The Sicilian (Crocidura sicula) and the Canary (C. canariensis) shrew (Mammalia, Soricidae): Peripheral isolate formation and geographic variation

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The Sicilian (*Crocidura sicula*) and the Canary (*C. canariensis*) shrew (Mammalia, Soricidae): peripheral isolate formation and geographic variation

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ABSTRACT

The skull and mandible morphometrics of two insular and endemic taxa (*C. sicula* and *C. canariensis*) from the Sicilian and Canary archipelagos, both having exactly the same karyotype were analysed by principal component and canonical variate analyses and related multivariate techniques. Information available in the literature was also employed to obtain a better approach to the systematics relationships in this taxon. Specimens of *C. suaveolens*, *C. leucodon*, *C. whitakeri* and *C. russula* from the Mediterranean, and *C. esuae* from the Pleistocene of Spinagallo (Sicily) were used as references. The results of multivariate analyses of the metric and non-metric characters of the skull and mandible, coupled with data from the biochemical and cytotaxonomic literature, have provided unanimous results pointing to the marked phenetic similarity of the *C. sicula* and *C. canariensis* taxa, that are ascribable to the same monophyletic group. On paleobiogeographic grounds, it is suggested that both taxa are two relict peripheral isolates, so dating today's disjointed distribution back to a colonization of the two archipelagos by a Maghrebi ancestral taxon, related to the *C. esuae* form, living in the Middle-Upper Pleistocene, and today probably extinct. In particular, the *C. canariensis* populations are morphologically very close to those of the smaller islands around Sicily (Marettimo, Gozo, Ustica), which have been isolated from Sicily for a long time; this could be explained by the similar adaptive responses on the islands and be caused by the Centrifugal Speciation Model. These findings are considered sufficient to guarantee conspecificity between *C. sicula* and *C. canariensis* and to place the latter taxonomically as a subspecies of *C. sicula*. A recent typological classification of *C. sicula* is also discussed and refuted.

INTRODUCTION

Recent studies (Vogel, 1988; Vogel et al., 1989; Sarà et al., 1990) have 'upset' previous interpretations of the systematics of the taxon *Crocidura*, Wagler, 1832, in the western Palearctic. The presence has emerged of a particular taxon *Crocidura sicula* which is a Sicilian-Maltese endemism, strictly insular and a probable relict from the Pleistocene. This taxon seems to be closely related to *C. canariensis*, also insular and endemic, recently discovered in the Canaries (Hutterer et al., 1987). Both have exactly the same karyotype (2n = 36, NF = 56, Nfa = 52), which is inexplicable in the light of various banding techniques or of chromosomic polymorphisms. Allozyme electrophoresis shows a genetic distance (D = 0.038) considered to be an index of conspecificity between mammals (Maddalena, 1990). However, the geographic variation of their morphometric characters does not seem to have been studied, with the exception of the lapidary affirmation (Molina & Hutterer, 1989): «New morphological studies of *C. sicula*, *C. canariensis* and *C. osorio* by one of us (R.H.) show that all three species are clearly separable on qualitative and quantitative characters».

Finally Hutterer (1991), backed by an otherwise acceptable framework of hypotheses on the relationships between Pleistocene and recent forms from the Mediterranean area, proposed a taxonomic classification of *C. sicula*, divided into four insular subspecies (one of which is diachronic); this in my opinion is typological and misleading, and moreover does not deal with, and therefore takes for granted, the heterospecificity of *C. canariensis*.

Rivers of ink have run in attempts to use and abuse the notion of subspecies in systematics. Subspecies is generally considered a segment of a continuum between populations within the taxon «species». On several occasions it has been highlighted how the spatio-temporal dimensions and confines of this segment depend greatly on the subjective criteria of the specialist's analysis and technique. The subspecies is tendentially considered a 'category' in modern definitions of species (Ghiselin, 1974) or as a class of objects, thus negating any objectively valid theoretical significance and conferring on it only practical utility (Mayr, 1970; Storer, 1982; Minelli, 1991).

The tendency today in evolutionary-systematics is to study a taxon through geographical variation and phylogenesis, to reconstruct its model of variation and polymorphism, the presence of discontinuity and the evolutionary processes which determine it, but certainly not to enumerate subspecies. Thus, the subspecies is not generally accorded the dignity of an evolutionary unit, and tends to be recognized as a formal taxonomic rank – i.e., geographic race – only in cases of (morphologically and/or genetically) polymorphic populations with separate areas of distribution from those of other conspecific populations. Even in these cases different formal

intraspecific levels (i.e., emergent interspecies, semispecies etc.) are proposed. The typological utilization of species and subspecies concepts, and the confusion of the two species notions (as category and taxon) seems recurring. It is appropriate to cite Brignoli (1988) who exhaustively confronted such problems starting with the example of the taxonomic status of the spider genus *Loxosceles*. His conclusions «...the *Loxosceles* species can be identified (within the order) by the places indicated on the map, by their genital morphology, by the relationship between their limbs and by good luck!» seem to be pertinent to this new contribution to the systematics of *Crocidura sicula* Miller, 1901.

Starting with the practical problem of how to classify *C. sicula* and *C. canariensis* taxonomically, this work will try to refute Hutterer's (1991) classification by further examining the geographic variation of *C. sicula* (cf. Sarà *et al.*, 1990) together with available literature information, so as to establish a better approach to the systematics relationships in this taxon.

MATERIALS AND METHODS

To analyse the biometric variation of *Crocidura* populations and the morphometric relationships between *C. sicula* and *C. canariensis*, material from the theriological collections of the Zoological Museum of the University of Palermo (MZPA, Palermo, Italy), the Institute of Zoology and Animal Ecology of the University of Lausanne (IZEA, Lausanne, Switzerland) and of the Museum of Natural Sciences, Tenerife (MNST, Santa Cruz de Tenerife, Spain) was used. The mandible and skulls were measured by a stereo-microscope provided with micrometric lenses and compared, even graphically, using diagnostic characters normally used in the literature of the biometric analysis of the *Crocidura* genus. Multivariate morphometric analyses (cf. Reyment *et al.*, 1984; Digby & Kempton, 1987) were carried out on the biometric data collected and log-transformed using the software SYN-TAX IV (Podani, 1990). The mandible and skull sample was not numerically nor by origin homogeneous, and so it had to be dealt with separately using different multivariate techniques. Table I shows the sample size of the single populations used in the multivariate analysis:

a) *metric characters of the mandible* - Four metric variables were measured: total length excluding incisor (UKL), height at the coronoid process (COH), length of molars (M1-M3), breadth of articular condylum (E), (cf. Sarà *et al.*, 1990) on 480 individuals from 15 populations. A multivariate analysis of variance (MANOVA) was carried out on mandible characters which thus led to a canonical analysis (CANVAR), so as to order the set of centroids of the 15 populations in the multivariate space of the first three canonical axes.

