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Pleistocene Calabrian and Sicilian bioprovinces

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Abstract

During the Pleistocene, southern Calabria was the area through which several mammalian taxa dispersed into the Sicilian island via the Straits of Messina. The rich fossil record of Sicily allowed for the construction of a fairly detailed bio-chronological frame that is dated by correlation of vertebrate bearing deposits with marine deposits. At present five Faunal Complexes (F.C.), characterised by the occurrence of different taxa, have been recognised. The two older Faunal Complexes (Monte Pellegrino F.C.'xes *Elephas falconeri* F.C.) include taxa with differently marked endemic features denoting the occurrence of an insular system made up of geographically isolated small islands, with very difficult and sporadic connections with the mainland. The Lower Pleistocene physiographic evidence fits closely with data coming from palaeontologic evidence. In the younger F.C.'xes (*E. mnaidriensis* F.C., Pianetti S. Teodoro F.C. and Castello F.C.), faunal composition is becoming more similar to that of the southern Italian peninsula, endemisation is more moderate becoming absent in the youngest assemblages. This behaviour denotes that temporary connections with southern Italy occurred more frequently and extensively during Late Middle Pleistocene and Late Pleistocene. Possibly a sort of filtering barrier affected the dispersals that gave rise to the former phase of population of the *E. mnaidriensis* F.C. preventing small mammals from the mainland from entering the island. The vertebrate fossil record of southern Calabria is rather poor and no mammal deposit is apparently older than the Late Middle Pleistocene. The occurrence at Bovetto of a continental fallow deer (*Dama dama* cf. *tiberina*), closely related to the endemic Sicilian species *D. carburangelensis* of the *E. mnaidriensis* F.C., may document the first Pleistocene connection of southern Calabria to the Italian peninsula and the dispersal of the forerunners of mammals of the *E. mnaidriensis* F.C. in Sicily. The well-diversified continental faunas coming from Archi and from Iannì di S. Calogero, both containing remains of *Homo sapiens neanderthalensis*, may document a post-Tyrrhenian dispersal event through the Catanzaro isthmus. Data are still lacking for the correlation of these faunal assemblages with the scarcely endemic faunas of the Late Pleistocene Contrada Pianetti–San Teodoro F.C. of Sicily. No record of the mammal assemblages that gave origin to the fauna of the Castello F.C. has been recovered so far in southern Calabria. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Keywords: Paleobiogeography; Pleistocene vertebrates; Endemic faunas; Sicily

1. Introduction

Insular environments are usually characterised by poorly diversified assemblages, the number of species present on islands being partially dependent on their size and on the availability and variety of resources of the island. The low biodiversity in insular systems is also conditioned by the intensity of geographic barriers that limit or even prevent migrations of taxa from continental areas. Finally, the entity of geographic isolation also tends to influence the degree of endemism of insular faunal assemblages.

Even with its severe limitations and uncertainties, the vertebrate fossil record provides a direct access to the chronological and palaeogeographical dimension of biological events and processes, and thus to the bio-geographic history of an area. In some cases, such as very ancient islands, palaeontology is the only possible approach.

The palaeogeography of Sicily, as well as its relationships with peninsular Italy, underwent several important changes from the Early Pleistocene to the Late Middle Pleistocene. During the Late Middle Pleistocene and the

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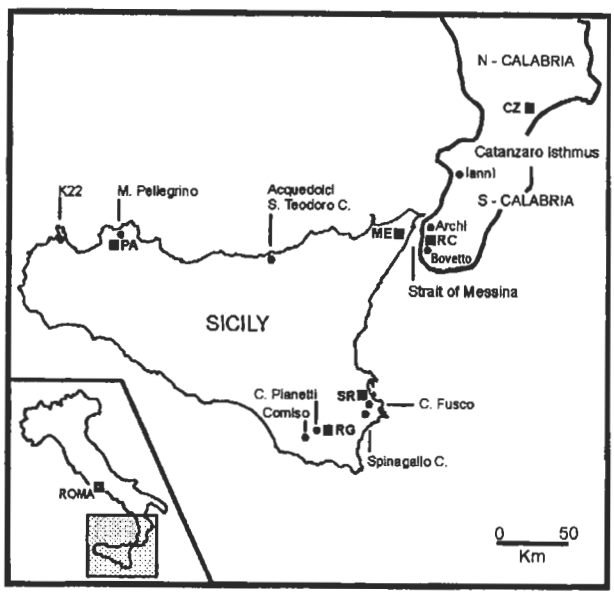

Fig. 1. Location of the sites quoted in the text. PA, Palermo; ME, Messina, SR, Siracusa; RG, Ragusa, RC, Reggio Calabria; CZ, Catanzaro.

Late Pleistocene, vertebrate dispersals from peninsular Italy through southern Calabria were conditioned by two palaeogeographic barriers, located in the area of the Straits of Messina and the Catanzaro isthmus (Fig. 1).

1.2. Historical backgrounds

Up to 1985, chronological schemes utilising Pleistocene mammals from Sicily were based on the assumption of the phyletic derivation of the dwarf elephant *Elephas falconeri* from the middle sized *E. mnaidriensis*, which is in turn a direct descendant of *E. antiquus* (Accordi, 1957, 1963, 1965; Accordi and Colacicchi, 1962; Ambrosetti, 1968; Ambrosetti et al., 1980; Gliozzi and Malatesta, 1984; Brugal, 1987; Kotsakis, 1979; Vaufrey, 1929). The smallest species (*E. falconeri*) was considered to be limited to the Early Würm period and to have evolved as a consequence of environmental stress linked to the Würmian climatic cooling. Most of the vertebrate remains came from cave deposits and little was known about their taphonomic and stratigraphic background.

