ΔΕΛΤΙΟ ΕΛΛΗΝΙΚΗΣ ΣΠΗΛΑΙΟΛΟΓΙΚΗΣ ΕΤΑΙΡΕΙΑΣ, ΤΟΜΟΣ XXI, 1993-1994
5ο ΔΙΕΘΝΕΣ ΣΥΝΕΔΡΙΟ, ΑΘΗΝΑ-ΚΡΗΤΗ, 7-11/11/1994 "ΑΝΑΠΤΥΞΗ, ΕΞΕΛΙΞΗ ΚΑΙ ΠΕΡΙΒΑΛΛΟΝ ΣΠΗΛΑΙΩΝ "

THE PLEISTOCENE SHREW FROM CRETE (CROCIDURA ZIMMERMANNI) IN A BROADER EVOLUTIONARY CONTEXT

By

JELLE W.F. REUMER

SUMMARY

The Cretan shrew *Crocidura zimmermanni* (Insectivora, Soricidae) is placed within a framework of taxonomic, biogeographic and evolutionary background. The shrew belonged to the subfamily Crocidurinae, and is unrelated to other living species in Europe. The species lived in Crete from the *Kritimys catreus* subzone onwards, and still exists in two small relic populations. It constitutes α relic of ancient *Crocidura* species, and of the Pleistocene endemic island faunas, and should be protected. Furthermore, the phenomenon seen in island faunas of smaller mammals increasing in size, is discussed and related to predation by avian raptors. The Cretan shrew, however, did not show this common response.

INTRODUCTION

Soricidae, or shrews, have been forming part of the European mammal fauna since the middle Oligocene, which implies a time span of roughly 30 million years (Mα). Their overall appearance has not changed much during this long period: shrews were, and are, small to very small mammals, with α characteristic dentition showing large incisors and dilambdodont upper molars.Occasionally, shrews settled on islands. One of the members of the peculiar, endemic and unbalanced vertebrate fauna from the Quaternary of Crete was the shrew *Crocidura zimmermanni* WETTSTEIN, 1953. In two earlier papers (Reumer, 1986, Reumer &Payne, 1986) the history of this species has been dealt with.The aim of the present paper is to place the Cretan shrew within a broader context of taxonomy, biogeography, and islandevolution.

THE CRETAN SHREW

At present, we can find three species of shrews in Crete: *C.zimmermanni* WETTSTEIN, 1953, *C. suaveolens canea*e MILLER, 1909 and *Suncus etruscus* (SAVI, 1822). There has been considerable controversy over the names of the two former taxa, see Reumer(1986) for a review of this. It was only a few years ago when Vogel (1986) proved the status of *C. zimmermanni* as an independant species. He did so by showing the unique karyotype of the species, which proved that it is unrelated to either of the three other Crocidura species presently living in Europe:*C. russula, C. suaveolens* and *C.*

*** Μυογαλές(*Soricidae*) στα νησιά, με ειδικές αναφορές στη Πλειστοκαινική μυγαλή της Κρήτης(*Crocidura Zimmermanni*).**

**** Jelle W.F. Reumer, Natuurmuseum Rotterdam, P.O.BOX 23452, NL - 3001 KL Rotterdam, The Netherlands.**

BULLETIN DE LA SOCIÉTÉ SPÉLÉOLOGIQUE DE GRÈCE, V.XXI, 1993-1994
5th INT.CONGRESS, ATHÈNES-CRÈTE, 7-11/11/1994 "CAVE DEVELOPMENT, EVOLUTION AND ENVIRONMENT"

leucodon. It will thus most probably be related to early or middle Pleistocene species,such as *C. Kornfeldi*.

Reumer (1986) concluded on morphological grounds that the living *C. zimmermanni* and the until then undescribed fossil shrew from the various Pleistocene localities (see Table 2)are the same species.

