THE QUATERNARY AVIFAUNA OF CRETE, GREECE

by

Peter D.M. WEESIE*

TABLE OF CONTENTS

* Institute for Earth Sciences, State University Utrecht, Budapestlaan 4, 3508 TA Utrecht, Netherlands.

Key-words : Avifauna, Quaternary, Crete, Systematics
Mots-clés : Avifaune, Quaternaire, Crète, Systématique

Palaeovertebrata, Montpellier, **18** (1): 1-94, 9 figs., 30 tab., 9 pls.
(Reçu le 2 Juin 1987, accepté le 3 Septembre 1987, publié le 1er Septembre 1988)

To the memory of my sister Karin

A reconstruction of some Pleistocene Cretan birds: *Gyps melitensis, Aquila chrysaetos simurgh, Athene cretensis* and *Garrulus glandarius.*

ABSTRACT

Pleistocene bird fossils have been studied from nine localities on Crete. Part of this material was described earlier by the author (Weesie, 1982) and will not be treated here in extenso, the results will be incorporated. More than one third of the over 10,000 fossil bird bones available could be identified ; they were found to represent at least 65 bird species.

The following species of the Pleistocene Cretan avifauna are new to the fauna of Crete : *Branta ruficollis, Haliaeetus albicilla, Gyps melitensis, Aquila chrysaetos simurgh* n. ssp., *Ketupa zeylomensis, Aegolius funereus, Dendrocopos leucotos, Zoothera dauma, Turdus iliacus* and *Pyrrhula pyrrhula* .

The Pleistocene Cretan avifauna differs less from comparable mainland avifaunas than (fossil) avifaunas from oceanic islands do. Still, the Pleistocene Cretan avifauna has two qualities that are characteristic of island avifaunas : the almost complete absence of a group of birds (the Galliformes) and the presence of two endemic (sub)species : the giant eagle *Aquila chrysaetos simurgh* n. ssp. and the long-legged owl *Athene cretensis* (Weesie, 1982). The new subspecies is described in the present study.

These endemic birds of prey were found in association with their supposedly principal prey species (now extinct as well) : endemic mice for the owl and endemic deer for the eagle. Endemic mammals have been found in association with endemic birds of prey on many islands, not only in the Mediterranean. There is evidence that the size of endemic birds of prey becomes optimally adapted to their feeding on certain endemic mammals, especially rodents.

Another characteristic of the Pleistocene Cretan avifauna is the great number of species of birds of prey. This appears to be a common characteristic of fossil avifaunas from caves on Mediterranean islands as well as from caves on the European mainland. However, we think that ecological conditions on Pleistocene Crete (especially the abundant presence of mice) helped to account for the high representation of birds of prey.

Furthermore, the fossil avifauna enables us to draw some conclusions about the climate and vegetation on Pleistocene Crete : it is concluded that the climate was cooler than today and that Crete was largely covered with forests.

Finally, the reasons for the extinction or disappearance from Crete of some bird species of the Pleistocene Cretan avifauna are discussed.

RÉSUMÉ

Des fossiles Pléistocènes d'oiseaux de neuf localités en Crète ont été étudiés. Une partie de ce matériel a été décrite déjà par l'auteur (Weesie, 1982) et ne sera pas traitée ici extensivement, les résultats seront incorporés dans le présent travail. Plus d'un tiers de la quantité de plus de 10,000 ossements disponibles pouvait être identifié et au moins 65 espèces d'oiseaux sont représentées dans cet ensemble.

Les espèces suivantes de l'avifaune Pléistocène de Crète sont nouvelles pour la faune de Crète : *Branta ruficollis, Haliaeetus albicilla, Gyps melitensis, Aquila chrysaetos simurgh* n. ssp., *Ketupa zeylonensis, Aegolius funereus, Dendrocopos leucotos, Zoothera dauma, Turdus iliacus* et *Pyrrhula pyrrhula* .

La différence entre l'avifaune Pléistocène de Crète et les avifaunes comparables du continent est moins grande que la différence entre ces dernières et les avifaunes provenant des îles océaniques. Néanmoins, l'avifaune Pléistocène de Crète possède deux qualités qui sont caractéristiques pour les avifaunes des îles: l'absence presque complète d'un groupe d'oiseaux (les Galliformes) et la présence de deux (sous-)espèces endémiques, c'est-à-dire l'aigle géant *Aquila chrysaetos simurgh* n. ssp. et la chouette aux pattes longues *Athene cretensis* (Weesie, 1982). La nouvelle sous-espèce est décrite dans la présente étude.

Ces rapaces endémiques ont été trouvés en association avec leur proie supposée principale (aujourd'hui éteinte aussi), c'est-à-dire des souris endémiques pour la chouette et des cerfs endémiques pour l'aigle. Des mammifères endémiques ont été trouvés en association avec des rapaces endémiques dans un grand nombre d'îles, et pas uniquement dans la Méditerranée. Il y a des preuves que la taille des rapaces endémiques s'adapte optimalement à la taille de leurs proies endémiques, spécialement à celle des rongeurs.

Un autre caractère de l'avifaune Pléistocène de Crète est le grand nombre d'espèces de rapaces. Cela paraît être une caractéristique normale des avifaunes fossiles provenant des grottes dans les îles Méditerranéennes et des grottes sur le continent d'Europe. Cependant nous pensons que les conditions écologiques en Crète à l'époque du Pléistocène (spécialement la présence abondante des souris) étaient aussi responsables pour la grande représentation des rapaces.

Ensuite, l'avifaune fossile nous permet de tirer quelques conclusions sur le climat et sur la végétation en Crète pendant la Pléistocène : elles nous démontrent que le climat était plus froid qu'aujourd'hui et que la Crète était largement couverte de forêts.

Finalement, les causes de l'extinction ou de la disparition de la Crète de quelques espèces d'oiseaux de l'avifaune Pléistocène sont discutées.

I.1. INTRODUCTION

The Pleistocene unbalanced endemic mammal fauna of Crete has become better known over the last two decades. During this period Dutch, British, Greek, German and Italian vertebrate paleontologists have collected and studied Pleistocene material. They -and earlier authors- have reported the following taxa :

A pigmy elephant *Elephas creticus* (BATE, 1907) ; a slightly larger elephant *E. creutzburgi* (KUSS, 1965) ; a continental elephant *E. antiquus* (BATE, 1907) ; a pigmy hippo, *Hippopotamus creutzburgi* (BOEKSCHOTEN & SONDAAR, 1965) ; eight species of endemic deer of the genus *Candiacervus* (de Vos, 1979, 1984) ; an endemic otter *Isolalutra cretensis* (SYMEONIDIS & SONDAAR, 1975) ; endemic *Muridae* of the genera *Kritimys* (three species) and *Mus* (two species) (MAYHEW, 1977), an endemic shrew *Crocidura zimmermanni* (REUMER, 1986) and bats.

This mammal fauna is characterized particularly by the absence of large carnivores and the presence of endemic species. Sondaar & Boekschoten (1967) concluded that Crete was an island during the Pleistocene. It was Sondaar (1971, 1977) who drew attention to the unbalanced character of the fauna and developed a model for the effect of insularity on mammal evolution. His model explains why certain kinds of mammals arrive on islands and it explains dwarfism and other evolutionary changes in mammals in terms of adaptations to island environments where there are no large carnivores.

Fossil bird remains have been collected by the Utrecht team from nine localities, which are also the richest ones for mammalian remains. Most fossil birds were found together with the stratigraphically young mammal fauna within the *Mus minotaurus* sub-zone of de Vos (1984). Some localities yielded a few bird fossils, some yielded several dozens. One site (Liko cave) is particularly rich in bird fossils. So far we have collected more than 10,000 specimens from this cave. Initial study of the Cretan material led to the description of an endemic, long-legged owl, *Athene cretensis* (WEESIE, 1982). This bird species is by far the most numerous in our material and is represented by 2639 identified fossil bones, deriving from at least 171 individuals.

An interesting problem, which presented itself from the beginning, was to find out whether or not the low diversity mammal fauna possibly affected the composition of the Cretan avifauna, especially with regard to the number and kind of birds of prey. Furthermore, we should like to know whether other "island characters" can be recognized in the avifauna. Up till now, it has been difficult to reconstruct the climate and vegetation of Pleistocene Crete, since most mammals are endemic. However, the sea is not a barrier for most birds and since the avifauna is varied it is possible to deduce something about the climate and vegetation. The purpose of this study, then, will be to describe the fossil birds and then try to reconstruct some aspects of the climate, vegetation and ecology of Crete in the Pleistocene.

I.2. ACKNOWLEDGEMENTS

I am especially grateful to Dr. C. Mourer-Chauviré (Lyon), Dr. P.Y. Sondaar (Utrecht) and Dr. J. de Vos (Leiden). Dr. P.Y. Sondaar introduced me to vertebrate paleontology and island biology, and Dr. C. Mourer-Chauviré introduced me to avian paleontology. The help of Dr. J. de Vos was indispensable in the accomplishment of the manuscript. I want to thank these people for their continuing support and for the many interesting discussions and pleasant hours we had.

The manuscript has benefited very much from the critical and stimulating comments of Prof. Dr. K.H. Voous (Huizen) and Dr. S.L. Olson (Washington), their help is greatly appreciated.

I thank Dr. C.J.O. Harrison (Tring) and Dr. L.E.M. de Boer (Rotterdam) for helping me with identification problems.

Dr. H. de Bruijn (Utrecht) and Dr. J. Wattel (Amsterdam) are thanked for general support.

I am also greatly indebted to Prof. Dr. P. Marks (Utrecht) for the way he accompanied me during the last part of my studies.

My special thanks to Dr. J.A. Alcover (Ciutat de Mallorca) for his friendly help and the stimulating collaboration.

Prof. Dr. N. Symeonidis (Athens) is thanked for allowing us to collect the Cretan fossils.

Thanks are due to Dr. C. Mourer-Chauviré, Dr. J.A. Alcover, Prof. Dr. H. de Lumley (Paris), Dr. C.J.O. Harrison, Dr. B. Engesser (Basle), Dr. A.T. Clason (Groningen) and Dr. G.F. Mees (Leiden) ,all of whom gave me access to various collections.

I thank Mr. T. van Kolfschoten for helping me operating the computer.

Furthermore, I thank Mr. J.P. Brinkerink for his indispensable help in the field and designing the cover, Mr. J. Luteijn for skilfully drawing the figures and reconstruction and preparing the photoplates, and Mr. W. den Hartog for photographing the material and the figures.

Miss S.M. McNab and Miss E.R.M. Franken are thanked for the correction of the english text.

Mr. H. van Essen kindly corrected the proofs.

I am grateful to Prof. Dr. M.D. Dermitzakis (Athens) for the Greek abstract.

The financial support of the Netherlands Organization for the Advancement of Pure Research (Z.W.O.) is gratefully acknowledged.

Mr. H. van Essen kindly corrected the proofs.

I am grateful to Prof. Dr. M.D. Dermitzakis (Athens) for the Greek abstract.

The financial support of the Netherlands Organization for the Advancement of Pure Research (Z.W.O.) is gratefully acknowledged.

II. LOCALITIES, MATERIAL, AGE, METHODS, TERMINOLOGY AND ABBREVIATIONS

1. LOCALITIES

Map fig. 1 gives the positions of the localities in Crete, from which the fossil bird remains came which are dealt with in the present study. All sites are karstic caves or fissures. Descriptions of these sites are given by Kuss (1970, 1973), Mayhew (1977) and Dermitzakis (1977).

Liko cave, the site that yielded by far the largest number of bird fossils, will be described below (see also Weesie, 1982).

Liko cave

The cave is named after the nearest village, Likotenaria, on the north-west coast of Crete, north-west of Georgioupolis. It is situated in Late Miocene limestones, a few metres above sea level, about ten metres from the coast, in the cliffs of Cape Drepanon. The cave is partly closed off from the outer world by slope breccia, through which a small entrance leads to the interior. It is about eight metres deep, five metres high from ground level and in the middle about four metres wide. Holes of the borer-mussel *Lithophaga lithophaga* in the walls indicate that the cave was once situated below sea level. Remnants of a calcite floor, visible along the walls c. three metres above the present ground level, may indicate that the cave was filled up earlier to a higher level (and, subsequently, was washed out by the sea). A breccious accumulation about three metres before the back of the cave separates it into a front and a rear part. The cavefill consists of red fossiliferous clay about three metres thick. One layer in the rear part (Li-b) consists of calcified sediment. In both parts of the cave several layers have been excavated in levels. The stratigraphical correlation of the upper and middle layers in the front part with those in the rear part is not clear. The lower layers in both parts partially overlap just underneath the breccious accumulation ; in fact they may be a single layer, continuing throughout the cave. In the front part of the cave, the levels have been

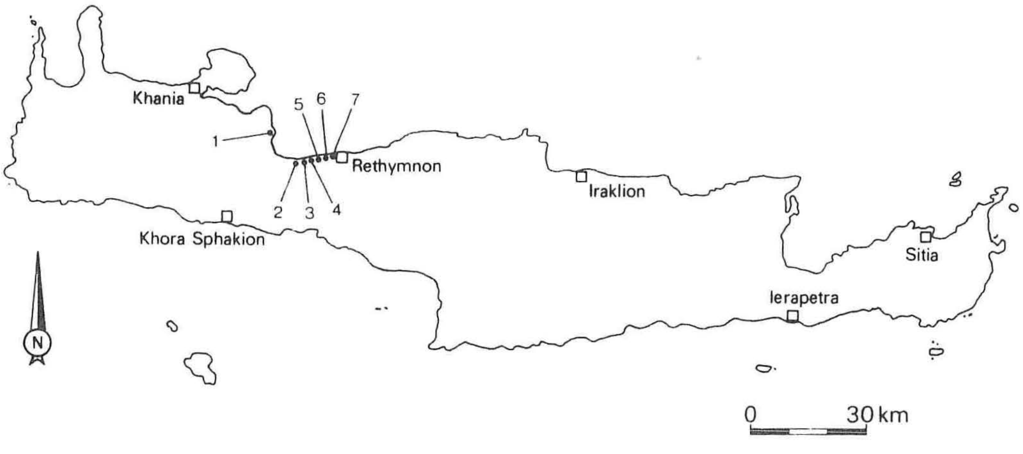


Fig. 1.- Map of Crete, indicating the localities yielding material studied here : 1. Liko cave, 2. Gerani II, IV, 3. Sourida, 4. Mavro Mouri, 5. Simonelli cave, 6. Gumbes B, C, 7. Rethymnon fissure.

denoted by (from above) the codes Li-A, Li-B, Li-C and Li-D, in the rear part by Li-a, Li-b, Li-c, Li-d and Li-e. The code Li-V indicates a layer consisting mainly of shells, occurring only along the walls of the cave in both the front and rear parts. The accidental mixture of material from different levels, e.g. Li-a and Li-b, led to codes such as Li-a/b. The code Li-O is given to material excavated erroneously without any indication of the level of origin.

The avian fossil material is not homogeneously distributed over the different layers. In the front part of the cave layer Li-B contains the most bird fossils, in the rear part the layers Li-a, Li-c and Li-d are the richest avian fossiliferous deposits (see also table 23). A thin layer in Li-c consists of fossil owl pellets (of *Athene cretensis*) composed mainly of bones of small mammals and birds (Mayhew, 1977).

In addition to fossil bird remains, Liko cave yielded remains of four size groups of endemic deer of the genus *Candiacervus* (de Vos, 1979, 1984), an endemic otter *Isolalutra cretensis* (Symeonidis & Sondaar, 1975, Willemsen, 1980), endemic *Mus minotaurus* and bats (Mayhew, 1977), and *Crocidura zimmermanni* (Reumer, 1986).

2. MATERIAL

The preservation of the fossil bones from all localities is, in general, good. Most of the fossils are completely mineralized and brown in colour. Black or white bones occur occasionally.

Most of the fossiliferous clay excavated from Liko cave was washed in the field over a one mm mesh sieve. The residues were sorted later in the laboratory. By this method the larger and more solid bones could be collected intact. Although the material was very carefully collected, it was inevitable that some break age of the fragile bones of small passerine species occurred during the digging up, the transport from the cave and the washing off of the matrix. Many of these bones were already broken before we isolated them. The bulk of the -mostly broken- specifically unidentifiable fossil bird bones consists of small passerine bones. The significance of these for the composition of the identified fossil avifauna will be discussed in the concluding chapter.

The material collected from layer Li-b is for the most part broken and was embedded in hard -calcified- sediment. Treatment in the laboratory with 10% acetic acid was sufficient for proper preparation of the larger bones in this sediment.

All the fossil material is stored in the fossil bird collection of the Institute for Earth Sciences, Utrecht.

3. AGE

The fossil bird material originates from cave and fissure deposits, which cannot be correlated in the field with deposits of established age. Neither fossil mammal nor fossil bird samples from these sites contain collagen, so radiocarbon dating cannot be used. De Vos (1984) gives a biozonation on the basis of many fossil mammal bearing localities, including all sites which yielded fossil birds, except for Gumbes B and C. If we use this biozonation, our localities fall within the youngest sub-zone, namely the *Mus minotaurus* sub-zone. This endemic mouse is probably of Late Pleistocene age and lived on Crete into the Holocene (Mayhew, 1977). It was encountered in large numbers in the upper levels of Liko cave.

4. METHODS

4.1. IDENTIFICATION

A paleontologist who wants to identify fossil bird bones will be confronted with a large number of species, interspecific uniform structures (especially within the Passeriformes) and sometimes considerable intraspecific variation (especially within the non-Passeriformes). Therefore, to identify a bird bone he will need to compare it with as many specimens of as many species as possible within any given family.

In this study comparison of the bones of the non-Passeriformes and (within the Passeriformes) the Corvidae with recent skeletal material available in the museums visited, in most cases yielded sufficient evidence to permit identification on species level. Sometimes, descriptions, measurements or pictures of bones given in literature could also be used for identification. In some cases, the exclusion of species living far beyond the western Palearctic reduced the number of related species with which a fossil bone was compared.

With regard to the remainder of the passeriform material, principally the complete humeri were studied. The humeri and coracoids are (after the cranium and mandibula) the most diagnostic bones in this group. Since the humerus is the most abundant bone in our fossil passeriform material, identification of the complete humeri is sufficient to give a reasonable picture of the small Passeriformes. However, in the future an integrated study of the other material in this group may provide a more complete picture. For some osteologically uniform families within the Passeriformes, such as the Turdidae and Emberizidae, size groups were established on the basis of measurements done on recent humeri. Each of these size groups corresponds to several species, so the groups are in fact species groups. Fossil humeri attributed to these species groups (based on corresponding osteology and size) belong to one of the species in the group, but it is impossible to conclude to which particular species.

To avoid confusion, in this study the term "osteolog(y)(ical)" refers exclusively to the shape of a bone and the term "morpholog(y)(ical)" refers to the shape and the size of a bone.

The comparisons were made in the Collection Regalia, Institut de Paléontologie Humaine (Paris), the Département des Sciences de la Terre, Université Claude Bernard (Lyon), the British Museum (Natural History) (Tring), the Naturhistorisches Museum (Basle), the Rijksmuseum van Natuurlijke Historie (Leiden) and the Biologisch-Archeologisch Instituut (Groningen).

4.2. STATISTICS

Measurements were taken with Vernier calipers and are given in O.1 mm units. The Student's t-test was used to compare some measurements. The symbols used in the tables are : N = number of measured specimens, M = mean of the measurements, Max = maximum, Min = minimum, SD = standard deviation. The probability values for each value of t and the corresponding degree of freedom are derived from statistical tables (Simpson *et al.*, 1960).

The minimum number of individuals of each bird species was counted. The censuses were made by counting the most abundant skeletal element of each species, either the rights or lefts, whichever were most numerous.

5. TERMINOLOGY

A general outline of a bird's skeleton is given in fig. 2.
The osteological terminology used is after Baumel (1979) and Jánossy (1983).

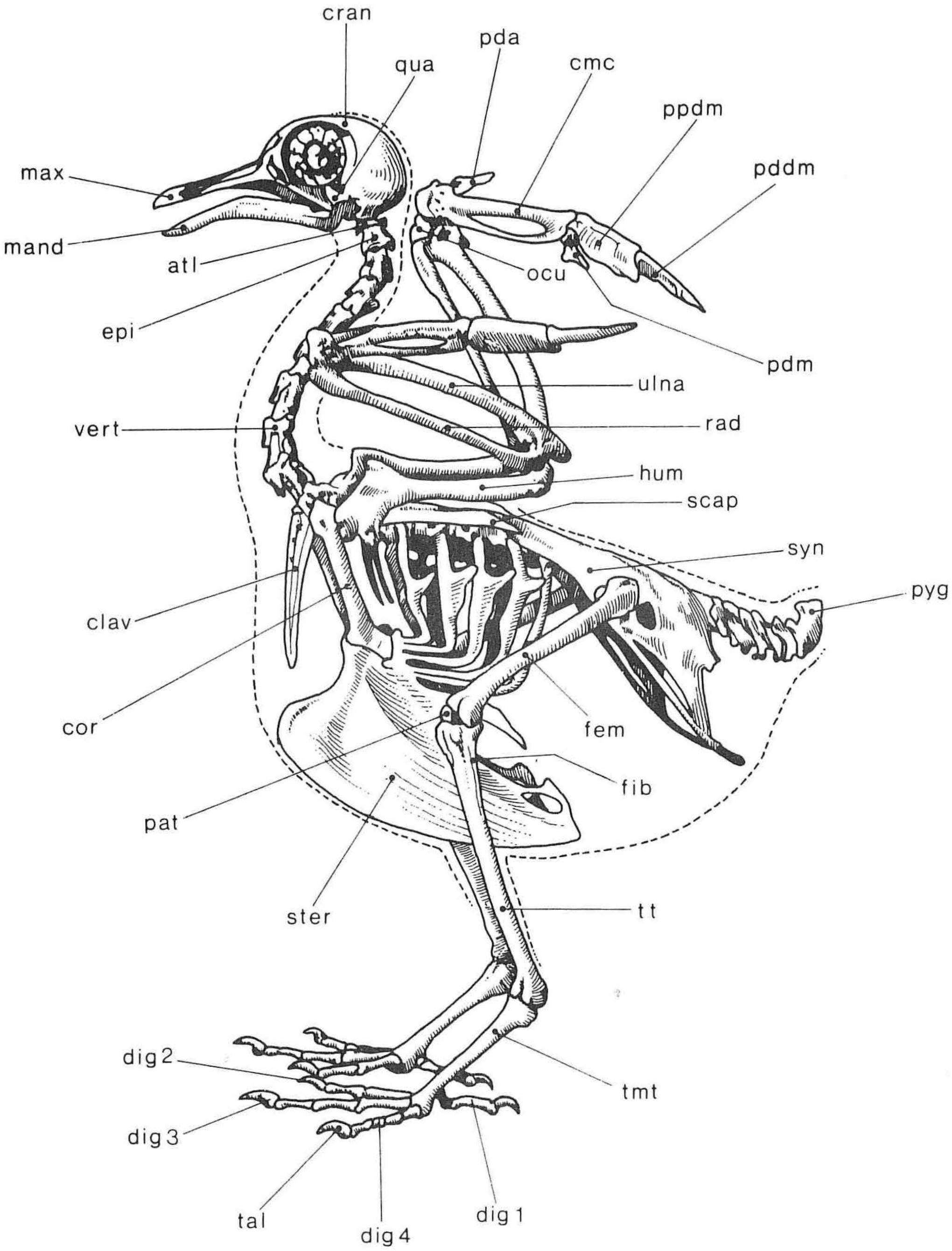


Fig. 2.- Skeleton of a pigeon (after Heilmann, 1927). Abbreviations : see II.6.1.

6. ABBREVIATIONS

6.1. OSTEOLOGICAL ABBREVIATIONS

Ant.	anterior
Atl.	atlas
Clav.	clavicula
Cmc.	carpometacarpus
Cor.	coracoid
Cran.	cranium/cranial
Diaph.	diaphysIS
Dig.	digit
Dist.	distal (is)
Epi.	epistropheus
Fem.	femur
Fib.	fibula
Fragm.	fragment
Hum.	humerus
Mand.	mandibula
Max.	maxilla
Ocu.	os carpi ulnare
Pat.	patella
Pda.	phalanx digiti alulae
Pddm.	phalanx distalis digiti majori
Pdm.	phalanx digiti minoris
Phal.	phalanx
Post.	posterior
Ppdm.	phalanx proximalis digiti majoris
Prox.	proximal (is)
Pyg.	pygostyl
Qua.	quadratum
Rad.	radius
Scap.	scapula
Ster.	sternum
Syn.	synsacrum
Tal.	talon
Tmt.	tarsometatarsus
Tt.	tibiotarsus
Vert.	vertebra

6.2. ABBREVIATIONS OF MUSEUM NAMES

BAI	Biologisch-Archeologisch Instituut (Groningen)
BMNH	British Museum (Natural History) (Tring)
IES	Institute for Earth Sciences (Utrecht)
IPH	Institut de Paléontologie Humaine (Paris)
MNCM	Museu de la Naturalesa de les Illes Balears (Ciutat de Mallorca)
NMB	Naturhistorisches Museum Basel (Basle)
RMNH	Rijksmuseum van Natuurlijke Historie (Leiden)
UCB	Université Claude Bernard (Lyon)
USNM	United States National Museum of Natural History (Washington)

6.3. ABBREVIATIONS OF LOCALITIES

Ge-II, IV	Gerani II, IV
Gu-B, C	Gumbes B, C
Li	Liko
MV	Mavro Mouri
Re	Rethymnon fissure
Sm	Simonelli cave
So	Sourida

III. SYSTEMATICS

General remarks

For most species or species groups, all fossil remains have been listed. However, for some species (those represented in Liko cave by a large number of fossil specimens) only a few characteristic skeletal elements are listed and delineated. In these cases the reader is referred to table 22 for the total number of fossil specimens per layer in Liko cave and to the original copy of the dissertation for an integral enumeration.

No morphological characters are given for those species of which the fossil representatives do not differ significantly from the living members of the species.

For each species an indication is given of the geographical areas in which it was found in the Pleistocene. Unless otherwise indicated, data on the distribution in the Pleistocene were derived from the Catalogue of Fossil Birds of Brodkorb (1962, 1964, 1967, 1970 and 1978).

For the modern distribution and habitat preference of the bird species Voous (1960), Cramp and Simmons (eds.) (1977, 1979, 1982), Cramp (ed.) (1985) and Harrison (1982) were consulted. The recent status of the bird species on Crete is based upon my own observations from 1979 up to 1985 and, mainly from the many reports in the literature, on the papers by Niethammer (1942), Stresemann (1943) and Vallianos (1984).

The sequence of bird species is from the list of recent Holarctic bird species (Voous, 1973, 1977).

Order **PROCELLARIIFORMES** FÜRBRINGER, 1888

Family **PROCELLARIIDAE** (BOIE, 1826) (Petrels and Shearwaters)

Genus *PUFFINUS* BRISSON, 1760

Puffinus puffinus cf. *P. p. yelkouan* (Brünnich, 1764)

(Manx Shearwater)

Matériel : * Gerani II (upper layer) ; Right hum. Ge-II5 (Plate I, fig. 1).

Nowadays, three subspecies of *P. puffinus* live in the western Palearctic : the Atlantic form *P. p. puffinus* , western Mediterranean *P. p. mauretanicus* and eastern Mediterranean *P. p. yelkouan* . Of these subspecies *P. p. mauretanicus* is the largest, followed by (in this order) *P. p. puffinus* and *P. p. yelkouan* (see table 1). We could compare the Cretan fossil humerus only with recent specimens of *P. p. puffinus* . The fossil bone is osteologically identical with its counterpart in this subspecies but it is smaller. In fact, the Cretan fossil humerus is only slightly smaller than its counterpart in *P. p. yelkouan* , so we tentatively attributed it to this form. *P. assimilis* , the only *Puffinus*--species in the western Palearctic which is smaller than *P. puffinus* , is considerably smaller than the latter species (see table 1), so its bones cannot possibly be confused with those of *P. puffinus* .

P. puffinus is known from the Pleistocene of Gibraltar, the Balearics (Alcover *et al.*, 1981), Sardinia, Italy and from some Pleistocene sites in North America.

Recently the species has been a frequent resident in the region. It breeds on the islets surrounding Crete, but probably not on Crete itself.

Manx Shearwater always lives out at sea ; it comes on land exclusively to breed.

Order **PELECANIFORMES** SHARPE, 1891
Family **PHALACROCORACIDAE** (BONAPARTE, 1853) (Cormorants)

Genus *PHALACROCORAX* **BRISSON, 1760**
Phalacrocorax aristotelis (LINN., 1761)
(Shag)

Material : * Liko cave ; Right fem. Li-B801 (Plate II, fig. 1).

Prox. right tt. Li-B802 (Plate II, fig. 2).

In this family the femur and tibiotarsus are characteristically bent. Three species occur in the western Palearctic ; they are clearly distinguishable in size : *P. carbo* is the largest, followed by (in this order) *P. aristotelis* and *P. pygmeus* .

The fossil bones were identified on the basis of comparisons with skeletons of *P. aristotelis aristotelis* . We could not compare them with the Mediterranean subspecies *P. aristotelis desmarestii* . Since this form is only slightly smaller than nominate *aristotelis* (Cramp and Simmons (eds.), 1977), it is probably impossible to seperate these subspecies based upon their size.

The Shag is known from Pleistocene sites in Norway, Scotland, Gibraltar, Monaco, Mallorca (Mourer-Chauviré *et al.*, 1977), Portugal, Italy and Sardinia (Malatesta & Suriano, 1970).

Nowadays the species inhabits most Mediterranean and western Palearctic Atlantic coasts. On Crete it still is a frequent resident ; it lives on high cliffs and rocky coasts.

Order **ANSERIFORMES** (WAGLER, 1831)
Family **ANATIDAE** VIGORS, 1825 (Swans, Geese and Ducks)

Genus *BRANTA* **SCOPOLI, 1769**
cf. *Branta ruficollis* (PALLAS, 1769)
(Red-Breasted Goose)

Material : * Liko cave ; Prox. right hum. Li-D801 (Plate I, fig. 2).

Fragm. of dist. right tmt. Li-0801.

B. ruficollis differs in size from all western Palearctic *Branta* and *Anser* species except for *Anser erythropus* . When comparing the proximal humerus of specimens of *B. ruficollis* and *A. erythropus* , we noted that the tuberculum dorsale in *A. erythropus* is placed more dorsally than in *B. ruficollis* , so that the proximal end of the crista pectoralis bends dorsally towards the tuberculum dorsale in *A. erythropus* , where it is rectilinear in *B. ruficollis* . The Cretan proximal humerus resembles *B. ruficollis* closely in this character and in its general morphology, so we tentatively attribute it to this species.

The Red-breasted Goose is known from the Pleistocene of England (Harrison &

Walker, 1977), possibly Java (Weesie, 1982a) and Hungary. It is known from the Holocene of Egypt as well (Moreau *in* Meinertzhagen, 1930). According to Moreau (1930), a pair of these birds is depicted on a panel of the tomb of Ne-fer-maat (ca 5,000 BP) at Medum, Egypt. The colour pattern of the head and neck in these birds differs significantly from that of the birds known today and suggests the existence of a distinct, formerly more western population, which is now extinct (Voous, pers. comm.). An immature bird was shot at Alexandria in 1874.

Today the species breeds in the west Siberian tundra, and it winters -on fields and steppes- around the Caspian and Black Seas, with Bulgaria and northern Greece as its most south-westerly area.

The presence of *B. ruficollis* in the Pleistocene of England, and possibly Crete and Java, and in the Holocene of Egypt, indicates that the species once had a wider distribution, which shrank for unknown reasons.

Genus *ANAS* LINN., 1758

Anas penelope LINN., 1758

(Wigeon)

Material : * Liko cave ; Dist. right cmc. Li-B804 (Plate II, fig. 3, x 2).

The Wigeon is known from the Pleistocene of Ireland, England, France (Mourer-Chauviré, 1975), Italy, Germany (Jánossy *in* Brunner, 1957, Jánossy, 1965), Czechoslovakia (Jánossy, 1972), Hungary, Israel (Tchernov, 1980) and Azerbaijan.

Nowadays the species has a Palearctic distribution and it is a rare winter visitor and migrant on Crete. It winters on sea coasts, marshes and floodland.

