

THE PLEISTOCENE AVIFAUNAS OF EUROPE

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ABSTRACT:The Pleistocene avifaunas from Europe include a few Tertiary relicts which progressively vanish during the Lower Pleistocene and the beginning of the Middle Pleistocene. These forms are mainly *Pavo* and *Palaeocryptonyx* in Western Europe, and *Francolinus* in Central Europe. During the Middle Pleistocene the characteristic association in Western Europe is *Perdix palaeoperdix* - *Corvus antecorax*, while in Central Europe the most characteristic elements are the Tetraoninae. In the Upper Pleistocene the cold elements become more and more abundant, in Western Europe as well as in Central Europe, and are mainly represented by *Lagopus lagopus*, *L. mutus*, *Nyctea scandiaca*, and *Pyrrhocorax graculus*. The avifaunas of the Mediterranean islands do not include a large number of endemic extinct forms, and among them, the most numerous so far known belong to the Strigiformes. The study of the frequency of the different parts of the avian skeleton recovered in the fossiliferous localities gives information about the agent responsible for the accumulation of the material.

KEYWORDS:FOSSIL BIRDS, UPPER PLIOCENE, PLEISTOCENE, WESTERN EUROPE, CENTRAL EUROPE, MEDITERRANEAN, EVOLUTION, BIOSTRATIGRAPHY, PALEOBIOGEOGRAPHY

RESUMEN:Las avifaunas pleistocénicas europeas incluyen una pequeña serie de relictos terciarios que desaparecen progresivamente durante el Pleistoceno inferior y principios del Pleistoceno medio. Los elementos más representativos de esta fauna son *Pavo* y *Palaeocryptonyx* en Europa occidental y *Francolinus* en Centroeuropa. Durante el Pleistoceno medio la asociación característica en Europa occidental es la formada por *Perdix palaeoperdix* - *Corvus antecorax* mientras que en Centroeuropa los elementos más característicos son los tetraoninos. En el Pleistoceno superior los elementos fríos se van haciendo cada vez más abundantes en todo el subcontinente y vienen representados por especies tales como *Lagopus lagopus*, *L. mutus*, *Nyctea scandiaca* y *Pyrrhocorax graculus*. Las avifaunas de las islas mediterráneas no incluyen gran número de formas endémicas extinguidas y, entre éstas, las más numerosas conocidas hasta el momento son estrigiformes. Los análisis de frecuencias de porciones esqueléticas recuperadas en los yacimientos proporcionan información acerca del agente responsable de la acumulación del material.

PALABRAS CLAVE: AVES FOSILES, PLIOCENO SUPERIOR, PLEISTOCENO, EUROPA OCCIDENTAL, CENTROEUROPA, MEDITERRANEO, EVOLUCION, BIOESTRATIGRAFIA, PALEOBIOGEOGRAFIA

INTRODUCTION

The Pleistocene avifaunas of Europe have been extensively studied since the 1950s, mainly in Central Europe, with the works of M. Kretzoi on the material from Belfia, in Rumania, but specially with the works of D. Janossy, who studied, as well as the Hungarian faunas, a certain number of faunas from Czechoslovakia, Austria, Poland, and from ex-Eastern Germany. A first biostratigraphical scheme on the European avifaunas from the Miocene to the Pleistocene was given by Janossy (1974a) in his work on the Middle Pleistocene avifauna of Hundsheim, in Austria. The whole of the studies on the Pliocene and Pleistocene avifaunas from the Carpathian Basin led up to a synthesis, published in six parts by Janossy (1976a, 1976b, 1977, 1979a, 1979b, 1980). These works have been continued in Poland by Bochenski (1989, 1991). Numerous new, extinct species or subspecies of birds have been described in the Pliocene and in the Lower and Middle Pleistocene.

In Western Europe the studied avifaunas mainly concern the Middle and Upper Pleistocene periods (Mourer-Chauviré, 1975a; Sánchez Marco, 1987a, 1987b). A few elements, however, are

known from more ancient localities, from the Pliocene or the Lower Pleistocene, and a certain amount of new material from these old periods has not yet been described due to a lack of time.

The chronological framework used in Central Europe is different from that of Western Europe and, in the present paper, I have tried to place all the fossiliferous avian localities in the same chronological sequence, using for the Pliocene the MN (Mammal Neogene) zones, defined by Mein (1976, 1990), and for the Pleistocene the MNQ (Mammal Neogene-Quaternary) zones, defined by Guérin (1982), slightly modified. The MNQ zones are also tentatively correlated with the Alpine glacial chronology. To place the Central European localities together with the Western European ones, I have used the works of Chaline (1986), and Chaline et al. (1985). The sequence so defined is only a tentative outline and will probably be modified as the progress of biostratigraphical studies continues (Table 1).

THE DISAPPEARANCE OF TROPICAL ELEMENTS AND TERTIARY RELICTS

The Tertiary avifaunas include numerous elements which belong to families whose present-day distribution is tropical, for example Secretary-birds, Colies, Parrots, Trogons, Turacos and so on... Most of these tropical elements disappear at the end of the Pliocene but some of them are still present at the beginning of the Pleistocene and progressively vanish during this period.

In Western Europe the main tropical elements of the end of the Tertiary are the Peafowls and the Junglefowls. The extinct species *Pavo bravardi*, which is very close to the Recent species *Pavo spiciferus*, the Green Peafowl, is present in France in the localities of Perpignan (MN 15), Ardé in the Perrier Mountain (MN 16), Saint-Vallier (MN 17), and Senèze (MN 18) (Mourer-Chauviré, 1989a, 1990). The locality of Senèze is now considered Upper Pliocene (Mein, 1990) and therefore one may consider that, in Western Europe, the Peafowls did not persist beyond the Plio/Pleistocene boundary.

The Recent genus *Gallus*, the Junglefowl, is represented by four species which live in India and South East Asia (Peters, 1963). One species of *Gallus* is present in the Pliocene of Perpignan (MN 15) (Depéret, 1897; Mourer-Chauviré, 1989a), and another species, *Gallus beremendensis*, has been described in the Pliocene of Beremend 5 (MN 16), in Hungary (Janossy, 1976b).

Another tropical element is the extinct genus *Palaeocryptonyx*, described in Perpignan (Depéret, 1897), which is also found in the Upper Pliocene of Montoussé 5 (MN 18) (Clot et al., 1976a) and of Cova de Ca Na Reia, at Ibiza (Alcover, 1989), and in other still unpublished localities such as Tourkoboumia 1, in Greece, and Cava Sud, at Soave, in Italy. *Palaeocryptonyx* is a small partridge, which could not have been very different from the Recent genus *Rollulus*, the Roulroul or Crested Wood-Partridge, from South East Asia. In France this genus does not persist beyond the Plio/Pleistocene boundary, but in Italy it may have persisted somewhat longer because, according to Chaline (1986), the locality of Cava Sud, at Soave, is correlated with the biozone of Les Valerots (MNQ 20) and corresponds to the end of the Menapian cold phase.