b) *Non-metric characters of the mandible* - 18 variables: Id = number of denticulations on the upper edge of I1; Igp = position of the groove on the medial side of I1; Igl = length of the groove; Ic = posterolingual cingulum; I2r = posterolingual ridge of I2; Pa = basal prominence on the anterior ridge of P4; Pl = lingual cusp - metaconid - of P4; Iex = posterior extension of P4; Pol = overlap of P4 over I2; MF = position of the mental foramen; M1c = length of the lingual cingulum of M1; M2c = lingual cingulum of M2; M3c = lingual cingulum of M3; M1e = postentoconid ledge of M1; M2e = postentoconid ledge of M2; M3e = postentoconid ledge of M3; M3t = talonid basin of M3; CE = elevation of the dorsal edge of the condyle relative to the line of the ventral edge of the temporalis fossa - were checked on 180 individuals from 12 populations using the method of Butler *et al.* (1989), which grades characters according to a derived-ancestor sequence. A comparison sample was sent to Prof.

TABLE I - *Origin and composition of samples used in multivariate analyses.*

Taxon	OTU	Canvar Mandible 4 metric variables	Cluster analysis Mandible 18 non-metric variables	Canvar Skull 14 metric variables	PCA Skull 14 metric variables
C. canariensis	Canaries	15	10	14	14
C. sicula	Favignana	16	10	0	3
C. sicula	Levanzo	6	4	0	0
C. sicula	Gozo	17	14	10	10
C. sicula	Marettimo	16	14	20	20
C. sicula	Ustica	12	10	13	13
C. sicula	Sicily	195	43	75	75
C. esuae	Sicily	9	13	0	1
C. leucodon	Italy	10	9	7	7
C. leucodon	Poland	4	4	4	4
C. russula	Pantelleria	0	18	0	0
C. russula	Sardinia	99	0	25	25
C. russula	Tunisia	25	0	11	11
C. russula	Morocco	15	4	15	15
C. suaveolens	Italy	20	14	14	14
C. whitakeri	Tunisia	16	13	0	12
C. whitakeri	Morocco	5	0	0	5
		480	180	208	229

Canvar, Canonical Variate Analysis; PCA, Principal Component Analysis.

Butler for standardization. Two synplesiomorphic (Igp, Igl), and two other non-objectively standardizable variables (I2r, Iex) were eliminated. The 14 remaining synapomorphic variables were processed by an agglomerative clustering method using the Gower coefficient for non-metric data. This method generated a hierarchical classification minimizing the inter-cluster distances of the 12 populations by way of a specific algorithm (see Podani, 1990).

c) *Metric characters of the skull* - 14 variables were measured: zygomatic width (LZ), palate length (PL), upper tooth-row length (UTL), incisor length (IL) of the second (aA2) and third (aA3) unicuspid, external buccal length (a1P4) and internal palatal length of the fourth premolar (a2P4), maximum width of the first (bM1), second (bM2) and third (bM3) molars, the median length of the first (aM1), second (aM2) and third (aM3) molars (Rzebik-Kowalska, 1988a; Sarà & Zanca, 1992) of 229 individuals from 15 populations. To ordinate the 15 populations in multivariate space, a centered PCA was carried out in which samples from 21 locations in Sicily were grouped as follows: 1 - South-East (Pleistocene from Spinagallo), 2 - North-East (Nebrodi mountains and Aetna), 3 - South-South East (Gela plain), 4 - East-Central (Sperlinga woods), 5 - West-Central (Sicani mountains and Ficuzza woods), 6 - South-West (Belice Valley), 7 - North-West (Palermo mountains), 8 - West (Trapani Province). Increasing the number of variables diminished the number of usable specimens (due to the degree of integrity of the material from owl pellets). Thus it was possible to repeat the analysis (MANOVA, CANVAR) carried out on the metric characters of the mandible on a reduced sample of 208 individuals from 11 populations; some *C. sicula* (Favignana, Levanzo, Spinagallo fossils) and *C. whitakeri* (Morocco and Tunisia) populations were excluded. The PCA was subsequently repeated on a sub-sample of 130 individuals from the 8 groups of locations in Sicily and 4 surrounding islands (Favignana, Marettimo, Gozo, Ustica), and the results were used to construct a Minimum-length Spanning Tree (MST). In multivariate practice, an MST is used to detect the distortion of pairs of points which look close together in a plot but are far apart if other dimensions are taken into account. The MST made it possible to show the morphometric relationships among the eight Sicilian locations and the four islands.

d) *Non-metric characters of the skull* - Hutterer *et al.* (1987) propose six diagnostic characters for *C. canariensis* vs *C. russula*; five of these from 172 individuals from 9 populations were checked to verify their diagnostic importance compared to *C. sicula*.

RESULTS

Morphometrics

Figure 1 shows the chart of the 15 OTU centroids, ordered by the metric characters of the mandible in the space determined from the first three canonical variables. *C. whitakeri, C. leucodon, C. suaveolens* and the Pleistocenic *C. esuae* are separate from the other populations. *C. russula* is in the same portion of multivariate space as *C. sicula* and *C. canariensis* showing a noteworthy geographic variation (Sarà & Zanca, 1992; Sarà & Vogel, unpublished data). The 36 chromosome population pool divides into two subgroups: i) small islands around Sicily (Levanzo, Favignana, Ustica, Gozo, Marettimo) plus the Canaries; ii) Sicily.

Figure 2 shows the hierarchical classification obtained from the graded non-metric variables of the mandible which groups the 12 populations according to common derived characters. Also, due to this approach, the 36 chromosome pool of OTUs figures in only one cluster
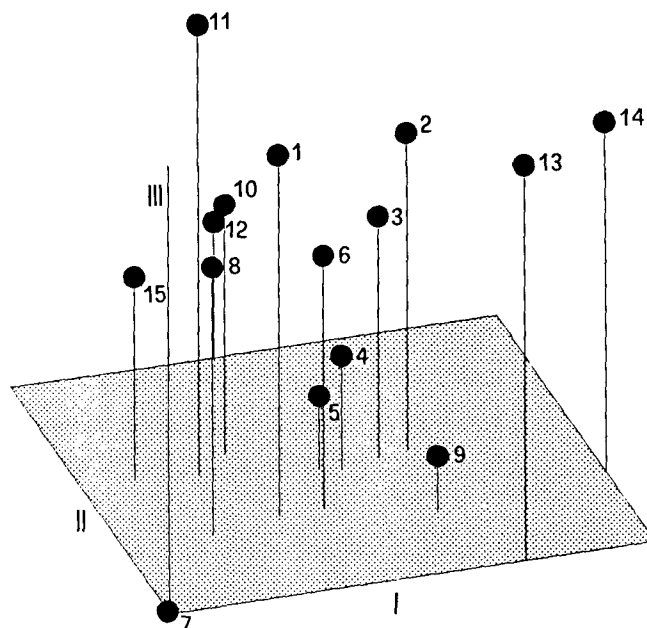