Anas querquedula LINN., 1758

(Garganey)

Material : * Liko cave ; Right cmc. Li-e801 (Plate II, fig. 4, x 2).
* Gumbes C ; Right cor. Gu-C4 (Plate II, fig. 5).

The Garganey is known from the Pleistocene of France, Monaco, Italy, Sardinia (Malatesta & Settepassi, 1954), Czechoslovakia, Hungary and Azerbaijan.

Nowadays the species breeds throughout the Palearctic, and it winters in the south of the Palearctic, and in the Afrotropical and Oriental faunal regions. It is a frequent winter visitor and migrant on Crete, where it possibly breeds. The Garganey occurs near all kinds of fresh water.

Order **ACCIPITRIFORMES** (VIEILLOT, 1816)

Family **ACCIPITRIDAE** (VIEILLOT, 1816) (Hawks, Eagles and Vultures)

Genus *HALIAEETUS* SAVIGNY, 1809

Haliaeetus albicilla (LINN., 1758)

(White-Tailed Eagle)

Material : * Liko cave ; Prox. right cmc. Li-V805 (Plate I, fig. 4).

Vert. Li-c803 (Plate I, fig. 3).

The White-tailed Eagle has been found in the Pleistocene of England, Holland (Junge, 1953), Belgium, Denmark, Norway, Sweden, Finland, Switzerland, Gibraltar, France (Mourer-Chauviré, 1975), Monaco, Italy, Hungary, Yugoslavia, Greece (Weesie, 1984) and Azerbaijan.

Today the species has a Palearctic distribution, but it is no longer found nesting on Crete, or on any other Greek island, probably due to direct extermination by man (Voous, 1960). The White-tailed Eagle lives near fresh water and coasts.

Genus *GYPAETUS* STORR, 1784

Gypaetus barbatus (LINN., 1758)

(Bearded Vulture)

Material : * Liko cave ; Right tmt. Li-B810 (Plate I, fig. 5).
* Mavro Mouri ; Fragm. of dist. right tmt. Mv-1 (Plate I, fig. 6).
* Gerani IV ; Fragm. of syn. Ge-IV1 (Plate I, fig. 8).

Pleistocene sites where the Bearded Vulture has been found are located in Belgium, France, Sardinia (Malatesta & Suriano, 1970), Spain, Monaco, Hungary and China.

Nowadays the species inhabits the Palearctic, Afrotropical and Oriental faunal regions, and it is a rare resident on Crete. The Bearded Vulture is typical for mountains and wind-swept plateaus.

Genus *GYPS* SAVIGNY, 1809

Gyps fulvus (Hablizl, 1783)

(Griffon Vulture)

Material : * Liko cave ; Fragm. of prox. right hum. Li-0803 (Plate I, fig. 9). Fragm. of syn. Li-a803 (Plate I, fig. 12).
* Rethymnon fissure ; Tal. dig. 1 Re-3 (Plate I, fig. 7).

The Griffon Vulture is known from Pleistocene sites in Belgium, Gibraltar, Spain (Villalta, 1964), Monaco, France (Mourer-Chauviré, 1975), Italy, Czechoslovakia, Israel and Azerbaijan.

Today the species lives in the Palearctic, Afrotropical and Oriental faunal regions; it is a frequent resident on Crete. The Griffon Vulture frequents open montane areas and plains.

Gyps melitensis LYDEKKER, 1890

Material : * Liko cave ; Fifth and sixth cervical vertebrae Li-c804, 805 (Plate III, figs. 1 and 2 respectively). Talon dig. 1 Li-0802 (Plate III, fig. 3).
* Simonelli cave ; Talon dig. 2 Sm-1 (Plate III, fig. 4).

The talon from Simonelli cave was collected on a spoil heap at the entrance to the cave.

Lydekker (1890) described this now extinct vulture from the Pleistocene of Malta. On the basis of the close osteological agreement of the fossil cervical vertebrae with those of the recent Griffon Vulture *Gyps fulvus* , Lydekker placed the new from in the genus *Gyps* . The new form closely resembled *G. fulvus* in other osteological characters as well, but it was about one fifth larger. The recent Black Vulture *Aegypius monachus* superficially resembles *G. fulvus* as well, but both species can be distinguished on the basis of small but distinct osteological differences (such as in the cervical vertebrae).

On the grounds of fossil evidence from the Middle Pleistocene of Austria, Jánossy (1974) concluded that *Gyps melitensis* is a mosaic form between *G. fulvus* and *A. monachus* . This is surprising, since *Aegypius* and *Gyps* are generally considered not to be closely related. Some skeletal elements of the Austrian fossil vulture closely resembled their counterparts in *G. fulvus* , while others showed osteological identity with *A. monachus* . This is exactly what we found in our Cretan fossil material.

The two fossil cervical vertebrae from Crete closely resemble their counterparts in recent *G. fulvus* with respect to the characteristics listed by Lydekker (1890), and their general appearance. However, we can add to the description of Lydekker that, in both *G. fulvus* and *A. monachus* , the presence and place of the pneumatic foramen at the base of each processus articularis caudalis varies. Our examination of recent specimens of these species showed that the presence of the foramina is not diagnostic for them, since, contrary to Lydekker's findings, the foramina are not present in all specimens of *G. fulvus* examined, nor are they absent in all specimens of *A. monachus* studied. In fossil vertebra Li-c805, they are on the dorsal (or outer) side of the base of each processus articularis caudalis, whereas in vertebra Li-c804 a single pneumatic foramen is on the ventral (or inner) side of the right processus articularis caudalis. The fossil vertebrae are about one fifth larger than their counterparts in recent *G. fulvus* .

The Cretan talon digit 1 is osteologically identical with that in *G. fulvus* , and the fossil talon digit 2 resembles its counterpart in *A. monachus* closely. Jánossy (1974) found the corresponding talons of the foot in his Austrian material and he noted, apart from the size difference, the same osteological affinities : the talon of the first digit resembled that in *G. fulvus* , whereas the talon of the second digit resembled that in *A. monachus* . The Cretan talon digit 1 is about 18 per cent larger than its counterpart in recent *G. fulvus* , and the talon digit 2 is 30-40 per cent larger than its counterpart in *A. monachus* . Table 2 gives the results of some measurements of the fossil talons and their recent counterparts. The scatter diagrams in fig. 3 illustrate the difference in the size of the fossil vulture and its recent relatives.

So, the osteological peculiarities of the Cretan fossil vulture correspond well with those of remains of *G. melitensis* . This, and the considerably larger size of the Cretan form as compared with recent *G. fulvus* and *A. monachus* , provide conclusive evidence that the Cretan vulture is in fact *G. melitensis* .

We have not yet been able to compare the remains of the Cretan vulture with specimens of *G. rüppelli* , which is the only related species that may have occurred on Pleistocene Crete. However, *G. rüppelli* is about 15 per cent smaller than *G. fulvus* (Cramp and Simmons (eds), 1979), so it cannot possibly be confused with *G. melitensis* , which is considerably larger than any modern Old World vulture.

In the same layers in Liko cave where fossil remains of *G. melitensis* were found, fossils of *G. fulvus* and *A. monachus* were encountered as well. Apparently, the three species lived together on Crete during some time in the Pleistocene. Boule

(1910) also found the three species together in Middle Pleistocene deposits in the caves at Grimaldi (Italy).

Furthermore, *G. melitensis* is known from Pleistocene sites in Hungary (Upper Pleistocene ; Jánossy, 1963), France (Upper Pleistocene ; Boule, 1921 and Mourer-Chauviré, 1975), Austria (Middle Pleistocene ; Jánossy, 1974) and Germany (Middle Pleistocene ; Mourer-Chauviré, 1977).

Genus *AEGYPIUS* SAVIGNY, 1809

Aegypius monachus (LINN., 1766)

(Black Vulture)

Material : * Liko cave ; seventh cervical vertebra Li-D807 (Plate I, fig. 10). Incomplete dist. right ulna Li-V855 (Plate I, fig. 11).

The fossil bones differ conspicuously from their counterparts in the only species with which *A. monachus* could possibly be confused morphologically : *G. fulvus* . In *A. monachus* , the seventh cervical vertebra is shorter and more heavily built than it is in *G. fulvus* . In the distal ulna, the sulcus tendineus at the base of the condylus dorsalis is more conspicuous in *A. monachus* than it is in *G. fulvus* . In the same bone, the cranial margin of the condylus dorsalis is located more obliquely on the longitudinal axis of the bone in *G. fulvus* than it is in *A. monachus* .

The Black Vulture has been found in the Pleistocene of Gibraltar, France, Monaco, Mallorca (Mourer-Chauviré *et al.*, 1977), Sardinia, Germany, Hungary, Israel, Azerbaijan and Mongolia.

Nowadays, the species has a southern Palearctic distribution. It occurs exceptionally on Crete in dry, open and mountainous country.

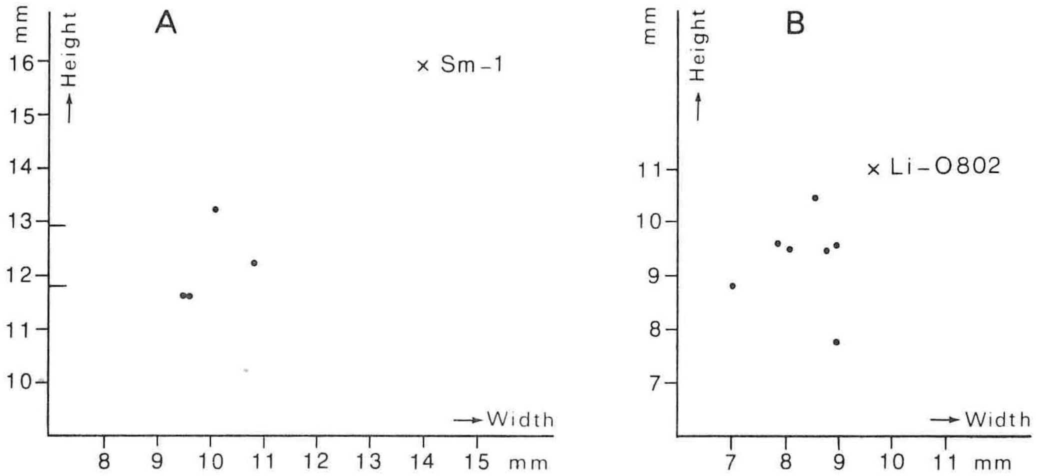


Fig. 3.- Height and width of the articular surface of the talons dig. 2 (A) and dig. 1 (B) of recent *A. monachus* and *G. fulvus* respectively (NMB, IPH, RMNH), and of fossil *G. melitensis* from Crete.

- : Height a.s. of two specimens of *A. monachus* (BMNH).

Genus *ACCIPITER* BRISSON, 1760

Accipiter gentilis (LINN., 1758)

(Goshawk)

Material : * Liko cave , (female :) Dist. left hum. Li-B813 (Plate III, fig. 5). Prox. left ulna Li-a/b801. Left rad. Li-a805 (Plate III, fig. 7). Prox. left rad. Li-a804. Right cor. Li-B812 (Plate III, fig. 6). Right fem. Li-B811 (Plate III, fig. 8). 2 Tal. dig. 2 Li-0804, Li-a/b802.
(male :) Dist. left ulna Li-V806.

A. gentilis and *A. nisus* resemble each other closely in the form of their bones. The size difference between the two species, and the size difference between the sexes in each species, permit identification of each sex in each species. The female of *A. gentilis* is the largest, followed by (in this order) the male of *A. gentilis* , the female of *A. nisus* and the male of *A. nisus* .

The size differences are illustrated by the different lengths of the humeri, given in table 3.

The Goshawk has been found in the Pleistocene of Finland, France (Mourer-Chauviré, 1975), Monaco, Italy, Australia, Czechoslovakia, Hungary, Azerbaijan, Israel (Tchernov, 1980) and California.

Today the species has a Holarctic distribution, it visits Crete exceptionally in winter. The Goshawk is a typical forest species.

Accipiter cf. *A. nisus* (LINN., 1758)

(Sparrowhawk)

Material : * Liko cave ; (female :) Dist. right ulna Li-B816. Right cmc. Li-B814 (Plate II, fig. 6). Dist. right tt. Li-B815 (Plate II, fig. 7). Dist. left tt. Li-A801. Ant. fragm. of left cor. Li-V807. Tal. dig. 1 Li-A803. Tal. dig. 2 Li-A802.
(male :) Left ulna Li-V808 (Plate II, fig. 8). Prox. right ulna Li-D810. Dist. left ulna Li-D809

We have not been able to compare the fossil material with the counterparts in *A. brevipes* , which is the only other western Palearctic member of the genus of the same size as *A. nisus* . Since the fossil bones are morphologically indistinguishable from their counterparts in *A. nisus* , they have been tentatively referred to the latter species.

The Sparrowhawk is known from the Pleistocene of Ireland, France, Spain (Mourer-Chauviré, 1980), Mallorca (Mourer-Chauviré *et al.*, 1977), Corsica, Gibraltar, Germany, Poland, Czechoslovakia, Austria, Hungary, and Israel.

Nowadays the species has a Palearctic distribution, and on Crete it is a rare resident, migrant and winter visitor. The Sparrowhawk lives in open, forested country.

Genus *BUTEO* LACEPEDE, 1799

Buteo buteo (LINN., 1758)

(Buzzard)

Material : * Liko cave ; Prox. right hum. Li-a801 (Plate III, fig. 9). Dist. left rad. Li-D808. Dist. right rad. Li-V803. Prox. right cmc. Li-D803. Right fem. Li-B805

(Plate II, fig. 9). Prox. left fem. Li-B806. Dist. left fem. Li-B807. Dist left tt. Li-D802. Right tmt. Li-a802 (Plate III, fig. 12). Cran. Li-c801 (Plate III, fig. 10). Left scap. Li-V802. Syn. Li-B808 (Plate III, fig. 11). Tal. dig. 4 Li-c802.
* Sourida fissure ; Ant. part of right cor. So-1.

Comparison of recent skeletons has demonstrated that the western Palearctic members of the genus (*B. buteo, B. lagopus* and *B. rufinus*) can hardly be distinguished on the basis of osteological differences. However, there are size differences between these species which enable specific identification of the fossil bones that can be referred to the genus. The bones of *B. buteo* are smaller than those of *B. rufinus* (Mourer-Chauviré, 1975). According to the measurements given by the latter author and our own comparisons, the wing bones and femur in *B. lagopus* are larger than in *B. buteo* (although there is some overlap). The tibiotarsus is about the same size in both species but the tarsometatarsus is smaller in *B. lagopus* than in *B. buteo* . This also results from the measurements made by Otto (1981) and Schmidt-Burger (1982). Since the fossil bones fall well wthin the size range of their counterparts in *B. buteo* , they were all attributed to this species. Subspecific identification is impossible, since the size ranges of most western Palearctic subspecies largely overlap (Cramp and Simmons (eds.), 1979).

The Buzzard is known from the Pleistocene of England, Denmark, Finland, France, Porto Santo (Pieper, 1985), Monaco (Boule, 1927), Italy, Sardinia, Hungary and Israel.

Nowadays the species has mainly a Palearctic distribution; it is a frequent resident and winter visitor to Crete. The Buzzard occurs in all kinds of open woodland.

Genus *AQUILA* BRISSON, 1760

Aquila chrysaetos (LINN., 1758)

(Golden Eagle)

Material : * Liko cave ; Dist. right tt. Li-D804 (Plate IV, fig. 1). Dist. right cmc. Li-D805 (Plate IV, fig. 2). Phal. 1 dig. 3 Li-D806 (Plate IV, fig. 3). Fragm. of syn. Li-d802 (Plate IV, fig. 5)
* Sourida fissure ; Phal. 2 dig. 2 So-2 (Plate IV, fig. 4).

The Golden Eagle is known from the Pleistocene in Scotland, Wales, France, Monaco, Italy, Spain (Villalta, 1964), Mallorca (Mourer-Chauviré *et al.*, 1977), Sardinia, Malta, Germany, Switzerland, Austria, Czechoslovakia, Hungary, Israel, Azerbaijan and from many sites in North America as well.

Nowadays it has a Holarctic distribution and it is a rare resident on Crete. The Golden Eagle frequents rocky montane areas.

Aquila chrysaetos simurgh n. ssp.

Holotype : Left tibiotarsus without proximal extremity Li-V804 (Plate V, fig. 3).
Paratypes : Left femur without trochanter femoris and condylus medialis Li-d801 (Plate V, fig. 2).
Sternum without upper posterior part Li-B809 (Plate IV, fig. 10, Plate V, fig. 1).

Name : After the mythological giant bird of prey Simurgh or Roc.
Type locality : Liko cave, Crete, Greece.
Age : Middle-Upper Pleistocene ?
Diagnosis : Subspecies of *A. chrysaetos* , in its known skeletal elements osteologically closely identical to the western Palearctic subspecies of *A. chrysaetos*, but larger.
Distribution : So far, known only from Crete.
Storage : The material is stored in the fossil bird collection of the Institute for Earth Sciences, Utrecht.

DESCRIPTION AND COMPARISONS WITH RECENT *AQUILA* SPECIES

Nowadays the genus *Aquila* comprises five species in the western Palearctic : *A. chrysaetos, A. heliaca, A. clanga, A. pomarina* and *A. rapax* . Morphologically, *A. chrysaetos* stands apart from its congeneric species. *A. chrysaetos* is larger than *A. heliaca* , which in turn is larger than *A. clanga, A. pomarina* and *A. rapax* . The only African *Aquila* -species that is about the same size as *A. chrysaetos* is *A. verreauxi* . The last two species can be distinguished from each other on the basis of osteological differences.

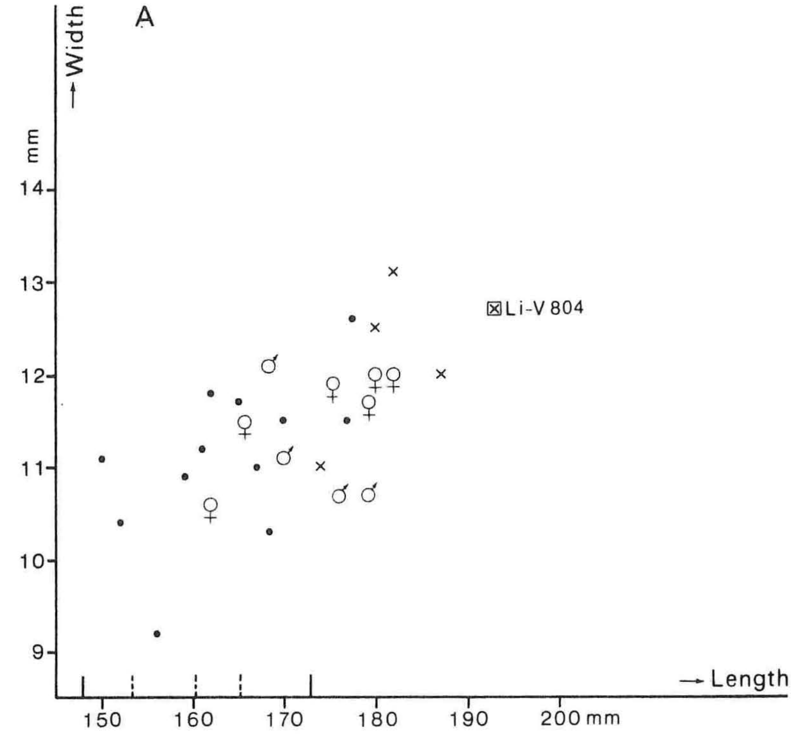
The fossil bones are morphologically identical with their counterparts in recent *A. chrysaetos* , except in size and apart from some small modifications in tibiotarsus and sternum. Yet, the latter differences are small and may be due to individual variation.

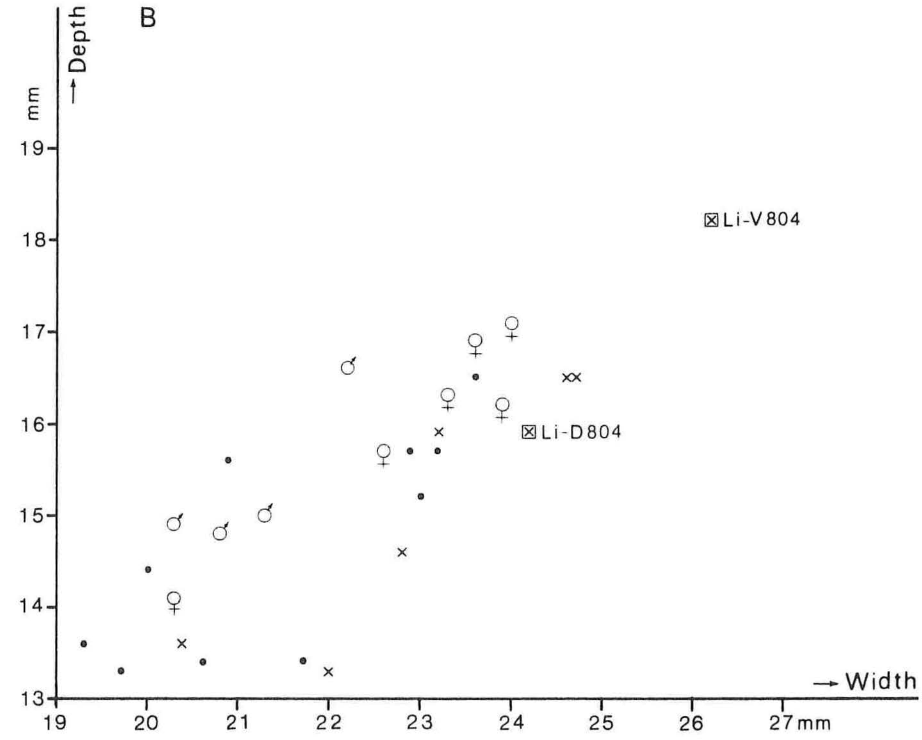
The tuberositas retinaculi musculi fibularis of the fossil tibiotarsus Li-V804 is less well developed than in the specimens of recent *A. chrysaetos* with which it was compared. In the same bone, the pons supratendineus is less delta-shaped than in recent *A. chrysaetos* , so it runs more along the longitudinal axis of the bone. The other morphological characteristics (except the size) of the fossil tibiotarsus are essentially the same as in recent *A. chrysaetos* . The shape of the distal condyles and of the incisura intercondylaris of the tibiotarsus distinguish *A. chrysaetos* from all its western Palearctic congeners. The condyles in *A. verreauxi* are smaller and more compressed in the longitudinal direction of the bone than in *A. chrysaetos* . The fossil tibiotarsus is significantly longer and stouter than in modern *A. chrysaetos* (see table 4 and fig. 4 A and B).

The fossil femur Li-d801 is osteologically identical with, and significantly larger than its counterpart in modern *A. chrysaetos* (see table 4 and fig. 4 C). The femur in *A. verreauxi* differs from the femur in *A. chrysaetos* by having a deeper impressio ansae musculi iliofibularis.

In the fossil sternum Li-B809, the spina externa of the rostrum sterni is smaller than in recent *A. chrysaetos* . However, since the fossil bone is slightly damaged at this spot it is not possible to get a clear picture of the spina externa. The tuberculi labri ventrales of the fossil sternum are better developed and protrude more cranially and laterally than in recent *A. chrysaetos* . The fossil sternum resembles its counterpart in recent *A. chrysaetos* closely in its general shape, more than in the western Palearctic congeners and *A. verreauxi* . It is significantly more heavily built than in recent *A. chrysaetos* (see table 4).

In summary, the fossil bones closely resemble their counterparts in recent *A. chrysaetos* . All measured parameters of the fossil form are significantly larger (from 11 to 20 per cent larger) than the means in recent *A. chrysaetos* , and fall well outside the size range of the western Palearctic subspecies of this species.


A
→ Width
mm
14
13
12
11
10
9
→ Length
150
160
170
180
190
200 mm
☒Li-V 804


B
→ Depth
mm
19
18
17
16
15
14
13
→ Width
19
20
21
22
23
24
25
26
27mm
☒Li-V 804
☒Li-D 804

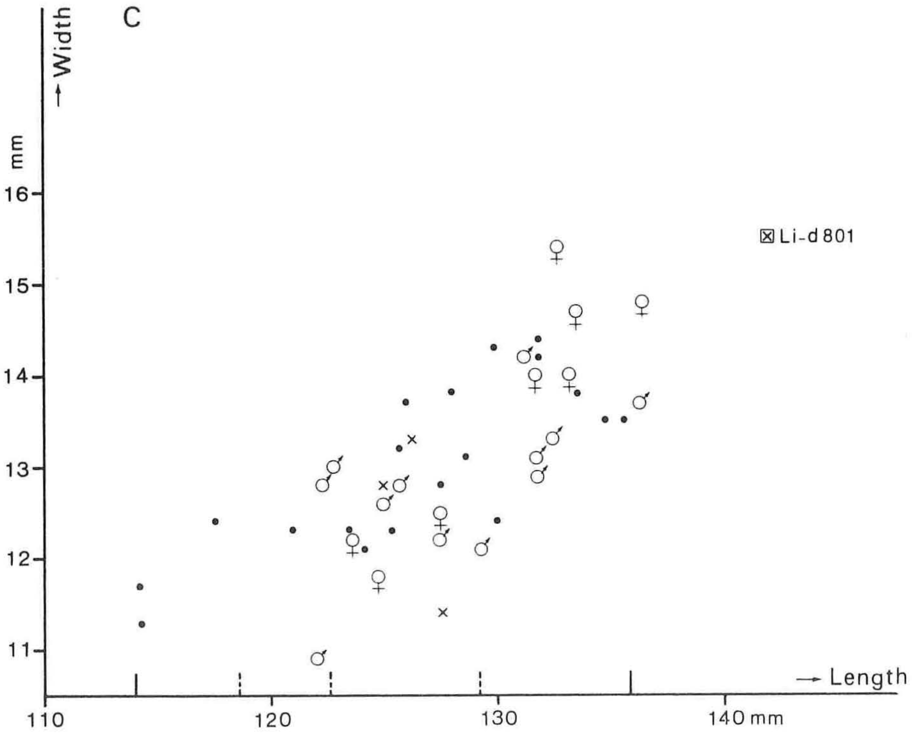


Fig. 4 A.- Length and width in the middle of the tibiotarsus of *A. chrysaetos* and *A. c. simurgh* n. ssp.
Explanation of symbols below.

Fig. 4 B.- Width and depth of the distal tibiotarsus of *A. chrysaetos* and *A. c. simurgh* n. ssp.
C.- Length and width in the middle of the femur of *A. chrysaetos* and *A. c. simurgh* n. ssp.
Explanation of symbols below.

Explanation of symbols used in fig. 4

- ♂ Recent male specimens of *A. chrysaetos*
- ♀ Recent female specimens of *A. chrysaetos*
- • Recent specimens of *A. chrysaetos* of unknown sex
- × Pleistocene specimens of *A. chrysaetos* from Monaco and France
- ⁝ Length of recent specimens of *A. chrysaetos* (Howard, 1932)
- | Minimum and maximum length of a series of Pleistocene specimens of *A. chrysaetos* from Rancho la Brea (Howard, 1932)
- Fossil specimen Li-D804 of *A. chrysaetos*
- ☒ Fossil specimens Li-V804 and Li-d801 of *A. chrysaetos simurgh* n. ssp.

COMPARISON WITH RECENT SUBSPECIES OF *A. CHRYSAETOS*

We know of five recent subspecies of *A. chrysaetos* : *A. c. chrysaetos* and *A. c. homeyeri* in Eurasia, *A. c. daphanea* and *A. c. japonica* in Asia and *A. c. canadensis* in east Siberia and North America (Vaurie, 1965). These subspecies differ in size and less importantly in colour, and within some of the subspecies there is also a slight, clinal size variation. The modern south European subspecies *A. c. homeyeri* is on average smaller than modern north European *A. c. chrysaetos* , but the size difference is not more than a few per cent (Vaurie, 1965). The skeletons of which we used the measurements for comparison with our fossil form were designated mainly as unspecified *A. chrysaetos* . Since most of them are of European origin, they will represent for the most part either *A. c. chrysaetos* or *A. c. homeyeri* . So the values of the means of our measurements will be intermediate between those of *A. c. chrysaetos* and *A. c. homeyeri* . Taking into account the nature of our comparative material and the size difference between *A. c. chrysaetos* and *A. c. homeyeri* , we can conclude that the size difference between *A. c. simurgh* and *A. c. homeyeri* will be greater than the size difference between *A. c. simurgh* and *A. c. chrysaetos* . In addition, the size difference between *A. c. simurgh* and *A. c. chrysaetos* will be smaller than is indicated in table 4. Nevertheless, we consider that this size difference of over ten per cent is sufficient to justify the recognition of the Cretan form as a separate subspecies.

COMPARISONS OF THE CRETAN FOSSIL EAGLE WITH OTHER FOSSIL *AQUILA* SPECIES

Two fossil species of the genus *Aquila* are known (Brodkorb, 1964) : *A. delphinensis* and *A. pennatoidus* from the Upper Miocene of France. *A. delphinensis* resembles modern *A. chrysaetos* in osteology but it is smaller. *A. pennatoidus* is smaller than *A. delphinensis* and its osteology resembles that in modern *Hieraaetus pennatus* (Gaillard, 1939). Consequently, *A. c. simurgh* is larger than both *A. delphinensis* and *A. pennatoidus* .

Mourer-Chauviré (1975) describes the subspecies *A. chrysaetos bonifacti* from the Middle Pleistocene of France. This form is osteologically identical with recent *A. chrysaetos* , but in most of its measurements it is smaller than the latter species, thus smaller than *A. c. simurgh* .

Miller (1911) and Howard (1932, 1947) reported a Golden Eagle from the Pleistocene of Rancho La Brea (California). The humeri and ulnae of that form are on average somewhat larger than in the modern species, the tarsometatarsi are on average shorter and the skull is lower, flatter and broader with a heavier beak and jaw than in the recent form (Howard, 1947). The massive sternum of *A. c. simurgh* suggests the presence of heavier wing bones in this form as well. The Cretan Pleistocene eagle may resemble the Rancho La Brea form in this respect. The femur and tibiotarsus of *A. c. simurgh* are longer and stouter than in recent *A. chrysaetos* . It is unlikely that the tarsometatarsus of *A. c. simurgh* , in contrast to the other leg bones, would be shorter than its counterpart in recent *A. chrysaetos* . So, the leg in *A. c. simurgh* is most probably longer than that in the Californian Pleistocene eagle.

ADDITIONAL OBSERVATIONS

Fossil remains of *A. chrysaetos* found in Liko cave fall entirely within the size range of the modern species. Table 5 shows the locations of the remains of *A. chrysaetos* and *A. c. simurgh* in the different layers in Liko cave. The coexistence of the two forms in the lower layer Li-d and the absence of *A. chrysaetos* in the upper layers of the cave, where *A. c. simurgh* is present, point to the possibility that *A. chrysaetos* was ancestral to *A. c. simurgh* .

The evolutionary history of the latter subspecies will be discussed in the concluding chapter.

Family **FALCONIDAE** VIGORS, 1824 (Falcons)

Genus *FALCO* LINN., 1758

Falco tinnunculus tinnunculus LINN., 1758

(Kestrel)

Material : * Liko cave ; 2 Right hum. Li-a815, Li-o805 (Plate II, fig. 11). Left hum. Li-V813. Prox. left hum. Li-o806. Left ulna Li-a817 (Plate II, fig. 10). Prox. left ulna Li-d805. 2 Right cmc. Li-B820 (Plate II, fig. 12), Li-B821. Prox. left cmc. Li-B822. 2 Dist. left cmc. Li-a818, 819. Right ppdm. Li-B824. Dist. left tt. Li-a816 (Plate II, fig. 13). Dist. right tt. Li-B825. Right cor. Li-a/b804 (Plate II, fig. 14). Ant. fragm. of left cor. Li-a/b805. Left scap. Li-V811. 2 Right scap. Li-V812, Li-D811.

* Gumbes B ; Dist. left cmc. Gu-B17.

