IS THERE ANY PALEONTOLOGICAL "TREATMENT" FOR THE "INSULAR SYNDROME" ?

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IS THERE ANY PALEONTOLOGICAL "TREATMENT" FOR THE "INSULAR SYNDROME" ?

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MAMMIFÈRES INSULAIRES
NÉOGÈNE
QUATERNAIRE
MÉDITERRANÉE
HORS MÉDITERRANÉE

RÉSUMÉ. – La paléontologie livre beaucoup d'exemples de faunes endémiques insulaires. Les endémismes consistent surtout en variations de taille, chez les Mammifères en particulier. Des exemples significatifs sont représentés par les Mammifères des îles méditerranéennes à partir du Tertiaire. Les associations insulaires à Mammifères sont marquées par un faible degré de diversité taxonomique, en raison de l'effet filtrant des liaisons avec la terre ferme. Les manifestations les plus communes d'endémisme sont representées par la réduction de la taille des Mammifères les plus grands, comme les Proboscidiens et les Artiodactyles, et l'augmentation de taille des Micromammifères, comme les Insectivores et les Rongeurs. On suppose que ces modifications résultent de l'isolements génétique des populations continentales, d'une réduction quantitative et qualitative de la disponibilité alimentaire, d'une altération de la compétition intraspécifique, de l'absence de Carnivores de grande taille, et probablement aussi de l'adaptation endothermique et/ou d'une défense contre les Oiseaux prédateurs pour les Micromammifères. Des exemples significatifs dans ce sens sont présentés, pour les faunes des îles méditerranéennes des Baléares, de Corse et de Sardaigne, de l'archipel toscan, des « îles fossiles » du Gargano et de la Calabre méridionale, de Sicile, de Malte, de Crète, de plusieurs îles égéennes et de Chypre. Il semble que pour produire ces spécialisations un temps relativement court soit suffisant, comme il est démontré dans le cas des Cerfs de Capri, Pianosa et des îles de Jersey et d'Oronsay hors de la région méditerranéenne, ainsi que dans le cas des Mammouths nains de l'île de Wrangel, dans l'Océan Arctique. L' homogénéité des caractères chez les Mammifères insulaires atteste le fait que leurs modifications endémiques représentent la règle et non l'exception. Est-il encore possible de concevoir un « syndrome d'insularité » ?

INSULAR MAMMALS
NEOGENE
QUATERNARY
MEDITERRANEAN
EXTRA-MEDITERRANEAN

ABSTRACT. – Many examples of endemic insular faunas are documented by the paleontological record. The endemisms consist mainly in size variations, which affect mammals in particular. Significant cases are shown by the mammals of the Mediterranean islands, at least since the Early Tertiary. The insular mammal assemblages are characterized by a very low taxonomic diversity, due to the filtering effects of the connections with the mainland areas. The commonest trends of endemization are the size decrease of large-sized mammals, such as Proboscideans and Artiodactyls, and the size increase of micromammals, such as Insectivores and Rodents. These modifications are generally supposed to be most of all a consequence of a genetic isolation from continental populations, a quantitative and qualitative reduction of food supply, an alteration of intraspecific competition, the lack of large-sized carnivores, and possibly, in micromammals, also endothermic adaptations and/or a defence from birds of prey. Among the Mediterranean island faunas, significant examples are those of the Balearics, Corsica and Sardinia, the Tuscan archipelago, the "fossil islands" of Gargano and Southern Calabria, Sicily, Malta, Crete, several Aegean islands and Cyprus. A relatively short time may be needed to produce these specializations, as the cases of the deer of Capri, Pianosa and of the extra-Mediterranean islands of Jersey and Oronsay and of the dwarf mammoths of Wrangel Island, in the Arctic Ocean, seem to suggest. The constance of patterns shown by the insular mammals attests to the fact that their endemic modifications are the normality and not the exception. Is all this not a possible "treatment" for the "insular syndrome"?

INTRODUCTION

The so-called "insular syndrome" consists in several characteristics which distinguish micromammals of the Mediterranean islands from their continental counterparts. It has been described as an essay of manifestations which comprise a decrease in species number (decrease in diversity), reduced pressure of predators and competitors, niche expansion, increase in population density, tendency for allopatry, genotypic and phenotypic modifications (e.g. gigantism), decrease in birth rate (Fons *et al.*, 1995). These factors also affect macromammals distributed in isolated habitats, though often with different responses (e.g. genotypic and phenotypic modifications may correspond to a tendency towards dwarfism). Paleontology permits to verify only some of these manifestations.

THE MONOTONOUS AND UNBALANCED ENDEMIC FAUNAS OF THE MEDITERRANEAN ISLANDS

According to paleontological evidence, many of the fossil mammalian faunas of the Mediterranean islands differed considerably from extant continental faunas. They were characterized by peculiarly evolved taxa. Fossils of Quaternary endemic mammals are known from the Balearics (Mallorca and Menorca), Ibiza, Corsica, Sardinia, the Italian islands of Pianosa (Tuscan archipelago) and Capri (facing the peninsula of Sorrento), Sicily, Malta, Lampedusa, Corfu, Crete, Kasos, Armathia, Karpathos, Cyclades (Milos, Amorgos, Delos, Seriphos, Kythnos, Naxos), Tilos, Rhodes and Cyprus. Each of these mammalian faunas, although monotonous in composition, at the order rank, on most of the islands, displayed peculiar endemic elements which differentiated each island fauna from one another. This is due to the fact that each island had a distinct geological history, being connected at different times to the closest landmass (Ambrosetti *et al.*, 1980). However, a common peculiarity of these insular faunas is that macromammals, mainly represented by deer, elephants and hippopotami, dispersed on islands often becoming dwarfed, while micromammals, represented by few groups of insectivores, such as shrews, by rodents and by lagomorphs, dispersed on islands becoming larger than their mainland counterparts (Sondaar, 1986).

