# BIOSTRATIGRAPHY OF AMPHIBIANS, REPTILES, BIRDS AND MAMMALS IN CORSICA AND THE ROLE OF MAN IN THE HOLOCENE FAUNAL TURNOVER

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## Summary

This paper presents the results of a study of seven late Pleistocene and Holocene faunal assemblages from Corsica. They greatly improve the number of chronostratigraphic data-sets available for amphibians, reptiles, birds and mammals from this island. Compared with those from several other recent excavations, they corroborate an earlier interpretation: the colonization of the island by man had little impact on the herpetofauna (a few introductions and no extinctions), a slightly more important impact on birds (mainly favouring some species) and a very strong one on mammals (complete turnover of the fauna).

## Résumé

Biostratigraphie des amphibiens, des reptiles et des mammifères en Corse et rôle de l'homme dans le renouvellement faunique holocène.

Cet article présente les résultats de l'analyse de sept nouveaux assemblages fauniques pleistocènes ou holocènes de Corse. Ils permettent d'augmenter de manière sensible le nombre des données chrono-stratigraphiques disponibles pour les amphibiens, les reptiles, les oiseaux et les mammifères en Corse. Comparés à d'autres résultats récents, ils confirment les interprétations émises précédemment : la colonisation de l'île par l'homme a eu un faible impact sur l'herpétofaune (petit nombre d'introductions et pas d'extinctions), un impact un peu plus important sur les oiseaux (effet favorable sur certaines espèces) et de très importantes conséquences pour les mammifères (complet renouvellement faunique).

## Zusammenfassung

Biostratigraphie der Amphibien, Reptilien, Vögel und Säugetiere in Korsika und der menschliche Einfluß auf die holozäne Fauna.

In diesem Beitrag werden die Ergebnisse der Untersuchung von sieben neuerdings ergrabenen Faunenensembles des späten Pleistozäns und Holozäns Korsikas vorgestellt. Sie erhöhen die Anzahl chronostratigraphisch gesicherter Daten bezüglich der Amphibien, Reptilien, Vögel und Säugetiere erheblich. Verglichen mit Werten aus anderen Grabungen erhärten sie die bisher gängige Annahme: geringer menschlicher Einfluß auf die Reptilienfauna (einige wenige "Importe", keine Ausrottung) ein etwas größerer Einfluß auf die Avifauna (mit einer Bevorzugung auf weniger Arten) und sehr starke Beeinflussung der Säugetierfauna (vollständige Umwandlung der Fauna).

## **Key Words**

Vertebrates, Corsica, Island, Human Impact, Late Pleistocene, Holocene.

## Mots clés

Vertébrés, Corse, Iles, Anthropisation, Pléistocène final, Holocène.

## Schlüsselworte

Wirbeltiere, Korsika, Insel, Menschlicher Einfluß, Spätpleistozän, Holozän.

During the Pleistocene, the terrestrial vertebrate fauna of Mediterranean islands evolved toward a heavy taxonomic endemism (Azzaroli, 1971; Sondaar, 1986; Davis, 1987; etc.). During the last 11,000 years (Holocene), these faunas underwent a partial turnover, mainly due to the colonization of the islands by modern man (Vigne, 1989; Cherry, 1990). The Mediterranean islands hence provide a very accurate "experimental" framework for the study of the impact of the successive

Holocene human activities on the evolution of the vertebrate fauna (i.e. extinction, immigration, modification of the dispersal area, etc.). Peculiarly, amphibians, reptiles, birds, small and large mammals have very different ecological characteristics, dispersal behaviours and cultural values for man. Archaeozoological analysis enables a story of how these different groups of animals reacted to human colonization and how these island faunas have evolved during the Holocene.

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Corsica is a Mediterranean island for which the last ten millennia are very well documented archaeozoologically. On this island, visits perhaps may have been made by Early and Middle Palaeolithic man (Bonifay, 1993) but cannot be considered for the moment as actual colonizations, i.e. the permanent presence of human groups living on island resources throughout the year and burying their dead on the island (Vigne, 1989). There is no evidence for a human presence in the Upper Palaeolithic. The first true colonization by modern man occurred at the beginning of the Holocene, during the 9th-8th millennia cal. BC (Camps, 1988; Vigne and Desse-Berset, 1995). For these reasons, Corsica provides us with an excellent case study of human impact on the different groups of vertebrates in a Mediterranean insular context.

Ten years ago, Vigne and Alcover (1985) reviewed West Mediterranean islands' faunal turnover for amphibians, reptiles and mammals, and suggested why some taxa became extinct while others survived to the present day. At that time, the Pleistocene fauna of Corsica was very poorly documented (Corte and Conca breccias, Maccinaggio cave; Deperet, 1897; Passemard, 1925; Tobien, 1935; Gasc, 1961; Bonifay, 1976; Brandy, 1978) and its composition was deduced from that of Sardinia, on the assumption that the two islands were joined by a landbridge during most of the last Glacial period. During the last ten years, excavations on Corsica have produced so many new data, including birds, that this question can now be reviewed using the example of Corsica alone.

The Quaternary herpetofauna of the Tyrrhenian Islands are still mainly known for Sardinia. Five sites have been studied: Su Casteddu (Villafranchian; Esu and Kotsakis, 1979), Sidanus (undeterminated Pleistocene; Sanchiz, 1979), Dragonara (upper Pleistocene; Kotsakis, 1980a), Corbeddu (early Holocene; Sondaar et al., 1984) and Su Guanu (undeterminated Holocene; Sanchiz, 1979; Kotsakis, 1983). They show that Discoglossus sp., Bufo viridis, Coluber sp., Emys orbicularis and Natrix sp., which are still present on the island, were present in the Pleistocene too. For the Pleistocene of Corsica, Gasc (1961) mentioned Discoglossus sp. and a large Lacertid from the Maccinaggio deposits (upper Pleistocene and recent mixed assemblage), and Kotsakis (1977) refers to Bufo sp. (without arguments). For the Holocene on the same island, the Araguina-Sennola shelter provided a record of Discoglossus sp. in the earlier layers (Preneolithic), Rana sp. (temporaria group) in the early and middle Neolithic ones and Bufo viridis in the Bronze Age (Vigne, 1985). The Chalcolithic layers of Terrina IV provided bones of *Emys orbicularis* (Cheylan, 1988). The 14th century deposit of Santa Maria Lavezzi provides evidence of *Podarcis tiliguerta* and *Coluber viridiflavus* (Bailon, in Vigne, 1994). These data suggested for Corsica (i) the great antiquity of *Discoglossus* sp., (ii) the Neolithic immigration of *Bufo viridis*, and (iii) the questionable immigration and rapid extinction of *Rana* sp. (*temporaria* group) during the Neolithic (Vigne, 1985; Vigne and Alcover, 1985). Among the eighteen species present (Delaugerre and Cheylan, 1992; nineteen if including *Natrix maura*; Fons *et al.*, 1991), only four have been mentioned as fossils.