In Central Europe, the tropical elements are mainly represented by the Francolins. The Recent genus *Francolinus* lives in the temperate and tropical regions, from the Middle East to the South of China, and in the whole of Africa (Peters, 1963). During the European Pliocene and Pleistocene, Francolins are represented by the following forms:

	Western Europe	Characteristic forms	Central Europe	Characteristic forms
MNQ zones 26 "Würm"	La Colombière Gigny-sur-Suran	* <i>Lagopus lagopus</i> * <i>Lagopus mutus</i>	Palank Pilisszanto Istalloskö	* <i>Lagopus lagopus</i> * <i>Lagopus mutus</i> * <i>Lyrurus tetrix</i>
25 "Riss-Würm"	Fontéchevade	* <i>Tetrao urogallus</i> * <i>Lyrurus tetrix</i>	K. Lambrecht Cave Varbo Süttö	* <i>Tetrastes bonasia</i> * <i>Tetrao urogallus</i>
24 "Riss"	La Fage Orgnac III (d-h.sup) Atapuerca-La Galeria	<i>Corvus antecorax</i> <i>P. palaeoperdix</i>	Solymar Castellum	* <i>Lagopus lagopus</i> * <i>Lagopus mutus</i>
23 "Mindel-Riss"	Lunel-Viel Orgnac III (h. inf-j)	<i>Corvus antecorax</i> <i>P. palaeoperdix</i> * <i>Tetrao urogallus</i> * <i>Lyrurus tetrix</i>		
22 "Mindel"	St-Estève-Janson Montoussé 3	* <i>Nyctea scandiaca</i> * <i>Pyrhocorax graculus</i> * <i>Tetrastes praebonasia</i> * <i>Tetrao urogallus</i> * <i>Lyrurus tetrix</i>	Uppony Vértesszöllös Tarkö Prezletice	* <i>First T. urogallus</i> * <i>First L. tetrix</i> • <i>Last F. capeki</i>
21 "Gunz-Mindel"	Cromer Forest Bed		Betfia 5 Kozi Grzbiet	* <i>Lagopus lagopus</i> * <i>Tetrao praeurogallus</i> * <i>Tetrastes praebonasia</i>
20 "Gunz"	Soave Bourgade Les Valerots	* <i>Palaeocryptonyx</i> * <i>First N. scandiaca</i> * <i>First L. lagopus</i>	Templomhegy Méhész Zalieski 1A	* <i>Francolinus capeki</i> * <i>Tetrao praeurogallus</i>
19	Mas Rambault	<i>Perdix palaeoperdix</i> <i>Corvus antecorax</i>	Betfia 2 Osztramos 2 & 8 D. Altenburg 4B	* <i>Francolinus capeki</i> * <i>Lyrurus partium</i>
MN Zones 18	Montoussé 5 Senèze	* <i>Palaeocryptonyx</i> * <i>Pavo bravardi</i> * <i>Lyrurus cf. partium</i>	Osztramos 3 Villany 3 & 5	* <i>Francolinus capeki</i> * <i>Francolinus minor</i>
17	Chilhac Saint-Vallier	* <i>Pavo bravardi</i> <i>Corvus antecorax</i>	Osztramos 7	* <i>Francolinus capeki</i> * <i>Francolinus minor</i> * <i>Tetrao (L.) conjugens</i>
16	Perrier	* <i>Pavo bravardi</i>	Rebielice Krolewskie Beremend 5	* <i>Francolinus capeki</i> * <i>Francolinus minor</i> * <i>Lagopus atavus</i> * <i>Gallus beremendensis</i>
15	Perpignan	* <i>Pavo bravardi</i> <i>Corvus praecorax</i> * <i>Palaeocryptonyx</i>	Weze Csarnota 2	* <i>Tetrao (L.) conjugens</i> * <i>Tetrao macropus</i> * <i>Lagopus sp.</i>

TABLE 1 - Comparison between the Western European and Central European avifaunas during the Plio-Pleistocene. MN and MNQ zones after Mein (1990) and Guérin (1982). For Western Europe, position of the sites after Chaline et al. (1985) and Chaline (1986) and characteristic forms after Depéret (1897), Clot et al. (1976a, 1976b), Mourer-Chauviré (1975a, 1980, 1989a, 1989b, 1990), and Sánchez Marco (1987a). For Central Europe, position of the sites and characteristic forms after Janossy (1974b, 1976a, 1976b, 1986) and Bochenski (1991). The black dots correspond to the Tertiary relicts and the asterisks to the cold elements.

Francolinus capeki, which goes from the Perpignan zone (MN 15) to the substage of Tarkö which corresponding to the Lower part of the Mindelian glacial stage (MNQ 22), with three successive subspecies, *F. capeki wenzensis*, *F. capeki villanyensis*, and *F. capeki capeki*; *Francolinus minor*, Pliocene age (MN 15 and 16); *Francolinus subfrancolinus*, Pliocene age (MN 17 and 18) (Janossy, 1986). The genus *Francolinus* disappears from Europe during the Mindelian glacial stage (MNQ 22), between the Tarkö and the Vértesszöllös substages (Janossy, 1986). The westernmost occurrence of this genus in the European Pleistocene is in the rich *Hippopotamus* locality of Untermassfeld, near Meiningen, in Germany, dating from the Lowest Biharian (MNQ 19 or 20) (Janossy, pers. comm.).

Other tropical elements that have been found in Central Europe are large storks, such as *Pelargosteon tothi*, which is related to Marabou Storks from Africa. *Pelargosteon tothi* has been described in the Early Middle Pleistocene of Betfia 5 (MNQ 21) in Rumania (Kretzoi, 1962). One element, designated as cf. *Pelargosteon tothi*, has also been found in the locality of Budapest-Varhegy, dating back to the Mindel (Tarkö substage, MNQ 22) (Janossy, 1979b), and another giant stork has been identified by Janossy (1965), in the locality of Voigtstedt, in Germany, also dating from the Mindel, and is considered by Janossy as a Tertiary relict. However it is difficult to be more precise about the affinities of these Ciconiidae, because they are represented by very fragmentary remains, mainly phalanges.

Tadorna tadorna, the Shelduck, can also be considered a Tertiary relict. At the present time its distribution is typically discontinuous. In Europe it breeds on the coasts of the North Atlantic, while in Central Asia it breeds on the shores of salt or brackish inland lakes, in the steppes, between latitudes of about 40° and 50° North (Voous, 1960). In the past it must have been widely and continuously distributed. It has been found in the Upper Pliocene at Chilhac, in the centre of France (MN 17) (Boeuf & Mourer-Chauviré, 1992), at Villany 3, in the South of Hungary, where it is very abundant (MN 18) (Mlikovsky, 1982), and its distribution was probably still continuous during the Middle Pleistocene; at that time it has been found at Voigtstedt, in Germany, and at Stranska Skala, in Czechoslovakia (MNQ 22) (Janossy, 1965, 1972).