On an overall view of the Mediterranean Pleistocene island faunas it can be observed that dwarfed proboscideans are known from thirteen islands, namely Cyprus (Bate, 1903a, 1904a, 1904b, 1904c; Vaufrey, 1929; Boekschoten & Sondaar,

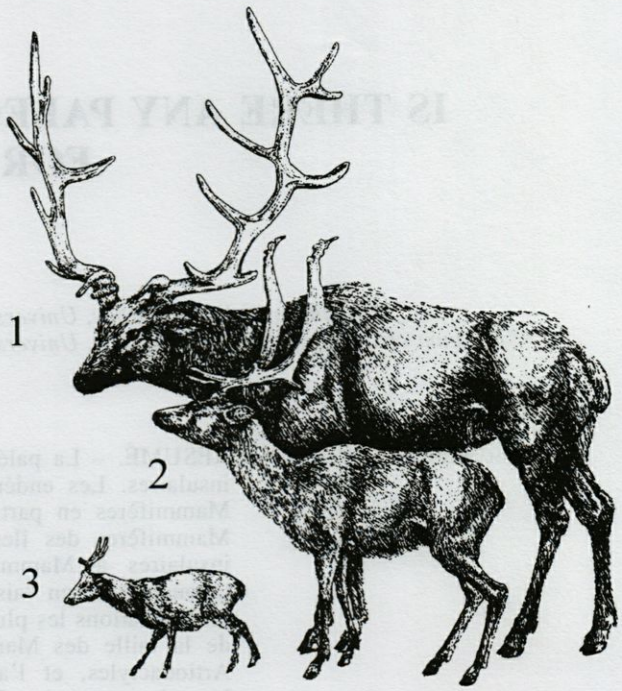

Fig. 1. – 1, *Megaloceros* (*Megaceroides*) *verticornis dendrocerus*, shoulder height: about 145-160 cm; 2, *Megaloceros* (*Megaceroides*) *algarensis*, shoulder height: about 80-100 cm; 3, *Megaloceros* (*Megaceroides*) *cretensis*, shoulder height: about 55-65 cm. Drawing by A. Azzaroli (1982).

1972; Reese, 1995); Rhodes and Tylos (Bachmayer *et al.*, 1984; Symeonidis *et al.*, 1973; Theodorou, 1985); Naxos, Delos and Serifos (Johnson, 1980; Davis, 1987); Kythnos (Caloi *et al.*, 1986; Kotsakis 1990); Milos and Kythira (Marinos & Symeonidis, 1977); Crete (Kuss, 1973; Sondaar, 1971; Theodorou, 1985; Schlager, 1991; Malta : Falconer, 1862; Leith Adams, 1870, 1875; Vaufrey, 1929; Bate, 1916; Zammit-Maempel, 1985); Sicily (Ambrosetti, 1968; Ambrosetti *et al.*, 1980) and Sardinia (Azzaroli, 1978; 1983), whereas, among artiodactyls, dwarfed hippopotami are reported from Cyprus (Bate, 1906; Boekschoten & Sondaar, 1972); Crete (Marinos & Simeonidis, 1977); Malta (Bate, 1916) and Sicily (Fabiani, 1928; Vaufrey, 1929; Accordi 1955 and 1962); dwarfed deer, reputed to derive from megalocerines, are known from Kasos (Kuss, 1969 and 1975); Karpathos (Sondaar, 1971; Kuss, 1975; Marinos & Simeonidis, 1977) and Sardinia and Corsica (Azzaroli, 1952; Caloi & Malatesta, 1974); other dwarfed deer, believed to have derived from cervines, from Rhodes (Kuss, 1975); Crete (Simonelli, 1907, 1908; Accordi, 1972; Kuss, 1975; De Vos, 1979 and 1984; Malatesta, 1980); Malta (Bate, 1916); Sicily (Accordi, 1955; Ambrosetti, 1968 and 1969; Azzaroli, 1962 and 1971); Capri (Azzaroli, 1962, 1977) and Pianosa (Stehlin, 1928; Azzaroli, 1962 and 1978); dwar-

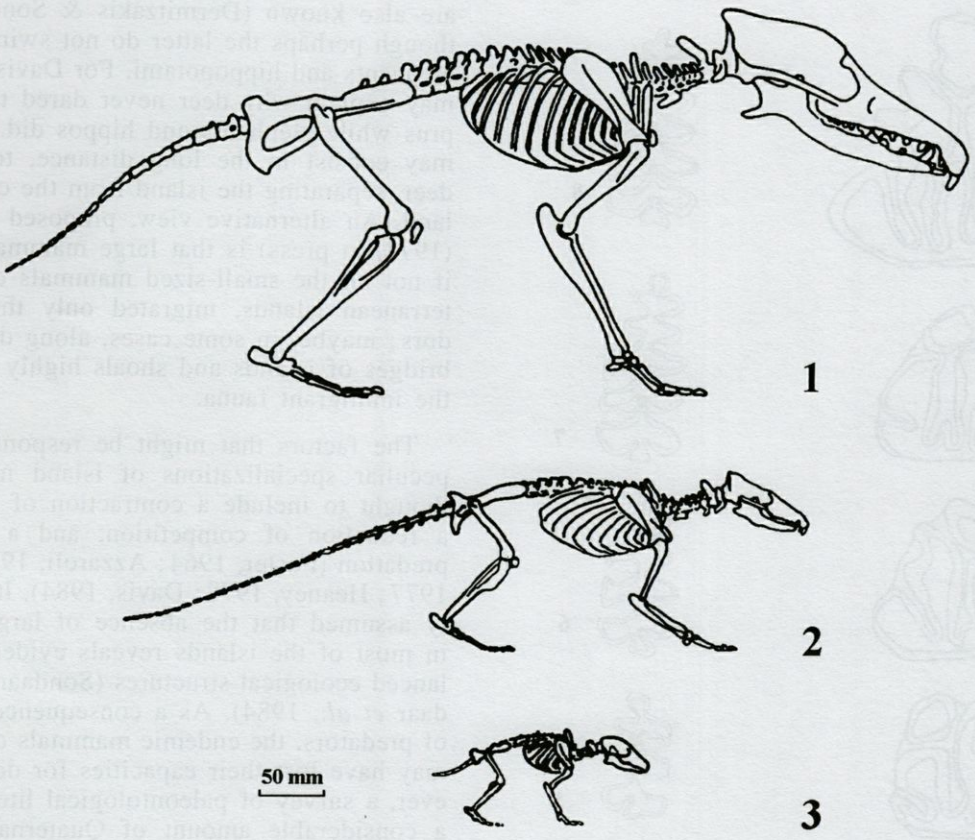

Fig. 2. – *Deinogalerix koenigswaldi* compared with living continental galericines. 1, *Deinogalerix koenigswaldi*; 2, *Echinosorex gymnurus*; 3, *Hylomys suillus*. Modified from Butler (1980).