THE TAXONOMIC CONTEXT

Crocidura zimmermanni is α member of the family Soricidae, order Insectivora. The systematical subdivision of the family although still subject to further studies - may be summarizedas follows:

Family: Soricidae GRAY, 1821 in which five subfamilies:
  Subfamily: Crocidosoricinae REUMER, 1987
  Subfamily: Allosoricinae FEJFAR, 1966
  Subfamily: Limnoecinae REPENNING, 1967
  Subfamily: Crocidurinae MILNE-EDWARDS, 1868-1874
  Subfamily: Soricinae FISCHER VON WALDHEIM, 1817
  in which six tribes:
    Tribe: Soricini FISCHER VON WALDHEIM, 1817
    Tribe: Blarinini KRETZOI, 1965
    Tribe: Notiosoricini REUMER, 1984
    Tribe: Amblycoptini KORMOS, 1926
    Tribe: Beremendini REUMER, 1984
    Tribe: Soriculini KRETZOI, 1965

In addition to this, I recognize α separate group of shrews within the tribe Soricini. This group comprizes, among others, the genera *Petenyia* and *Blarinella*. A detailed study of this group is forthcoming; it may warrant separation as a distinct soricine tribe. A total of eleven distinct groups of shrews can thus be recognized. Not α 11 of these are of interest to our present subject: two groups (the subfamily Limnoecinae and the tribe Notiosoricini) are exclusively American.

Shrews (Soricidae) most probably originated in Asia and they are known on the European continent from the Early Oligocene onward (Hugueney, 1976; Reumer, 1994α). They showed α considerable diversification during the Miocene and the Pliocene,especially in the Holarctic region.

The oldest shrews known belonged to the Crocidosoricinae. TheCrocidosoricinae gave rise to the other subfamilies of shrews (Limnoecinae, Allosoricinae, Soricinae, Crocidurinae; see Reumer 1987, 1989 and 1992). The Crocidosoricinae come into the fossil record in the early Oligocene; their last occurrence in the European continent is in several Spanish localities of early Vallesian age (Late Miocene, zone MN 9).

The Allosoricinae show α range from the Early Miocene (MN 3,Wintershof-West, Germany) to the late Pliocene (MN 16, Betfia13, Roumania and Mala Cave, Poland, see Reumer 1992).Members of the tribe Soricini are not met in the European fossil record until the latest Miocene (MN 13, Maramena, Greece: οωη observation).

Hemisorex from Stubersheim 3 (Early Miocene, MN3-4, Germany:Ziegler 1989) is the first record of α member of the Petenyiα/Blarinella group. The genus *Hemisorex* is here attributed to this group on the basis of morphological similarities in the dentition and the mandibular structure. The attribution follows the suggestion of Baudelot (1972). A member of this group still lives in Asia today.

The tribe Amblycoptini, which also has α representative living in Asia today, first appeared in the early Vallesian (Late Miocene, MN 9) of Spain (Gibert 1975).

Members of the tribe Blarinini reached Europe coming from America in the early Ruscinian (Podlesice, Poland: Kowalski1956), but are noω again restricted to America.

Soriculini (or Neomyini as they are often called) are first found in Maramena, Greece (latest Miocene, MN13; own observation); they still abound in Eurasia. Beremendini form a small tribe, that originated in the early Ruscinian of central Europe (Osztramos 1 and 9, Hungary, MN14) and became extinctin the Pleistocene (Reumer 1984).

Finally, the subfamily Crocidurinae comes into the fossil record. The enigmatic character of this late appearance warrants discussion elsewhere; it can here be concluded that the oldest record known so far is from Apolakkia on the island of Rhodes, Greece (MN 15; Van de Weerd et al. 1982). Crocidurinaeare nowadays particularly developed in Africa. However, the fossil record from Africa is extremely scanty and obscure. Nocertain records of pre-Pleistocene shrews are known from this continent, but the enormous recent proliferation of shrews of the subfamily Crocidurinae in Africa suggests a long history.

Mediterranean island shrews may thus theoretically have come from both Europe and Africa, as both continents had and have shrews as components of the mammal fauna. There is also a large amount of taxonomic groups from which island shrews could have derived.

THE BIOGEOGRAPHIC CONTEXT

Table 1 shows a taxonomic difference between the western Mediterranean shrews and those from the central and eastern Mediterranean islands during the Pleistocene.

