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Variation and evolution of the Sicilian shrew: Taxonomic conclusions and description of a possibly related species from the Pleistocene of Morocco (Mammalia: Soricidae)

Rainer Hutterer

Abstract. A synthesis is given on the temporal and geographical size variation of the shrew *Crocidura sicula* Miller, 1901. It is shown that Pleistocene populations from Sicily and Malta, previously regarded as a separate taxon, have evolved to the present-day populations of Sicily, the Egadi Islands, and Gozo. Due to sea level changes, probably all these islands were temporarily connected by landbridges during the Pleistocene. Subsequent geographical isolation led to the evolution of at least three morphologically distinct extant populations, two of which are named as new. In addition, a possibly related new species from the Pleistocene of Morocco is described.

Key words. Mammalia, Soricidae, *Crocidura*, Sicily, Malta, Egadi Is., Morocco, size variation, evolution, taxonomy.

Introduction

The shrews of the Mediterranean Islands have been subject of contradictory taxonomic opinions for many years. This is especially true for Sicily, the Egadi Islands, and Malta (Fig. 1). It is the merit of Vogel (1988) to have shown that the *Crocidura* species of Sicily has a particular karyotype and represents an endemic species. More recently, the same karyotype was found in shrews of Gozo, which led Vogel et al. (1989) to the conclusion that all extant populations of Sicily, Gozo, and the Egadi Islands probably form one biological species, for which the name *Crocidura sicula* Miller, 1901 is available. However, Vogel et al. (1989) and Sarà et al. (1990) found considerable morphological variation within the species. Furthermore, extinct populations of Malta and Sicily, described by Malec & Storch (1970), Storch (1970) and Kot-sakis (1986), could not yet be correctly classified. This paper gives a synthesis of variation and taxonomy of all these populations, based on fossil and recent material, and an idea of their possible evolution. The contents were presented verbally at the "XIIIème Colloque International de Mammalogie" at Banyuls-sur-Mer (France), 13—15 October 1989, and a summary was included in the proceeding of that congress (Hutterer 1990).

Material and Methods

The material studied consists of shrews preserved in alcohol, study skins and skulls, owl pellet material, and fossil remains, representing ca. 3105 fossil and 86 extant specimens. 7 principal samples were studied: 1) Malta, Ghar Dalam Cave, Last Interglacial; Storch (1974) dated this level as Early Pleistocene but Zammit Maempel (1989) as Middle Pleistocene; 2) idem, Last Glacial; 3) idem, Neolithic period (see Malec & Storch 1970, and Storch 1970, for details on the excavation); 4) Gozo, Recent (see Vogel et al. 1989); 5) Sicily, Spinagallo, Last Glacial (data

