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Evolution and Extinction of Plio-Pleistocene Island Ungulates

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Summary

The pattern of faunal evolution on islands differs fundamentally from that on the mainland. The patterns of faunal evolution of the Pliocene-Pleistocene Japanese and Mediterranean islands are reviewed and compared, in order to understand the origin of their differences. In general, it can be said that the major faunal turnovers on the mainland are triggered by global climatological changes. On the islands, it were mainly changes in paleogeography and the new arrival of predators, among others humans. Three types of Pleistocene islands are recognized. Firstly, continental islands, for example Sardinia/Corsica, secondly, oceanic-like islands, for example Crete, Cyprus, Central Ryukyu Islands, Japan, and thirdly, islands connected with the mainland through a filter bridge, for example Late Pleistocene Sicily and Japan. The origin of the founder population of the first type is a Pliocene mainland fauna, while the second type is colonized by overseas sweepstake dispersal. The third type is characterized by filter dispersal from the continent.

The lack of transitional faunas between the founder population and the endemic population has led us to the conclusion that the evolutionary scenario in the ungulate fauna on islands of the first and second type is characterised by rapid major evolutionary changes in the founder poulation, explained as adaptation to the island environment, followed by a relatively static period, which in some cases ends abruptly with a dramatic faunal turnover. The duration of this equilibrium differs from island to island, but as a rule comes to an end after new arrivals. Again there is no transitional fauna between the original endemic fauna and the newer endemic fauna. This is seen on Crete during the Late Pleistocene, where the dwarf hippo and dwarf elephant are replaced by deer and a larger elephant, both endemic. On some islands, the arrival of humans caused a dramatic faunal turnover, as on Sardinia during the early Paleolithicum, or only extinctions without the arrival of new taxa, as on Cyprus. Neolithization of islands causes extinction of the endemic impoverished island fauna, which is replaced by domesticated live stock they brought in.

The third type of island is less predictable in its faunal content, as the effect of a filter bridge is highly dependent on the nature of the filter. In the case of Sicily, the ungulate fauna is characterized by a gradually replacement, where the smaller endemics of the

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previous period coexist with the newly arrived mainland taxa.

Introduction

Zoogeographically, three types of islands can be recognized: continental and oceanic islands (Darlington, 1957) and oceanic-like islands (Alcover *et al*., 1998).
Continental islands became isolated from the mainland through subsidence of the isthmus of a peninsula, and thus its ancestral fauna is in principle a mainland fauna. The arrival is characterized through corridors or filters (*sensu* Simpson, 1965). Example is Sardinia during the Early Pliocene, with a hyenid in the impoverished fauna. The opposite situation takes place when an island gradually becomes connected to the mainland, and a mainland fauna arrives through filters or corridors. Examples are Sicily and Japan during the Late Pleistocene, when the *Equus hydruntinus* and *Sinomegaceros* faunas respectively meet the *E. mnadriensis* and *Palaeoloxodon naumanni* fauna.
Oceanic islands have arisen beneath the sea, and the ancestral fauna came overseas. Oceanic-like islands have been connected to the mainland in a remote past, and the ancestors of the present fauna came overseas, as in the case of true oceanic islands. In both cases, oceanic as well as oceanic-like islands, the most common arrival is through sweepstake dispersal (*sensu* Simpson, 1965), in which case only a very few taxa will be successful colonizors of the island: only those that swim and/or float and live in herds, like elephants and deer (Sondaar, 1977). Examples are Sicily during the Middle Pleistocene with the *Elephas falconeri* fauna and Crete during the late Middle / early Late Pleistocene with the *Candiacervus* fauna (De Vos & Dermitzakis, 1986).

The paleogeography of many islands is complex, with subsequent submerging and emerging, due to sea level changes and tectonic processes. For example, Crete was part of the mainland during the Miocene, submerged in the Pliocene, and got its present shape in the Pleistocene. Other islands are nowadays part of the mainland, like Monte Gargano (Southern Italy), now a peninsula, but an island in the Miocene/Pliocene (Freudenthal, 1971) with an endemic deer (Leinders, 1984; Van der Geer, 1999). Archipelagoes, finally, are not necessarily a unit, for example, the Northern Ryukyu Islands should be reckoned to Japan in zoohistorical respect, while the Central and Southern Ryukyu Islands form an independent island group.

Sicily

From the Early Pleistocene through the Holocene four different faunal associations can be recognized on Sicily. From old to young these are as follows.

1. Monte Pellegrino fauna, Palermo, Early / Middle Pliocene, MN 14-15. This fauna is characterised by an endemic micro-fauna, with a large murid (*Apodemus maximus*), a glirid (cf. *Maltamys*), a large sized ctenodactilid (*Pellegrinia panormensis*), a leporoid (*Hypolagus* sp), a soricid (*Episoriculus* sp) and a mustelid (*Mustelercta arzilla*). The origin of this faunule is best explained through an ancestral stock of a continental

association which became isolated soon after the Messinian (Kotsakis, 1990). It replaced the balanced Gravitelli fauna (MN 13, Alberdi *et al*., 1997), consisting of the hippo *Hexaprotodon crusafonti*, several bovids (*Gazella deperdita, 'Antilope', Tragoceros,* ?*Parabos),* a rhino, and an elephant (*Zygolophodon borsoni*). Zampetti *et al*. (2000) suggest a 'passive' arrival (through isolation) of the Monte Pellegrino fauna during the Turolian to Middle Pliocene, in which period indeed a very high sea level can be observed (Haq *et al*., 1998), however, none of the large Gravitella taxa are found sofar in the Pellegrino fauna. This has probably a taphonomic reason, as from the Gravitella fauna no small mammals are known, while the Pellegrino fauna contains only micromammals, which bear an African stamp.

2. *Elephas falconeri* fauna, Spinagallo (lower cavity; Accordi & Colacicchi, 1962), Comiso, Chiaramonte Gulfi (Bonfiglio et al., 1992); early Middle Pleistocene, 0,7 Ma - 0,3 Ma. This is a typically unbalanced, impoverished island fauna, which is characterized by *Elephas falconeri (E. melitensis* is just the smaller form of this sexually dimorphic species, Ambrosetti, 1968*)*, *Crocidura sicula* (= *C. esuae*, see Hutterer, 1991), *Leithia cartei* and *Leithia melitensis*. Left overs from the preceding Monte Pellegrino fauna are not known. The association of a pygmy elephant with an endemic soricid and one or two rodent taxa is common for Pleistocene Holarctic islands and indicates that the founder population came on the island by sweepstake dispersal. Sicily was therefore an oceanic island in the early Middle Pleistocene. The time interval between the Pellegrino fauna and *Elephas falconeri* fauna is characterized by vulcanic activity (eolian vulcanismus) and this, together with eustatic sea-level changes, might have caused the extinction of the Monte Pellegrino fauna (Agnesi *et al*., 1998). During this period, Sicily's shape was very similar to the present shape (Agnesi *et al*., 1998).
3. *Elephas mnaidriensis* fauna, Spinagallo (main cave), Coste di Gigia, Acquedolci (Bonfiglio, 1992), Maddalena Peninsula (Accordi, 1963), Contrada Cimillà (Bonfiglio *et al*., 1992); late Middle Pleistocene, 0,3 Ma - 0,02 Ma. In the middle Galerian, the dwarf elephant *E. falconeri* is replaced by an elephant, in size and proportion, more close to the mainland forms. In addition, the other newly arrived ungulates are also closely related to the late Middle Pleistocene mainland ungulates, and are all somewhat reduced in size (about 20%). The ungulates present are *Bos primigenius siciliae*, *Bison priscus siciliae*, *Hippopotamus pentlandi, Cervus siciliae*, and *Megaceroides carburangelensis*. In association with these ungulates, *Canis lupus* and *Panthera leo spelaea* are found. The micromammals (*Crocidura sicula, Leithia melitensis*) are remnants of the preceeding fauna. The *E. mnaidriensis* fauna is a balanced, slightly impoverished mainland fauna, and indicates that the ancestral stock came overland. This is confirmed by the low sea level during that period (Haq *et al*., 1998). The fauna points to a certain degree of isolation, explained as a peninsula not reachable from the mainland for all taxa (filter route). Although not in association, lithic artefacts are found along the terraces of the rivers Simento, Dittaino, and Gornalunga that can be placed in the same time interval
4. *Equus hydruntinus* fauna, S. Teodoro, Castello, Late Pleistocene, 0,02 Ma. In the middle Galerian (late MmQ 4), again a clear faunal change can be observed , resulting