Fossil records of avifauna from Mediterranean islands have been compiled by Alcover et al. (1992) for the Middle and Late Pleistocene. Some data have been added for the Pleistocene (Ferrandini and Salotti, 1995) and overall for the Holocene with the long stratigraphy of the Araguina-Sennola shelter (Vigne, 1988), with the late Antiquity site of Castellu (Vigne and Marinval-Vigne, 1988) and with the historical deposits of the Lavezzi island (Vigne et al., 1991). Despite a scarcity of studies of fossil birds in Corsica, and with more than 85 recorded taxa, this island is the richest of the eleven Mediterranean islands (which possess a total of 160 taxa of birds). The general history of the avifauna of Corsica has also been discussed, mainly from biological analyses, by Blondel (1986) and Blondel and Vigne (1993) who emphasized that Holocene colonizers are mainly small generalist species.

In Sardinia (Kotsakis, 1980b; Azzaroli, 1981; Palombo, 1981; Sondaar et al., 1986), the latest Pleistocene (non flying terrestrial) large mammals comprised only a deer (Megaloceros cazioti), a canid (Cynotherium sardous), a small lagomorph (Prolagus sardus), a large vole (Tyrrhenicola henseli), a large mouse (Rhagamys orthodon) and a large shrew (Episoriculus similis/corsicanus). A few other mammal species, mostly otters, may have become extinct at the beginning of the Holocene (Vigne, 1990). Until now, Pleistocene mammal fossils have been very scarce in Corsica, and are only represented by the assemblages from Maccinaggio (Bonifay, 1976) and Castiglione (Salotti and Ferrandini-Cevaren, 1993; Ferrandini and Salotti, 1995). But it is probable that the composition of the living mammals has not been very different from the one in Sardinia. However, by the 8th millennium cal. BC, i.e. in the Corsican Preneolithic layers, both the deer and the canid appear to have been absent, while the four small mammals were attested up to the beginning of Historical Times (Vigne, 1990, 1992). Meanwhile, more than twenty species, both wild and domestic, immigrated from the nearby mainland during less than six millennia, presumably being introduced by man (Vigne, 1988, 1992).

### Sites, material and methods

This paper will consider four new sites: Castiglione (Ct; only for the herpetofauna), Gritulu (Gt), Monte Leone (ML) and Monte di Tuda (T) (tab. 1). Gt was excavated by J. Magdeleine, Ct by J. Ferrandini-Cevaren and M. Salotti (1995), and the two others by one of us (J.-D. V.). They are located either in the southern or in the northern parts of the island, all on calcareous substrata and at low altitude. Most of them were excavated by soundings, the sediment having been sieved through thin mesh (1 or 1.5 mm) with water (ML, T) or not (Gt, Ct). For two of them (ML and T), the water sieving residues were exhaustively sorted under the microscope. No quantitative approach could be attempted because the collecting methods, although good, were different for each site, because the samples were sometimes too small, and because their biological and historical validities are different depending on whether mammals, amphibians and birds (see below).

In addition, the herpetofauna of Araguina-Sennola (Preneolithic, Neolithic and Bronze Age; Vigne, 1985, 1988) has been revised.

For all other stratigraphic units, excepted for Gt, chronological attributions are given by radiocarbon dating. All of them could be calibrated except Castiglione A, we shall use calibrated dates in this article.

#### Results

Tables 2 to 4 show the presence of the taxa in each stratigraphic unit, classified from the older to the younger. For all three groups, we only took into account bones which could be identified to species or genus. Taxa have been classified systematically for amphibians, reptiles and mammal, alphabetically for birds (since the taxonomic arrangement depends on the authors), and large mammal are shown separately from the small ones.

At Gt, all the mandibles of *Prolagus* are large; P/<sub>3</sub> are thick-set, with a small anteroconulid, without a distal notch, the protoconulid being always smaller than the protoconid. These characters indicate *P. sardus* rather than *P. figaro*, and excludes a date older than the beginning of the Upper Pleistocene (Lopez-Martinez and Thaler, 1975). An accelerator radiocarbon dating was not possible due to the absence of collagen, but the absence of *Enhydrictis*, which is attested in CtA (Ferrandini and Salotti, 1995), suggests that Gt is later than CtA. In 1996, new excavations in this cave indicated that the main fossil deposits failed after the Würm, probably during the late Glacial (Vigne and Magdeleine, unp.).

All the identifications of the herpetofauna of Araguina-Sennola (Vigne, 1985) have been confirmed, except the bones attributed to *Rana* sp. (*temporaria* group):

**Table 1**: Main characteristics of the seven new vertebrate assemblages referred to in this paper. CtA includes only herpetofauna, from Ferrandini and Salotti, 1995. SU: stratigraphic unit.

	Castiglione 1 A (1)	Gritulu	Monte	e Leone		Monte di Tuda				
District	Haute-Corse	Haute-Corse	Corse	-du-Sud		Haute-Corse				
Commune	Oletta	Luri	Bon	ifacio		Olmetta-di-Tuda				
Altitude asl	120 m	150 m	60	) m						
Site	Deep cave	Cave porch	Rock	shelter	Cave porch					
Excavation	4 soundings (? m³)	1 sounding (2,5 m <sup>3</sup> )	4 soundin	gs (2,8 m <sup>3</sup> )	n <sup>3</sup> ) 2 soundings (5 m <sup>3</sup> )					
Collection	(water?) sieving (? mesh)	dry sieving; 1.5 mm	water sie	ving; 1 mm	v	water sieving; 1 mm				
method	naked eye sorting?	naked eye sorting	microsco	pic sorting	r	microscopic sorting				
Stratigraphy	A	3 to 8	SU 5	SU 4	Biozone 3	Biozone 2	Biozone 1			
14C date	Older than LGQ: 31560±1450 bp	no radiocarbon date	ETH-8305: 8225±80 bp	Ly-6099: 5855±95 bp (upper limit of the layer)	GifA-92061: 2510±120 bp to GifA-92363: 2180±90 bp	GifA-92366: 2090±70 bp & GifA-91436: 1960±120 bp	GifA-91437: 610±120 bp (lower limit of the biozone)			
Calibrated date (2 sigma ranges)	-		7433-7035 BC	4934-4470 BC	864-409 BC to 393-151 BC	348 BC-42 AD & 322 BC-283 AD	1224-1459 AC to Present			
Chronological Attribution and	Final Riss / Early Würm	Late Pleistocene (Late Glacial)	Corsican Preneolithic	Early Neolithic	Iron Age to Early Roman	Roman	Middle Ages to Present			
Abreviation	CtA	Gt	ML5	ML4	Т3	T2	Tl			

**Table 2**: Presence (X) of the species of amphibians and reptiles in the seven fossil assemblages: NISP, number of identified specimens; for other abreviations, see tab. 1.