In conclusion, some tropical elements, or Tertiary relicts, persisted in Europe as recently as the Middle Pleistocene, in the Mindel glacial stage.

THE TYPICAL AVIFAUNAS OF THE LOWER AND MIDDLE PLEISTOCENE AND THE APPEARANCE OF THE "COLD ELEMENTS" (ZONES MNQ 19 TO 24)

In Western Europe the typical elements of the Lower and Middle Pleistocene are *Corvus antecorax*, a primitive form of Raven, and *Perdix palaeoperdix*, a primitive form of Grey Partridge, which appear together in France, during the Lower Pleistocene, in the locality of Mas Rambault (MNQ 19) and persist until the end of the Middle Pleistocene (MNQ 24) (Mourer-Chauviré, 1975a). They are also known in Spain, in the locality of Atapuerca (Sánchez Marco, 1987a, 1987b).

In the meantime, in Central Europe, the avifaunas are dominated by the Tetraoninae, which appear as early as the Lower Pliocene, Perpignan zone (MN 15), at Weze, in Poland (Janossy, 1974b; Bochenski, 1991). All the Tetraoninae have shortened and feathered tarsi and are adapted to rather

cold climates. Janossy (1974), and Bochenski (1991) have defined a succession of different species of Tetraoninae, which evolved and gave rise to the Recent European forms:

In the lineage of *Tetrao urogallus*, the Capercaillie, the first known ancestor is *Tetrao macropus*, in the Pliocene (MN 15 and 16), then *Tetrao praeurogallus* from the Late Pliocene (MN 18) to the Early Middle Pleistocene (MNQ 22, Tarkö substage), and, finally, *Tetrao urogallus*, from the Middle Pleistocene (MNQ 22, Vértesszöllös substage) to the Present.

In the lineage of *Lyrurus tetrrix*, the Black Grouse, the first known ancestor is *Tetrao (Lyrurus) conjugens* in the Pliocene (MN 15 to 17), then *Lyrurus partium* from the Late Pliocene (MN 18) to the Early Middle Pleistocene (MNQ 22, Tarkö substage), and, finally, *Lyrurus tetrrix* from the Middle Pleistocene (MNQ 22, Vértesszöllös substage) to the Present.

In the lineage of *Lagopus lagopus* and *L. mutus*, the Willow Grouse and the Ptarmigan, the earliest form, *Lagopus* sp., appears in the Lower Pliocene (MN 15), at Weze, in Poland (Janossy, 1974b; Bochenski, 1991), then *Lagopus atavus* is found in the Upper Pliocene (MN 16 and 17). The extant species *Lagopus lagopus* first appears in France, in the locality of Les Valerots, and in Poland, in the locality of Kozi Grzbiet, at about the same time (MNQ 20-21). The formation of the Recent species *Lagopus mutus* probably took place by isolation in mountainous regions during the Mindel-Riss interglacial (MNQ 23), since both Recent species, *L. lagopus* and *L. mutus*, occurred together, in the same localities, since the Riss glacial stage (MNQ 24). They are found during the Riss in the localities of La Fage, in France (Mourer-Chauviré, 1975a), and Hunas, in Germany (Janossy, 1976a). *Tetrastes praebonasia*, the ancestor of the Recent Hazel Hen, *Tetrastes bonasia*, is known both in Central and Western Europe, in the localities of Hundshheim, Austria (Janossy, 1974a), Tarkö, Hungary (Janossy, 1976a), Kozi Grzbiet, Poland (*T. cf. praebonasia*, Bochenski, 1989), and Montoussé 3, France, in the Pyrénées mountains (Clot et al., 1976b), in the Early Middle Pleistocene (MNQ 21 and 22). The Recent form is only known from the Riss-Würm interglacial (MNQ 23) in Central Europe (Janossy, 1976a) and in France it appears only during the Holocene (Figure 1).

The Tetraoninae are always present in the avifaunas of Central Europe during the Lower and Middle Pleistocene, while in Western Europe they just appear briefly from time to time, for example *Lyrurus cf. partium* at Senèze, in the center of France (MN 18) (Stehlin, 1923), *Lagopus lagopus* at Les Valerots, in Burgundy (MNQ 20) (Chaline et al., 1985), *Tetrao urogallus*, *Lyrurus tetrrix* and *Tetrastes praebonasia*, at Montoussé 3, in the Pyrénées (MNQ 22) (Clot et al., 1976b), but they do not become settled at this time. For example, they are totally missing in the very rich and very cold avifauna of Saint-Estève-Janson, in the Durance Valley (MNQ 22) (Mourer-Chauviré, 1975a).

In Western Europe the Tetraoninae became settled only in Southern France at the time corresponding to certain layers of Orgnac 3, which are attributed to the Mindel-Riss interglacial (MNQ 23), and where they are associated to forest forms (Mourer-Chauviré, 1975a). They became more frequent only during the Riss glacial stage (MNQ 24), and, afterwards, both species of Grouse, *Lagopus lagopus*, the Willow Grouse, and *Lagopus mutus*, the Ptarmigan, become the most common elements of the Würmian avifaunas (MNQ 26) (Figure 1).

In Western Europe, one of the most frequent elements is *Corvus corax*, the Raven, either represented by its ancestral form, *Corvus antecorax*, or by its Recent form. Strangely enough this lineage is very poorly represented in Central Europe. *Corvus cf. corax* is quoted by Janossy (1986) at Tarkö, but in his previous works, he considered the large corvid from Tarkö as belonging to the extinct species *Corvus pliocaenus janossyi*. The Recent form, *Corvus corax*, is only known in a few Würmian localities (Janossy, 1979a).