in all local ungulates being replaced by normal sized mainland taxa: *E. hydruntinus, E. caballus, Bos primigenius, Cervus elaphus*. This period coincides with the lowest sea level since the Miocene (Haq *et al*., 1998). Of special interest is the first occurence of a member of the genus *Equus*. The faunal turnover is not abrupt, as in the faunal complex of Castello elements of the *Elephas mnaidrienses* are found in association with *Equus hydruntinus*. In the Late Pleistocene cave deposits of Sicily there is evidence for the association of the *E. hydruntinus* fauna and lithic artefacts made by *Homo sapiens* (Bonfiglio & Piperno, 1996).

The successive faunas can be summarized thus,

1. Monte Pellegrino fauna, origin: continental island fauna, age: Early-Middle Pliocene, extinction: submerging of the island.
2. *Elephas falconeri* fauna, origin: oceanic island fauna, age: ca 700.000-300.000, extinction: arrival of balanced continental fauna by filter bridge
3. *Elephas mnadriensis* fauna, origin: mainland fauna, age: 300.000-20.000, extinction: arrival of mainland fauna by land connection
4. *Equus hydruntinus* fauna, origin: land connection, age: 20.000-10.000

Mallorca / Menorca

There is a well-documented sequence of terrestrial vertebrates from the Gymnesic Islands, mostly in karstic deposits (Alcover, 1992; Sondaar *et al*., 1995b), from which it becomes clear that Mallorca / Menorca can be considered true islands in the whole Plio-Pleistocene paleozoographical unit, and not continental islands, as their fauna is not balanced, moreover, there are no indications for the presence of a mainland fauna on the islands. Obviously, even during the Messinian event, there was no full land vertebrate fauna interchange, possibly due to salty deserts that acted as an ecological filter (Alcover, 1987).

The following faunal units are recognized,

1. *Insulotragus* fauna, Mallorca, Early / Middle Pliocene. The new caprid genus *Insulotragus* includes the larger *M. pepgonellae* (Early or Middle Pliocene), and the smaller *M. antiquus* (late Middle Pliocene) (Bover & Alcover, this volume). This fauna came on the Gymnesics during the Messinian event (5.35 Ma ago), and replaced the endemic Miocene *Gymnesicolagus* fauna (S. Margalida, S. Llorenç on Mallorca, Punta Nati 2 on Menorca) . *Insulotragus* might be very well related to the Plio-Early Pleistocene caprine of Sardinia, but not directly with *Nesogoral*, whose ancestral stock came in the Middle Pleistocene on the island Sardinia/Corsica (fig. 1). *Insulotragus antiquus* is found in assemblages with the glirid *Hypnomys waldreni*. It might be that during the same period a peculiar insular vertebrate assemblage populated Menorca, consisting of a giant tortoise (*Cheirogaster gymnesica*), a giant leporid (aff. *Alilepus* n. sp.) with low gear locomotion (Alcover, 2000), and a large dormouse (*Muscardinus cyclopeus*), but the fauna has not been dated yet. An alternative dating is an intra-

Messinian age (Agustí & Moyà-Solà, 1990).
2. *Myotragus kopperi* - *Hypnomys intermedius* fauna, Mallorca, Plio-Pleistocene boundary or Early Pleistocene. This caprine differs essentially from the previous *Insulotragus* by monophyodonty of the incisors (Bover & Alcover, 2000a), more medial orbits and fusions in the tarsus (Bover & Alcover, this volume). It is the first occurrence of the genus *Myotragus* on the Gymnesic Islands.
3. *Myotragus bateae* - *Hypnomys* sp. fauna, Mallorca, Early / Middle Pleistocene. The species *M. bateae* was originally named *M. batei* Crusafont and Angel 1966, but renamed and emended by Bover & Alcover 2000b), to include the Menorcan material previous assigned to *M. binigausensis*.
4. *Myotragus balearicus* - *Hypnomys morpheus*, Mallorca, late Middle Pleistocene to Holocene. On Menorca, *M. balearicus* and *H. mahonensis* are found in Late Pleistocene and in Holocene deposits; for the Middle Pleistocene, no remains have been recovered. It has been suggested (Sondaar *et al*., 1995b) that *M. balearicus* replaced *M. binigausensis* on Menorca.

The successive faunas can be summarized thus,

1. *Insulotragus* fauna, origin: mainland fauna, age: Pliocene, extinction: evolution into the next fauna
2. *Myotragus* faunas, origin: oceanic island fauna, age: Late Pliocene-Holocene, extinction: arrival Neolithic humans

From the faunal units it becomes clear that the whole Pleistocene period is characterized by stasis. The fauna did not effectively change in composition, nor did *Myotragus* itself change much in morphology from the Early Pliocene until colonization of the islands by humans took place (Alcover *et al*., 1994; Alcover *et al*., 1998; Sondaar *et al*., 1995b). Only a very gradual change in the composition of the Gymnesic Island fauna takes place. There are some evolutionary changes on the specific level in *Myotragus*, however, these changes cannot be related to global events. Gradually, the genus *Myotragus* evolved endemic insular characters, like hypsodonty, reduction in dental elements, and a low-gear locomotion. The low-gear locomotion is not only inferred from anatomy, but also from footprints (Quintana, 1993). M*yotragus* became extinct in the Holocene.
The Gymnesic Islands could be classified as oceanic-like islands during the Plio-Pleistocene, and in the Holocene till the arrival of *Homo*.

Eivissa / Formentera

The Pityusic islands differ in their faunas from all other Mediterranean islands, as they have only two faunal units in Plio- / Pleistocene period, and moreover, the second faunal unit is an exceptionally unbalanced fauna, with only flying vertebrates, and one land vertebrate (Sondaar *et al*., 1995b). The lack of land mammals is paralleled by Pleistocene Hawaii only (Seguí & Alcover, in press). The two biozones are as follows,

1. glirid fauna, Cova de Ca Na Reia, Pliocene - Early Pleistocene. The fossil record of

the Pityusic Islands of this period is extremely poor. The element that in first instance was determined as a caprid incisor (Alcover *et al*., 1981) turned out to be a right tibia of a glirid instead (Alcover *et al*., 2000). Other land vertebrates are two glirids (*Hypnomys* sp. and *Eivissia canarreiensis*), and a big-sized tortoise (*Cheirogaster* sp.). The glirid fauna colonized the western Mediterranean islands during the Messinian (Alcover, 2000), and replaced the Ses Fontalles fauna (Late Miocene), characterized by two bovids (*Tyrrhenotragus* sp., a caprine), a dormouse (*Eliomys* sp.) and a large ochotonid (*Alilepus* sp.).