fed Rupicaprinae-like bovids from Mallorca and Menorca (Bate, 1909; Alcover *et al.*, 1981; Burleigh & Clutton-Brock, 1980; Andrews, 1915; Azzaroli, 1982) and Sardinia (Gliozzi & Malatesta, 1980), while dwarfed oxes are reported from Pianosa (Azzaroli, 1978) and Sicily (Brugal, 1987). Endemic large-sized micromammals are represented in most of the Mediterranean islands (Petronio, 1970; Azzaroli, 1982; Alcover *et al.*, 1981; Vigne, 1992; Mayhew, 1977; Bate, 1903b).

The same modifications are documented in older insular faunas from the Mediterranean area and in others from extra-Mediterranean islands. The existence of "fossil islands" is attested by the endemic faunas of the Miocene Abruzzo-Apulian (Freudenthal, 1972; Butler, 1980; De Giuli *et al.*, 1986a; Mazza, 1986a, b, 1987; Mazza *et al.*, 1995; Mazza & Rustioni, in press) and Tuscan-Sardinian paleobioprovince (Stehlin, 1910; Hürzeler & Engesser, 1976; Hürzeler, 1982, 1983, 1987; Engesser, 1983, 1989; Cordy & Ginesu, 1994; Kotsakis *et al.*, in press) and by the Late Pleistocene ones of Southern Calabria (Bonfiglio, 1978; Bonfiglio & Berdar, 1986). The extra-Mediterranean record includes the mammoths distributed in Wrangel Island, in the Arctic Ocean, which progressively reduced their size between 7.000 and 4.000 yr B.P. (Lister, 1993), the dwarfed deer from the Last Interglacial deposits of Jersey, Channel Islands (Lister, 1989) and those from the Mesolithic deposits of Oronsay, in Inner Hebrides (Grigson, 1981), which were imported by man between about 6.000 and 5.400 yr B.P. and then rapidly became dwarfed.

A peculiar aspect of the Late Pleistocene endemic mammal faunas of the Mediterranean islands is that they are all unbalanced. Large groups, such as perissodactyls, are entirely missing. Outside the Mediterranean, islands with Pleistocene unbalanced faunas occur in the Japanese archipelago, Indonesia, the Canary islands, Madagascar, and off the coast of California.

Not all the faunal elements of the Mediterranean islands arrived at the same time. Some genera are probably relicts from the Tertiary; others are distinctly Pleistocene forms, but there are differences in the degree of specialisation between the ultimate species of the same genus or group in the different island faunas. It is commonly assumed that, before becoming dwarfed, elephants, hippopotami, deer and, presumably, also the oxes of Pianosa and Sicily reached the islands from the closest mainland by temporary landbridges that originated from the lowering of the

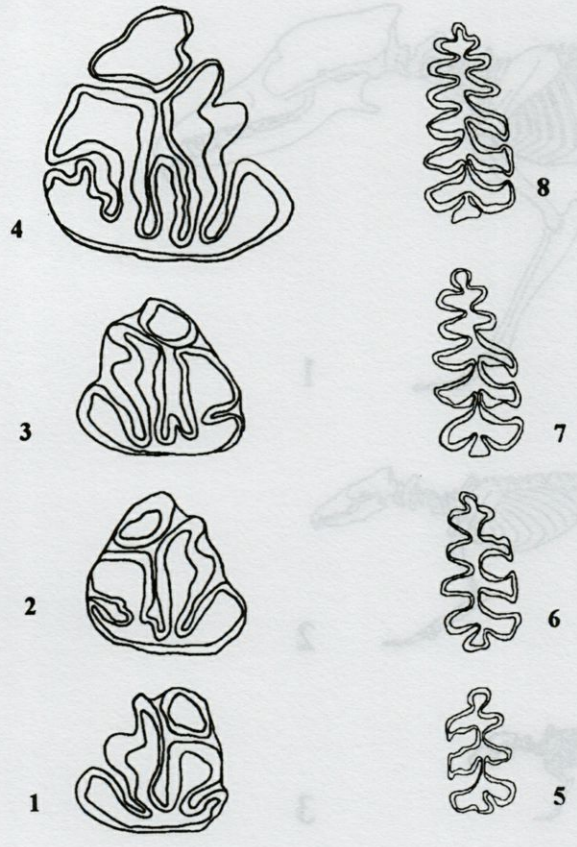

Fig. 3. – 1-4, Gargano *Prolagus* evolutionary sequence from the *P. apricenicus* morphotype (1-3) to the *P. imperialis* morphotype (4); 5-8, Gargano *Microtia* evolutionary sequence from the most primitive (5) to the most derived morphotype (8). Not to scale.

sea-level during the Pleistocene Ice Ages. According to Azzaroli (1971; 1977; 1983), this may be the case of Sardinia and Sicily (Palombo, 1985). On the basis of tectonic arguments, Malatesta (1980) observed that Crete also may have been united to continental Greece during the Pleistocene. However, as noted by Davis (1987), it is difficult to explain why the Pleistocene faunas of the latter islands are relatively rich, compared to that of Cyprus. Perhaps only few species migrated to Cyprus, which was relatively difficult to reach (Azzaroli, 1977). In fact, the bathymetric contours prove that Cyprus was never connected to the mainland, even during the numerous and protracted Pleistocene glacial episodes (Swiny 1988). Sondaar (1977) observed that island faunas were dominated by good swimmers such as elephants, hippopotami and deer and therefore deduced that continental mammals mainly swam to colonize islands. Some authors agreed with this view suggesting that elephants perhaps swam to at least some of the Mediterranean islands (Johnson, 1980). New evidence today shows unequivocally that elephants are actually excellent swimmers. The swimming abilities of hippopotami and deer are also known (Dermitzakis & Sondaar, 1978), though perhaps the latter do not swim as well as elephants and hippopotami. For Davis (1987) this may explain why deer never dared to reach Cyprus while elephants and hippos did. The reason may consist in the long distance, too great for deer, separating the island from the closest mainland. An alternative view, proposed by Azzaroli (1978, in press) is that large mammals and most if not all the small-sized mammals of the Mediterranean islands, migrated only through corridors; maybe, in some cases, along discontinuous bridges of islands and shoals highly selective on the immigrant fauna.