Though the fossil material is slightly stouter than in recent *F. t. tinnunculus* , it is osteologically identical with it. Jánossy (1972) described a subspecies *F. t. atavus* from several Lower Pleistocene sites in Central Europe. Mourer-Chauviré (1975) ascribed Middle Pleistocene material from France to this subspecies. *F. t. atavus* is larger than recent *F. t. tinnunculus* , and the former form has a more proximally situated foramen vasculare distale and a somewhat deeper sulcus extensorius in the tarsometatarsus than the latter (Jánossy, 1972). Unfortunately, we have no tarsometatarsus in our Cretan material. Comparison with measurements given by Mourer-Chauviré (1975) showed that biometrically the Cretan form stands more or less in between *F. t. tinnunculus* and *F. t. atavus* . Since the dimensions of our material do not generally exceed the dimensions of recent *F. t. tinnunculus* by more than c. five per cent, and since in 5 cases out of 24 the dimensions of the Cretan material are smaller than in recent *F. t. tinnunculus* , we have attributed the Cretan material to this subspecies of the Kestrel.

The Kestrel is known from Pleistocene sites in Ireland, England, France, Monaco (Mourer-Chauviré, 1975), Madeira (Pieper, 1985), Gibraltar, Mallorca (Florit & Alcover, in press), Corsica, Sardinia (Malatesta & Suriano, 1970), Italy, Switzerland, Czechoslovakia, Hungary, Israel, Azerbaijan and China.

Today it has a Palearctic, Afrotropical and Oriental distribution. The Kestrel is a common resident and migrant on Crete in all kinds of open country.

Falco subbuteo LINN., 1758

(Hobby)

Material : * Liko cave ; Dist. left ulna Li-a807. Dist. left tt. Li-B817 (Plate II, fig.15).

The Hobby is known from the Pleistocene in France, Gibraltar, Italy, Hungary and Israel (Tchernov, 1980).

Its recent range is Palearctic, Afrotropical and Oriental, and it is a rare migrant on Crete. The Hobby inhabits open woodland.

Falco eleonorae GENE, 1839

(Eleonora's Falcon)

Material : * Liko cave ; Left hum. Li-d804 (Plate II, fig. 16). Dist. left ulna Li-B818. Dist. right ulna Li-a814. Prox. right ulna Li-a812. Prox. right rad. Li-a811. Right fem. Li-a809 (Plate II, fig. 17). Dist. right fem. Li-V810. Dist. left tt. Li-a808 (Plate II, fig. 18). Prox. left tt. Li-a810. Prox. right tt. Li-a813. Right tmt. Li-a/b803 (Plate II, fig. 19). Dist. right tmt. Li-d803. 2 Left scap. Li-B819, Li-d883. Right scap. Li-c894.

The fossil bones are osteologically identical with their counterparts in recent *F. eleonorae* , and most of them are slightly larger. In our opinion, this difference in size is too small for the material to be attributed to a new subspecies. In this matter we agree with Harrison (pers. comm.) who considers that generally there must be a size difference of at least ten per cent to justify the erection of a new (sub)species.

Eleonora's Falcon is known from Pleistocene sites in Gibraltar, Mallorca (Florit & Alcover, in press) and Italy.

Nowadays, the species breeds on rocky coasts throughout the Mediterranean and on the north-west coast of Africa, and it winters in East Africa. Eleonora's Falcon also breeds in several colonies on the islets off Crete's north coast.

Falco peregrinus TUNSTALL, 1771

(Peregrine Falcon)

Material : * Liko cave ; Right cmc. Li-a806 (Plate II, fig. 20).
Prox. left cmc. Li-V809.

The Peregrine has been found in the Pleistocene of Ireland, England, France, Gibraltar, Spain (Villalta, 1964), Monaco, Italy, Sardinia (Malatesta & Suriano, 1970), Switzerland, Czechoslovakia, Hungary, Azerbaijan and it is known from several Pleistocene sites in North America as well.

Today it is a cosmopolitan species, and a rare resident on Crete. It occurs in all kinds of open areas.

Order **GALLIFORMES** (TEMMINCK, 1820)
Family **PHASIANIDAE** VIGORS, 1825 (Game Birds)

Genus *COTURNIX* BONNATERRE, 1791

Coturnix coturnix (LINN., 1758)

(Quail)

Material : * Liko cave ; Prox. right hum. Li-A808 (Plate II, fig. 21, x2).

Within the family, the Quail is the smallest species in the western Palearctic.

It is known from Pleistocene sites in Ireland, England, France, Monaco, Spain (Villalta, 1964), Mallorca (Alcover *et al.*, 1981), Corsica, Sardinia, Malta (Fischer & Stephan, 1974); Italy, Germany, Czechoslovakia, Austria, Hungary, Israel, Mongolia and China.

Today the species has a Palearctic, Afrotropical and Oriental distribution. It is a frequent breeding species and migrant on Crete, living in grasslands and fields.

Order **GRUIFORMES** (BONAPARTE, 1854)
Family **RALLIDAE** VIGORS, 1825 (Rails)

General remark

The species identified in this study are distinguishable in size from the other western Palearctic species of the family. Within the family, the largest western Palearctic species is *Porphyrio porphyrio* , followed by (in this order) *Fulica cristata* , *Fulica atra, Gallinula chloropus, Crex crex* and *Rallus aquaticus, Porzana porzana, Porzana parva* and *Porzana pusilla* .

Genus *PORZANA* VIEILLOT, 1816
Porzana porzana (LINN., 1766)
(Spotted Crake)

Material : * Liko cave ; Right hum. Li-d806 (Plate II, fig. 22, x1.5). Prox. right hum. Li-c806. Left cor. Li-c938 (Plate II, fig. 23, x1.5).

The Spotted Crake has been found in the Pleistocene of France (Mourer-Chauviré, 1975), Monaco, Spain (Villalta, 1964, Mourer-Chauviré, 1980), Mallorca (Alcover *et al.*, 1981), Italy, Switzerland, Germany (Jánossy, 1965), Czechoslovakia, Poland, Hungary and Israel.

In recent times, the species has a Palearctic, Afrotropical and Oriental distribution. It is a migrant and winter visitor on Crete in uncertain numbers, and it possibly breeds there. The Spotted Crake lives in thick vegetation near fresh water.

Genus *GALLINULA* BRISSON, 1760
Gallinula chloropus (LINN., 1758)
(Moorhen)

Material : * Liko cave ; Right hum. Li-B826 (Plate VI, fig. 1).

The Moorhen is known from the Pleistocene of Ireland, England, France, Monaco, Italy, Czechoslovakia, Israel, and from several Pleistocene sites in North America, Cuba and Brazil.

Nowadays it is semicosmopolitan. On Crete, it is a frequent resident, migrant and winter visitor, always to be found near fresh water.

Genus *FULICA* LINN., 1758
Fulica atra LINN., 1758
(Coot)

Material : * Gumbes B ; Left cor. Gu-B18 (Plate VI, fig. 2, x1.5).

The Coot has been found in the Pleistocene of Ireland, France (Mourer-Chauviré, 1975), England, Wales, Monaco, Italy, Czechoslovakia (Jánossy, 1983a) and Azerbaijan.

Today the species has a Palearctic and Oriental distribution. It is a rare resident, and a common migrant and winter visitor to Crete. The Coot is always to be found near fresh water.

Order **CHARADRIIFORMES** (HUXLEY, 1867)
Family **GLAREOLIDAE** BREHM, 1831 (Pratincoles and Coursers)

Genus *GLAREOLA* BRISSON, 1760
Glareola species group

This species group comprises *G. pratincola* (LINN., 1766), Collared Pratincole and *G. nordmanni* FISCHER, 1842, Black-winged Pratincole.

Material : * Liko cave ; Prox. right hum. Li-a 877 (Plate II, fig. 24, x1.5).

We could compare our fossil humerus only with the humeri of recent specimens of *G. pratincola* , from which it is indistinguishable in size and osteology. *G. pratincola* and *G. nordmanni* , the only modern representatives of the genus in the western Palearctic, are closely related and they are sometimes treated as races of a single species (Harrison, 1982). The osteology of these species will, most probably, be very similar so the fossil humerus may represent either the one or the other species.

The Collared Pratincole may have been found in the Pleistocene of France (its identification is uncertain) (Mourer-Chauviré, 1975). The Black-winged Pratincole has so far not been reported in the fossil state.

Nowadays, both species have a Palearctic, Afrotropical and Oriental distribution. The Collared Pratincole is a frequent migrant on Crete, the Black-winged Pratincole has only been observed exceptionally on the island. Both species frequent open grassy or sandy areas near fresh or salt water.

Family **SCOLOPACIDAE** VIGORS, 1825 (Waders)

Genus *CALIDRIS* MERREM, 1804
Calidris canutus (LINN., 1758)
(Knot)

Material : * Liko cave ; Dist. left tmt. Li-V814 (Plate VI, fig. 3, x2).

The tarsometatarsus is osteologically identical with the recent specimens of *C. canutus* with which it was compared, and it is slightly stouter. Since the Knot is by far the largest species in its genus, it is easily distinguishable by its size from its osteologically similar congeners.

The species is known from the Pleistocene of England, France (Mourer-Chauviré, 1975) and Italy (Cassoli, 1980).

Today the breeding grounds of the Knot are scattered over the tundras of the Holarctic, it migrates southwards along the Atlantic coasts down to South Africa and Patagonia. It is a very rare winter visitor to the eastern Mediterranean and it frequents flat sandy coasts and river mouths.

Genus *SCOLOPAX* LINN., 1758

Scolopax rusticola LINN., 1758

(Woodcock)

Material : * Liko cave ; Left hum. Li-B827 (Plate VI, fig. 4). Left ulna. Li-a879 (Plate VI, fig. 5). 2 Left cmc. Li-B803, Li-a881 (Plate VI, fig. 7). Right cmc. Li-a880. Right cor. Li-A804 (Plate VI, fig. 10). Right fem. Li-0807 (Plate VI, fig. 8). Dist. right tt. Li-B833 (Plate VI, fig. 6). Right tmt. Li-B835 (Plate VI, fig. 9). Fragm. of syn. Li-B836 (Plate VI, fig. 11). See table 22 for the total number of skeletal elements per layer.

* Gerani IV ; Right cmc. Ge-IV2.

The fossil bones are at the large end of the size range of this species. For the fossil carpometacarpi this is illustrated in table 6. The measurements show that the size variation in the recent Woodcock is large (Fraguglione, 1982).

Large-sized *S. rusticola* is also known from the Pleistocene of France (Mourer-Chauviré, 1975). Furthermore, the species is known from Pleistocene sites in Norway, Belgium and Italy (Fraguglione, 1982), Mallorca (Mourer-Chauviré *et al.*, 1977), Austria (Jánossy, 1974), Ireland, England, Denmark, Germany, Poland, Monaco, Sardinia, Czechoslovakia and Hungary.

Today the species has a Palearctic and Oriental distribution, and it is a frequent winter visitor on Crete in forest areas with thick and preferably humid undergrowth.

Order **COLUMBIFORMES** (LATHAM, 1790) (Pigeons)
Family **COLUMBIDAE** (ILLIGER, 1811)

Genus *COLUMBA* LINN., 1758

In Europe, the genus *Columba* comprises three osteologically uniform species. By its larger size *C. palumbus* , Wood Pigeon ,is easily distinguishable from *C. oenas,* Stock Dove, and *C. livia* , Rock Dove. The last two species differ very little in size so their fossil remains are difficult to identify. Yet, on the basis of small osteological differences in the sternum, ulna and tarsometatarsus as described by Fick (1974) we were able to attribute some of our fossil bones to either *C. oenas* or *C. livia* .

In the sternum of *C. oenas* , the spina externa of the rostrum sterni protrudes more or less parallel to the spina interna, and in *C. livia* the spina externa is more dorsally directed towards the spina interna. On the basis of this difference, we attributed 3 sterna to *C. oenas* , while 3 incomplete sterna were left unidentified.

In the proximal ulna of *C. oenas* , the depressio musculi brachialis begins circa one mm distally from the cotyla ventralis, and the shape of the tuberculum ligamenti collateralis ventralis is roughly an isosceles triangle. In *C. livia* , the depressio musculi brachialis begins further distally from the cotyla ventralis, the triangle of the tuberculum ligamenti collateralis ventralis seems distally cut off and projects into the depressio musculi brachialis. On the basis of this difference, 2 ulnae were attributed to *C. livia* , 6 complete and 8 proximal ulnae to *C. oenas* , and 2 complete, 3 proximal and 11 distal ulnae were left unidentified. The unidentified proximal ulnae show an intermediate position of the depressio musculi brachialis.

In the tarsometatarsus, the crista medialis hypotarsi is more or less square in lateral view in *C. livia* , while in *C. oenas* its distal border runs obliquely distally. On the grounds of this difference 2 tarsometatarsi have been attributed to *C. livia* , 3 to *C. oenas* and the remaining 11 bones of which the hypotarsus is missing were left unidentified.

According to Fick (1974), these are the only osteological differences between *C. oenas* and *C. livia* . It proved impossible for us to detect any other osteological differences between these species, so, on the basis of osteology, we had to leave the rest of our material unidentified. However, since there is a small size difference between the two species we tried to identify part of our material provisionally on the basis of this fact, in order to estimate the ratio in which the two species are represented in our material.

Boule (1910) found that most bones of *C. oenas* are slightly more thick-set than those of *C. livia* . This is confirmed for the humerus by Mourer-Chauviré (1975), who found a significant difference between the widths in the middle of this bone, the mean width in *C. oenas* being larger. For this purpose she used measurements of a sample of recent and fossil humeri identified by Boule.

When comparing recent specimens of *C. oenas* and *C. livia* , we noted that the bones of the wing are generally a little longer and heavier in *C. oenas* , and in *C. livia* the bones of the leg are somewhat larger. The same trend is to be found in the measurements made by Ballmann (1976) and in those of Fick (1974) ; however ,the latter author concluded that both species are equal in size. In table 7 we combine the minimum and maximum values of the measurements of the length of the humerus in recent *C. oenas* and *C. livia* , as given in Fick (1974), in Mourer-Chauviré (1975) and include our own measurements taken in the BMNH.

If we assume that the size ranges as given in table 7 and fig. 5 represent the actual variation in this character of both species, we can provisionally identify our fossil humeri by locating their place on the scale. The ones shorter than 42.9 mm are attributed to *C. livia* (3 specimens), the ones longer than 46.4 mm are assigned to *C. oenas* (3 specimens), and the ones falling in the area of overlap are left unidentified (21 specimens). Table 7 and fig. 5 give the size ranges of the widths in the middle of the humerus of *C. oenas* and *C. livia* . Of the 21 humeri left unidentified in view of their length, we can now, by locating their place on the scale given in fig. 5, provisionally attribute another 11 specimens to *C. oenas* , and 10 specimens remain unidentified. Table 8 summarizes the measurements of the length and the width in the middle of the fossil Cretan humeri attributed to *C. oenas, C. livia* and to either *C. oenas* or *C. livia* .

The above method is only valuable if we assume that there is no size difference between the Pleistocene and the Recent species, and that the size ranges reflect correctly the actual size ranges in *C. oenas* and *C. livia* . In this case, the method was applied only for the humerus, as we had only a few measurements of the other limb bones at our disposal. The method provides an estimate of the ratio in which both species are present in our fossil material. In table 9 the number of the identified ulnae on osteological grounds are compared with the number of the identified humeri on biometrical grounds. In both cases, the ratio in which the two species are present in our material is roughly 7 (*C. oenas*) to 1 (*C. livia*).

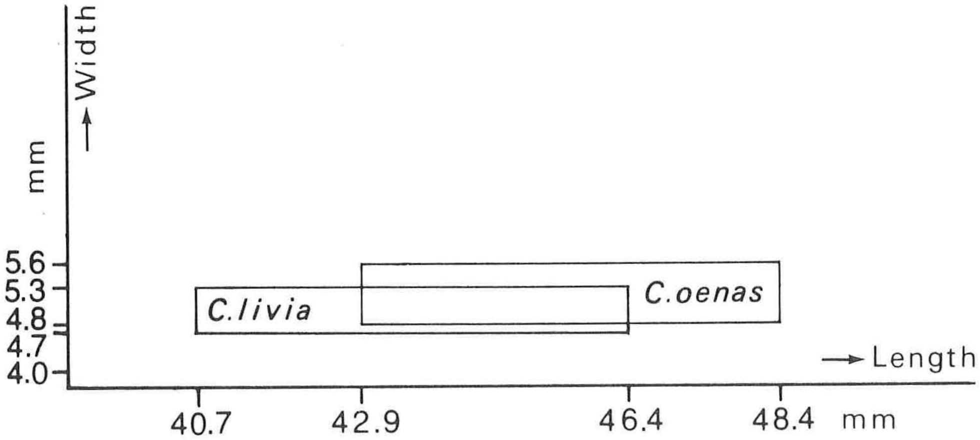


Fig. 5.- Size ranges of the humerus of *C. oenas* and *C. livia* , as observed by different authors. The height of each horizontal bar indicates the range of the width in the middle, and the length of each bar indicates the range of the length of the humerus.

Columba livia GMELIN, 1789

(Rock Dove)

Material : * Liko cave ; 2 Left hum. Li-d809, 812 (Plate VI, fig. 12). Right hum. Li-c810. 2 Right ulnae Li-d826, Li-V817 (Plate VI, fig. 14). Right tmt. Li-d832.
* Gumbes B ; Left tmt. Gu-B19 (Plate VI, fig. 13).

The Rock Dove is known from the Pleistocene in Ireland, England, Portugal, Spain, Mallorca (Alcover *et al.*, 1981), Gibraltar, France, Monaco, Corsica, Sardinia, Italy, Switzerland, Germany, Czechoslovakia, Greece (Weesie, 1984), Israel, Azerbaijan and China.

Today the wild Rock Dove has a Palearctic, Afrotropical and Oriental distribution, and in its domesticated form it has spread all over the world. It is a common resident on Crete in open, rocky and mountainous areas.

Columba oenas LINN., 1758

(Stock Dove)

Material : * Liko cave ; 5 Right hum. Li-B843, 844, 851, Li-c814, Li-d824. 7 Left hum. Li-B837, 838, 840, Li-a833, Li-d810, 822, 823, 2 Right ulnae Li-a836, 837 (Plate VI, fig. 17). 4 Left ulnae Li-a834, 835, Li-a/b810, Li-d818. 3 Prox. left ulnae Li-a838, Li-c817, 818. 5 Prox. right ulnae Li-B823, Li-a/b811, 812, Li-c816, 819. 3 Sterna Li-0810, Li-c/d804, Li-d833. Left tmt. Li-B854. 2 Right tmt. Li-B859 (Plate VI, fig. 16), Li-c829.

* Gumbes C ; 2 Left hum. Gu-C5, 8 (Plate VI, fig. 15).

The Stock Dove has been found in the Pleistocene of England, Spain, Gibraltar, Monaco, France (Mourer-Chauviré, 1975), Italy, Czechoslovakia, Hungary, Poland and Israel.

Nowadays it is distributed within the Palearctic. The species occurs exceptionally on Crete. It is a typical bird of forest and open wooded country.

Unspecified *Columba oenas* or *Columba livia*

Material : * Liko cave ; see table 22 for the number of skeletal elements per layer.
* Gumbes B ; Dist. left hum. Gu-B20. Dist. left ulna Gu-B21.
Prox. left ulna Gu-B22.
* Gumbes C ; Dist. left rad. Gu-C9.
* Gerani II (upper layer) ; Left cor. Ge-II7. Dist. left tmt. Ge-II8.

Columba palumbus LINN., 1758
(Wood Pigeon)

Material : * Liko cave ; Right hum. Li-a859 (Plate VI, fig. 19). Left cmc. Li-c847 (Plate VI, fig. 21). Left cor. Li-a862 (Plate VI, fig. 18). Right tt. Li-B887 (Plate VI, fig. 22). Fragm. of syn. Li-a/b818 (Plate VI, fig. 20). See table 22 for the total number of skeletal elements per layer.
* Gumbes B ; Dist. right tt. Gu-B23.

The Wood Pigeon is known from Pleistocene sites in Ireland, England, Belgium, France, Spain, Gibraltar, Monaco, Italy, Corsica, Switzerland, Austria (Jánossy, 1974), Czechoslovakia, Poland, Hungary, Greece and Israel.

Recently it has a Palearctic and Oriental distribution. It is a frequent resident and winter visitor to Crete, living in forests and open wooded country.

Order **STRIGIFORMES** (WAGLER, 1830)
Family **TYTONIDAE RIDGWAY**, 1914 (Barn Owls)

Genus *TYTO* **BILLBERG**, 1828
Tyto alba (SCOPOLI, 1769)
(Barn Owls)

Material : * Liko cave ; Left hum. Li-b801 (Plate VII, fig. 1). Prox. right ulna Li-B902 (Plate VII, fig. 2). Right cmc. Li-D812 (Plate VII, fig. 4). Dist. left fem. Li-a887 (Plate VII, fig. 5). Dist. right tt. Li-B906 (Plate VII, fig. 6). Right tmt. Li-a890 (Plate VII, fig. 7). Left cor. Li-c858 (Plate VII, fig. 3). Fragm. of cran. Li-d864 (Plate VII. fig. 9). Max. Li-c/d805 (Plate VII, fig. 8). See table 22 for the total number of skeletal elements per layer.
* Gumbes B ; Prox. left cmc. Gu-B25.

Osteologically the fossil material is identical with recent *T. alba* but it is a little larger than most of the recent specimens from the European mainland with which it was compared. Since this size difference does not exceed c. five per cent, we did not place the Cretan Barn Owl in another subspecies. Study of recent skeletal material of *T. alba* shows that size differences of up to c. ten per cent occur between Palearctic forms. Various giant insular forms of the Barn Owl are known ; In the Mediterranean *T. sanctialbani, T. robusta* and *T. gigantea* (Ballmann, 1973, 1976) from the Miocene island of Gargano (Italy) and *T. balearica* from the Plio-Pleistocene of the Balearic islands (Mourer-Chauviré *et al.*, 1980). Other giant barn owls ; *T. pollens, T. ostologa, T. noeli* and *T. riveroi* are known from the Pleistocene of the West Indies (Olson, 1985). All these forms differ by more than c. ten per cent in size from recent *T. alba* and the two largest species, *T. gigantea* and *T. riveroi* , are about twice the size of *T. alba* .

The Barn Owl already had a cosmopolitan distribution during the Pleistocene and is known from Palearctic Pleistocene sites in Ireland, Madeira (Pieper, 1985), Portugal, Spain, France, Monaco, Mallorca (Mourer-Chauviré *et al.*, 1977), Malta (Fischer & Stephan, 1974), Italy, Sardinia (Malatesta & Suriano, 1970), Switzerland, Poland, Greece and Israel. In the New World it has been found in Pleistocene sites in North America, the Bahamas, the Dominican Republic and Brazil.

In Recent times the Barn Owl is almost cosmopolitan. It inhabits all kinds of open country and at present it is a rare resident on Crete.

Family **STRIGIDAE** VIGORS, 1925 (Typical Owls)

Genus *OTUS* PENNANT, 1769

Otus scops (LINN., 1758)

(Scops Owl)

Material : * Liko cave ; (female :) Right hum. Li-B889 (Plate VII, fig. 11, x2). Dist. left hum. Li-c890. 3 Prox. right hum. Li-B890, Li-c891, Li-d853. Dist. left tt. Li-d854 (Plate VII, fig. 14, x2). 2 left tmt. Li-B892 (Plate VII, fig. 12, x2), Li-a864. 2 Dist. left tmt. Li-a865, Li-c849. 2 Prox. right tmt. Li-B893, 894. 2 Dist. right tmt. Li-a866, Li-B895. 3 Phal. 2 dig. 3 Li-B981, Li-a867, Li-c889. Dist. right cmc. Li-a959. (male :) Right tmt. Li-c848 (Plate VII, fig. 13, x2). Left hum. Li-B891 (Plate VII, fig. 10, x2). Dist. right hum. Li-a946.
* Gumbes C ; (female :) Dist. right tt. Gu-C6.

The sexual dimorphism (the female is larger) permits identification of the sex.

The Scops Owl has been found in Pleistocene sites in France (Mourer-Chauviré, 1975), Monaco, Mallorca (Ballmann & Adrover, 1970), Italy, Malta (Fischer & Stephan, 1974), Switzerland, Poland, Hungary, Azerbaijan and Israel.

Nowadays it has a Palearctic, Afrotropical and Oriental distribution. It is a common resident on Crete, inhabiting open forested and cultivated areas with trees.

Genus *KETUPA* LESSON, 1830

Ketupa zeylonensis (GMELIN, 1788)

(Brown Fish Owl)

Material : * Liko cave ; Left hum. without prox. extremity Li-D816 (Plate IV, fig. 6).

Though the fossil bone is slightly worn distally, it agrees closely with its counterpart in a recent specimen of *K. zeylonensis* from Thailand (USNM 429219). It differs from the humerus of modern *Bubo bubo* in that it is smaller, the fossa musculi brachialis is proximally less deeply excavated and the epicondylus ventralis proceeds not so far laterally, so that the width of the distal extremity is also relatively smaller.

So far, the Brown Fish Owl has been recorded only from the Pleistocene in India and Israel (Tchernov, 1980). Today it has a scattered Palearctic and Oriental distribution, with as its most western populations the relicts in Israel and possibly south Turkey, i.e. at least circa 500 km east of Crete. It lives near fresh water in forests and open wooded country, feeding mainly on fish.

Genus *ATHENE* BOIE, 1822

Athene cretensis WEESIE, 1982

(Cretan Little Owl)

This species is thought to be an endemic island form. It differs from is putative mainland ancestor *A. noctua* in having a slightly larger over-all body size, longer wings and a morphologically different humerus, and disproportionately longer legs (Weesie, 1982).

In addition to the material of this species already described, the following fossil bones of this species have been recognized :

Material : * Liko cave :

Right fem. Li-b404 (Plate VII, fig. 15). Dist. right hum. Li-c230 (Plate VII, fig. 16). Syn. Li-c724 (Plate VII, fig. 17). Right tt. Li-B173 (Plate VII, fig. 18). Max. Li-d717 (Plate VII, fig. 19).

See table 22 for the total number of skeletal elements per layer.

* Gumbes B ; Dist. right fem. Gu-B23.

* Gumbes C ; Dist. right hum. Gu-C10. Diaph. of right hum. Gu-C11. Right fem. Gu-C12. Prox. right fem. Gu-C14. Dist. left fem. Gu-C13. 2 Phal. 1 dig. 1.

Genus *ASIO* BRISSON, 1760

Asio flammeus (PONTOPPIDAN, 1763)

(Short-eared Owl)

Material : * Liko cave ; Prox. left ulna Li-d855 (Plate VII, fig. 21).

* Gerani II ; Right tmt. Ge-II6 (Plate VII, fig. 20).

* Rethymnon fissure ; Dist. right fem. Re-4. Prox. left tt. Re-5.

* Gumbes B : Phal. 2 dig. 2 Gu-B24.

* Gumbes C : Phal. 2 dig. 2 Gu-C7.

The Short-eared Owl is known from the Pleistocene in England, Portugal, Spain, France, Monaco, Corsica, Italy, Switzerland, Germany, Austria, Poland, Czechoslovakia, Hungary, Rumania, Azerbaijan and from several sites in North America.

Nowadays the species has a Holarctic and Neotropical distribution, and it is an exceptional migrant on Crete. It inhabits open country with low vegetation and scrub.

Genus *AEGOLIUS* KAUP, 1829

Aegolius funereus (LINN., 1758)

(Tengmalm's Owl)

Material : * Liko cave ; Prox. left hum. Li-a868 (Plate VII, fig. 23). Dist. left rad. Li-c850. Right cmc. Li-c851 (Plate VII, fig. 22). Right cor. Li-a869. Right fem. Li-a870 (Plate VII, fig. 25). Prox. left fem. Li-a871. Dist. left fem. Li-a872. 2 Left tt. Li-B896, 897 (Plate VII, fig. 26). 2 Prox. right tt. Li-B898, Li-c852. Prox. left tt. Li-d856. 2 Dist. left tt. Li-a873, Li-c853. 3 Dist. right tt. Li-a874, 875, Li-d857. 3 Left tmt. Li-B899, Li-c854, Li-d858. 2 Right tmt. Li-a876 (Plate VII, fig. 24), Li-d859. Fragm. of right tmt. Li-d860. Prox. right tmt. Li-e802.

The fossil material is slightly longer and slightly more slender than the recent material with which it was compared. The difference is too small (less than five per cent) for it to be classified as a separate form.

Tengmalm's Owl is known from the Pleistocene in France (Mourer-Chauviré, 1975), Italy (Cassoli, 1980), Poland, Hungary, Czechoslovakia (Jánossy, 1972) and New Mexico. It has also been found in Pleistocene and Paleolithic deposits in Attica, Greece (Mourer-Chauviré, 1981 and pers. comm.).

Recently, the species has a Holarctic distribution. It possibly occurs in northern Greece, but not in the middle and south of this country. Its occurrence as far south as Crete may be the result of climatic changes that occurred during the Pleistocene Glacial periods. The species is a sedentary forest bird, characteristic for coniferous forests, but it also lives in mixed forest.

Order **CAPRIMULGIFORMES** (RIDGWAY, 1881)
Family **CAPRIMULGIDAE** VIGORS, 1825 (Nightjars)

Genus *CAPRIMULGUS* LINN., 1758

Caprimulgus cf. *C. europaeus* LINN., 1758

(European Nightjar)

Material : * Liko cave ; Right hum. Li-B912 (Plate VII, fig. 27).

Though the fossil bone is identical in morphology with its counterpart in *C. europaeus* , it may belong to the closely related *C. ruficollis* . Comparison of these species revealed that they are osteologically indistinguishable. The length of the fossil humerus falls at the smaller end of the size range of the humerus in recent *C. europaeus* (see table 10). Since *C. ruficollis* has slightly longer wings than *C. europaeus* (Cramp (ed.), 1985), we tentatively attributed the fossil humerus to *C. europaeus* .

The European Nightjar is known from Pleistocene sites in England, Italy, Hungary and Czechoslovakia (Jánossy, 1972).

Nowadays it breeds in the Palearctic and it winters in the tropics. It is a rare summer visitor and migrant on Crete. The species frequents open, dry country and pine forests.

Order **APODIFORMES** PETERS, 1940
Family **APODIDAE** (HARTERT, 1897) (Swifts)

General remark

The Apodidae stand osteologically apart from the other Palearctic bird families. The humerus and ulna are extremely short and thick-set, and the sulcus extensorius on the anterior tarsometatarsus runs distally up to the trochleae. *Apus melba* is by far the largest species of the genus in the western Palearctic, followed by (in this order) : *Apus apus* and *Apus pallidus* , *Apus unicolor* , *Apus caffer* and finally by *Apus affinis* .

Genus *APUS* SCOPOLI, 1777
Apus cf. *A. apus*
(Swift = Martinet noir)

Material : * Liko cave ; 2 Right hum. Li-V824, Li-d865. Left hum. Li-d866 (Plate VI, fig. 23, x1.5). Left ulna Li-d867 (Plate VI, fig. 26, X1.5). Left tmt. Li-a893 (Plate VI, fig. 28, x1.5). Dist. left tmt. Li-V801.

The fossil bones are identical in morphology with their counterparts in *A. apus* . However, they might represent the closely related species *A. pallidus* . The latter species is osteologically very similar to the former, and it is about the same size. Since the only specimen of *A. pallidus* studied (in the IPH) is a little larger than most specimens of *A. apus* studied, we tentatively attributed the fossil material to the latter species.

The Swift is known from Pleistocene sites in England, France (Mourer-Chauviré, 1975), Monaco, Corsica, Sardinia, Italy, Hungary, Czechoslovakia (Jánossy, 1972) and Israel.

Today it breeds in the Palearctic and it winters in the Afrotropical and the Oriental faunal regions. The Swift is a common summer visitor and migrant on Crete. It is to be found in villages and towns, on rocky coasts, in the mountains and in forested areas.

Apus melba (LINN., 1758)
(Alpine Swift)

Material : * Liko cave : Right hum. Li-c861 (Plate VI, fig. 24, x1.5). 2 Left ulnae Li-a892 (Plate VI, fig. 25, x1.5), Li-c862. Right cor. Li-B1023 (Plate VI, fig. 27 x1.5). Left cor. Li-B1024.

A. melba has been found in the Pleistocene of Gibraltar, France (Mourer-Chauviré, 1975, 1980), Mallorca (Ballmann & Adrover, 1970), Italy, Sardinia, Hungary, Czechoslovakia (Jánossy, 1972) and Israel.

Today the species has a Palearctic, Afrotropical and Oriental distribution. It is a common summer visitor and migrant on Crete, living on rocky coasts and in the mountains.