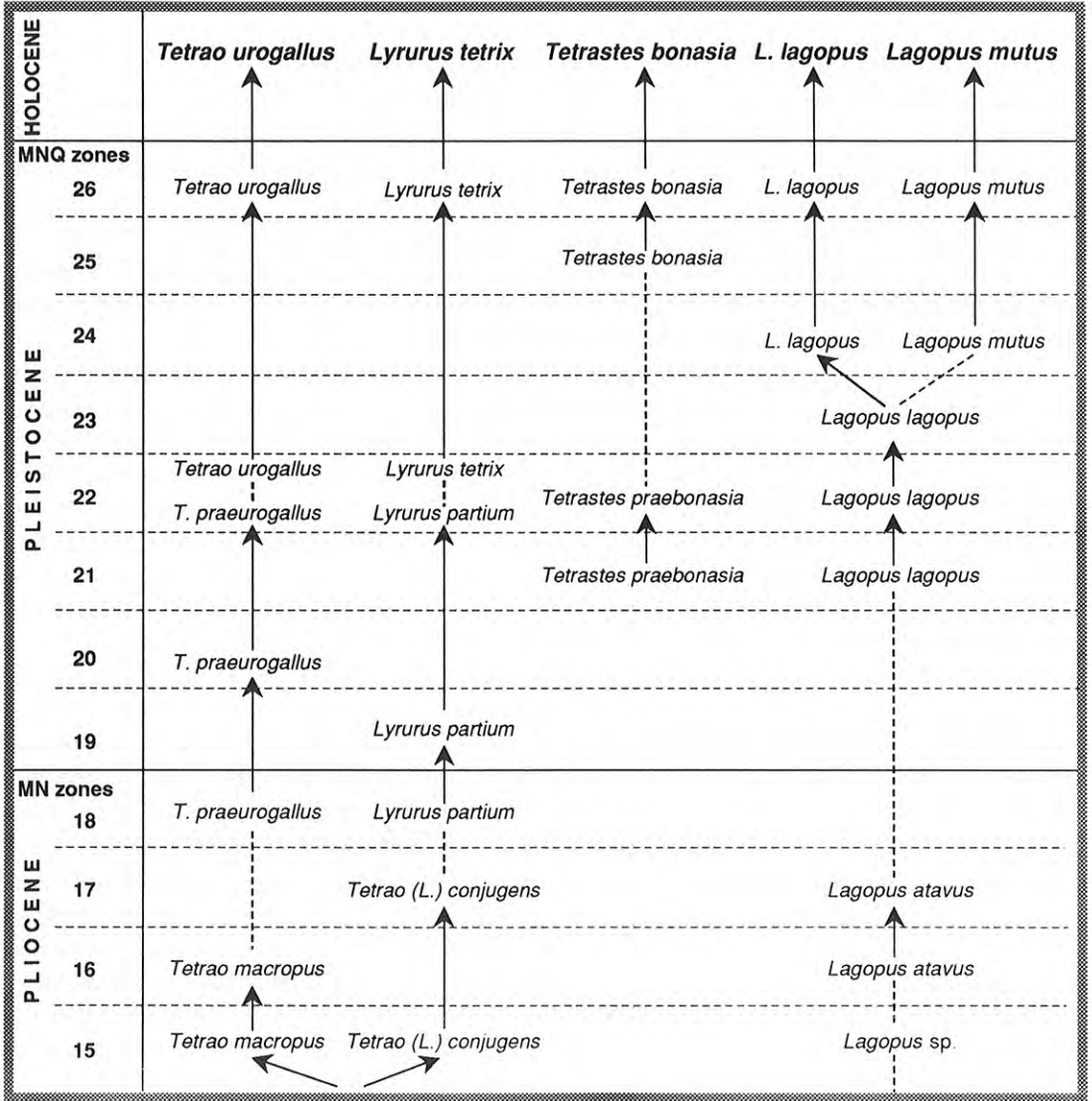


FIGURE 1 - Evolution of the different lineages of Tetraoninae in Europe after Bochenski (1991), Chaline et al. (1985), Clot et al. (1976b), Janossy (1976a, 1986), Mourer-Chauviré (1975a), replaced in the chronological framework of the MN (Mein, 1990) and MNQ (Guérin, 1982) zones.

Among the cold elements which appear as early as the first cooling stages, is the Snowy Owl, *Nyctea scandiaca*. It has been known in France since the Lower Pleistocene, at Bourgade, near the Mediterranean shore (Gunz glacial stage, MNQ 20) (Mourer-Chauviré, 1980). Later it is very abundant in Saint-Estève-Janson, during the Mindel glacial stage (MNQ 22). Among the material from Saint-Estève-Janson, there are subadult bones, and it is therefore probable that it was nesting at this time in the Durance valley (Mourer-Chauviré, 1975a). It is found again during each glacial stage

and during the Würm it is very abundant in South West France, for example in the locality of Le Morin, in the Gironde department (Mourer-Chauviré, 1975a). It is also known in Spain, in Erralla Cave (Eastham, 1985), in Gibraltar (Eastham, 1968), and it reached the extreme South of Italy, in the locality of Romanelli, Terra d'Otranto (Cassoli et al., 1977). Curiously, it is very rare in Central and Eastern Europe, where it only appears at the end of the Riss-Würm in Kalman Lambrecht Cave, in Hungary, (Janossy, 1963) and in the beginning of the Würm in Binagady, Azerbaïdjan (Burchak-Abramovitch, 1975); after that it is only known in Central Europe from a few Würmian localities (Janossy, 1977).

Another cold element is the Alpine Chough, *Pyrrhonorax graculus*, which is very abundant in the Mediterranean cold avifaunas. At present it breeds in the mountains above altitudes of 1400 m (Voous, 1960), but during the glacial stages it probably lived at lower altitudes, probably down to sea-level. In Central Europe it is known as early as the Pliocene, in Csarnota 2 (MN 15), and during the Lower and Middle Pleistocene (Betfia 2: MNQ 19, Mészáros: MNQ 20, Betfia 5: MNQ 21, Tarkö, Hundsheim, Stranska Skala: MNQ 22) (*Pyrrhonorax* aff. *graculus* and *Pyrrhonorax graculus vetus*) (Kretzoi, 1962; Janossy, 1972, 1974a, 1979a). But in Western Europe it seems to appear only during the Middle Pleistocene, in particular in the locality of Saint-Estève-Janson (Mindel, MNQ 22), where it is extremely abundant (Mourer-Chauviré, 1975a).

THE GREAT DEVELOPMENT OF THE COLD AVIFAUNAS

It is mainly during the last glacial stage, Würmian or Weichselian (MNQ 26), that avifaunas which include a great majority of cold forms are to be found. The most widespread are *Lagopus lagopus*, the Willow Grouse, *Lagopus mutus*, the Ptarmigan, *Nyctea scandiaca*, the Snowy Owl, and *Pyrrhonorax graculus*, the Alpine Chough. During the cold stages, the other Tetraoninae such as *Tetrao urogallus*, the Capercaillie, and *Lyrurus tetrix*, the Black Grouse, decrease, to increase again at the end of the Würm or during the Holocene.

During the Middle Würm, Ptarmigans prevailed in Hungary (Istallosko, Janossy, 1986), as well as in France (Gigny-sur-Suran, layers XX to IX, Mourer-Chauviré, 1989b), then Willow Grouse prevailed in Hungary (Pilisszanto, Janossy, 1986), as in France (Gigny-sur-Suran, layers VII to V, Mourer-Chauviré, 1989b) or Belgium (Coléoptère cave, Mourer-Chauviré, 1983a), corresponding to a colder climate, which was similar to the boundary between the taïga and the tundra zones. Then Ptarmigans and Black Grouse become prevalent again, for example in Szekszard-Palank, in Hungary (Janossy, 1986).

During this period all the northern part of Europe was covered by a very large ice-cap. The marine species which at present nest in this area, such as the Fulmars (*Fulmarus glacialis*), Long-tailed Ducks (*Clangula hyemalis*), Scoters (*Melanitta fusca* and *nigra*), Eiders (*Somateria mollissima*), Brent and Red-Breasted Geese (*Branta bernicla* and *ruficollis*), some shorebirds, Phalaropes (*Phalaropus*), Skuas (*Stercorarius*), Gulls (*Larus*), Little Auks (*Plautus alle*) etc ... at that time probably nested far southwards, along the Atlantic coasts, from the South of Great Britain to Gibraltar and on the northern shores of the Mediterranean.