Fig. 1 - Canonical analysis results for the mandible. All the con-specific populations *C. russula* (3), *C. whitakeri* (2) and *C. sicula* (6) vary geographically and are interseparated on the I-III canonical axes. The highest phenetic variability range is among the insular populations of *C. sicula*. There is a phenetic convergence between allopatric *C. russula* and the *C. sicula* of Sicily (in fact long confused with *C. russula*). The Pleistocene *C. esuae* is distinct from the *C. sicula* populations, while *C. canariensis* lies within the insular variability of the latter. 1, *C. canariensis*. Canaries; 2, *C. sicula*, Favignana; 3, *C. sicula*, Levanzo; 4, *C. sicula*, Gozo; 5, *C. sicula*, Marettimo; 6, *C. sicula*, Ustica; 7, *C. leucodon*, Italy plus Poland; 8, *C. russula*, Sardinia; 9, *C. suaveolens*, Italy; 10, *C. sicula*, Sicily; 11, *C. russula*, Tunisia; 12, *C. russula*, Morocco; 13, *C. whitakeri*, Tunisia; 14, *C. whitakeri*, Morocco; 15, *C. esuae*, Spinagallo.

which then splits into three sub-groups: i) Levanzo and Favignana, islands close to Sicily, plus Ustica; these islands share a more similar grade of derived characters with Sicily and Spinagallo (ii) than the more distant Gozo, Marettimo, and Canaries (iii).

Figure 3 shows the chart of 15 OTUs on the first two principal components obtained from the metric variables of the skull. The first axis (size component according to Jolicoeur & Mosimann, 1960) explains the main percentage of total variance, and orders the populations in a gradient of diminishing size from right to left. Nearly all the variables concur on the formation of the first axis (Table II), the main contribution in terms of variance being made, however, by the zygomatic width (LZ) and palate length (PL). The populations are further distinguished on the second axis by the decreasing values of some dental variables: the length of the third unicuspid (aA3), the medial and buccal length of the premolar (a1P4, a2P4), the maximum width of the first molar (bM1), and on the third axis the width (bM3) and length (aM3) of the third molar. Figure 4 shows the order in space of the first three canonical variables of the set reduced to 11 OTUs. The ordering in multivariate space
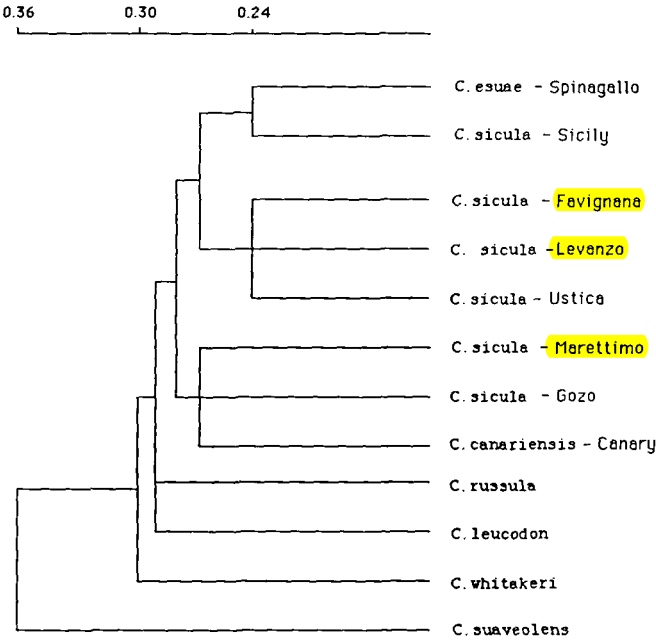
Fig. 2 - Hierarchical classification obtained by using the graded non-metric characters derived from the mandible. The insular populations of *C. sicula* subdivide (D = 0.264) into two groups: the first, formed by the islands furthest from Sicily (Marettimo, Gozo and the Canaries), being the first and oldest colonization. The second (D = 0.246) consists of other islands (Favignana, Levanzo) isolated or probably colonized (Ustica) more recently from the mother island (Sicily).

TABLE II - *Variance percentage of variables accounted for by each component. The underlined values show the highest contribution for each axis. All the correlations of the underlined variables to the axes are positive, except a1P4 and bM1 to the F2, whose correlation is negative.*

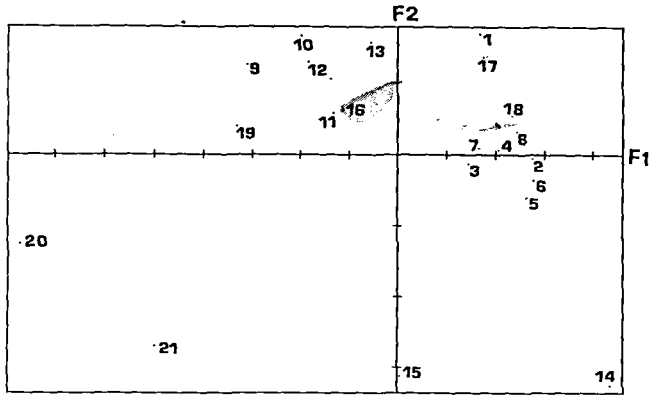| Variable	F1	F2	F3
LZ	84.546	5.034	1.783
LP	91.149	0.004	4.420
UTL	78.938	1.105	14.117
LI	60.514	19.634	0.445
aA2	61.494	10.366	0.522
aA3	63.956	32.809	0.090
a1P4	59.372	28.614	0.561
a2P4	23.891	50.296	3.763
aM1	74.624	13.789	0.288
aM2	75.406	6.497	0.221
aM3	49.189	0.668	44.237
bM1	62.035	26.570	1.717
bM2	77.031	12.118	2.462
bM3	58.823	1.129	27.336

Fig. 3 - PCA results of the metric variables of the skull. The ordination derived from the first two components (F1 = 65.4% of total variance and F2 = 15.8%) suggests a grouping of the 21 populations congruent with the results from other analyses (e.g. karyotype). The taxa with different karyotypes (shaded areas) are morphologically distinct, but the populations (2-8) living in Sicily are also distinct from the pool of the small islands, in whose variability lies *C. canariensis* (9-13). *C. esuae* is separate from its descendents *C. sicula*; finally, the convergence should be noted between the populations of *C. sicula* and *C. russula* already revealed by the mandible analysis. 1, *C. esuae*, Spinagallo; 2 - 8, *C. sicula*, Sicily; 9, *C. sicula*, Favignana; 10, *C. sicula*, Gozo; 12, *C. sicula*, Ustica; 13, *C. canariensis*, Canaries; 14, *C. leucodon*, Italy; 15, *C. leucodon*, Poland; 16, *C. russula*, Morocco; 17, *C. russula*, Sardinia; 18, *C. russula*, Tunisia; 19, *C. suaveolens*, Italy; 20, *C. whitakeri*, Morocco; 21, *C. whitakeri*, Tunisia.

of the metric characters of the skull carried out by PCA is analogous ot that worked out with CANVAR, both reflecting the same spatial relationships between the OUTs obtained for the metric characters of the mandible (Fig. 1).

