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A morphometrical review of the *Sorex araneus-arcticus* species group from the Iberian Peninsula (Insectivora, Soricidae)

María José López-Fuster & Jacint Ventura

Abstract. A review of the morphometry and geographical distribution of *Sorex araneus*, *S. coronatus* and *S. granarius* from the Iberian Peninsula is presented. Multivariate analyses based on mandible and skull parameters were carried out. The results of cluster and principal component analyses revealed a clinal size variation of these species, especially notable in the case of *S. coronatus*, within their Iberian range. This fact determines the biometrical overlapping between *S. granarius* and *S. coronatus* in the West and between the latter species and *S. araneus* in the East. In an attempt to solve the species determination of these shrews, especially in the sympatric areas, discriminant analyses based on mandible and also on skull parameters from Iberian specimens were carried out. Results suggest that, at least in the Northwest of the Iberian Peninsula, the sympatric area of *S. coronatus* and *S. granarius* is probably larger than generally accepted. Parapatry or syntopy in this area remain to be demonstrated.

Key words. *Sorex araneus*, *Sorex coronatus*, *Sorex granarius*, morphometry, multivariate analyses, Iberian Peninsula.

Introduction

In the Iberian Peninsula the *Sorex araneus-arcticus* group is represented by three species of the European *araneus* group, defined by Hausser et al. (1985): *Sorex araneus* Linnaeus, 1758, *S. coronatus* Millet, 1828 and *S. granarius* (Miller, 1910). The common shrew, *S. araneus*, is distributed through the eastern Pyrenees and Catalan Pre-Pyrenees and is completely isolated from other European populations of the species (Sans-Coma 1979; Gosálbez et al. 1981; López-Fuster et al. 1985). Millet's shrew, *S. coronatus*, extends from the Pyrenees in the East to Galicia in the West, and probably to the south through the Sistema Ibérico (García Dory 1977; Nores 1979; López-Fuster et al. 1985; López-Fuster & Ventura 1987; Brunet-Lecomte & Delibes 1988; Hausser 1990a). The Iberian shrew, *S. granarius*, stretches from Sistema Central to the mouth of the Tajo River and northwards to Galicia (Niethammer 1970; Gisbert et al. 1988; Brunet-Lecomte & Delibes 1988; Hausser 1990b). According to previous studies, the distribution areas of these two latter species overlap in parts of Galicia, León and probably in the Sistema Ibérico as well (Brunet-Lecomte & Delibes 1988; Hausser 1990a, b). Moreover, the areas of *S. araneus* and *S. coronatus* overlap, at least, in the Aran and Boí Valleys (Lleida), although it has not been shown whether there is a mutual exclusion between the two species in these regions, similar to that reported by Hausser (1978) in Switzerland and France (López-Fuster et al. 1985).

It is well known that the species of the European *araneus* group are morphologically and biometrically similar, so cytogenetic or biochemical analyses are

often the only way to ensure correct specific determination (Meylan & Hausser 1978; Hausser et al. 1975; Catzefflis et al. 1982; Hausser & Zuber 1983). Nevertheless, it has been shown that multivariate analyses, based on craniometrical characters, can provide a satisfactory approach to the determination between these species, and may be very useful when cytogenetic and biochemical analyses are not available or cannot be used, e. g. in owl-pellet material. Until now, the morphometrical differentiation between *S. coronatus* and *S. araneus* could be attained mainly by means of the discriminant function of Hausser & Jammot (1974), which was calculated from central-European specimens. Although this function has been applied to some Spanish populations (Sans-Coma 1979; López-Fuster 1983; López-Fuster et al. 1985), its efficiency has not been demonstrated in the Iberian sympatric area. On the other hand, a discrimination between *S. coronatus* and *S. granarius* must be performed on the basis of subjective criteria of shape and size (Miller 1912; Hausser et al. 1975; Nores 1979), or by the vague method proposed by Brunet-Lecomte & Delibes (1988), based on the simultaneous application of two very complicated discriminant functions. All these multivariate methods are carried out using mandible measurements, thus lacking biometrical procedures that would permit the specific determination by skull parameters.