2. birds and bats fauna, Late Pleistocene. The fossil record of this period is well documented, and comprises only flying vertebrates (birds and insectivorous bats), one land vertebrate (a lacertid lizard, *Podarcis pityusensis*), and several land gastropods (Alcover *et al*., 1994). The birds and bats did not evolve to endemic species. The sea eagle *Haliaeetus albicilla* can be considered the superpredator on these islands, as on other oceanic islands without terrestrial mammals (Alcover & McMinn, 1994).

The successive faunas can be summarized thus,

1. Glirid fauna, origin: mainland fauna, age: Early Pliocene - late Middle Pleistocene, extinction: natural disaster of unknown origin
2. Avifauna, origin: by air, age: late Middle Pleistocene-Holocene, extinction: partially existent.

A natural disaster in the Middle Pleistocene may have caused the extinction of the endemic landtaxa, except for a few gastropods and the lizard (Alcover *et al*., 1994; Alcover, 2000). After this event, the Pityusic Islands were not recolonized by terrestrial vertebrates. A system of marine currents (Florit *et al*., 1989), similar to the existing, might have hampered overseas dispersal to the Pityusics (Alcover, 1989). The prehistoric humans, with their knowledge of marine navigation, were the first terrestrial vertebrates to reach the island again.

Japan

Plio-Pleistocene mammal biozonation of the mainland of Japan is mainly based upon proboscideans (e.g. Takai, 1938; Ikebe, 1959; Kamei *et al*., 1988; Taruno, 1999). Six biozones can be recognized after the extinction of *Zygolophodon sendaicus* (Takahashi & Namatsu, 2000). Fortunately, the horizon and the age of several proboscidean fossils are known accurately (Taruno, 1999), because Japanese Plio-Pleistocene strata have been well studied by teprochronology, paleomagnetic stratigraphy and other dating methods. Correlation of horizons is possible by means of volcanic ash deposits (Satoguchi *et al*., 1999). Most of the faunas are unbalanced, impoverished endemic faunas, which indicates an island environment. In the Late Pleistocene, a mainland Asian fauna, including *Homo sapiens*, arrives in the territory. The following seven biozones can be recognized, excluding Hokkaido.

1. *Stegodon shinshuensis* fauna (Early Pliocene, 4-3 Ma). The molars of this stegodont

are similar to those of *S. zdanskyi* from northern China, Early Pliocene to Early Pleistocene (Taruno, 1991), and are therefore interpreted as a mainland form. However, the similarity between the two species can also point to *S. zdansky* as being the ancestor of the island species *S. shinshuensis*, as there is sofar no indication of association with other mainland taxa, such as carnivores. The *S. shinshuensis* fauna is therefore most likely an unbalanced fauna. There is an eustatic sealevel rise during this biozone (Nakagawa, 1981).

2. *Stegodon aurorae* fauna (Late Pliocene to Early Pleistocene, 2.5-1 Ma). This stegodont is relatively small with a shoulder height of 2 m, and had relatively hypsodont molars (Taruno, 1991). On the basis of cranial morphology, *S. shinshuensis* might have been ancestral to the endemic *S. aurorae*, which means that Japan was an island in this period. The endemic Japanese stegodont is not found in China nor in the Korean peninsula (Zong, 1995).
3. *Mammuthus protomammonteus* fauna (Early Pleistocene, 1.0 - 0.7 Ma). Other ungulates of this fauna are the endemic *Cervus kazusensis* and a "*Bubalus*" sp. (Kawamura *et al*., 1989). The molars of this mammoth differ from the other Holarctic *trogontherii*-stage forms by their small size and narrow crown. Only the form from Taiwan, described as *M. armeniacus taiwanicus* might be similar (Takahashi & Namatsu, 2000). The large inter-individual variation gave rise to a lot of confusion, and subsequent, the division into several types: *M. meridionalis* subsp., *M. paramammonteus shigensis, M. armeniacus proximus* by Otsuka *et al*. (1985), *M. protomammonteus, M. proximus, M. paramammonteus, M. shigensis, M*. cf. *meridionalis* by others (Matsumoto, 1926; Takai, 1938; Matsumoto, 1939; Matsumoto & Ozaki, 1959; Otsuka, 1978; Kamei & Otsuka, 1981), but is more easily explained as the common variability seen in island megafauna. If that is true, than Japan must have been an oceanic-like island in the Early Pleistocene. This is confirmed by the sea-level, which attained its highest level (about 150-200 metres above present level) during this period (Nakagawa, 1981; Kimura, 2000).
4. *Stegodon orientalis* fauna (Middle Pleistocene, 0.7-0.4 Ma, dating in Taruno & Kamei, 1993). At the same period, *S. orientalis* was also present in China and Taiwan (Zong, 1995). Other elements of this horizon are *Rhinoceros sinensis*, *Bubalus* and *Nipponicervus* (Taruno & Yamamoto, 1978), and maybe also *Panthera youngi* (Shikama, 1965). Japan might have been connected by a filter bridge to the mainland during the Middle Pleistocene, but more data are needed to confirm this. The sea level kept on lowering gradually (Naruse, 1981).
5. *Palaeoloxodon naumanni* fauna (Middle to Late Pleistocene, 0.3 - 0.13 Ma). Remains of this medium-sized elephant (shoulder height less than 3 m) are the most abundant proboscidean fossils known from Japan (Takahashi & Namatsu, 2000), and are also abundant on the Penghu Islands of Taiwan (Hu & Tao, 1993). On the Penghu Islands, a smaller and a larger sized *P. naumanni* are found both, whereas in Japan only the smaller sized type occurs. The larger sized type is found also at two Chinese localities (Liu, 1977) and at the bottom of the East China Sea (Otsuka, 1978; Takahashi & Namatsu, 2000), but its molars cannot be distinguished from those of the smaller type (Chow, 1957; Chang, 1964). If the smaller sized form with relatively large molars

turns out to be a dwarfed form, then Japan should be considered an island during the Middle to Late Pleistocene. The site that yielded the most *P. naumanni* specimens (Locality L, Otsuka, 1989) is also abundant in deer (six different *Cervus* subspecies, and two *Elaphurus* spp.), which also indicates a variability typical for oceanic-like islands. Towards the end of this period, there is an eustatic sea-level lowering, but a temporary rise (more than 20 metres above present level) occurred between 0.15 and 0.1 Ma y. B.P., dated by fission track and paleomagnetic chronology (Nakagawa, 1981).

