Resolving riddles and presenting new puzzles in Chonorinidae Phylogenetics

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The Sierra del Cadí

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In the chapters 6, 7 and 8 new data on the land snail species *Abida secale* (Draparnaud, 1801) are presented. In chapter 6 the phylogenetic relations between the populations of the morphologically defined subspecies of *A. secale* are dealt with. Chapter 7 describes the morphological variation in the species in relation to altitude. A hypothesis on the processes responsible for the observed incongruence between the distributional patterns of the subspecies on the one hand and some DNA markers on the other hand, is presented in chapter 8 (pp. 123-124).

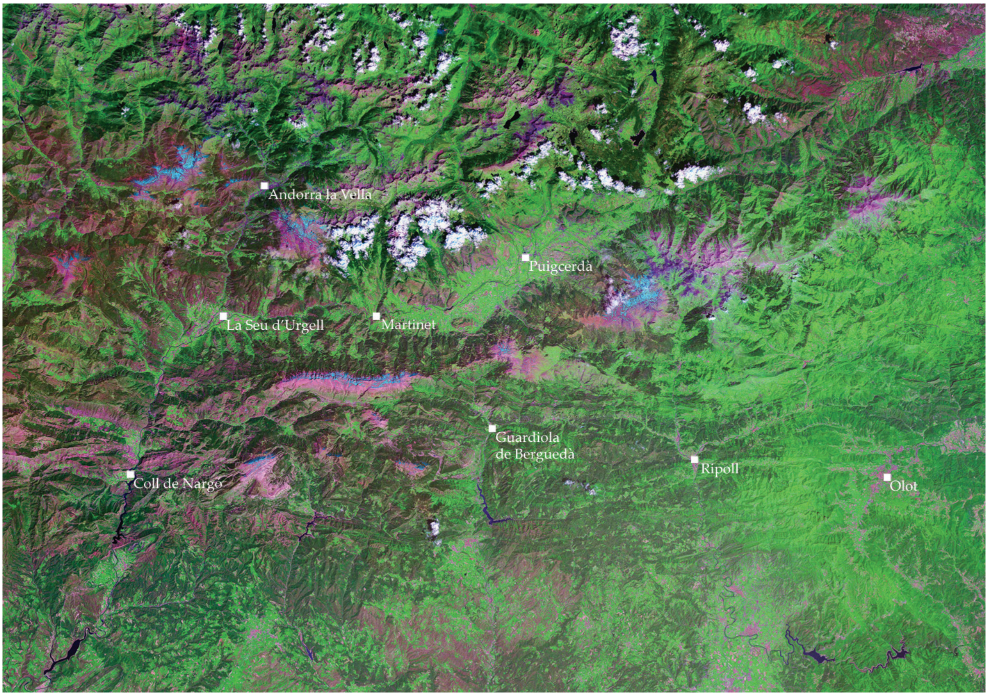
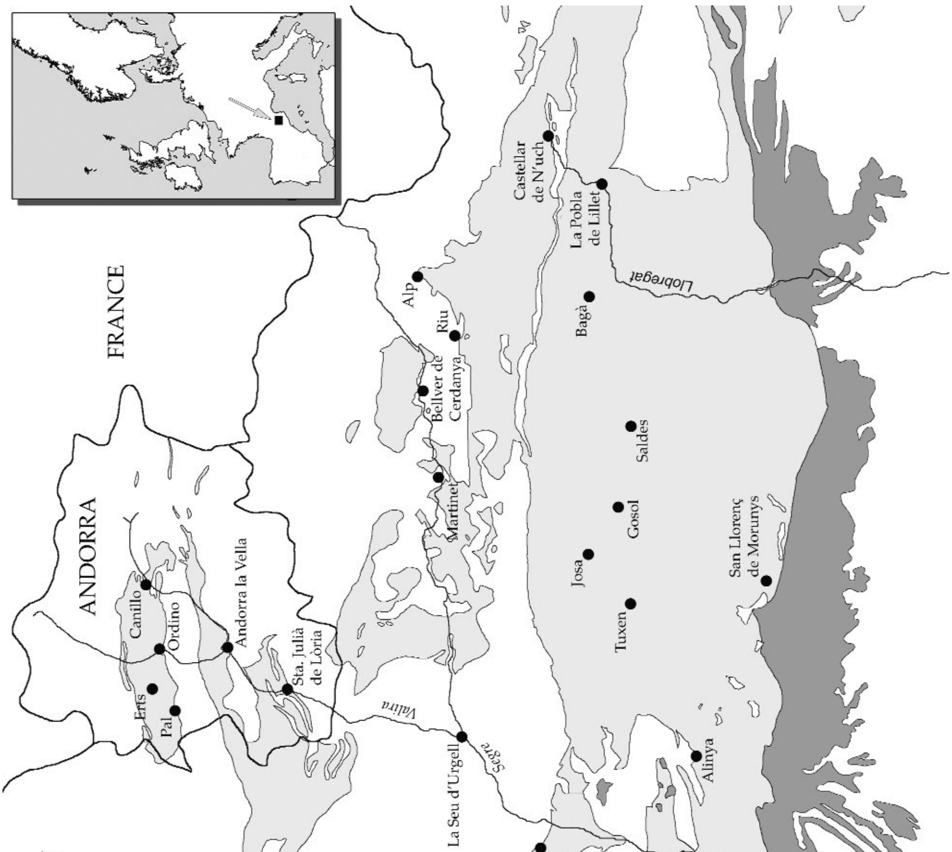