The factors that might be responsible for the peculiar specializations of island mammals are thought to include a contraction of food supply, a reduction of competition, and a decrease in predation (Foster, 1964; Azzaroli, 1971; Sondaar, 1977; Heaney, 1978; Davis, 1984). It is commonly assumed that the absence of large carnivores in most of the islands reveals evidence of unbalanced ecological structures (Sondaar, 1977; Sondaar *et al.*, 1984). As a consequence of the lack of predators, the endemic mammals of the islands may have lost their capacities for defence. However, a survey of paleontological literature yields a considerable amount of Quaternary carnivore fossil species (Pomel, 1853; De Gregorio, 1886; Bate, 1903b; Bate, 1935; Thenius, 1951 and 1962; Ficcarelli & Torre, 1967; Kurtén, 1968; Boekschoten & Sondaar, 1972; Symeonidis & Sondaar, 1975; Malatesta, 1977; Malatesta, 1978; Kotsakis, 1980; Mourer Chauvirè *et al.*, 1980; Alcover *et al.*, 1981; Azzaroli, 1982; Esu *et al.*, 1986; Burgio & Fiore, 1988; Van der Geer, 1988; Weesie, 1988; Eisenmann, 1990; Vigne, 1992; Willemsen, 1992; Wolsan, 1993; Steensma & Reese, in press).

Foster (1964) summarized, in rather general terms, the effects of selective forces on living insular mammals as compared to those distributed on the nearest mainland areas. Size increase is the inevitable price to pay for decreasing of the selective pressure in the restricted insular environments with limited food resources (Reyment, 1983). Size increase, on the other hand, finds a number of different explanations. Butler (1980) suggested that the increase in size of micromammals may likely be a consequence of a paucity of ungulate herbivores. Although the increase in size causes an increase in intraspecific competition, it has an undoubted advantage in terms of endothermic control, because of the more suitable body surface/body volume relation. From studies of island squirrels in southern Asia, Heaney (1978) showed that limited food supply and reduced interspecific competition are also important in determining size. On islands with few species, larger rodents might have evolved to exploit a wider

range of food (Davis, 1987). The increased size of rodents might also have some correlation with the lack of carnivores (Sondaar, 1977). Rodents usually escape predators by hiding in crevices : hence their small size. The absence of carnivores on Mediterranean islands would permit, on the contrary, the survival of larger individuals, which could compete more successfully for limited food resources. Thus dormice of giant proportions would evolve (Davis, 1985). However, island rodents will still be the main item for mainland birds of prey which are present in large numbers on the islands. In fact, a characteristic of fossil island avifaunas is the great number of continental and endemic birds of prey (Sondaar, 1977). There are also mammals which did not change significantly on the islands : for example, lagomorphs, many insectivores and some of the rodents which coexist with the giant forms. Probably on the island they found an ecological niche similar to that existing on the mainland (Sondaar, 1977). This might be the case of *Crocidura zimmermanni* Wettstein, 1953, an endemic "normal size" soricid which has been documented from Crete since early Pleistocene times. The terminal Pleistocene fauna of Corsica and Sardinia is characterized by the occurrence of *Prolagus sardus* (Wagner, 1829), an ochotonid lagomorph the size of a big rat. This animal, which is comparable to hares and rabbits, probably produced many offspring in a rather short time and it is likely that it provided an inexhaustible source of food for the Pleistocene predators of Sardinia and Corsica.

CONCLUSIVE REMARKS

Paleontological evidence shows that Mediterranean and extra-Mediterranean fossil island faunal communities are mainly characterized, compared with coeval mainland communities, by lower diversity, an unbalanced composition and a reduced pressure of predators, mostly due to an absence of large-sized carnivores. A reduction of competition is commonly observed in island communities. This is actually documented in the initial phase of colonization of island habitats. In later times the modifications in body size and species composition seem to be aimed exactly to reduce the inter- and intraspecific competition and to pass to K-selection (specialization and decrease in birth rate : the contrary of r-selection).

Whether the species density modifies in insular conditions cannot be demonstrated on paleontological grounds, but the cases of *Prolagus sardus* and of the Miocene Gargano *Prolagus* seem to suggest that the density may be more or less analogous to that of extant mainland lagomorphs.

The cases of the dwarf deer of Capri (Azzaroli, 1977), of Pianosa (Azzaroli, 1978) and of the dwarf oxes of Pianosa (Azzaroli, 1978) and Sicily (Brugal, 1987) seem to suggest that a relatively short time may be sufficient to produce the endemization of insular faunas, of the order of a few thousands of years. Dwarf mammoths have been reported from Wrangel Island, in the Arctic Ocean, which became dwarfed between 7.000 and 4.000 yr B.P. (Lister, 1993). Outside the Mediterranean basin, other two cases size reduction are represented by the Last Interglacial deer of the island of Jersey, Channel Islands (Lister, 1989), and the Mesolithic deer of the island of Oronsay, in Inner Hebrides (Grigson, 1981). The latter was imported by man between about 6.000 and 5.400 yr B.P. and then became dwarfed.

The archaeozoological record tells us that present day island mammals of the Mediterramean were mostly introduced by Man and that the ecological impact with the new incomers doomed most of the previously distributed endemic forms to a rapid disappearance at least after the Neolithic colonization (7th millennium B.C.) (Alcover, 1980; Davis, 1984; Vigne, 1992; Masseti, 1993). The example of the deer of Oronsay supports the hypothesis that also macromammals introduced by Man in the Mediterranean islands probably undergo a process of endemization. This tendency towards endemization may also explain the occurrence of extant insular micromammals of larger size in respect to their continental counterparts, such as *Crocidura suaveolens cyrnensis,* in Corsica, *Eliomys quercinus liparensis*, in Lipari, *Apodemus sylvaticus ilvanus*, in Elba, *A. sylvaticus hermani*, in Pantelleria (cf. Amori & Masseti, in this volume).