Order **PICIFORMES** (MEYER and WOLF, 1810)
Family **PICIDAE** VIGORS, 1825 (Woodpeckers)

Genus *DENDROCOPOS* **KOCH, 1816**
Dendrocopos leucotos (BECHSTEIN, 1803)
(White-backed Woodpecker)

Material : * Liko cave ; Right fem. Li-B980 (Plate VIII, fig. 2).
* Gumbes C ; Left hum. Gu-C24 (Plate VIII, fig. 1).

D. leucotos is distinguishable from the other woodpeckers in the western Palearctic by its size : it is larger than the other *Dendrocopos* - and *Picoides* -species in the region, and it is smaller than the *Picus* -and *Dryocopos* -species.

The White-backed Woodpecker is known from the Pleistocene in France (Mourer-Chauviré, 1975), Austria and Czechoslovakia.

In Recent times the species has a Palearctic distribution. It is a rare resident in northern Greece but it is absent from the south Aegean islands. The White-backed Woodpecker inhabits thick mixed and broad-leaf forest.

Order **PASSERIFORMES** (LINN., 1758)

General remarks

It is well known that the Passeriformes are a large and osteologically uniform order. Some families are morphologically clearly distinguishable from the other families in the order (in this study the Alaudidae, the Hirundinidae, the Prunellidae and the Corvidae) but other families are very similar to one another (in this study the Muscicapidae-Turdidae-Sturnidae and the Fringillidae-Emberizidae). Within the families, morphological similarities are even greater. If one studies the morphology of a passeriform bone very carefully, taking into account the size ranges of the species to which it may belong, one does not necessarily arrive at a definite identification. The most diagnostic passerine elements are the skull and the parts of the bill, but they are scarcely represented in our material.

The availability of recent comparative osteological material is another problem. Not all the western Palearctic passeriform species are present in the collections of the museums visited.

Consequently, the identified species have often been given a cf. identification status. Jánossy (1983) gives identification keys and morphological characteristics for the humerus in passeriform families and species. This work has helped me greatly to confirm or correct my own identifications.

In all, we have collected ca 7,000 fossil passeriform bones on Crete. The most numerous skeletal element in this bulk is the humerus (ca 1,100 specimens). Since the osteological characteristics of the humerus are more conspicuous than those of the other wing and leg bones, we have studied principally the undamaged humerus material of this group. The fossil material belonging to the Corvidae is larger and has been studied in its entirety.

Family **ALAUDIDAE** (VIGORS, 1825) (Larks)

Genus *CALANDRELLA* KAUP, 1829

cf. *Calandrella brachydactyla* (LEISLER, 1814)
(Short-toed Lark)

Material : * Liko cave ; Left hum. with worn distal extremity Li-d868 (Plate IX, fig. 1, x2).

The humerus in *C. brachydactyla* is smaller than in the other western Palearctic lark species, and it has a somewhat deeper fossa tricipitalis (Jánossy, 1983).

The Short-toed Lark is known from the Pleistocene in France and the Ukraine.

Nowadays it has a Palearctic, Afrotropical and Oriental distribution. It is a frequent summer visitor and migrant on Crete in open, dry, often rocky or sandy country.

Family **HIRUNDINIDAE** VIGORS, 1825 (Swallows and Martins)

Genus *HIRUNDO* LINN., 1758

cf. *Hirundo daurica* LINN., 1771
(Red-rumped Swallow)

Material : * Liko cave ; 2 Left hum. Li-c863 (Plate IX, fig. 2, x3), Li-c864. Right hum. Li-B913.

The humerus in the Hirundinidae is charactrized by its thick-set form. The fossil humeri are larger than in *Ptyonoprogne obsoleta, Delichon urbica* and *Riparia riparia* , and they are comparable in size to *Hirundo rustica* and *H. daurica* . Though the fossil bones are osteologically indistinguishable from their counterparts in both these species, they are closer in size to *H. daurica*, in which the humerus is a little more heavily built than in *H. rustica* . Even so, the fossil bones might belong to *Ptyonoprogne rupestris* , but we were unable to compare our material with this species.

The Red-rumped Swallow has been found in the Pleistocene of France, Monaco (Mourer-Chauviré, 1975), Italy and Israel.

Nowadays it has a Palearctic, Afrotropical and Oriental distribution. It is a frequent migrant and a rare summer visitor to Crete, living in open country, on coasts and in mountains.

Family **PRUNELLIDAE** RICHMOND, 1908 (Dunnocks)

Genus *PRUNELLA* VIEILLOT, 1816

Prunella collaris (SCOPOLI, 1769)
(Alpine Dunnock)

Material : * Liko cave ; 6 Left hum. Li-a901 (Plate IX, fig. 3, x2), Li-a902-904, Li-b803, 807. 3 Right hum. Li-0816, Li-B1017, Li-a900.

P. collaris is larger than the only other western Palearctic member of the family, *P. modularis* .

The Alpine Dunnock has been found in the Pleistocene of France, Italy, Czechoslovakia and the south Aegean island of Karpathos (Greece) (Weesie, 1984).

In Recent times it lives scattered throughout the southern Palearctic, and it is a rare resident on Crete. It inhabits rocky areas above the tree line, descending in wintertime to lower rocky country, though rarely to sea-level.

Family **TURDIDAE** BONAPARTE, 1838 (Thrushes, Chats, Wheatears and Robins)

General remarks

The western Palearctic Turdidae can be divided into two size groups : on the one hand the small *Saxicola-, Phoenicurus-, Oenanthe-, Erithacus* - and *Luscinia* -species and on the oher hand the larger *Monticola-, Turdus* - and *Zoothera* -species. Jánossy (1983) gives some morphological characteristics of the family and its members. Western Palearctic Turdidae species such as *Cercotrichas galactotes, Irania gutturalis, Cercomela melanura* and some *Oenanthe* -species belong to the smaller size group but culd not be studied in the museums visited. Therefore, the fossil specimens tentatively attributed to one of the species in this size group, have still to be compared with these species.

Erithacus - and *Luscinia* -species

The genera *Erithacus* and *Luscinia* stand apart from the genera *Saxicola, Phoenicurus* and *Oenanthe* osteologically in that they have a less deeply excavated fossa tricipitalis in the proximal humerus.

Genus *ERITHACUS* CUVIER, 1800

cf. *Erithacus rubecula* (LINN., 1758)

(Robin)

Material : * Liko cave ; 6 Left hum. Li-a895, 896, Li-a/b845, Li-c905, Li-d869, 887. 4 Right hum. Li-V841, Li-a/b846 (Plate IX, fig. 4, x3), Li-a/b847, 848.

The humeri in *E. rubecula* (which is the only species in the genus) are on average smaller than in the western Palearctic *Luscinia* -species, although there is an overlap. Table 11 gives the measurements of the humeri in recent *E. rubecula, L. luscinia* and *L. megarhynchos* . Jánossy (1983) gives some osteological differences between these species.

The fossil humeri are osteologically identical with their counterparts in modern *E. rubecula* and fall within the size range of this species too ; their measurements are given in table 11.

The Robin has been found in Pleistocene sites in Ireland, England, France, Mallorca (Alcover *et al.*, 1981), Corsica, Italy, Denmark, Hungary, the Ukraine and Israel.

In Recent times it has a Palearctic distribution and is a common winter visitor and migrant on Crete ; it inhabits montane forest areas.

Saxicola-, Phoenicurus- and *Oenanthe* -species

Jánossy (1983) lists some osteological differences between the genera *Phoenicurus* and *Oenanthe* . Size differences between the various species of these genera exist and help to identify them ; they will be dealt with in the following section. Tables 12 and 13 give the length and width in the middle and the size ranges of the humeri of some species in this group. *O. leucura* is the largest species, followed by (in this order) *O. oenanthe, O. hispanica* and *O. deserti* . The size ranges of the humeri of *O. hispanica* and *P. ochruros* overlap considerably, but the humerus of the latter species is on average shorter and is a little more slenderly built than that of the former species. The humeri in *P. phoenicurus* are on average smaller than in *P. ochruros* , and they are more stoutly built than in *P. moussieri* . The size ranges of the humeri of *P. phoenicurus* and *S. rubetra* overlap largely, and *S. torquata* is the smallest species in this group.

Genus *OENANTHE* VIEILLOT, 1816

Oenanthe cf. *O. hispanica* LINN., 1758

(Black-eared Wheatear)

Material : * Liko cave ; 4 Left hum. Li-B914 (Plate IX, fig. 5, x3), Li-a894, 897, 960. 2 Right hum. Li-a899, 961.

We have not been able to compare the fossil material with more than one specimen of *O. deserti* . Since the fossil humeri are identical in osteology with and fall within the size range of modern *O. hispanica* , they have been tentatively attributed to this species. Their measurements are given in table 12.

As far as we know, the Black-eared Wheatear has not yet been recorded from the Pleistocene.

Today it has a Palearctic and Afrotropical distribution. It is a common summer visitor and migrant on Crete, inhabiting open, dry and stony country.

Monticola- , Turdus- and *Zoothera* -species

The *Monticola-* species stand apart from the *Turdus* - and *Zoothera* -species osteologically in that they have the crus dorsale fossae completely separating the fossa tricipitalis and the fossa pneumoanconaea (Jánossy, 1983) and have a more dorso-ventrally placed tuberculum ventrale.

Z. dauma is far larger than the largest *Turdus* -species, where as it is osteologically similar.

Genus *MONTICOLA* BOIE, 1822

Monticola cf. *M. solitarius* (LINN., 1758)

(Blue Rock Thrush)

Material : * Liko cave ; Right hum. Li-c906 (Plate IX, fig. 6, x2). Left hum. Li-V842.

M. solitarius is osteologically indistinguishable from *M. saxatilis* , which is the only other species in the genus in the western Palearctic. Although the size ranges of these species overlap, *M. saxatilis* seems to be slightly smaller (see table 14). The fossil humeri are osteologically identical with their counterparts in the recent *Monticola*-species, and since their dimensions exceed those of recent *M. saxatilis* , but fall within the size range of the humerus of *M. solitarius* (as far as we know it, see table 14), they were tentatively attributed to the latter species.

The Blue Rock Thrush is known from the Pleistocene of France.

In Recent times it has a southern Palearctic, Afrotropical and Oriental distribution. The species is a frequent resident on Crete, inhabiting rocky areas.

Genus *ZOOTHERA* VIGORS, 1832
cf. *Zoothera dauma* (LATHAM, 1790)
(White's Thrush)

Material : * Liko cave ; 5 Right hum. Li-B986, Li-a962, Li-c907, 908, Li-d888 (Plate IX, fig. 7, x2). 2 Left hum. Li-B987, Li-c910. 2 Prox. left hum. Li-c909, Li-B989. Worn left hum. Li-B988.

We could compare the fossil humeri with only one, incomplete recent specimen in the IPH. The proximal half of this humerus is morphologically identical withthe fossil specimens, and the distal half of it is missing. The lengths and widths in the middle of the fossil humeri tentatively attributed to White's Thrush are given in table 15.

White's Thrush has been found in the Pleistocene of Monaco, Italy and Corsica, and possibly France (Mourer-Chauviré, 1975).

In Recent times it lives in the eastern Palearctic and Oriental faunal region, it is absent in Western Europe. The different range of this species in the Pleistocene was possibly associated with a Glaciation. White's Thrush is a typical forest bird.

Turdus - species

The humerus in the *Turdus*- (and *Zooohera* -) species can be distinguished from that in the other passeriform genera by the confluent fossa tricipitalis and fossa pneumo anconaea, partly separated by a reduced crus dorsale fossae (Jánossy, 1983). Within the genus, the species are osteologically very uniform, but they differ in size. On the basis of our measurements of the length of the humerus of modern western Palearctic *Turdus*-species, we can divide these species into four size groups (see fig. 6). On the basis of its length, each fossil humerus, attributed to the genus on osteological grounds, has been placed in one of these size groups. The only modern western Palearctic *Turdus*-species not included is *T. ruficollis* , so all the fossil humeri, placed in one of the size groups, have still to be compared with this species.

Genus *TURDUS* LINN., 1758
Turdus cf. *T. iliacus* LINN., 1766
(Redwing)

Material : * Liko cave ; 3 Left hum. Li-B990 (Plate IX, fig. 8, x2), Li-a963, Li-a/b850. 2 Right hum. Li-a964, Li-a/b851.

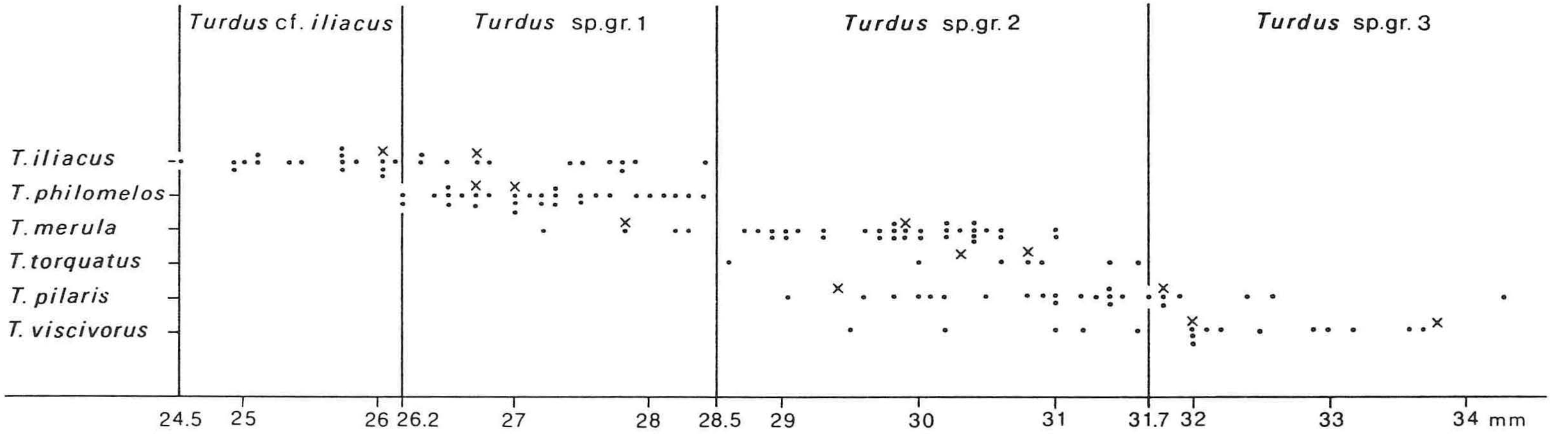


Fig. 6.-- Length of the humerus of some modern *Turdus* -species (IPH, BMNH, NMB, RMNH, UCB). Minimum and maximum values of the measurements of Jánossy (1983) are indicated by a cross.

The fossil *Turdus* -humeri that are shorter than 26.2 mm (see fig. 6) have been tentatively attributed to this species, since it is the smallest *Turdus* -species present in the western Palearctic.

The Redwing is known from the Pleistocene of Ireland, England, Belgium, Portugal, France, Monaco, Spain (Mourer-Chauviré, 1980), Mallorca, Italy, Switzerland, Czechoslovakia, Austria, Hungary, Rumania, the Ukraine and the Georgian SSR.

Nowadays the Redwing has a Palearctic distribution ; it winters in the southern part of its range, although it is unknown at present on Crete. The species frequents open forested country.

Turdus species group 1

The fossil *Turdus* - humeri with a length of between 26.2 and 28.5 mm were attributed to this species group, which comprises at least one of the following species : *T. iliacus*, Redwing, *T. philomelos,* Song Thrush, and *T. merula* , Blackbird (see fig. 6).

Material : * Liko cave ; 22 Left hum. Li-B991, 992, Li-a965-972, Li-a/b852-856, Li-a/b857 (Plate IX, fig. 9, x2), Li-a/b858-860, Li-c911, 912, Li-c/d809. 26 Right hum. Li-O829-831, Li-V843, Li-B993-997, Li-a973-977, Li-a/b861-867, Li-d889, Li-c913-915, Li-e805.
* Gumbes B ; 2 Left hum. Gu-B40, 41.

Turdus species group 2

The fossil *Turdus* -humeri with a length of between 28.5 and 31.7 mm were attributed to this species group, which comprises at least one of the following species : *T. merula* Blackbird, *T. torquatus* Ring Ouzel, *T. pilaris* Fieldfare and *T. viscivorus* Mistle Thrush (see fig. 6).

Material : * Liko cave ; 42 Left hum. Li-O832, 833, Li-V844-848, Li-B998-1008, Li-a978, 979, 981, Li-a980 (Plate IX, fig. 10, x2), Li-a/b868-873, Li-c916-926, Li-c/d810, Li-d890, 891. 34 Right hum. Li-O834-836, Li-V849, 850, Li-B1009-1015, Li-a982-984, Li-a/b874-880, Li-c927-931, Li-d892-898.

Turdus species group 3

The fossil *Turdus* -humeri with a length of over 31.7 mm were attributed to this species group, which comprises at least one of the following species : *T. pilaris,* Fieldfare, and *T. viscivorus* , Mistle Thrush (see fig. 6).

Material : * Liko cave ; 3 Right hum. Li-B1016, Li-c932 (Plate IX, fig. 11, x2), Li-d899.

The *Turdus* -species which are possibly present in our material ; *T. philomelos, T. merula, T. viscivorus, T. pilaris* and *T. torquatus* have been recognized from Pleistocene sites all over Europe.

In Recent times, all of these species have been recorded from Crete except the

Ring Ouzel *T. torquatus* . The Blackbird, *T. merula* , is a common resident on Crete, whereas the Mistle Thrush, *T. viscivorus* , and the Fieldfare, *T. pilaris* , are rare winter visitors. The Song Thrush, *T. philomelos* , is a common winter visitor to Crete. All these species indicate fairly open forested country.

Family **MUSCICAPIDAE** VIGORS, 1825

Genus *MUSCICAPA* **BRISSON, 1760**

cf. *Muscicapa striata* (PALLAS, 1764)
(Spotted Flycatcher)

Material : * Liko cave ; Right hum. Li-a898 (Plate IX, fig. 12, x3).

The fossil humerus is osteologically indistinguishable from its counterpart in *M. striata* and is at the large end of the size range in this species (see table 16). *M. striata* is the largest western Palearctic species in its family. It is distinguishable from Turdidae-species of about the same size (such as the *Phoenicurus-* and *Saxicola-* species) in having the fossa tricipitalis of the proximal humerus less deep than the fossa pneumoanconaea.

The Spotted Flycatcher has been found in the Pleistocene of Mallorca (Alcover *et al.*, 1981).

In Recent times, the species has a Palearctic, Afrotropical and north west Oriental distribution. On Crete it is a rare summer visitor and a frequent migrant, living principally in forested country.

Family **CORVIDAE** VIGORS, 1825 (Jays, Magpies and Crows)

General remark

This osteologically homogeneous family comprises 13 species in the western Palearctic. It is possible to arrange these species according to their size. The largest species is *Corvus corax* , followed by (in this order) the *Corvus rhipidurus* and *Corvus ruficollis* size group, then by the *Corvus corone* and *Corvus frugilegus* size group, then by the *Pyrrhocorax pyrrhocorax, Pyrrhocorax graculus* and *Corvus monedula* size group, then by the *Pica pica, Garrulus glandarius* and *Nucifraga caryocatactes* size group, and finally by *Cyanopica cyanus* and *Perisoreus infaustus* . These (groups of) species can be identified according to the proportions of their bones. Jánossy (1954, 1962) reported proportional differences in the humerus and femur of several of the above listed species.

In addition to the size differences, there are also osteological differences between the various species. These facilitate the identification of these species, especially in cases where size differences are marginal.

Genus *GARRULUS* **BRISSON, 1760**

Garrulus glandarius (LINN., 1758)
(Eurasian Jay)

Material : * Liko cave ; Left hum. Li-a908 (Plate VIII, fig. 3). Left ulna Li-B922

(Plate VIII, fig. 4). Right cmc. Li-B985 (Plate VIII, fig. 5). Left fem. Li-a915 (Plate VIII, fig. 6). Left tmt. Li-O821 (Plate VIII, fig. 8). See table 22 for the total number of skeletal elements per layer.

* Gerani II (upper layer) ; Prox. left hum. Ge-II9.
* Mavro Mouri ; Dist. left tt. MV-2.
* Gumbes B ; Prox. right hum. Gu-B27. Dist. right ulna Gu-B39. Prox. right ulna Gu-B28. Right tt. Gu-B29 (Plate VIII, fig. 7). Prox. left tt. Gu-B30. Dist. left tt. Gu-B31. Dist. right tt. Gu-B32. Dist. right tmt. Gu-B33.
* Gumbes C ; Right hum. Gu-C15. Prox. right hum. Gu-C16. Dist. left hum. Gu-C17. Dist. right tt. Gu-C18. Dist. left tmt. Gu-C19. Prox. right tmt. Gu-C20.

• Comparison of the fossil material with recent Corvidae-species

The bones in modern *G. glandarius* are on average smaller than in *P. pica*, they are about the same size as in *N. caryocatactes* (Jánossy, 1954) and they are much larger than in *C. cyanus* . In palmar view, the proximal epiphysis of the humerus in *G. glandarius* differs from its counterpart in *P. pica* (Jánossy, 1954, fig. 17). In anconal view, the distal end of the crus dorsale fossae of the proximal humerus is placed more towards the axis of the bone in *P. pica* than in *G. glandarius* . In comparison with its counterpart in *N. caryocatactes* , the fossa olecrani of the distal humerus of *G. glandarius* is better developed and it is situated more proximally and more caudally. In the proximal humerus of the latter species, the fossa tricipitalis is smaller and the crus dorsale fossae is lower than in *N. caryocatactes* . The crista bicipitalis bends more sharply ventrally and the crista pectoralis ends further distally in *G. glandarius* than in *N. caryocatactes* .

In addition to showing a close general resemblance with their counterparts in *G. glandarius* , the fossil humeri show the above mentioned osteological characteristics of *G. glandarius* so they were attributed to this species, though they are smaller. Table 17 gives the measurements of the lengths of the humeri in both the modern and the fossil form. The length of the fossil humeri is 91.5 per cent of the length in modern *G. glandarius* , and the Student's t-test indicates a significant difference between the two forms. The modern skeletons of which we used the measurements were designated mainly as unspecified *G. glandarius* .

The leg bones in *G. glandarius* are distinctly smalle rhan those in *P. pica* , and they are more heavily built than those in *N. caryocatactes* . The fossil femora are morphologically identical with those in recent *G. glandarius* , and the ratio between their width in the middle and their total length corresponds to that given by Jánossy (1962) for *G. glandarius* . The fossil tibiotarsi and tarsometatarsi are the same size as their counterparts in modern *G. glandarius* . A comparison of the size of the leg bones of the fossil and recent form of *G. glandarius* is given in table 17.

The fossil ulnae and carpometacarpi are smaller than those in *P. pica, G. glandarius* and *N. caryocatactes* . The osteology of these fossils is undoubtedly corvid. However, it is not possible to detect an osteological difference in the ulnae and carpometacarpi of the last-mentioned species. Since we did not encounter *P. pica* and *N. caryocatactes* among the more numerous and positively identified fossil humeri and leg bones of approximately the same size, we assume that these species are not represented in our fossil material and ascribe the fossil ulnae and carpometacarpi to *G. glandarius* . The length of these fossil bones is 92.2 and 91.8 per cent respectively of that of their counterparts in recent *G. glandarius* , and this is a significant difference as well (see table 17).

In summary, the length of the major wing bones of Pleistocene Cretan *G. glandarius* is about 90 per cent of that in Recent *G. glandarius* , and the legs in both forms are the same size. Osteologically, both forms are identical.

• Modern *Garrulus glandarius* : its distribution and the variation in its subspecies

Nowadays, *G. glandarius* , the Eurasian Jay, has a Palearctic and Oriental distribution, and in Europe it is the only representative of its genus. In all there are eight groups of subspecies of *G. glandarius* (Vaurie, 1959). These comprise in the western Palearctic the *G. g. glandarius* group in Europe, the *G. g. cervicalis* group in north-west Africa and the *G. g. atricapillus* group in Turkey and the Middle East (Harrison, 1982). These groups of subspecies differ not only in colouring but also in size. Within each of these groups, the subspecies also vary in (mainly) colouring and in size. Within the European group of subspecies, Voous (1953) distinguishes 11 subspecies, whereas Vaurie (1959) recognizes only 9. With the exception of the isolated populations in the Mediterranean region (in Spain, and on Corsica, Sardinia and Crete), these subspecies intergrade with one another with respect to colouring and size. According to Voous (pers. comm.), and as is usual in non-migratory passerines, the wing length variation in the European subspecies of *G. glandarius* reflects variation in ove-rall body-size, and allometrical wing length differences (with equal body-sizes) do not occur. We think, however, that this needs to be confirmed for the isolated Mediterranean populations. It is possible that these populations differ allometrically from the mainland subspecies. All we know now is that the modern Cretan subspecies *G. g. cretorum* has a different colouring (Voous, 1953) and that it is "noticably smaller on the basis of both wing length and weight" (Watson, 1964) than the Greek mainland form *G. g. graecus* . Future biometrical comparison of the major wing and leg bones of the fossil and recent jays from Crete with each other and with the modern mainland subspecies will fill this gap, and will probably lead to subspecific recognition of Pleistocene, Cretan *G. glandarius* .

The Eurasian Jay has been found in the Pleistocene of Ireland, England, Spain, France, Belgium, Luxembourg, Corsica, Sardinia (Malatesta & Settepassi, 1954), Italy, Switzerland, Germany, Denmark, Czechoslovakia, Austria, Hungary, Poland, Rumania, Moldavia, the Ukraine, Russia and Israel.

The species lives exclusively in forested country and occurs up to the tree line.

• The *Pyrrhocorax pyrrhocorax* , *Pyrrhocorax graculus* and *Corvus monedula* size group

The bones of modern *P. graculus* are smaller than those of modern *P. pyrrhocorax* , and they are about equal in length but much more thick-set than in modern *C. monedula* . Table 18 gives some measurements of the fossil humeri attributed to any one of these three species. The tarsometatarsus of *C. monedula* is distinguishable from its counterpart in *P. pyrrhocorax* and *P. graculus* in that it has only one foramen vasculare distale, where the last two species have two.

Genus *PYRRHOCORAX* TUNSTALL, 1771

Pyrrhocorax graculus (LINN., 1766)

(Alpine Chough)

Material : * Liko cave ; Left hum. Li-B942 (Plate VIII, fig. 15). Right cmc. Li-c883 (Plate VIII, fig. 17). Left tmt. Li-a926 (Plate VIII, fig. 18). The total number of skeletal elements per layer is given in table 22.
* Gerani IV ; Right ulna Ge-IV3 (Plate VIII, fig. 16). Left cmc. Ge-IV4. Right cmc. Ge-IV5.

The Alpine Chough has been found in the Pleistocene of England, Wales, France, Monaco, Spain, Gibraltar, Mallorca, Corsica, Sardinia (Malatesta & Suriano, 1970), Italy, Switzerland, Czechoslovakia, Austria, Hungary, Rumania, Ukraine and Israel.

Today the species has a southern Palearctic distribution and it lives in the same habitat as the Red-billed Chough, though it usually occurs in higher mountains than the latter species. The Alpine Chough is a rare resident on Crete.

Pyrrhocorax pyrrhocorax (LINN., 1758)

(Red-billed Chough)

Material : * Liko cave ; Right hum. Li-a/b827 (Plate VIII, fig. 9). Dist. left ulna Li-B934 (Plate VIII, fig. 10). Right cmc. Li-B937 (Plate VIII, fig. 11). Right tt. Li-a921 (Plate VIII, fig. 13). Right tmt. Li-B941 (Plate VIII, fig. 14). Right cor. Li-a/b830 (Plate VIII, fig. 12). The total number of skeletal elements per layer is given in table 22.

The Red-billed Chough has been found in the Pleistocene of France, Monaco, Mallorca (Mourer-Chauviré *et al.*, 1977), Menorca (Reumer, 1982), Sardinia (Malatesta & Settepassi, 1954), Luxemburg, Portugal, Spain, Gibraltar, Italy, Switzerland, Germany, Austria, the Ukraine, Georgian SSR and Azerbaijan.

In Recent times it has a south Palearctic distribution and is a frequent resident on Crete, living in mountainous, rocky areas with grasslands.

Genus *CORVUS* LINN., 1758

Corvus monedula LINN., 1758

(Jackdaw)

Material : * Liko cave ; Right hum. Li-B849 (Plate VIII, fig. 19). Left ulna Li-B957 (Plate VIII, fig. 20). Left cmc. Li-O823 (Plate VIII, fig. 23). Right cor. Li-V836 (Plate VIII, fig. 24). Left tt. Li-a936 (Plate VIII, fig. 21). Right tmt. Li-a940 (Plate VIII, fig. 22). The total number of skeletal elements per layer is given in table 22.
* Gumbes B ; Prox. left hum. Gu-B34. Left cmc. Gu-B35. Dist. left tmt. Gu-B37. Prox. right tmt. Gu-B36. Dist. right tmt. Gu-B38.
* Gumbes C ; Dist. right ulna Gu-C21. Dist. right tt. Gu-C23. Dist. right tmt. Gu-C22.
* Mavro Mouri ; Prox. left tmt. MV-IV3.

* Gerani IV ; Dist. left tt. Ge-IV6.
* Sourida ; Dist. right tmt. So-3.

The Jackdaw has been found in the Pleistocene of Ireland, England, Belgium, Portugal, Spain, France, Mallorca (Mourer-Chauviré *et al.*, 1977), Corsica, Italy, Germany, Switzerland, Czechoslovakia, Austria, Hungary, Rumania, Poland, Moldavia, Ukraine, Russia, Israel and China.

Nowadays it has a Palearctic distribution and is a locally frequent resident on Crete. It inhabits open forested country.

Corvus species group

This species group comprises *C. corone* LINN., 1758, Carrion and Hooded Crows, and *C. frugilegus* LINN., 1758, Rook.

Material : * Liko cave ; Right hum. Li-a942 (Plate VIII, fig. 25). Right ulna Li-O825 (Plate VIII, fig. 27). Right cmc. Li-V838 (Plate VIII, fig. 26). Dist. right tt. Li-B978 (Plate VIII, fig. 28). Right ppdm. Li-B979 (Plate VIII, fig. 29). The total number of skeletal elements per layer is listed in table 22.

It proved impossible to distinguish the skeletal elements of the modern Crows from those of Rooks on the basis of morphology.

Both *C. corone* and *C. frugilegus* have been found in many Pleistocene sites in the Palearctic.

Nowadays both species have a Palearctic distribution as well. The Hooded Crow *C. corone cornix* is a common resident on Crete, but the Carrion Crow *C. corone corone* does not occur in eastern Europe. The Rook is not found on Crete today. The Crows and the Rooks inhabit all kinds of open country.

Corvus corax LINN., 1758
(Raven)

Material : * Gumbes B ; Dist. left hum. Gu-B26 (Plate IV, fig. 7).

The Raven is by far the largest species of the western Palearctic Corvidae.

It is known from the Pleistocene of Ireland, Scotland, England, Spain, Mallorca, France, Belgium, Monaco, Sardinia, Malta, Italy, Switzerland, Germany, Norway, Czechoslovakia, Austria, Hungary, the Ukraine, Abkhazia, Azerbaijan, Israel and North America.

Nowadays the Raven has a Holarctic distribution and it is a frequent resident on Crete. It inhabits almost all kinds of country.

Family **STURNIDAE** VIGORS, 1825 (Starlings)

Genus *STURNUS* **LINN., 1758**
Sturnus species group

The fossil bones represent at least one of the following species : *S. vulgaris* LINN., 1758 Common Starling, *S. unicolor* Temminck, 1820, Spotless Starling, *S. roseus* (LINN., 1758) Rosy Starling.

Material : * Liko cave ; 4 Left hum. Li-V851 (Plate IX, fig. 13, x2). Li-B1018, 1019, Li-c933. 3 Right hum. Li-B1020, Li-c934, Li-d900.

The proximal humerus in the Sturnidae is characterized by the fact that the crus dorsale fossae completely separates the deep fossa tricipitalis from the fossa pneumo anconaea (Jánossy, 1983). On examining the humeri of the three modern western Palearctic *Sturnus* -species, *S. vulgaris, S. unicolor* and *S. roseus* , we did not find any osteological or metrical differences between them, so the fossil bones may in fact belong to any one of these species.

Common Starlings are known from many European Pleistocene sites, the Spotless and Rosy Starling have been found at some European Pleistocene sites only.

