Resolving riddles and presenting new puzzles in Chonorinidae Phylogenetics

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7

Altitudinal gradients and shell morphology in *Abida secale:* *Ecophenotypic variation and subspecies*

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INTRODUCTION

It is well known in land snails and other organisms, including humans, that the more extreme conditions at higher altitudes as compared to the lowlands may induce an ecological and evolutionary response (see for example: Buria & Stahel, 1983; Berner et al., 2004; Beall, 2006; Dillon et al., 2006). The temperatures are lower, the atmospheric pressure is lower, negatively influencing the oxygen percentage in the air, and the season available for growth and reproduction is shorter. Usually there is also a difference between north- versus south-facing slopes. The adaptation to such a relatively hostile environment may be both ecophenotypic and genetically induced (Berven, 1982; Baur & Rabout, 1988; Cuauhtémoc et al., 2006).

High-altitude populations in land snails have been studied by several authors. Clinal variation has been observed in life history traits (Baur & Baur, 1998), body size and shell shape (Hausdorf, 2003; Gittenberger, 1991; Gittenberger et al., 2003), as well as species diversity (Tattersfield et al., 2001). Some species are exclusively adapted to high-altitudes, like for example the eastern Pyrenean helicid snail *Arianta canigonensis* (Boubée, 1833), which is not known from below 2200 m altitude (A.J. de Winter, personal observation), or the helicid Alpine snail *Cylindrus obtusus* (Draparnaud, 1805), which is usually found (far) above 1500 m altitude in Austria (Klemm, 1973). Other species or species groups occur along a large altitudinal range, sometimes reaching from sea level to mountain summits. A species from that category is *Abida secale* (Draparnaud, 1801).

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 northern Italy, France and northeastern Spain (Gittenberger, 1973; Kerney, 1963; Kerney et al., 1983). The morphological differentiation is small over the largest part of its range. An exception to this uniformity is found in the southwestern part of the species' range. In a small part of SE. France and NE. Spain the species shows an extreme morphological differentiation. This has led to the description of three subspecies from the French part of the Pyrenees, one from Andorra, and an astonishing eleven from the province of Catalunya, Spain (Kokshoorn & Gittenberger [chapter 8, p. 123]).

The geographical distribution of *Abida secale* and its morphologically defined subspecies is rather well known, but sofar hardly any attention has been paid to variation in shell morphology along altitudinal gradients. A striking case where altitudinal variation has been documented concerns the Comabona Mtn in the Sierra del Cadí, south of Andorra. Here we find in the valleys two clearly distinguishable subspecies of *A. secale*, viz. *A. s. brongersmai* at the northern side and *A. s. brauniopsis* in the south. From high altitudes here, i.e. the Collado de Tancalaporta at 2000 m, two additional subspecies have been described, viz. *A. s. cadica* (Westerlund, 1902) and *A. s. cadiensis* Gittenberger, 1973. These two taxa are readily distinguishable and their alleged sympatric occurrence led Gittenberger (1973) to locate the ends of an '*Abida secale* ringspecies' at high altitudes in the Sierra del Cadí. This hypothesis was
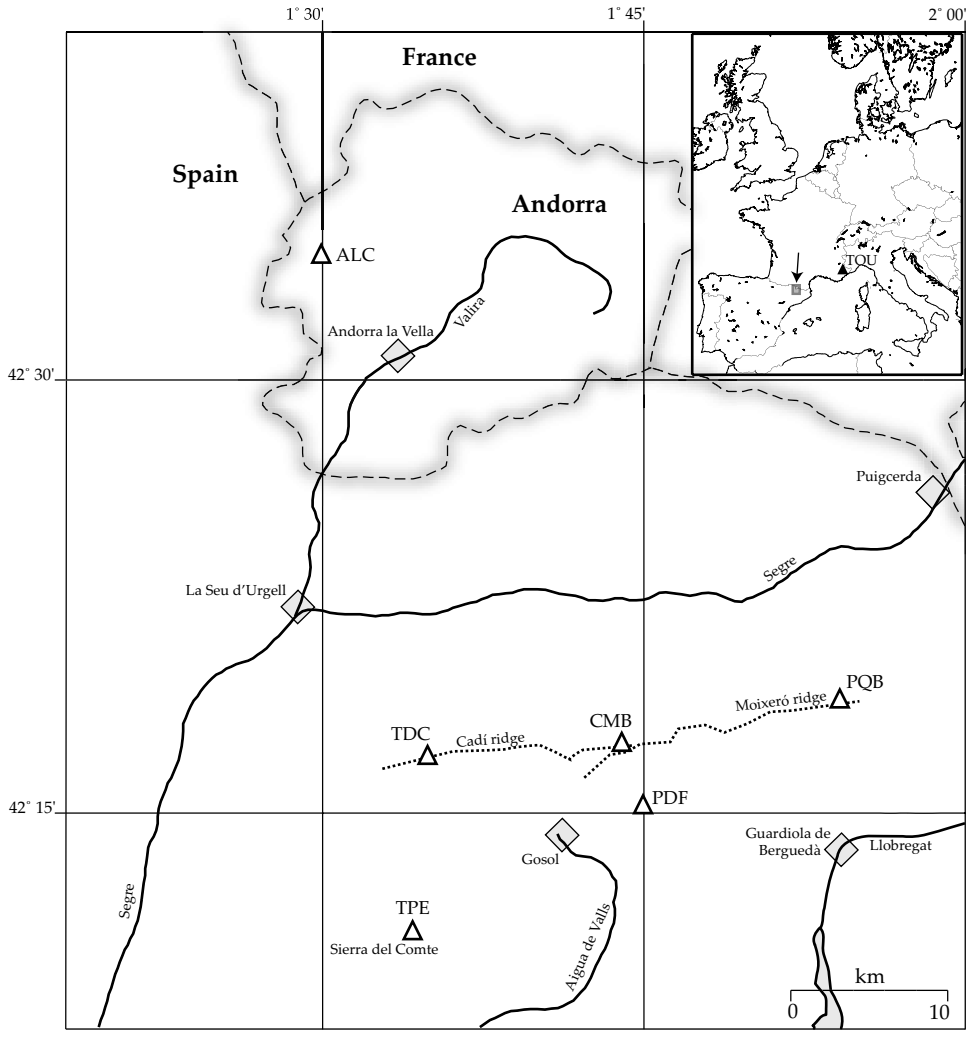
Fig. 1. Map of the study area. The Tournon mountain (TOU) lies outside the map area. Mercator projection