Figure **1**. Landsat-5 satellite imagery of northeastern Spain derived from NASA's GeoCover dataset, available through http://zulu.ssc.nasa.gov/mrsid/. This is a Short-Wavelength Infrared (SWIR) RGB image using band 2 (visible green light, shown in blue), band 4 (near-infrared, in green) and band 7 (mid-infrared, in red). The resulting image shows water in dark blue, while snow is bright blue. Green is vegetation, where dark green are forests and shrubs and light green grasses or crops. The pink to magenta or lavender and reddish and brownish colors are bare rocks or soil or urban area's. The white area's in the image are clouds.


FRANCE
ANDORRA
SPAIN
Canillo
Ordino
Andorra la Vella
Erts
Pal
Sta. Julià de Lòria
Valira
La Seu d'Urgell
Segre
Noves de Segre
Coll de Nargó
Noguera
Sort
La Pobla de Segur
15 km
Alinya
Tuxen
Josa
Gosol
Saldes
San Llorenç de Morunys
Bagà
La Pobla de Lillet
Castellar de N'uch
Llobregat
Alp
Riu
Bellver de Cerdanya
Martinet

Abida secale shows very complex, incongruent patterns in both shell morphology and geographical distribution in a small part of its range, i.e. NE Spain, Andorra and southern France. The centre of this area is situated in the Spanish part of the Pyrenees, in and around the Serra del Cadí. Therefore, some basic information on geology, climate and topography of the area is provided, which may contribute to a better understanding of the patterns that are observed and the processes we subsequently inferred.

Abida secale is a lithotrophic species that is always found associated with rocks with a high calcium content. In most cases this is limestone but the species has also been found on conglomerate rocks, as well as with rocks of vulcanic origin with very little free calcium. This rather strict habitat preference may have caused its patchy distribution throughout its range. The species may be present in one limestone 'island' but be absent from the next. Calcium rich rock types are abundant in the eastern Pyrenees, the area with the highest diversity in *A. secale* forms, though not only in that part of Europe.

According to Hartevelt (1970), from whom the following information about the geological history was taken, the Pyrenees were uplifted during the Alpine orogeny, which ended for the Pyrenees in the late Eocene (middle Alpine), c. 37 Mya. The uplift was caused by the collision of the African and the European continental plates. The uplift of the Cadí, Moixeró and Pedraforca mountains can only roughly be dated as occurring later on, during the Oligocene-Pliocene (1.8 – 33.7 Mya). The Cadí and Moixeró mountain ranges consist of nearly continuous limestones of Upper Cretaceous (southern unit) and Carboniferous – Triassic (northern unit) age. The conglomerates south of the area are somewhat younger, dating back to the Upper Eocene – Oligocene (Saura & Teixell, 2006, and references therein). Our map showing the distribution of calcareous rocks (fig. 2) was derived from the Instituto Geologico y Minero de España (IGME) geological map no. 24 (Berga, 1:200,000). The same basic map is used to plot the provenance of all individuals that were sequenced (chapter 6, p. 88).

Figure 1 is an infrared satellite image of the area. It shows landcover and landuse in different colors (see figure caption). In combination with fig. 3 this gives an impression of the elevation and location of the major mountain ranges. The distribution of the subspecies of *A. secale* (Chapter 8, p. 126, fig. 2) appears to be mainly correlated with the geomorphology of the area.

Figure 4 gives the main climatological conditions. Both the average annual temperatures (4a) and the total amount of annual precipitation (4d) are mapped with 1

Figure **2**. Distribution of limestone (light grey) and other possibly calcium rich soils (conglomerates, dark grey) in northeastern Spain and Andorra.