Southern Calabria was considered a "fossil island" as evidenced by the occurrence in early Late Pleistocene deposits of a small sized elephant (*Elephas* cf. *antiquus*) (Azzaroli, 1982; Bonfiglio and Berdar, 1986), and of a cervid, coming from Bovetto, which was considered a dwarf megalocerine (*Megaceroides calabriae*) closely related to the Sicilian endemic deer, *M. carburangelensis* (Bonfiglio, 1978).

Since 1985, new stratigraphic, aminostratigraphic and taphonomic investigations have deeply changed the knowledge of Pleistocene vertebrates in Sicily (Bada et al., 1991; Belluomini and Bada, 1985; Bonfiglio, 1987, 1991, 1992a, b, 1995; Bonfiglio and Insacco, 1992; Bonfiglio et al., 1993, 1996, 1997, 2000, 2001; Burgio and Cani, 1988; Chilardi and Gilotti, 1996).

Actually, most of the Sicilian mammalian fossils are found in "morphological" traps such as caves and fissures, rather common in the carbonate mountain ranges of northern Sicily and in the Hyblean Plateau. Another important category of deposits is represented by ancient shorelines, beach deposits and marine terraces, which are frequently associated with a lagoon or swamp. Limnic deposits related to small freshwater basins also occur, often in relation to coastal and fully marine deposits.

Fossil documentation of Quaternary vertebrates in Sicily is not evenly distributed in time. A trend is evident towards a richer fossil record from the Early Pleistocene to the Late Glacial, fossils of the latter age being most widespread. The geographic distribution could be related to taphonomical factors and to effective differences in palaeogeography in the insular system (Bonfiglio and Burgio, 1992), while the reason why the number of sites and stratigraphic levels varies so greatly with respect to time (younger sites are much more numerous) has never been investigated in detail. This pattern, widespread in regions in which tectonic activity is very intense, is probably partially due to the destruction of older deposits by intense erosion.

The rich fossil record of Sicily allowed for the construction of a fairly detailed bio-chronological frame that is dated by the correlation of vertebrate bearing deposits with marine deposits and with ancient shorelines.

On the basis of extensive new evidence, the Pliocene–Quaternary vertebrate associations can be arranged into five phases or Faunal Complexes (F.C.) which are characterised by the occurrence of different taxa showing, on average, a decreasing degree of endemism (Tables 1 and 2).

The vertebrate fossil record of southern Calabria is, on the contrary, rather poor. No mammal deposits from southern Calabria are apparently older than the Late Middle Pleistocene and their correlation with coastal and marine deposits is subjected to the interference of a very intense geodynamic activity. Furthermore, mainly for taphonomic reasons but also due to sampling and excavation methods, the faunal assemblages are rather poor and no small mammal has been recovered so far.

Nevertheless, palaeobiogeographic data coming from the Sicilian palaeobioprovince fit closely with palaeontologic evidence coming from southern Calabria and with the Plio–Pleistocene palaeogeographic features that are known from the literature.

2. Late Pliocene–Early Pleistocene

2.1. Palaeontological evidence from Sicily

Monte Pellegrino Faunal Complex (Table 1) is the oldest Quaternary fossil record so far known and is documented only in the very restricted geographic area of Monte

Table 1
Composition of Quaternary Faunal Complexes of Sicily. Avifauna is listed in Table 2

"Monte Pellegrino"	"*Elephas falconeri*"	"*Elephas mnaidriensis*"	"Grotta S. Teodoro Pianetti"	"Castello"	Holocene
Pannonictis arzilla	*Vulpes* sp.	*Panthera leo*	*Crocuta crocuta*	*Canis lupus*	*Canis* cf. *lupus*
	Nesolutra trinacriae	*Crocuta crocuta*	cf. *spelaea*	*Vulpes vulpes*	*Vulpes vulpes*
Asoriculus burgioi		cf. *spelaea*	*Canis* cf. *lupus*		*Felis silvestris*
Apodemus maximus	*Elephas falconeri*	*Canis lupus*	*Vulpes vulpes*	*Equus caballus*	*Martes* sp.
Leithia sp.		*Nesolutra trinacriae*	*Ursus* cf. *arctos*	*Equus hydruntinus*	*Mustela* cf. nivalis
Maltamys cf. *gollcheri*	*Crocidura esuae*	*Ursus* cf. *arctos*		*Sus scrofa*	*Ursus* sp.
Pellegrinia	*Leithia cartei*		*Elephas mnaidriensis*	*Cervus elaphus*	*Monachus monachus*
panormensis	*Leithia melitensis*	*Elephas mnaidriensis*	*Sus scrofa*	*Bos primigenius*	
Hypolagus sp.	*Maltamys gollcheri*	*Sus scrofa*	*Equus hydruntinus*		*Sus scrofa*
	Bats, several species	*Hippopotamus pentlandi*	*Cervus elaphus siciliae*	*Erinaceus europaeus*	*Cervus* sp.
Testudo graeca		*Cervus elaphus siciliae*	*Bos primigenius siciliae*	*Crocidura* cf. *sicula*	*Bos primigenius*
	Birds	*Dama carburangelensis*		*Microtus* (*Terricola*)	
		Bos primigenius siciliae	*Erinacues* cf. *europaeus*	ex. gr. *savii*	*Erinaceus europaeus*
	Emys orbicularis	*Bison priscus siciliae*	*Crocidura* cf. *sicula*	*Apodemus sp*	*Crocidura* sp.
	Testudo hermanni		*Apodemus* cf. *silvaticus*	*Lepus europaeus*	Chiroptera indet
	Geochelone sp.	*Erinaceus europaeus*	*Microtus* (*Terricola*)		*Microtus* (*Terricola*)
	Lacerta	*Crocidura* aff. *esuae*	ex. gr. *savii*	Birds	cf. *savii*
	siculomelitensis	*Leithia* cf. *melitensis*	Chiroptera		*Apodemus* sp.
	Lacerta viridis	*Maltamys* cf. *wiendincitensis*			*Arvicola terrestris*
	Lacerta sp.		Birds		*Mioxus glis*
	Coluber cf.	Birds			
	viridiflavus		*Podarcis* sp.		Birds
	Natrix sp.	*Emys orbicularis*	Gekkonidae		
		Testudo hermanni	*Testudo* sp.		Turtle indet.
	Discoglossus cf.	*Lacerta siculomelitensis*	Anura		*Emys orbicularis*
	pictus				*Lacerta viridis*
	Bufo cf. *viridis*	*Discoglossus* cf. *pictus*	*Hyla* gr. *H. arborea*		*Bufo bufo*
	Hyla sp.		*Rana* sp.		*Bufo viridis*
			Bufo cf. *viridis*		
					Fishes