based on the observation that the subspecies in the valleys around the mountain range are interconnected by intermediates. From the Collado de Tancalaporta two forms without intermediates are represented in collections, thus suggesting a case of intraspecific isolation in conformity with the ringspecies model. This hypothesis could neither be confirmed nor convincingly falsified by Kokshoorn & Gittenberger [chapter 6]. During fieldwork near the Collado de Tancalaporta, neither a truly sympatric and syntopic occurrence, nor intermediate forms have been observed. On the

one hand, populations of both forms come as close as hundreds of meters, but an overlap was not observed. On the other hand, our molecular data suggest that there is, or recently has been, gene flow between *A. s. cadica* and *A. s. cadiensis* and not a relatively large genetic distance, supposed to have accumulated over a series of ring-like interconnected populations. Fieldwork has also made clear that high-altitude forms of *Abida secale* occur in several other mountain ranges in the area. These forms are similar to *A. s. cadiensis* and *A. s. cadica* (Kokshoorn & Gittenberger [chapter 8]).

We investigated the morphological variation along altitudinal transects. Using six morphometric parameters, the relation of these characters to altitude and geography (north- versus south-side and geographical distribution) was analysed.

MATERIAL AND METHODS

STUDY SITES

Snails were collected along four altitudinal transects on both the northern and the southern side of the Comabona (CMB) and the Pedro dels Quattre Battles (PQB) in the Sierra del Cadí and the Sierra Moixero. Material from high altitudes at five mountains elsewhere was examined for comparison, i.e. from the Alt de la Capa in Andorra, the Pedraforca and the Torre del Cadí in the Sierra del Cadí, the Tossa Pelada in the Sierra del Comte, southwest of the Sierra del Cadí, and the Tournon in the French Alps (fig. 1). The sample from the Tournon was kindly provided by Mr. O. Gargominy, Paris, France. Samples and collection numbers are given in table 1.

The altitudinal transects were dived in categories (altitude zones or AltZone). AltZone 1 (the foot of the mountain) ranges from 900 – 1,500 m, AltZone 2 from 1,501 – 1,700 m, AltZone 3 from 1,701 – 2,200 m and AltZone 4 from 2,201 – 2,500 m alt. The summit (AltZone 5) was defined as >2,501 m alt.