	CtA	Gt	ML5	ML4	Т3	T2	T1
NISP	28	10	118	13	167	41	19
Discoglossus sp.	X	X	X	X	X	X	X
Discoglossus sardus					X	X	X
Bufo viridis	X	X	X	X	X	X	X
Hyla (arborea) sarda	X			X	X	X	X
Rana kl. esculenta					X	X	X
Gekkonidae					X	X	X
Archaeolacerta bedriagae	X			X	X	X	X
Podarcis tiliguerta	X		X	X	X	X	X
Coluber viridiflavus	X		X	X	X	X	X
Natrix natrix	X		X	X	X	X	X

**Table 3**: Presence (X) of the species of birds in six of the seven fossil assemblages: MNI, minimum number of individuals; for other abbreviations, see tab. 1.

	Gt	ML5	ML4	<b>T3</b>	T2	T1		Gt	ML5	ML4	Т3	T2	T1
MNI	28	2	80	7	36	85	MNI	28	2	80	7	36	85
Acrocephalus							Lanius excubitor/minor				X		
arundinaceus (?)						X	Larus canus/R. tridactyla			X			
Alauda arvensis					X	X	Luscinia megarhynchos					X	X
Anthus cf. pratensis			X				Miliaria calandra						X
Anthus spinoletta						X	Motacilla cf. alba						X
Apus apus						X	Muscicapa striata						X
Aquila chrysaetos	X					X	Oenanthe hispanica			X			
Asio flammeus			X				Oenanthe oenanthe						X
Athene noctua			X				Otus scops			X			
Bubo insularis	X	X					Pandion haliaetus	X					
Buteo lagopus (?)	X						Parus ater						X
Calidris canutus						X	Parus cf. major	X		X			X
Calidris sp.			X				Passer gr. domesticus			X	X	X	X
Carduelis cannabina			X				Petronia petronia				X		X
Carduelis carduelis			X		X	X	Phoenicurus sp.	?		X			
Carduelis chloris			X		X	X	Phylloscopus sp.			X			
Circaetus gallicus	X						Porzana porzana			X			
Coccothraustes							Pyrrhocorax sp.			X			
coccothraustes			X		X	X	Pyrrhocorax graculus					X	
Columba livia	X		X				Rallus aquaticus			X			
Coracias garrulus			X				Regulus sp.						X
Coturnix coturnix	X		X			X	Saxicola cf. rubetra			X			X
Corvus corone					X		Streptopelia turtur			X			
Corvus corax	X		X				Sturnus sp.	X			X	X	X
Corvus monedula	X		?		X		Sylvia atricapilla						X
Emberiza cf. cirlus					X	X	Sylvia cf. borin	X					
Erithacus rubecula	?		X	X	X	X	Sylvia cf. melanocephala	X		X			X
Falco peregrinus			X				Sylvia hortensis (?)						X
Falco subbuteo			X				Sylvia sp.			X			
Falco tinnunculus	X						Tringa ochropus	X					
Falco vespertinus			X				Troglodytes troglodytes			X			
Ficedula sp.			X				Turdus cf. philomelos	X		X			X
Fringilla coelebs							Turdus merula/torquatus	X		X			
/montifringilla	X		X		X	X	Turdus viscivorus			X		X	
Garrulus glandarius					X		Tyto alba			X			
Gypaetus barbatus	$\mathbf{x}$						Upupa epops			X			X
Jynx torquilla						X	Cr. pa cpops						
Lanius collurio/senator	X												

	Gt	ML5	ML4	Т3	<b>T2</b>	<b>T1</b>
Large mammals (NISP)	207	0	0	0	0	0
Cynotherium sardus Megaloceros cazioti	X X					
Small mammals (MNI)	661	124	90	1633	883	378
Erinaceus europaeus Episoriculus corsicanus Suncus etruscus	X	X	X	X X X	X X X	X X
Crocidura suaveolens Prolagus sardus Glis glis	X	X	X	X X X	X X X	X
Eliomys quercinus Rhagamys orthodon Apodemus sylvaticus	X	X	X	X X X	X X X	X X
Mus musculus domesticus Rattus rattus Tyrrhenicola henseli	X	X	X	X X	X X X	X X

**Table 4**: Presence (X) of the species of large and small mammals in six of the seven fossil assemblages: MNI, minimum number of individuals; NISP, number of identified specimens; for other abbreviations, see tab. 1.

some of them have been re-identified as *Discoglossus* and the others as *Bufo viridis*, according to the osteological criteria of Bailon (1991).

## Comparison with ancient and recent data

In order to interpret the results of this study, we collected a corpus of published palaeontological, archaeozoological and zoological data, most of them having never been used in a synthesis. Fossil samples are as follows.

- Pleistocene birds of Corsica according to Alcover et al. (1992), mainly coming from the Pleistocene layers of Maccinagio.
- The older assemblage of Castiglione (CtA, tab. 1) which also provided bird and mammal bones (Ferrandini and Salotti, 1995).
- A later assemblage of Castiglione (CtB: LGQ: 14.950 ± 260 bp, final Würm) placed before ML5 and provided data for mammals only (Ferrandini and Salotti, 1995).
- Layer 7 of Basi (B7), dated to the end of the 7th millennium cal. BC (Vigne, 1988) is approximately contemporaneous with ML4, and provided mainly mammal bones.
- The Neolithic and Bronze Age layers of Araguina-Sennola, between ML4 and T3, provided data for all four taxonomic groups (Vigne, 1985, 1988). No chronological differentiation has been taken into account for the herpetofauna; for birds we distinguished assemblages from the middle and recent Neolithic (AN) from those of the final Neolithic and Bronze Age (AB); for mammals, we distinguished four chronological groups, i.e. middle Neolithic

(A14), late Neolithic (A12), Bronze Age (A6), and final Bronze Age - Iron Age (A5).