Pellegrino, close to the town of Palermo (Burgio and Fiore, 1997; Thaler, 1972). The faunal assemblage has been recovered from soil deposits infilling karst fissures.

The taxa of the Monte Pellegrino faunal complex have been considered indicative of a Late Pliocene–Early Pleistocene age by Thaler (1972), although Burgio and Fiore (1997) considered it to be Early Pleistocene (Late Villafranchian).

The poorly diversified fauna includes species with different degrees of endemism and of different geographical affinity, indicating a polyphasic origin. After the first report by Thaler (1972), some of the taxa have been revised more recently but our knowledge of this very peculiar and intriguing faunal assemblage is still not exhaustive.

Hypolagus and Pannonictis (*Pannonictis* in particular) are characterised by moderately endemic features with respect to both size and morphology (Burgio and Fiore, 1997). The potential ancestors appear to be typical European forms, not found so far in northern Africa.

This shrew *Asoriculus burgioi* is about twice as large as the *Asoriculus* representatives from the mainland, but, in comparison with them, is not particularly modified (Masini and Sarà, 1998). Its occurrence in Sicily parallels the occurrence of *Nesiotites* in the Balearics and in Corsica/Sardinia, suggesting a separate origin for the two taxa within a clade of common ancestors. *Asoriculus* is well documented in Europe from the Early Pliocene, and it has also been found recently in northern Africa, in Late Pliocene–Early Pleistocene deposits (Geraads, 1995; Rzebik-Kowalska, 1988). This finding complicates the palaeobiogeographical picture, making any hypothesis of its geographic provenance more uncertain.

The endemic dormice *Leithia* nov. sp. was quoted by Thaler (1972), but this taxon has not been studied in detail. There is, however, a certain consensus in the literature regarding them as one of the direct precursors of the better known and better described *Leithia* and *Maltamys* from the Middle to Late Pleistocene of Sicily and Malta (Zammit Maempel and De Bruijn, 1982). They have been assigned to the tribe *Eliomyini* and, according to some authors, they are the direct offspring of a taxon, no better identified than *Eliomys* sp. (Daams and De Bruijn, 1995). These authors considered *Leithia* and *Maltamys* as relics of a scarcely known older (Messinian) population phase and these elements have remained isolated in the Sicilian Maltese archipelago for the entire Pliocene and most of the Quaternary.

The presence of *Pellegrinia panormenis* in the Monte Pellegrino assemblage is enigmatic. This rodent has been described by Thaler (1972) as a strongly endemic form belonging to Ctenodactilids, a rodent family that nowadays

Table 2
Composition of Quaternary avifauna of Sicily: (E) indicates endemic species of Siculo-Malthese archipelago; (↑) indicates extinct species