In this study we undertake a review of the morphometry and geographical distribution of the species of the European *araneus* group in the Iberian Peninsula. Likewise, in order to facilitate their morphometrical species diagnosis, especially in areas of sympatry, discriminant analyses of mandible measurements from Iberian specimens are presented. In addition, and whenever possible, discriminant analyses of skull variables are also performed.

Material and methods

For analyses, 157 skulls and 351 mandibles of shrews from 48 localities of the Iberian Peninsula were used (Tab. 1, Fig. 1). Specific determination was carried out taking into account morphological and morphometrical traits (Miller 1912; Hausser & Jammot 1974; Hausser et al. 1975; Nores 1979) and the geographical origin of the specimens.

The following measurements were taken: TCL: total cranium length; CBL: condylobasal length; RL: rostral length; SCL: skull case length; SBL: staphylion-basion length; UDS: length of the upper dental series; P⁴-M³: P⁴-M³ length; IOW: interorbital width; ZW: zygomatic width; SCW: skull case width; α : labial mandibular length; β : articular process length; γ : inclination of the coronoid process; δ : mandibular foramen; IAL: incisor-angle length; ML: mandibular length; AL: articular length of the mandible; ITF: length of the internal temporal fossa; LDS: length of the lower dental series; C-M₃: C-M₃ length; M₁-M₃: M₁-M₃ length; LM₃: M₃ length; CH: coronoid height. Cranial measurements, AL and CH were taken with a Mitutoyo caliper. The other variables were measured with a Reichert Mak MS or a Nikon measurescope, according to the method described by Hausser & Jammot (1974). For measurement definitions, see López-Fuster & Ventura (1987) and Gisbert et al. (1988).

To summarize the geographical size variation of the species of the *Sorex araneus-arcticus* group in the Iberian Peninsula, cluster and principal component analyses were performed by means of the NTSYS-pc programs (Rohlf 1988), using the arithmetic averages of several populations reported in previous studies (see Sans-Coma 1979; López-Fuster 1983; López-Fuster & Ventura 1987; Gisbert et al. 1988). Samples of each species used in these analyses were as follows: *S. araneus* from the Catalan Pyrenees and Andorra (see Sans-Coma 1979; López-Fuster 1983); *S. coronatus* from the Aran Valley (Lleida), Hautes Pyrénées (France), Huesca, Guipúzcoa and Navarra, Asturias, and León (see López-Fuster & Ventura 1987); *S.*

Table 1: List of the material studied. S: species (A: *S. araneus*; C: *S. coronatus*; G: *S. granarius*); N: number of skulls (Sk) and mandibles (Md); M: material from captures (Cp) or owl-pellets (Ow); Coll.: collection (BAUB: Biologia Animal, Universitat de Barcelona; UZA: Unidad de Zoología Aplicada, Madrid; IZEA: Institut de zoologie et d'écologie animale, Lausanne).