The western Mediterranean Pleistocene shrews belonged to the genus Nesiotites, a member of the tribe Soriculini (Neomyini) of the subfamily Soricinae. Several species have been described from five islands. Majorca harboured the species *N. Ponsi* REUMER, 1979 and *N. hidalgo* BATE, 1945. On the adjacent island of Menorca lived *N. meloussae* PONS & MOYA, 1980, as well as *N.hidalgo*. In both cases *N. hidalgo* is the younger species, geologically speaking. The same genus lived on the large Franco-italian islands: *N. corsicanus* BATE, 1945 on Corsica, and *N. similis* BATE, 1945 on Sardinia.

As pointed out by Reumer (1984), this endemic island taxon is a direct descendant of the Plio/Pleistocene European species. A *soriculus gibberodon* (PETENYI, 1864), which was forced into southern refuges due to the climatic deterioration of the Quaternary. This took place most probably in relation to the world-wide cooling event some 2.4 Ma ago (Reumer, 1989). We therefore assume that these shrews originate from Europe.

All other Mediterranean island shrews belong to the genus *Crocidura*, a member of the subfamily Crocidurinae. The onlyexception to this statement, is a Late Miocene or Early Pliocene shrew from the former island of Gargano (now part of the Italian continent), which is an as yet undescribed member of the extinct subfamily Crocidosoricinae, see Table 1. From the Pleistocene and/or Holocene, we know of *Crocidura's* from Sicily (*C. esuae* KOTSAKIS, 1984), from Malta (as yet undescrid), from Cyprus (*C. suaveolens praecypria* REUMER & OBERLI,1988, most probably not an endemic but introduced by humans),and the Cretan shrew. This list will certainly not be complete.

The fossil *Crocidura* from Crete most probably reached the island from either Greece or Asia Minor. *Crocidura* is known to have been present in this part of Europe from the late Ruscinian onwards. Van de Weerd et al. (1982) reported *Crocidura sp.* from the late Ruscinian of Apolakkia on the island of Rhodes (which was connected to the continent at the time).Reumer & Doukas (1985) described a *Crocídura sp.* from the early Villányian of Tourkobounia 1 (Athens, Greece) and *C.kornfeldi* KORMOS, 1934 from the early Biharian localities of Tourkobounia 2, 3 and 5. This dates the earliest possible arrival of the shrew in Crete to a period not before the late Ruscinian.

In general, the mechanism by which terrestrial small mammal swere transported from the mainland into islands must have been rafting. Although some shrews are good swimmers (especially the water shrews to which the genus *Asoriculus* belonged), they are certainly unable to cover considerable distances at sea.Water shrews are bound to clear fresh-water environments such as streams and ponds and they have never been recorded fromcoastal marine habitats. Iη addition to this, shrews have special dietary requirements. Due to their extremely small body size and their high metabolic rate, shrews can survive no more than a few hours without eating (see Vogel, 1980 andChurchfield, 1990 for this aspect of soricid physiology). This requirement prevents any venture into open water: even if they would have been able to swim into the open sea, they would have starved to death after a few hours.

Rafting has been proposed more often as α natural means of reaching islands. Large parts of floating vegetation have been reported to flow into the open sea from river mouths. Provided an adequate size and an abundant invertebrate food supply such "floating islands" could very well have harboured one or more living shrews.

ISLAND EVOLUTION

As stated, the island of Crete harboured endemic and unbalanced mammal faunas during the Quaternary. The same phenomenon is known from many other Mediterranean islands as well as from islands in other parts of the world. As a rule, such unbalanced endemic associations consisted of (dwarfed) large herbivores of the Orders Proboscidea (Elephantidae), Artiodactyla (Bovidae, Cervidae, or Hippopotamidae), Rodentia (mostly Muridae or Gliridae) and Insectivora (mostly Soricidae),sometimes supplemented with certain Carnivora (Lutrinae) and non-mammalian vertebrates (tortoises, frogs, endemic birds,etc.). Due to specific environmental circumstances present in islands we can often observe evolutionary phenomena unlike those in continental biota.