Elephas falconeri F.C.	*Elephas mnaidriensis* F.C.	Pianetti-S. Teodoro F.C.	Castello F.C.
Geronticus eremita	*Tachybaptus ruficollis*	*Branta* sp.	*Calonectris diomedea*
Cygnus cfr. *C. cygnus*	*Podiceps cristatus*	*Falco columbarius*	*Puffinus yelkouan*
Cygnus equitum (E)	*Podiceps auritus*	*Falco tinnunculus*	*Podiceps cristatus*
Anser erythropus	*Phalacrocorax carbo*	*Coturnix coturnix*	*Phalacrocorax aristotelis*
Branta cfr. *B. ruficollis*	*Pelecanus crispus*	*Alectoris graeca*	*Anser erythropus* ?
Anas crecca/querquedula	*Ixobrychus minutus*	*Vanellus vanellus*	*Anser fabalis* ?
Anas penelope	*Botaurus stellaris*	*Pluvialis* cf. *P. apricaria*	*Branta leucopsis* ?
Marmaronetta angustirostris	*Egretta garzetta*	*Scolopax rusticola*	*Falco tinnunculus*
Accipiter gentilis	*Ardea cinerea*	*Columba livia/oenas*	*Falco naumanni*
Accipter nisus	*Plegadis falcinellus*	Hirundinidae indet.	*Alectoris graeca*
Falco tinnunculus	*Cygnus falconeri* (E)	*Turdus* sp.	*Rallus aquaticus*
Falco subbuteo	*Anser anser*	*Pyrrhocorax pyrrhocorax*	*Crex crex*
Falco eleonorae	*Anser fabalis*	*Pyrrhocorax graculus*	*Tetrax tetrax*
Falco columbarius	*Anser albifrons*	Passeriformes indet	*Columba livia*
Coturnix coturnix	*Anas plathyrhyncjos*		*Columba palumbus*
Rallus acquaticus	*Anas acuta*		*Cuculus canorus*
Fulica atra	*Anas strepera*		*Athene noctua*
Grus grus	Anas querquedula		Asio otus
Grus melitensis (E)	*Anas crecca*		*Strix aluco*
Tetrax tetrax	Aythya fuligula		Apus apus/pallidus
Recurvirostra avosetta	*Mergus merganser*		*Picus viridis*
Scolopax rusticola	*Oxyura leucocephala*		*Hirundo daurica/rustica*
Limosa limosa/lapponica	*Pandion halietus*		*Garrulus glandarius*
Larus minutus	*Gyps melitensis* (↑)		*Pyrrhocorax pyrrhocorax*
Larus ridibundus	*Aquila heliaca*		*Pyrrhocorax graculus*
Pterocles alchata	*Accipiter gentiles*		*Corvus monedula*
Columba livia/oenas	*Accipiter nisus*		*Corvus corone*
Columba palumbus	*Falco tinnunculus*		*Corvus corax*
Streptopelia turtur	*Falco columbarius*		*Sturnus unicolor/vulgaris*
Tyto n. sp. (E)	*Coturnix coturnix*		*Sturnus roseus*
Otus scops	Fulica atra		Carduelis chloris
Athene n. sp. (E)	*Grus grus*		*Emberiza* sp.
Asio otus	*Otis tetrax*		Passeriformes indet
cfr. *Surnia ulula*	*Otis tarda*		
Caprimulgus cfr. *C. europaeus*	*Scolopax rusticola*		
Apus apus/pallidus	*Numenius phaeopus*		
Tacymarptis melba	*Pterocles orientalis*		
Dendrocopos leucotos	*Columba palumbus*		
Picus viridis	*Columba oenas*		
Calandrella brachydactyla	*Bubo bubo*		
Lullula arborea	*Strix aluco*		
Hirundo daurica/rustica	*Athene noctua*		
Anthus sp.	*Asio otus*		
Prunella modularis	*Tacymarptis melba*		
Erithacus rubecula	*Coracias garrulous*		
Oenanthe cfr. *O. hispanica*	*Picus viridis*		
Monticola solitarius	*Hirundo daurica/rustica*		
Turdus sp.	*Anthus* sp.		
Sylvia sp.	*Erithacus rubecula*		
Phylloscopus sibilatrix/collybita	*Turdus viscivorus*		
Lanius senator	*Turdus merula*		
Pica pica	*Sylvia* sp.		
Pyrrhocorax graculus	*Pica pica*		
Pyrrhocorax pyrrocorax	*Pyrrhocorax pyrrhocorax*		
Corvus monedula	*Corvus corone*		
Corvus corax	*Sturnus unicolor/vulgaris*		
Corvidae n. sp. (E)	*Fringilla coelebs*		
Sturnus vulgaris/unicolor			
Petronia petronia			
Fringilla coelebs/montifringilla			
Serinus sp.			
Carduelis chloris			
Carduelis sp.			
Pyrrhula pyrrhula			
Coccothraustes coccothraustes			
Emberiza sp.			

has an exclusive African distribution. Ctenodactilids probably originated in Asia in the Oligocene; the oldest African representative of the family dates to the Middle Miocene (Locality: Beni Mellal). Ctenodatilids are also known from Sardinian deposits of Early Miocene age. According to Thaler, *Pellegrinia* has derived characteristics of the African stock of Ctenodictilids, thus indicating a dispersal from that region. Again, a Late Miocene (Messinian) age has been cited for this dispersal.

The information derived from the poorly studied *Apodemus maximus* is limited to the observation that this mouse is more than twice as large as the living *A. sylvaticus*. The size increase, comparable to that observed in *Asoriculus*, indicates that this taxon underwent a certain amount of differentiation in insular conditions.

To summarise, the composition of the Monte Pellegrino fauna—unique for the Mediterranean islands—suggests it may have been derived in part from an older, not locally known, population phase (Messinian age? Azzaroli, 1974; Azzaroli and Guazzone, 1979) and partially from younger dispersals from Europe.

2.2. Physiographic evidence

Plio–Pleistocene palaeogeographic evolution of southern Calabria has been controlled mainly by tectonics. In southern Calabria three main blocks have been recognised, represented by the Cape Vaticano, the Aspromonte and the Serre horsts (Fig. 2(A)), which are bounded by regional fault systems. Beginning from Early Pliocene up to the present, the three massifs show an uplifting tendency. Diachronic deep Pliocene–Early Pleistocene marine basins are located among the uplifting areas and at their margins (Catanzaro, Mesima, Gioia Tauro, Monte Torre, Monasterace, Reggio Calabria basins) (Barrier et al., 1993; Fabbri et al., 1980; Gignoux, 1913; Selli et al., 1977).

The evolution of these sedimentary basins is controlled by synsedimentary faults that belong to the recognised regional fault systems and to the regional tilting of the uplifting areas (Barrier, 1987; Barrier et al., 1990, 1993; Fabbri et al., 1980).