MORPHOLOGICAL MEASUREMENTS

To characterize the general morphology of the shells, six parameters were selected that are commonly used to distinguish subspecies in *Abida secale*, viz. shell height (SH), width of the body whorl (SW), apertural height (AH) and width (AW), 'protrusion' of the aperture (P) and the number of whorls (W). The 'protrusion' was measured at a 90º angle to the shell's axis, from the body whorl to the frontal edge of the aperture. The number of whorls was counted as illustrated in Kerney & Cameron (1979: 13). Shells were measured using a 'Wild M5©' stereo microscope and an ocular with a scale. All measurements were converted to millimeters. Only undamaged shells were measured, so that for all shells all six characters are available.

STATISTICAL ANALYSES

The inter-correlation between the six morphological characters was tested with

Mountain		AltZone	Transect	Sample	Altitude	Subspecies at the foot
1	Alt de la Capa, Andorra	Summit		BK0747	2,492	*A. secale andorrensis*
2	Comabona, Sierra del Cadí, Spain	1 (900 - 1,500 m, Foot)	North	100570	1,300	*A. secale brongersmai*
		2 (1,501 - 1,700 m)		100539	1,625	
		3 (1,701 - 2,200 m)		100573	2,000	
				100576	2,125	
		4 (2,201 - 2,500 m)		100582	2,250	
				104122	2,430	
		1 (900 - 1,500 m, Foot)	South	100546	1,430	*A. s. brauniopsis*
		2 (1,501 - 1,700 m)		100568	1,700	
		3 (1,701 - 2,200 m)		104085	1,820	
				104087	1,972	
		4 (2,201 - 2,500 m)		104126	2,429	
		Summit		104124	2,511	
3	Pedro dels Quattre Batlles, Sierra Moixero, Spain	1 (900 - 1,500 m, Foot)	North	100613	1,325	*A. secale margaridae*
		2 (1,501 - 1,700 m)		-	-	
		3 (1,701 - 2,200 m)		104107	2,023	
		4 (2,201 - 2,500 m)		104105	2,326	
		1 (900 - 1,500 m, Foot)	South	104093	934	*A. s. lilietensis*
		2 (1,501 - 1,700 m)		-	-	
		3 (1,701 - 2,200 m)		100535	2,000	
		4 (2,201 - 2,500 m)		104083	2,366	
				104101	2,400	
		Summit		104103	2,530	
4	Pedraforca, Sierra del Cadí, Spain	Summit		99135	2,300	West: *A.secale brauniopsis*, East: *A. s. lilietensis*
5	Tossa Pelada, Port del Comte, Sierra del Comte, Spain	Summit		54960	2,100	*A. secale tuxensis*
6	Torre de Cadí, Sierra del Cadí, Spain	Summit		99118	2,400	*A. secale tuxensis*
7	Tournon mountain, Thorame, Hautes Alpes, France	Summit		CB16	2,665	*A. secale secale*

Mtn	Transect	Data	AltZone 1	AltZone 2	AltZone 3	AltZone 4	Summit
CMB	North	n	18	13	37	41	
		ShellHeight (SH)	8.82±0.14	8.94±0.16	7.76±0.09	6.55±0.07	
		ShellWidth (SW)	2.71±0.03	2.88±0.04	2.62±0.03	2.46±0.02	
		ApertureHeight (AH)	2.65±0.03	2.61±0.04	2.47±0.03	1.99±0.02	
		ApertureWidth (AW)	2.04±0.03	1.91±0.05	1.93±0.02	1.71±0.02	
		Protrusion (P)	2.64±0.03	3.23±0.06	2.54±0.02	2.37±0.02	
		Whorls (W)	9.31±0.09	9.77±0.12	8.48±0.10	7.93±0.06	
		Factor	-0.87±0.08	-1.26±0.11	-0.26±0.06	0.65±0.05	
	South	n	6	11	14	10	20
		ShellHeight (SH)	9.62±0.29	10.23±0.38	8.77±0.29	6.66±0.12	6.1±0.09
		ShellWidth (SW)	2.63±0.04	2.73±0.03	2.67±0.04	2.38±0.02	2.29±0.02
		ApertureHeight (AH)	2.77±0.08	2.74±0.05	2.54±0.08	1.91±0.03	1.85±0.03
		ApertureWidth (AW)	2.03±0.03	2.05±0.04	2.03±0.05	1.66±0.02	1.62±0.02
		Protrusion (P)	2.92±0.06	3.2±0.08	3.05±0.05	2.31±0.03	2.18±0.03
		Whorls (W)	10.17±0.23	10.47±0.19	9.59±0.17	8.75±0.13	8.12±0.10
		Factor	-1.26±0.11	-1.61±0.16	-1.02±0.19	0.67±0.05	1.06±0.07
PQB	North	n	13		16	18	
		ShellHeight (SH)	11.14±0.18		8.45±0.11	6.59±0.08	
		ShellWidth (SW)	3.13±0.04		2.89±0.04	2.53±0.02	
		ApertureHeight (AH)	3.23±0.04		2.71±0.03	2.06±0.03	
		ApertureWidth (AW)	2.42±0.04		2.05±0.02	1.74±0.03	
		Protrusion (P)	2.97±0.03		2.72±0.06	2.33±0.03	
		Whorls (W)	10.11±0.09		8.58±0.06	8.02±0.07	
		Factor	-2.44±0.08		-0.9±0.09	0.54±0.08	
	South	n	12		20	49	21
		ShellHeight (SH)	7.67±0.12		8.2±0.12	6.35±0.07	6.02±0.07
		ShellWidth (SW)	2.34±0.04		2.4±0.02	2.46±0.02	2.40±0.02
		ApertureHeight (AH)	2.19±0.03		2.28±0.03	2.02±0.02	1.91±0.02
		ApertureWidth (AW)	1.75±0.02		1.79±0.02	1.70±0.01	1.63±0.01
		Protrusion (P)	2.13±0.05		2.25±0.02	2.27±0.02	2.18±0.02
		Whorls (W)	9.13±0.09		9.58±0.10	7.91±0.07	7.53±0.08
		Factor	0.36±0.07		0.03±0.08	0.73±0.05	1.05±0.05