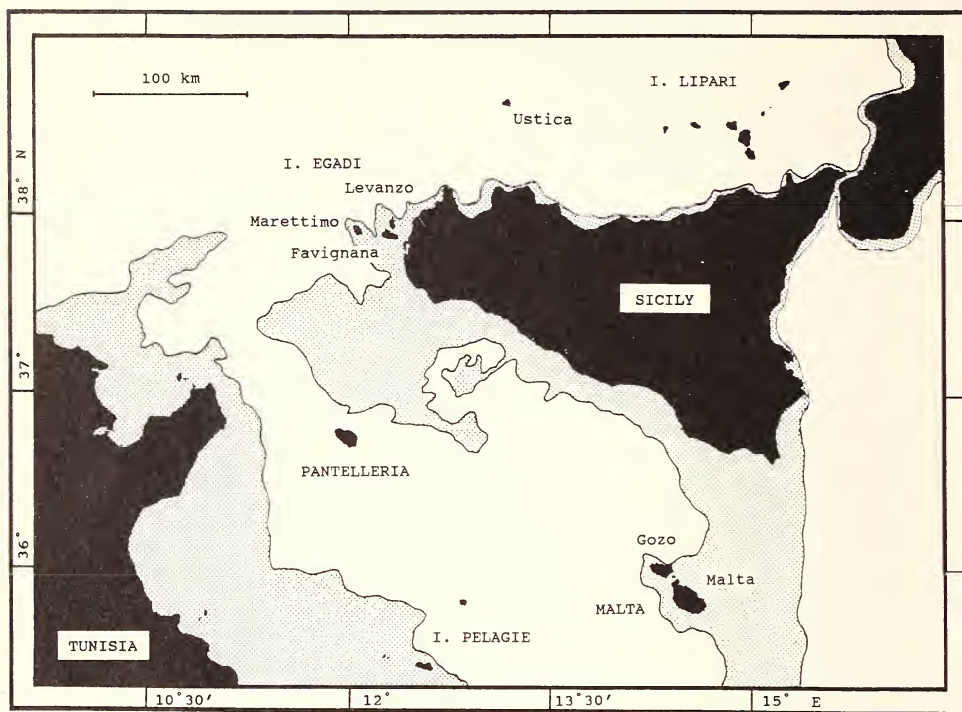


Fig. 1: Map of Sicily and surrounding archipelagos. The stippled area shows the extension of land to a depth of less than 200 meters below present sea surface.

taken from Kotsakis 1986); 6) Sicily, Recent (see Hagen 1954; Klemmer & Krampitz 1954; Vogel 1988); 7) Egadi Islands, Recent (see Krapp 1970). External measurements were taken from specimen tags; all other measurements were taken by the author with an electronic caliper and a binocular measuring system. Drawings were made with a camera lucida. Voucher specimens are deposited in the following collections: Institut de zoologie et d'écologie animale, Lausanne (IZEA), Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków (PAS), Senckenberg-Museum, Frankfurt (SMF), Centre de Paleontologie, Université Claude Bernard, Lyon (UCBL), Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK), Museo Civico di Storia Naturale, Verona (MCV), private collection of J. Niethammer, Bonn (CNB), private collection of P. J. Schembri, Malta (CSM), Ghar Dalam Cave and Museum, Malta (GDCM).

Results

Characters of extinct and extant populations

All extant populations of *C. sicula* are characterized by a sharply bicoloured body and tail. The rostrum of the skull is flat and slender, and the infra-orbital bridge is narrow. The most characteristic tooth is P^4 : its parastyle is massive and angular like a brick, and the dorsal edge of the cingulum is undulated, not straight (Vogel et al. 1989). The same characters are found in fossil specimens from Malta (Fig. 2). In principle, the form of the parastyle is similar in Pleistocene and Present populations,

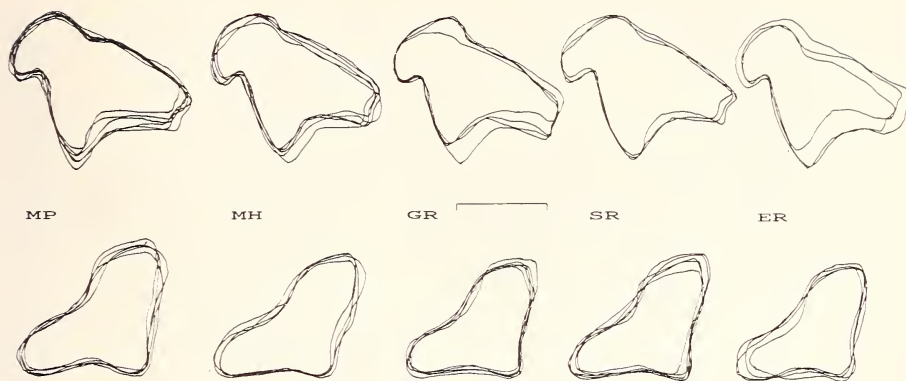


Fig. 2: Superimposed outlines of the external view of the fourth upper premolar (upper row) and the posterior view of the condylar process of the mandible (below) for samples of *Crocidura sicula* from (MP) Malta, Pleistocene, (MH) Malta, Holocene, (GR) Gozo, Recent, (SR) Sicily, Recent, and (ER) Egadi Islands, Recent. Scale is 1 mm.

however, the angular form is more constant in the extant shrews of Sicily, Egadi, and Gozo. The same applies to the condylar process of the mandible. Its shape is rather characteristic in shrews (see Hutterer 1987; Molina & Hutterer 1989); in *Crocidura sicula* it is relatively short and stout and differences between the examined populations only concern the size (Fig. 2). Other characters checked but not shown here do not indicate any fundamental difference between them, either.