The endemization of island faunas is the result of a normal and repetitive reorganization of few faunal entities distributed in restricted areas with limited resources and in the absence of large-sized carnivores. In its common acception, a "syndrome" is a "number of symptoms which collectively indicate an often abnormal condition of the body" (Oxford advanced learner's dictionary of current English, 1974). The part of a community which underwent endemization would thus represent the "symptoms" which on the whole form the "insular syndrome". We should thus expect that a residual part of the fauna would be "normal", in the sense of maintaining its original continental aspect and composition. This, however, is never verified on islands, provided a sufficient time of endemization (Zammit-Maempel, 1989), as demonstrated by several paleontological examples. By and large, the impression is that all the modifications that occur in island mammals may be the necessary result of a tendency towards a redefinition of ecological equilibria under very peculiar environmental conditions (cf. MacArthur

& Wilson, 1967; Blondel & Vigne, 1993). The pioneer faunas are in obvious state of disequilibrium in insular environment and are subjected to r-selection. Later on, the modifications in body size and population density are aimed to reduce the inter- and intraspecific competition and thus tend to reestablish new equilibria. K-selection conditions are finally reached.

In the light of all this facts, is it still the case to talk about "insular syndrome"?

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REFERENCES

ACCORDI B., 1955. *Hippopotamus pentlandi* H. von Meyer del Pleistocene di Sicilia. *Paleontogr. Italica* **50** : 52 p.

ACCORDI B., 1962. Some data on the Pleistocene stratigraphy and related pygmy mammalian faunas of Eastern Sicily. *Quaternaria* **6** : 415-430.

ACCORDI B., 1972. Lo scavo della "Grotta Simonelli" con cervi nani del Quaternario, effettuato a Creta nel 1971 dall'Istituto di Geologia e Paleontologia dell'Università di Roma, con il finanziamento dell'Accademia Nazionale dei Lincei. *Quad. Acc. Naz. Lincei* **167** : 1-17.

ALCOVER J.A., 1980. Note on the origin of the present mammalian fauna from the Balearic and the Pityusic islands. *Miscellania zool.* **6** : 141-149.

ALCOVER J.A., S. MOYA'-SOLA' & J. PONS-MOYA', 1981. Les Quimeres del Passat. Editorial Moll, Ciutad de Mallorca, 261 p.

AMBROSETTI P., 1968. The Pleistocene dwarf elephants of Spinagallo (Siracusa, South-eastern Sicily). *Geol. Romana* **7** : 277-398.

AMBROSETTI P., 1969. Rappresentanti del genere *Leithia* nel Pleistocene della Sicilia. Scritti in onore di Angelo Pasa. *Mus. Civ. St. Nat. Verona, Mem. Fuori Ser.* **3** : 75-80.

AMBROSETTI P., A. AZZAROLI & T. KOTSAKIS, 1980. Mammiferi del Plio-Pleistocene delle isole. *In* I Vertebrati Fossili Italiani, catalogo della mostra di Verona : 243-248.

AMORI G. & M. MASSETI. Does the occurrence of predators on Central Mediterranean islands affect the body size of micromammals? 13[e] Coll. Internat. Mammalogie, Banyuls-sur-Mer, 13-15 Oct. 1995, in this volume.

ANDREWS C.W., 1915. A descritpion of the skull and skeleton of a peculiar modified Rupicaprinae Antelope (*Myotragus balearicus*) with a notice as a new variety (*Myotragus volcaiens* var. *major*). *Phyl. Trans. Roy. Soc. London* (B) **206** : 281-305.

AZZAROLI A., 1952. La sistematica dei cervi giganti e i cervi nani delle isole. *Atti Soc. Tosc. Sc. Nat.*, **59** : 119-127.

AZZAROLI A., 1962. Il naniso dei cervi insulari. *Paleont. It.* **26** : 1-31.

AZZAROLI A., 1971. Il significato delle faune insulari quaternarie. *Le Scienze* **30** : 84-93.

AZZAROLI A., 1977. Considerazioni sui mammiferi fossili della isole mediterranee. *Boll. Zool.* **44** : 201-211.

AZZAROLI A., 1978. Fossil mammals from the island Pianosa in the Northern Tyrrhenian Sea. *Boll. Soc. Paleont. It.* **17** : 15-27.

AZZAROLI A., 1979. Critical remarks of some Giant Deer (genus *Megaceros* Owen) from the Pleistocene of Europe. *Paleontograph. It.* **71** : 5-16.

AZZAROLI A., 1982. Insularity and its effects on terrestrial vertebrates : evolutionary and biogeographic aspects. *In* Palaeontology; Essential of Historical Geology. Edited by E. Montanaro Gallitelli. S.T.E.M. Mucchi, Modena, 193-215.

AZZAROLI A., 1983. Biogeografia dei mammiferi della Sardegna. *Lavori Soc. It. Biogeogr.* **8** : 35-52.

AZZAROLI A., 1990. Lezioni di Paleontologia dei Vertebrati. Pitagora Editrice, Bologna, 375 p.

AZZAROLI A., in press. Processes of island colonization by terrestrial organisms. *Lavori Soc. It. Biogeogr.* **18** : 000.

BACHMAYER F., N. SYMEONIDIS, R. SEEMANN & H. ZAPFE, 1984. Die Ausgrabungen in der Zwergelefantehöle der Insel Tilos (Dodecanes, Griechenland) im Jahr 1983. *Akad. Wissenschaft Mathem-Naturw. Kl. Abt. I*, 193. Bd 6 bis **10** : 321-328.

BATE D.M.A., 1903a. Preliminary note on the discovery of a pygmy elephant in the Pleistocene of Cyprus. *Proc. Roy. Soc. London* **73** : 498-500.

BATE D.M.A., 1903b. The mammals of Cyprus. *Proc. Zool. Soc. London* **2** : 341-348.