In Recent times only the Common Starling is known from Crete, where it is a frequent winter visitor. The Common and the Spotless Starling frequent open forested country, whereas the Rosy Starling inhabits more open, bare, rocky and mountainous country.

Family **FRINGILLIDAE** VIGORS, 1825 (Finches)

The humeri in the various genera of this family are rather uniform, and resemble the humeri in the Emberizidae. Jánossy (1983) gives osteological charactristics of some genera within the Fringillidae ; these will be given here where a genus or a species has actually been identified in the fossil material. Size differences between most species in the family exist, but are often marginal and size ranges often overlap. Table 19 gives the measurements of the humerus of some modern species in the family. Within the family, *Coccothraustes coccothraustes* and *Pinicola enucleator* are the largest species, followed by (in this order) *Loxia pytyopsittacus, Loxia curvirostra, Carduelis chloris,* then by *Fringilla coelebs, Pyrrhula pyrrhula* and *Fringilla montifringilla, Carpodacus erythrinus, Loxia leucoptera, Carduelis cannabina, Carduelis flavirostris, Carduelis carduelis, Serinus serinus* and *Carduelis citrinella, Carduelis spinus, Carduelis flammea* and *Carduelis linaria* . Western Palearctic Fringillidae species not included in this survey are some *Serinus* -species, *Carduelis hornemanni, Loxia scotica* and various *Rhodopechys* - and *Carpodacus* -species, so the identified species (groups) have still to be compared with these species.

Genus *FRINGILLA* LINN., 1758

The proximal humerus in this genus is characterized by a long crista pectoralis, a well-developed very thin crus dorsale fossae with thickened margin, a broadened crus ventrale fossae with a small depression in it, and a weak tuberculum ventrale (Jánossy, 1983).

Fringilla species group

This species group comprises *F. coelebs* Linn., 1758, Chaffinch and *F. montifringilla* Linn., 1758, Brambling. The humeri of these species are osteologically identical and their size ranges overlap completely (see table 19).

Material : * Liko cave ; 3 Right hum. Li-B1021, Li-a985, Li-c936. 6 Left hum. Li-V852, Li-B1022 (Plate IX, fig. 14, x2), Li-a986, Li-a/b882, 883, Li-c937.

The fossil humeri show the osteological characteristics of the genus and fall within the size range of both *F. coelebs* and *F. montifringilla* . In addition to differing in their osteology, the fossil humeri attributed to this species group differ from those in the *Emberiza* -species of about the same size (*Emberiza* species group 1) in that they are slightly more stoutly built.

Both Chaffinch and Brambling are known from various Pleistocene sites in Europe.

In Recent times, both species have a Palearctic distribution. *F. coelebs* is a common resident on Crete, and *F. montifringilla* is a frequent migrant there. Both species inhabit open forested country.

Genus *CARDUELIS* BRISSON, 1760

Carduelis chloris (LINN., 1758)

(Greenfinch)

Material : * Liko cave ; 3 Right hum. Li-a987 (Plate IX, fig. 15, x2), Li-a988, Li-c866. Mand. Li-V853 (Plate IX, fig. 16, x2).

The humerus in *C. chloris* is stoutly built, proximally and distally broadened with a short crista pectoralis, the fossa tricipitalis is shallower than the fossa pneumoanconaea, and the two fossae are not quite confluent (Jánossy, 1983). The fossil humeri show these characteristics and fall within the size range of the recent species too. They are slightly more stoutly built than in the *Fringilla* -species. The mandibula in modern *C. chloris* is more heavilly built than in the *Fringilla* -species, though it is by no means as heavy as in *Coccothraustes coccothraustes* . The fossil mandibula agrees perfectly in size and osteology with the mandibula in recent *C. chloris*.

The Greenfinch is known from the Pleistocene in Ireland, England, France, Italy, Malta, Switzerland, Poland, the Ukraine and Israel.

Nowadays it is found throughout the western Palearctic, it is a frequent resident and migrant and a common winter visitor to Crete. It inhabits open woodland.

Genus *PYRRHULA* BRISSON, 1760

cf. *Pyrrhula pyrrhula* (LINN., 1758)

(Bullfinch)

Material : * Liko cave ; Right hum. Li-a989 (Plate IX, fig. 17, x2).

The proximal humerus in this species is characterized by a long crista pectoralis and (in comparison with the *Fringilla* - species) a more dorsally extending crus dorsale fossae (Jánossy, 1983). The fossil humerus is osteologically identical with its counterpart in modern *P. pyrrhula* and falls within its size range too.

The Bullfinch is known from the Pleistocene of Ireland, France, Mallorca (Florit & Alcover, in press), Sardinia, Italy, Switzerland, Austria, Germany, Hungary and Czechoslovakia.

Nowadays it is found throughout the Palearctic, but it is not known from Crete. The species inhabits mainly coniferous forest.

Genus *COCCOTHRAUSTES* BRISSON, 1760
Coccothraustes coccothraustes (LINN., 1758)
(Hawfinch)

Material : * Liko cave ; 2 Max. Li-V825, Li-a905 (Plate IV, fig. 8, x2). 3 Fragm. of mand. Li-V826, Li-a906, 907 (Plate IV, fig. 9, x2).

The maxilla and mandibula in modern *C. coccothraustes* are easily distinguishable from those in the other western Palearctic passerine species in that they are very short and thick-set.

The Hawfinch has been found in the Pleistocene of England, Spain (Mourer-Chauviré, 1980), Madeira (Pieper, 1985), Mallorca, France, Sardinia, Malta, Italy, Austria, Hungary, Poland, Czechoslovakia, Rumania, yhe Ukraine and Israel.

Today it has a Palearctic distribution and is an exceptional winter visitor to Crete. It lives in forests and open wooded country.

Family **EMBERIZIDAE** VIGORS, 1831 (Buntings)

The humerus in this family resembles that in the Fringillidae. Yet, it is characterized in the genus *Emberiza* by the light, elongated form, the short crista pectoralis, the large and confluent fossa tricipitalis and fossa pneumoanconaea, which are hardly intersected by the reduced crus dorsale fossae (Jánossy, 1983). Within the genus, the species are osteologically very uniform, although there are size differences : *E. calandra* is the largest species, followed by (in this order) *E. citrinella, E. hortulana, E. cirlus* and *E. schoeniclus* (see table 20 and fig. 7). Western Palearctic members of the genus not included in this study are *E. caesia, E. cineracea, E. melanocephala, E. cia* and *E. striolata* , so the identified humeri have still to be compared with these species.

Genus *EMBERIZA* LINN., 1758
cf. *Emberiza calandra* LINN., 1758
(Corn Bunting)

Material : * Liko cave ; 2 Right hum. Li-a/b820, Li-e806 (Plate IX, fig. 18, x2).

Both fossil humeri closely resemble the humerus in modern *E. calandra* , and also fall within the size range of this species (see table 20, fig. 7). In addition to osteological differences, the humerus of *E. calandra* is a little more slenderly built than in the Fringillidae-species of nearly the same size (i.e. *P. enucleator* and *C. coccothraustes*).

The Corn Bunting has been found in the Pleistocene of England, France, Germany, Czechoslovakia, Hungary, Israel and the Ukraine.

Nowadays it inhabits the western Palearctic, it is a common resident and migrant on Crete in dry open country.

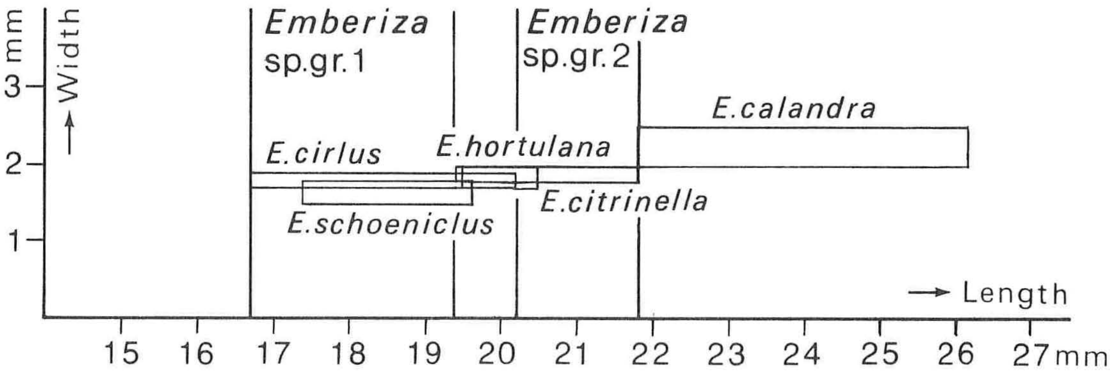


Fig. 7.- Size ranges of the humerus of some modern *Emberiza* -species. The height of each horizontal bar indicates the range of the width in the middle of the humerus, and the length of each bar indicates the range of the length of the humerus.

Emberiza species group 1

This species group comprises the *Emberiza* -species in which the length of the humerus varies between 16.7 and 19.4 mm (see fig. 7). So it includes *E. cirlus* , Cirl Bunting, and *E. schoeniclus* , Reed Bunting. It excludes *E. hortulana, E. citrinella* and *E. calandra.*

Material : * Liko cave ; 3 Right hum. Li-a/b881, Li-c935, Li-c/d811 (Plate IX, fig. 19, x2).

The fossil humeri show the osteological characteristics of the genus and fall within the size range of this species group (see fig. 7, tables 20, 21). In addition to the osteological differences, the humerus in the *Emberiza* -species of this size group differs from that in the Fringillidae species of about the same size (i.e. *F. coelebs, F. montifringilla*) in that it is more slenderly built.

Emberiza species group 2

This species group comprises the *Emberiza* -species in which the length of the humerus varies between 20.2 and 21.8 mm (see fig. 7). So it includes *E. citrinella,* Yellowhammer, and *E. hortulana* , Ortolan Bunting. It excludes *E. cirlus, E.*

schoeniclus and *E. calandra* .

Material : * Liko cave ; 4 Left hum. Li-a991 (Plate IX, fig. 20, x2), Li-a/b884, Li-d901, 902.

The fossil humeri show the osteological characteristics of the genus and fall within the size range of this species group (see fig. 7, tables 20, 21). They are a little more thick-set than the humeri in *Emberiza* species group 1.

Emberiza -species belonging to one of the species groups and recorded from the Pleistocene are *E. hortulana, E. citrinella* and *E. schoeniclus* .

In addition to *E. calandra* , we also find on modern Crete ; *E. citrinella, E. hortulana, E. cirlus, E. cia, E. caesia* and *E. melanocephala* . With the exception of *E. schoeniclus* , which is a reed-land species, the *Emberiza* -species are generally associated with arid, open country.

IV. THE LOCALITIES AND THEIR SPECIES CONTENTS

1. GENERAL REMARKS

In this study we are dealing with assemblages of fossil bird bones from caves and fissures. Together these assemblages form our fossil avifauna. Obviously this fossil avifauna will not correspond completely to the actual fauna from which it is derived, but its composition will be determined by the nature of the localities and the way in which the fossils were deposited. For example, the avifauna deposited in fossiliferous layers formed in a moor will be quite different from that in a nearby cave, although both fossil faunas descend from the same avifauna. Furthermore, small passerine species may be under-represented in our fossil avifauna, because of the fragility of their bones. The tiny bones of small passerines have a poorer chance of becoming fossilized than the bones of more robust species, and once fossilized they are more likely to break during collection than larger, more solid bones. In our study of the small passerine species we chose to study principally complete humeri ; this method therefore may also have led to under-representation of these species.

In summary, then, we can say that the composition of our fossil avifauna is influenced by taphonomic processes and the representation of the species will not accurately reflect the original composition of the avifauna. Both factors will be discussed in the appropriate sections.

2. NUMBER OF IDENTIFIED SPECIES AND THEIR FOSSIL REMAINS

It proved possible to identify in all 3590 fossil bird remains out of the over 10,000 collected from 9 localities (including the material treated in 1982). Tables 22, 23, 24 and 25 show the bird species identified, the number of their fossil remains, the minimum number of their individuals and the approximate number of unidentified specimens per locality and per layer in Liko cave. The unidentified part of the fossil material consists largely of fragments of small passerine bones. The identified part comprises 13 orders, 24 families and 65 species (or species groups). 13 species are represented by 1 specimen, 51 species are represented by 2-84 specimens ; *Athene cretensis* with 2639 identified specimens is the species with by far the largest representation.

3. SPECIES ASSOCIATION FROM LIKO CAVE (TABLE 22, FIG. 8)

The species association we find in Liko cave gives us some clues about how the cave was filled up. The great number of bird species (62) indicates that the cave was probably connected with the outer world by a sink-hole. It is unlikely that raptors and the independent entry of species were exclusively responsible for the presence of such a varied avifauna, although both factors may have played a role.

The numerical abundance of *Athene cretensis* (see fig. 8) indicates that Liko cave was probably a place where this bird was born, lived, died and was fossilized. This was confirmed by the presence of a thin layer of fossil owl pellets in Li-c. The pellets were found to consist mainly of bones of small mammals and birds (Mayhew, 1977). The size of these pellets indicated that they most probably came from *Athene cretensis*. Bones of this species are abundantly present in layer Li-c.

After *Athene cretensis* (minimum 163 individuals), the species most abundantly represented in Liko cave are : *Turdus* sp. gr. 2 (min. 44 ind.), *Turdus* sp. gr. 1 (min. 28 ind.), *Garrulus glandarius* (min. 18 ind.), *Corvus monedula* (min. 16 ind.), *Tyto alba* and *Columba oenas* (min. 12 ind.) and *Otus scops* (min. 9 ind.). Of these species, *Corvus monedula, Tyto alba, Columba oenas* and *Otus scops* may have used the cave for roosting or breeding. *Athene cretensis, Tyto alba* and *Otus scops* may have been responsible for bringing in mice and small passerines. The abundant presence of *Turdus* sp. gr. 1 and 2 of *Garrulus glandarius* is difficult to explain. It is unlikely that these species entered the cave by themselves. A possible explanation is that they were brought into the cave as prey species of Peregrine Falcons. This raptor preys upon birds such as thrushes and jays, and it may have used the cave for roosting as well. The Peregrine Falcon may also have brought into the cave species such as *Anas penelope, Anas querquedula, Coturnix coturnix, Gallinula chloropus, Calidris canutus, Scolopax rusticola, Glareola* sp. gr., *Columba oenas, Columba livia, Columba palumbus, Caprimulgus europaeus, Dendrocopos leucotos, Pyrrhocorax pyrrhocorax, Pyrrhocorax graculus, Corvus* sp. gr., *Corvus monedula, Zoothera dauma, Turdus iliacus* and *Sturnus* sp. gr.. The fact that so few Peregrine individuals (i.e. 2) were found in Liko cave does not contradict this hypothesis. In France, caves have been found to contain many bones of prey species of avian raptors, while they hardly contain bones of the raptors themselves (Mourer-Chauviré, pers. comm.). Besides the Peregrine, Eleonora's Falcon may have brought small bird species into the cave.

In addition to *Athene cretensis, Corvus monedula, Tyto alba, Otus scops, Columba oenas, Falco peregrinus* and *Falco eleonorae*, the following species may have entered the cave by themselves : *Phalacrocorax aristotelis, Falco tinnunculus, Columba livia, Apus melba, Apus apus, Hirundo daurica, Monticola solitarius, Pyrrhocorax pyrrhocorax, Pyrrhocorax graculus* and *Sturnus* sp. gr.

In conclusion we can say that part of the fossil avifauna from Liko cave was probably introduced through a sink-hole into which cadavers of birds (and probably also of mammals) fell or were washed. The owl *Athene cretensis* lived in the cave, and probably together with *Tyto alba* and *Otus scops* was responsible for bringing in small mammals and birds. Diurnal raptors such as *Falco peregrinus* and *Falco eleonorae* may have brought in many bird species as prey. The cave was probably also used -for shelter, roosting or even breeding- by a number of non-predatory bird species.

Nowadays, the Blue Rock Thrush *Monticola solitarius* is the only bird species known to breed in Liko cave.

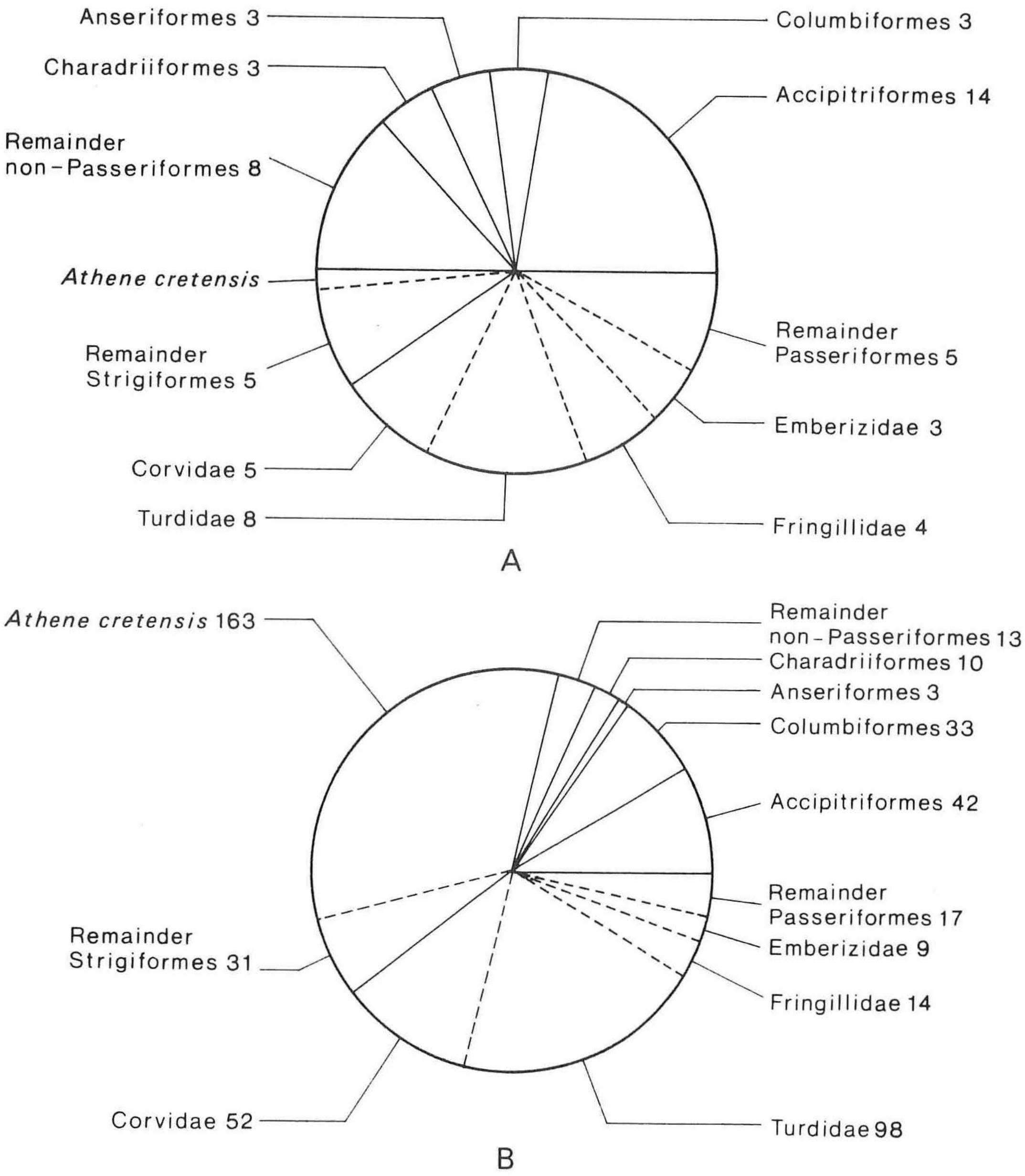


Fig. 8.- The number of bird species within the main groups represented in Liko cave (A) and the minimum number of individuals within these groups (B).

4. SPECIES ASSOCIATIONS FROM THE OTHER LOCALITIES

The other localities yielded far fewer fossil bird remains than Liko cave (tables 24 and 25). In view of the small number of species in each locality it would be speculative to draw conclusions from their species association. One can say that all bird species from these sites are equally represented by one or a few individuals, except for *Athene cretensis* (minimum 8 individuals), *Garrulus glandarius* (min. 6 ind.), *Corvus monedula* (min. 5 ind.) and *Asio flammeus* (min. 4 ind.).

With the exception of *Puffinus puffinus, Fulica atra* and *Corvus corax*, all species from these localities are also present in Liko cave.

V. COMPARISON OF THE PLEISTOCENE AND RECENT AVIFAUNAS AND THE PALEOENVIRONMENT ON PLEISTOCENE CRETE

1. GENERAL REMARKS

For a comparison of the Pleistocene and the Recent avifaunas of Crete we include in the Pleistocene avifauna all the bird species that have been recorded so far from all the Pleistocene sites on Crete. So we also include the Gannet *Morus bassana* and the White-fronted Goose *Anser albifrons* , reported from Simonelli cave by Suriano (in Malatesta, 1980). We choose to ignore -provisionally- the age differences between the localities, so that our picture of the Pleistocene avifauna will be as complete as possible.

The Recent avifauna of Crete contains within 17 orders, 50 families with 224 sedentary and migratory birdspecies (Vallianos, 1984). In the Pleistocene avifauna, 13 orders with 25 families and 67 species have so far been recognized (table 26).

2. COMPARISON OF THE COMPOSITION OF THE PLEISTOCENE AND RECENT AVIFAUNAS

Fig. 9 shows the composition of the Pleistocene and Recent avifaunas divided into main bird orders and, within the Passeriformes, into main bird families. Table 26 lists the number of species within each order -and, for the Passeriformes, within each family- of the Pleistocene and Recent avifaunas.

The main differences in the composition of the Pleistocene and Recent avifaunas are :

- the Accipitriformes, the Strigiformes and (within the Passeriformes) the Corvidae and Turdidae are over-represented in the Pleistocene avifauna.
- the Ciconiiformes, the Charadriiformes and (within the Passeriformes) the Sylviidae and Motacillidae are under-represented in the Pleistocene avifauna.

Passeriformes

We have already pointed to the under-representation of the small members of this order in the Pleistocene avifauna. The absence of the tiny Sylviidae (with no less than 24 species in the Recent avifauna) and of the Motacillidae in the Pleistocene avifauna may well be due to the extreme fragility of their bones.

There are also good reasons for the over-representation of the Corvidae and Turdidae in the Pleistocene avifauna : members of both families are either good prey species for avian raptors or are likely to enter caves and fissures by themselves.

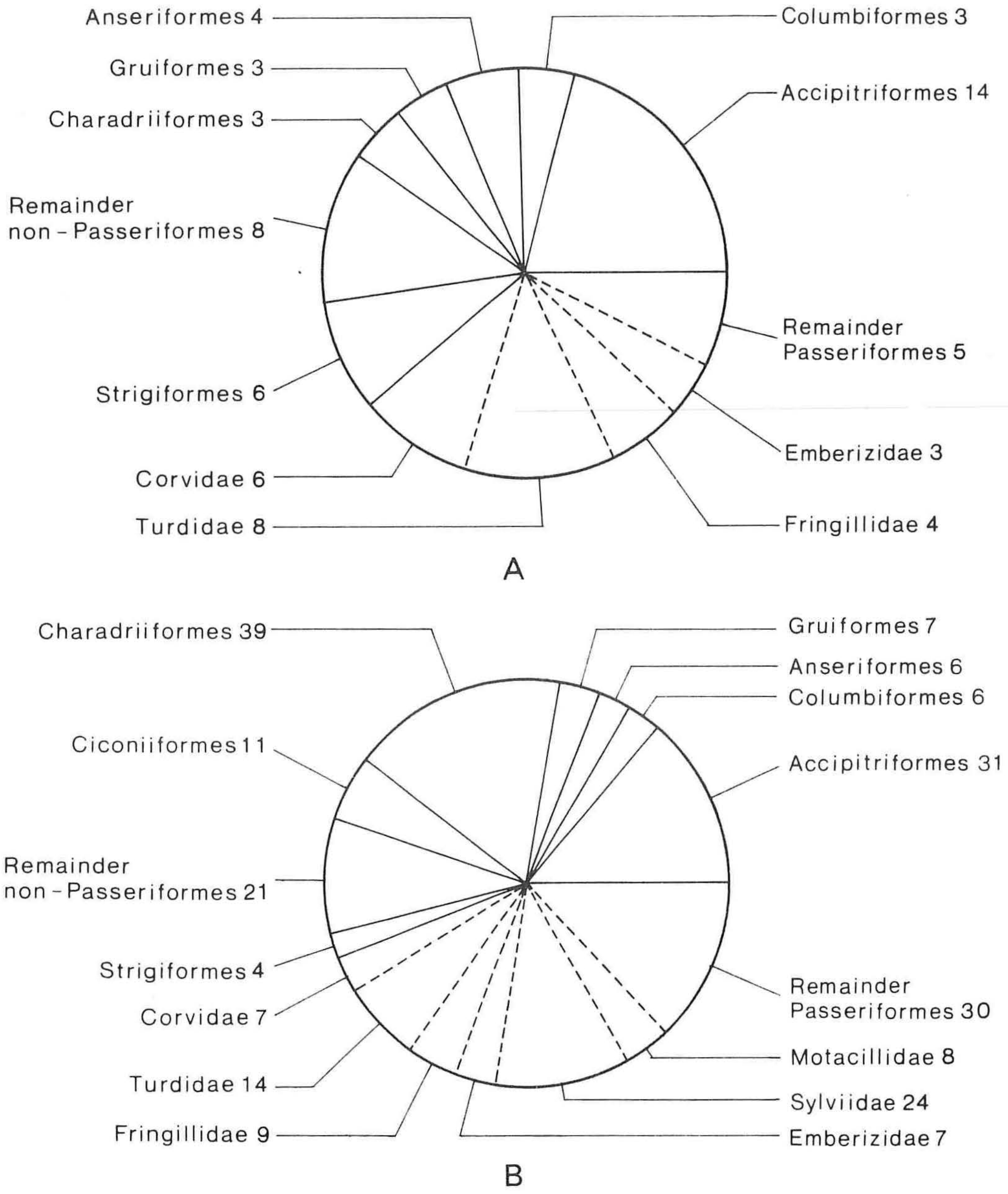


Fig. 9.- The number of bird species within the main groups of the Pleistocene (A) and Recent (B) avifaunas of Crete.

Ciconiiformes

The absence of this group in the Pleistocene avifauna might be explained by the fact that most members of this order rarely leave the water's edge. Furthermore, especially the larger species are not attractive prey species for most avian raptors. Members of this order are in fact rarely encountered in karstic localities (Mourer-Chauviré, pers. comm.).

Charadriiformes

This large order comprises many coastal and wetland species. Their under-representation in the Pleistocene avifauna may indicate that in those days the cave was situated much further from the sea than today, and that (coastal) wetlands were not plentiful on Pleistocene Crete.

Accipitriformes and Strigiformes

The relative abundance of birds of prey species -especially the Strigiformes- in the Pleistocene avifauna is striking in comparison with their representation in the Recent avifauna. The number of owl species in the Pleistocene avifauna (six) is higher than in the Recent avifauna (four). Naturally, the Passeriformes are under-represented in the Pleistocene avifauna so the representation of the birds of prey will actually have been smaller than indicated in fig. 9A. But, even if we -provisionally- increase the proportion of the Passeriformes in the Pleistocene avifauna to the same proportion as in the Recent one, the representation of the birds of prey remains much larger than in the Recent Cretan avifauna. As will be shown below, a high proportion of birds of prey species is a common characteristic of fossil avifaunas from caves. It has often been suggested in the literature, and we share this opinion, that this is probably due to the attractiveness of caves for raptors. Nevertheless, we think that ecological conditions on Pleistocene Crete also helped to account for the high representation of birds of prey. This will be discussed in more detail later.

3. COMPARISON OF THE CLIMATIC ZONES INHABITED BY THE SPECIES OF THE PLEISTOCENE AND RECENT AVIFAUNAS

In table 27, all neospecies of the Pleistocene avifauna of Crete are listed, and for each species the climatic zones in which they occur are given. The climatic zones have been defined by Harrison (1982), they include : Arctic (A), Subarctic (SA), Boreal (B), Temperate (T), Warm Temperate (WT), Subtropical (STr) and Tropical (Tr). Most bird species listed occur in a range of climatic zones. In these cases, only the extreme northern and southern climatic zones are indicated. In table 28, the number of bird species within the same ranges of climatic zones is compared for the Pleistocene and the Recent avifaunas of Crete. It appears that relatively more species with a more northern distribution range occur in the Pleistocene avifauna than in the Recent avifauna, and that relatively more species with a more southern distribution range occur in the Recent avifauna than in the Pleistocene avifauna. In other words ; the Pleistocene avifauna of Crete comprises more northern and fewer southern bird species than the Recent avifauna of the island. So, if our fossil avifauna is -with respect to climatic preference- a random sample of the avifauna that actually lived on Crete, we can conclude that the climate on Crete during the deposition of the fossiliferous sediments was cooler than it is today. Still, some typically Mediterranean species (such as *Gypaetus barbatus, Gyps fulvus, Falco eleonorae, Hirundo daurica, Oenanthe hispanica* and *Monticola solitarius*) occur in the fossil avifauna too.

The assumption that the climate on Pleistocene Crete was cooler than today is further supported by the presence of fossil remains of bird species for which at present, the climate on Crete is almost certainly too warm :

- *Morus bassana* . The most southern breeding populations of this species are today to be found off the coast of France, some 1,000 km further north than Crete.

Since this species comes on land only when breeding (Cramp & Simmons (eds.), 1977), the fossil evidence of it may indicate that it actually bred on Pleistocene Crete.

- *Branta ruficollis* winters nowadays further to the north and east of Crete.
- *Aegolius funereus* is a typically "cold" taiga species with a boreal and montane distribution. The presence of this species so far south during the Pleistocene is remarkable.
- *Dendrocopos leucotos* and *Pyrrhula pyrrhula* are boreal forest species whose southernmost distribution boundaries today are in northern Greece and south-western Turkey.

4. THE HABITATS OF THE SPECIES AND THE PALEOENVIRONMENT

Each bird species is indicative for the habitat(s) in which it normally occurs. If we assume, following Moreau (1954), that the habitat requirements of bird species have hardly changed at all since the Pleistocene, then our fossil birds should tell us something about the paleoenvironment of Pleistocene Crete. However, since different habitats support different numbers of bird species and since the bird species of each habitat will probably not be represented in the same ratio in the Pleistocene avifauna, it is impossible to draw precise conclusions about the extent of the various habitats on Pleistocene Crete. In table 27, the characteristic habitats are indicated for each species of the fossil avifauna. Since the habitats are generalized to a certain extent and linked arbitrarily with the species, they can give only a general impression of the paleoenvironment on Pleistocene Crete. We use the following habitats : Arid, Rocks (AR), Steppe (S), Wide range (WR), Open woodland (OW), Forest (F), Fresh water (FW), Mountains (M) and Coast (C).

About half the Pleistocene avifauna (32 species) indicates an open woodland and forest habitat. So, these habitats probably occupied a large part of Pleistocene Crete, larger than today. Most bird species indicate the presence of mixed broad-leaf and conifer forest. There must also have been mountains (13 species), and arid and rocky country (8 species). Fresh water was present (11 species) ; in mountainous country it was probably in the form of rivers and streams. Steppe-land (3 species) was probably scarce on Pleistocene Crete.

VI. CHARACTERISTICS OF THE PLEISTOCENE CRETAN AVIFAUNA, A BASIS FOR DISCUSSION AND SPECULATION

The fossil avifauna can be characterized in the following way :

1. It contains relatively more representatives of temperate and boreal zones than the recent avifauna, but nevertheless includes some typically Mediterranean species. Many of the birds represented are characteristic for open woodland and forest.
2. The absence of the Galliformes (with the exception of *Coturnix coturnix*).
3. The presence of many bird of prey species. The number of owl species (i.e. six) is larger than in the recent avifauna (i.e. four).
4. The presence of endemic birds of prey : the large eagle *Aquila chrysaetos simurgh* and the long-legged owl *Athene cretnesis* .