In Sicily also the establishment of an extensional tectonic regime from the Early Pleistocene onwards resulted in the collapse of peripheral zones and led to the creation of a series of deep marine basins which occupied large areas until the end of the Early Pleistocene (Bonfiglio and Burgio, 1992; Bonfiglio and Piperno, 1996; Di Geronimo, 1979; Di Geronimo and Costa, 1978; Di Geronimo et al., 1980; Grasso and Lentini, 1982; Ruggieri and Unti, 1974, 1977; Sprovieri, 1982).

To summarise current knowledge, geological observations do not provide details on identifying the route and the age of dispersal of the Monte Pellegrino F.C.

It is possible to assume a vicariance from more ancient non-documented phases and later dispersal from Italian peninsula. Data are too poor to allow a palaeogeographical reconstruction.

3. Early Middle Pleistocene

3.1. Palaeontologic evidence from Sicily

The *E. falconeri* Faunal Complex (Tables 1 and 2) is even poorer than the preceding one in mammalian biodiversity. The dormice from Monte Pellegrino are still present

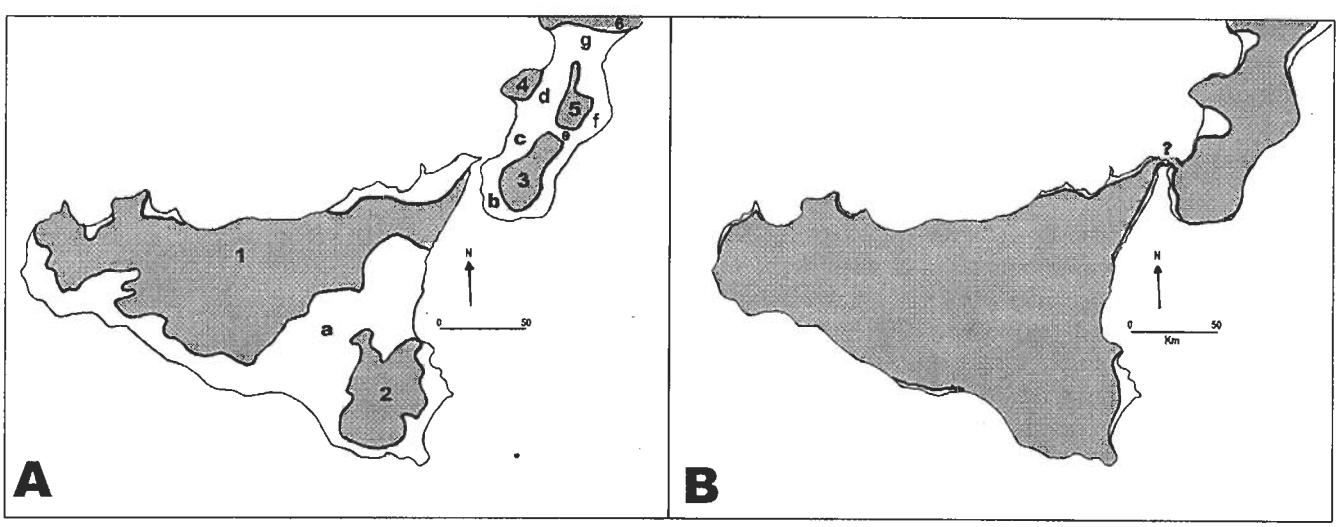

Fig. 2. Palaeogeographic maps of Sicily and southern Calabria. (A) Upper Pliocene–Lower Pleistocene. Lands: 1, Northern-Central Sicily; 2, Hyblean Plateau; 3, Aspromonte Massif; 4, Cape Vaticano M.; 5, Serre M.; 6, Northern Calabria. Basins: a, Gela channel; b, Reggio Calabria; c, Gioia Tauro; d, Mesima; e, Monte Torre; f, Monasterace; g, Catanzaro. (B) Upper Pleistocene. "?" indicates the Strait of Messina area which in turn has probably acted as a filtering barrier and/or a land bridge.

in the insular system, while all the other small mammals are apparently extinct.

The shrew *Crocidura esuae* is an endemic species, of uncertain bio-geographic affinity (Kotsakis, 1986). The genus *Crocidura* is recorded in Italy from the Late Pliocene (Montagnola Senese Locality; Fondi, 1972; Maul et al., 1998) and occurs widely in the Quaternary, probably correlating with a degree of climatic aridity in Europe (Reumer, 1984; Rzebik-Kowalska, 1995). Approximately coeval occurrences are the oldest evidence of this genus in eastern Africa (Late Pliocene at Omo Valley and Laetoli), while its oldest record in northern Africa is more recent, dating back to the Middle Pleistocene (Butler, 1980). At present no more detailed information is available in the literature on the origin of this endemic species. It deserves a more thorough investigation.

Large mammals include the pigmy elephant *E. falconeri*, strongly reduced in size, and a member of the Lutrinae (genus *Lutra*). The occurrence of a small bear and of "*Vulpes*" is considered uncertain and deserves further investigation. Neither the ancestor nor the geographic provenance of *E. falconeri* has been determined unequivocally. Even though its derivation from a Paleoloxodontine elephant is accepted by several authors, its possible origin from European *E. antiquus* stock, or from a north African species, is still a matter for discussion.

Moreover, also the composition of this faunal complex reveals a polyphasic origin; some taxa are relics from the preceding phase and others are "newcomers" that probably entered the island through a strongly filtering barrier.