S	Locality	N		M	Coll.
		Sk	Md		
A	1 Grells, Girona	—	1	Cp	BAUB
A	2 Sant Quirze de Besora, Barcelona	1	1	Cp	BAUB
A	3 Setcases, Girona	1	1	Cp	BAUB
A	4 Queralbs, Girona	32	34	Cp	BAUB
A	5 La Molina, Girona	5	5	Cp	BAUB
A	6 Andorra	14	15	Cp	BAUB
A	7 Ainet de Besan, Lleida	—	2	Cp	BAUB
A	8 La Guingueta, Lleida	—	2	Cp	BAUB
A	9 Son del Pí, Lleida	1	1	Cp	BAUB
A	10 Sant Maurici, Lleida	—	1	Cp	BAUB
C	11 Betrén, Lleida	—	39	Ow	BAUB
C	12 Arrós, Lleida	31	—	Cp	BAUB
C	13 Jaca, Huesca	26	26	Cp	BAUB
C	14 Ruesta, Zaragoza	—	10	Ow	BAUB
C	15 Las Ilces, Santander	1	1	Cp	BAUB
C	16 Fuente Dé, Santander	2	2	Cp	BAUB
C	17 Arenas de Cabrales, Asturias	1	1	Cp	BAUB
C	18 Covadonga, Asturias	6	6	Cp	BAUB
C	19 Riberas, Asturias	5	5	Cp	BAUB
C	20 Puerto del Pontón, León	3	3	Cp	BAUB
C	21 Cuerres, Asturias	—	31	Ow	BAUB
C	22 Noreña, Asturias	—	15	Ow	BAUB
C	23 Priañes, Asturias	—	11	Ow	BAUB
C	24 Camuño, Asturias	—	9	Ow	BAUB
G	25 Grado del Pico, Segovia	—	2	Ow	UZA
G	26 Riofrío de Riaza, Segovia	—	9	Ow	UZA
G	27 Puerto de Fuenfría, Segovia	—	1	Cp	UZA
G	28 Alto de Guarramillas, Madrid	—	1	Cp	UZA
G	29 Santiago del Collado, Avila	—	1	Cp	UZA
G	30 El Barco de Avila, Avila	—	53	Ow	UZA
G	31 Candelario, Salamanca	—	13	Ow	UZA
G	32 Villasrubias, Salamanca	—	1	Ow	UZA
G	33 Hervás, Cáceres	—	3	Ow	UZA
G	34 Baños de Montemayor, Cáceres	—	1	Ow	UZA
G	35 Rascafría, Madrid	3	3	Cp	IZEA
G	36 Piedrahita, Avila	2	2	Cp	IZEA
G	37 Candelario, Salamanca	6	6	Cp	IZEA
G	38 Arines, Pontevedra	1	1	Ow	BAUB
G	39 Puebla del Caramiñal, La Coruña	—	2	Ow	BAUB
G?	40 Brandomil, La Coruña	—	3	Ow	BAUB
G	41 Pontedueme, La Coruña	7	2	Ow	BAUB
G?	42 Montfero, La Coruña	—	2	Ow	BAUB
G	43 El Ferrol, La Coruña	1	1	Cp	UZA
G	44 San Ciprián, Lugo	—	1	Cp	UZA
G	45 Villalba, Lugo	2	2	Cp	BAUB
G	46 Castro Caldelas, Orense	5	6	Ow	BAUB
G	47 Lago de la Baña, León	1	1	Cp	UZA
G?	48 Corullón, León	—	12	Ow	BAUB

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Table 2: Descriptive statistics of jaw measurements of *Sorex granarius* (GU: Guadarrama; GR: Gredos; GA: Galicia; Gisbert et al. 1988), *S. coronatus* (LE: León; AS: Asturias; NG: Navarra and Guipúzcoa; HU: Huesca; FR: Hautes Pyrénées, France; VA: Vall d'Aran; López-Fuster & Ventura 1987) and *S. araneus* (AN: Andorra; López-Fuster 1983; QU: Queralbs; Sans-Coma 1979).