The problem of the long legs

Kotsakis (1986) described remains of *Crocidura* from Upper Pleistocene (Würmian) sediments of Spinagallo, Sicily, as a new species, *Crocidura esui* (now *C. esuae*, corrected by Hutterer 1990, according to the rules of the ICZN), and he and Esu et al. (1988) also referred fossils from the Ghar Dalam Cave, Malta, to the new species. Its diagnostic character is a very long tibia, which led the author to the speculation that the species was adapted to aquatic habits. However, in a review of anatomical adaptations of shrews (Hutterer 1985) it was shown that semiaquatic species are only known in the subfamily Soricinae, not Crocidurinae. Moreover, a comparison of tibia length and skull size (Tab. 1) demonstrates that within the 7 populations both variables decreased from the Pleistocene to Present. The longer legs of the Pleistocene shrews were associated with larger body size. As there is no other character which would separate *C. esuae* from Holocene populations of *C. sicula*, I prefer to include it into the latter species.

Size changes from the Pleistocene to Present

A comparison of several cranial and skeletal measurements of the 7 populations shows a remarkable variation in size; fig. 3 gives an example. In general, the Pleistocene samples are the largest, and the Recent ones the smallest. There is always overlap between a least two samples. Maximum reduction in size is 25 %. This trend

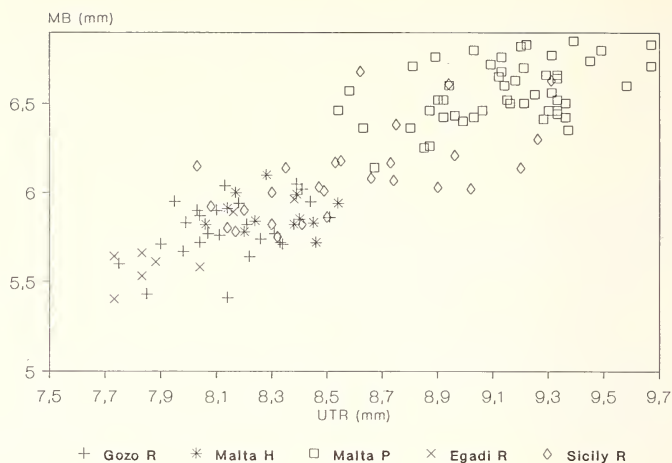


Fig. 3: A scatter diagram of upper tooththrow length (UTR) versus maxillary breadth (MB) for five populations of *Crocidura sicula*. R = Recent, H = Holocene, P = Pleistocene.

Table 1: Length of tibia (TL) and maxillary breadth (MB) in living and extinct populations of *Crocidura sicula* (sensu lato).

Locality / Period	TL \pm sd	n	MB \pm sd	n
Malta, Ghar Dalam / Early Pleistocene	16.3 \pm 0.6	200	6.6 \pm 0.2	51
Sicily, Spinagallo / Upper Pleistocene [Kotsakis 1986]	[15.1–17.6]	17	[6.0–6.2]	3
Malta, Ghar Dalam / Upper Pleistocene	14.9	1	—	—
Sicily / Recent	13.5 \pm 0.5	20	6.1 \pm 0.2	24
Malta, Ghar Dalam / Neolithic	12.5 \pm 0.8	5	5.9 \pm 0.1	12
Gozo / Recent	12.3	2	5.8 \pm 0.1	27
Egadi Is. / Recent	12.3	1	5.7 \pm 0.2	8

Table 2: Length and width of the upper third molar in living and extinct populations of *Crocidura sicula*.

Locality / Period	M ³ -Length	M ³ -Width	n
Malta, Ghar Dalam / Early Pleistocene	0.66 \pm 0.06	1.30 \pm 0.05	10
Sicily, Spinagallo / Upper Pleistocene [Kotsakis 1986]	—	[1.35]	2
Sicily / Recent	0.60 \pm 0.04	1.27 \pm 0.08	13
Malta, Ghar Dalam / Neolithic	0.56 \pm 0.04	1.22 \pm 0.03	6
Gozo / Recent	0.56 \pm 0.00	1.25 \pm 0.05	7
Egadi / Recent	0.52 \pm 0.03	1.11 \pm 0.05	8