Table **2**. The six measurements of *A. secale* shells collected from the Comabona (CMB) and Pedro dels Quattre Battles (PQB) Mountains in Northern Spain, averaged per AltZone and for the summits ± 1 SE.

Table **1**. Samples used in this study.

	SH	SW	AH	AW	P	W	Factor
Shell Height (SH)	1.00	0.65	0.91	0.81	0.71	0.89	-0.95
Shell Width (SW)		1.00	0.77	0.79	0.85	0.39	-0.82
Aperture Height (AH)			1.00	0.90	0.75	0.71	-0.95
Aperture Width (AW)				1.00	0.77	0.60	-0.91
Protrusion (P)					1.00	0.51	-0.85
Whorls (W)						1.00	-0.78
Factor							1.00

Table **3**. The correlation matrix with Spearman rank R-values between the six measurements of *A. secale* shells collected from CMB and PQB in Northern Spain. Because all correlations were significant at the p-level of 0.001, a factor was calculated using Factor Analyses. This factor explained 79.6% of all variance and is included in the correlation matrix.

	Effect	SS	Degr. of Freedom	F	p
Shell Height					
Mountain	Random	11.95	1.00	0.52	0.49
Transect	Random	102.56	2.00	0.89	0.48
AltZone	**Random**	**378.63**	**3.00**	**9.70**	**0.00**
Mountain*Transect*AltZone	**Random**	**103.57**	**9.00**	**37.14**	**0.00**
Error		93.89	303.00		
Shell Width					
Mountain	Random	0.05	1.00	0.05	0.82
Transect	Random	4.62	2.00	2.70	0.14
AltZone	Random	4.08	3.00	2.72	0.11
Mountain*Transect*AltZone	**Random**	**3.98**	**9.00**	**29.18**	**0.00**
Error		4.59	303.00		
Aperture Height					
Mountain	Random	0.42	1.00	0.23	0.64
Transect	Random	9.23	2.00	1.27	0.37
AltZone	**Random**	**23.43**	**3.00**	**8.60**	**0.01**
Mountain*Transect*AltZone	**Random**	**7.22**	**9.00**	**36.20**	**0.00**
Error		6.72	303.00		
Aperture Width					
Mountain	Random	0.15	1.00	0.22	0.65
Transect	Random	2.71	2.00	1.42	0.32
AltZone	**Random**	**5.32**	**3.00**	**4.42**	**0.04**
Mountain*Transect*AltZone	**Random**	**3.20**	**9.00**	**28.26**	**0.00**
Error		3.81	303.00		
Protrusion					
Mountain	Random	4.68	1.00	2.72	0.13
Transect	Random	4.39	2.00	0.84	0.48
AltZone	Random	14.14	3.00	3.89	0.05
Mountain*Transect*AltZone	**Random**	**9.62**	**9.00**	**50.66**	**0.00**
Error		6.39	303.00		
Whorls					
Mountain	Random	8.76	1.00	1.09	0.33
Transect	Random	41.61	2.00	1.00	0.44
AltZone	**Random**	**138.84**	**3.00**	**11.07**	**0.00**
Mountain*Transect*AltZone	**Random**	**33.38**	**9.00**	**18.28**	**0.00**
Error		61.48	303.00		
Factor					
Mountain	Random	8.75	1.00	0.66	0.44
Transect	Random	57.34	2.00	1.15	0.39
AltZone	**Random**	**153.98**	**3.00**	**6.83**	**0.01**
Mountain*Transect*AltZone	**Random**	**59.73**	**9.00**	**52.63**	**0.00**
Error		38.21	303.00		