		n	\bar{x}	sd	min.	max.		n	\bar{x}	sd	min.	max.	
α	GU	13	6.11	0.11	5.93	6.33	β	GU	13	1.09	0.10	0.94	1.26
	GR	73	6.30	0.18	5.80	6.59		GR	73	1.14	0.08	0.87	1.29
	GA	20	6.29	0.20	5.80	6.72		GA	20	1.15	0.08	1.00	1.29
	LE	32	6.49	0.22	5.93	6.99		LE	32	1.18	0.08	1.00	1.36
	AS	46	6.47	0.18	6.06	6.72		AS	46	1.19	0.09	1.00	1.45
	NG	24	6.60	0.11	6.46	6.85		NG	24	1.25	0.10	1.07	1.49
	HU	29	6.69	0.17	6.33	6.99		HU	29	1.24	0.09	1.13	1.49
	FR	33	6.71	0.15	6.46	6.99		FR	33	1.26	0.06	1.10	1.39
	VA	31	6.78	0.14	6.33	7.12		VA	31	1.27	0.08	1.10	1.46
	AN	20	6.91	0.20	6.59	7.25		AN	19	1.16	0.06	1.03	1.29
	QU	41	7.18	0.11	6.85	7.38		QU	41	1.18	0.09	1.03	1.36
γ	GU	13	1.93	0.16	1.68	2.26	δ	GU	13	0.14	0.11	0	0.38
	GR	73	1.87	0.14	1.51	2.29		GR	73	0.19	0.08	0	0.41
	GA	20	1.89	0.15	1.52	2.23		GA	20	0.19	0.09	0.04	0.37
	LE	32	1.88	0.21	1.45	2.45		LE	32	0.15	0.10	0	0.37
	AS	46	1.95	0.17	1.55	2.33		AS	46	0.15	0.09	0	0.34
	NG	24	1.97	0.15	1.62	2.23		NG	24	0.19	0.08	0.04	0.37
	HU	29	2.00	0.14	1.78	2.26		HU	29	0.19	0.08	0.04	0.37
	FR	33	1.97	0.18	1.62	2.23		FR	33	0.16	0.07	0.04	0.29
	VA	31	2.01	0.18	1.62	2.36		VA	31	0.10	0.09	0	0.36
	AN	19	1.88	0.11	1.71	2.07		AN	19	0.26	0.09	0.11	0.44
	QU	41	1.89	0.15	1.59	2.19		QU	41	0.33	0.09	0.15	0.57
IAL	GU	10	11.29	0.25	10.94	11.60	LDS	GU	11	6.89	0.19	6.59	7.25
	GR	60	11.42	0.29	10.94	11.99		GR	58	6.90	0.23	6.33	7.25
	GA	15	11.71	0.24	11.33	12.13		GA	15	7.18	0.18	6.85	7.38
	LE	32	12.01	0.35	11.07	12.65		LE	32	7.42	0.27	6.72	8.04
	AS	46	12.24	0.33	11.33	12.78		AS	46	7.60	0.27	6.85	8.04
	NG	24	12.57	0.26	11.99	13.05		NG	24	7.81	0.19	7.51	8.17
	HU	29	12.61	0.27	11.99	13.18		HU	29	7.74	0.25	7.25	8.37
	FR	33	12.70	0.26	12.26	13.18		FR	33	7.93	0.21	7.64	8.30
	VA	31	12.68	0.28	11.86	13.18		VA	31	7.85	0.30	6.72	8.17
	AN	16	12.81	0.22	12.52	13.18		AN	19	7.97	0.21	7.38	8.30
	QU	37	12.80	0.18	12.20	13.80		QU	40	8.07	0.15	7.60	8.30
M_1-M_3	GU	11	3.62	0.09	3.56	3.82	LM_3	GU	11	1.01	0.04	0.97	1.07
	GR	62	3.61	0.10	3.43	3.95		GR	55	1.00	0.04	0.94	1.10
	GA	16	3.70	0.10	3.56	3.82		GA	16	1.01	0.03	0.94	1.07
	LE	32	3.85	0.10	3.69	4.09		LE	32	1.05	0.04	1.00	1.13
	AS	46	3.81	0.12	3.56	4.09		AS	46	1.04	0.04	0.97	1.13
	NG	24	3.95	0.08	3.82	4.09		NG	24	1.06	0.03	1.03	1.13
	HU	29	3.90	0.10	3.69	4.09		HU	29	1.07	0.03	1.03	1.13
	FR	33	4.01	0.10	3.82	4.22		FR	33	1.08	0.03	1.03	1.13
	VA	31	3.94	0.09	3.82	4.09		VA	31	1.07	0.03	1.03	1.16
	AN	19	3.96	0.10	3.82	4.09		AN	19	1.06	0.03	1.00	1.13
	QU	41	3.96	0.07	3.82	4.09		QU	41	1.10	0.03	1.03	1.16
AL	GU	13	9.07	0.18	8.80	9.40	CH	GU	13	4.26	0.14	4.00	4.50
	GR	71	9.05	0.22	8.60	9.50		GR	73	4.23	0.14	3.90	4.60
	GA	20	9.11	0.26	8.70	9.60		GA	20	4.29	0.18	4.00	4.60
	LE	32	9.28	0.25	8.70	9.80		LE	32	4.29	0.15	4.00	4.70
	AS	46	9.38	0.25	8.80	9.80		AS	46	4.44	0.16	4.10	4.90
	NG	24	9.69	0.18	9.40	10.10		NG	24	4.63	0.11	4.40	4.90
	HU	29	9.78	0.26	9.30	10.30		HU	29	4.63	0.16	4.30	4.90
	FR	33	9.83	0.19	9.40	10.20		FR	33	4.68	0.12	4.50	5.00
	VA	31	9.93	0.17	9.50	10.20		VA	31	4.74	0.15	4.40	5.00
	AN	19	9.81	0.27	9.20	10.30		AN	18	4.64	0.14	4.40	4.90
	QU	41	10.18	0.23	9.60	10.80		QU	40	4.74	0.14	4.50	5.00