The extinct Great Auk, *Pinguinus impennis*, which disappeared during the XIXth century, nested along the Atlantic and Mediterranean coasts of the Iberian Peninsula and Italy at that time. During the Pleistocene it has been found at Figueira Brava, in Portugal (Mourer-Chauviré et al., 1991), Gibraltar (Bate, 1928; Eastham, 1968), Cueva of Nerja, in Spain (Boessneck et al., 1980; Eastham, 1986), the Arene Candide (Cassoli, 1980), Archi (Ascenzi et al., 1971), and Romanelli (Blanc, 1927; Cassoli et al., 1977), in Italy. It is therefore not very surprising that Palaeolithic rock paintings of the Great Auk have been recently found in the submarine Cosquer Cave, near Marseille (Clottes et al., 1992). It has also been found at Porto Santo, in the Madeira Archipelago (Pieper, 1985).

In the Figueira Brava Cave, in Portugal, other species which at present nest in the tundra and winter at sea, (such as Red-throated Diver, *Gavia stellata*, Common Scoter, *Melanitta nigra*, Velvet Scoter, *Melanitta fusca*, Long-tailed Duck, *Clangula hyemalis*, and the Razorbill, *Alca torda* (Mourer-Chauviré et al., 1991) have been also identified. The Gannet, *Sula bassana*, which nests farther to the South, and an extinct species of shearwater, *Puffinus holei*, recently described from the Pleistocene of Canary Islands (Walker et al., 1990), were also present in Figueira Brava.

THE MEDITERRANEAN INSULAR AVIFAUNAS

The Mediterranean Islands are not located very far from the mainland and that is probably the reason why they do not have a great number of endemic extinct species. A synthetic work on these avifaunas, by Alcover et al., was published in 1992. Some extinct species, or subspecies, have already been described and more will be probably found in the future. The extinct forms known at present are the following:

Procellariiformes:

- *Puffinus nestori*, Upper Pliocene of Cova de Ca Na Reia, Ibiza (Alcover, 1989).

Anseriformes:

- *Cygnus equitum*, the Giant Maltese Swan, Upper Pleistocene of Malta (Bate, 1916; Northcote, 1988, 1992).

- *Cygnus falconeri*, the Dwarf Maltese "Swan-Goose", Upper Pleistocene of Malta (Lydekker, 1890; Bate, 1916; Northcote, 1982b).

Accipitriformes:

- *Aquila chrysaetos simurgh*, a large form of Golden Eagle, Pleistocene of Crete (Weesie, 1988).

- *Gyps melitensis*, a large form of Vulture, Pleistocene of Malta and Crete (Lydekker, 1890; Bate, 1916; Weesie, 1988). This form, described in Malta, has also been found in the Middle and Upper Pleistocene of the European mainland.

Gruiformes:

- *Grus primigenia*, a large form of crane, similar in size to the Sarus Crane, Pleistocene of Majorca and Ibiza (Northcote et al., 1988; Florit et al., 1989). This form is known from a few Upper Pleistocene localities on the continent.

- *Grus melitensis*, a large form of crane, Upper Pleistocene of Malta (Lydekker, 1890, 1891; Northcote, 1982a, 1992).

Strigiformes:

- *Tyto melitensis*, a presumed large form of Barn Owl, Upper Pleistocene of Malta (Lydekker, 1890,

1891; Bate, 1916). This form does not actually differ very much from the Recent Barn Owl, *Tyto alba* (Mourer-Chauviré et al., 1980).

- *Tyto balearica*, a large form of Barn Owl, Upper Pliocene of Majorca and Menorca (Mourer-Chauviré et al., 1980). This form, however, was not endemic to the Balearics, since a bird of comparable size was living on the mainland during the same period (Mourer-Chauviré et al., 1988).

- *Bubo insularis*, a dwarf form of Eagle Owl, Pleistocene of Sardinia and Corsica (Mourer-Chauviré et al., 1986).

- *Athene cretensis*, a large form of the Little Owl, Pleistocene of Crete and Armathia (Weesie, 1982; Alcover et al., 1992).

Among the Passeriformes a new subspecies of *Corvus antecorax* occurred in Ibiza as late as the Holocene; a new species of Fringillidae appears in Majorca, and possibly a new subspecies of *Garrulus glandarius*, the Jay, in Crete. All these forms are still undescribed (Weesie, 1988; Alcover et al., 1992).

Among the forms which no longer, or very rarely, occur on these islands, *Otis tarda*, the Great Bustard, has been found in Malta (Bate, 1916), Ibiza (Florit et al., 1989), and was extremely abundant in the Upper Pleistocene of Cyprus (Simmons, 1991; Mourer-Chauviré, in preparation).

With the exception of the quail, *Coturnix coturnix*, which is the only migratory phasianid, and of *Palaeocryptonyx* sp. in the Upper Pliocene of Ibiza, the insular avifaunas of the Mediterranean are characterized by the lack of Phasianidae. This absence stands in sharp contrast with the mainland avifaunas, where the Phasianidae are often the most abundant elements.

THE RELATIVE ABUNDANCE OF SKELETAL ELEMENTS

During the course of my research on Pleistocene birds from both archaeological and non-archaeological sites, I realized that the distribution of the main long bones was not always related only to their robustness. In the case of medium-sized birds, such as Willow Grouse, Ptarmigans, Partridges, hunted by large nocturnal birds of prey such as Eagle Owls or Snowy Owls, there is an over-representation of the tarsometatarsi and, to a lesser extent, of the carpometacarpus. This had already been reported by Dupont (1872), Boessneck et al. (1973), then by myself (1975a, 1975b, 1983b), Vilette (1983), and recently again by Baales (1992).

In the case of cave sites, it is necessary to distinguish between those birds which were living in situ, in the rocky cliffs surrounding the caves, such as *Columba livia*, the Rock Dove, or *Pyrhrocorax graculus*, the Alpine Chough, and species which had been brought to the site by predators. In the first instance, the different skeletal elements have an almost homogeneous representation. It is only in those birds which did not live in the cliffs and were not hunted by Man, that an over-representation of tarsometatarsi and, secondarily, of carpometacarpus is to be found. This has been recorded in the medium-sized Galliformes, which are often the most abundant items, but also in Anseriformes, Accipitriformes, Charadriiformes, and the Strigiformes, as in the localities of Orgnac 3 (Mourer-Chauviré, 1975a), or La Fage (Mourer-Chauviré, 1975b). It is also necessary to group birds according to size. This over-representation is observed only in medium-sized birds.