Table **4**. Results from the General Linear Models to test the effects of altitude on six measurements of A. secale shells collected from two mountains in Northern Spain, with the factor that explained 79.6% of the variation among these variables. Type I hierarchical variance reduction was used with "Mountain" entered first, followed by "Transect", "AltZone" and the interaction effect between these categorical predictors.
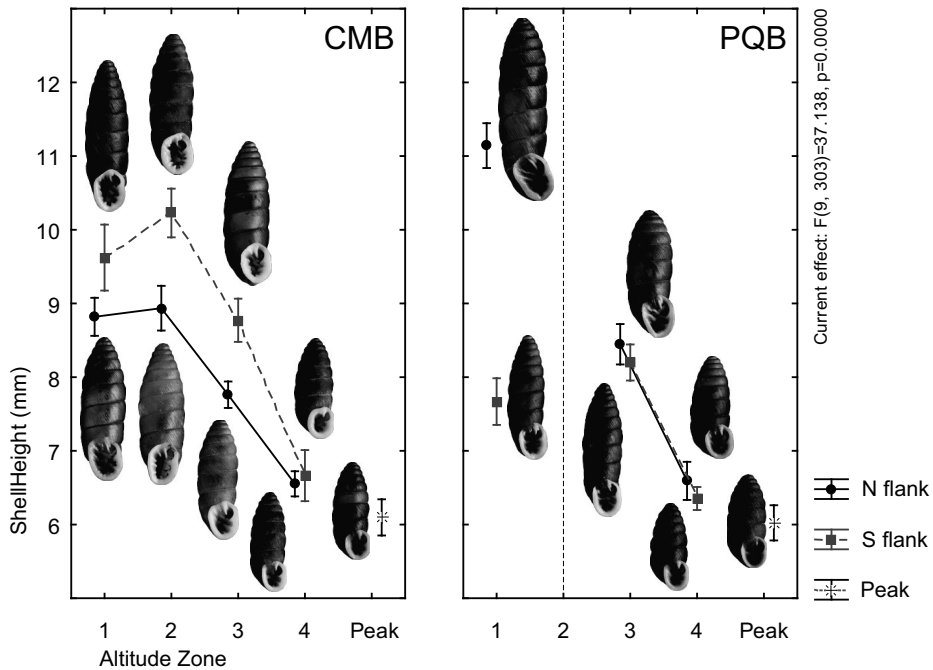
Figure **2**. Example of clinal variation observed across the altitudinal gradients, here for Shell Height (SH).