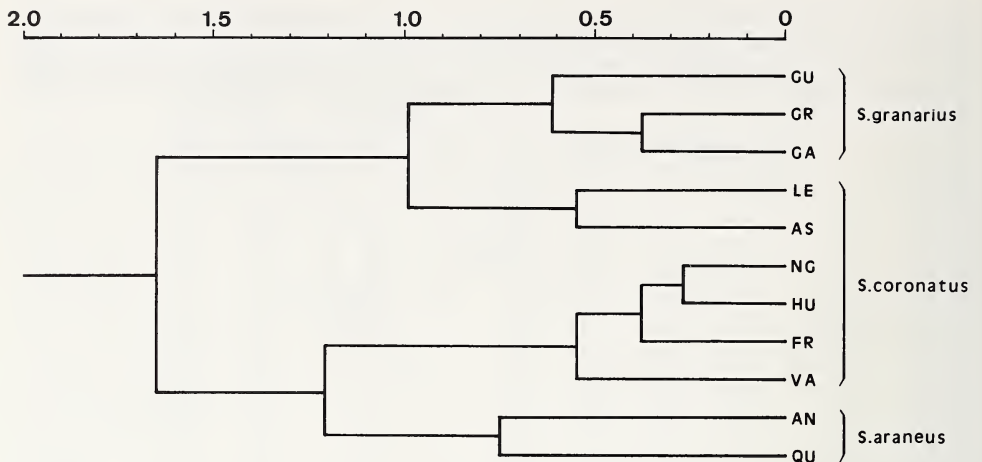


Fig. 2: Distance phenogram depicting the morphometrical relationships between samples of *S. granarius* (GU: Guadarrama; GR: Gredos; GA: Galicia), *S. coronatus* (LE: León; AS: Asturias; NG: Navarra and Guipúzcoa; HU: Huesca; FR: Hautes Pyrénées, France; VA: Vall d'Aran) and *Sorex araneus* (AN: Andorra; QU: Querals). Cophenetic correlation coefficient is 0.78.

distinguished, one corresponding to *S. araneus*, characterized by high values of the mandibular foramen, and the other containing the large size specimens of *S. coronatus*, with lower values of δ (Tab. 2). Samples of *S. granarius* were located on the left side of the diagram, because of their small size, whereas the smaller specimens of *S. coronatus* occupied an intermediate position in the diagram.

The distribution of the samples in the canonical space coincide with their geographical location and provide evidence of a clinal size variation in the Iberian Peninsula, reported in previous studies: size decrease from East to West in *S. araneus* (López-Fuster 1983) and *S. coronatus* (Nores 1979; López-Fuster & Ventura 1987), and a slight size increase from South to North in *S. granarius* (Gisbert et al. 1988). This clinal variation, which is especially notable in *S. coronatus*, determines that its metrical values overlap substantially with those of *S. araneus* in the East and *S. granarius* in the West (Tab. 2). This hinders the specific determination based on univariate statistical analyses in or near sympatric areas. In an attempt to solve this problem, discriminant analyses of mandible and skull parameters were carried out. As for the mandible, the discriminant analysis between *S. araneus* and *S. coronatus* was performed with specimens from localities 1–10 and 13–14, respectively (Tab. 1). The function obtained included five variables and classified 96.77 % of the individuals correctly (Tab. 4), with three specimens wrongly classified from Andorra. To assess its efficiency, the function was applied to a sample of *S. coronatus* from Betrán (locality 11, Tab. 1), and 96.15 % of the cases were classified correctly. Except for LDS, the variables selected in our function coincided with those of Hausser & Jammot (1974), calculated for central-European animals. However, when their function was applied to the mandibles from Betrán, only 70.49 % of the cases were