6. *Palaeoloxodon naumanni* - *Sinomegaceros yabei* fauna (Late Pleistocene, 0.13 - 0.016 Ma). In the Upper Kuzuü Formation, *P. naumanni* is found together with nother *Paleoloxodon*, *Canis lupus*, *Nyctereutes vivverrinus*, *Ursus arctos*, *Meles*, *Mustela*, *Felis pardus, Macaca* cf. *fuscata*, many rodent taxa, etcetera (Shikama, 1949), indicating a balanced mainland fauna. The ungulates of this fauna are *Alces alces*, *Sinomegaceros yabei*, *Bison* sp., *Bos primigenius* and *Equus hemionus*, which are indicative for a balanced mainland fauna.. *P. naumanni* is a remnant of the previous zone. At the end of this period, the sea level reached its lowest level (140 m below present according to Iseki (1975), 100 m according to Hoshino (1978), 80 ± 5 m according to Ohshima (1980) at 0.02 to 0.017 Ma (radiocarbon dated, Kaizuka & Moriyama, 1969). This coincides not only with the coldest vegetation in the region (Suzuki & Kamei, 1981), but also with the last occurrence of *P. naumanni* (radiocarbon age 16,720 ± 880 y. B.P., Okumara *et al*., 1982).
7. *Homo sapiens* - *Sus scrofa* fauna (Late Pleistocene - Holocene). Human remains have been found in several sites on Honshu. *Sus scrofa* and *Cervus nippon* are the dominant species, but at Lake Nojiri-ko (Nagano Prefecture), elements from the preceding *Palaeoloxodon naumanni* - *Sinomegaceros yabei* fauna seem to be present at the horizon with stone and bone artefacts. The Jomon people don't exhibit adaptations for an island environment, although they show the same physical features as Upper Paleolithic people from continental Asia and Europe (Yamaguchi, 1982, 1992), whereas they are considered of Neolithic Age on the ground of their ceramics and stable houses.

The successive faunas can be summarized thus,

1. *Stegodon shinshuensis* fauna, origin: Northern Chinese mainland, age: Pliocene, extinction: local evolution into next unit
2. *Stegodon aurorae* fauna, origin: oceanic island fauna, age: Early Pleistocene, extinction: arrival mainland taxa
3. *Mammuthus protomammonteus* fauna, origin: Southern Chinese (?) mainland, age: late Early Pleistocene-Middle Pleistocene, extinction: arrival mainland taxa (filter bridge)
4. *Stegodon orientalis* fauna, origin: mainland, age: Middle Pleistocene, extinction: gradual change into next unit
5. *Palaeoloxodon naumanni* fauna, origin: mainland China plus local evolution (filter bridge), age: Late Pleistocene, extinction: gradual change into next unit

6. *Palaeoloxodon-Sinomegaceros* fauna, origin: mainland (filter bridge), age: Late Pleistocene, extinction: arrival of humans by filter/land bridge
7. *Homo sapiens-Sus scrofa* fauna, origin: mainland China, age: late Late Pleistocene-Holocene, extinction: still existent.

Ryukyu Islands

The Ryukyu island arc is situated between Kyushu (Japan) in the North and Taiwan in the South, and is separated from these islands by a sea deeper than 200 meters. To the West the Okinawa Trough is found, and to the East the Philippine Sea. The archipelago consists of three island groups: Northern Ryukyu Islands (Yakushima, Tanegashima, Tokara Islands), Central Ryukyu Islands (Okinawa, Kume, Ie, Amami-Oshima, Tokunoshima), and Southern Ryukyu Islands (Yonaguni, Yaeyama, Iriomote, Ishigaki, Miyako), separated by two straits: the Tokara Gap (= Watase Line) between the Northern and the Central Group, and the Kerama Gap between the Central and the Southern Group. Several typical faunal assemblages are recognised during the Pleistocene on the Central and Southern Groups, whereas the Northern Group follows the mainland of Japan in palaeo-faunistical respect, as a result of connection to Kyushu during global sea level changes. The Pliocene is only known by an isolated find of *Trilophodon* on Miyako Island, which should be synonymized with the Japanese *Zygolophodon sendaicus* (Otsuka, 1983).

Otsuka & Takahashi (2000) on the other hand, recognize seven different faunal assemblages from Miocene to the Holocene, as they consider the Ryukyu Islands as a consistent unit. Each find on one of the many islands is interpolated onto the whole archipelago, resulting in the creation of virtual assemblages that possibly never existed. If, however, we seperate the archipelago into three groups on the ground of clear sea straits, and strictly limit finds to the proper islands, a different and more consistent picture arises. The Central and the Southern Group were oceanic-like islands during the whole Pleistocene, had impoverished and unbalanced faunas, and were never connected to the mainland of Asia, in contrast to the mainland of Japan, which had a balanced Late Pleistocene fauna, and was connected to the mainland of Asia in that period. The Northern Ryukyu Islands were several times connected to Kyushu, and follow Japan in zoohistorical respect.

1. *Cervus-Leopoldamys* fauna (Imadomari-Akagimata assemblage), latest Pliocene - Early Pleistocene, ca 1.5 - 1.3 Ma (Northern Okinawa), corresponding to Otsuka & Takahashi's (2000) level 2. Elements of this fauna are a large rodent *Leopoldamys*, *Muntiacus* sp., a large deer (Haneji Formation), and possibly *Mammuthus* or *Paleoloxodon* (only one, incomplete molar is found, Cape Kyan, Southern Okinawa). The deer, that is in proportion similar to *Cervus nippon* (Matsumoto & Otsuka, 2000), is considered the ancestor of *Cervus astylodon* (Otsuka & Takahashi, 2000), but this is not very likely, as the following period (1.3 - 0.2 Ma, Okinawa Trough Stage and Ryukyu Coral Sea Stage) saw the practically complete submerging of the Ryukyu land area (Kimura, 2000). It is supposed that this fauna is a latest Pliocene immigrant fauna from Central China (Jin & Zheng, 1998; Huang, 1998; Jin *et al.*, 1999; Huang *et al.*,

1991). The Central Ryukyu Islands seem to have had an impoverished and unbalanced subset of the mainland fauna during the Early Pleistocene. The dry East China Sea (Kimura, 2000) possibly acted as a filter bridge, comparable to the Messinian salinity crisis in the Mediterranean.

2. *Manouria - Geoemyda* fauna, Middle Pleistocene, ca. 0.18 - 0.13 Ma (Okinawa, Amami), corresponding to Otsuka & Takahashi's (2000) level 3. The giant tortoise *Manouria*, the marsh tortoise *Geoemyda japonica*, and the box tortoises *Cistoclemmys* sp. and *Cuora* sp., are endemic to these islands. The Central Ryukyu Islands were clearly oceanic-like islands during the Middle Pleistocene. On Kume, some cervid molars (?*Dicrocerus*) are found, but identification is still questionable, and possibly they belong to the next faunal stage.
3. *Cervus astylodon* - *Manouria* fauna, Late Pleistocene, 0.035 - 0.02 Ma (Okinawa, Ie, Kume, Amami, Tokunoshima, Ishigaki), corresponding to Otsuka & Takahashi's (2000) level 4. The fauna is dominated by endemic deer: *Cervus astylodon, Dicrocerus* sp. and at least two muntiacs. *Geoemyda* and *Manouria* of the previous stage are still present. Matsumoto & Otsuka (2000) recognizes at least four morphotypes of *C. astylodon* on Kume Island alone, which all display the typical features dwarfism, fusion of tarsal bones, and reduction in autopodium length. On Tokunoshima also an endemic rabbit, the still living *Pentalagus furnessi*, occurs. The Central Ryukyu Islands were oceanic-like islands during the Late Pleistocene. At the end of this period the sea level was low again, coinciding with the replacement of the megafauna.
4. *Homo sapiens* - *Sus scrofa* fauna, latest Pleistocene, ca. 0.018 - 0.015 Ma (Yaeyama, Miyako, Okinawa), radiocarbon age 18,250 ± 650 y. B.P. and 16,600 ± 30 y. B.P. (Kobayashi *et al*., 1974). Other elements of this fauna on the Southern Group are *Capreolus miyakoensis*, *Sus scrofa*, *Felis* sp., *Microtus fortus*, and an elephant of which the systematic position is still unclear (Tokunaga, 1940; Otuka, 1941; Kamei, 1970; Otsuka, 1996). Pre-neolithic human bones have been found in Pinza-abu Cave on Miyako (Sakura, 1981), and on Okinawa, amongst others in the Minatogawa fissure (Suzuki, 1982; Baba *et al*., 1998), that might show adaptations to an island environment (Baba *et al*., 1998; Baba, 2000). The accompagnying faunal remains on Okinawa are not yet studied, but it seems that only wild boar was found together with the human fossils (Otsuka, pers. comm. 2000). This fauna is clearly impoverished. The Southern Ryukyu Islands seem thus to have been connected to the mainland during the Late Pleistocene, which is confirmed by the paleogeography (Kimura, 2000) and the balanced mainland fauna, whereas the Central Group remained oceanic-like with an unbalanced, impoverished fauna.

