accidental, successful, dispersal event, closely related species might not be able anymore to colonize the same area because of the competitive exclusion principle (Gause's Law). The fact that the prime species originated relatively recently suggests that their status is only temporary. However, if *Solatopupa similis* is considered the prime species in *Solatopupa*, we have to conclude that prime species may be relatively old elements as well (Ketmaier et al., 2006; Kokshoorn & Gittenberger [Chapter

2]). For the moment being, prime species are best defined on the basis of only their evolutionary success, i.e. the relative size of their geographic ranges. To be called a remnant species, an additional criterion is necessary. The phylogenetic relationships should be known to differentiate between either (1) an early stage in speciation, with a population or relatively small group of populations, that became isolated only recently, or (2) a secondary situation, with stability or a decrease in range in a remnant taxon, contrasting with speciation events and/or a prominent range expansion in the sister group.

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