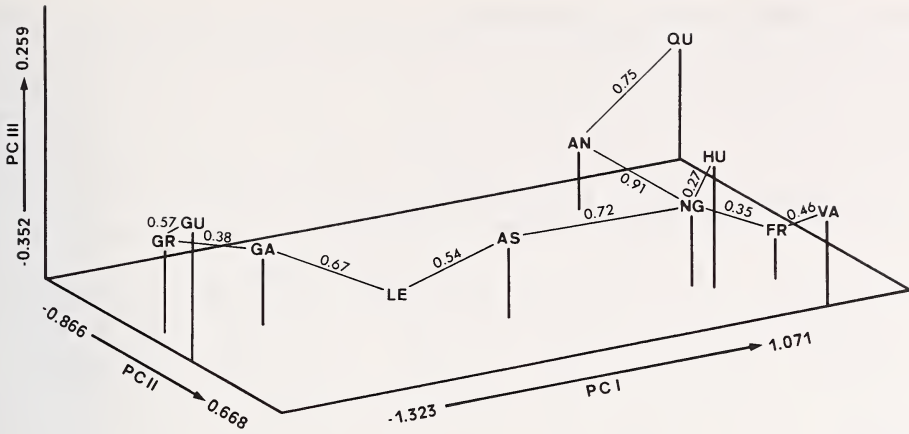


Fig. 3: Projection of the first three axes from principal component analysis of mandible characters and minimum spanning tree showing distances between nearest neighbours. (*S. granarius*: GU: Guadarrama; GR: Gredos; GA: Galicia; *S. coronatus*: LE: León; AS: Asturias; NG: Navarra and Guipúzcoa; HU: Huesca; FR: Hautes Pyrénées, France; VA: Vall d’Aran; *S. araneus*: AN: Andorra; QU: Qeralbs).

Table 3: Character loadings for the three components of the principal components analysis.

Variable	I	II	III
α	0.920	-0.351	0.008
β	0.764	0.553	-0.175
γ	0.460	0.823	0.317
δ	0.351	-0.890	0.173
IAL	0.984	-0.011	-0.088
LDS	0.983	-0.063	-0.098
M_1 - M_3	0.963	0.046	-0.224
LM_3	0.955	-0.115	0.017
AL	0.979	-0.093	0.142
HC	0.973	0.064	0.168

well classified. The important geographical variation of the *araneus* group species over their distribution area (Loch 1977; Hausser 1984) recommends the use of our function for the Iberian specimens, even though it includes one more variable than the formula of Hausser & Jammot (1974).

It has been demonstrated that jaw measurements are more appropriate than skull measurements to analyse morphometrical relationships between shrews (e.g. Hausser & Jammot 1974). However, a discriminant analysis on skull parameters between *S. araneus* and *S. coronatus* was performed, in order to provide supplementary information about the morphometrical differences between these two species in Spain. In spite of the restriction that the function can have for owl-pellet material, it can be easier to apply to captured animals, especially when mandibular variables are dif-

Table 4: Results of the discriminant analyses.