Table III shows the percentage presence of the state of the two non-metric skull characters, the pterygoid fossa and the foramina incisiva in the populations of the individual islands in the Canary and Sicily archipelagos. The two characters vary between the populations of the various islands and do not seem to be diagnostic, and therefore do not serve to identify or distinguish the *C. sicula* and *C. canariensis* populations. As regards the other characters reported by Hutterer *et al.*, (1987), a consistent difference can only be noted in the form of the basisphenoid bridge (the «baguette osseuse» of the French authors) which is flat and in the form of an X in the *C. sicula* populations, while it is raised and with a different design in *C. canariensis*.

The multivariate analysis results affirm the great phenetic similarity of the skull and mandible of the 36 chromosome OTUs. *C. canariensis* is associated in multivariate space with the micro-insular populations of *C. sicula* (Gozo, Marettimo) which have been isolated longer from the populations of the mother island; this despite the type of variable (metric *vs* non-metric), analysis (PCA or CANVAR ordination *vs* hierarchical classification) or sample (skull *vs* mandible). The Pleistocene specimens of Spinagallo are biometrically distinct from recent *C. sicula* populations, but do not show a pronounced mandible plesiomorphy with respect to those of Sicily. Finally, the constant morphometric convergence should be noted of the *C.*

TABLE III - *The percent presence of the two skull character states in the insular populations* C. sicula *and* C. canariensis. *Their high variability invalidates their use as diagnostic characters.*

| Taxon	OTU	Foramina incisiva			Pterygoid fossa		
		% presence of character state A	% presence of character state B	*n*	% presence of character state A	% presence of character state B	*n*
C. sicula	Sicily	81.2	18.2	77	27.6	72.4	76
C. sicula	Favignana	41.7	58.3	12	0.0	100.0	12
C. sicula	Levanzo	66.3	33.3	3	0.0	100.0	3
C. sicula	Marettimo	95.0	5.0	20	15.0	85.0	20
C. sicula	Ustica	28.6	71.4	14	92.8	7.1	14
C. sicula	Gozo	92.3	7.7	13	100.0	0.0	13
C. canariensis	Fuerteventura	12.5	87.5	14	0.0	100.0	15
C. canariensis	Lanzarote	36.4	63.6	11	9.0	91.0	11
C. canariensis	Montaña Clara	80.0	20.0	5	0.0	100.0	8
				169			172

n, number of specimens.
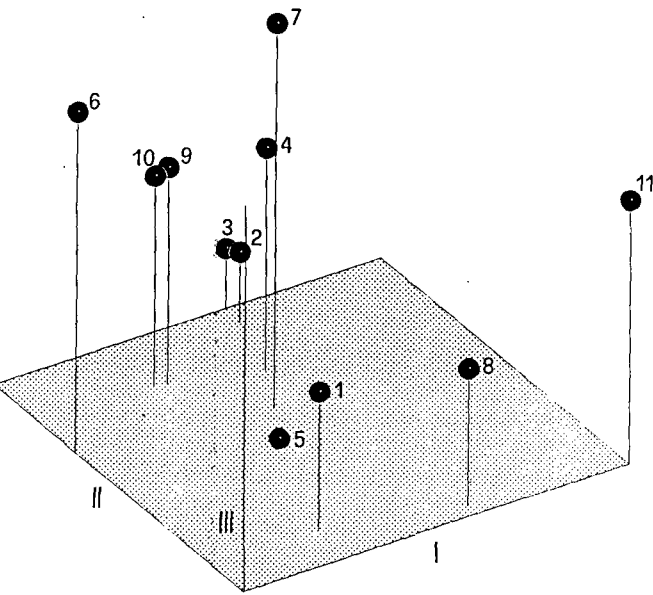
Fig. 4 - Canonical analyses of the skull variables carried out on a smaller number of OTUs indicate the same relationships in multivariate space of the first three canonical axes (I-III) already noted in the PCA (Fig. 3). 1, *C. sicula*, Sicily, 2, *C. sicula*, Marettimo; 3, *C. sicula*, Gozo; 4, *C. sicula*, Ustica; 5, *C. canariensis*, Canaries; 6, *C. leucodon*, Italy; 7, *C. leucodon*, Poland; 8, *C. russula*, Morocco; 9, *C. russula*, Sardinia; 10, *C. russula*, Tunisia; 11, *C. suaveolens*, Italy.

russula populations toward the allopatric populations of *C. sicula-canariensis*.

In the case of *C. sicula*, it was possible to analyse the skull intrapopulation variability comparing seven existing geographical OTUs of the mother island with those of four small islands and with the Pleistocene sample. Figure 5 shows the MST constructed from the PCA
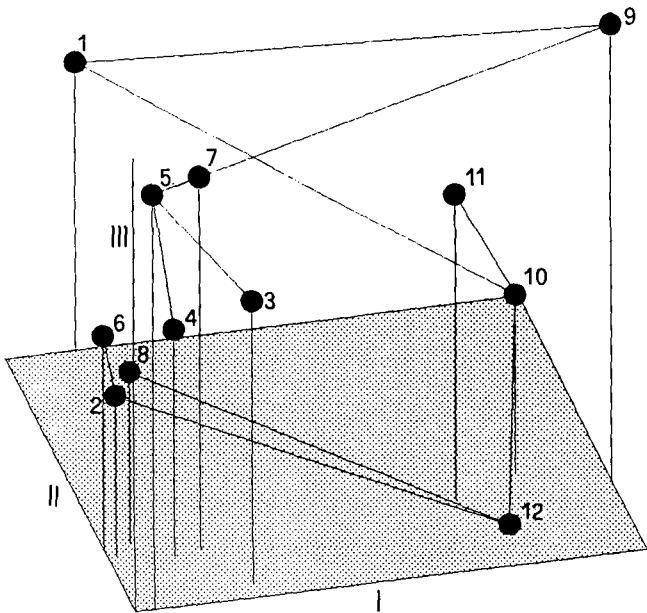
Fig. 5 - The Minimum Spanning Tree connections among *C. sicula* populations. The Pleistocene *C. esuae* is separated from the modern form just as the small islands are separated from Sicily. During the Middle-Pleistocene, Roman regression (250 000 - 170 000 years B.P.) *C. esuae* probably spread towards the north, south and west of the island and originated the first nucleus of the Egadi and Maltese islands. A secondary contact between Sicily and Favignana probably took place during during the Wurmian glaciation (Post-Tyrrhenian regression) or later by human passive introduction. Shrews must have come in two different steps from western and north-eastern Sicily to the volcanic island of Ustica. 1, South-East (Pleistocene from Spinagallo); 2, North-East (Nebrodi mountains and Aetna); 3, South-South East (Gela plain); 4, East-Central (Sperlinga woods); 5, West-Central (Sicani mountains and Ficuzza woods); 6, South-West (Belice Valley); 7, North-West (Palermo mountains); 8, West (Trapani Province); 9, Favignana; 10, Marettimo; 11, Gozo; 12, Ustica.