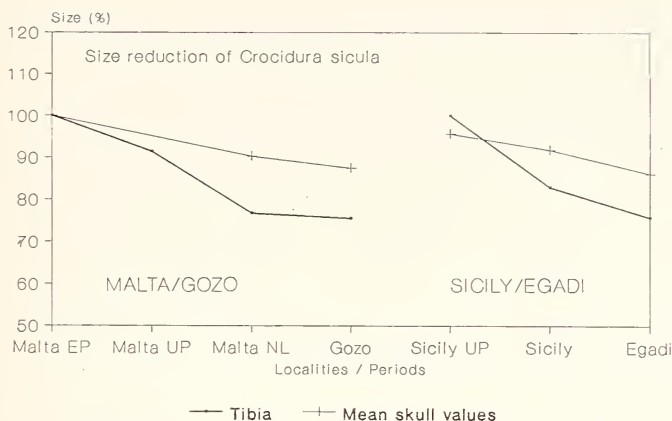


Fig. 4: Size reduction of *Crocidura sicula* from the Pleistocene to Present. Mean values for tibia length and for five skull measurements expressed as percentages of the Pleistocene population of Ghar-Dalam Cave, Malta. EP = Early Pleistocene, UP = Upper Pleistocene, NL = Neolithic, other samples from extant populations.

also counts for the tooth size, for example of M^3 (Tab. 2). A detailed comparison (Tab. 3) also shows that the extant populations differ considerably in their dimensions, Sicily being largest, and Gozo and Egadi smallest. It is also interesting that the size reduction is more pronounced for the tibia length than for the skull size (Fig. 4).

Discussion

No substantial character differences could be found between Pleistocene shrews of Malta and Sicily, previously referred to *C. esuae*, and between Holocene and Recent populations of *C. sicula*. Moreover, it was found that the tibia length varies with body size. Therefore I see no reason to distinguish different species in this group. This conclusion is also supported by the low genetical distances reported by Madalena & Vogel (1990). However, a temporal size reduction of 25 % has never been documented for a shrew and seems quite unusual. Fig. 4 also shows that the extremities suffered more size reduction than the skull, which seems logical, as there appears to be a limit for the reduction of the brain and dentition. However, it remains unknown whether a part of the tibia-lengthening was due to adaptive processes. An answer to this question would require a detailed knowledge of the landscape of Malta and Sicily during the Pleistocene. Today, large parts of these islands are covered by rocky country, a condition which would favour adaptations for climbing, including lengthening of the limbs.

The conformity of the Pleistocene populations of Malta and Sicily and the diversity of the extant island populations is easily explained by looking at the geological setting of the area (Fig. 1). According to Donn et al. (1962) and other authors,

Table 3: Some cranial measurements of living and extinct populations of *Crocidura sicula* (see also table 1).

Measurement	Malta Pleist.	Malta Holoc.	Gozo Recent	Sicily Recent	Egadi I. Recent
Condylolincisive l.	—	—	18.35±0.4 (7)	19.41±0.6 (17)	18.07±0.4 (7)
Greatest width	—	—	8.46±0.2 (7)	8.93±0.3 (14)	8.45±0.2 (7)
Postglenoid w.	6.63 (2)	6.17±0.0 (3)	5.90±0.1 (10)	6.30±0.2 (20)	5.81±0.2 (7)
Interorb. w.	4.53±0.1 (10)	4.03±0.1 (11)	3.81±0.1 (11)	4.01±0.2 (22)	3.83±0.1 (7)
Upper tooththrow l.	9.14±0.3 (51)	8.31±0.1 (12)	8.16±0.2 (28)	8.61±0.3 (23)	7.95±0.2 (8)
Lower tooththrow l.	8.18±0.5 (3)	—	7.69±0.1 (8)	7.95±0.3 (24)	7.43±0.2 (8)
Coronoid process height	4.96±0.1 (25)	4.47±0.2 (6)	4.36±0.1 (8)	4.65±0.2 (24)	4.27±0.1 (8)

Table 4: Weight (g) and external measurements (mm) of extant populations of *Crocidura sicula*. Range, mean and sample size given.