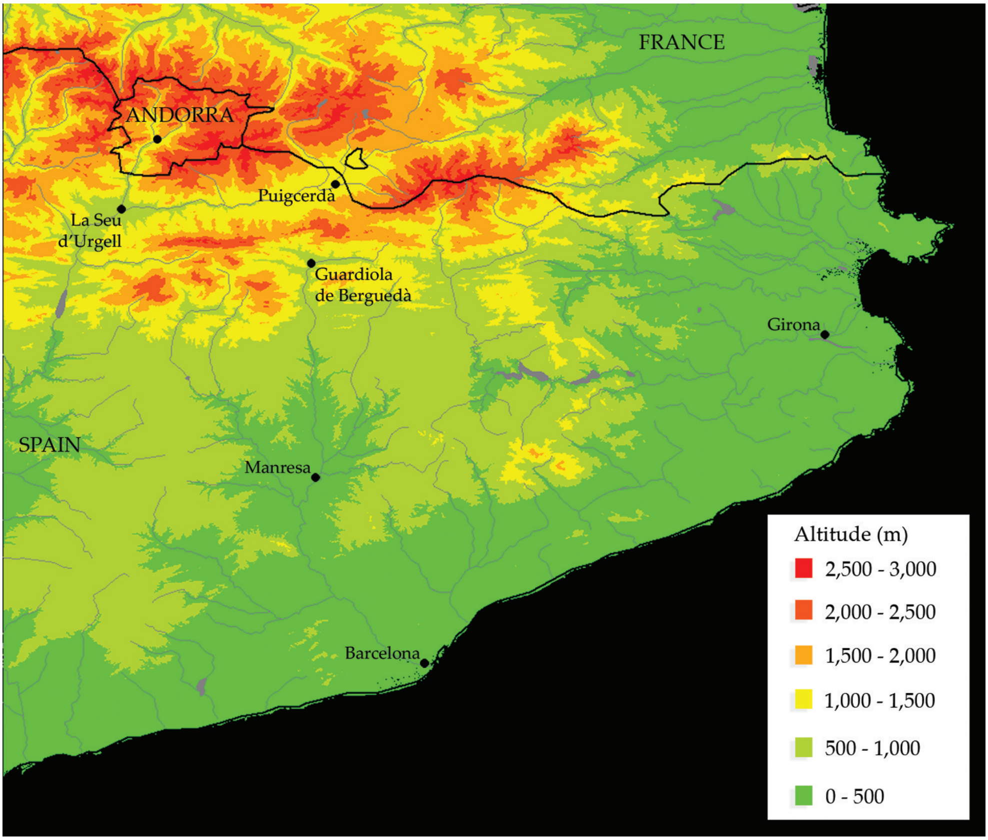
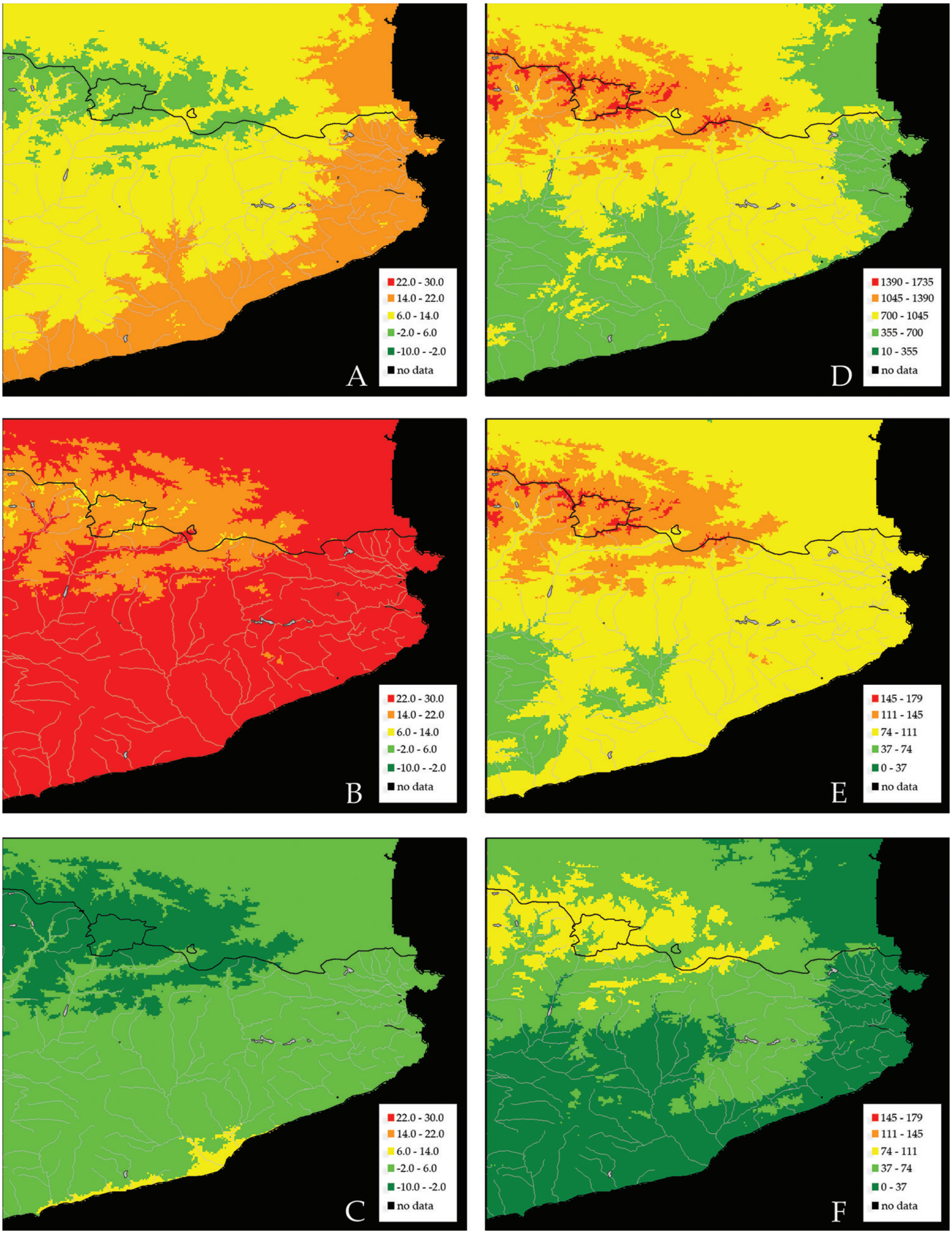