The successive faunas of the Central Ryukyus can be summarized thus,

1. *Cervus-Leopoldamys* fauna, origin: unknown, age: Early Pleistocene (?), extinction: unknown. Status and age of this fauna is uncertain due to the poor fossil record
2. *Manouria-Geoemyda* fauna, origin: mainland of China by sweepstake dispersal, age: late Middle Pleistocene-Late Pleistocene, extinction: arrival of mainland taxa by

sweepstake dispersal

3. *Cervus astylodon-Manouria* fauna, origin: mainland of China by sweepstake dispersal, age: Late Pleistocene, extinction: arrival of *Homo sapiens* and *Sus scrofa* around 0.02 Ma by sweepstake dispersal
4. *Homo sapiens-Sus scrofa* fauna, origin: mainland of China, age: late Late Pleistocene, extinction: arrival of Mesolithic humans

Crete

In the Early Pleistocene, Crete got its present configuration (Sondaar *et al.,* 1986a). During the Pliocene, Crete was probably submerged, as the Miocene *Hipparion* fauna (MN 9-MN 12) is overlain by Tortonian foraminifera beds and marine deposits (De Bruijn *et al*., 1971; Sondaar *et al*., 1986a; Benda *et al*., 1974).

After emersion, Crete became an oceanic-like island which was colonized by sweepstake dispersal, and can be considered an example for colonization, neso-evolution of ungulates, and finally extinction of the endemic island ungulates. The successful Cretan Pleistocene ungulates were hippopotamids, elephants and cervids.

Mayhew (1996) distinguishes 5 bio-zones based on the endemic Pleistocene murid species of Crete. These species belong to two genera, the larger *Kritimys* and the smaller *Mus*. If we look at the ungulates, there is one faunal turnover. The extinction of the dwarf elephant, *Elephas creticus,* and the dwarf hippo, *Hippopotamus creutzburgi* and the arrival of the cervids and a larger elephant characterize this turnover. At the same time, the endemic *Kritimys* is replaced by *Mus*.

The faunal assemblages can be summarized as follows,

1. *Elephas creticus - Hippopotamus creutzburgi* fauna, or the *Kritimys* Zone (*sensu* De Vos, 1984), several localities, Early and early Middle Pleistocene. The earliest land vertebrates from this fauna are from the locality Siteia 1. Besides *Kritimys* aff. *kiridus* material (Mayhew, 1977, 1996), a rib of *H. creutzburgi* was found (Spaan, 1996). The dwarf *H. creutzburgi* had a more unguligrade stance, compared to its possible ancestor (*H. antiquus* Desmarest, 1822 (= *H. major* Cuvier, 1824), and is an endemic insular hippo (Capasso Barbato *et al*., 1982; Spaan, 1996). The dwarf elephant *E. creticus* is associated with *Kritimys* (Cape Maleka 1, Mayhew, 1977, 1996; this site is somewhat younger in age than Siteia 1, based upon the evolutionary stage of *Kritimys*). The youngest association of *E. creticus* with *H. creutzburgi* is Katharo 1 (absolute dated (AAR and ESR) around 400.000 years, Reese *et al*., 1996). The probable ancestors of *Kritimys catreus* and of the soricid *Crocidura zimmermanni* are of a Late Pliocene / Early Pleistocene mainland stock (Mayhew, 1996; Reumer, 1986). During the Early and early Middle Pleistocene, Crete was an oceanic-like island, with an unbalanced, impoverished endemic fauna.
2. *Elephas creutzburgi - Candiacervus* fauna, or the *Mus* Zone (*sensu* De Vos, 1984), late Middle and Late Pleistocene. The younger sites (Gerani 5) are absolute dated 127.450 ± 20%, with the youngest locality Gerani 2, AAR dated 47.000 ± 20% (Reese, 1996); Early Neolithic deposits covered the Pleistocene deposits in this cave.

The earliest occurrence of *Mus* on Crete is at the Stavros Micro site; the earliest find of the cervid *Candiacervus* is in Charoumbes 2, and the earliest find of *Elephas* and *Candiacervus* together Charoumbes 3. De Vos (1979, 1984, 1996) recognizes six morphotypes in the endemic genus *Candiacervus*, explained as adaptive radiation of the ancestral stock (De Vos, 2000; Van der Geer, this volume). Capasso Barbato (1992) came to two different ancestors for the deer (*Megaloceros* (*Candiacervus*) for the smaller species, and *Cervus* (*Leptocervus*) for the larger species), based upon cladistic analysis applied to the postcranial material. However, especially the postcranial of endemic island ungulates differ essentially from that of their mainland ancestor. She (Capasso Barbato, 1992) even states that "*M. (C.) ropalophorus*, however, maintained similar morphological features of skull, teeth and postcranial skeleton even if metapodials were proportionally thinner than those of the continental forms", but this is true only for *Candiacervus* sp. V and *C*. sp. VI (*sensu* De Vos, 1984), whereas *C. ropalophorus, C*. spp. II, *C. cretensis* have the typically short and robust metapodials, and *C. rethymnensis* is comparable to the mainland species *Cervus elaphus*. Thus, postcranial material might be useful to recognize different morphotypes within the island taxa, but cannot be used in defining the ancestral form from the mainland (De Vos, 1979, 2000).

Crete was an oceanic-like island again during the late Middle to Late Pleistocene, with an unbalanced endemic fauna, that was different from the previous period, indicating a temporary easy access from the mainland. The dramatic faunal turnover between the two main zones might be placed somewhere in the Middle Pleistocene, possibly related to the low sea level in the late Middle Pleistocene, MmQ2 and MmQ3 (Haq *et al*., 1998).

The successive faunas can be summarized thus,

1. *Elephas-Hippopotamus* fauna, origin: mainland Europe, age: Early-Middle Pleistocene, extinction: arrival of mainland taxa by sweepstake dispersal
2. *Candiacervus* fauna, origin: mainland Europe, age: late Middle Pleistocene-Holocene, extinction: arrival of mainland taxa

A remark about the biostratigraphy of the Cretan deer should be made here. This biostratigraphy concerns the faunal units 2 and 3 in Capasso Barbato's view (1992), and only faunal unit 3 in De Vos' view (1996, revision of Dermitzakis & De Vos, 1987). Erroneously, Capasso Barbato (1992) placed cervids in her biostratigraphic scheme in the localities Stavros Macro, Charoumbes 4 and Charoumbes 5 of the *Kritimys* zone. Sondaar and De Vos were the collectors of these sites and never found a trace of cervid fossils. Probably she (Capasso Barbato, 1992) confused localities of Kuss (1965, 1975) with those excavated by Sondaar and De Vos, which are different in age, and based her scheme mainly on Dermitzakis & De Vos (1987), without seeing the revision of this scheme (De Vos, 1996).