- The Terrina IV deposits (Chalcolithic; Vigne, 1988) are contemporaneous with A12 and provided both mammal and reptile bones.
- Castiglione provided also late Classical Antiquity deposits (CtD: between 260 and 430 cal. AD; Ferrandini and Salotti, 1995) with mammal bones. It occurs between the biozones 2 and 1 of T.
- The Santa Maria Lavezzi deposits (SML) are dated to the 14<sup>th</sup> and to the 17<sup>th</sup> centuries, between CtD and biozone 1 of T. For our purpose, it provided important data for birds and reptiles (Vigne *et al.*, 1991; Vigne, 1994).
- Numerous data concerning the large mammals of the Middle Ages (just before biozone 1 of the Monte di Tuda) have been collected by Vigne (1988, 1992, 1994).

With the exception of birds (Alcover *et al.*, 1992), results from Maccinaggio (upper Pleistocene; Gasc, 1961; Bonifay, 1976) have not been used because they are only partly published and come from layers not yet well dated.

In addition, we used data about the modern-day fauna of Corsica (amphibians and reptiles: Delaugerre and Cheylan, 1992; birds: Thibault, 1983; mammals: Vigne, 1988, 1992).

### **Discussion**

# Taphonomy and significance of the fossil assemblages

What is the significance of all these fossil assemblages with respect to the living fauna? The bone accumulation

processes in most of them has not been studied. Generally, the amphibian, reptile, passeriform, large bird, small mammal and large mammal bones in these sites have accumulated by different processes.

Pleistocene large birds and mammals died in the caves or were brought by predators into the caves, as is suggested by the presence of large portions of skeletons and strong digestive erosion of bones at Gritulu (Vigne, unpub.). This kind of accumulation can hardly give a complete picture of the living fauna for such a small number of sites. Most of the Holocene large birds and mammals (sometimes including *Prolagus*; Vigne *et al.*, 1987) come from archaeological deposits (Basi, Araguina-Sennola, Terrina IV, Medieval sites) where they were deposited by humans, i.e. selected by hunters. In all these cases, data must be considered as resulting from accidental processes or biased by hunter choice.

However, the processes of accumulation for amphibians, reptiles and small birds such as passerines are poorly understood. These taxa regularly occur in the diet of Mediterranean insular owls; and when they are associated with a lot of small mammal bones in fossil assemblages (ML4, T, SML), one must probably consider them to be derived from owl pellets. But they are always scarce in the diet of owls today (when the species diversity in the biota is large, especially for small birds) and the pattern of raptor selection is incompletely known (Andrews, 1990).

Large accumulations of small mammal bones (mainly: Ct, Gr, ML4, T, SML) should be considered as raptor (mainly owl) pellet remains (Chaline, 1977) and are probably of better ecological significance. Owl pellet accumulations, especially those of *Tyto alba* in Corsica (Libois, 1984), give an accurate idea of small mammal living communities, at least from a qualitative point of view (Dodson, 1973; Chaline *et al.*, 1974; Denys, 1985; Andrews, 1990; etc.). Some evidence has been collected for owl pellet accumulations at Gr and ML4 (Vigne, unpub.; Grouard, 1994), and it has been demonstrated for T (biozone 1; Sanchez *et al.*, 1997).

For these reasons, results for small mammals are probably much more reliable. The others (large mammal, birds, amphibians and reptiles) cannot be considered as complete and reliable indications of the living fauna. They only give evidence of presence. Absences of species can only be deduced when consistently missing from several successive sites over a wide distribution.

Since most of the sites are situated at a low altitude, the data will give poor indications for mountain species, especially for the ones which could have found refuge in the mountains after a strong competition with new invaders or just prior to their extinction.

### Herpetofauna (tab. 5)

Today, the herpetofauna of Corsica is rich with 18 species (Delaugerre and Cheylan, 1992) while the fossil records include only 8 taxa. One explanation for the scarcity of fossil taxa is the difficulty in distinguishing bones of the three species of Corsican Gekkonidae and the two Discoglossus (D. sardus and D. montalentii; Clark and Lanza, 1990). If we exclude these taxa, the recorded species still represent less than 60% of the living ones. The absence of Euproctus montanus and Salamandra salamandra can be explained because bones of urodeles are more fragile, owls do not predate urodeles (M. Cheylan, in litt.) and these two species live in biota (fast flowing water and forests respectively) to which the predators have difficulty in gaining access. Algyroides fitzingeri is probably absent because of its very small size. The arrival of Podarcis sicula (and Testudo hermanni?) in Corsica is probably too recent (Delaugerre and Cheylan, 1992) to be recorded in our fossil assemblages.

Discoglossus sp. is attested throughout the Quaternary, and as early as the Miocene (Sanchiz and Sanz, 1980). Good data are now available for a continuous presence of Bufo viridis in Corsica from the Pleistocene, as well as in Sardinia (Kotsakis, 1980a), while Vigne (1985) thought it was a Holocene immigrant. Emys orbicularis is only attested in one Neolithic site in Corsica (TIV; Cheylan, 1988), but it was probably present in Corsica from the upper Pleistocene at least, since it has been recorded in Sardinia in the upper Pleistocene (Monte San Giovanni, Caloi et al., 1980)(1). A ranid has been mentioned in the Pliocene of Sardinia (Capu Mannu; Pecorini et al., 1974), but Rana sp. described from the Villafranchian of Su Casteddu (Sardinia; Esu and Kotsakis, 1979) must be considered as dubious, osteological criteria rather suggesting Discoglossus. According to present data, it would seem that the only Rana of the Quaternary of Corsica, R. kl. esculenta, immigrated to Corsica during the Holocene. A Gekkonid has been identified from the Pliocene of Capo Mannu (Pecorini et al., 1974), which could be Phyllodactylus, the only endemic genus of gecko in Corsica, rather than Hemidactylus or Tarentola, which are generalists and are widely distributed throughout the Mediterranean Basin (Castanet and Guyétant, 1990).

<sup>(1)</sup> More recent excavations at Ct (1995) brough evidence for the upper Pleistocene presence of *E. orbicularis* in Corsica too (Bailon, unpub.).