BATE D.M.A., 1904a. Further note on the remains of *Elephas Cypritotes* from a cave-deposit in Cyprus. *Phyl. Trans. Roy. Soc. London* B **197** : 347-460.

BATE D.M.A., 1904b. Further note on the remains of *Elephas Cypriotes* Bate. *Geol. Magazine* V **1** : 325-326.

BATE D.M.A., 1904c. Further note on the remains of *Elephas Cypriotes* Bate from a cave-deposit in Cyprus. *Proc. Roy. Soc. London* : 120-121.

BATE D.M.A., 1906. The Pygmy Hippopotamus of Cyprus. *Geol. Mag.* **3** : 241-245.

BATE D.M.A., 1909. Preliminary note on a new artiodactyle from Majorca, *Miotragus balearicus*, gen. et sp. nov. *Geol. Magazine* **6** : 385-388.

BATE D.M.A., 1916, On a small Collection of Vertebrate Remains from the Har Dalam Cavern. Malta : with Note on a new species of the genus *Cignus*. *Proc. Zool. Soc. London* **28** : 421-426.

BATE D.M.A., 1935. Two new mammals from the Pleistocene of Malta, with notes on the associated fauna. *Proc. Zool. Soc. London* : 247-264.

BLONDEL J. & J.D. VIGNE, 1993. Space, Time, and Man as Determinants of Diversity of Birds and Mammals in the Mediterranean Basin. *In* : Species Diversity in Ecological Communities, R.E. Ricklefs & D. Schluter Eds., Chicago University Press : 135-146.

BOEKSCOTEN G.J. & P.Y. SONDAAR, 1972. On the fossil mammals of Cyprus. *Konikl. Nedrel. Akad. Vetensch. Proceed.* **75** : 306-338.

BONFIGLIO L., 1978. Resti di cervide (Megacero) nell'Eutirreniano di Bovetto (RC). *Quaternaria* **20** : 87-108.

BONFIGLIO L. & A. BERDAR, 1986. Gli elefanti del Pleistocene superiore di Archi (RC) : nuove evidenze di insularità della Calabria durante il ciclo Tirreniano. *Boll. Soc. Paleont. Ital.* **25** (1) : 9-34.

BRUGAL J.P., 1987. Cas de "nanisme" insulaire chez l'auroch. *Acta 112^{e} Congr. Natl. Soc. Sav. Lyon* **2** : 53-66.

BURGIO E. & M. FIORE, 1988. *Nesolutra trinacriaea* n. sp., loutra quaternaria della Sicila. *Boll. Soc. Palent. Ital.* **27** : 259-275.

BURLEIGH R. & J. CLUTTON-BROCK, 1980. The Survival of *Myotragus balearicus* Bate, 1909, into the Neolithic on Mallorca. *Jour. Arch. Sci.* **7** : 385-388.

BUTLER P.M., 1980. The giant erinaceid insectivore *Deinogalerix* Freudenthal from the Upper Miocene of Gargano, Italy. *Scripta Geol.* **57** : 1-72.

CALOI L., T. KOTSAKIS & M.R. PALOMBO, 1986. La fauna a vertebrati terrestri del Pleistocene delle isole del Mediterraneo. *Geologica Romana* **25** : 235-256.

CALOI L. & A. MALATESTA, 1974. Il cervo pleistocenico di Sardegna. *Mem. Ist. Ital. Paleont. Um.* **2** : 163-247.

CAPASSO BARBATO L., 1992. Nuova specie di Cervide del Pleistocene di Creta. *Atti Acc. Naz. Lincei* **9** : 183-220.

CORDY J.M. & S. GINESU, 1994. Fiume Santo (Sassari, Sardaigne, Italie) : un nouveau gisement à Oréopitèque (*Oreopithecidae, Primates, Mammalia*). *C. R. Acad. Sci. Paris* **318** (2) : 697-704.

DAVIS S.J.M., 1984. Khirokitia and its mammal remains. A Neolithic Noah's ark. ital : Le Brun A. Ed. : Fouilles récentes à Khirokitia (Chypre), 1977-1981, vol. 1, Editions Recherches sur les Civilisations, Paris : 147-162.

DAVIS S.J.M., 1985. Tiny elephants and giant mice. *New Scientist* **3** : 25-27.

DAVIS S.J.M., 1987. The Archaeology of Animals. B.T. Batsford Ltd, London, 224 p.

DERMITZAKIS S.J.M. & P.Y. SONDAAR, 1978. The importance of fossil mammals in reconstructing paleogeography with special reference to the pleistocene Aegean archipelago. *Ann. Geograph. Pays Helleniques* **29** : 808-840.

DE GIULI C., F. MASINI, D. TORRE & V. BODDI, 1986. Endemism and bio-chronological reconstructions : the Gargano case history. *Boll. Soc. Paleont. Ital.* **25** (3) : 267-276.

DE VOS J., 1979. The endemic Pleistocene deer of Crete. I-II. *Proc. Kon. Ned. Akad. Wetensch.* B **82** : 59-90.

DE VOS J., 1984. The endemic Pleistocene deer of Crete. *Verh. Kon. Ned. Akad. Wetensch. Afd. Natk. Eerste Reeks* **31** : 1-100.

EISENMANN V., 1990. Caractères juvéniles et affinités systématiques du crâne de *Cynotherium sardous*, canidé endémique pléistocène de Sardaigne. *C. R. Acad. Sci. Paris* **310** : 433-439.

ENGESSER B., 1983. Die jungtertiären Kleisäuger des Gebietes der Maremma. 1 Teil : Gliridae (Rodentia, Mammalia). *Eclog. Geol. Helv.* **76** (3) : 763-780.

ENGESSER B., 1989. The late Tertiary small mammals of the Maremma region (Tuscany, Italy). 2nd part : Muridae and Cricetidae (Rodentia, Mammalia). *Boll. Soc. Paleont. Ital.* **28** (2-3) : 227-252.

ESU D., T. KOTSAKIS & E. BURGIO, 1986. I vertebrati e i molluschi continentali pleistocenici di Poggio Schinaldo (Palermo, Sicilia). *Boll. Soc. Geol. It.* **105** : 233-241.