	Sicily	Egadi Islands	Gozo
Weight	6.4—10.5 8.5 (10)	4.5—8.0 5.8 (7)	4.2—9 6.9 (5)
Head and body length	62—77 70.0 (23)	60.5—69.5 63.7 (8)	55—70 58.8 (9)
Tail length	28—45 36.7 (23)	32—35.5 33.6 (7)	30—36 31.7 (8)
Hindfoot length	11—13.5 12.4 (23)	11—11.7 11.3 (6)	11—12 11.5 (9)
Ear length	6—10.5 7.6 (15)	7.5—9 7.9 (5)	6.5—8 7.3 (5)

worldwide submarine terraces have been observed at a depth range of 142—154 meters; these terraces are older than 30.000 years B. P. During the Middle Pleistocene, the sea level was even 160—180 m lower than it is at present (Heaney 1986). In other words, Sicily, Malta, and the Egadi Islands formed one island during the Pleistocene (but there must have been also a landbridge to the mainland of Italy; see Caloi et al. 1988, Thake 1985, and Malatesta 1957). With rising sea levels at the end of the Pleistocene the sub-islands were separated and the shrews living on them underwent separate evolutionary processes. Separate evolutionary ways are also indicated by the highly derived condition of the third upper molar in the Egadi Island shrews (Tab. 2), in contrast to the more primitive condition in the other populations.

Taxonomic conclusions

Following the preceding results and discussion, I propose a new taxonomic arrangement for the Sicilian shrew.

Crocidura sicula esuae Kotsakis, 1986

Crocidura esui Kotsakis, 1986: 51 (Spinagallo, Sicily).

Emendation: Kotsakis (1986: 2) named the taxon after Dr. Daniela Esu; according to articles 31 (a) and 32 (d) of the ICZN (1985), the name must be corrected to *esuae* (Hutterer 1990: 215).

Diagnosis: Large shrews with the characters of *C. sicula* and a very long tibia (Tab. 2).

Distribution and material: Pleistocene of Spinagallo, Sicily, Italy (Kotsakis 1986; Esu et al. 1986; Bonfiglio & Kotsakis 1987; Caloi et al. 1988) and Ghar Dalam Cave, Malta (ca. 3080 SMF; 3 GDCM; 10 ZFMK).

Crocidura sicula sicula Miller, 1901

Crocidura sicula Miller, 1901: 41 (Palermo, Sicily).

Crocidura caudata Miller, 1901: 42 (Palermo, Sicily).

Diagnosis (modified from Vogel et al. 1989): A medium-sized shrew in the size range of *C. suaveolens* and *C. russula*, in general sharply bicoloured with a whitish undersurface but sometimes washed with grey, whitish fore- and hindfeet, and a bicoloured tail. Rostrum of skull rather flat and slender but bimaxillary region broad as in *C. russula*. Infra-orbital bridge narrow. Tips of the second and third upper unicuspid teeth usually in one line with the tip of the parastyle of the P⁴; parastyle massive and angular like a brick (Fig. 2), dorsal edge of the cingulum of P⁴ undulated, not straight; third upper molar narrow. Largest of the extant subspecies.

Distribution and material: Sicily, Italy (22 CNB; 3 IZEA; 14 SMF; 3 ZFMK). Specimens found in owl pellets from Ustica are probably not autochthonous but may have been brought by owls from Sicily (Sarà et al. 1990).

Crocidura sicula aegatensis n. subsp.

Holotype: ZFMK 89.392, skin and skull of adult male, collected 23 March 1969 by F. Krapp, field number 35/69; Egadi Islands, Marettimo, Casa Sarraceno. — **Paratypes:** 7 further specimens, listed in detail by Krapp (1970), from Levanzo (1 ZFMK) and Favignana (5 ZFMK; 1 MCV).

Diagnosis: A considerably small subspecies of *C. sicula*; weight and body size smaller, tail and hindfoot shorter (Tab. 4); all cranial distances smaller (Tab. 3); fourth upper molar extremely reduced (Tab. 2).

Distribution: Egadi Islands, Italy (see Krapp 1970, for details).

Etymology: Named for the "Aegates Insulae", as the Romans called these islands.

Crocidura sicula calypso n. subsp.

Holotype: ZFMK 89.418, adult male, preserved in alcohol, skull extracted, collected 22 October 1986 by S. Schembri and D. M. Johnson; Gozo (Malta), Is-Saqwi, Xlendi Valley. — **Paratypes:** 34, all from Gozo (Is-Saqwi, San Blas Valley, Xaghra, Munxar), collected 1981–1989 by M. Borg, D. M. Johnson, P. J. Schembri, S. Schembri, J. Sultana and P. Vogel (2 CSM; 18 CNB; 9 IZEA; 20 ZFMK).