It is often observed that mammals in islands show changingbody sizes (Sondaar, 1977). Large herbivores had atendency to become smaller (Bovidae from the Baleares, Hippopotamidae from Cyprus and Crete, Elephantidae from Crete, Malta and Sicily,to name but a few) or to radiate (Cervidae from Crete, De Vos, 1984). Small mammals often became larger. We know of Pleistocene large Muridae from the Canary Islands (*Canariomys*; Crusafont & Petter, 1964), from Crete (the genus *Kritimys*; Mayhew, 1977), as well as from many islands in S.E.A sia and other parts of the world. The Baleares, Ibiza, and Malta harboured large dormice (subgenera of *Eliomys*, see references in Reumer, 1994b). Another famous example are the murids and the giant hedgehog (*Deinogalerix*) from the Miocene island of Gargano, Italy (Freudenthal, 1972). Increasing sizes of island shrews have been described from the Baleares (the genus *Nesiotites*, see Reumer, 1980) and from Cyprus (*Crocidura suaveolens praecypria*, see Reumer & Oberli, 1988).

It is thus noteworthy that the Cretan shrew *C. zimmermanni* is reported to have remained in stasis throughout its existence (Reumer, 1986). This apparent stasis also applies to the endemic murid *Mus minotaurus* from the Cretan late Pleistocene.

I do not know of extensive studies into the evolutionary mechanism that caused increasing sizes of small mammals in islands. The genetic background of any island population is influenced by the reduced amount of genotypic diversity of the original colonizing individuals (the founder principle; Mayr, 1977; White, 1978). It subsequently depends on the nature of the selective pressures exerted upon the species what the phenotypic outcome will be.

In the case of small mammals (such as rodents and shrews) αn important selective pressure is predation. In the case of living shrews, predation by owls, kestrels and other raptors, weasels, stoats, foxes, snakes, and domestic cats has been reported

(Churchfield, 1990). Their most important predators are owls.In the case of small rodents, the spectrum of predators will not be much different. Mammalian predators prefer rodents to shrews, due to the smelly and distasteful character of the latter.

Most environmental circumstances are not, or will not have been, much different in the larger Mediterranean islands when compared to the situation on the mainland. Everyone who has visited these regions can imagine that for a shrew living in the middle of Crete, the habitat will be virtually identical as for a shrew living in, for example, the Peloponnesos. What differed during the Pleistocene was the set of predators. Almost all endemic unbalanced island faunas lack terrestrial predators. There are, with a few exceptions, no canids, no felids, no musteline mustelids in any of the known Pleistocene island biota. The small mammals are thus only preyed upon by avian predators: owls and diurnal raptors. It is this ecological difference between the habitats in islands and on the meinland that must provide the selective force towards increasing sizes in small mammals.

Owls are to some extent selective towards prey size. Wijnandts (1984) showed that Dutch Long-eared owls (*Asio otus*) took mammal prey with an average body weight of 19.2 gram, with most prey ranging between 18-22 gram. Andrews (1990) showed a similar result for English Barn owls (*Tyto alba*), hardly taking prey with mandible lengths over 17 mm. Larger species, such as *Arvicola sp.*, *Rattus sp.*, or *Oryctolagus cuniculus* are only taken as neonates or juveniles, and even then rarely (own observation).

It may thus seem that small mammals can "escape" predation by birds of prey simply by increasing their body size and by thus "moving" themselves out of the commmon prey spectrum. I hypothesize that this may be the selective force causing small mammals in island ecosystems to become larger. Terrestrial predators are able to handle larger prey by not swallowing them as a whole but dismembering them instead. Owls do not do this. The absence of terrestrial (mammalian) predators from island ecosystems could mean the absence of selective forces against larger body size.

It is not known why *Crocidura zimmermanni* (and *Mus minotaurus* for that matter, which only oscillated in size but did not show an increase; Mayhew, 1977) did not increase in size during their period in the endemic fauna in Crete. If the hypothesis mentioned above is correct, it could be because they were preyed upon by terrestrial mammals.

Crete had a Pleistocene otter (*Lutrogale cretensis* (SYMEONIDIS & SONDAAR, 1975], see Willemsen, 1992). Otters are a common member of Mediterranean island faunas, most probably due to the fact that they are the only Carnivora that do habitually swim. However, they are considered to have fed mainly on fish and shellfish, and not so much on terrestrial mammals (Willemsen, 1992). Otters may not therefore have been an important factor in the Cretan shrew's ecosystem. In addition, the Cretan otter is found only in Liko cave, so that it will hot have had an important impact on the small mammals during their entire range.