Figure **3**. Digital altitude data mapped for northeastern Spain. Data were derived from the CGIAR-CSI / NASA Shuttle Radar Topography Mission (SRTM) and have a spatial resolution of 3 arcseconds (app. 90 m). The vertical error is 16 m. Jarvis A., H.I. Reuter, A. Nelson, E. Guevara, 2006, Hole-filled seamless SRTM data V3, International Centre for Tropical Agriculture (CIAT), available from http://srtm.csi.cgiar.org.

Figure **4**. Climate data mapped for northeastern Spain. Data were derived from the WorldClim database (data description: Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones and A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978). Data have a spatial resolution of 1 km. 4 A; Average annual temperature, 4 B; Maximum temperature in the warmest month, 4 C; Minimum temperature in the coldest month, 4 D; Total annual precipitation, 4 E; Precipitation in the wettest month, 4 F; Precipitation in the driest month. Temperatures are in degrees Celcius, precipitation in mm.


22.0 - 30.0
14.0 - 22.0
6.0 - 14.0
-2.0 - 6.0
-10.0 - -2.0
no data
A
1390 - 1735
1045 - 1390
700 - 1045
355 - 700
10 - 355
no data
D
22.0 - 30.0
14.0 - 22.0
6.0 - 14.0
-2.0 - 6.0
-10.0 - -2.0
no data
B
145 - 179
111 - 145
74 - 111
37 - 74
0 - 37
no data
E
22.0 - 30.0
14.0 - 22.0
6.0 - 14.0
-2.0 - 6.0
-10.0 - -2.0
no data
C
145 - 179
111 - 145
74 - 111
37 - 74
0 - 37
no data
F

square kilometer resolution. These values are flanked by the maximum (4b) and minimum (4c) temperatures and the precipitation in the wettest (4e) and dryest (4f) month. These conditions are of course strongly influenced by the terrain elevation (compare with fig. 3). The differences are closely related with the location of the various mountain ranges and altitudes. Both the fluctuations in temperature and precipitation, as well as the average temperature and total annual precipitation do not differ strongly between the northern Segre valley (where *A. s. brongersmai* and *A. s. margaridae* occur) and the area south of the Cadí / Moixeró mountains (where *A. s. tuxensis*, *A. s. brauniopsis* and *A. s. lilietensis* are found). Furthermore, the distributional range of *A. s. tuxensis* spans a range of climatic differences, from the relatively dry and hot southern Segre valley to more average local conditions. It may be concluded that the observed temperature or precipitation patterns, do not correspond with the distribution of the *A. secale* subspecies.

References

HARTEVELT, J.J.A., 1970. Geology of the Upper Segre and Valira valleys, Central Pyrenees, Andorra/Spain. -- Leidse Geologische Mededelingen 45: 167-236.

SAURA, E., & A. TEIXELL, 2006. Inversion of small basins: effects on structural variations at the leading edge of the Axial Zone antiformal stack (Southern Pyrenees, Spain). -- Journal of Structural Geology 28(11): 1891-2120.