When birds were hunted and brought into the cave by Man, there is usually, an over-representation of humeri and femora in the medium-sized Galliformes, whereas the

tarsometatarsi are often the least abundant bones. The bones can also present cut or burn marks. In the case of large-sized birds, such as the Great Bustards from Cyprus, there is a strong over-representation of the scapular part of the coracoid, which is also the most robust part of the skeleton, and in this site many of the bones are burnt.

CONCLUSIONS

Although there are differences in the faunal composition between the Western European and the Central European avifaunas, extinct forms which are common for these two areas have also been found, and thus make it possible to bring to the fore evolutionary phenomena which occurred at the scale of the whole European subcontinent. These common extinct species or subspecies are:

Strix intermedia Janossy, a form that is intermediate between the Recent *Strix aluco* and *Strix uralensis*. It has been found in four localities in Hungary, Czechoslovakia, Austria, and in France at Saint-Estève-Janson; for all these localities, age MNQ 22 (Janossy, 1974a, 1977; Mourer-Chauviré, 1975a).

Tetrastes praebonasia Janossy, an ancestor of the Recent *Tetrastes bonasia* (already indicated in paragraph III). It has been found in three localities in Hungary, Poland, Austria and in France at Montoussé 3, in the Pyrénées; age MNQ 21 - MNQ 22 (Janossy, 1974a, 1976a; Clot et al., 1976b; Bochenki, 1989).

Falco antiquus Mourer-Chauviré, a form that is intermediate between the Recent *Falco rusticolus* and *Falco cherrug*. It has been found in France, at La Fage (Mourer-Chauviré, 1975a) and in Hungary, at Horvölgy (*Falco* aff. *antiquus*, Janossy, 1977, 1980); age MNQ 24.

Falco tinnunculus atavus Janossy, a subspecies slightly larger than the Recent *Falco tinnunculus*. It has been found in five localities in Austria, Czechoslovakia, Rumania, Hungary (Janossy, 1977, 1981), age MNQ 19 to MNQ 22, and in six localities in France (Mourer-Chauviré, 1975a; Chaline et al., 1985), age MNQ 20 to MNQ 24.

Corvus pliocaenus (Portis) and *Corvus pliocaenus janossyi* Mourer-Chauviré, found in Rumania and Hungary (Janossy, 1979a, 1980; Jurcsak et al., 1988), age MNQ 21 and MNQ 22. It was much more frequent in Western Europe being known in Italy (Regalia, 1902), in Spain, in Majorca (Mourer-Chauviré et al., 1977), in France from seven localities (Mourer-Chauviré, 1975a, 1981, Philippe et al., 1980), and in Greece (unpublished data), age MNQ 18 to MNQ 24.

Pica pica major Janossy, a subspecies slightly larger than the Recent *Pica pica*. It has been found in six localities in Hungary, Austria, Czechoslovakia (*P. pica major* and *P. aff. pica major*, Janossy, 1972, 1974a, 1979a), age MN 15 to MNQ 22, and in France in two localities (Mourer-Chauviré, 1975a), age MNQ 22 and MNQ 23.

Pyrhocorax graculus vetus Kretzoi, a subspecies slightly smaller than the Recent *Pyrhocorax graculus*. Described by Kretzoi (1962) in Betfia 5, Rumania (MNQ 21), it has been found in France in nine localities (Mourer-Chauviré, 1975a; Clot et al., 1976b), age MNQ 22 to MNQ 24.

Statistical comparisons of the dimensions of the main long bones between fossil and Recent populations, however, show that the variations are not always related to evolutionary phenomena

occurring in a continuous way in the same direction, but can be punctual responses of certain populations to particular ecological conditions, restricted in space and time.

It will be necessary to continue these studies to obtain a more precise knowledge of the evolution of these Plio-Pleistocene European avifaunas.

BIBLIOGRAPHY

- Alcover, J.A. (1989) - Les aus fossils de la Cova de Ca Na Reia. *Endins* 14-15: 95-100.
- Alcover, J.A.; F. Florit; C. Mourer-Chauviré & P. Weesie (1992) - The avifaunas of the isolated Mediterranean islands during the Middle and Late Pleistocene. *Natural History Museum of Los Angeles County, Science Series*, 36: 273-283.
- Ascenzi, A. & A. Segre (1971) - Il giacimento con mandibola neandertaliana di Archi (Reggio Calabria). *Accademia nazionale dei Lincei*, ser. VIII, vol. L (6): 763-771.
- Baales, M. (1992) - Accumulations of bones of *Lagopus* in Late Pleistocene sediments. Are they caused by Man or Animals?. *Cranium* 9(1): 17-22.
- Bate, D.M.A. (1916) - On a small collection of vertebrate remains from the Har Dalam cavern, Malta; with note on a new species of the genus *Cygnus*. *Proceedings of the zoological Society of London* 1916: 421-430.
- Bate, D.M.A. (1928) - Excavation of a mousterian rock-shelter at Devil's tower, Gibraltar. The animal remains. *Journal of the royal anthropological Institute* 58: 92-113.
- Blanc, G.A. (1927) - Sulla presenza di *Alca impennis* Linn. nella formazione pliocenica superiore di grotta Romanelli in Terra d'Otranto. *Archivio per l'Antropologia e l'Etнологia* 58(1-4): 34 p.
- Bochenski, Z. (1989) - Ptaki - Aves. In: Kowalski, K. (ed.): History and Evolution of the terrestrial fauna of Poland. *Folia quaternaria* 59-60: 89-108.
- Bochenski, Z. (1991) - Pliocene grouse of the genus *Lagopus* from Poland. *Acta zoologica cracoviensia* 34(2): 563-577.
- Boessneck, J. & A. von den Driesch (1973) - Die jungpleistozänen Tierknochenfunde aus der Brillenhöhle. In: Riek, G.: Das Paläolithikum der Brillenhöhle bei Blaubeuren, Teil II. *Forschungen und Berichte zur Vor- und Frühgeschichte in Baden-Württemberg* 4(II): 105 p.
- Boessneck, J. & A. von den Driesch (1980) - Tierknochenfunde aus vier Südspanischen Höhlen. *Studien über frühe Tierknochenfunde von der Iberischen Halbinsel* 7: 1-83.
- Bocuf, O. & C. Mourer-Chauviré (1992) - Les oiseaux des gisements d'âge Pliocène supérieur de Chillac, Haute-Loire, France. *Compte Rendus de l'Académie des Sciences de Paris*, sér. II, 314: 1091-1096.
- Burchak-Abramovitch, N.I. (1975) - Die pleistozäne Vogelfauna der UdSSR. *Quartärpaläontologie* 1: 87-105.
- Cassoli, P.F. (1980) - L'Avifauna del Pleistocene superiore delle Arena Candide (Liguria). *Memorie dell'Istituto italiano di Paleontologia umana*, nov. ser., 3: 156-234.
- Cassoli, P.; A.G. Segre & E. Segre (1977) - Evolution morphologique et écologique de la côte de Castro (Pouilles) dans le Pléistocène final. *Colloque international du CNRS n° 271: La fin des temps glaciaires en Europe, Talence, 24-28 mai 1977*. CNRS édit.: 325-332.
- Chaline, J. (1986) - Continental faunal units of the Plio-Pleistocene of France. *Memorie della Società geologica Italiana* 31: 175-183.
- Chaline, J.; J. Renault-Miskovsky; G. Brochet; R. Clement-Dels; D. Jammot; C. Mourer-Chauviré; J. Bonvalot; J. Lang, N. Leneuf & A. Pascal (1985) - L'Aven des Valerots (Nuits-Saint-Georges, Côte d'Or), site de référence du Pléistocène inférieur. *Revue de Géologie dynamique et de Géographie physique* 26(2): 109-118.
- Clot, A.; J. Chaline; E. Heintz; D. Jammot; C. Mourer-Chauviré & J.C. Rage (1976a) - Montoussé 5 (Hautes-Pyrénées), un nouveau remplissage de fissure à faune de vertébrés du Pléistocène inférieur. *Geobios* 9(4): 511-514.