Almost all the endemic taxa of the *E. falconeri* Faunal Complex are typical of the Sicilian Siculo-Maltese archipelago (Bonfiglio, 1992c).

From the *E. falconeri* Faunal Complex assemblages also comes a rich typical endemic avifauna which is contained in cave deposits of the Palermo area (Luparello, Marasà, Poggio Schinaldo) as well as in the limnic deposits at Comiso and in fissure-filling deposits of the Hyblean Plateau (Spinagallo; Pavia, 1999; Contrada Annunziata; Ragusa).

The avifauna of the *E. falconeri* F.C. (Pavia, 2000) includes five endemic species, three of them are a new record and have not been described yet: *Cygnus equitum*, *Grus melitensis*, *Tyto* nov. sp. and Corvidae nov. sp.. These species have endemic features, such as the gigantism of *Tyto* nov. sp., the dwarfing of *C. equitum*, the peculiar morphologies observed, for instance, in lengthened forelimbs of *Athene* nov. sp. Typical continental taxa (i.e. Galliforms) are lacking and some endemic species are also typical of the Sicilian-Maltese archipelago.

No records of the mammal assemblages that dispersed in Sicily and gave origin to the fauna of the *E. falconeri* F.C. have been recovered so far in southern Calabria.

3.2. Physiographic evidence

The *E. falconeri* F.C. denotes the occurrence of an insular system made up of strongly geographically isolated small islands, with very difficult and sporadic connections with the mainland.

The oldest occurrence of this F.C. occurs in the Hyblean Plateau where the vertebrate assemblage is contained in limnic deposits that overlie clays and sands of the uppermost Early Pleistocene and in turn are overlain by Early Middle Pleistocene marine sands (Bonfiglio and Insacco, 1992). This continental limnic succession, made up of by paleosoils, lacustrine and aeolian deposits, constitutes the evidence of the first connection of the Hyblean Plateu with the northern sector of Sicily in the Pleistocene (Conti et al., 1980).

At the beginning of the Middle Pleistocene, the evolution of southern Calabria was characterised by the uplifting of the three main blocks, which is diachronic and affected by tilting (Barrier et al., 1990, 1993; Fabbri et al., 1980). In the uppermost Early Pleistocene, the closing of the Monte Torre basin is documented while marine basin persists around the three main blocks.

Basically, the palaeogeography of southern Calabria prevented the dispersal of terrestrial faunas from the Italian peninsula, while paleobiological data support a connection between Sicily and Malta. In fact all the endemic taxa of the *E. falconeri* F.C. are recognised in Malta (Bonfiglio, 1992c).

According to Bonfiglio and Piperno (1996) the distribution of the *E. falconeri* assemblages in south-eastern and western Sicily and the scattered traces of Lower Palaeolithic artefacts in the Hyblean Plateau and along the area linking it to western Sicily, might suggest that the dispersal events of humans and of some faunal elements have followed the same route. According to the latter authors, the hypothesis of an African provenance for both *E. falconeri* and human populations through the Sicilian–Tunisian isthmus, as a result of tectonic controlled changes of sea bed depth during the Early Pleistocene (see Alimen, 1975; Kelling and Stanley, 1972; Vaufrey, 1929), should at least merit a fresh and more detailed re-consideration.

4. Late Middle Pleistocene–Late Pleistocene

4.1. Palaeontologic evidence from Sicily

The large-mammal assemblage of the *E. mnaidriensis* Faunal Complex (Tables 1 and 2) is almost completely renewed with respect to the preceding F.C. The pigmy *E. falconeri* is extinct, while the faunal composition is more balanced and includes top predators such as the lion and the spotted "cave" hyena. The only significant absence is that of perissodactyls (rhinos and horses). The herbivorous taxa (bison, aurochs, fallow deer, red deer, hippo) are moderately modified with respect to the cogeneric or cospecific taxa

from the mainland; the endemic nature of the fauna is apparent mainly from the modest reduction in size. The continental forerunner of most of these taxa has been fairly accurately identified. For instance, *E. mnaidriensis* can be easily seen as a smaller, but not extremely modified, descendant of *E. antiquus*, a rather common taxon throughout Europe. The red deer *Cervus elaphus* is slightly reduced in size (about 20%). *Dama carburangelensis* (previously identified as *M. carburangelensis*) is probably derived from fallow deer populations (*D. dama tiberina*) widespread in central and southern Italy during the Late Middle Pleistocene (Abbazzi et al., 2001).

The faunal composition is quite similar to that found in the southern Italian peninsula and indicates a large island, with abundant resources and a well-developed trophic chain. In Malta, faunal assemblages containing taxa of the *E. mnaidriensis* F.C. also occur, but they lack some taxa (hyena, bison, lion, aurochs, wild boar) with respect to the Sicilian assemblages (Bonfiglio, 1992c).

A peculiarity of this fauna is the very low biodiversity of small mammals, which are represented only by survivors from the *E. falconeri* F.C. (*Leithia*, *Maltamys* and *Crocidura esuae*); *Maltamys*, however, is represented by different species. The knowledge of the composition of the avifauna is still incomplete because bird remains have been collected systematically only in three sites (Pavia, 2001). One endemic species, *Cygnus falconeri*, occurs, while the endemic species of the previous F.C. became extinct, except *Grus melitensis* whose persistence is, however, questionable. Typical continental taxa (i.e. Galliforms) are still lacking. On the whole, the avifauna assemblages are partially renewed like the mammal fauna.