<i>Sorex araneus</i> vs. <i>Sorex coronatus</i>				
Mandible				
Discriminant function:				
$d1 = 3.9698 \alpha - 10.1922 \beta - 3.7647 \gamma + 5.9951 \delta + 1.9362 \text{LDS} - 25.2155$				
Discriminant value: <i>S. araneus</i> > -0.7006 > <i>S. coronatus</i>				
Actual group	N	Predicted group		% Correct
		<i>S. araneus</i>	<i>S. coronatus</i>	
<i>S. araneus</i>	61	58	3	95.10
<i>S. coronatus</i>	32	0	32	100.00
Total	93	58	35	96.77
Skull				
Discriminant function:				
$d2 = -1.6867 \text{CBL} + 2.1048 \text{RL} + 4.5365 \text{SCL} - 6.3072 \text{ZW} + 0.1764$				
Discriminant value: <i>S. araneus</i> > 0.1255 > <i>S. coronatus</i>				
Actual group	N	Predicted group		% Correct
		<i>S. araneus</i>	<i>S. coronatus</i>	
<i>S. araneus</i>	35	34	1	97.10
<i>S. coronatus</i>	36	2	34	94.40
Total	71	36	35	95.77
<i>Sorex coronatus</i> vs. <i>Sorex granarius</i>				
Mandible				
Discriminant function:				
$d3 = 0.8181 \text{ML} + 3.6415 \text{LDS} + 2.3643 \text{CH} - 44.4485$				
Discriminant value: <i>S. coronatus</i> > 0.2959 > <i>S. granarius</i>				
Actual group	N	Predicted group		% Correct
		<i>S. granarius</i>	<i>S. coronatus</i>	
<i>S. granarius</i>	63	62	1	98.40
<i>S. coronatus</i>	45	3	42	93.30
Total	108	65	43	96.30

ficult to measure. The analysis was performed with specimens from localities 2–6, 9 and 12–13, respectively (Tab. 1), and it furnished a function based on four variables, which classified 95.77 % of the cases correctly (Tab. 4). Three specimens were incorrectly classified, one *S. araneus* from Andorra and two *S. coronatus* from Jaca (Huesca).

In the case of *S. coronatus* and *S. granarius* the discriminant analysis on mandible measurements was carried out with specimens from localities 21–24 and 25–34, respectively (Tab. 1), and it furnished a function with three variables and with 96.30 % of correct classification (Tab. 4). Three specimens of *S. coronatus* from

Asturias (two from Noreña and one from Camuño) and one of *S. granarius* from Gredos (El Barco de Avila) were classified incorrectly. This function was applied to morphologically, geographically or even cytologically determined specimens from localities 15–20, 35–37 (Tab. 1), and gave 100 % of correct classification. Subsequently, the function was also applied to those specimens of doubtful specific determination according to their geographical origin (localities 38–48, Tab. 1). In this case, of the 17 animals from Galicia initially assigned to *S. granarius*, four (two from Montfero and two from Brandomil, La Coruña) were classified as *S. coronatus*. Likewise, 7 out of 12 presumed *S. coronatus* from Corullón (León) were determined by the function as *S. granarius*. These results can be attributed to two main causes. On the one hand, the clinal size variation observed in both species determines that in the Northwest of the Iberian Peninsula specific discrimination by means of multivariate analysis on metrical traits does not attain the degree of efficiency that is obtained when animals from allopatric areas are considered. Indeed, it has been reported that the variation of the mandibular morphometry of the species analysed is at first a function of eco-geographical conditions (Hausser et al. 1985). Since these species share the same ecological niche (Hausser 1984), they converge to a similar size in the parapatric areas. On the other hand, although the syntopy between two species of the *Sorex araneus-arcticus* group is rare (Hausser 1978; Graf et al. 1979), it could explain the presence of *S. coronatus* and *S. granarius* in the samples of Corullón and Brandomil. Similar results have been reported in other localities from the Iberian Peninsula, such as Sedano (Niethammer 1956; Hausser 1984) and Cascajares (Brunet-Lecomte & Delibes 1988), in Burgos. Thus, it cannot be ruled out that the overlapping area of *S. coronatus* and *S. granarius* is larger than generally accepted. Our results about the presence of both species in León confirm the previous findings of Brunet-Lecomte & Delibes (1988), according to which *S. granarius* spreads further from western León to the East. Moreover, we suggest that *S. coronatus* can also have a larger distribution area, extending to the northwestern coast of Galicia. According to the data about the comparative ecology of the *Sorex araneus* complex (Hausser 1978, 1984; Hausser et al. 1985), in this extensive overlapping area *S. granarius* and *S. coronatus* must be mostly parapatric and mutually exclusive. This mutual exclusion, which is mainly a sharp altitudinal one in the mountainous areas between *S. coronatus* and *S. araneus*, remains to be analysed.

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Dra. M. J. López-Fuster, Dr. Jacint Ventura, Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Avinguda Diagonal, 645, 08028-Barcelona, Spain.

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