Sardinia-Corsica

The cirno-sardinian massif differs from the other Mediterranean islands, as the genus *Homo* colonized the massif several times with success, which had a dramatic impact on the faunal evolution. The human arrival can be considered a natural disaster: a new large predator arrived on the island.
Altogether four different faunal units can be recognized during the Pliocene-Holocene of Sardinia / Corsica (Ginesu & Cordy, 1997; Sondaar, 1987, 1998, 2000; Vigne, 1998; Van der Made, 1999). These are, from oldest to youngest (table 1),

1. the *Rhagapodemus minor* - caprid fauna, Su Casteddu, Campidanu, Mandriola, and Orosei 6, Pliocene / Early Pleistocene. The fauna is balanced and impoverished, consisting of a caprid, *Sus sondaari*, *Chasmaporthetes*, *Apodemus mannu* and *Prolagus figari*. The ancestral fauna is a Late Miocene / Early Pliocene mainland fauna, as indicated by the presence of the murid *R. minor* (type locality Mandriola, Pliocene), which is similar to the mainland *Rhagapodemus* (Martin Suarez & Mein, 1998). *P. figari* is also found in Perpignan (MN 14) (Van der Made, 1999). The relation between this fauna, and the Late Miocene fauna with *Maremmia lorenzi*, *Tyrrhenotragus gracillimus*, *Oreopithecus bambolii* and a crocodile (Cordy & Ginesu, 1994; Kotsakis *et al*., 1997) on Sardinia is not yet clear, caused by a gap in the fossil record. The association of a hyena with terrestrial elements (Ginesu & Cordy, 1997) points to an isolation of a mainland fauna, rather than an overseas dispersal; the island should therefore be considered continental (Sondaar, 2000). The fauna lacks the classical characteristics of island endemics, such as low gear locomotion. However, *Apodemus mannu* seems large, and *Sus sondaari* evolved size decrease together with increased crown height, increased enamel thickness, loss of p1, simplification of molar structure and reduction of premolar size (Van der Made, 1999), which indicates an increased ability to grind abrasive food (Van der Geer, this volume).
2. the *Tyrrhenicola* - *Nesogoral* fauna, Orosei, early Middle Pleistocene. The dominant ungulate of this fauna is *Nesogoral*. Other elements are *Tyrrhenicola henseli* and *Prolagus sardus*. The ancestor of *Nesogoral* (possibly *Gallogoral*, see fig. 1) came by sweepstake dispersal during the Middle Pleistocene on the island. The dramatic faunal turnover with the extinction of all ungulates and arrival of the ancestral stock of *Nesogoral* is difficult to understand without taking the impact of human colonization into account. Human presence is suggested by archaeological complexes (Martini, 1992), of which the two oldest are compared with clactonian complexes from the continent. The oldest complex (Coa de sa Mua, Perfugas) is interpreted as Middle Pleistocene. The success of the probable colonization might have depended on the presence of *Prolagus* with its high reproduction rate and large enough size to provide the necessary proteins to support a viable human population (Sondaar *et al.*, 1986b; Sondaar & Van der Geer, 2000).
3. the *Tyrrhenicola* - *Megaloceros* fauna, Dragonara, Corbeddu; late Middle / Late Pleistocene. This fauna is the best known of all Plio-Pleistocene associations, and is represented by large bone accumulations in cave deposits (Malatesta, 1970; Caloi & Malatesta, 1974; Klein Hofmeijer, 1996; Sondaar *et al*., 1984), and consists mainly of

Megaloceros cazioti, *Cynotherium sardous*, *Prolagus sardus*, *Tyrrhenicola henseli* and *Rhagamys orthodon*. The faunal turnover consists of the extinction of *Nesogoral* and the arrival of *Megaloceros*, whose first occurrence is ESR dated 450.000 ± 20% yBP (pers. comm. D.S. Reese to Van der Made, 1999). This insular fauna deviates from the expected pattern, as *M. cazioti* has mainland proportions, and a fox-sized canid is present. A second human successfull colonization might be the explanation for the unusual composition (Sondaar, 2000; Sondaar & Van der Geer, 2000). This is supported by the presence of a palaeolithic industry (Sa Pedrosa-Pantallino, Sassari), apparently older than the last glaciation (Arca *et al*., 1982; Bini *et al*. 1993; Martini, 1992) and a human phalanx from Corbeddu, dated around 20.000 yBP (Sondaar *et al*., 1995a).

4. the *Tyrrhenicola* - *Prolagus* fauna, latest Late Pleistocene - Holocene. A third dramatic faunal turnover took place around 9.000 yBP, and is characterized by the extinction of *Megaloceros* and the arrival of Mesolithic modern humans (Vigne, 1998). For a period of about thousand years, ungulates were lacking. The Paleolithic (Late Pleistocene) is recognized (Bonifay, 1994), and also the Mesolithic (Vigne, 1998; Lanfranchi, 1998). In the Mesolithic sites, pottery and domesticated animals are not found, while the typical Late Paleolithic deer *Megaloceros* must have been extinct. Obsidian artefacts that mark the beginning of the Early Neolithic, are missing (Vigne, 1998). The Corsican Mesolithic hunter-gatherer sites can be placed in the 9th millennium (Vigne, 1998), which date is confirmed by a human skeleton from Araguina-Sennola abri (Lanfranchi *et al*. 1973; Duday 1975; Lanfranchi, 1998), and by two human fossils (maxilla and temporal bone) from Corbeddu Cave, Sardinia (Spoor & Sondaar, 1986; Klein Hofmeijer *et al*., 1987; Sondaar *et al*., 1991).

The successive faunas can be summarized thus (fig. 2),

Rhagapodemus minor-caprid fauna, origin: mainland of Europe through full land connection, age: Early Pliocene-Middle Pleistocene, extinction: arrival of *Homo erectus* (?) in early Middle Pleistocene
Nesogoral - *Tyrrhenicola* fauna, origin: mainland of Europe by sweepstake dispersal, age: Middle Pleistocene, extinction: arrival of archaic *Homo sapiens*
Megaloceros cazioti fauna, origin: mainland of Europe by sweepstake dispersal, age: late Middle Pleistocene-Early Holocene, extinction: arrival of Mesolithic modern *Homo sapiens*

It appears that the transition between the different Pleistocene faunas is not gradual, but catastrophic instead. The changes are characterized by an extinction of large herbivores/omnivores, and an arrival of new herbivores from the mainland. On the whole, after each transition, or faunal turnover, there is a loss in total number of large herbivores. In all the Pleistocene and Early Neolithic faunas, *Prolagus* is abundant. There are four dramatic faunal turnovers, with extinctions and arrivals of herbivores, in some cases in association with archaeological complexes. The boundaries between the faunal

units are sharp, characterized by extinctions which point to a catastrophic event. There are two faunal turnovers in the Pleistocene and two in the Holocene.
On morphological characters Gliozzi & Malatesta (1980) discuss the possible origin of *Nesogoral* and *Myotragus*. The classic idea is that the ancient fore runners of both Nemorhaedini reached the islands in the widespread Mediterranean emersion of the Messinian. However, they state that *Nesogoral* is closer in morphology to *Gallogoral* and *Nemorhaedus*, and our results confirm their observation. The caprid of the preceding *Chasmaporthetes* fauna probably arose from the same stock as *Myotragus* from the Balearics (fig. 1).