Bada et al. (1991) assigned an age of 200 ± 40 Ky to this faunal complex. ESR dating for teeth enamel of *E. mnaidriensis* and *Hippopotamus pentlandi* from Contrada Fusco (Rhodes, 1996) provided an age ranging between 146.8 ± 28.7 and 88.2 ± 19.5 Ky.

Where correlated with sediment of littoral environments, the assemblages of the *E. mnaidriensis* Faunal Complex are associated with deposits dated as Late Middle Pleistocene and/or Late Pleistocene (Bonfiglio and Burgio, 1992; Bonfiglio et al., 1996).

4.2. Palaeontologic evidence from southern Calabria

A recent revision of the supposed dwarf megalocerine "*M. calabriae*" from Bovetto and the comparison of the Calabrian specimen with "*M. carburangelensis*" (Abbazzi et al., 2001) shows that the Calabrian and Sicilian "megacerine" deer belong to genus *Dama*. In particular, the Calabrian form is comparable to *D. dama tiberina*, a fallow deer documented in the Italian peninsula during the Late Middle Pleistocene (MIS 7) while *D. carburangelensis* is an endemic species strictly related with the mainland species.

At the site of Bovetto, the remains of *D. dama tiberina* are associated with remains of *Hippopotamus* cf. *amphibius* (Marra, 2000) and of an elephant.

The occurrence of a non-endemic fallow deer in southern Calabria and of its possible direct descendant *D. carburangelensis*, a moderately endemic fallow deer, in the *E. mnaidriensis* complex of Sicily, could indicate the assemblage from Bovetto as an evidence of the dispersal of the taxa of the *E. mnaidriensis* F.C. through southern Calabria.

4.3. Physiographic evidence

The above-mentioned palaeontological evidences also involve the Pleistocene palaeobiogeographic reconstructions of southern Calabria and Sicily (Fig. 2(B)) and suggest that the elements of the mega and large fauna have dispersed through some kind of filter barrier which has prevented small mammals from entering the island. Such a kind of barrier could be a partially emerged sea floor or a swampy lagoonal system. The dispersal route must have been the Catanzaro isthmus and the Messina Straits.

According to Bonfiglio (1978), the sedimentary succession of Bovetto referred to Eutyrrhenian, comprises three units (5, 6, 7 and Figs. 2, 4 in Bonfiglio, 1978) that are separated from each other by reddish horizons (remnants of palaeosoils?). The remains of *D. dama* cf. *tiberina* come from the base of unit 6. In Sauret's (1980) opinion, the succession of Bovetto represents a sequence of infilling, which was controlled by tectonics, and therefore is relatively thick with respect to other terrace deposits outcropping in the same area, considered Eutyrrhenian in age. From Fig. 25(C) in Sauret (1980), it is apparent that a tension fault cuts the series of Bovetto. The great variation in thickness of the series (from 10 m close to the ancient shoreline to about 30 m at the other side of the fault) suggests, according to the same author, that the beginning of the infilling of the sedimentary basin (unit 5, in Bonfiglio, 1978) preceded the deposition of the *Strombus bubonius* sands (Units 6 and 7 in Bonfiglio, 1978). From Sauret's data it emerges that the deposition of the Eutyrrhenian transgressive series of Bovetto was at first due to an extensional tectonic phase and only in the upper part of the sequence (gravel with *S. bubonius*) to the eustatic transgression corresponding to MIS 5e. The lower part of the "Eutyrrhenian" series of Bovetto, where the remains of *D. dama* cf. *tiberina* were found, could be correlated to the end of Middle Pleistocene.

The pre-Tyrrhenian age of *D. dama* cf. *tiberina* is consistent with bio-chronological data about the dispersal in Sicily of the *E. mnaidriensis* Faunal Complex. Dispersal of *D. dama* cf. *tiberina* through the Catanzaro isthmus may have occurred late during the Late Middle Pleistocene partial emersion, which followed the deposition of Plio–Pleistocene bathial sediments. Possibly in a second time, still during the Late Middle Pleistocene, *D. dama* cf. *tiberina* and other ancester taxa of the *E. mnaidriensis* complex dispersed to Sicily in correspondence of an exten

sional tectonic phase, perhaps coeval to MIS 6 (Bonfiglio and Burgio, 1992; Bonfiglio et al., 2000).

5. Late Pleistocene

5.1. Palaeontologic evidence from Sicily

The Pianetti–San Teodoro F.C. (Tables 1 and 2) date to the last glacial cycle. The faunal history of this period is dominated by extinction events (hippopotamus, endemic dormice and *Crocidura esuae*), and by the dispersal of equids (*Equus hydruntinus*) and of mainland small mammals, which are represented by taxa still present in Sicily (*Microtus* (*Terricola*), *Crocidura* cf. *sicula*, *Apodemus* cf. *sylvaticus*, *Erinaceus europaeus*) (Bonfiglio et al., 2001). Almost all of the large mammals belonging to this F.C. seem to be inherited from *E. mnaidriensis* F.C. The only taxon that shows a certain degree of endemism is *Crocidura sicula*. Even though the affinities of this shrew are still not well established, its morphological features are sufficient to rule out the possibility of a derivation from the older Sicilian endemic *Crocidura esuae*.

Endemic species of avifauna are lacking from the assemblages of the Pianetti–Grotta di S. Teodoro F.C. (Pavia, 2000); *Alectoris graeca*, a galliform at present represented in Sicily by the endemic subspecies *Alectoris graeca whitakeri*, occurs.