FABIANI R., 1928. Cenni sulle raccolte di Mammiferi quaternari del Museo geologico della R. Università di Palermo e sui risultati di nuovi assaggi esplorativi. *Boll. Assoc. Min. Sic.* **4** : 25-34.

FALCONER H. 1862. On the fossil remains of *Elephas melitensis*, an extinct pygmy species of elephant and on other mammalia, etc., from the ossiferous caves of Malta. *Paleont. Mem. Notes* **2** : 292-308.

FICCARELLI G. & D. TORRE, 1967. Il mustelide *Enhydrictis galictoides* del Pleistocene della Sardegna. *Paleontogr. Ital.* **63** : 139-160.

FONS R., M.D.L. MATHIAS, S. MAS-COMA & R. LIBOIS, 1995. The insular syndrome : the case of micromammals and their helminth parasites. Abstract Book 2nd European Congr. Mammalogy, Southhampton Univ., 217.

FOSTER J.B., 1964. Evolution of mammals on islands. *Nature* **202** : 234-235.

FREUDENTHAL M., 1971. Neogene vertabrates from the Gargano Peninsula, Italy. *Scripta Geol.* **3** : 1-10.

GLIOZZI E. & A. MALATESTA, 1980. The Quaternary goat of Capo Figari (Northeastern Sardinia). *Geol. Romana* **19** : 295-347.

GRIGSON C., 1981. Mammals and Man on Oronsay : Some Preliminary Hypotheses Concerning Mesolithic Ecology in the Inner Hebrides. *B.A.R. Int. Ser.* **94** : 163-180.

HEANEY L.R., 1978. Island area and body side in insular mammals : evidence from the tri-colored squirrel (*Callosciurius prevosti*) of southeast Asia. *Evolution*, **32** : 29-44.

HOUTIKAMER J.L. & P.Y. SONDAAR, 1979. Osteology of the fore limb in the Pleistocene dwarf hippopotamus from Cyprus with special reference to phylogeny and function. *Kon. Ned. Akad. Wetensch.* **82** : 411-448.

HÜRZELER J.H., 1982. Sur le suidé du lignite de Montebamboli (prov. Grosseto, Italie). *C. R. Acad. Sci. Paris* sér. 2, **296** : 697-699.

HÜRZELER J.H., 1983. Un alcélaphiné aberrant (Bovidé, Mammalia) des "lignites de Grosseto" en Toscane. *C.R. Acad. Sc. Paris* s. 2, **296** : 497-503.

HÜRZELER J.H., 1987. Die Lutrinen (Carnivora, Mammalia) aus dem "Grosseto-lignit" der Toskana. *Schweiz. Pal. Abh.* **110** : 25-48.

HÜRZELER J.H. & B. ENGESSER, 1976. Les faunes de mammifères néogènes du bassin de Baccinello (Grosseto, Italie). *C.R. Acad. Sci. Paris*, sér. 2, **283** : 333-336.

JOHNSON D.L., 1980. Problems in the land vertebrate zoogeography of certain islands and the swimming powers of elephants. *Journ. Biogeography* **7** : 383-398.

KOTSAKIS T., 1980. Osservazioni sui vertebrati quaternari della Sardegna. *Boll. Soc. Geol. It.* **99** : 151-165.

KOTSAKIS T., 1990. Isular and non insular vertebrate fossil faunasin the Eastern Mediterranean islands. International Symposium "Biogeographical Aspects of Insularity". *Atti Conv. Lincei* **85** : 289-334.

KOTSAKIS T., G. MARRAS & M.R. PALOMBO. An *Oreopithecus* fauna from Late Miocene of Sardinia. *Riv. It. Pal. Strat.* in press.

KURTÉN B., 1968. Pleistocene Mammals of Europe. Weidenfeld & Nicholson, London, 317 p.

KUSS S.E., 1969. Die erste pleistozäne Säugetierfauna der Insel Kasos (Griechenland). *Ber. Naturf. Ges. Freiburg. i. Br.* **58** : 169-177.

KUSS S.E., 1973. Die pleistozäne Säugetierfaunen der Mediterranean Inseln. Ihr Alter und ihre Herkinft. *Ber. Naturf. Ges. Freiburg. i. Br.* **63** : 49-71.

KUSS S.E., 1975. Die pleistozäne Hirsche der ostmediterranen Inseln Kreta, Kasos, Karpathos und Rhodos (Griechenland). *Ber. Naturf. Ges. Freiburg. i Br.* **65** : 25-79.

LEINDERS J.M. & P.Y. SONDAAR, 1974. On functional fusion in footbones of ungulates. *Z. Säugetierk.* **39** : 109-115.

LEITH ADAMS A. 1870. Notes of a naturalist in the Nile Valley and Malta. Edmonston & Douglas, Edinburgh.

LEITH ADAMS A. 1875. On the dentition and osteology of the Maltese fossil elephant. *Trans. Zool. Soc. London* **9**.

LISTER A.M., 1989. Rapid dwarfing of red deer on Jersey in the Last Interglacial. *Nature* **342** : 539-542.

LISTER A.M., 1993. Mammoths in miniature. *Nature* **362** : 288-289.

McARTHUR R.H. & E.O. WILSON, 1967. The Theory of Island Biogeography. Princeton, N.J., Princeton University Press, 203 p.

MALATESTA A., 1980. Dwarf deer and other Late Pleistocene fauna from Simonelli Cave in Crete. *Acad. Naz. Lincei Quad.* **249** : 1-97.

MASSETI M., 1993. Post-Pleistocene variations of the non-flying terrestrial mammals of some Italian islands. *Suppl. Ric. Biol. Selvaggina* **21** : 201-209.

MAZZA P., 1986a. *Prolagus* (Ochotonidae, Lagomorpha, Mammalia) from Neogene fissure fillings in Gargano (Southern Italy). *Boll. Soc. Paleont. Ital.* **25** (2) : 159-185.

MAZZA P., 1986b. Further data on the Gargano (Southern Italy) *Prolagus* (Ochotonidae, Lagomorpha, Mammalia). *Boll. Soc. Paleont. Ital.* **25** (3) : 203-211.