Diagnosis: Distinctly smaller than the nominal subspecies, slightly larger than *aegatensis* (Tabs 2–4). Third upper molar not as much reduced as in *aegatensis* (Tab. 2). The most colourful extant subspecies; hands, feet, belly and undersurface of tail always whitish (figured in Vogel et al. 1989, 1990).

Distribution and further material: Gozo (Malta); recently extinct populations of Malta Island (12 SMF) may also be referred to this taxon.

Etymology: Named for the beautiful nymph Calypso, who, according to Greek mythology, lived in a cave near Ramla Bay on Gozo. The subspecific epithet is a noun in apposition.

A possibly related species from the Pleistocene of North Africa

It is now clear that the Pleistocene shrew of the Sicilian-Maltese archipelago evolved to the present-day forms. However, the origin of the Pleistocene shrew itself is not known. Vogel (1988) proposed a relationship between *C. sicula* and the Canarian endemic *C. canariensis* (Hutterer et al. 1987), an assumption which was supported by Maddalena (1990), and Maddalena & Vogel (1990). However, Michaux et al. (1991) recently found fossils of *C. canariensis* in an Upper Pleistocene deposit of Fuerteventura, showing that the Canary shrew formed a separate lineage since at least 30.000 years. Hutterer (1987) and Molina & Hutterer (1989) found morphological similarities between *C. canariensis* and the North African *C. whitakeri* and *C. tarfayaensis*. It is likely that all four species form one clade.

An extinct, yet undescribed species may be added to this tentative clade. It is characterized by an extremely enlarged parastyle at P⁴, which one may interpret as the exaggerated condition of the brick-like parastyle found in *C. sicula*. I therefore hypothesize that the new fossil may represent an ancestor of some of the species of the *C. sicula* group. A brief diagnosis of the new taxon is given below to announce its former existence, however, a more comprehensive description will be given later in a paper on fossil shrews of Morocco.

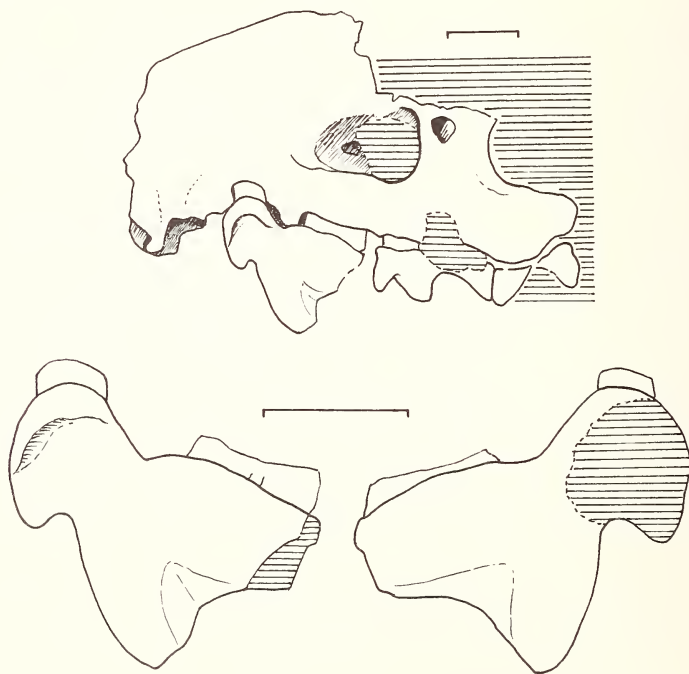


Fig. 5: *Crocidura maghrebiana* n. sp., holotype SMF 86/156, frontal part of skull and left and right P⁴ in labial view. Scales represent 1 mm; hatched areas indicate missing parts (left P⁴) or parts covered by sediment.

Crocidura maghrebiana n. sp. (Fig. 5)

Crocidura cf. *viaria*: Rzebik-Kowalska 1988: 75–80.

Holotype: SMF 86/156, partial skull with P^4-M^3 preserved, “Carrière Thomas (kleine Spalte), Höhle”, Middle Pleistocene of Morocco; leg. J.-L. Franzen & G. Storch 1973; other specimens referable to the new taxon are deposited in SMF, PAS and UCBL.

Measurements of holotype: Maxillary breadth 6,99; maximum length of upper P^4 in labial view 1,98; maximum height 1,83 mm.