- Clot, A.; J. Chaline; D. Jammot; C. Mourer-Chauviré & J.C. Rage (1976b) - Les poches ossifères du Pléistocène moyen et inférieur de Montoussé (Hautes-Pyrénées). *Bulletin de la Société d'Histoire naturelle de Toulouse* 112(1-2): 146-161.
- Clottes, J.; A. Beltran; J. Courtin & H. Cosquer (1992) - La grotte Cosquer (Cap Morgiou, Marseille). *Bulletin de la Société préhistorique française*, 89(4): 98-128.
- Depéret, C. (1897) - Les animaux pliocènes du Roussillon. *Mémoires de la Société géologique de France*, Paléontologie, 3: 198 p.
- Dupont, M.E. (1872) - *L'homme pendant les âges de la pierre dans les environs de Dinant-sur-Meuse*. Muquardt, Bruxelles.
- Eastham, A. (1968) - The avifauna of Gorham's Cave, Gibraltar. *Bulletin of the Institute of Archaeology* 7: 37-42.
- Eastham, A. (1985) - The Magdalenian Avifauna at Erralla Cave. *Munibe* 37: 59-80.
- Eastham, A. (1986) - The birds of the Cueva de Nerja. In: Jordá Pardo, J.F. (ed.): *La Prehistoria de la Cueva de Nerja* (Málaga). *Trabajos sobre la Cueva de Nerja*. Num. 1, Universidad de Málaga: 109-130.
- Florit, X.; C. Mourer-Chauviré & J.A. Alcover (1989) - Els Ocells pleistocènics d'Es Pouas, Eivissa. Nota preliminar. *Bulleti de la Institucio Catalana d'Historia Natural* 56 (Sec. Geol., 5): 35-46.
- Guérin, C. (1982) - Première biozonation du Pléistocène européen, principal résultat biostratigraphique de l'étude des Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur d'Europe occidentale. *Geobios* 15(4): 593-598.
- Janossy, D. (1963) - Letztinterglaziale Vertebraten-Fauna aus der Kalman Lambrecht-Höhle (Bükk-Gebirge, Nordost Ungarn) I. *Acta zoologica* IX(3-4): 293-331
- Janossy, D. (1965) - Vogelreste aus den altpleistozänen Ablagerungen von Voigtstedt in Thüringen. *Paläontologische Abhandlungen*, Abt. A, II(2-3): 337-361.
- Janossy, D. (1972) - Die mittelpleistozäne Vögelfauna der Stranska Skala. *Anthropos, Studia Musei Moraviae* 20: 35-64.
- Janossy, D. (1974a) - Die mittelpleistozäne Vogelfauna von Hundsheim (Niederösterreich). *Sitzungsberichten der Österr. Akademie der Wissenschaften, Mathem.-naturw. Kl., Abt. I*, 182(6-8): 211-257.
- Janossy, D. (1974b) - Upper Pliocene and Lower Pleistocene Bird remains from Poland. *Acta Zoologica Cracoviensia*, XIX(21): 531-564.
- Janossy, D. (1976a) - Plio-Pleistocene bird remains from the Carpathian basin. I. Galliformes. 1. Tetraonidae. *Aquila* 82: 13-36.
- Janossy, D. (1976b) - Plio-Pleistocene bird remains from the Carpathian basin. II. Galliformes. 2. Phasianidae. *Aquila* 83: 29-42.
- Janossy, D. (1977) - Plio-Pleistocene bird remains from the Carpathian basin. III. Strigiformes, Falconiformes, Caprimulgiformes, Apodiformes. *Aquila* 84: 9-36.
- Janossy, D. (1979a) - Plio-Pleistocene bird remains from the Carpathian basin. IV. Anseriformes, Gruiformes, Charadriiformes, Passeriformes. *Aquila* 85: 11-39.
- Janossy, D. (1979 b) - Plio-Pleistocene bird remains from the Carpathian basin. V. Podicipediformes, Ciconiiformes, Otidiformes, Columbiformes, Piciformes. *Aquila* 86: 19-33.
- Janossy, D. (1980) - Plio-Pleistocene bird remains from the Carpathian basin. VI. Systematical and geographical catalogue. *Aquila* 87: 9-22.
- Janossy, D. (1981) - Die altpleistozänen Vogelfaunen von Deutsch-Altenburg 2 und 4 (Niederösterreich). *Beiträge zur Paläontologie von Österreich* 8: 375-391.
- Janossy, D. (1986) - *Pleistocene vertebrate faunas of Hungary*. Developments in Paleontology and Stratigraphy, n° 8, Elsevier: 208 p.
- Jurcsak, T. & E. Kessler (1988) - Evoluția Avifaunei pe teritoriul României (III). Filogenie și sistematică. *Complexul Muzeal Județean Bihor* XVIII: 647-688.
- Kretzoi, M. (1962) - Vogelreste aus der altpleistozänen Fauna von Belfia. *Aquila* 67-68: 167-174.
- Lydekker, R. (1890) - On the remains of some large extinct birds from the Cavern-deposits of Malta. *Proceedings of the zoological Society of London* 1890: 403-410.