**Table 5**: Presence (X) of the species of amphibians and reptiles in the ten fossil assemblages arranged in chronological sequence, and probable chronostratigraphic distribution (greyish): NISP, number of identified specimens; for other abbreviations, see tab. I and text.

	CtA	Gt	ML5	ML4	A	TIV	Т3	T2	SML	T1	Pres.
NISP	28	10	118	13	15	34	167	41	6	19	
Discoglossus sp. (2 species)	X	X	X	X	X		X	X		X	X
Discoglossus sardus							X	X		X	X
Bufo viridis	X	X	X	X	X		X	X		X	X
Hyla (arborea) sarda	X			X			X	X		X	X
Archaeolacerta bedriagae	X			X			X	X		X	X
Podarcis tiliguerta	X		X	X			X	X	X	X	X
Coluber viridiflavus	X		X	X			X	X	X	X	X
Natrix natrix	X		X				X	X		X	X
Emys orbicularis						X					X
Rana kl. esculenta							X	X		X	X
Gekkonidae (3 species)							X	X		X	X
Testudo hermanni											X
Podarcis sicula											X
Natrix maura											X
Eurpoctus montanus	?	?	?	?	?	?	?	?	?	?	X
Salamandra salamandra	?	?	?	?	?	?	?	?	?	?	X
Algyroides fitzingeri	?	?	?	?	?	?	?	?	?	?	X
Discoglossus montalentii	?	?	?	?	?	?	?	?	?	?	X

Finally, with respect to the Holocene colonization of Corsica by man, reptile and amphibian species are of two kinds: species present before (= "autochthonous") and species which immigrated after man.

Among the "autochthonous" species, all those suggested as such by Vigne and Alcover (1985) are confirmed: Discoglossus sp., Hyla (arborea) sarda, Archaeolacerta bedriagae, Podarcis tiliguerta, Coluber viridiflavus and Natrix natrix. Now, we can add B. viridis and Emys orbicularis, which have probably been on the island for a very long time without becoming markedly endemic. The evidence for a great antiquity of B. viridis in Corsica refutes the hypothesis of a recent immigration suggested by the littorally restricted distribution of the species today (Delaugerre and Cheylan, 1992). Although they are still unknown in the fossil record, Euproctus, Salamandra, Algyroides (and probably Phyllodactylus) might also be considered as "autochthonous" because of their endemism. Among these twelve "autochthonous" taxa, it is however necessary to distinguish "old endemics" (such as E. montanus, A. bedriagae, D. montalentii...), from "neoendemics" (such as P. tiliguerta, N. natrix, H. (arborea) sarda...) which probably immigrated during the MioPliocene. But their dates of immigration are still unknown for many of these "autochthonous" taxa (such as *E. orbicularis*, *C. viridiflavus*, etc.).

Species only recorded in the Holocene are *Rana* kl. *esculenta* and the two other Gekkonids (they possibly immigrated during the Iron Age); these taxa could have been introduced by humans; *Podarcis sicula* is not known in the fossil record but, according to Delaugerre and Cheylan (1992), it must be included in this second category too.

It is presently impossible to decide if *Testudo herman- ni* comes under the first or the second category.

#### Avifauna (tab. 6)

A total of 119 bird taxa have been recorded from the Corsican fossil assemblages (Alcover *et al.*, 1992; Vigne, 1988; Vigne *et al.*, 1991; present paper), 74 of them still nest regularly or occasionally on the island (Thibault, 1983). Hence they represent 57.5% of the 127 present-day nesting species, which is a rather good representation. The present study adds 29 new taxa.

Species which are both presently (i.e. 19th-20th centuries) frequent visitors or migrants (Thibault, 1983) and only recorded once as fossil have been considered to be

**Table 6**: Presence (X) of the species of birds in the eleven fossil assemblages arranged in chronological sequence, and probable chronostratigraphic distribution (grey): MNI, minimum number of individuals; for other abbreviations, see tab. 1 and text.

	Alc	CtA	Gt	ML5	ML4	AN	AB	Т3	Т2	SML	Т1	Nesting
NMI	_	_	28	2	80	65	11	7	36	62	85	
Acrocephalus paludicola	X											
Fratercula arctica	X											
Gyps fulvus	X											
Anser erythropus	X											
Corvus corone/frugilegus	X											
Buteo lagopus (?)			X									
Bubo insularis	X	X	X	X								
Circaetus gallicus			X									
Ficedula sp.				100	X							
Pyrrhocorax sp.					X							
Accipiter gentilis	X	2	3.05 2.05 2.05 2.05								1	
Accipiter nisus	X											
Anas crecca	X									X		
Anas penelope	X											
Anas platyrhynchos	X					X						
Anthus spinoletta	X										X	
Apus melba	X											
Aquila chrysaetos	X		X				X				X	
Asio flammeus		X			X	X						
Asio otus	X					X						
Aythya fuligula	X											
Buteo buteo	X					X						190507
Caprimulgus europaeus	X											
Carduelis chloris	X	100			X				X		X	
Circus aeruginosus	X											
Coccothraustes coccothraustes	X				X				X		X	
Columba livia	X		X		X		X			X		
Columba oenas/livia	X				X							
Columba palumbus	X	X				X						
Coracias garrulus	X				X	X						
Corvus monedula			X		?	ALTER S			X			
Coturnix coturnix	X		X		X						X	
Corvus corax	X		X		X							
Crex crex	X											
Cuculus canorus	X											
Dendrocopos major	X											
Emberiza cf. cirlus	X					?			X		X	
Erithacus rubecula	X		?		X	Constant of		X	X		X	
Falco naumanni	X								1			

Table 6: continued	Alc	CtA	Gt	ML5	ML4	AN	AB	Т3	Т2	SML	T1	Nesting
NMI	_	_	28	2	80	65	11	7	36	62	85	
Falco naumanni	X											
Falco peregrinus	X				X		X					
Falco subbuteo	X				X							
Falco tinnunculus	X		X									
Falco vespertinus					X							
Fringilla coelebs/montifringilla	X		X		X				X		X	1
Galerida cristata	X											
Galinago media	X											
Gallinago galinago	X											
Gallinula chloropus	X											
Gypaetus barbatus	1		X									
Haliaetus albicilla	X											
Hirundo rustica	X											
Lanius collurio/senator	X		X									
Lanius excubitor/minor	X					X	X	X				
Limosa limosa	X											
Lullula arborea	X											la barbara
Luscinia megarhynchos	X								X		X	
cf. Marmaronetta angustirostris						X						
Merops apiaster	X											
Milvus migrans	X					X	X					
Oriolus oriolus	X											
Otus scops	X				X		X					
Pandion haliaetus			X									
Parus cf. major			X		x	X					X	
Petronia petronia	X							X			X	
Phalacrocorax aristotelis	X					X	X			X		
Phoenicurus sp.	X		?		X							
Porzana parva	X											
Porzana porzana	X				X							
Porzana pusilla	X											
Prunella collaris	X											See and
Pyrrhocorax graculus	X	X							X			
Rallus aquaticus	X				X							
Saxicola rubetra	X				X						X	
Scolopax rusticola	X					X	X					
Strurnus sp.	X		X					X	X		x	
Sylvia atricapilla	X										X	10.00
Sylvia cf. borin	170		X									
Sylvia cf. melanocephala			X		X						X	0.13
Tadorna tadorna	X					X					2	
Tringa erythopus	X											
Tringa ochropus			X									