Spearman Rank correlations. Subsequently, factor analyses were used to combine inter-correlated variables into a single factor. This factor represents a certain amount of the variability of the data. To test for the effect of altitude on each of the morphological measurements and factor, General Linear Models (GLMs) with Type I hierarchical variance reduction were used. The categorical predictor "Mountain" was tested first, followed by "Transect" and "AltZone". In addition, the interaction effect between these three categorical predictors was included ("Mountain"*"Transect"*"AltZone") to test whether effects of altitude differed between transects and mountains. To quantify the width of morphological variation within altitudinal zones, the Coefficient of Variation (CoV), i.e. the standard deviation divided by the mean, was calculated for each of the six measurements. The relation between altitude and CoV was tested with one-way ANOVA's. All analyses were carried out using Statistica 6.0 (©StatSoft).
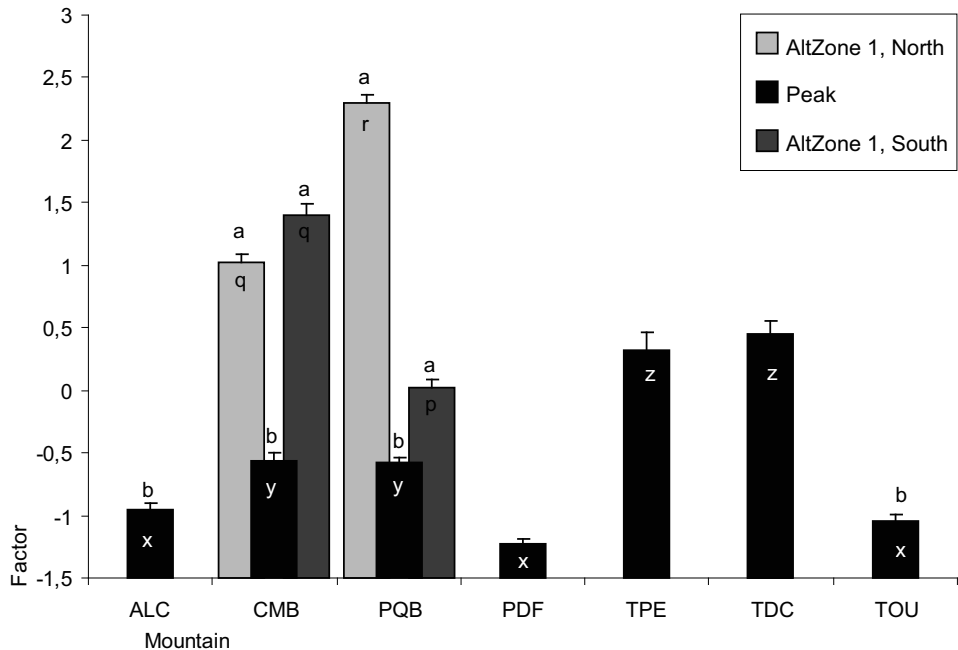
Figure **3**. Graph with the results from the general linear model with subsequent Tukey HSD (unequal n) posthoc tests for the factor between the seven summits and between foot and summit for the PEDRO DELS QUATTRE BATTLES and COMABONA mountain. The factor itself explains 79.6% of the variation in the 6 measurements.

a and b: Significant differences between foot and summit within one mountain

x, y and z: Significant differences between summits

p,q and r: Significant differences between feet.

RESULTS

In total 372 shells were measured (table 2). The measured characters were significantly correlated at the $p<0.001$ level (table 3). Because of this correlation between the six measured characters it was decided to calculate a factor. This factor explains 79.6% of all variation in the data and was negatively correlated to each of the 6 measurements (table 3).

Except for shell width and protrusion of the aperture, all measurements were significantly correlated with altitude (table 4), with the largest values in the valleys and the smallest at the highest localities (i.e. fig. 2). However, for all measurements there was a significant interaction effect between the three categorical predictors (i.e. mountain, transect and altitude zone) in that the differences were largest between the two subspecies (*A. secale margaridae* and *A. secale lilietensis*) at the foot

	$F_{(4-11)}$	p
Shell Height	1.02	0.44
Shell Width	2.29	0.12
Aperture Height	1.27	0.34
Aperture Width	1.95	0.17
Protrusion	2.28	0.13
Whorls	0.71	0.60

Table **5**. ANOVA results to test for the effects of AltZone on the value of the Coefficient of Variation for each of the six measurements of shells collected on the Comabona and Pedro dels Quattre Battles Mts in northern Spain.

of the Pedro dels Quattre Battles. Between 2,200 and 2,500 m altitude (AltZone 4), and between the two summits, none of the measurements differed significantly. Moreover, there were no differences in measurements of the shells collected from the summits at the two mountains. The Coefficient of Variation (CoV) did not differ between the altitudinal zones (table 5), i.e. there is no difference in the variability of the measured characters between the altitudinal zones.

Samples taken from the summits of both the Pedro dels Quattre Battles and the Comabona *together* differed significantly from the samples from the other 5 mountains (fig. 3). There we see that the samples from the Alt de la Capa (Andorra), Pedraforca (Spain) and Tournon (France) do not differ significantly (in the measured characters), and neither do those from the Port del Comte and Torre del Cadí (Spain).

DISCUSSION

We observed a strong convergence between the measurements of the samples from AltZone 3 (i.e. between 1,701 – 2,200 m alt.) in transects 1 and 2 on the Pedro dels Quattre Battles (fig. 2). This might be explained by the presence of the Coll de Pal, just east of the summit. This mountain pass, situated at c. 2,100 m altitude, may enable contact, i.e. gene flow, between the two series of populations from the north and the south flank of the mountain. This might explain the rapid morphological convergence between both transects at such relatively low altitude as compared to the Comabona mtn.