The associations of "Pianetti–S. Teodoro" F.C. come from fissure-filling (Contrada Pianetti; K 22 site, upper levels) and cave (San Teodoro) deposits, that are not correlated to marine deposits and have not yet been dated radiometrically (Bonfiglio et al., 1997, 1999, 2001; Di Maggio et al., 1999). The faunal composition of this F.C. is probably not completely known, since only a few sites have been discovered so far and one of them (S. Teodoro cave) has not yet been completely investigated.

The dispersal to Sicily of the ground vole, which has a fossorial habit, and of horses, that prefer open landscapes, might imply that a fully exposed connection (a temporary land bridge related to eustatic lowstand) had formed, perhaps more than once during the last glaciation.

5.2. Palaeontologic evidence from southern Calabria

The vertebrate deposits outcropping at S. Francesco di Archi and Iannì di San Calogero hills rest on marine sediments referred to the Eutyrrhenian marine cycle and underlie brackish lagoon deposits (Bonfiglio and Berdar, 1986; Bonfiglio et al., 1986). The occurrence of an *Elephas* of reduced size in lower levels of the Archi section (Bonfiglio and Berdar, 1986) may suggest that a certain isolation of southern Calabria occurred during the Tyrrhenian.

The well-diversified continental faunas coming from the upper levels of the Archi section and those coming from Iannì di S. Calogero both contain remains of *Homo neanderthalensis* and may document a post-Tyrrhenian dispersal event through the Catanzaro isthmus. Data are still lacking for correlation of the faunas from the upper levels of S. Francesco di Archi and Iannì di San Calogero hills with the scarcely endemic faunas of the Late Pleistocene Contrada Pianetti–San Teodoro Faunal Complex.

5.3. Physiographic evidence

Even though the new issues from Bovetto do not justify the occurrence of an "ancient" (Middle Pleistocene) southern Calabrian palaeo-island any more, nevertheless, they do not exclude the possibility of a more recent insular phase (Tyrrhenian age?), as suggested by the smaller sized elephant from a little known stratigraphic series at Vallone Corvo and at the S. Francesco di Archi hill in southern Calabria too (Bonfiglio and Berdar, 1986). New research on the diverse mammal assemblages coming from these sites can clarify this point.

6. Late Glacial

The continental type faunal assemblages of the Castello F.C. (Tables 1 and 2) demonstrate that faunal exchanges become easier, so that the mammalian population of Sicily becomes very similar to that of the southern Italian peninsula, even though less diversified (Bonfiglio et al., 2000, 2001). Also humans entered the island probably during Late Glacial.

Endemic species of avifauna are lacking from the assemblages of the Castello F.C., which still contains *Alectoris graeca* (Pavia, 2000).

No records of the mammal assemblages that dispersed in Sicily and gave origin to the fauna of the Castello F.C. have been recovered so far in southern Calabria.

6.1. Physiographic evidence

The composition of the two younger two F.C. denotes that temporary connections with southern Italy occurred. Variation in palaeogeography caused by tectonics and gla cial and eustatic marine cycles, which are not easy to recognise in the geological record, have controlled the processes and timing of Late Pleistocene–Late Glacial vertebrate faunal dispersion in southern Calabria and in Sicily.

7. Conclusions

The Pleistocene vertebrate fossil record from Sicily and southern Calabria provides the only direct access to the chronological and palaeogeographical dimension of biological events concerning these two areas.

The oldest Sicilian Faunal Complexes (Monte Pellegrino F.C. and *E. falconeri* F.C.), characterised by strongly endemic faunal assemblages, denote the occurrence of an insular system made up of geographically isolated small islands, with very difficult and sporadic connections with the mainland. The occurrence of two taxa with European affinity in the oldest F.C. is an indirect demonstration of a dispersal route from the Italian peninsula. Unfortunately, palaeogeographic data do not provide more precise information on the route followed by dispersals for this complex and for the following *E. falconeri* F.C.

Temporary connections between Sicily and southern Italy through southern Calabria occurred more frequently and extensively during the Late Middle Pleistocene and Late Pleistocene, as indicated by:

- starting from the *E. mnaidriensis* F.C. to the Castello F.C., the faunal composition is more similar to that of the southern Italian peninsula;
- endemism becomes more and more moderate, being absent in the youngest assemblages;
- a delay occurs in the age of dispersal of large and small mammals respectively, as shown by the occurrence within the *E. mnaidriensis* F.C. of endemic rodents and insectivores directly descended from those of the *E. falconeri* F.C. and the occurrence of not non-endemic rodents and insectivores in the younger Pianetti–San Teodoro F.C. A sort of filtering barrier could affect the dispersals in the former phase of the population, preventing small mammals from the mainland from entering the island.

Dispersal of land mammals in southern Calabria might have occurred in the Middle Pleistocene when the Catanzaro isthmus emerged after the long lasting deposition of Plio–Pleistocene bathial deposits that are well known and intensively studied in the area. Unfortunately, vertebrate fossils are poorly documented and the few known sites give the following indications:

- the fauna from Bovetto could testify the connection of southern Calabria with peninsular Italy and could be coeval of mammals that spread in Sicily giving the *E. mnaidriensis* faunal complex;
- the vertebrate of S. Francesco di Archi and Iannì di San Calogero may document a dispersal event through the Catanzaro isthmus after the Eutyrrhenian marine cycle. Relationships with "Pianetti–S. Teodoro" F.C. are still unknown.

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