Table 6: end.	Alc	CtA	Gt	ML5	ML4	AN	AB	Т3	Т2	SML	T1	Nesting
NMI	_	_	28	2	80	65	11	7	36	62	85	
Tringa totanus	X											
Turdus cf. philomelos	X		X		X	X	X			X	X	d
Turdus merula/torquatus	X		X		X	X	X			X		
Turdus viscivorus	X				X	X	X		X	X		
Tyto alba		X			X		X		X			
Upupa epops	X				X						X	
Vanellus vanellus	X											
Otis tetrax	X	?	?	?	?	?	?	?	?	?	?	
Corvus corone	?	?	?	X								
Anthus cf. pratensis					X	X						
Athene noctua					X	X						
Calidris sp.					X					X		
Carduelis cannabina					X							1
Carduelis carduelis					X				X		X	
Larus canus/Rissa tridactyla					X							
Oenanthe hispanica					X							
Passer gr. domesticus					X			X	X	X	X	
Phylloscopus sp.					X					X		
Troglodytes troglodytes					X							
Corvus cf. frugilegus						X						
Netta rufina						X						
Puffinus yelkouan						X				X		
Streptopelia turtur						X						85616
Alauda arvensis						6.E Z 23/00; p to 16/0	X		X		X	
Sterna cf. hirundo							X					
Alectoris sp.							PETER MEDICAL CO.			X		
Garrulus glandarius									X			
Calonectris diomedea									1	X		
Acrocephalus arundinaceus (?)										0.000.000.002.00	X	
Apus apus											X	
Calidris canutus											X	
Jynx torquilla											X	
Miliaria calandra											X	
Motacilla cf. alba											X	
Muscicapa striata											X	
Oenanthe oenanthe											X	
Parus ater											X	
Regulus sp.											X	
Sylvia hortensis (?)											X	
,												

present on the island from the Pleistocene to the present time. These include Anas penelope, Crex crex, Falco vespertinus, Galerida cristata, Gallinago media, G. gallinago, Haliaeetus albicilla, Limosa limosa, cf. Marmaronetta angustirostris, Porzana parva, P. pusilla, Prunella collaris, Sylvia cf. borin, Tringa ochropus, T. totanus, and Vanellus vanellus. We have not made the same extrapolation for Circaetus gallicus and overall for Acrocephalus paludicola because they are presently too rare in Corsica, or for Corvus corone/frugilegus, Ficedula sp. and Pyrrhocorax sp., because identification to species has not been possible. The chrono-stratigraphic distribution of these last five taxa cannot be determined with present-day available data.

Five other species are only known from the Pleistocene and are presently absent from Corsica. They have been considered as extinct. Among them, *Bubo insularis* is the only Corsico-Sardinian endemic; its presence in ML5 indicates that it became extinct during the Holocene, i.e. not as a result of climatic events. However, three others (*Buteo lagopus, Anser erythropus* and *Fratercula arctica*), now living in northern Europe, have completely disappeared from Corsica. This "retreat" northwards can probably be correlated with the post-glacial shift northwards of cold conditions. *Gyps fulvus* also disappeared from Corsica (but not from Sardinia) but it is very difficult to know when (see above: taphonomy).

In the Pleistocene assemblages, we must emphasize the large number of raptors, which suggests a high trophic diversity (mainly birds). This hypothesis is corroborated by the presence of *F. vespertinus* and *F. subbuteo*: these two raptor birds nest late in the year, which necessitates a relative abundance of prey after the end of the nesting season of most bird species (Cramp and Simmons, 1977-80).

Table 6 shows that 79 taxa are both attested at CtA, Gt or by Alcover *et al.*,  $(1992)^{(2)}$  and still nesting, migrants or frequent visitors to Corsica. Even if the status of these taxa could have changed during the last 20,000 years, all of them can be considered to have lived continuously in Corsica. All ecological communities are represented. Typical forest species such as *Turdus merula* are especially rare, as well as species inhabiting medium and low maquis (mainly Sylviidae), the smallest of them (tab. 6; *Sylvia* sp.) being indistinguishable on the bases of their bones. Conditions of preservation being generally good for the sites, it does not seem that this could be the main reason for their absence. About 22 of the 79 taxa (27.8%, up to 29% if we exclude fresh water and sea birds; Carduelinae,

Erithacus rubecula, Fringilla sp., Turdus philomelos, Sturnus sp., etc.) are more or less associated with fallow lands (open vegetation to bush) and none of them disappeared during the sequence. Fallow lands are always a rich biota because of a strong edge effect (Frochot, 1981).

Table 6 also shows that 31 taxa are found only after the beginning of the Neolithic. Many of them, especially fresh water and sea birds, may have been present in Corsica during the Pleistocene without any fossil record. Among others, forest taxa are very rare, possibly partly because of the low altitude of the archaeological sites, which could only be reached by them when they left the mountains during winter. More numerous again (12 taxa) are taxa associated with low to medium vegetation, such as Anthus cf. pratensis, Carduelinae, Oenanthe sp., Alauda arvensis, Sylvia hortensis, etc. They represent 39% of the 31 taxa, or up to 50% if we exclude fresh water and sea birds. This is significantly higher (e > 1.96) than in the group of species present throughout the Quaternary and suggests that open and low vegetation species have been favoured among these possibly Holocene immigrants, probably reflecting man's influence upon the vegetation. This probably happened as early as the end of the Neolithic (Reille, 1992).