variance-covariance matrix which, related to the geological events of the region, allows us to hypothesize some of the stages of morphological evolution which took place between the Pleistocene populations and the existing ones. The Spinagallo sample is positioned far apart from the other locations and shows connections with some small islands (Marettimo and Favignana). The MST sequence suggests a colonization by way of the route which, during Pleistocene, joined Sicily to these islands, and would affirm that different populations were responsible at different times for the colonization of the small islands around Sicily. Favignana shrews also appear morphometrically related to the West-Central OTU and without any contact with Marettimo, i.e., at least a second invasion from Sicily occurred later than the Pleistocene, whereas the Ustica shrews must have come both from North-Eastern and Western populations.

Paleobiogeography

The proposed (Maddalena, 1990) monophyletic origin of *C. canariensis* and *C. sicula* was investigated on a paleontological and biogeographical basis, and it would thus seem opportune to summarize the main data available.

Crocidura canariensis is distributed exclusively on the eastern islands and islets of the Canary archipelago (Lanzarote, Fuerteventura, Lobos, Montaña Clara). The first two were once part of the African Continental Mass and are denominated 'continental' as opposed to the Western 'oceanics' (Rothe & Schimcke, 1968: 78, 237 *apud* Kunkel, 1976).

The Canaries flora and fauna, both recent and Tertiary, generally originate from West Africa and the Iberian peninsula. While an African origin for *C. canariensis* seems certain, it is interesting to note that there exist endemic taxa (Umbelliferae, Labiatae, Clethraceae) with a detached Macaronesic-East Mediterranean distribution which attests to a dispersion of North Mediterranean elements in South-West Africa and as far as Macaronesia before the drying of the Sahara in the Holocene (Davis & Hedge, 1971: 236-238; *apud* Kunkel, 1976). The oldest *C. canariensis* known is from the Upper Pleistocene (Fuerteventura), and aged at least 30 000 years (Michaux *et al.*, 1991); later it is normally found in Holocene deposits (5 000 - 3 000 years B.P.) associated with the modern (*Apodemus sylvaticus*) and endemic (*Malpaisomys insularis*) murid fauna (Hutterer *et al.*, 1988).

Crocidura sicula is found in Sicily, in the Egadi archipelago (Marettimo, Levanzo, Favignana), and in Gozo and Ustica, and is considered extinct in Malta and Lampedusa.

These islands, excluding Ustica which is of volcanic origin, formed a single insular mass during the Rissian glaciation (Roman regression; 250 000 - 170 000 years B.P.), from which the Maltese islands were the first to separate, followed by the Egadis. Of these, Marettimo was the first to separate during the Quaternary, and

therefore has been isolated longer, which is confirmed by zoogeographic analysis (Massa, 1974).

During the Pleistocene, in deposits both from Malta (Ghar el Salaam) and Sicily (Spinagallo) there was a form named *C. esui* (Kotsakis, 1986), amended to *C. sicula esuae* by Hutterer (1991). The presumed age of the taxon *esuae* is however much older than that reported previously (59 000 - 70 000 years); in fact, by employing the method of isoleucine racemization (Bada *et al.*, 1991), the fauna of Spinagallo has been dated back to the Middle Pleistocene (455 000 ± 90 000 years B.P.). The presence of *C. esuae*, the Pleistocene ancestor of *C. sicula* (Kotsakis, 1986; Hutterer, 1991) is therefore much earlier and not a contemporary of the fossil forms of *C. canariensis*. Furthermore, it is nearly contemporary with the Milazziano (800 000 - 500 000 years B.P.). On the other hand, until the Milazziano, Sicily was divided into two insular stumps, of which the southern (Iblea island) was probably connected to the Maghreb (La Greca, 1961).

Accepting this reconstruction, and above all the data of Bada *et al.*, (1991), and the Milazziano connection between the Iblea island and the Maghreb, it is possible to date today's disjointed distribution of the taxon *sicula-canariensis* back to a colonization of the two archipelagos by an ancestral taxon living in the Middle-Upper Pleistocene.

During the Middle Pleistocene, at the same time as the Spinagallo fauna, there could have existed in North Africa a taxon whose range extended as far as the Iblea island (where Spinagallo is situated); such a taxon must then have colonized part of the Canary archipelago. (The colonization would have had to be at a later stage, given the paleontological data available, even though further research could backdate the presence of *canariensis*). Nothing is known of such a central Maghrebi population, of its structure or destiny; it might have become extinct or evolved[1], in any case leaving two extreme and distant isolates.

DISCUSSION

The bio-evolutionary process to substantiate such a paleogeographic reconstruction could lie in the speciation models which include the peripheral isolates (Mayr, 1963). Normally, these are made up of small

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[1] In the Plio-Pleistocene in Morocco and Algeria, *C. russula*, a large (*C.* ref. *viaria*) and two other small fossil forms *C.* ref. *marocana* (found together with *C. whitakeri*), and *C. jaegeri* were already present (Rzebik-Kowalska, 1988b). Hutterer (1991) instituted a new species *C. maghrebiana*, thus renaming *C.* ref. *viaria* of Rzebik-Kowalska (1988b) and hypothesizing a monophyletic group which includes *sicula, canariensis, tarfayaensis, whitakeri* and *maghrebiana*, but inexplicably does not account for *C. marocana*. It is probable that some of the taxa cited by Hutterer (1991) form a monophyletic group, but the phylogenetic relationships within the group should be further investigated both as regards *C. marocana* and between *C. sicula* and *C. whitakeri*.

isolated or semi-isolated populations distributed near the periphery of a large portion of the species range; generally they have quite distinct characters from the central population and for this reason are considered an important component of evolutionary divergence (Mayr, 1963; Mayr & Ashlock, 1991). It is true today, as it was in Darwin's time, that the assignation of a taxonomic rank to geographic isolates, particularly to very strongly characterized ones, tends to be arbitrary. There are literally thousands of geographic isolates which are classified as species by some authors and subspecies by others (Mayr, 1982).