Diagnosis: Large *Crocidura* with a characteristic upper P^4 in which the parastyle constitutes about one third of the entire tooth surface in labial view and is set apart from the body of the tooth by a distinct constriction (Fig. 5). Additional descriptions, figures and measurements are given by Rzebik-Kowalska (1988).

Distribution: Extinct; known from two Mid-Pleistocene sites in Morocco: Irhoud Derbala Virage (Rzebik-Kowalska 1988, PAS; also UVBL), and Carrière Thomas, near Casablanca (SMF).

Etymology: The species epithet is derived from the Maghreb region.

Discussion: The new fossil species is best characterized by the anvil-like shape of the parastyle of P^4 ; in this character it resembles most *C. sicula* (“brick-like”, fig. 2), *C. whitakeri*, *C. tarfayaensis*, and *C. canariensis* (Molina & Hutterer 1989: figs 6, 7, 9). *C. maghrebiana* n. sp. is larger than all these species (comparative measurements of MB in Hutterer 1987, and Molina & Hutterer 1989) but smaller than the African *C. viaria* to which Rzebik-Kowalska (1988) assigned some of the fossils under study. On morphological, biochemical (Maddalena & Vogel 1990, Hutterer et al., in press), and paleogeographical grounds I hypothesize that *sicula*, *canariensis*, *tarfayaensis*, *whitakeri* and *maghrebiana* n. sp. are members of the same monophyletic group. Fig. 6 presents a tentative framework of their distributions. Their actual distributions are still poorly known, and only recently Egypt has been included into the range of *C. whitakeri* (Hutterer, in press). The newly described *C. cossyrensis* Contoli, 1989, from Pantelleri (Contoli 1990, Contoli et al. 1989) is not considered here as it seems to be related to *C. russula* (Sarà et al. 1990) and is still insufficiently known. Also *C.*

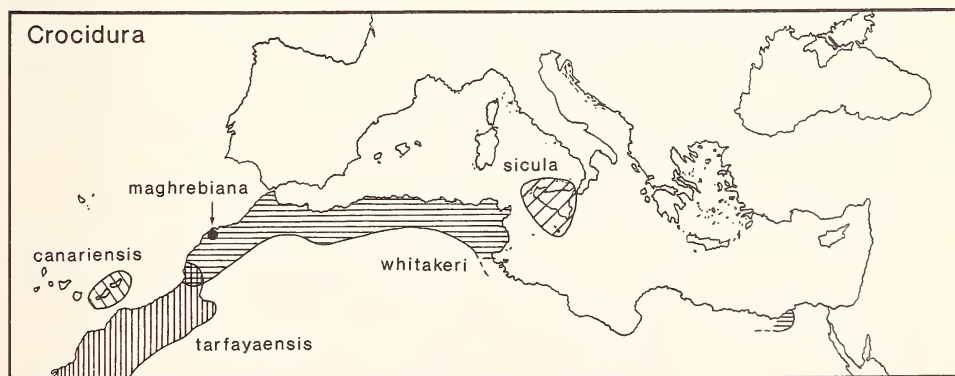


Fig. 6: Map of the Mediterranean Region with approximate limits of the distributions of the species of the *C. sicula* group indicated.

aleksandrisi Vesmanis, 1977, from Cyrenaica, Libya, is not mapped because I regard it as an isolated species with yet unknown affinities.

Zusammenfassung

Die Variation der Sizilienspitzmaus *Crocidura sicula* in Zeit und Raum wurde untersucht und die Ergebnisse in einer Synthese zusammengefaßt. Pleistozäne Populationen von Sizilien und Malta, die bisher als eigene Art betrachtet werden, müssen als Vorfahren der heutigen Populationen Siziliens, der Ägadischen Inseln und von Gozo (Malta) angesehen werden. Während des Pleistozäns waren alle diese Inseln als Folge von Meeresspiegelschwankungen zeitweise durch Landbrücken verbunden. Darauf folgende geographische Isolation führte zur Evolution von mindestens drei morphologisch unterscheidbaren Rezentpopulationen, von denen zwei neu benannt werden. Darüberhinaus wird eine neue Art aus dem Pleistozän von Marokko beschrieben, die möglicherweise eine Ausgangsform für die rezenten Arten der "*Crocidura sicula* Gruppe" gewesen ist.

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Dr. Rainer Hutterer, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 162, D-5300 Bonn 1.

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Autor(en)/Author(s): Hutterer Rainer

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