MAZZA P., 1987. *Prolagus apricenicus* and *Prolagus imperialis* : two new Ochotonids (Lagomorpha, Mammalia) of the Gargano (Southern Italy). *Boll. Soc. Paleont. Ital.* **26** (3) : 233-243.

MAZZA P. & M. RUSTIONI. The fossil Artiodactyls from Scontrone (Abruzzo, Central Italy). *Boll. Soc. Paleont. Ital.*, Modena in press.

MAZZA P., M. RUSTIONI, G. ARUTA & E. DI CARLO, 1995. A Messiniam *Prolagus* from Capo di Fiume quarry (Palena, Abruzzo, Central Italy). *Boll. Soc. Paleont. Ital.* **34** (1) : 55-66, Modena.

MOURER-CHAUVIRE' C., J.A. ALCOVER, S. MOYA' & J. PONS, 1980. Une nouvelle forme insulaire d'effraie géante, *Tyto balearica* n. sp. (Aves Strigiformes) du Plio-Pléistocène des Baléares. *Geobios* **3** : 803-811.

PALOMBO M.R., 1985. I grandi mammiferi pleistocenici delle isole del Mediterraneo : tempi e vie di migrazione. *Boll. Soc. Paleont. It.* **24** : 201-224.

PETRONIO C., 1979. I roditori pleistocenici della grotta di Spinagallo. *Geologica Rom.* **9** : 149-194.

REESE D.S., 1995. The Pleistocene vertebrate sites and fauna of Cyprus. Geol. Surv. Dept. Min. Agriculture Natural Resources and Environ., Bull. 9, Nicosia.

REYMENT R.A., 1983. Palaeontological aspects of island biogeography : colonization and evolution of mammals on Mediterranean islands. *Oikos* **41** : 299-306.

SIMONELLI V., 1907. Mammiferi quaternari dell'isola di Candia. I. *Mem. Acc. Sc. Inst. Bologna* VI **4** : 455-471.

SIMONELLI V., 1908. Mammiferi quaternari dell'isola di Candia. II. *Mem. Acc. Sc. Inst. Bologna* VI **5** : 103-111.

SCHLAGER N., 1991. Archäologische Gelandeprospektion Südostkreta. Erste Ergebnisse. *Österr. Archäol. Inst. Berichte Materialen* **2** : 3-26.

SONDAAR P.Y., 1971. Palaeozoogeography of the Pleistocene Mammals from Aegean. *In* STRID A. (Ed.) : Evolution in the Aegean. *Opera Botanica* **20** : 65-70.

SONDAAR P.Y., 1977. Insularity and its Effects on Mammal Evolution. Hecht M.K. Goody P.C. Hecht B.M. Eds., Major Patterns in Vertebrate Evolution. NATO Advanced Study Inst., (A) 14. Plenum Press, New York/London : 671-707.

SONDAAR P.Y., 1986. The island Sweepstakes. *Natural History* **9** : 50-57.

SONDAAR P.Y., G. KLEIN HOFMEJIER, M. SANGES & D. ESU, 1984. First report on a Paleolithic culture in Sardinia. *B.A.R. Int. Ser.* **229** : 29-47.

SONDAAR P.Y., M. SANGES, T. KOTSAKIS & P.L. DE BOER, 1986. The Pleistocene Deer Hunter of Sardinia. *Geobios* **19** : 17-25.

STEENSMA K.J. & D.S. REESE. The Aetokremnos Genet. First Report Volume in press.

STEHLIN H.G., 1910. Zur Revision der europäischen Anthracotherien. *Verhandl. Naturforsch. Gesellsch. Basel* **21** : 165-185.

STEHLIN H.G., 1928. Ueber eine altepleistozäne Säugetierfauna von der Inzel Pianosa. *Ecl. Geol. Helv.* **21** : 433-469.

SWINY S., 1988. The Pleistocene fauna of Cyprus and recent discoveries on the Akrotiri peninsula. *Report Dep. Ant. Cyprus* **1** : 1-14.

SYMEONIDIS N., F. BACHMEYER & H. ZAPFE, 1973. Grabungen in der Zwergelefanten-Höle "Charkadio" auf der Inseln Tilos (Dodecanese, Griechenland). *Ann. Naturhistor. Mus. Wien* **77** : 133-139.

SYMEONIDIS N. & P.Y. SONDAAR, 1975. A new otter from the Pleistocene of Crete. *Ann. Geol. Pays Hellen.* **27** : 11-24.

THENIUS E., 1951. Die neuen paläontologischen Ausgrabungen in Hunsheim (NO). *Anz. Österr. Akad. Wiss. math. naturw.* 341-343.

THENIUS E., 1962. Die Grosssäugetiere des Pleistozäns von Mitteleuropa. *Z. Säugetierk.* **27** : 65-83.

THEODOROU G.E., 1985. Pleistocene elephants from Crete (Greece). *Modern Geology* **10** : 235-242.

VAUFREY R., 1929. Les éléphants nains des Iles méditerranéennes et la question des isthmes pléistocènes. *Arch. Inst. Paléont. Humaine* Mem 6, Masson et C. Eds., Paris.

VIGNE J.-D., 1992. Zooarcheology and the biogeographical history of the mammals of Corsica and Sardinia since the last ice age. *Mammal Review* **2** : 87-96.

WALDREN W.H., 1982. Balearic prehistory ecology and cultura. The excavation and study of certain caves, rock shelters and settlements. *B.A.R. Int. Ser.* 149.

WEESIE P.D.M., 1988. The Quaternary Avifauna of Crete, Greece. *Palaeovertebrata* **18** : 1-94.

WILLEMSEN G.F., 1992. A revision of Pliocene and Quaternary Lutrinae from Europe. *Scripta Geol.* **101** : 1-115.

WOLSAN M., 1993. Phylogeny and classification of early European *Mustelidae* (Mammalia, Carnivora). *Acta theriol.* **38** : 345-384.

ZAMMIT-MAEMPEL G., 1985. Biology and ecology of Ghar Dalam Cave, Malta. *Att. Soc. Tosc. Sc. Nat. Mem.* **92** : 351-374.

ZAMMIT-MAEMPEL G., 1989. Ghar Dalam cave and deposits. P.E.G. Ltd, Malta. 74 p.

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