As regards the potential role, and therefore the importance of temporal and/or spatial isolation in speciation, even if new species and evolutionary novelties are usually aspects of peripheral isolates, it is not true that they are exclusive to them (Mayr, 1970; Endler, 1977). It is important to remark that speciation processes and involved patterns (sympatry or allopatry) of populations are distinct and independent aspects. Each can therefore be implicated simultaneously or singularly (isolation without speciation and viceversa). Spatial and/or temporal isolation is therefore a necessary but not sufficient cause for speciation, and populations are not automatically ascribable to different species just because they are isolated by topographic barriers or have strongly disjointed distributions.

The traditional model of speciation connected with

peripheral isolates is the Peripheral Isolates Model (PIM) or the variously defined allopatric speciation models (Mayr, 1963; Bush, 1975; Wiley, 1981). Brooks & McLennan (1991) recognize three main modes of peripheral isolate formation which generate the PIM: casual colonization, alternating episodes of dispersion and isolation, and vicariant peripheral isolation. A fourth, but no less important mode, is by contraction of the species range (Frey, 1993).

Frey (1993) describes an allopatric speciation model called the Centrifugal Speciation Model (CSM) whose predictions differ from those of the PIM. The CSM assumes that the 'centre' and not the 'periphery' is the principal source of evolutionary change, the central population becoming highly derived while the peripherals remain relatively plesiomorphic and demonstrate slow rates of evolutionary change. The CSM predictions, when peripheral isolates are formed by the retraction of a species range, correspond to the situation outlined for the taxon *sicula-canariensis*. There is a slow rate of appearance of new characters in the two peripheral archipelagos which is substantiated by the results of karyotype, allozyme electrophoresis and morphometrics.

Further research in North Africa would probably confirm definitively the group's phylogenesis, identifying all the components of the clade and therefore:

a) the destiny (evolution or extinction) of the central

TABLE IV - *The ratios between the most significant skull variables valid for the taxonomic classification of* Crocidura *species*

Taxon	OTU	LP/LZ	aA2/aA3	a1P4/a2P4	bM1/aM1	bM2/aM2	bM3/aM3
C. s. sicula	Sicily	1.31	0.86	2.23	1.86	1.96	2.20
C. s. sicula	Favignana	1.30	0.85	2.27	1.86	1.84	2.06
C. s. sicula	Marettimo	1.29	0.87	2.09	1.80	1.87	2.29
C. s. sicula	Gozo	1.29	0.87	2.16	1.92	1.87	2.34
C. s. sicula	Ustica	1.28	0.79	1.98	1.86	1.92	2.21
C. s. canariensis	Canaries	1.34	0.86	2.02	1.70	1.88	2.13
C. s. canariensis	Mean	1.30	0.85	2.13	1.83	1.89	2.21
	SD*	0.02	0.03	0.11	0.07	0.04	0.10
C. leucodon	Italy	1.25	0.88	2.63	1.92	1.93	2.23
C. leucodon	Poland	1.22	0.95	2.75	2.08	1.98	2.28
C. russula	Morocco	1.31	0.83	2.19	1.80	1.87	2.28
C. russula	Sardinia	1.27	0.81	2.14	1.69	1.85	2.21
C. russula	Tunisia	1.26	0.84	2.17	1.82	1.91	2.25
C. suaveolens	Italy	1.26	0.87	2.33	1.76	1.80	1.97
C. whitakeri	Morocco	1.29	1.01	2.23	2.11	2.16	2.34
C. whitakeri	Tunisia	1.25	1.15	2.67	2.09	2.22	2.35
C. esuae	Sicily	1.25	0.88	2.06	1.80	1.81	2.17

LP, palate length; LZ, zygomatic length; aA2 and aA3, second and third unicuspid lengths; bM1, bM2, bM3, maximum width of the first, second and third molars; aM1, aM2, aM3, medial length of the first, second and third molars.
*, standard deviation.

population. It is worth remembering that the karyotype and allozyme characteristics of *tarfayaensis* and *whitakeri* are still unknown (ref. Note 1) and that in Africa (Burundi) Maddalena (1990) has found in *C. luna* a stock of 2n = 36; NF = 56 chromosomes;

b) the fossil remains of a Pleistocene Maghrebi ancestor which ought to be morphologically related to *C. esuae*.

Closely related taxa tend to be phenotypically similar to each other as a consequence of at least three different biological processes: phylogenetic niche conservationism, phylogenetic time lags and similar adaptive responses (Harvey & Pagel, 1991).

The selective forces determined by the shared insularity condition (relative simplicity of ecosystems; small physical size and area; climatic analogies between the Canary and Mediterranean islands; Kunkel, 1976) can explain the slow evolutionary rate of the taxon *sicula-canariensis*. Insularity, in this case, acts as a cohesive force balancing the genetic divergence due to isolation and different founder events and substituting the cohesive force of gene flow (cf. Case, 1978; Davis, 1983).

Sondaar (1977) suggested that the evolution of insular Pleistocene mammal fauna was clearly directed involving a strong selective pressure which was similar on different islands. Not surprisingly, the *canariensis* shrews are morphometrically similar to those of the small Sicilian islands. The 36 chromosome populations thus show similar adaptive responses (relative size reduction and related changes in shape) to similar selective pressures due to insular conditions.

CONCLUSION

After having examined the morphometric relationships and the information available for the taxonomic classification of the group *sicula-canariensis* some general conclusions can be drawn.

The best possible classification is to consider *C. canariensis* as a synonym of *C. sicula* such that the various populations of the monophyletic taxon *sicula-canariensis* are grouped together; the Canary shrew should thus be named, according to the nomenclature law of priority, *C. sicula canariensis*.

On the basis of the multivariate analysis results, without instituting a diachronic subspecies, it would be more opportune to consider *C. esuae* as a chronospecies which has been replaced by the modern *sicula*. The evolution of the *C. sicula* populations must have been due to successive geographic isolation during the Milazziano and the Quaternary glaciations, and probably also to different environmental and climatic conditions. The populations of the islands furthest from Sicily (Gozo, Marettimo and Ustica) are in fact more distant phenetically from those of the nearest islands (Levanzo and Favignana). The morphometric characters of these small islands are found in some of the Sicilian populations, for which it seems impossible to recognize the subspecific characters of *aegatensis* and *calypso* which are also not present in north-eastern and north-western Sicilian populations (Fig. 5). The external morphometric characters (size, mantle colour etc.) and some

TABLE V - *Mean and standard deviation of skull (from LZ to bM3) and mandible (from UKL to COH) variables of* C. sicula *and* C. canariensis.