Some species, even present as early as the Pleistocene, have been more clearly favoured by man. Gypaetus barbatus certainly exploited Megaloceros carcasses during the Pleistocene (Vigne, forthcoming), but it has certainly been favoured by the Neolithic increase of mammal breeding (Vigne, 1988), since it is very dependent on this activity (Thibault et al., 1993). Since the extinction of Megaloceros might have occurred several millennia earlier than the appearance of husbandry (see below, mammals), it is not impossible that Gypaetus barbatus became extinct from Corsica (not from Sardinia, where endemic deer survived till much later; Sondaar et al., 1986) and re-colonized the island during the Neolithic. Taxa typical of low mediterranean vegetation such as Coturnix coturnix, Enanthe sp., Alauda arvensis and Anthus cf. pratensis, which could have lived on the island during the Würm cold period, may have flourished as a result of agriculture, mainly after the drastic deforestations during the Roman and Medieval periods (Reille, 1992; Vigne and Valladas, 1996). Among these taxa, Alectoris sp., generally one of the most frequent genera in Mediterranean Neolithic sites (Vilette, 1983) but absent from those of Corsica, can be considered to have been introduced by man during Historical Times (Blondel and Vigne, 1993), the oldest record for this genus being the Late Antiquity (6th century AD; Vigne and Marinval-Vigne, 1989).

<sup>(2)</sup> However we should point out that Callonectris diomedea has never been attested in a secure Pleistocene layer (Mayaud and Schaub, 1950).

Passer domesticus needs a special mention. Tchernov (1993) suggested that it became commensal in the Near East during the Natufian period, i.e. at the beginning of the Holocene (11<sup>th</sup>-12<sup>th</sup> millennia BC), but the date and method of arrival of this allochthonous species in Western Europe is not known. Present data may also indicate an early date (ML4, early Neolithic, before the 5<sup>th</sup> millennium BC). Although obtained on an island, it can be taken as a good terminus ante quem for the whole Western Mediterranean Basin. Hence, it seems that the insularity of Corsica did not impede the arrival on the island of the important cultural indicators such as commensal species (the sparrow or the black rat; Vigne, 1994; Vigne and Valladas, 1996) as well as domestic animals (Vigne, 1987a) or ceramic (Camps, 1988).

#### Mammals (tab. 7)

The data presented here confirm the general views expressed above in the introduction and provide a more accurate picture of what happened as follows.

The absence of all modern taxa from the times before the early Neolithic, which, up to now, was only suggested by similarities with Sardinia and by a very small number of Corsican fossil assemblages (see references in the introduction), is confirmed by three new important assemblages, two from Castiglione and one from Gritulu. The only exception may be *Sus* sp. determined in the Riss-Würm assemblage of Castiglione; but, without any further precision from the authors (Ferrandini and Salotti, 1995), it is more probable that these bones belong to a descendent of

**Table 7**: Presence (X) of the species of mammals in the 16 fossil assemblages arranged in chronological sequence, and probable chronostratigraphic distribution (grey): MNI, minimum number of individuals; NISP, number of identified specimens; other abbreviations, see tab. 1 and text.

	CtA	CtB	Gt	ML5	ML4	B7	A14	A12	TIV	A6	A5	Т3	Т2	CtD	MA	SML	T1	Pres.
NISP (large mammals)	-	-	207	0	0	1137	487	567	1743	633	171	0	0	_	14973	473	0	
MNI (small mammals)	-	_	661	124	90	1	65	81	13	2	4	1633	883	_	54	70	378	
Sus sp.	X																	
cf. Enhydrictis	X																	
Megaloceros cazioti	X		X															
Cynotherium sardus	X		X								W-1000 - 1000 - 1000 - 1000							
Episoriculus corsicanus	X	X	X	X	X		X	X		X	X	Χ	X					
Rhagamys orthodon	X	X	X	X	X		X	X	X	X	X	X	X					
Tyrrhenicola henseli	X	X	X	X	X		X	X		X	X	X	X					
Prolagus sardus	X	X	X	X	X	X	X	X		X	X	Х	Х	?				
Vulpes vulpes						X	X	X	X						X			X
Sus scrofa						X	X	X	X	X	X				X			X
Erinaceus europaeus							X					X	X				X	X
Apodemus sylvaticus								X		X		X	X	X		X	X	x
Ovis musimon									X						X			χ.
Myoxus glis									X			X	X					X
Mus m. domesticus												X	X	X		X	X	x
Suncus etruscus												X	X	X			X	х
Crocidura suaveolens												X	X	X		X	X	х
Eliomys quercinus												X	X	X		X	X	X
Rattus rattus													X	X		X	Χ	X
Lepus capensis															X		X	x
Ursus arctos															X			
Cervus elaphus															X	X		
Mustela nivalis																		X
Felis libyca reyi																		X
Oryctolagus cuniculus																		X
Rattus norvegicus																		Х

Sus nanus described from the *Tyrrhenicola* fauna of the Capo Figari (Sardinia; Made, 1988), than to *Sus scrofa*, which, if native to Corsica, would probably have been recorded from the Preneolithic sites (Vigne and Desse-Berset, 1995).

Sus cf. nanus as well as Enhydrictis are probably confirmed as being mainly pre-Würmian or early Würmian taxa in Corsica, as they are in Sardinia (Palombo, 1981; Vigne, 1990). Megaloceros cazioti and Cynotherium sardous survived until the Würm, but their apparent absence at CtB (Ferrandini and Salotti, 1995; they are however recorded at Gt, which seems a little bit more recent that CtB) as well as their more secure absence from the Preneolithic sites such as ML (Vigne and Desse-Berset, 1995) may indicate a rather early extinction, perhaps before the Holocene arrival of man (Vigne, in press) and probably earlier than the Sardinian one (Sondaar et al., 1986).

The persistence of the four endemic small mammal species into Historical Times (Vigne, 1987b, 1988) is confirmed by the data from the Monte di Tuda cave. The stratigraphy of that site did not allow a determination of whether they became extinct at the end of the Antiquity or during the early or central Middle Ages. The mention of Prolagus in the CtD could indicate the late Classical Antiquity, but the same layer of that site also gave a more recent radiocarbon dating (840  $\pm$  140 BP, i.e. 1220 cal. BC; Ferrandini and Salotti, 1995). The question of the extinction date of these species remains open for the present.

There have been important improvements in our understanding of when modern species of small mammal arrived. The combined data of the water sieved fauna from ML4 and from T3, which provided the first fossils of *Eliomys quercinus*, *Crocidura suaveolens* and *Suncus etruscus* for Corsica, indicate that these three species, as well as *Apodemus sylvaticus*, *Mus musculus* and *Glis glis* (Vigne, 1992), were introduced to Corsica between the end of the early Neolithic and the beginning of the Iron Age, i.e. between 4400 and 1000 cal. BC.