- Lydekker, R. (1891) - *Catalogue of the fossil birds in the British Museum (Natural History)*. British Museum Publ.: 368 p.
- Mein, P. (1976) - Biozonation du Néogène méditerranéen à partir des Mammifères. *Proceedings of the VIth Congress, R.C.M.N.S.*, 2: 78-81.
- Mein, P. (1990) - Updating of Mn zones. In: Lindsay, E.H. et al. (eds.): *European Mammal chronology*. Plenum Press: 73-90.
- Mlikovsky, J. (1982) - Taxonomisch Identität der *Anas submajor* Janossy 1979 (Aves: Anseriformes) aus dem Oberpliozän Ungarns. *Vestník Československé Společnosti Zoologické* 46: 199-202.
- Mourer-Chauviré, C. (1975a) - Les oiseaux du Pléistocène moyen et supérieur de France. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon* 64: 624 p.
- Mourer-Chauviré, C. (1975b) - Les oiseaux (Aves) du gisement pléistocène moyen des Abîmes de la Fage à Noailles (Corrèze). *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon* 13: 89-112.
- Mourer-Chauviré, C. (1980) - La faune d'oiseaux du Pléistocène en Europe occidentale. In: Problèmes de stratigraphie quaternaire en France et dans les pays limitrophes. *Supplément au Bulletin de l'Association française d'Etude du Quaternaire*, nouv. sér., 1: 353-358.
- Mourer-Chauviré, C. (1981) - Les oiseaux du Pléistocène moyen de la Caune de l'Arago à Tautavel. *Colloque international du CNRS, Tautavel, 22-28 juin 1981, Prétirage*: 205-212.
- Mourer-Chauviré, C. (1983a) - Les oiseaux de la couche 5 de la grotte du Coléoptère à Bomal-sur-Ourthe (Belgique). *Société wallonne de Paléontologie*, mém. n° 5: 53-65.
- Mourer-Chauviré, C. (1983b) - Les Oiseaux dans les habitats préhistoriques : gibier des hommes ou proies des rapaces ? In: Grigson, C. & J. Clutton-Brock (eds.): *Animals and Archaeology*, vol. 2, Shell Middens, Fishes, and Birds. *British Archaeological Reports, International series* 183: 111-124.
- Mourer-Chauviré, C. (1989a) - A Peafowl from the Pliocene of Perpignan, France. *Palaeontology* 32(2): 439-446.
- Mourer-Chauviré, C. (1989b) - Les Oiseaux. In : La Baume de Gigny (Jura) sous la direction de M. Campy, J. Chalain et M. Vuillemeij. *XXVII^{eme} suppl. à Gallia-Préhistoire*: 121-129.
- Mourer-Chauviré, C. (1990) - Les paons du Pliocène et du Pléistocène inférieur d'Europe. Biostratigraphie et Paléocécologie. In : Journée Louis David. *Documents des Laboratoires de Géologie de Lyon*, H. S. 9: 77-91.
- Mourer-Chauviré, C; S. Moya & R. Adrover (1977) - Les oiseaux des gisements quaternaires de Majorque. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon* 15 suppl.: 61-64.
- Mourer-Chauviré, C.; J.A. Alcover; S. Moya & J. Pons (1980) - Une nouvelle forme insulaire d'effraie géante, *Tyto balearica* n. sp. (Aves, Strigiformes) du Plio-Pléistocène des Baléares. *Geobios* 13(5): 803-811.
- Mourer-Chauviré, C. & M.T. Antunès (1991) - Présence du grand pingouin, *Pinguinus impennis* (Aves, Charadriiformes) dans le Pléistocène du Portugal. *Geobios* 24(2): 201-205.
- Mourer-Chauviré, C. & A. Sánchez Marco (1988) - Présence de *Tyto balearica* (Aves, Strigiformes) dans des gisements continentaux du Pliocène de France et d'Espagne. *Geobios* 21(5): 639-644.
- Mourer-Chauviré, C. & P.D.M. Weesie (1986) - *Bubo insularis* n. sp., forme endémique insulaire de grand-duc (Aves, Strigiformes) du Pléistocène de Sardaigne et de Corse. *Revue de Paléobiologie* 5(2): 197-205.
- Northcote, E.M. (1982a) - The extinct Maltese crane *Grus melitensis*. *Ibis* 124: 76-80.
- Northcote, E.M. (1982b) - Size, Form and Habit of the extinct Maltese swan *Cygnus falconeri*. *Ibis* 124: 148-158.
- Northcote, E.M. (1988) - An extinct "swan-geese" from the Pleistocene of Malta. *Palaeontology* 31(3): 725-740.
- Northcote, E.M. (1992) - Swans (*Cygnus*) and Cranes (*Grus*) from the Maltese Pleistocene. *Natural History Museum of Los Angeles County, Science Series*, 36: 285-291.
- Northcote, E.M. & C. Mourer-Chauviré (1988) - The extinct crane *Grus primigenia* MILNE-EDWARDS in Majorca (Spain). *Geobios* 21(2): 201-208.

- Peters, J.L. (1963)** - *Check-list of Birds of the World*, vol. II, 2nd edition. Harvard Univ. Press, Cambridge.
- Philippe, M.; C. Mourer-Chauviré & J. Evin (1980)** - Les gisements paléontologiques quaternaires des Causses de Martel et de Gramat (Corrèze et Lot) : Faunes et chronologie. *Nouvelles Archives du Muséum d'Histoire naturelle de Lyon* 18 suppl.: 57-67.
- Pieper, H. (1985)** - The fossil land birds of Madeira and Porto Santo. *Bocagiana* 88: 6 p.
- Regalia, E. (1902)** - Sette uccelli pliocenici del Pisano e del Valdarno superiore. *Palaeontographia italica* VIII: 219-238.
- Sánchez Marco, A. (1987a)** - Aves fosiles de Atapuerca. In: Aguirre, E.; E. Carbonell & J.M. Bermudez de Castro (eds.): *El Hombre fósil de Ibeas y El Pleistoceno de la Sierra de Atapuerca*. I. Junta de Castilla y Leon, Consejería de Cultura y Bienestar Social: 67-73.
- Sánchez Marco, A. (1987b)** - Saalian *S.L.* avian findings in the Northern Iberian Plateau. In: Mourer-Chauviré, C. (ed.): *L'Evolution des Oiseaux d'après le Témoignage des Fossiles*. *Documents des Laboratoires de Géologie de Lyon* 99: 193-196.
- Simmons, A. (1991)** - Humans, island colonization and Pleistocene extinctions in the Mediterranean: the view from Akrotiri *Aetokremnos*, Cyprus. *Antiquity* 65 (249): 857-869.
- Stehlin, G. (1923)** - Die oberpliocäne Fauna von Senèze (Haute-Loire). *Eclogae geologicae Helvetiae* XVIII(2): 268-281.
- Vilette, P. (1983)** - Avifaunes du Pléistocène final et de l'Holocène dans le Sud de la France et en Catalogne. *Atacina* 11: 190 p.
- Voous, K.H. (1960)** - *Atlas of European birds*. Nelson, London, 284 p.
- Walker, C.; G.M. Wragg & C.J.O. Harrison (1990)** - A new shearwater from the Pleistocene of the Canary islands and its bearing on the evolution of certain *Puffinus* shearwaters. *Historical Biology* 3: 203-224.
- Weesie, P.D.M. (1982)** - A pleistocene endemic island form within the genus *Athene*: *Athene cretensis* n. sp. (Aves, Strigiformes) from Crete. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, Series B, 85(3): 323-336.
- Weesie, P.D.M. (1988)** - The Quaternary avifauna of Crete, Greece. *Palaeovertebrata* 18(1): 94 p.