	LZ	LP	UTL	LI	aA2	aA3	a1P4	a2P4	aM1	aM2	aM3	bM1	bM2	bM3	UKL	M1-M3	E	COH
Sicily	6.06	7.93	8.63	1.59	0.76	0.89	1.97	0.88	1.14	1.03	0.59	2.12	2.02	1.29	10.46	3.88	0.88	4.59
	0.18	0.24	0.22	0.08	0.05	0.05	0.06	0.06	0.05	0.04	0.04	0.09	0.07	0.07	0.29	0.15	0.08	0.16
Favignana	5.61	7.19	7.90	1.49	0.69	0.82	1.79	0.84	1.08	1.00	0.53	1.94	1.84	1.14	9.72	3.59	0.78	4.32
	0.17	0.27	0.25	0.09	0.02	0.03	0.07	0.07	0.04	0.01	0.06	0.09	0.05	0.16	0.47	0.18	0.08	0.22
Marettimo	5.72	7.40	8.44	1.47	0.74	0.84	1.83	0.88	1.08	0.99	0.51	1.94	1.85	1.17	10.05	3.74	0.93	4.37
	0.14	0.23	0.23	0.07	0.05	0.06	0.06	0.04	0.04	0.04	0.03	0.06	0.05	0.08	0.28	0.10	0.04	0.14
Levanzo	na	na	na	na	na	na	na	na	na	na	na	na	na	na	9.76	3.70	0.81	4.34
															0.18	0.09	0.07	0.18
Gozo	5.71	7.36	8.43	1.54	0.73	0.84	1.88	0.87	1.06	0.99	0.54	2.03	1.84	1.25	9.94	3.73	0.90	4.36
	0.11	0.24	0.24	0.07	0.05	0.05	0.04	0.03	0.05	0.05	0.05	0.09	0.08	0.09	0.27	0.12	0.05	0.11
Ustica	5.93	7.49	8.43	1.50	0.67	0.85	1.77	0.90	1.10	0.99	0.49	2.01	1.91	1.11	10.15	3.69	0.92	4.57
	0.17	0.25	0.11	0.06	0.04	0.05	0.05	0.04	0.03	0.02	0.08	0.06	0.05	0.05	0.38	0.10	0.06	0.14
Canaries	5.79	7.74	8.63	1.60	0.74	0.86	1.83	0.90	1.14	1.00	0.53	1.94	1.89	1.14	10.39	3.73	0.92	4.73
	0.17	0.24	0.41	0.07	0.05	0.06	0.07	0.05	0.06	0.07	0.06	0.07	0.06	0.06	0.50	0.12	0.07	0.28
Spinagallo	6.06	7.60	8.20	1.60	0.85	0.96	1.91	0.93	1.12	1.05	0.60	2.01	1.90	1.30	10.79	4.08	0.95	4.79
	0.27	0.36	na	na	na	0.07	0.06	0.12	0.03	0.04	na	0.02	0.05	na	0.15	0.10	0.08	0.14

na, not available.

non-metric characters of the skull, on which Hutterer (1991) based his classification, do not seem taxonomically useful because they vary greatly between the different island populations (Table III).

In view of these results, the subspecies proposed by Hutterer (1991) appear to be unfounded; the subdivision according to geographical origin is unfounded because, due to multivariate biometry and paleogeographic evidence, it would be more correct to speak, were it the case, of a Gozo plus Marettimo and Ustica subspecies.

The need is also noted for different complementary approaches in a thorough systematics examination of the species having the 2n = 36, NF = 56 and Nfa = 52 karyotype.

Comparative analyses are necessary for models of variation and for phenotypical and genetic correlation (Cheverud, 1988; Cheverud et al., 1989) before being able to define a particular species as a real biological entity on the basis of certain intrinsic properties (Zunino & Palestrini, 1991). One wonders, in other words, whether it is possible in the near future to work out a systematics of the group which is the (one hopes stable) result of an analysis that integrates different methodological approaches (i.e., total evidence: Kluge, 1989; but for a review of parsimony methods and consensus trees, see Minelli, 1993). The research is ongoing on insular populations of *C. sicula* (e.g. Sicily *vs* Marettimo and Ustica) and includes an analysis of both molecular (by RAPD analysis of DNA: Sarà et al., unpubl.) and ecoethological characters (by Specific Mate Recognition Systems definition) which could give unexpected results as to the levels of speciation reached by these populations.

The proposed taxonomic classification is as follows:

– *Crocidura sicula canariensis* Hutterer, Lopez-Jurado & Vogel, 1987 **status nov.** *Crocidura canariensis* Hutterer, Lopez-Jurado & Vogel, 1987: 1354 (loc. typ.: Canary Islands: Fuerteventura).

– *Crocidura esuae* Kotsakis, 1986 **status nov.** *Crocidura sicula esuae* Hutterer 1991: 246 (loc. typ.: Sicily: Spinagallo).

– *Crocidura sicula sicula* Miller, 1901 **status nov.** *Crocidura sicula aegatensis* Hutterer, 1991: 247 (loc. typ.: Egadi islands: Marettimo) and *Crocidura sicula calypso* Hutterer, 1991: 247 (loc. typ.: Maltese Islands: Gozo).

Diagnosis: a polytypical taxon of *Crocidura*, characterized by a karyotype of 2n = 36, NF = 56, Nfa = 52 and notable geographic variation. Of average size, with biometric measurements of the skull and mandible usually between those of the smallest *C. whitakeri* and *C. suaveolens* and the largest *C. russula* and *C. leucodon*. The average palate to zygomatic length ratio (1.3) is higher than for any other species. The second unicuspid is smaller than the third, as in all the other species except *C. whitakeri*, but the ratio between the second and third

unicuspid is on average lower (0.85) than in other species (0.88-0.95) except *C. russula* (0.83). The length/width ratio of the premolars and molars in the occlusal view (Table IV) is quite characteristic. Other biometrical differences in skull and mandible, which are useful for discriminating among island populations, are reported in Table V.

Distribution: *C. sicula canariensis*: Canary Islands (Lanzarote, Fuerteventura, Lobos and Montana Clara); *C. sicula sicula*: Sicily, Egadi Islands, Gozo and Ustica; extinct in Malta and Lampedusa.

REFERENCES

Bada J. L., Belluomini G., Bonfiglio L., Branca M., Burgio E., Delitala L., 1991 - Isoleucine epimerization ages of Quaternary mammals from Sicily. Il Quaternario, 4: 49-54.

Brignoli P. M., 1988 - Ragni, specie e filosofia. *In*: G. Ghiara, P. Lupurini, G. Mancino & R. Nobili (eds), Il problema biologico della specie. Collana U.Z.I., Problemi di Biologia e Storia della Natura, Mucchi, Modena, pp. 293-308.

Broocks D. R., McLennan D. A., 1991 - Phylogeny, ecology and behavior: A research program in comparative biology. University of Chicago Press, Chicago, 434 pp.

Bush G. L., 1975 - Modes of animal speciation. Ann. Rev. Ecol. Syst., 6: 339-364.