Now, owing to the Monte di Tuda stratigraphic sequence (Vigne and Valladas, 1996), greater precision is available for the date of arrival of the black rat (*Rattus rattus*) to Corsica (4<sup>th</sup>-2<sup>nd</sup> centuries cal. BC) and to the whole Western Mediterranean Basin (Audoin-Rouzeau and Vigne, 1994 and this volume).

In general, the mammals of Corsica can be divided into five categories (modified from Vigne, 1988: 225-227):

(i) Pleistocene endemic large mammals which became extinct before the Holocene arrival of man (Sus sp., Enhydrictis cf. galictoides and probably Cynotherium sardous and Megaloceros cazioti);

- (ii) modern species which were introduced by man from the beginning of the Post-Glacial (15 wild species plus the well known domestic ones), either on purpose or by accident;
- (iii) feral species derived from domestic or tamed ones: bear (*Ursus arctos*, probably introduced as a tamed animal; Poplin *et al.*, 1988), the wild boar (*Sus scrofa*, derived from the domestic pig; Popescu *et al.*, 1980) and the moufflon (derived from the early Neolithic sheep; Poplin, 1979; Poplin and Vigne, 1983; Geddes, 1985; Vigne, 1988;
- (iv) Pleistocene endemic small mammals, whose extinction was brought about by man during the first millennium AD, probably by the combined effects of increasing competition with modern species (such as the black rat) and of man's modifications to the landscape (Vigne and Marinval-Vigne, 1991; Vigne and Valladas, 1996);
- (v) modern species which have never been found as fossils: *Mustela nivalis*, probably long resident on the island (Vigne, 1988), *Felis lybica reyi* (early feralized from the domestic cat; Vigne, 1988; Arrighi and Salotti, 1988), *Oryctolagus cuniculus* (probably very recently introduced; Dubray and Roux, 1984) and *Rattus norvegicus* (very rare and introduced in the 18th century AD; Vigne and Villié, 1995).

#### Conclusion

From the point of view of their representation, the available fossil data provide a more complete picture of mammals (75% of present species are represented in fossils) than of birds (57% represented) and of amphibians and reptiles (44% represented) (tab. 8 and fig. 1).

On the whole, fossil data indicate extinctions of Pleistocene species, immigration of modern ones and the establishment of feral populations (mammals only).

The extinction rate (number of late Pleistocene species which became extinct, tab. 8) is nil for amphibians and reptiles (all known Pleistocene species are still alive, perhaps sometimes with reduced distribution), very low for birds (6%) which had a very low degree of endemism, and greatest for mammals, all taxa (endemics) being extinct during the end of the Pleistocene or during Historical Times. Chronological evidence suggests that the large mammals (Megaloceros and Cynotherium) may have become extinct before the colonization of the island by modern man. All boreal birds probably disappeared from the islands as they did from the whole Mediterranean area with the end of the last Ice Age. The extinctions of large mammals and of these birds were probably caused by climatic changes. The persistence of Bubo insularis into the Holocene probably

Birds

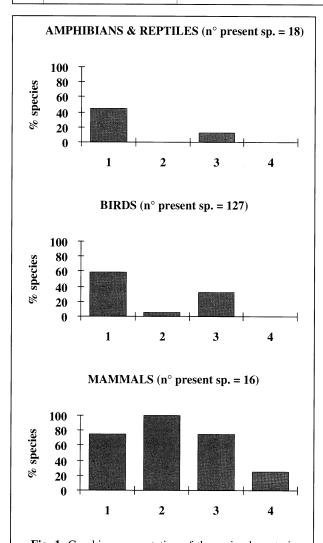
Mammal

		Total number of species present today	Late Pleistocene species	Modern species registered as fossil	Late Pleist. species extinct (extinction rate)	Modern sp. immigrated Holocene (immig. rate)	Modern species with feral origin
Nb	Amphibians/Reptiles	18	7	8	0	1	0
	Birds	127 (nesting)	86	73 (nesting)	5	(maximum) 23	0
	Mammal	16	6	12	6	9	3
%	Amphibians/Reptiles			44.4	0.0	12.5	0.0

57.5

75.0

Table 8: Main characteristics of the three taxonomic groups as in the discussion herein.



**Fig. 1**: Graphic representation of the main characteristics of the three taxonomic groups according to the data in tab. 8: sp., species; 1, proportion of present-day species registered as fossil; 2, extinction rate; 3, immigration rate; 4, feralization rate.

reflects its adaptation to preying upon *Prolagus* (Alcover *et al.*, 1992). The impact of man may be the reason for the extinction of this bird and without doubt provoked the extinction of *Prolagus*, *Rhagamys*, *Tyrrhenicola* and *Episoriculus*, all of which suffered from the arrival of the black rat and from the drastic Roman and Medieval clearance of vegetation (Vigne and Marinval-Vigne, 1991; Vigne and Valladas, 1996). The amphibians and reptiles appear to have successfully resisted both climatic changes and the influence of man.

31.5

75.0

0.0

25.0

5.8

100.0

The immigration rate can be represented by the number of Holocene immigrants with respect to the number of known (nesting, for birds) fossil species. For amphibians and reptiles, it is only 12.5% (only one species: Rana kl. esculenta), but this very low rate is probably underestimated because of the absence of a good fossil record of modern Gekkonidae, Podarcis sicula and Natrix maura (immigration rate = 26% if they all immigrated). The immigration rate seems higher for birds, but the percentage of 31.5% is probably an over-estimate because a lot of species were probably present as early as the Pleistocene but are not attested as fossil (such as the endemic Sitta whitehaedii). Previous analysis suggests that the immigration of birds was facilitated by the modification of the landscape by Holocene man. For mammals, all the present taxa immigrated during the Holocene, this immigration rate (100%) suggesting an unnatural process, i.e. introduction by man (Vigne, 1992).

Finally, the Holocene colonization of Corsica by man has had very little effect on the herpetofauna (small number of immigrations), only facilitated the immigration of a small number of open field birds but brought about a complete turnover of mammals. This conclusion confirms, with much more fossil evidence, the one already proposed by Vigne and Alcover (1985), and shows that the impact of man on insular vertebrate communities is a complex phenomenon which could have been very important as early as the beginning of the Holocene.

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