Cyprus

The Pleistocene fauna of Cyprus contains only two large herbivores: a dwarf elephant and a dwarf hippo. These taxa remain almost without any evolutionary change on the island, obviously far away from mainland influences. The Pleistocene fauna of Cyprus is a classical example of stasis in an endemic insular fauna. This stasis was only disturbed in the latest Late Pleistocene, when humans arrived on the island, and caused the extinction of the herbivores due to overkill, combined with their slow reproduction rate and unaquintedness with predators. Thus, only two faunal units can be defined for the period under consideration,

1. *Elephas cypriotes* - *Phanourios minutus* fauna; Pliocene to Late Pleistocene (see also dates given by Reese, 1996). More than 90% of the fossils belong to the dwarf hippo, which indicates that the environment was quite favorable for *P. minutus.* The dwarf hippo is an endemic insular species, as it was well adapted to walking on rocky soil and to climbing, but not to running, and its dentition was lophodont, typical for a browser (Sondaar & Boekschoten, 1967; Boekschoten & Sondaar,1972; Houtekamer & Sondaar, 1979; Spaan, 1996). Accordingly, Cyprus must have been forested or at least covered with shrubs. Fossil hippos from localities that differ in age, are quite similar in morphology and do not show different evolutionary stages on which a relative age could be based (Boekschoten & Sondaar, 1972; Houtekamer & Sondaar 1979). The molars of the dwarf elephant *Elephas cypriotes* suggests an ancestry from the Pliocene/Early Pleistocene *Mammuthus meridionales* from the mainland. At the end of the period, humans arrived during the latest Late Pleistocene. Dwarf hippos and dwarf elephants are found together with a lithic industry and burnt bones and shells at the site Akrotiri Aetokremnos (Mandel & Simmons, 1997; Simmons, 1988, 1999), dated mid ninth millennium BC. In the older stratum 4, the bulk of the remains belongs to the hippo (>98%), whereas this percentage is less than 20% in the younger stratum 2 (Reese, 1996), likely due to human consumption (Simmons, 1996; Reese, 1996). The dramatic decrease in the consumption of hippo and a simultaneous increase in the consumption of shellfish and birds is explained as reduction in number, caused by overkill (Simmons, 1999; Sondaar & Van der Geer, 2000). Such an event can be considered an extinction event, instead of a turnover, as no successfull re-colonization occurs.

The fauna can be summarized thus,

Phanourios-Elephas fauna, origin: mainland Europe by sweepstake dispersal, age: Early Pleistocene-late Late Pleistocene, extinction: arrival of humans by boat

Cyprus was colonized by a mainland elephant and hippo in the Late Pliocene - Early Pleistocene. They arrived on an oceanic-like island by sweepstake dispersal. After punctuated evolutionary processes they obtained the typical island adaptation. There was a stasis in the faunal evolution till the arrival of humans in the latest Late Pleistocene - Early Holocene.

Discussion and conclusion

At least seven faunal changes can be recognized in the Plio/Pleistocene of the Holarctic mainland, in a time span of around 4.5 million years from MN 14 (Early Pliocene) to MmQ 4 (Late Pleistocene). These successive faunal units are characterized by invasions, extinctions and local evolution. A relation between these faunal turnovers and global climatological changes is in many cases clear. Such a clear relation is not found on islands.

Two types of Plio/Pleistocene islands can be recognized: continental and oceanic-like islands. Though the origin of these faunas are completely different, the faunal evolutionary pattern is similar. Oceanic-like islands, Crete, Cyprus and the like, are colonized overseas by sweepstake dispersal, while the ancestral fauna of a continental island as Sardinia was an Early Pliocene mainland fauna. In both cases a fast evolutionary change can be recognized, which can be explained as an adaptation to the restricted island environment. On the oceanic-like islands, without large predators, dwarf herbivores evolve (fig. 2).

On Sardinia this change includes a loss of diversity, extinction of Proboscidae, equids, rhinos and the like, but at the same time evolution of endemic bovids. The hyena *Chasmaporthetes* survives. In both cases, continental and oceanic-like islands, there is a stasis in the faunal evolution, once an endemic insular fauna is established. The fauna remains more or less stable in composition and morphology, and is not affected by global climatic changes (fig. 3).

After an endemic fauna has evolved, adapted to the insular environment, there is a period of stasis, which can be probably disturbed, resulting in an extinction event, and often but not always, the arrival of a new colonizer. Examples are Crete with a transition from the *Kritimys* to the *Mus* zone around 0.3 Ma, and Sardinia with a transition from the *Chasmaporthetes* to the *Nesogoral* fauna around 0.7-0.8 Ma. In both the extinction event is followed by a recovery phase, effectuated by new colonizers. In the case of Sardinia-Corsica the recovery phases are of a antropogenic character, in other words, the endemic island fauna apparently evolved in association with *Homo*. The new arrivals came by sweepstake dispersal on the islands. If the dispersal route is a filter bridge, a different pattern will arise. Example is Sicily, where *Elephas falconeri* is succeeded by the

Elephas mnadriensis fauna at around 0.3 Ma. This fauna is an impoverished but balanced mainland fauna with endemic features whose ancestors came by filter bridge on the island. A long time the island was completely isolated from the mainland, but at periods of low sea level, the new invadors could pass the filter bridge. Around 20.000 BP the land connection must have been completed, and most endemics became extinct. Another example is Japan, where the *Palaeoloxodon naumanni* fauna replaces the *Stegodon orientalis* fauna around 0.3 Ma.

The stasis can be disturbed, mostly abruptly but sometimes gradually, and will result in a faunal turnover. An abrupt turnover is seen, for example, on Crete and on Sicily during the late Middle Pleistocene, where, amongst others, an endemic, dwarfed elephant is replaced with a larger elepant. On other islands, the stasis is only gradually disturbed, for example Sicily and Japan between 0.3 Ma and 0.016 Ma, when these islands became slowly more and more connected to the mainland (filter bridge), and the island faunas (*E. mnadriensis* - *P. naumanni* fauna resp.) were gradually superseded by mainland faunas (*Equus* and *Sinomegaceros* resp.). The stasis is as a rule abruptly disturbed if humans are involved. Human colonizations take place in the Middle Pleistocene on, for example, the continental island Sardinia, in the Late Pleistocene on the Ryukyu Islands, and in the Holocene on the oceanic-like islands like Cyprus and Crete. From archaeological complexes it can be learned that Sardinia was probably colonized by humans as early as the Middle Pleistocene. The reason for this early succesful colonization can be found in the presence of the ochotonid *Prolagus* on this continental island. The taphonomy of the Mesolithic Corsican sites is suggestive for the explanation that the *Prolagus* population, through its high reproductive rate, could support a viable human hunter-gatherer population over a longer period, without becoming exhausted. On the other hand, the colonization of oceanic-like islands by Paleolithic / Mesolithic hunter-gatherer societies must have led to a dramatic reduction of the dwarf herbivores. Furthermore, the lack of ecological alternatives on the Pleistocene oceanic-like islands made Pre-neolithic human colonization unsuccessful. Cyprus provides such an example.