Another possible reason for the apparent stasis could have been the absence of predation. This can be excluded, first of all because several owl species and many diurnal raptors have been found (Weesie, 1982). An endemic owl (Athene cretensis WEESIE, 1982) has been reported with terrestrial adaptations. Terrestrial owls have been reported from other islands as well (e.g., Ballmann, 1973, 1976) where apparently the absence of terrestrial mammalian predators opened a new niche. Predation by raptors will thus have been present; there seems no reason to believe that Crete would have been different in this respect from other Mediterranean islands: birds of prey can fly!

When small mammals on other islands became larger, while they remained in stasis in Crete, there must have been an ecological difference between Crete at the

time of the Mus-zone on the one hand, and all other islands on the other. I must leave this problem unanswered.

BIOSTRATIGRAPHY

As far as Crete is concerned, we have had two different unbalanced endemic faunas, see Table 2 and Dermitzakis & De Vos, 1987. The *Kritimys* zone (see Mayhew, 1977 for stratigraphical units) witnessed a dwarfed elephant, dwarfed hippos, a giant mouse and in its later part (the *K. catreus* subzone) the shrew, amongst other elements. The Mus zone witnessed a large elephant, radiating deer (into six different size groups, from animals of 40 cm withers height to animals about the size of Alces; see De Vos, 1984), a small mouse and the shrew. There are reports of predators from the *Mus minotaurus* subzone: an endemic otter and an endemic terrestrial owl. The Cretan shrew has thus been reported from the *K. Catreus* subzone of the *Kritimys* zone, and from the entire Mus zone. The faunal turn-over that demarcated both zones was apparently survived without any problem.

island	**shrew taxon**
LATE MIOCENE_EARLY PLIOCENE	
Gargano (Italy)	**Crocidosoricinae gen. et sp. indet.**
PLEISTOCENE_HOLOCENE	
Majorca	***Nesiotites ponsi***
	N. hidalgo
Menorca	***Nesiotites meloussae***
	N. hidalgo
Corsica	***Nesiotites corsicanus***
Sardinia	***Nesiotites similis***
Sicily	***Crocidura esuae***
Malta	***Crocidura sp.***
Crete	***Crocidura zimmermanni***
HOLOCENE	
Cyprus	***Crocidura suaveolens praecypria***

Table 1. Fossil Soricidae of the major Mediterranean islands.

stratigraphy		**selected localities**
RECENT		**Nida and Omalos plains**
		Liko a,A,B,C,D
***Mus* zone**	***Mus minotaurus* subzone**	**Rethymnon fissure**
		ilatos 2
		Stavros Cave inside
	***M. bateae* subzone**	**Stavros Micro**
***Kritimys* zone**	***K. catreus* subzone**	**Xeros**
	***K.Kiridus* subzone**	

Table 2. Biostratigraphical presence of *Crocidura zimmermanni*: the shrew was absent during the *Kritimys kiridus* subzone of the *Kritimys* zone, but from the *K. catreus* subzone onwards it has been present. It survives in the Nida and Omalos high plains of Central Crete.

HISTORICAL DEVELOPMENTS

The original endemic mammal faunas on the Mediterranean islands, Crete included, became extinct due to anthropogenic factors such as hunting, attempted domestication, predation by introduced carnivores, competition with introduced species, and habitat destruction. The extinction process in the islands was certainly not a sudden process, but one that took several millenia. This has several reasons. In the first place, introductions by man of other mammal species - wanted or unwanted did not happen at once. Furthermore it will have taken different lengths of time for different species to respond to the changes in their environment. Some data are known for a few islands (e.g., Menorca, see Reumer & Sanders, 1984; and Crete, papers in this volume), but in general the picture of introductions and extinctions is still wanting for most of the Mediterranean islands.

When focusing oη the Cretan shrew *Crocidura zinunerman,*it can be concluded that this species has been present in Cretefrom the *Kritimys catreus* subzone onwards (Reumer, 1986). During all the rest of the Pleistocene it was the only insectivore. *C. suaveolens caneae* was introduced into Crete around 1700-1550 years BC; *Suncus etruscus* is found as early as 1370 - 1200 years BC. *C. zimmermanni* has still been found in archeological levels in Kommos (S. Crete) dated also around 1370-1200 years BC. Iη younger levels it was absent, while the two introduced shrews were present (see Reumer & Payne, 1986, for details oη these data).