1.1. THE CLIMATE AND SURFACE AREA FLUCTUATIONS OF PLEISTOCENE CRETE

It was concluded above that the temperate character of the Pleistocene avifauna and the presence of some "cold" species suggest a cooler climate than today. Obviously, this cool period may well have been related to a Glaciation. It is well known that (as a result of larger polar ice-masses) lower sea levels occurred during the Glaciations. If this happened in the eastern Mediterranean as well, this may have meant that Crete had a larger surface than nowadays. Coastal terraces on the north and east coast of Crete indicate that oscillations in the sea level occurred in the past. However, these may also have been effected by tectonic activities, which are known to have occurred in the area. Whatever the cause, we have evidence that the surface of Crete varied in size during the Pleistocene.

At present, Liko cave is situated at a distance of c. ten metres from the sea, on a broad, steep slope which runs down to below sea level. Sea level fluctuations in the past may have caused alternately submersion of the cave, and increase in the distance from the cave to the sea. We find evidence of both events ; holes of a borer-mussel (*Lithophaga lithophaga*) in the walls of Liko cave indicate submersion before the cave had its present contents, and the great number of land birds found in the cave and the near-absence of Charadriiformes (see V.2.) indicate that in Pleistocene times the cave was much further from the sea than it is today.

1.2. THE PALEOBIOGEOGRAPHY OF SOME BIRDSPECIES IN RELATION TO THE CLIMATE AND VEGETATION ON PLEISTOCENE CRETE

Nowadays, Crete is sparsely forested, the forests being restricted to a few mountain areas. It was concluded above, considering the great number of forest species in the Pleistocene Cretan avifauna, that Crete was probably more forested than it is today. This conclusion is supported by palynological evidence : Both Zohary and Orshan (1965) and Greuter (1975) postulate that in pre-neolithic times Crete was largely covered with forest. It appears that at present only a few remnants of the former vegetation are left on the island (Bottema, 1980).

According to Moreau (1954), when the Glaciations were at their peak, broad-leaved and mixed woodlands in Europe were confined to the most favourable (= warm) parts of the Mediterranean peninsulas. In the Palearctic, the changing climatic and ecological conditions during the Pleistocene Glaciations were of special importance for forest birds. When, during a Glaciation, forests disappeared in large areas of continental Europe, forest birds sought refuge in the most southerly parts which were still forested. Only small remnant populations of forest birds survived in south western and south eastern Europe (Voous, 1960) and Italy (Moreau, 1954). Harrison (1982) too considers Greece and west Turkey to have been a potential glacial refuge area for western Palearctic forest birds. During the Interglaciations and after the last Glaciation, the forests -and with them the forest birds- spread northwards again.

In view of the probability that the Pleistocene Cretan avifauna lived in a cooler period than today, the fossil avifauna may well partly represent such a refuge population of forest birds. *Accipiter gentilis, Columba oenas* and *Coccothraustes coccothraustes* are typical forest species of the Cretan fossil avifauna which recently occur exceptionally on Crete. Furthermore, it is notable that of the five northern bird species in the fossil avifauna which are lacking in Crete's modern avifauna, three are typically forest species : *Aegolius funereus, Dendrocopos leucotos* and *Pyrrhula pyrrhula* .

The remarkable occurrence of *Zoothera dauma* (which today has a strictly oriental distribution) in the Pleistocene avifauna may also be linked with climatic changes and their effect upon the vegetation in Eurasia. The species is also known from the Pleistocene of Monaco, Corsica, Italy (Brodkorb, 1978) and possibly France (Mourer-Chauviré, 1975). It is known that various oriental steppe species invaded Europe during the Glaciations. However, oriental forest species such as *Zoothera dauma* have rarely been encountered in Europe.

Another oriental forest element in the Pleistocene avifauna is *Ketupa zeylonensis.* This species has an oriental distribution, but there are some residual populations in the Middle East. Its occurence on Pleistocene Crete is the most westward known occurrence so far.

Naturally, not only forest birds were forced southward during a cold Pleistocene period, but whole avifaunas were to be found in more southerly locations. This may be illustrated by the presence of the Gannet *Morus bassana* . As discussed earlier, the fossil evidence of this species may indicate that it bred on Pleistocene Crete. If so, this would mean an important shift southward, for the recent breeding grounds of this species are some 1,000 km further north. As far as is known, there have been no other recordings of *Morus bassana* from the Pleistocene in the Mediterranean (Brodkorb, 1962). According to Moreau (1954), it is quite possible that *Morus bassana* , and other marine species now confined to the Atlantic, actually bred in the Mediterranean during the Glaciations. *Branta ruficollis* is another water bird of the Pleistocene Cretan avifauna which at present has a more northern distribution.

Various typically Mediterranean bird species (*Gypaetus barbatus, Gyps fulvus, Falco eleonorae, Hirundo daurica, Oenanthe hispanica* and *Monticola solitarius*) stayed "at home" i.e. did not move to other areas during this colder Pleistocene period. Apparently they tolerated lower (average) temperatures. This may be explained by the fact that most of these species inhabited mountainous country, and could descend to lower, warmer altitudes.

2. THE ABSENCE OF MOST GALLIFORMES

With the exception of the Quail *Coturnix coturnix* , the Galliformes are not present in the Pleistocene Cretan avifauna. This is in sharp contrast with most Quaternary cave avifaunas from the European mainland, which are often dominated by members of this order (Lambrecht, 1933). Species within the galliform genera *Lagopus, Tetrao, Lyrurus, Tetrastes, Alectoris* and *Perdix* were brought into the continental caves mainly as prey species of avian raptors. Since most members of these genera are essentially sedentary and short-distance fliers (again, with the exception of *Coturnix coturnix*), they rarely cross open stretches of sea and they are, consequently, not present in most Pleistocene Mediterranean island avifaunas. Migratory *Coturnix coturnix* which has a good flying ability and is also a favourite prey of avian raptors, is to be found in most Pleistocene Mediterranean island avifaunas. Its presence in the Cretan fossil avifauna is therefore not surprising.

The Chukar Partridge *Alectoris chukar* is the only galliform on Crete today besides *Coturnix coturnix* . The species is sedentary and reached Crete probably from the Turkish mainland, via Rhodos and Karpathos (it is does not occur on the Greek mainland). Recent Cretan *Alectoris chukar* differs slightly from Turkish *Alectoris chukar cypriotes* in colour and size, but is still attributed to it (Cramp and Simmons (eds.), 1979).

3. THE ABUNDANCE OF BIRDS OF PREY

The abundance of birds of prey can be explained in terms of 1. the number of species present and 2. the population density of these species. It has been pointed to above, that taphonomic processes and the habits of the species involved determine largely the composition of a fossil avifauna. It is therefore difficult to reconstruct population densities of bird species. Yet, the number of bird of prey species found is useful information, it informs us about ecological diversity and can be used for comparison with other avifaunas.

The number of both diurnal and nocturnal bird of prey species in the Pleistocene Cretan avifauna is relatively higher than in Crete's Recent avifauna (see fig. 9). This is illustrated in table 29 as well. In this table the number of species within Accipitriformes and Strigiformes in the Recent avifaunas of the Greek mainland and of Crete are given, as well as the number of species within these orders in some fossil avifaunas from caves from the European mainland and from some Mediterranean islands.

It appears that the Recent avifaunas of Greece and Crete differ from all fossil avifaunas in having a much lower proportion of Strigiformes, and their proportion of Accipitriformes is lower in 16 out of the 24 cases. The proportion of both orders combined is lower in the recent avifaunas than in all fossil avifaunas. As mentioned earlier, the over-representation of raptors in fossil avifaunas from caves is generally thought to be a result of the attractiveness of caves for birds of prey.

Furthermore, although the proportion of Strigiformes is highest in a fossil island avifauna (Gargano), and the lowest proportions of Strigiformes occur in fossil mainland avifaunas, we find that most fossil mainland and fossil island avifaunas from caves contain a comparatively high proportion of Strigiformes. The same holds -to a lesser extent- for the Accipitriformes, an exception being the Balearics with a very low proportion of Accipitriformes. The proportion of Accipitriformes and Strigiformes combined in fossil mainland avifaunas differs very little from that in fossil island avifaunas, but is highest in an island avifauna (Gargano).

So, despite the general absence of mammalian carnivores in fossil faunas from Mediterranean islands, these faunas do generally not contain more species of bird of prey than fossil mainland faunas.

Still, the number of owl species in the Pleistocene Cretan avifauna is among the 6 highest of the 24 avifaunas listed in table 29, and the proportion of diurnal birds of prey in the Cretan fossil avifauna is also relatively high. We think that the abundant presence of endemic murids on Pleistocene Crete may help to explain this phenomenon. According to Mayhew (1977), these murids went through periods of overcrowding. Gliwicz (1984) also found that island populations of rodents differ from open mainland populations of the same species by higher density. A dense population of endemic murids may well have formed a rich food supply for the birds of prey. On Pleistocene Crete, the raptors could fully exploit this niche, which on the continent is always partly occupied by mammalian carnivores. When a bird of prey specialized in feeding on the murids (for example *Athene cretensis*) it may have left the exploitation of part of its original niche (in this case the feeding on insects and small reptiles) to other avian raptors (*Otus scops, Aegolius funereus*).

4. THE ENDEMIC BIRDS OF PREY

Athene cretensis

The evolutionary history of *Athene cretensis* as discussed in Weesie (1982) will be summarized here. The supposedly ancestral mainland Little Owl *Athene noctua* is generally sedentary and is inclined to a terrestrial way of life. For instance, the species may pursue mice by running over the ground. The distance of Pleistocene Crete from the mainland was, apparently, sufficiently large to establish genetic isolation of the Cretan population of *Athene noctua* . Long-legged *Athene cretensis* developed in the absence of mammalian carnivores, and in the presence of (sometimes abundantly available) endemic murids. Analysis of fossil owl pellets from Liko cave demonstrated that *Athene cretensis* probably fed mainly on endemic *Mus minotaurus* . The fossils from the deposits in the rear part of Liko cave provide evidence of a gradual increase in the length of the legs of *Athene cretensis* . In the same layers, Mayhew (1977) found a significant size increase of *Mus minotaurus*. The long legs of *Athene cretensis* are considered to reflect an adaptation to a mainly terrestrial life style. However, the discovery of a humerus of *Athene cretensis* in a deposit in a hollow of unknown age on the island of Armathia (Pieper, 1984) may prove that this species was still able to fly a considerable distance. Armathia is a very small island north west of Kasos, some 50 km from Crete. In view of the small size of Armathia and Kasos, it is not realistic to suppose that a form similar to *Athene cretensis* evolved on these islets. From the Pleistocene of nearby Karpathos the mainland form *Athene noctua* has been reported (Weesie, 1984).

Aquila chrysaetos simurgh

Modern Golden Eagles feed mainly on medium-sized mammals. These must have formed an important food source for the Pleistocene Cretan Eagles as well. The (young of the) various species of endemic deer, elephant and hippopotamus are of appropriate prey size for the eagles. For instance, the smallest species of endemic deer, *Candiacervus ropalophorus* , had a shoulder height of about 40 cm (de Vos, 1984). Fossil evidence from Liko cave proves that the Pleistocene Cretan eagles lived contemporaneously with several species of endemic deer. Sondaar (1977) points out that the population density of endemic deer fluctuated considerably, and that overpopulation must have occurred several times. It is likely, then, that the Cretan Golden Eagle population fed for a great deal on the endemic deer. Furthermore, the Pleistocene Cretan eagle population may well have been reproductively isolated during some part of the Pleistocene, since the distance of Crete from the mainland was sufficiently large (ca 40 km, Sondaar, pers. comm.) to form a geographical barrier. In these circumstances it is conceivable that endemic *Aquila chrysaetos simurgh* actually evolved on the island.

So far, we have no fossil evidence that *Aquila chrysaetos simurgh* lived contemporaneously with the Cretan dwarf elephants and hippopotamus, though this may be proved by future investigations. Nevertheless, it is tempting to speculate about the origin of the old fable of the "Roc", a giant bird able to carry elephants through the air. Lambrecht (1933, p. 220) depicts an ancient Persian picture of a flying bird with three relatively small elephants in its claws. The caption of this picture refers to the bird as Simurgh, or Roc. Lambrecht supposes that the elephants in the picture represent dwarf elephants from the Mediterranean islands. As for the bird, he agreed with Lydekker (1890) that it might represent *Gyps melitensis* , a giant vulture from the Pleistocene of Malta (now known from Crete as well). However, vultures usually feed on carrion and they never carry away their entire prey. Modern Golden Eagles on the other hand sometimes fly around with their prey, especially when feeding their young. The large Cretan eagle may have carried off (baby) dwarf elephants from time to time and this could have been the origin of the fable.

VII. SOME REMARKS ON ISLAND AVIFAUNAS AND THE SPECIATION OF BIRDS OF PREY ON ISLANDS

Island avifaunas commonly differ from mainland avifaunas in having 1. fewer resident bird species than equivalent mainland areas and 2. a number of endemic (sub)species. The number of resident bird species is thought to be directly correlated to the distance of the island from the mainland and to its size (MacArthur & Wilson, 1967), and to the diversity of habitats it provides (Watson, 1964, Lack, 1969, 1976). The degree of endemism of an island avifauna is considered to be influenced by the degree of isolation of the island (distance from the mainland and other islands and the length of the period of isolation), and by the ecological peculiarities of the island (Lack, 1969, 1976).

One can recognize these phenomena in the fossil record of islands. An extreme example are the birds from the Hawaiian Islands (3800 km from the nearest mainland), nearly 99 per cent of which are endemic land birds (Olson & James, 1982).

Although the distance of Crete from the mainland during the Pleistocene was not very long (ca 40 km), the Cretan fossil avifauna 1. lacks various bird species which commonly occur in fossil mainland avifaunas and 2. contains two endemic (sub)species. The number of endemic forms is by far not so large as in oceanic avifaunas and this is undoubtedly related to the vicinity of the mainland. This is in sharp contrast to the Pleistocene mammal fauna of Crete, of which almost all species are endemic.

The only endemic birds of the Cretan fossil avifauna are birds of prey (with the possible exception of *Garrulus glandarius* ssp.). As has been pointed to earlier, endemic deer and mice roamed on Crete, from time to time, in large numbers. So, the habitats of the birds of prey on Pleistocene Crete were different from those on the mainland because of the difference in food supply. This explains -together with genetic isolation- the speciation of the endemic birds of prey. For non-predatory birds the environment on Pleistocene Crete was probably less different from that on the mainland.

Speciation of endemic birds of prey in association with endemic mammals has been encountered repeatedly on islands. From the Mediterranean we know of the giant endemic barn owls *Tyto gigantea* and *Tyto robusta* from the Miocene island of Gargano (Ballmann, 1973, 1976) and *Tyto balearica* from the Plio-Pleistocene Balearics (Mourer-Chauviré *et al.*, 1980), all of which were associated with endemic rodents. Furthermore, we find three endemic species of eagles of the genus *Garganoaetus* from Gargano in association with endemic deer (Ballmann, 1973, 1976). This association of endemic birds of prey with endemic mammals is also known from oceanic islands. For instance, in the West Indies we know of the giant barn owls *Tyto pollens, Tyto ostologa, Tyto noeli* and *Tyto riveroi* (Wetmore, 1922, 1937, Arredondo, 1976), all associated with large extinct rodents which seem to have been their principal food (Brodkorb, 1959). Other endemic raptors from the West indies were the giant eagle *Titanohierax gloveralleni,* the giant vulture *Antillovultur varonai* and the giant owl *Ornimegalonix oteroi* . These species have also been found in association with endemic rodents and/or edentates (Olson and Hilgartner, 1982).

It appears that birds of prey on islands, irrespective of their generic identity, tend to specialize in the available, often endemic, mammal prey species. The subsequent size of the raptors may be considered as the best possible adaptation to feeding on the prey in question. This is also illustrated in the genus *Bubo* . The Eagle Owl *Bubo bubo* of the Mediterranean mainland region feeds principally on the Rabbit *Oryctolagus cuniculus* . A smaller, endemic form within the genus, *Bubo insularis* from the

Pleistocene on Sardinia and Corsica, is believed to have fed mainly on the endemic hare *Prolagus sardus*, which in turn is smaller than *Oryctolagus cuniculus* (Mourer-Chauviré *et* Weesie, 1986). On Crete, large endemic *Athene cretensis* fed principally on large, endemic *Mus minotaurus* . The large endemic eagle *Aquila chrysaetos simurgh* took mainly endemic deer as its prey.

VIII. DISAPPEARANCE AND EXTINCTION OF VARIOUS PLEISTOCENE CRETAN BIRD SPECIES

Various bird species of the Pleistocene Cretan avifauna are no longer present on Crete today. The species that have disappeared are listed in table 30. In all, 3 (sub)species (4%) of the Pleistocene Cretan avifauna (67 species) are extinct, 10 extant bird species (15%) of the fossil avifauna live no longer on Crete and another 6 species (9%) occur nowadays only exceptionally on the island.

As pointed out before, the climatic changes that have occurred on Crete since the Pleistocene were probably the major reason for the absence nowadays of the temperate and boreal species: *Morus bassana, Branta ruficollis, Aegolius funereus, Dendrocopos leucotos* and *Pyrrhula pyrrhula* . At present all these species live at more northerly latitudes. The disappearance of the large forests on Crete (which in turn may be related to climatic changes and the influence of man) probably played a role in the withdrawal of the forest species *Accipiter gentilis, Columba oenas, Aegolius funereus, Dendrocopos leucotos, Pyrrhula pyrrhula, Zoothera dauma* and *Coccothraustes coccothraustes* . The meagre forest cover of Crete today is probably hardly able to support these species.

The absence of suitable habitat may prevent *Anser albiforns* and *Calidris canutus* from visiting the island.

The absence of *Asio flammeus* and *Turdus iliacus* is surprising, as they winter at present throughout the Mediterranean. Perhaps they may still be found and have simply been overlooked.

The extinction of the endemic bird species of Pleistocene Crete may have been due to various circumstances. *Athene cretensis* has been encountered in the upper layer of Gerani II, together with remains of *Mus minotaurus*, domesticated animals and traces of human activities. De Vos (1984) considers the extinction of *Mus minotaurus* after the arrival of man (thought to have taken place ca 8,000 B.P. (Cherry, 1981)), to be a result of competition with *Rattus rattus* and recent *Mus* , which accompany every human invasion. The extinction of *Athene cretensis* may well have been linked with the extinction of its main prey species *Mus minotaurus* . Possibly, *Rattus rattus* and carnivores which arrived with man directly extirpated ground-dwelling *Athene cretensis*.

According to evidence from Gerani II the extinction of the endemic deer is with regard to at least one species, *Candiacervus ropalophorus* , linked with the arrival of man and his domestic animals. The extinction of the deer may in its turn have led to the extinction of their principal predator *Aquila chrysaetos simurgh* . Other possible explanations for the disappearance of *Aquila chrysaetos simurgh* are the intermingling with mainland *Aquila chrysaetos* or niche competition with the latter species, followed by extinction. As we may consider endemic *Aquila chrysaetos simurgh* to be a better adapted predator on endemic deer than newly invaded *Aquila chrysaetos*, extinction of the deer may have placed *Aquila chrysaetos* in a more advantageous position.

So, the extinction of the endemic birds *Aquila chrysaetos simurgh* and *Athene cretensis* is probably linked with the arrival of man and his (domestic) animal companions.

More recently, man is responsible for the disappearance of *Haliaeetus albicilla* from the island (Voous, 1960). This would also account for the almost complete absence of *Aegypius monachus*.

Actually it is not certain whether *Ketupa zeylonensis* still occurs in its most western territories in south Turkey. In Israel the species is rapidly declining due to human expansion (Cramp (ed.), 1985), which may have caused its disappearance from Crete as well.

Since the beginning of this century, deforestation and agricultural developments began to impoverish the then still rich and unspoiled Cretan biotope (Vallianos, 1984). The large-scale tourist and agricultural developments of the last few decades, and unlimited hunting, are at present endangering the Cretan natural environment and its avian inhabitants to an unacceptable extent. The existence of many bird species, especially the vultures and eagles for which Crete once was famous, and many water birds, is directly endangered due to hunting and habitat destruction. This impoverishment of the natural environment including the bird life on islands is alas an all too common phenomenon in our times. On Crete, the once rich and varied avifauna is likely to perish unless fully protected nature reserves are established without delay.

REFERENCES

ALCOVER J.A., MOYA-SOLA S., PONS-MOYA J., 1981. - Les quimeres del passat. *Institució Catalana d'història natural*, Memória núm. 11, Ciutat de Mallorca.

ARREDONDO O., 1976. -The great predatory birds of the Pleistocene of Cuba. *in*: Storrs L. Olson, ed. - Collected Papers in Avian Paleontology Honoring the 90th Birthday of Alexander Wetmore. *Smithsonian Contributions to Paleobiology*, 27: 169-187, 11 fig., 8 tables.

BALLMANN P., 1973. - Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien). *Scripta Geol.*, 17: 1-75, Taf 1-7, Leiden.

BALLMANN P., 1976. - Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien), zweiter Teil. *Scripta Geol.*, 38: 1-59, Taf 1-7, Leiden.

BALLMANN P. & ADROVER R., 1970. - Yacimiento paleontológica de la cueva de Son Bauzá (Mallorca). *Acta geol. hispan.*, Madrid, 5 (2): 58-62.

BATE D.M.A., 1907. - On Elephant remains from Crete, with description of *Elephas creticus . Proc. Zool. Soc. London*: 238-250.

BAUMEL J. *et al.*, 1979. - Nomina anatomica avium. *Academic Press*, London.

BOEKSCHOTEN G.J. & SONDAAR P.Y., 1965. - The Pleistocene of the Katharo basin (Crete) and its Hippopotamus. *Bijdragen Dierkunde*, 36: 17-44.

BOTTEMA S., 1980. - Palynological investigations of Crete. *Review of palaeobotany and palynology*, 31: 193-217.

BOULE M., 1910. - Géologie et paléontologie, *in*: de Villeneuve, Boule, Verneau et Cartailhac - Les grottes de Grimaldi, t. 1, fasc. 2, 3 et 4. Imprimerie de Monaco, 362 p., 48 fig., 41 pl.

BOULE M., 1921. *in*: R. de Saint-Périer - Le Solutréen supérieur de la Grotte des Harpons à Lespague (Haute-Garonne). *Ass. fr. Avanc. Sci.*, Rouen, 8 p., 5 fig.

BOULE M. & VILLENEUVE L. de, 1927. - La grotte de l'Observatoire à Monaco. *Arch. Inst. Paléont. hum.*, Paris, mém. 1, 113 p., 16 fig., 26 pl.

BRODKORB P., 1959. - Pleistocene Birds from New Providence Island, Bahamas. *Bull. Florida State Mus. Biol. Sci.*, 4(11): 349-371, 3 pl., 1 map, 3 tables.

BRODKORB P., 1962. - Catalogue of fossil birds, part 1 (Archaeopterygiformes through Ardeiformes). *Bull. Florida State Mus. Biol. Sci.*, 7(4): 179-293.

BRODKORB P., 1964. - Catalogue of fossil birds, part 2 (Anseriformes through Galliformes). *Bull. Florida State Mus. Biol. Sci.*, 8(3): 195-335.

BRODKORB P., 1967. - Catalogue of fossil birds, part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). *Bull. Florida State Mus. Biol. Sci.*, 11(3): 99-220.

BRODKORB P., 1970. - Catalogue of fossil birds, part 4 (Columbiformes through Piciformes). *Bull. Florida State Mus. Biol. Sci.*, 15(4): 163-266.

BRODKORB P., 1978. - Catalogue of fossil birds, part 5 (Passeriformes). *Bull. Florida State Mus. Biol. Sci.*, 23(3): 139-228.

CASSOLI P.F., 1980. - L'Avifauna del Pleistocene Superiore delle Arene Candide (Liguria). *Memorie dell'Istituto Italiano di Paleontologia Umana*, 3: 155-234.

CHERRY J.F., 1981. - Pattern and process in the earliest colonization of the Mediterranean Islands. *Proceedings of the Prehistoric Society*, 47: 41-68.

CRAMP S. & SIMMONS K.E.L. (eds.), 1977. - The birds of the Western Palearctic, Vol. I.

CRAMP S. & SIMMONS K.E.L. (eds.), 1979. - The birds of the Western Palearctic, Vol. II.

CRAMP S. & SIMMONS K.E.L. (eds.), 1982. - The birds of the Western Palearctic, Vol. III.

CRAMP S. (ed.) 1985. - The birds of the Western Palearctic, Vol. IV.

DERMITZAKIS M.D., 1977. - The quaternary fossil mammals in the caves and karstic holes of Crete Island and their significance. *Bull. de la Société Spéléologique de Grèce*, vol. XIV: 152-190.

DERMITZAKIS M.D. & SONDAAR P.Y., 1978. - The importance of fossil mammals in reconstructing paleogeography with special reference to the Pleistocene Aegean Archipelago. *Annales Géologiques des Pays Helléniques*, 29: 808-840, Athènes.

FICK O., 1974. - Vergleichend morphologische Untersuchungen an Einzelknochen Europäischer Tauben. Dissertation, München.

FISCHER K. & STEPHAN B., 1974. - Eine pleistozäne Avifauna aus der Ghar Dalam-Höhle, Malta. *Z. geol. Wiss.*, Berlin, 2(4): 515-523.

FLORIT X. & ALCOVER J.A., in press. - Els ocells del Pleistocè Superior de la Cova Nova (Capdepera, Mallorca).

FRAGUGLIONE D., 1982. - La Bécasse fossile (*Scolopax rusticola* L.). Son origine, son expansion géographique au cours des millénaires. *La Mordorée*, 143: 3-27.

GAILLARD C., 1939. - Quelques oiseaux Oligocènes, Miocènes et Pliocènes. *Arch. Mus. Hist. nat. Lyon*, 15: 35-37.

GLIWICZ J., 1984. - Rodents on islands: living in a crowd. *Acta Zool. Fennica* , 172: 95-98.

GREUTER W., 1975. - Die Insel Kreta, eine geobotanische Skizze. Inst. ETH Stiftung, Rübel, Zürich, 55: 141-197.

HARRISON C.J.O. & WALKER C.A., 1977. - A re-examination of the fossil birds from the Upper Pleistocene in the London Basin. *London Naturalist*, 56: 6-9.

HARRISON C.J.O., 1982. - An Atlas of the birds of the Western Palaearctic. Collins, London.

HEILMANN G., 1927. - The origin of birds. Dover Publications, Inc., New York.

HOWARD H., 1932. - Eagles and eagle-like vultures of the Pleistocene of Rancho la Brea, California. *Carnegie Inst. of Wash., Publ.*, 429: 1-82, 29 pls., 3 text figs.

HOWARD H., 1947. - An ancestral Golden Eagle raises a question in taxonomy. *Auk*, 64: 287-291.

INGERSOLL E., 1923. - Birds in legend, fable and folklore. Singing Tree Press, Detroit (1968).

JÁNOSSY D., 1954. - Fossile Ornis aus der Höhle von Istallosko. *Aquila*, 55-58: 205-223.

JÁNOSSY D., 1957. - Die Vögelreste. *in*: G. Brunner - Die Breitenberghöhle bei Gössweinstein/Ofr. Eine Mindel/Riss und postglaziale Mediterrane Fauna. *Neues Jb. Geol. Paläont.*, 7-9: 352-378, 385-403, 18 fig.

JÁNOSSY D., 1963. - Letztinterglaziale Vertebrata fauna aus der Kalman Lambrecht-Höhle (Bükk-Gebirge, Nordost Ungarn). *Acta zool.*, 9(3-4): 293-331.

JÁNOSSY D., 1965. - Vogelreste aus den altpleistozänen Ablagerungen von Voigtstedt in Thüringen. *Pal. Abh.*, Berlin, A, II(2-3): 335-361.

JÁNOSSY D., 1972. - Die mittelpleistozäne Vögelfauna der Stránska Skála (CSSR). *Anthropos*, 20: 35-64, 6 fig., 2 pl

JÁNOSSY D., 1974. - Die mittelpleistozäne Vogelfauna von Hundsheim (Nieder- österreich). *Sitzungsberichte der Österr. Akad. Wiss., Math.-naturw. Kl.*, Abt I, 182(6-8): 211-257, 5 Abb., Wien.

JÁNOSSY D., 1983. - Humeri of Central European smaller Passeriformes. *Fragmenta Mineralogica et Paleontologica*, 11: 85-112.

JÁNOSSY D., 1983a. - Die mittelpleistozäne Vogelfauna von Prezletice bei Prag (CSSR). *Schiftenr. geol. Wiss.*, Berlin, 19/20: 247-269.

JUNGE G.C.A., 1953. - Fossil bones of a White-tailed Eagle, *Haliaeetus albicilla* (L.) from the Tegelen clay. *Proc. Kon. Ned. Akad. Wetensch.*, Amsterdam, B, 56(3): 285-290.

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

KUSS S.E., 1965. - Eine pleistozäne Säugetierfauna der Insel Kreta. *Ber. Naturf. Ges. Freiburg i. Br.*, 55(2): 271-348.

KUSS S.E., 1970. - Abfolge und Alter der pleistozänen Säugetierfaunen der Insel Kreta. *Ber. Naturf. Ges. Freiburg i. Br.*, 60(1): 35-83.

KUSS S.E., 1973. - Die pleistozänen Säugetierfaunen der ostmediterranen Inseln. *Ber. Naturf. Ges. Freiburg i. Br.*, 93 (1-2): 49-71.

LACK D., 1969. - The number of bird species on islands. *Bird Study*, 16 (4): 193-209.

LACK D., 1976. - Island biology illustrated by the land birds of Jamaica. 445 pages, 14 plates, 58 figures, 48 tables, 29 appendices. Oxford: Blackwell Scientific Publications.

LAMBERT A., 1957. - A specific check list of the birds of Greece. *Ibis*, 99: 43-68.

LAMBRECHT K., 1933. - Handbuch der Palaeornithologie. Bornträger, Berlin.

LYDEKKER R., 1890. - On the remains of some large extinct birds from the cavern-deposits of Malta. *Proc. Zool. Soc. London*, XXVIII: 403-411.

MACARTHUR R.H. and WILSON E.O., 1967. - The theory of island biogeography. 203 p., 60 fig., 13 tabl. Princeton University Press, New Yersey.

MALATESTA A. & SETTEPASSI F., 1954. - Fossili delle formazioni continentali Quaternari. *Boll. Serv. Geol. It.*, 76: 33-39, Roma.

MALATESTA A. & SURIANO F., 1970. - Avifauna pleistocenica di Alghero (Sardegna). *Boll. Serv. Geol. It.*, 91: 149-158, Roma.

MALATESTA A., 1980. - Dwarf deer and other late Pleistocene fauna of the Simonelli cave in Crete. *Academica Nazionale deï Linceï*, Quaderno N.249, Roma.

MAYAUD A., 1932. - Considérations sur la morphologie et la systématique de quelques Puffins. I. Les races de *Puffinus puffinus* . *Alauda*, 4: 41-78.

MAYHEW D.F., 1977. - The endemic Pleistocene murids of Crete I and II. *Proc. Kon. Ned. Akad. Wetensch.*, Amsterdam, B, 80(3): 182-214.

MILNE-EDWARDS A., 1867-71. - Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France. 4 Volumes, Masson, Paris.

MILLER L.H., 1910. - The condor-like vultures of Rancho la Brea. *University of California publications (geology)* , 6 (1): 1-19.

MOREAU R.E., 1930. - The birds of ancient Egypt. *in:* R. Meinertzhagen - Nicoll's Birds of Egypt (Based on notes by Michael J. Nicoll. With maps). 2 Vol. Hugh Rees, London.

MOREAU R.E., 1954. - The main vicissitudes of the European avifauna since the Pliocene. *Ibis*, 96: 411-431.

MOURER-CHAUVIRÉ C., 1975. - Les oiseaux du Pléistocène moyen et supérieur de France. *Docum. Lab. Géol. Fac. Sci. Lyon*, No. 64: 1-624.

MOURER-CHAUVIRÉ C., 1977. - Die Vogelreste aus den Mittelpleistozänen Mosbacher Sanden bei Wiesbaden (Hessen). *Mz. Naturw. Arch.*, 16: 35-46.

MOURER-CHAUVIRÉ C., MOYA S. & ADROVER R., 1977. - Les oiseaux des gisements Quaternaires de Majorque. *Nouv. Arch. Mus. Hist. nat. Lyon*, 15: 61-64.

MOURER-CHAUVIRÉ C., 1980. - Las aves del sitio de ocupacion achelense de Aridos-1 (Arganda, Madrid). *Ocupaciones Achelenses en el Valle del Jarama. Publicaciones de la Excelentisima Diputacion Provincial de Madrid:* 145-160.