Faunal turnovers, always consisting of an extinction event and in many cases also of a recovery phase, are mainly linked to changes in the palaeogeography, which opened possibilities to reach islands. Global climatological changes had impact on the sea level, and through this indirectly on the palaeogeography. In a number of cases, the result was dramatically, as filter bridges came into existence and sea straits between islands and the mainland became narrower. This is the most parsimonious explanation for the fact that extinction events on several islands are especially clear around 0.7-0.8 Ma, 0.3-0.2 Ma and another one at 0.02 Ma. However, on Cyprus and Mallorca there is no such extinction event. Perhaps local sea currrents or the distance to the mainland made it impossible to reach the island. Another question to solve is why especially after 0.8 Ma faunal turnovers took place so frequently, compared to the previous period. Perhaps this might be explained by the fact that from that period on humans were able to cross sea straits, but sofar only on Sardinia / Corsica the relation human colonization and extinction events are well established. On Cyprus, the arrival of a human population the

Late Pleistocene caused extinction of the dwarf elephant and dwarf hippo, but here the hunter-gatherer society was not succesfull, most likely because of lack of food resources after this extinction.

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Figures

Fig. 1. Fauna list of Sardinia/Corsica from the Early Pleistocene till the Early Neolithic.

	Pleistocene			Holocene	
	Early	Middle	Upper	Mesolithic	Early Neolithic
	Cava 6	Cava 10	Cava 7, Corbeddu 2, 3	Araguina	Corbeddu
Macaca majori	x	x			
Talpa tyrrhenica	x	x			
Nesiotites similis	x	x	x	x	
Prolagus sp.	x	x	x	x	x
Leporoid	x				
Tyrrhenicola sp.		x			
Tyrrhenicola henseli			x	x	x
Rhagamys minor	x	x			
Rhagamys orthodon			x	x	x
Glirid	?	?			
Chasmaporthetes	x				
Mustelid sp. 1	x				
Mustelid sp. 2	x	x			
Cynotherium sp.	x	x?			
Cynotherium sardous			x		
Nesogoral melonii		x			
Nesogoral sp. 2		x			
Sus nanus	x				
Caprine sp. nov.	x				
Megaloceros cazioti			x		
Domestic animals					x

Sondaar, P.Y., Van der Geer, A.A.E. 2005. Evolution and Extinction of Plio-Pleistocene Island Ungulates. In: E. Crégut-Bonnoure (ed.). Les ongulés holarctiques du Pliocène et du Pléistocene. Quaternaire, International Journal of the French Quaternary Association, hors-série 2005, 2: 241-256. Paris: Maison de la Géologie

Fig. 2. Relation different human colonization waves and extinction/arrival of island herbivores on Sardinia/Corsica. After each new colonization there is an extiction event of large endemic herbivores, which are replaced by new arrivals. However, there is a loss in total number of herbivore taxa after each colonization event. Probably after the arrival of modern Mesolithic *Homo sapiens* the last large herbivore *Megaloceros cazioti* became extinct.

	Pleistocene			Holocene	
	Early	Middle	Late	Mesolithic	Early Neolithic
	Campidanu, Mandriola, Su Casteddu, Orosei 6	Orosei 10	Dragonara, Corbeddu 2, 3	Araguina	Corbeddu 1
Faunal unit	*Chasmaporthetes* *R. minor* *Prolagus* caprid	*Tyrrhenicola* *R. minor* *Nesogoral* *Prolagus*	*Tyrrhenicola* *R. orthodon* *Megaloceros* *Cynotherium* *Prolagus*	*Tyrrhenicola* *R. orthodon* *Prolagus*	Cattle *R. orthodon* *Prolagus*
Sus sondaari	x				
Caprine sp.	x				
Nesogoral melonii		x			
Megaloceros cazioti			x	x?	
Domestic animals					x
Homo sp.		x (Coa 'e sa Mua, Perfugas)			
Homo sapiens archaic			x (Sa Pedrosa-Pantallino, Sassari; Corbeddu 2)		
Homo sapiens modern				x (Araguina-Sennola; Corbeddu 1, 2)	x (Corbeddu 1)

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Fig. 3. Global analysis of several Holarctic insular faunas from the Pliocene to the Late Pleistocene. Only mammalian taxa and giant tortoises are given, except for Eivissa, where birds play a major role. Legenda: * = endemic insular taxon, about 20 % enlarged or reduced in size, ** = endemic insular taxon, giant or dwarf, more than 20 %. From the data presented it becomes clear that faunal successions are not the same on all islands. They are highly dependent on local factors, such as accessibility, area, geography. Some features, however, are shared by all true islands. The composition of endemic insular faunas is always impoverished, often unbalanced, and their taxa show peculiar characteristics not found in mainland taxa. Endemic insular taxa can evolve from isolated subsets of the mainland fauna (continental islands) or from ancestral taxa that reach the island by sweepstake dispersal (oceanic and oceanic-like islands) or by a filter bridge (continental islands). In the last case, a mixture of endemics with mainland taxa can occur, indicating a progressive connection with the mainland. Another common phenomenon is the replacement of dwarf elephants with elephants that are just slightly smaller than their mainland relatives.

	Early / Middle Pliocene	Late Plio/Early Pleistocene	Early Pleistocene	early and middle Middle Pleistocene	late Middle Pleistocene	Late Pleistocene
Ma	5,35 - 2,5	2,5 - 1,8	1,8 - 0,8	0,8 - 0,3	0,3 - 0,125	0,125 - 0,01
MU, Agusti *et al.*, 1987	MN 14-15	MN 16-17	MmQ 3	MmQ4		
Land Mammal age	Ruscinian	Villafranchian		Galerian		Aurelian
Sicily	*Apodemus **Maltamys *Hypolagus	-	-	**Elephas falconeri **Leithia	*Elephas mnaidriensis *Hippopotamus pentlandi *Bos, *Bison **Leithia	Equus hydruntinus *Elephas mnadriensis Bos, Bison Homo sapiens
Crete	-	-	**Elephas creticus *Hippopotamus creutzburgi *Kritimys		*Elephas creutzburgi **Candiacervus *Mus minotaurus	
Sardinia	Rhagapodemus minor caprid Sus sondaari Chasmaporthetes Prolagus figari			*Tyrrhenicola henseli *Nesogoral *Prolagus sardus Homo	*Tyrrhenicola henseli Megaloceros cazioti *Cynotherium sardous *Prolagus sardus *Rhagamys orthodon Homo	*Tyrrhenicola henseli *Prolagus sardus *Rhagamys orthodon Homo
Mallorca	Insulotragus Hypnomys waldreni	*Myotragus kopperi *Hypnomys intermedius	**Myotragus bateae **Hypnomys onicensis	**Myotragus balearicus **Hypnomys morpheus		
Menorca	*Alilepus sp. *Muscardinus cyclopeus	?				
Eivissa	*Alilepus Tyrrhenotragus Eliomys caprid	**Hypnomys **Eivissia Aves		Aves		
Cyprus		**Elephas cypriotes **Phanourios minutus				
Central Ryukyu Islands	Zygolophodon sendaicus	Cervus Leopoldamys Muntiacus	-	-	**Manouria *Geoemyda	**Manouria **Cervus astylodon *Pentalagus furnessi
Japan	*Stegodon shinshuensis	**Stegodon aurorae	*Mammuthus protomammonteus *Cervus kazusensis	Stegodon orientalis Nipponicervus	*Palaeoloxodon naumanni *Cervus	*Palaeoloxodon naumanni Sinomegaceros Homo

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