All Pleistocene localities mentioned in Table 2 are found close to the coast and just above sea-level. This means that *C. zimmermanni* was, at that time, living abundantly in the Cretan lowlands. Its scarcity in the archeological samples from Kommos suggests that it had already been replaced by the introduced species in the lowland area around Kommos. It was probably forced to a refuge in somewhat more elevated and climatically more severe areas, where it still survives. As stated before (Reumer & Payne, 1986), more data are needed from other archeological sites before we can form any proper picture of the time and the rapidity of the process of replacement.

The present-day population of *C. zimmermanni,* which lives in two elevated regions of Crete only, isa relic in two senses. In the first place, it is a descendant of the early and middle Pleistocene group of *Crocidura* species that is no longer living, containing e.g. *C. Kornfeldi.* In addition, it is the only known survivor of the wonderful world of endemic species that was found in most of the larger Mediterranean islands during the Pleistocene. For both reasons, *C. zimmermanni* deserves active conservation. This shrew, the Cretan shrew, should be listed in international conservation lists as either Endangered or Vulnerable.

LITERATURE

Andrews, P. 1990. Owls, Caves and Fossils. Natural History Museum Publications, London: 231 pp. **Ballmann, P. 1973.** Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien). Scripta Geologica 17: 1-75.

Ballmann, P. 1976. Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien), zweiter Teil. Scripta Geologica 38: 1-59. Baudelot, S. 1972. ,tude des chiropteres, insectivores et rongeurs du Miocene de Sansan (Gers). These, Universite ÑaulSabatier, Toulouse. Soricidae: 76-139.

Churchfield, S. 1990. The natural history of shrews. Cornell University Press, Ithaca, New York: 178 pp.

Crusafont-Pairo, M. & F. Petter. 1964. Un murine geant fossile des Iles *Canaries Canariomys* bravoi gen. nov., sp. nov. Mammalia, 28: 607-612.

Dermitzakis, M. and J. De Vos. 1987. Faunal succession and the evolution of mammals in Crete during the Pleistocene. Neues Jahrbuch f. Geologie u. Paläontologie, Abh. 173 (3): 377-408.

De Vos, J. 1984. The endemic Pleistocene deer of Crete. Verhandelingen Koninklijke Nederlandse Akademie vav Wetenschappen, afd. Natuurkunde, 1e reeks, 31: 1-100.

Freudenthal, M. 1972. *Deinogalerix koenigswaldi* nov. Gen., nov. spec., a giant insectivore from the Neogene of Italy.Scripta Geologica 14: 1-19.

Gibert, J. 1975. New insectivores from the Miocene of Spain. Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B 78: 108-133.

Hugueney, M. 1976. Un stade primitif dans 1'evolution des Soricinae (Mammalia, Insectivora): Srinitium marteli nov.gen., nov. sp. de 1'Oligocene moyen de Saint-Martin-de-Castillon (Vaucluse). Comptes rendus, Académie des Sciences, Paris,serie D, 282: 981-984.

Kowalski, K. 1956. Insectivores, bats and rodents from the Early Pleistocene bone breccia ïs Podlesice near *Kroczyce* (Poland). Acta Palaeontologica Polonica, 1 (4): 331-398.

Mayhew, D.F. 1977. The endemic Pleistocene murids of Crete. Proceedings Koninklijke Nederlandse Akademie vav Wetenschappen, Ser. B 80 (3): 182-214.

Mayr, E. 1977. Populations, Species, and Evolution. Harvard University Press, Cambridge (MA) and London, 453 pp.

Reumer, J.W.F. 1980. Ïn the Pleistocene shrew *Nesiotites hidalgo Bate*, 1944 from Majorca (Soricidae, Insectivora). Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, ser. B 83 (1): 39-68.

Reumer, J.W.F. 1984. Ruscinian and early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary. Scripta Geologica 73: 1-173.

Reumer, J.W.F. 1986. Notes ïn the Soricidae (Insectivora, Mammalia) from Crete. É. The Pleistocene species *Crocidura zimmermanni*. Bonner zoologische Beitraerge 37 (3): 161-171.

Reumer, J.W.F. 1987. Redefinition of the Soricidae and the Heterosoricidae (Insectivora, Mammalia), with the description of the Crocidosoricinae, a new subfamily of Soricidae. Revue de Paleobiologie, 6 (2): 189-192.