Butler P. M., Thorpe F. L. S., Greenwood M., 1989 - Interspecific reations of African Crocidurinae shrews (Mammalia: Soricidae) based on a multivariate analysis of manibular data. Zool. J. Linn. Soc., 96: 373-412.

Case T. J., 1978 - A general explanation for insular body trends in terrestrial vertebrates. Ecology, 59: 1-18.

Cheverud J. M., 1988 - A comparison of genetic and phenotypic correlations. Evolution, 42: 958-968.

Cheverud J. M., Wagner G. P., Dow M. M., 1989 - Methods for the comparative analysis of variation patterns. Syst. Zool., 38: 201-213.

Davis S. J. M., 1983 - Morphometric variation of house mice *Mus domesticus* in Britain and Faröe. J. Zool., Lond., 199: 521-534.

Digby P. G. N., Kempton R. A., 1987 - Multivariate analysis of ecological communities. Chapman & Hall, London New York, 206 pp.

Endler J. A., 1977 - Geographic variation, speciation and clines. Princeton University Press, Princeton, 246 pp.

Frey J. K., 1993 - Modes of peripheral isolate formation and speciation. Syst. Biol., 42: 373-381.

Ghiselin M. T., 1974 - A radical solution to the species problem. Syst. Zool., 23: 536-544.

Harvey P. H., Pagel M. D., 1991 - The comparative method in evolutionary biology. Oxford University Press, Oxford, 239 pp.

Hutterer R., 1991 - Variation and evolution of the Sicilian shrew: Taxonomic conclusions and description of a possibly related species from the Pleistocene of Morocco (Mammalia: Soricidae). Bonn. zool. Beitr., 42: 241-251.

Hutterer R., Lòpez-Jurado L. F., Vogel P., 1987 - The shrews of the Eastern Canary Islands: a new species (Mammalia: Soricidae). J. nat. Hist., 21: 1347-1357.

Hutterer R., Lopez-Martinez N., Michaux J., 1988 - A new rodent from Quaternary deposits of the Canary islands and its relationships withy Neogene and recent Murids of Europe and Africa. Paleovertebrata, 18: 241-262.

International Commission Zoological Nomenclature, 1985 - International Code of Zoological Nomenclature. Int. Trust Zool. Nomenclature & British Museum Nat. Hist., London, 145 pp.

Jolicoeur P., Mosimann J. E., 1960 - Size and shape variation in the Painted Turtle a principal component analysis. Growth, 24: 339-354.

Kluge A. G., 1989 - A concern for evidence and a phylogenetic hypothesis of relationships among Epichrates (Boidae, Serpentes). Syst. Zool., *38*: 7-25.

Kotsakis T., 1986 - *Crocidura esui* n. sp. (Soricidae, Insectivora) du Pléistocène de Spinagallo (Sicile orientale, Italie). Geologica Rom., *23*: 51-64.

Kunkel G., 1976 - Biogeography and ecology in the Canary Islands. W. Junk Publ., The Hague, 511 pp.

La Greca M., 1961 - Considerazioni sull'origine e la costituzione della Fauna di Sicilia. Arch. bot. biogeogr. ital., *6*: 2-23.

Maddalena T., 1990 - Systematics and biogeography of Afrotropical and Palearctic shrews of the genus *Crocidura* (Insectivora: Soricidae) an electrophoretic approach. *In*: G. Peter & R. Hutterer (eds), Vertebrates in the tropics. Museum A. Koenig, Bonn, pp. 297-308.

Massa B., 1974 - Appunti sulla biogeografia delle Isole Egadi. L'universo, *5*: 789-804.

Mayr E., 1963 - Animal species and evolution. Belknap Press of Harvard University Press, Cambridge, Massachusetts, 865 pp.

Mayr E., 1970 - Population, species and evolution. Belknap Press of Harvard University Press, Cambridge, Massachusetts, 566 pp.

Mayr E., 1982 - The growth of biological thought. Diversity evolution and inheritance. Belkap Press of Harvard University Press, Cambridge, Massachusetts, 932 pp.

Mayr E., Ashlock P. D., 1991 - Principles of systematic zoology. McGraw Hill, New York, 457 pp.

Michaux J., Hutterer R., Lopez-Martinez N., 1991 - New fossil faunas from Fuerteventura, Canary Islands: Evidence for a Pleistocene age of endemic rodents and shrews. C. R. Acad. Sci. Paris, *312*: 801-806.

Minelli A., 1991 - Introduzione alla sistematica biologica. Muzzio, Padova, 138 pp.

Minelli A., 1993 - Biological Systematics, the state of art. Chapman & Hall, New York, 387 pp.

Molina O. M., Hutterer R., 1989 - A cryptic new species of *Crocidura* from Gran Canaria and Tenerife, Canary Islands (Mammalia, Soricidae). Bonn. zool. Beitr., *40*: 85-97.

Podani J., 1990 - SYN-TAX IV, user's manual. ICEM, Trieste, 145 pp.

Reyment R. A., Blackith R. E., Campbell N. A., 1984 - Multivariate morphometrics. Academic Press, New York, 233 pp.

Rzebik-Kowalska B., 1988a - Studies on the genus *Crocidura* (Insectivora, Mammalia) in Algeria. Acta zool. Cracov., *31*: 176-192.

Rzebik-Kowalska B., 1988b - Soricidae (Mammalia, Insectivora) from the Plio-Pleistocene and Middle-Quaternary of Morocco and Algeria. Folia Quaternaria, *47*: 51-90.

Sarà M., Zanca L., 1992 - Metric discrimination and distribution of the species of *Crocidura* occurring in Tunisia. Acta Theriol., *37*: 103-116.

Sarà M., Lo Valvo M., Zanca L., 1990 - Insular variation in central Mediterranean *Crocidura* Wagler, 1832. Boll. Zool., *57*: 283-293.

Sondaar P. Y., 1977 - Insularity and its effect on mammal evolution. *In*: M. K. Hecht, P. C. Goody & B. M. Hecht (eds), Major pattern in vertebrate evolution. Plenum Publ. Co., New York, pp. 671-707.

Storer R. W., 1982 - Subspecies and the study of geographic variation. Auk, *99*: 599-601.

Vogel P., 1988 - Taxonomical and biogeographical problems in Mediterranean shrews of the genus *Crocidura* (Mammalia, Insectivora) with reference to a new karyotype from Sicily (Italy). Bull. Soc. Vaud. Sci. nat., *79*: 37-48.

Vogel P., Hutterer R., Sarà M., 1989 - The correct name, species diagnosis and distribution of the Sicilian shrew. Bonn. zool. Beitr., *40*: 243-248.

Wiley E. O., 1981 - Phylogenetics: The theory and practice of phylogenetic systematics. J. Wiley & Sons, New York, 439 pp.

Zunino M., Palestrini C., 1991 - El concepto de espece y la biogeografia. An. Biol., *17*: 85-88.