The CoV, used to compare morphological variability across altitudinal zones, does not support a scenario with increasing altitude as an increasingly strong selective force acting on shell morphology. It is evident that altitude influences shell morphology in these snails. Shell height, aperture height and width and the number of whorls all decrease with increasing altitude. However, selection appears to be relaxed. The variation width (in the measured characters) does not decrease with increasing altitude, as would be expected if increasing altitude would increase selective pressure. This absence of strict selection might explain the absence of a significant correlation between altitude and shell height as was demonstrated by Uribe et
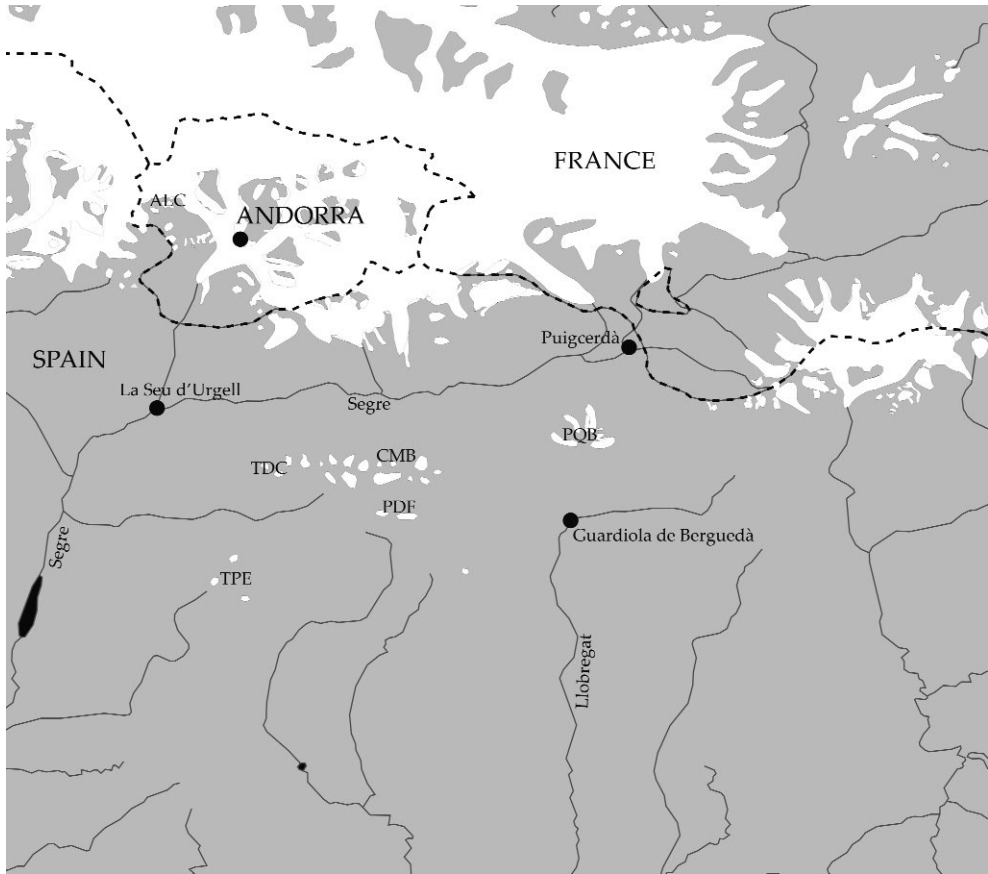
Figure **4**. Maximum extent of glaciers (white) during the Last Glacial Maximum.
Map data derived from Ehlers & Gibbard, 2004. The map has no projection.

al. (2007). Our data support a significant correlation between the measurements and the altitudinal zones. Our sampling points are rather far apart (altitudinally, not geographically, table 1). In the study by Uribe et al. the sampling points are much closer together. Because other factors than altitude, like differences in microhabitat and genetic determination as well as random variation, will strongly influence shell shape in local populations (i.e. Kokshoorn & Gittenberger [Chapter 8, p. 123]), this will be of more influence on the statistical results when the samples are taken at close proximity.