Reumer, J.W.F. 1989. Speciation and evolution in the Soricidae (Mammalia: Insectivora) in relation with the paleoclimate. Revue suisse de Zoologie, 96 (1): 81-90.

Reumer, J.W.F. 1992. The taxonomical position of the genus Paenelimnoecus Baudelot, 1972 (Mammalia: Soricidae): a resurrection of the subfamily Allosoricinae. Journal of Vertebrate Paleontology, 12 (1): 103-106.

Reumer, J.W.F. 1994a. Phylogeny and distribution of the Crocidosoricinae (Mammalia, Soricidae). Én J.F. Merritt, G.L. Kirkland, Jr, and R.K. Rose, eds., Advances in the Biology of Shrews. Carnegie Museum of Natural History Special Publication 18: 486 pp

Reumer, J.W.F. 1994b. *Eliomys (Hypnomys)* onicensis nomen novum, to replace the *homonym Hypnomys intermedius* Reumer, 1981 (Rodentia: Gliridae) from Majorca. Zeitschrift fûr Säugetierkunde, 59: in print.

Reumer, J.W.F. and C.S. Doukas. 1985. Early Pleistocene Insectivora (Mammalia) from Tourkobounia (Athens,Greece).Proceeding Koninklijke Nederlandse Akademie íáç Wetenschappen, ser. Â 88 ß): 111-121.

Reumer, J.W.F. & U. Oberli. 1988. Shrews (Mammalia: Soricidae) from a Bronze Age deposit in Cyprus, with the description of a new subspecies. Bonner zoologische Beitrûge 39 (4): 305-314.

Reumer, J.W.F. and S. Payne. 1986. Notes on the Soricidae (Insectivora, Mammalia) from Crete. II. The shrew remains from Minoan and Classical Kommos. Bonner zoologische Beitraege 37 (3): 173-182.

Reumer, J.W.F. and E.A.C. Sanders. 1984. Changes in the vertebrate fauna of Menorca in prehistoric and classical times. Zeitschrift für Säugetierkunde, 49 (6): 321-325.

Sondaar, P.Y. 1971. Insularity and its effect in mammal evolution. In M.K. Hecht, P.C. Goody and B.M. Hecht, eds., Major patterns in vertebrate evolution. Plenum, New York: 671-707.

Symeonides, N. and P.Y. Sondaar. 1975. A new otter from the Pleistocene of Crete. Annales geologiques des Pays Helleniques 27: 11-24.

Van de Weerd, A., J.W.F. Reumer and J. de Vos. 1982. Pliocene mammals from the Apolakkia Formation (Rhodes, Greece). Proceedings Koninklijke Nederlandse Akademie ían Wetenschappen, ser. B 85(1): 89-112.

Vogel, P. 1980. Metabolic levels and biological strategies in shrews. In K. Schmidt-Nielsen, L. Bolis and C.R. Taylor, eds., Comparative physiology: primitive mammals. Cambridge University Press, Cambridge: 170-180.

Vogel, P. 1986. Der Karyotyp der Kretaspitzmaus, *Crocidura zimmermanni* Wettstein, 1953 (Mammalia, Insectivora). Bonner zoologische Beiträge 37 (1): 35-38.

Weesie, P.D.M. 1982. A Pleistocene endemic island form within the genus Athene: Athene *cretensis* n.sp. (Aves, Strigiformes) from Crete. Proceedings Koninklijke Nederlandse Akademie ían Wetenschappen, ser. B, 85 (3): 323-336.

White, M.J.D. 1978. Modes of speciation. W.H.Freeman and Company, San Francisco, 455pp.

Willemsen, G.F. 1992. A revision of the Pliocene and Quaternary Lutrinae from Europe. Scripta Geologica 101: 1-115.

Wijnandts, Ç. 1984. Ecological energetics of the Long-eared (Asio otus). Ardea 72: 1-92.

Ziegler, R. 1989. Heterosoricidae und Soricidae (Insectivora, Mammalia) aus dem Oberoligozän und Untermiozän Sûddeutschlands. Stuttgarter Beitrûge zur Naturkunde, Ser. B, 154: 1-73.