MOURER-CHAUVIRÉ C., ALCOVER J.A., MOYA S. & PONS J., 1980. - Une nouvelle forme insulaire d'effraie geante, *Tyto balearica* n. sp., du Plio-Pléistocène des Baleares. *Géobios*, 13 (5): 803-811, 1 fig., 1 tabl., 1 pl.

MOURER-CHAUVIRÉ C., 1981. - Les oiseaux de la grotte de Kitsos (Attique, Grèce). *in*: La grotte préhistorique de Kitsos (Attique) sous la direction de Nicole Lambert. Éditions A.D.P.F., Paris, et École Française d'Athènes, t. 11, p. 595-606, pl. LVIII, tabl. 115.

MOURER-CHAUVIRÉ C. & WEESIE P.D.M., 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.

NIETHAMMER G., 1942. - Uber die Vogelwelt Kretas. *Ann. Nat. hist. Mus. Wien*, 53 (2): 5-59.

OLSON S.L. & HILGARTNER W.B., 1982. - Fossil and subfossil birds from the Bahamas. *in*: Storrs L. Olson, ed. *Smithsonian Contributions to Paleobiology*, 48: 22-56, Fig. 2-12, Tab. 5-12.

OLSON S.L. & JAMES H.F., 1982. - Prodromus of the fossil avifauna of the Hawaiian Islands. *Smithsonian Contributions to Zoology*, 365: 1-59, 12 figs., 5 tables.

OLSON S.L., 1985. - The fossil record of birds. Pages 79-238, 11 figs. *in*: D.S. Farner, J.R. King and K.C. Parkes (eds.). - Avian Biology, Vol. 8, Academic Press, New York, London.

OTTO C., 1981. - Vergleichend morphologische Untersuchungen an Einzelknochen in Zentraleuropa vorkommender mittelgrosser Accipitridae. I. Schädel, Brustbein, Schultergürtel und Vorderextremität. Dissertation, München.

PIEPER H., 1984. - Eine neue *Mesocricetus*-Art (Mammalia: Cricetidae) von der griechischen Insel Armathia. *Stuttgarter beitr. Naturk.*, B, 107: 1-9.

PIEPER H., 1985. - The fossil land birds of Madeira and Porto Santo. *Bocagiana*, 88: 1-6.

REUMER J.W.F., 1982. - Some remarks on the fossil vertebrates from Menorca, Spain. *Proc. Kon. Ned. Akad. Wetensch.*, Amsterdam, B, 85 (1): 77-87.

REUMER J.W.F., 1986. - Notes on the Soricidae (Insectivora, Mammalia) from Crete. I. The Pleistocene species *Crocidura zimmermanni* . *Bonn. zool. Beitr.*, 37: 161-171.

SCHMIDT-BURGER P., 1982. - Vergleichend morphologische Untersuchungen an Einzelknochen in Zentraleuropa vorkommender mittelgrosser Accipitridae. II. Becken und Hinterextremität. Dissertation, München.

SIMPSON G.G., ROE A. & LEWONTIN R.C., 1960. - Quantitative zoology, revised edition. Hartcourt, Brace & World Inc., New York.

SONDAAR P.Y. & BOEKSCHOTEN G.J., 1967. - Quaternary mammals in the South Aegean Island arc, I and II. *Proc. Kon. Ned. Akad. Wetensch.*, Amsterdam, B, 70: 556-576.

SONDAAR P.Y., 1971. - Paleozoogeography of the Pleistocene mamals from the Aegean. *in*: A. Strid (ed.) - Evolution in the Aegean. *Opera Botanica*, 30: 65-70.

SONDAAR P.Y., 1977. - Insularity and its effect on mammal evolution. *in*: M.K. Hecht and P.C. Goody, eds. Major patterns in vertebrate evolution, Proc. 1976, Nato Adv. Study Inst.: 671-707, New York.

STRESEMANN E., 1943. - Uberblick über die Vögel Kretas und den Vogelzug in der Agäis. *J. Orn.*, Berlin, 91: 448-514.

SYMEONIDIS N. & SONDAAR P.Y., 1975. - A new otter from the Pleistocene of Crete. *Annales Géologiques des Pays Helléniques*, 27: 11-24, Athènes.

TCHERNOV E., 1980. - The Pleistocene birds of Ubeidiya, Jordan Valley. The Israel Academy of Sciences and Humanities, Jérusalem, 83 p., 12 fig., 23 tabl., 6 pl.

VALLIANOS C., 1984. - Les oiseaux observés en Crète. *Biologia Gallo-Hellenica*, 11(1): 111-127.

VAURIE C., 1959. - The Birds of the Palaearctic fauna. Order Passeriformes. Witherby ed., London.

VAURIE C., 1965. - The Birds of the Palaearctic fauna, Non Passeriformes. Witherby ed., London.

VILLALTA J.F., 1964. - Datos para un catalogo de las aves fosiles del Cuaternario Espanol. *Speleon*, 15: 79-102.

VOOUS K.H., 1953. - The geographical variation of the Jay (*Garrulus glandarius*) in Europe: a study on individual and clinal variation. *Beaufortia*, 30(2): 1-41. Zoological Museum Amsterdam.

VOOUS K.H., 1960. - Atlas of European Birds. Nelson ed., London, 284 p., 355 fig., 419 maps.

VOOUS K.H., 1973. - List of recent Holarctic bird species, Non-Passerines. *Ibis*, 115: 612-638.

VOOUS K.H., 1977. - List of recent Holarctic bird species, Passerines. *Ibis*, 119: 223-250, 376-406.

VOS J. de, 1979. - The endemic Pleistocene deer of Crete I and II. *Proc. Kon. Ned. Akad. Wetensch.*, B, 82(1): 59-90.

VOS J. de, 1984. - The endemic Pleistocene deer of Crete. *Verh. Kon. Ned. Akad. Wetensch. Afd. Natk*, Eerste Reeks, Deel 31.

WATSON G.E., 1964. - Ecology and evolution of passerine birds on the islands of the Aegean Sea. Ph. D. dissertation, Yale University.

WEESIE P.D.M., 1982. - A Pleistocene endemic island form within the genus *Athene: Athene cretensis* n. sp. (Aves, Strigiformes) from Crete. *Proc. Kon. Ned. Akad. Wetensch.*, Amsterdam, B, 85(3): 323-336.

WEESIE P.D.M., 1982a. - The fossil bird remains in the Dubois collection. Modern Quaternary research in southeast Asia, 7: 87-90.

WEESIE P.D.M., 1984. - On some Pleistocene bird fossils from the south Aegean island of Karpathos (Greece). *Géobios*, 17(6): 845-849, 1 fig.

WETMORE A., 1922. - Remains of birds from caves in the Republic of Haiti. *Smiths. Miscell. Coll.*, 74: 1-4, 2 figs.

WETMORE A., 1937. - Bird remains from cave deposits on Great Exuma Island in the Bahamas. *Bull. Mus. comp. Zool.*, 80: 427-441, 16 figs., 1 pl.

WILLEMSEN G.F., 1980. - Comparative study of the functional morphology of some Lutrinae, especially *Lutra lutra*, *Lutrogale perspicillata* and the Pleistocene *Isolalutra cretensis*. *Proc. Kon. Ned. Akad. Wetensch.*, Amsterdam, B, 83(3): 289-326.

WRAGG G., 1985. - The comparative biology of Fluttering Shearwater and Hutton's Shearwater and their relationship to other shearwater species. Master Applied Sciences, Univ. Canterbury.

ZOHARY M. and ORSHAN G., 1965. - An outline of the geobotany of Crete. *Isr. J. Bot.*, 14 (Suppl.): 1-49.

						N	Min	Max	M
P.p. mauretanicus	MAYAUD, 1932	82,3	83,5	82,8		11	81,3	88,7	84,3
	ALCOVER, pers. comm.	81,3	84,0	85,5	83,0				
		83,4	86,5	88,7	86,4				
P.p. puffinus	BMNH	83,3	83,4	80,8	79,5	11	78,7	83,4	80,9
		78,7	80,0						
	RMNH	80,5							
	MAYAUD, 1932	78,7	82,1						
	WRAGG, 1985	80,7	82,1						
P.p. yelkouan	MAYAUD, 1932	74,3	77,8	78,7	79,0	8	74,3	79,0	77,7
		79,0	78,8						
	WRAGG, 1985	75,5	78,3						
P. assimilis	WRAGG, 1985	59,1	61,5	59,0	58,7	13	56,9	65,4	60,6
		61,5	61,1	64,6	65,4				
		63,0	62,6	57,2	57,5				
		56,9							
Fossil Ge-II5		73,6							

Table 1. The length of the humerus (in mm) in the three recent western Palearctic subspecies of *Puffinus puffinus*, in *P. assimilis*, and the length of the Cretan fossil bone.

G. fulvus	N	Min	Max	M	*G. melitensis*	Size difference
Height a.s. of talon dig. 1	7	7,8	10,5	9,3	11,0	18,3 %
Width a.s. of talon dig. 1	7	7,0	9,0	8,3	9,7	16,9 %
A. monachus						
Height a.s. of talon dig. 2	6	11,6	13,2	12,2	15,9	30,3 %
Width a.s. of talon dig. 2	4	9,5	10,8	10,0	14,0	40,0 %

Table 2. Comparison of the height and width (in mm) of the articular surfaces (a.s.) of the talons dig. 1 and dig. 2 in recent *G. fulvus* and *A. monachus* respectively, with their counterparts in fossil, Cretan *G. melitensis*.

		N	Min	Max	M
A. gentilis	female	4	97,6	98,6	98,2
A. gentilis	male	3	85*	89,8	86,9
A. nisus	female	13	57*	63,2	60,6
A. nisus	male	8	48*	54,5	51,1

Table 3. The length of the humerus (in mm) in *A. gentilis* and *A. nisus*, as measured in the RMNH, NMB and MNCM. Values marked with * have been obtained by extrapolation.

Tibiotarsus Li-V804	*Aquila chrysaetos simurgh* n. ssp.	*Aquila chrysaetos*						
		N	Min	Max	M	SD	t	Size diff.
Length	193,0*	22	150,0	182,0	168,3	9,3334	2,6	14,7 %
Distal width	26,2	22	19,3	24,0	21,9	1,4915	2,8	19,6 %
Distal depth	18,2	21	13,3	17,1	15,2	1,1853	2,5	19,7 %
Width in the middle	12,7	22	9,2	12,6	11,3	0,7583	1,8	12,4 %
Femur Li-d801								
Length	142,0*	40	114,2	136,4	127,9	5,5583	2,5	11,0 %
Width in the middle	15,5	40	10,9	15,4	13,1	1,0174	2,3	18,3 %
Sternum Li-B809								
Width over tuberculi labri ventrales	55,1	37	41,0	51,0	45,7	2,4853	3,7	20,6 %

Table 4. Comparison of some parameters (in mm) of the bones of fossil *A. c. simurgh* n. ssp. and the same parameters of their counterparts in modern *A. chrysaetos* . Values marked with * have been obtained by extrapolation. The size difference between the two forms is given as a percentage of the mean values in *A. chrysaetos* .

A. chrysaetos		*A. c. simurgh*	
Front part	Rear part	Front part	Rear part
		Li-V(1)	Li-V(1)
		Li-B(1)	
Li-D(3)	Li-d(1)		Li-d(1)

Table 5. The layers in Liko cave in which fossil remains of *A. chrysaetos* and *A. c. simurgh* have been found. The number of fossils is given in parentheses. There is no known stratigraphical correlation between the layers in the front and those in the rear part of the cave. The fossil bone found in layer Li-V comes from either the front or the rear part of Liko cave.

Recent								
Fraguglione, 1982	37,5	38,5	39,0	38,0				
BMNH	37,2	35,9	37,7	37,5	37,5	38,4	36,5	37,0
RMNH	38,3	37,0	38,9	39,2	37,7			
NMB	37,7	37,0	39,1	36,4				
UCB	37,5	36,8	36,7					
MNCM	37,7	41,8	37,5	37,4	36,8			
Pleistocene								
France (Fraguglione, 1982)			37,0	38,5	39,0			
Crete Li-B803			40,0					
Li-a880			40,0					
Li-a881			41,6					
Ge-IV2			39,0					

	N	Min	Max	M	SD
Recent	29	35,9	41,8	37,73	1,1449
Pleistocene Crete	4	39,0	41,6	40,15	1,0755

Table 6. The length (in mm) of the carpometacarpus of Recent and Pleistocene *S. rusticola* .

	C. oenas			*C. livia*		
Length	N	Min	Max	N	Min	Max
FICK (1974)	18	42,9	48,4	8	40,7	46,4
MOURER-CHAUVIRÉ (1975)	5	44,8	47,0	10	42,2	46,4
BMNH	5	45,9	47,4	3	42,3	44,2
Combined	28	42,9	48,4	21	40,7	46,4
Width						
FICK (1974)	18	4,8	5,5	8	5,0	5,2
MOURER-CHAUVIRÉ (1975)	5	5,1	5,6	10	4,7	5,3
Combined	23	4,8	5,6	18	4,7	5,3

Table 7. Ranges (in mm) of the lehgth and width in the middle of the humerus of recent *C. oenas* and *C. livia*, as observed by different authors.

C. oenas	47,0	47,3	47,8	44,5	44,8	45,3	45,8	44,9	44,4	44,6
	5,6	5,8	5,7	5,4	5,5	5,4	5,6	5,5	5,4	5,4
	46,0	42,9	46,0	45,9						
	5,5	5,4	5,6	5,4						
C. livia	42,3	41,5	42,3							
	5,2	4,8	5,2							
C. oenas or *C. livia*	45,8	45,0	44,4	45,7	44,8	44,0	43,6	43,4	45,7*	43,4*
	5,3	4,9	5,1	5,4	5,3	5,3	5,2	5,0	5,2	5,2

Table 8. The length and width in the middle (in mm) of the fossil humeri attributed to *C. oenas, C. livia* and either to *C. oenas* or *C. livia* . Values marked with * have been obtained by extrapolation.

	C. oenas	*C. livia*	*C. oenas* or *C. livia*	Total
Ulna	14	2	4	20
Humerus	14	3	10	27

Table 9. The number of the identified ulnae and humeri of *C. oenas* and *C. livia* .

	IPH		RMNH				IES	MNCM
C. ruficollis	39,1						39,0	
C. europaeus	36,5	34,3	36,6	39,3	38,6	36,7		34,8
Fossil Li-B912	35,2							

Table 10. Length (in mm) of the humerus of recent *C. europaeus* and *C. ruficollis* , and of the fossil humerus Li-B912.

									N	Min	Max	M	SD
Erithacus rubecula			16,4	16,6	15,9	16,2	16,8	15,7	22	15,4	17,7	16,16	0,5508
					1,4	1,5	1,5	1,5	20	1,4	1,6	1,50	0,0686
	16,0	16,5	16,4	15,9	16,0	17,7	15,8	15,5					
	1,5	1,4	1,6	1,4	1,5	1,6	1,5	1,4					
	16,1	17,0	16,3	15,5	15,5	16,3	15,4	16,1					
	1,5	1,6	1,6	1,5	1,5	1,5	1,5	1,4					
Luscinia megarhynchos				16,7	17,0	16,8	15,8	17,0	7	15,8	17,9	17,01	0,7290
						1,5	1,2	1,6	5	1,2	1,6	1,48	0,1643
					17,9	17,9							
					1,5	1,6							
Luscinia luscinia			18,0	18,3	18,2	16,4	17,2	18,6	6	16,4	18,6	17,78	0,8256
					1,6	1,5	1,7	1,8	4	1,5	1,8	1,65	0,1291
Fossil cf. *Erithacus rubecula*				16,2	17,5	16,1	16,1	16,0	10	15,5	17,5	16,24	0,5125
				1,5	1,6	1,5	1,5	1,5	10	1,5	1,6	1,52	0,0422
				15,5	16,2	16,3	16,0	16,5					
				1,6	1,5	1,5	1,5	1,5					

Table 11. Length and width in the middle (in mm) of the humerus of recent *E. rubecula, L. megarhynchos* and *L. luscinia* (BMNH, IPH, NMB, RMNH, UCB). The same measurements of the fossil humeri tentatively attributed to *E. rubecula* (in the same order as listed above). Underscored numbers are from Jánossy (1983).

								N	Min	Max	M	SD
Saxicola torquata			15,3	16,1	15,9	15,6	15,9	5	15,3	16,1	15,76	0,3130
				1,4	1,4	1,4	1,5	4	1,4	1,5	1,43	0,0500
Saxicola rubetra		15,6	17,3	16,9	16,3	17,1	16,4	11	15,2	17,3	16,43	0,6467
		1,4	1,5	1,5	1,4	1,5	1,6	10	1,4	1,6	1,50	0,0816
		16,6	16,9	15,9	15,2	16,5						
		1,6	1,5		1,4	1,6						
Phoenicurus moussieri			16,0					1			16,0	
			1,3					1			1,3	
Phoenicurus phoenicurus			15,5	15,1	15,4	15,8	15,6	12	15,1	17,8	16,12	0,7814
			1,5	1,5	1,4	1,5	1,5	10	1,4	1,6	1,51	0,0568
	15,9	17,8	16,0	16,7	16,2	17,2	16,2					
	1,5	1,5	1,5			1,6	1,6					
Phoenicurus ochruros			17,5	18,3	17,7	18,2	17,8	7	17,2	18,3	17,76	0,3867
					1,6	1,8	1,6	5	1,5	1,8	1,60	0,1225
				17,6	17,2							
				1,5	1,5							
Oenanthe deserti		20,3	19,8	18,7	19,6	19,2		5	18,7	20,3	19,52	0,6058
Oenanthe hispanica		2,0	1,8					2	1,8	2,0	1,90	0,1414
Oenanthe leucura		22,8						1			22,8	
		2,0						1			2,0	
Fossil *Oenanthe* cf. *O. hispanica*		18,1	17,6	17,7	18,3	18,5	18,3	6	17,6	18,5	18,08	0,3601
		1,7	1,7	1,7	1,6	1,8	1,8	6	1,6	1,8	1,72	0,0753

Table 12. Length and width in the middle (in mm) of the humerus of some members of the genera *Saxicola, Phoenicurus* and *Oenanthe* (BMNH, IPH, NMB, RMNH, UCB). The same measurements of the fossil humeri tentatively attributed to *O. hispanica* (in the same order as listed above). Underscored numbers are from Jánossy (1983); this goes for all other occurrences of "Jánossy (...)", which I shall simply underscore from now.

	Oenanthe oenanthe						*Oenanthe hispanica*					
	Length			Width			Length			Width		
	N	Min	Max	N	Min	Max	N	Min	Max	N	Min	Max
JÁNOSSY (1983)	10	17,8	20,2	10	1,8	2,0	4	17,0	19,0	4	1,6	1,9
This paper	5	18,7	20,3	2	1,8	2,0	4	17,7	18,3	2	1,6	1,7
Combined	15	17,8	20,3	12	1,8	2,0	8	17,0	19,0	6	1,6	1,9

Table 13. Ranges (in mm) of the length and width in the middle of the humerus of *O. oenanthe* and *O. hispanica*, as observed by two authors.

						N	Min	Max	M	SD
Monticola	26,6	26,9	26,5	24,6	23,5	8	23,5	27,2	26,01	1,2766
solitarius	2,6	2,4	2,5	2,5	2,1	8	2,1	2,6	2,44	0,1506
	26,5	26,3	27,2							
	2,5	2,4	2,5							
Monticola	24,3	24,6	25,0	25,2	24,2	7	24,2	25,9	24,83	0,5908
saxatilis	2,2	2,4	2,4	2,3	2,5	7	2,2	2,5	2,37	0,0951
	24,6	25,9								
	2,4	2,4								
Fossil *Monticola*			25,9	26,5						
cf. *M. solitarius*			2,6	2,5						

Table 14. Length and width in the middle (in mm) of the humerus of recent *M. solitarius* and *M. saxatilis* (BMNH, IPH, NMB, RMNH). The same measurements of fossil *Monticola* cf. *M. solitarius* (in the same order as listed). The measurement of Jánossy (1983) underscored.

Length	38,1	37,9	38,3	38,6	36,5	38,2	37,5
Width	3,8	3,7	3,8	3,9	3,8	3,9	3,9

Table 15. Length and width in the middle (in mm) of the fossil humeri tentatively attributed to *Z. dauma* (in the same order as listed above).

							N	Min	Max	M	SD
Muscicapa	16,1	16,7	16,3	15,3	16,5	17,2	8	15,3	17,2	16,30	0,5477
striata		1,5	1,6	1,4	1,6	1,6	7	1,4	1,6	1,53	0,0756
		16,2	16,1								
		1,5	1,5								
Fossil		16,7					1			16,7	
Li-a898		1,6					1			1,6	

Table 16. Length and width in the middle (in mm) of the humerus of recent *M. striata* (BMNH, IPH, NMB, RMNH, UCB). The same measurements of the fossil humerus tentatively referred to this species.

	Recent *Garrulus glandarius*					Pleistocene Cretan *Garrulus glandarius*					
	N	Min	Max	M	SD	N	Min	Max	M	SD	t
Hum.	26	38,5	43,9	41,3	1,4788	19	35,1	40,9	37,8	1,5763	7,6
Ulna	22	44,9	52,3	48,8	2,1666	6	43,0	48,2	45,0	2,1433	3,8
Cmc.	23	24,6	28,9	26,8	1,0369	3	24,0	25,1	24,7	0,5859	3,4
Fem.	21	35,6	42,9	38,2	1,7408	2	37,9	38,9	38,4	0,7071	0,2
Tt.	20	56,2	63,3	59,7	2,3990	2	63,1	63,3	63,2	0,0707	2,0
Tmt.	20	39,3	45,0	42,2	1,6441	4	40,6	43,0	42,0	1,1087	0,2

Table 17. Comparison of the length (in mm) of the wing and leg bones of Pleistocene Cretan *G. glandarius* and the same parameters of Recent *G. glandarius* (BAI, BMNH, IPH, NMB, RMNH, including measurements given by Jánossy, 1954).

Pyrrhocorax	57,0	53,5								
pyrrhocorax	5,7	5,6								
Pyrrhocorax	45,6	46,3	43,6	42,8						
graculus	5,2	5,6	5,1	4,8						
Corvus	46,7	47,1	47,2	44,6	48,3	45,5	45,0	46,9	44,7	49,2
monedula	4,8	4,6	4,5	4,5	4,7	4,6	4,5	4,6	4,6	5,1

Table 18. Length and width in the middle (in mm) of the fossil humeri attributed to *P. pyrrhocorax, P. graculus* and *C. monedula.*

								N	Min	Max	M	SD
Carduelis		13,4	13,1					2	13,1	13,4	13,25	0,2121
linaria		1,4	1,3					2	1,3	1,4	1,35	0,0707
Carduelis		13,4	14,0	13,4	13,6			4	13,4	14,0	13,60	0,2828
flammea		1,4	1,5	1,4	1,4			4	1,4	1,5	1,43	0,0500
Carduelis		14,0	14,1	13,8	13,7	14,0	14,0	12	13,4	14,3	13,94	0,2392
spinus		1,4	1,6	1,4	1,5	1,4	1,5	12	1,4	1,6	1,47	0,0651
		14,3	13,8	13,4	14,2	14,0	14,0					
		1,4	1,5	1,5	1,5	1,4	1,5					
Serinus		17,1	16,7	14,0	15,4	15,0	15,0	14	14,0	17,1	15,30	0,9232
serinus		1,6	1,6	1,4	1,5	1,4	1,6	14	1,3	1,6	1,47	0,0914
14,9	15,0	15,7	14,8	16,7	14,8	14,5	14,6					
1,5	1,4	1,3	1,4	1,5	1,5	1,5	1,4					
Carduelis			15,1	15,7	15,9	14,7		4	14,7	15,9	15,35	0,5508
citrinella			1,5	1,5	1,7	1,5		4	1,5	1,7	1,55	0,1000
Carduelis		15,6	17,0	16,3	16,0	16,3	15,8	26	14,4	17,0	15,90	0,5963
carduelis		1,6	1,8	1,7	1,7	1,7		25	1,4	1,8	1,61	0,0971
15,1	16,1	16,1	16,3	15,9	15,8	16,1	15,9					
1,5	1,5	1,6	1,6	1,6	1,5	1,6	1,7					
16,3	16,1	16,1	16,2	15,9	15,9	16,6	15,5					
1,7	1,6	1,8	1,6	1,6	1,5	1,7	1,6					
14,4	15,1	16,6	14,5									
1,5	1,6	1,6	1,4									
Carduelis			15,9	15,5	16,2	17,0	15,4	6	15,4	17,0	16,03	0,5820
flavirostris			1,6	1,6	1,6	1,7	1,6	6	1,6	1,7	1,62	0,0408
			16,2									
			1,6									

Table 19. Length and width in the middle (in mm) of the humerus of some Fringillidae-species (BMNH, IPH, MNCM, NMB, RMNH, UCB). Underscored numbers are from Jánossy (1983).

								N	Min	Max	M	SD
Carduelis		16,7	15,8	16,4	17,3	17,1	15,6	16	15,5	17,3	16,56	0,5476
cannabina			1,6	1,6	1,8	1,7	1,7	15	1,5	1,8	1,68	0,0862
16,8	16,3	16,9	16,4	16,8	16,9	15,5	16,9					
1,7	1,6	1,7	1,7	1,7	1,7	1,5	1,8					
16,4	17,2											
1,6	1,8											
Loxia			18,0					1			18,0	
leucoptera			2,0					1			2,0	
Carpodacus			18,7	17,5	18,2			3	17,5	18,7	18,13	0,6028
erythrinus			1,8	1,8	1,8			3			1,8	
Fringilla			19,2	19,1	17,5	18,7	19,0	14	17,5	19,6	18,65	0,6124
montifringilla					1,6	1,7	1,9	12	1,6	2,0	1,82	0,1115
19,1	19,6	18,2	17,7	19,1	18,3	18,4	19,0					
2,0	1,9	1,8	1,8	1,9	1,8	1,7	1,9					
18,2												
1,8												
Pyrrhula		18,1	19,1	18,9	17,7	17,7	17,9	20	17,7	21,2	18,82	0,9972
pyrrhula		1,8	1,8	1,9	1,7	1,8	1,7	19	1,7	2,2	1,86	0,1300
19,0	17,7	18,0	18,6	19,3	18,2	18,0	20,1					
1,9	1,8	1,7	1,8	1,9	1,8		1,9					
19,2	18,2	19,2	21,2	19,9	20,4							
1,8	2,2	1,9	2,0	1,9	2,1							
Fringilla		18,8	19,7	19,2	19,3	18,4	18,2	29	17,1	19,8	18,94	0,5559
coelebs		1,9	1,9	1,8	2,0	2,0		27	1,6	2,0	1,83	0,1171
18,9	19,2	19,4	19,1	19,6	18,6	19,3	18,7					
	1,9	1,9	1,8	1,8	1,8	1,9	1,8					
19,3	18,8	19,2	18,7	19,4	19,1	17,1	18,6					
1,8	1,8	1,6	1,8	1,9	2,0	1,6	1,8					
18,3	18,8	19,3	19,8	19,5	18,7	18,4						
1,6	2,0	1,9	1,8	1,9	1,7	1,7						

Table 19. (continued)

								N	Min	Max	M	SD
Carduelis		19,8	19,5	18,9	19,0	19,4	19,3	26	18,6	20,0	19,17	0,3762
chloris		2,0	1,8	1,8	1,8	2,0		24	1,7	2,0	1,84	0,0929
19,4	19,0	18,9	19,1	19,7	18,8	19,0	18,7					
	1,9	2,0	1,9	1,8	1,8	1,8	1,7					
19,0	19,1	18,9	18,7	19,4	19,2	19,7	19,3					
1,7	1,8	1,9	1,8	1,8	1,8	1,8	1,9					
18,6	20,0	19,3	18,6									
1,7	1,8	2,0	1,9									
Loxia			18,1	20,3	19,9	20,0	19,9	17	18,1	20,8	19,68	0,8393
curvirostra			2,1	2,3	2,1	2,2	2,2	15	2,0	2,3	2,16	0,0828
20,5	19,2	18,2	19,8	20,6	19,2	20,3	19,7					
2,2	2,1			2,3	2,1	2,1	2,1					
20,8	20,3	19,4	18,3									
2,2	2,2	2,0	2,2									
Loxia			20,4	21,1	20,1			3	20,1	21,1	20,53	0,5132
pytyopsittacus				2,3	2,1			2	2,1	2,3	2,20	0,1414
Pinicola			23,0	23,9	23,7	23,0	22,2	8	22,2	25,0	23,35	0,8485
enucleator			2,3	2,3	2,3	2,3		5	2,3	2,4	2,32	0,0447
22,8	23,2	25,0										
		2,4										
Coccothraustes			23,6	25,6	23,7	24,2	25,8	24	22,4	25,8	23,95	0,7951
coccothraustes			2,1	2,5	2,4	2,5	2,6	21	2,1	2,7	2,38	0,1446
23,0	24,2	22,4	23,5	23,3	23,5	23,8	24,9					
			2,3	2,2	2,2	2,4	2,5					
25,0	23,8	23,4	23,5	23,6	24,0	23,4	24,3					
2,7	2,3	2,4	2,4	2,2	2,3	2,3	2,5					
23,7	23,7	24,8										
2,4	2,3	2,4										

Table 19. (continued)

									N	Min	Max	M	SD
Emberiza			25,3	24,1	21,8	23,9	24,0	26,2	12	21,8	26,2	24,23	1,2743
calandra			2,4	2,2	2,1	2,2	2,2	2,5	10	2,0	2,5	2,25	0,1434
	23,9	25,5	24,7	24,6	24,6	22,1							
	2,3	2,3			2,3	2,0							
Fossil cf. *Emberiza*						24,9	24,2						
calandra						2,5	2,2						
Emberiza				20,9	21,4	20,0	20,8	20,8	21	19,4	21,8	20,54	0,6538
citrinella				2,0	1,9	1,9	1,9	1,8	18	1,8	2,0	1,94	0,0698
	20,9	20,3	20,1	19,6	19,4	21,0	20,4	20,8					
	2,0	2,0	1,8			2,0	2,0	2,0					
	20,3	21,8	21,7	20,0	20,0	19,8	20,3	21,0					
		2,0	1,9	1,9	1,9	1,9	2,0	2,0					
Emberiza			20,3	20,0	20,0	20,5	19,8	20,0	13	19,5	20,5	19,99	0,2753
hortulana			2,0	1,9	1,9	1,9	2,0	1,9	11	1,7	2,0	1,89	0,0944
	19,5	19,7	20,1	19,7	20,0	20,3	20,0						
	1,8	1,7	2,0			1,8	1,9						
Emberiza			19,9	16,7	19,3	19,7	19,4	19,9	10	16,7	20,2	19,28	0,9705
cirlus			1,9	1,7	1,8	1,8	1,8	1,8	10	1,7	1,9	1,79	0,0568
	20,2	19,2	19,3	19,2									
	1,8	1,8	1,7	1,8									
Emberiza				18,8	18,6	17,5	18,4	18,7	11	17,4	19,6	18,42	0,6780
schoeniclus				1,7	1,5	1,6	1,7	1,6	11	1,5	1,8	1,65	0,0934
	19,2	18,0	19,6	17,9	17,4	18,5							
	1,7	1,5	1,7	1,7	1,7	1,8							

Table 20. Length and width in the middle (in mm) of the humerus of some modern *Emberiza* species (BMNH, IPH, MNCM, NMB, RMNH, UCB). The same measurements of the fossil humeri tentatively attributed to *E. calandra* (in the same order as listed). Underscored numbers are from Jánossy (1983).

	Li-a/b881	Li-c935	Li-c/d811	
Emberiza sp. gr. 1	19,3 1,9	19,0 1,8	19,1 1,8	
	Li-a/b884	Li-a991	Li-d901	Li-d902
Emberiza sp. gr. 2	20,3* 1,9	20,6 2,0	20,7 2,0	21,6 2,1

Table 21. Length and width in the middle (in mm) of the fossil humeri attributed to *Emberiza* species group 1 and 2. The value obtained by extrapolation is marked with *.