We know from the fossil record that *Abida secale secale* was already present in central Europe about 60,000 years bp (Moine et al, 2005). However, the presence of the species at high altitudes in the Alps is most likely of Holocene origin. We assume

that if *A. secale* would have survived the extensive glaciations of the Last Glacial Maximum (LGM: c. 18,000 years ago) amidst the ice on nunataks in the Alps, this should have left morphological traces. However, there is hardly any morphological variation (beside size differences) between populations at the foot of the mountains and those on the summits. The situation in the central Pyrenees is not comparable to that in the Alps. In the Pyrenees, and especially in the pre-Pyrenees like the Sierra del Cadí, the glacier extent was limited (Ehlers & Gibbard, 2004) (fig. 4). Allthough it is unlikely that a suitable habitat would continuously have been available at high altitudes in the Cadí/Moixero mountains during the LGM (Hartevelt, 1970: 232), there could still have been a reasonable amount of altitudinal variation in habitat. Climatic conditions that now apply to the habitat of *A. secale* above 2,000 m altitude, would have been present at that time at much lower altitudes. Even now climatic conditions are strongly influenced by the complex geology of the area. The sheltered Gresolet valley east of the Pedraforca for instance, harbours typical high-altitude species and forms (i.e. *Pyrenaearia* sp.) at a mere 1,600 m (pers. obs.). Hence, there is no reason to accept that the high-altitude forms that we encounter at present in the centre of morphological diversity originated from lowland populations only after the LGM, as is most probably the case in the Alps. In the Pyrenees, the altitudinal clines had more time to differentiate, as compared to the situation the Alps. With more time being available, more conspicuous contrasts could develop.

What's in a name?

The value of infraspecific taxonomic ranks has been a point of discussion for a long time. Many infraspecific ranks have been used, i.e. forma, natio, variety, race, etc. The more general use of the subspecies category came with the introduction of Mayr's biological species concept (Mayr, 1942). Its acceptance by the International Commission on Zoological Nomenclature (ICZN) in 1960 was instrumental in proliferating its use, despite strong opposition (i.e. Wilson & Brown, 1957). Mayr (1942) defined subspecies as genetically distinct, geographically separate populations, belonging to the same species and, therefore, interbreeding freely in contact-zones (Wilson & Brown, 1953).

The original description of *A. s. cadiensis* was based on few samples. Nevertheless, there was already material available from two different mountain ranges. In the type series (Gittenberger, 1973: 112) there are 4 shells from "Port de Comte südlich vom Tossa Pelada, 2100 m … (RMNH 54960)". These are apparently from the Sierra de Port del Comte, situated southwest of the Sierra del Cadí, where the Tossa Pelada is a peak of 2,373 m high, and not from the Sierra del Cadí itself (as was stated by Gittenberger, 1973). So the original type series suggests a disjunct distribution for *A. s. cadiensis*. The fact that the shells from the two mountain ranges differ in size (fig. 3) and somewhat in general shell shape, was either overlooked or neglected. However, it does illustrate that these shells are very similar.

With much more material from high altitudes available for study now, we could demonstrate that despite a more general similarity, there may be differences in the measured characters between specimens from summits in different mountain ranges (fig. 3). Apart from that, shells from high altitudes in different mountain chains, even when not differing in size, differ from each other in other characters, like sculpture and/or general shape, apertural dentition and/or shape, which are not used in this study (Kokshoorn & Gittenberger, [chapter 8, pp. 123-140]). This fact is illustrated, for instance, by the absence of significant differences in the measured characters between the subspecies at the foot of the Comabona mtn. Although *A. s. brongersmai* (northern flank) and *A. s. brauniopsis* (southern flank) are clearly different in their morphology (i.e. Kokshoorn & Gittenberger, [chapter 8, pp. 131-133, pls. 4-5]), the measured characters do not show significant differences (fig. 2 and 3).

These additional characters, which may be overlooked at first sight, strongly suggest that the forms occurring at high altitudes in different mountain chains, have different sister-group taxa in the valleys. This view is strongly supported by the intermediate populations that are known for several of the taxa that are here discussed.

There is clearly a geographical component in the distributional pattern of the high-altitude taxa. These taxa have different sister-groups and, as a consequence, their own unique evolutionary histories. Therefore, classifying all of them as a single taxon cannot be an option, because that would result in an unnatural entity. Uniting the high-altitude forms with their associated closest relatives in the valleys would imply that extremely variable taxa are created, distributed from the valleys to the summits. The descriptions of these taxa would have to be broadened to such an extent that they can hardly be differentiated anymore. More serious than this practical problem, is the fact that doing so would imply that these geographically restricted, genetically determined forms are neglected in zoological nomenclature, while they form a key aspect of the enigmatic centre of diversity in *A. secale*. A comparable diversity in forms from high altitudes is found nowhere else in the large range of *A. secale*. We therefore see no satisfying solution other than to introduce four new subspecific taxa in *A. secale* (see chapter 8, pp. 134-140). This will bring the total number of subspecies in this species to 17, all but one restricted the extreme south of the species' distribution.

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