Layer	Li-O	V	A	B C	D	a	a/b	b	c	c/d	d	e	T	I
P. aristotelis				2									2	1
B. ruficollis	1				1								2	1
A. penelope				1									1	1
A. querquedula												1	1	1
H. albicilla		1							1				2	2
G. barbatus				1									1	1
G. fulvus	1					1							2	1
G. melitensis	1								2				3	1
A. monachus		1			1								2	2
A. gentilis	1	1		3		2	2						9	4
A. nisus		2	3	3	2								10	5
B. buteo		2		4	3	2			2				13	5
A. chrysaetos					3						1		4	2
A. c. simurgh		1		1							1		3	3
F. t. tinnunculus	2	3		5	1	5	2				1		19	7
F. subbuteo				1		1							2	2
F. eleonorae		1		2		7	1		1		3		15	5
F. peregrinus		1				1							2	2
C. coturnix			1										1	1
P. porzana									2		1		3	2
G. chloropus				1									1	1
Glareola sp. gr.						1							1	1
C. canutus		1											1	1
S. rusticola	2	1	1	11		7	1		2	1	3		29	8
C. livia		1							1		4		6	4
C. oenas	1			9		6	3		6	1	6		32	12
C. livia/oenas	3	3		36	7	33	11	3	34	3	34	1	168	10
C. palumbus	1	2	1	11		5	4		5				29	7
T. alba	4	3	1	12	4	10		2	6	1	6		49	12
O. scops				8		6			5		2		21	9
K. zeylonensis					1								1	1
A. cretensis	94	198	60	578	17	619	281	120	383	6	220	13	2589	163

Table 22. The bird species identified, the number of their remains for each layer in Liko cave, the total number of their remains in Liko cave (under "T") and (under "I") the minimum number of their individuals in Liko cave.

Layer	Li-O	V	A	B C	D	a	a/b	b	c	c/d	d	e	T	I
A. flammeus											1		1	1
A. funereus				4		9			5		5	1	24	8
C. europaeus				1									1	1
A. apus		2				1					3		6	3
A. melba				2		1			2				5	3
D. leucotos				1									1	1
C. brachydactyla											1		1	1
H. daurica				1					2				3	3
P. collaris	1			1		5		2					9	7
E. rubecula		1				2	4		1		2		10	7
O. hispanica				1		5							6	4
M. solitarius		1							1				2	2
Z. dauma				4		1			4		1		10	7
T. iliacus				1		2	2						5	3
Turdus sp. gr. 1	3	1		7		13	16		5	1	1	1	48	28
Turdus sp. gr. 2	5	7		18		7	13		16	1	9		76	44
Turdus sp. gr. 3				1					1		1		3	3
M. striata						1							1	1
G. glandarius	5			19		16	6		16		5		67	18
P. graculus		4		7		7	3		6		2		29	8
P. pyrrhocorax		1		9		4	5						19	4
C. monedula	2	6	1	27 1	5	16	4		3	2	6		73	16
Corvus sp. gr.	3	3		5	1	5	1		1				19	6
Sturnus sp. gr.		1		3					2		1		7	5
Fringilla sp. gr.		1		2		2	2		2				9	6
C. chloris		1				2			1				4	4
P. pyrrhula						1							1	1
C. coccothraustes		2				3							5	3
E. calandra							1					1	2	2
Emberiza sp. gr. 1							1		1	1			3	3
Emberiza sp. gr. 2						1	1				2		4	4

Table 22. (continued)

	Li-o	V	A	B	C	D	a	a/b	b	c	c/d	d	e	T
i.s.	130	253	68	803	1	46	810	364	127	519	17	322	18	3478
u.s.	241	313	192	959	60	112	1678	771	356	1086	50	656	88	6562
t.s.	371	566	260	1762	61	158	2488	1135	483	1605	67	978	106	10,040

Table 23. The number of identified specimens (i.s.), the approximate number of unidentified specimens (u.s.) and the approximate total number of specimens (t.s.) for each layer in Liko cave. Totals under "T".

	Gu-B	Gu-C	Ge-II	Ge-IV	So	Sm	Re	MV	T	I
P; p. yelkouan			1						1	1
A. querquedula		1							1	1
G. barbatus				1				1	2	2
G. fulvus							1		1	1
G. melitensis						1			1	1
B. buteo					1				1	1
A. chrysaetos					1				1	1
F. t. tinnunculus	1								1	1
F. atra	1								1	1
S. rusticola				1					1	1
C. livia	1								1	1
C. livia/oenas	3	1	2						6	3
C. oenas		2							2	2
C. palumbus	1								1	1
T. alba	1								1	1
O. scops		1							1	1
A. cretensis	25	16	7				2		50	8
A. flammeus	1	1	1				2		5	4
D. leucotos		1							1	1
Turdus sp. gr. 1	2								2	2
G. glandarius	8	6	1					1	16	6
P. graculus				3					3	1
C. monedula	5	3		1	1			1	11	5
C. corax	1								1	1

Table 24. The bird species identified for each locality on Crete other than Liko cave, the number of their remains, the total number of their remains (under "T") and (under "I") the minimum number of their individuals.

	Gu-B	Gu-C	Ge-II	Ge-IV	So	Sm	Re	MV	T
i.s.	50	32	12	6	3	1	5	3	112
u.s.	127	48	2	27	5		13	8	230
t.s.	177	80	14	33	8	1	18	11	342

Table 25. The number of identified specimens (i.s.), the approximate number of unidentified specimens (u.s.) and the approximate total number of specimens (t.s.) for each locality on Crete other than Liko cave. Totals under "T".

Order	Pleistocene	Recent	Passeriform family	Pleistocene	Recent
			Alaudidae	1	5
Podicipediformes		3	Hirundinidae	1	5
Procellariiformes	1	2	Motacillidae		8
Pelecaniformes	2	4	Troglodytidae		1
Ciconiiformes		11	Prunellidae	1	2
Anseriformes	4	6	Turdidae	8	14
Accipitriformes	14	31	Sylviidae		24
Galliformes	1	2	Muscicapidae	1	3
Gruiformes	3	7	Paridae		3
Charadriiformes	3	39	Sittidae		1
Columbiformes	3	6	Certhiidae		1
Cuculiformes		1	Oriolidae		1
Strigiformes	6	4	Laniidae		4
Caprimulgiformes	1	1	Corvidae	6	7
Apodiformes	2	3	Sturnidae	1	1
Piciformes	1	1	Passeridae		3
Coraciiformes		4	Fringillidae	4	9
Passeriformes	26	99	Emberizidae	3	7
TOTAL	67	224		26	99

Table 26. The bird orders -and the number of species within each order- present in the Pleistocene and Recent avifaunas of Crete (left). The bird families -and the number of species within each family- within the Passeriformes in both avifaunas (right).

		HABITAT							
	CLIMATIC ZONES	AR	S	WR	OW	F	FW	M	C
Puffinus puffinus	B-Tr								C
Morus bassana	SA-STr								C
Phalacrocorax aristotelis	SA-STr								C
Anser albifrons	A-WT		S				FW		
Branta ruficollis	A-T						FW		C
Anas penelope	SA-WT						FW		C
Anas querquedula	B-STr						FW		
Haliaeetus albicilla	SA-T						FW		C
Gypaetus barbatus	WT							M	
Gyps fulvus	WT-STr							M	
Aegypius monachus	WT							M	
Accipiter gentilis	SA-WT					F			
Accipiter nisus	SA-STr				OW	F			
Buteo buteo	B-Tr			WR					
Aquila chrysaetos	B-WT							M	
Falco tinnunculus	B-Tr			WR					
Falco subbuteo	B-STr				OW				
Falco eleonorae	WT-STr								C
Falco peregrinus	A-Tr			WR					
Coturnix coturnix	T-STr		S						
Porzana porzana	B-STr						FW		
Gallinula chloropus	B-STr						FW		
Fulica atra	B-STr						FW		
Glareola sp. gr.	T-Tr						FW		C
Calidris canutus	A-Tr								C
Scolopax rusticola	B-WT					F			
Columba livia	T-STr	AR						M	C
Columba oenas	B-WT				OW	F			
Columba palumbus	B-WT				OW	F			
Tyto alba	T-Tr				OW				
Otus scops	T-Tr				OW				
Ketupa zeylonensis	WT				OW	F	FW		
Asio flammeus	SA-STr		S		OW		FW		
Aegolius funereus	B-T					F			
Caprimulgus europaeus	B-Tr				OW				
Apus apus	B-Tr					F		M	C
Apus melba	T-Tr							M	C
Dandrocopos leucotos	B-T					F			
Calandrella cinerea	WT-Tr	AR							

Table 27. The climatic zones and habitats of the neospecies of the Pleistocene avifauna of Crete. Abbreviations : see text.

					HABITAT				
	CLIMATIC ZONES	AR	S	WR	OW	F	FW	M	C
Hirundo daurica	WT-Tr	AR			OW			M	C
Prunella collaris	T-WT							M	
Erithacus rubecula	B-STr					F			
Oenanthe hispanica	WT-STr	AR							
Monticola solitarius	WT-STr	AR						M	C
Zoothera dauma	B-STr					F			
Turdus iliacus	SA-WT				OW				
Turdus sp. gr. 1	SA-WT				OW				
Turdus sp. gr. 2	B-WT				OW				
Turdus sp. gr. 3	B-WT				OW				
Muscicapa striata	B-Tr					F			
Garrulus glandarius	B-WT				OW	F			
Pyrrhocorax graculus	WT							M	
Pyrrhocorax pyrrhocorax	T-WT							M	
Corvus monedula	B-WT				OW				
Corvus sp. gr.	SA-WT			WR					
Corvus corax	A-WT			WR					
Sturnus sp. gr.	SA-STr	AR			OW			M	
Fringilla sp. gr.	SA-WT				OW				
Carduelis chloris	B-WT				OW				
Pyrrhula pyrrhula	B-WT					F			
Coccothraustes coccothraustes	T-WT				OW	F			
Emberiza calandra	T-WT				OW				
Emberiza sp. gr. 1	SA-STr	AR			OW				
Emberiza sp. gr. 2	SA-STr	AR			OW				
Number of indications for each habitat		8	3	5	23	15	11	13	14

Table 27 (continued)

		CLIMATIC ZONES								
	N	"Colder"		"Wide Range"			"Warmer"			
		A-T SA-T B-T	A-WT SA-WT B-WT	A-STr SA-STr B-STr	A-Tr SA-Tr B-Tr	T-STr T-Tr	T-WT	WT	WT-STr WT-Tr	STr
Pleistocene avifauna	64	4 6,3	18 28,1	14 21,9	8 12,5	6 9,4	4 6,3	4 6,3	6 9,4	
Recent avifauna	224	2 0,9	41 18,3	30 13,4	52 23,2	38 17,0	14 6,3	10 4,5	36 16,1	1 0,4

Table 28. The number of bird species, and -underscored- their share expressed as a percentage in the various ranges of climatic zones, for both the Pleistocene and Recent avifaunas of Crete. Abbreviations : see text.

	Reference		S	A	R	S:R	A:R	SA:R
Modern avifauna								
Greek mainland	Lambert,	1956	4	20	192	1:48	1:10	1:8
Crete	Vallianos,	1984	3	10	92	1:31	1:9	1:7
Fossil avifauna (island)								
Crete	This paper		6	14	47	1:8	1:3	1:2
Balearics	Alcover *et al.*,	1981	4	3	39	1:10	1:13	1:6
Malta	Lambrecht, 1933, Fischer,	1974	3	4	25	1:8	1:6	1:4
Sardinia	Kotsakis, 1980, Weesie, in prep.		6	12	32	1:5	1:3	1:2
Gargano	Ballmann, 1973,	1976	7	5	11	1:2	1:2	1:1
Fossil avifauna (mainland)								
Istallosko;	Jánossy,	1954	4	3	22	1:6	1:7	1:3
Breitenberg-Höhle;	Jánossy,	1957	4	2	23	1:6	1:12	1:4
Subalyuk-Höhle;	Jánossy,	1962	2	5	15	1:8	1:3	1:2
Kalman Lambrecht-Höhle;	Jánossy,	1963	2	6	19	1:10	1:3	1:2
Stránska Skála;	Jánossy,	1972	6	10	74	1:12	1:7	1:5
Hundsheim;	Jánossy,	1974	2	3	27	1:14	1:9	1:5
La grotte Tournal;	Mourer-Chauviré,	1975	1	3	16	1:16	1:5	1:4
La grotte de l'Escale;	Mourer-Chauviré,	1975	5	13	47	1:9	1:4	1:3
La grotte I de Mas des Caves;	Mourer-Chauviré	1975	4	3	26	1:7	1:9	1:4
Locus VIII du Lazaret;	Mourer-Chauviré,	1975	7	10	56	1:8	1:6	1:3
La grotte du Salpêtre;	Mourer-Chauviré,	1975	3	4	28	1:9	1:7	1:4
La grotte du Prince;	Mourer-Chauviré,	1975	6	10	43	1:7	1:4	1:3
La grotte de l'Observatoire;	Mourer-Chauviré,	1975	3	9	23	1:8	1:3	1:2
La grotte de la Crouzade;	Mourer-Chauviré,	1975	1	5	16	1:16	1:3	1:3
La grotte de la Balauzière;	Mourer-Chauviré,	1975	1	4	26	1:26	1:7	1:5
La grotte des Romains ;	Mourer-Chauviré,	1975	4	5	52	1:13	1:10	1:6
La grotte Jean Pierre N° 1;	Mourer-Chauviré,	1975	4	4	40	1:10	1:10	1:5
La grotte du Rond du Barry;	Mourer-Chauviré,	1975	5	3	51	1:10	1:17	1:6
La grotte de la Baume;	Mourer-Chauviré,	1975	4	3	31	1:8	1:10	1:4

Table 29. The number of species within Accipitriformes (A), Strigiformes (S) and the remaining number of species (R), the ratio in which these groups occur, in two modern avifaunas and in some fossil avifaunas from caves on various Mediterranean islands and from caves on the European mainland. In the modern avifaunas exceptional and rare species are excluded. SA : Strigiformes and Accipitriformes combined.

Morus bassana
Anser albifrons
Branta ruficollis
Haliaeetus albicilla
** *Gyps melitensis*
* *Aegypius monachus*
* *Accipiter gentilis*
** *Aquila chrysaetos simurgh*
* *Calidris canutus*
* *Columba oenas*
Ketupa zeylonensis
* *Asio flammeus*
** *Athene cretensis*
Aegolius funereus
Dendrocopos leucotos
Zoothera dauma
Turdus iliacus
Pyrrhula pyrrhula
* *Coccothraustes coccothraustes*

Table 30. Those bird species of the Pleistocene avifauna of Crete which are lacking or occur exceptionally in the Recent avifauna. Extinct species are marked with **, exceptional species with*.

CAPTIONS OF PLATES

All figures approximately natural size, except where enlargement is indicated.
N.B.: In the text the plates are indicated by roman numerals.

PLATE 1

Fig. 1- *Puffinus* cf. *P.p. yelkouan*: Right hum. Ge-115
Fig. 2- cf.*Branta ruficollis*: Prox. right hum. Li-D801
Fig. 3- *Haliaeetus albicilla*: Vert. Li-c803
Fig. 4- *Haliaeetus albicilla*: Prox. right cmc. Li-V805
Fig. 5- *Gypaetus barbatus*: Right tmt. Li-B810
Fig. 6- *Gypaetus barbatus*: Fragm. of dist. right tmt. Mv-1
Fig. 7- *Gyps fulvus*: Tal. dig. 1 Re-3
Fig. 8- *Gypaetus barbatus*: Fragm. of syn. Ge-IV1
Fig. 9- *Gyps fulvus*: Fragm. of prox. right hum. Li-0803
Fig. 10- *Aegypius monachus*: 7th cervical vert. Li-D807
Fig. 11- *Aegypius monachus*: Fragm. of dist. right ulna Li-V855
Fig. 12- *Gyps fulvus*: Fragm. of syn. Li-a803

PLATE 2

Fig. 1- *Phalacrocorax aristotelis*: Right fem. Li-B801
Fig. 2- *Phalacrocorax aristotelis*: Prox. right tt. Li-B802
Fig. 3- *Anas penelope*: Dist. right cmc. Li-B804 (x2)
Fig. 4- *Anas querquedula*: Right cmc. Li-e801(x2)
Fig. 5- *Anas querquedula*: Right cor. Gu-C4
Fig. 6- *Accipiter* cf. *A. nisus* (female): Right cmc. Li-B814
Fig. 7- *Accipiter* cf. *A. nisus* (female): Dist. right tt. Li-B815
Fig. 8- *Accipiter* cf. *A. nisus* (male): Left ulna Li-V808
Fig. 9- *Buteo buteo*: Right fem. Li-B805
Fig. 10- *Falco tinnunculus tinnunculus*: Left ulna Li-a817
Fig. 11- *Falco tinnunculus tinnunculus*: Right hum. Li-0805
Fig. 12- *Falco tinnunculus tinnunculus*: Right cmc. Li-B820
Fig. 13- *Falco tinnunculus tinnunculus*: Dist. left tt. Li-a816
Fig. 14- *Falco tinnunculus tinnunculus*: Right cor. Li-a/b804
Fig. 15- *Falco subbuteo*: Dist. left tt. Li-B817
Fig. 16- *Falco eleonorae*: Left hum. Li-d804
Fig. 17- *Falco eleonorae*: Right fem. Li-a809
Fig. 18- *Falco eleonorae*: Dist. left tt. Li-a808
Fig. 19- *Falco eleonorae*: Right tmt. Li-a/b803
Fig. 20- *Falco peregrinus*: Right cmc. Li-a806
Fig. 21- *Coturnix coturnix*: Prox. right hum. Li-A808 (x2)
Fig. 22- *Porzana porzana*: Right hum. Li-d806 (x1.5)
Fig. 23- *Porzana porzana*: Left cor. Li-c938 (x1.5)
Fig. 24- *Glareola* sp. gr.: Prox. right hum. Li-a877 (x1.5)

PLATE 3

Fig. 1a- *Gyps melitensis*: 5th cervical vert. Li-c804 ventral view
Fig. 1b- *Gyps melitensis* : 5th cervical vert. Li-c804 dorsal view
Fig. 2a- *Gyps melitensis* : 6th cervical vert. Li-c805 ventral view
Fig. 2b- *Gyps melitensis*: 6th cervical vert. Li-c805 dorsal view
Fig. 3a,b- *Gyps melitensis* : Tal. dig. 1 Li-0802 lateral view
Fig. 3c- *Gyps melitensis* : Tal. dig. 1 Li-O802 proximal view
Fig. 4a,b- *Gyps melitensis* : Tal. dig. 2 Sm-1 lateral view
Fig. 4c- *Gyps melitensis* : Tal. dig. 2 Sm-1 proximal view
Fig. 5- *Accipiter gentilis* (female): Dist. left hum. Li-B813
Fig. 6- *Accipiter gentilis* (female): Right cor. Li-B812
Fig. 7- *Accipiter gentilis* (female): Left rad. Li-a805
Fig. 8- *Accipiter gentilis* (female): Right fem. Li-B811
Fig. 9- *Buteo buteo* : Prox. right hum. Li-a801
Fig. 10- *Buteo buteo* : Cran. Li-c801
Fig. 11- *Buteo buteo* : Syn. Li-B808
Fig. 12- *Buteo buteo* : Right tmt. Li-a802

PLATE 4

Fig. 1- *Aquila chrysaetos*: Dist. right tt. Li-D804
Fig. 2- *Aquila chrysaetos*: Dist. right cmc. Li-D805
Fig. 3- *Aquila chrysaetos*: Phal. 1 dig. 3 Li-D806
Fig. 4- *Aquila chrysaetos*: Phal. 2 dig. 2 So-2
Fig. 5- *Aquila chrysaetos*: Syn. Li-d802
Fig. 6- *Ketupa zeylonensis*: Dist. left hum. Li-D816
Fig. 7- *Corvus corax*: Dist. left hum. Gu-B26
Fig. 8- *Coccothraustes coccothraustes*: Max. Li-a905 (x2)
Fig. 9- *Coccothraustes coccothraustes*: Mand. Li-a907 (x2)
Fig. 10-*Aquila chrysaetos simurgh* n. ssp.: Sternum Li-B809

PLATE 5

Fig. 1- *Aquila chrysaetos simurgh* n. ssp.: Sternum Li-B809
Fig. 2a- *Aquila chrysaetos simurgh* : Left fem. Li-d801 caudal view
Fig. 2b- *Aquila chrysaetos simurgh*: Left fem. Li-d801 cranial view
Fig. 3a- *Aquila chrysaetos simurgh*: Left tt. Li-V804 caudal view
Fig. 3b- *Aquila chrysaetos simurgh*: Left tt. Li-V804 cranial view

PLATE 6

Fig. 1- *Gallinula chloropus*: Right hum. Li-B826
Fig. 2- *Fulica atra*: Left cor. Gu-B18 (x1.5)
Fig. 3- *Calidris canutus*: Dist. left tmt. Li-V814 (x2)
Fig. 4- *Scolopax rusticola*: Left hum. Li-B827
Fig. 5- *Scolopax rusticola*: Left ulna Li-a879
Fig. 6- *Scolopax rusticola*: Dist. right tt. Li-B833
Fig. 7- *Scolopax rusticola*: Left cmc. Li-a881
Fig. 8- *Scolopax rusticola*: Right fem. Li-O807
Fig. 9- *Scolopax rusticola*: Right tmt. Li-B835
Fig. 10-*Scolopax rusticola*: Right cor. Li-A804
Fig. 11-*Scolopax rusticola*: Syn. Li-B836
Fig. 12-*Columba livia*: Left hum. Li-d812
Fig. 13-*Columba livia*: Left tmt. Gu-B19
Fig. 14-*Columba livia*: Right ulna Li-V817
Fig. 15-*Columba oenas*: Left hum. Gu-C8
Fig. 16-*Columba oenas*: Right tmt. Li-B859
Fig. 17-*Columba oenas*: Right ulna Li-a837
Fig. 18-*Columba palumbus*: Left cor. Li-a862
Fig. 19-*Columba palumbus*: Right hum. Li-a859
Fig. 20-*Columba palumbus*: Syn. Li-a/b818
Fig. 21-*Columba palumbus*: Left cmc. Li-c847

Fig. 22-*Columba palumbus*: Right tt. Li-B887
Fig. 23-*Apus* cf. *A. apus*: Left hum. Li-d866 (x1.5)
Fig. 24-*Apus melba*: Right hum. Li-c861 (x1.5)
Fig. 25-*Apus melba*: Left ulna Li-a892 (x1.5)
Fig. 26-*Apus* cf. *A. apus*: Left ulna Li-d867 (x1.5)
Fig. 27-*Apus melba*: Right cor. Li-B1023 (x1.5)
Fig. 28-*Apus* cf. *A. apus*: Left tmt. Li-a893 (x1.5)

PLATE 7

Fig. 1- *Tyto alba*: Left hum. Li-b801
Fig. 2- *Tyto alba*: Prox. right ulna Li-B902
Fig. 3- *Tyto alba*: Left cor. Li-c858
Fig. 4- *Tyto alba*: Right cmc. Li-D812
Fig. 5- *Tyto alba*: Dist. left fem. Li-a887
Fig. 6- *Tyto alba*: Dist. right tt. Li-B906
Fig. 7- *Tyto alba*: Right tmt. Li-a890
Fig. 8- *Tyto alba*: Max. Li-c/d805
Fig. 9- *Tuto alba*: Cran. Li-d864
Fig. 10- *Otus scops* (male): Left hum. Li-B891 (x2)
Fig. 11- *Otus scops* (female): Right hum. Li-B889 (x2)
Fig. 12- *Otus scops* (female): Left tmt. Li-B892 (x2)
Fig. 13- *Otus scops* (male): Right tmt. Li-c848 (x2)
Fig. 14- *Otus scops* (female): Dist. left tt. Li-d854 (x2)
Fig. 15- *Athene cretensis*: Right fem. Li-b404
Fig. 16- *Athene cretensis*: Dist. right hum. Li-c230
Fig. 17- *Athene cretensis*: Syn. Li-c724
Fig. 18- *Athene cretensis*: Right tt. Li-B173
Fig. 19- *Athene cretensis*: Max. Li-d717
Fig. 20- *Asio flammeus*: Right tmt. Ge-II6
Fig. 21- *Asio flammeus*: Prox. left ulna Li-d855
Fig. 22- *Aegolius funereus*: Right cmc. Li-c851
Fig. 23- *Aegolius funereus*: Prox. left hum. Li-a868
Fig. 24- *Aegolius funereus*: Right tmt. Li-a876
Fig. 25- *Aegolius funereus*: Right fem. Li-a870
Fig. 26- *Aegolius funereus*: Left tt. Li-B897
Fig. 27- *Caprimulgus* cf. *C. europaeus*: Right hum. Li-B912

PLATE 8

Fig. 1- *Dendrocopos leucotos*: Left hum. Gu-C24
Fig. 2- *Dendrocopos leucotos*: Right fem. Li-B980
Fig. 3- *Garrulus glandarius*: Left hum. Li-a908
Fig. 4- *Garrulus glandarius*: Left ulna Li-B922
Fig. 5- *Garrulus glandarius*: Right cmc. Li-B985
Fig. 6- *Garrulus glandarius*: Left fem. Li-a915

Fig. 7- *Garrulus glandarius*: Right tt. Gu-B29
Fig. 8- *Garrulus glandarius*: Left tmt. Li-O821
Fig. 9- *Pyrrhocorax pyrrhocorax*: Right hum. Li-a/b827
Fig. 10- *Pyrrhocorax pyrrhocorax*: Dist. left ulna Li-B934
Fig. 11- *Pyrrhocorax pyrrhocorax*: Right cmc. Li-B937
Fig. 12- *Pyrrhocorax pyrrhocorax*: Right cor. Li-a/b830
Fig. 13- *Pyrrhocorax pyrrhocorax*: Right tt. Li-a921
Fig. 14- *Pyrrhocorax pyrrhocorax*: Right tmt. Li-B941
Fig. 15- *Pyrrhocorax graculus*: Left hum. Li-B942
Fig. 16- *Pyrrhocorax graculus*: Right ulna Ge-IV3
Fig. 17- *Pyrrhocorax graculus*: Right cmc. Li-c883
Fig. 18- *Pyrrhocorax graculus*: Left tmt. Li-a926
Fig. 19- *Corvus monedula*: Right hum. Li-B849
Fig. 20- *Corvus monedula*: Left ulna Li-B957
Fig. 21- *Corvus monedula*: Left tt. Li-a936
Fig. 22- *Corvus monedula*: Right tmt. Li-a940
Fig. 23- *Corvus monedula*: Left cmc. Li-O823
Fig. 24- *Corvus monedula*: Right cor. Li-V836
Fig. 25- *Corvus* sp. gr.: Right hum. Li-a942
Fig. 26- *Corvus* sp. gr.: Right cmc. Li-V838
Fig. 27- *Corvus* sp. gr.: Right ulna Li-O825
Fig. 28- *Corvus* sp. gr.: Dist. right tt. Li-B978
Fig. 29- *Corvus* sp. gr.: Right ppdm. Li-B979

PLATE 9

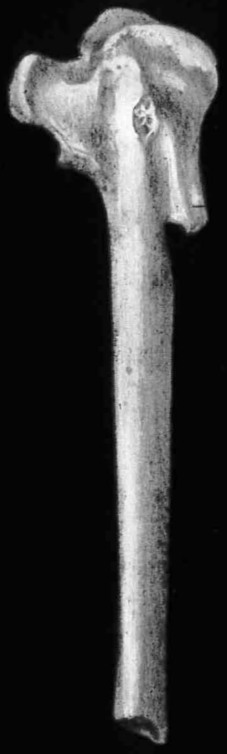
Fig. 1- cf. *Calandrella brachydactyla*: Left hum. Li-d868 (x2)
Fig. 2- cf. *Hirundo daurica*: Left hum. Li-c863 (x3)
Fig. 3- *Prunella collaris*: Left hum. Li-a901 (x2)
Fig. 4- cf. *Erithacus rubecula*: Right hum. Li-a/b846 (x3)
Fig. 5- *Oenanthe* cf. *O. hispanica*: Left hum. Li-B914 (x3)
Fig. 6- *Monticola* cf. *M. solitarius*: Right hum. Li-c906 (x2)
Fig. 7- cf. *Zoothera dauma*: Right hum. Li-d888 (x2)
Fig. 8- *Turdus* cf. *T. iliacus*: Left hum. Li-B990 (x2)
Fig. 9- *Turdus* sp. gr. 1: Left hum. Li-a/b857 (x2)
Fig. 10- *Turdus* sp. gr. 2: Left hum. Li-a980 (x2)
Fig. 11- *Turdus* sp. gr. 3: Right hum. Li-c932 (x2)
Fig. 12- cf. *Muscicapa striata*: Right hum. Li-a898 (x3)
Fig. 13- *Sturnus* sp. gr.: Left hum. Li-V851 (x2)
Fig. 14- *Fringilla* sp. gr.: Left hum. Li-B1022 (x2)
Fig. 15- *Carduelis chloris*: Right hum. Li-a987 (x2)
Fig. 16- *Carduelis chloris*: Mand. Li-V853 (x2)
Fig. 17- cf. *Pyrrhula pyrrhula*: Right hum. Li-a989 (x2)
Fig. 18- cf. *Emberiza calandra*: Right hum. Li-e806 (x2)
Fig. 19- *Emberiza* sp. gr. 1: Right hum. Li-c/d811 (x2)
Fig. 20- *Emberiza* sp. gr. 2: Left hum. Li-a991 (x2)

PLATE 1


1


2


3

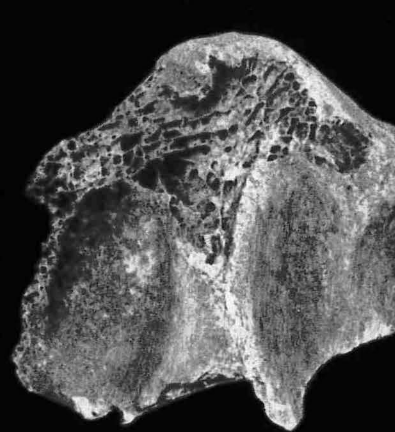

4


5


6


7


8


9


10

11

12

PLATE 2


1


2


3


4


5


6


7


8


9


10


11


12


13


14


15


16


17


18


19


20


21


22


23


24

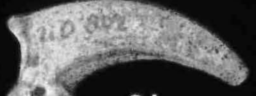
PLATE 3


1a


2a


3a


3c


3b


4a


4c


4b


1b

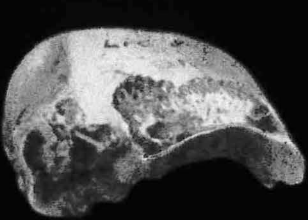

2b


5


7


8


9


10

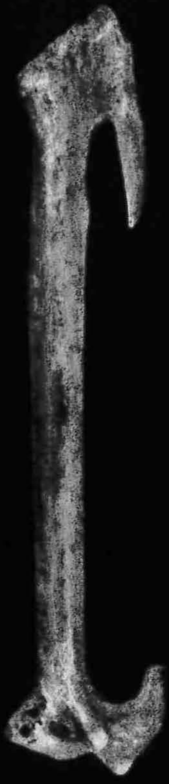

11


12

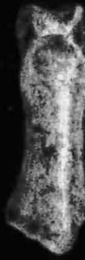

6

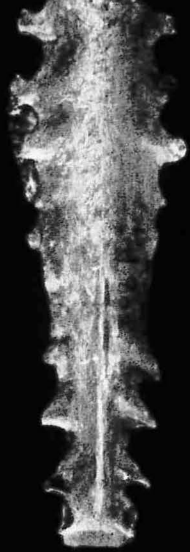
PLATE 4


1


2


3


4


5


6

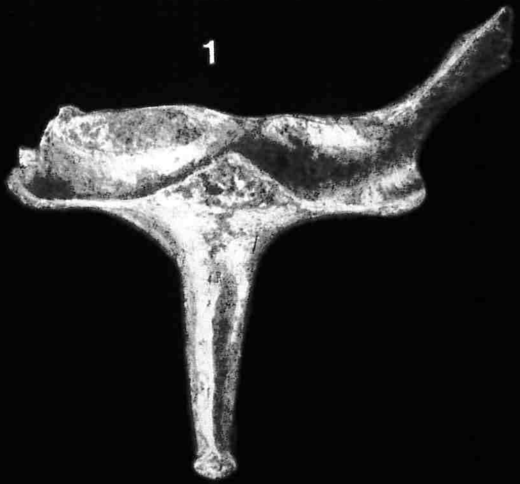

7


8


9


10

1



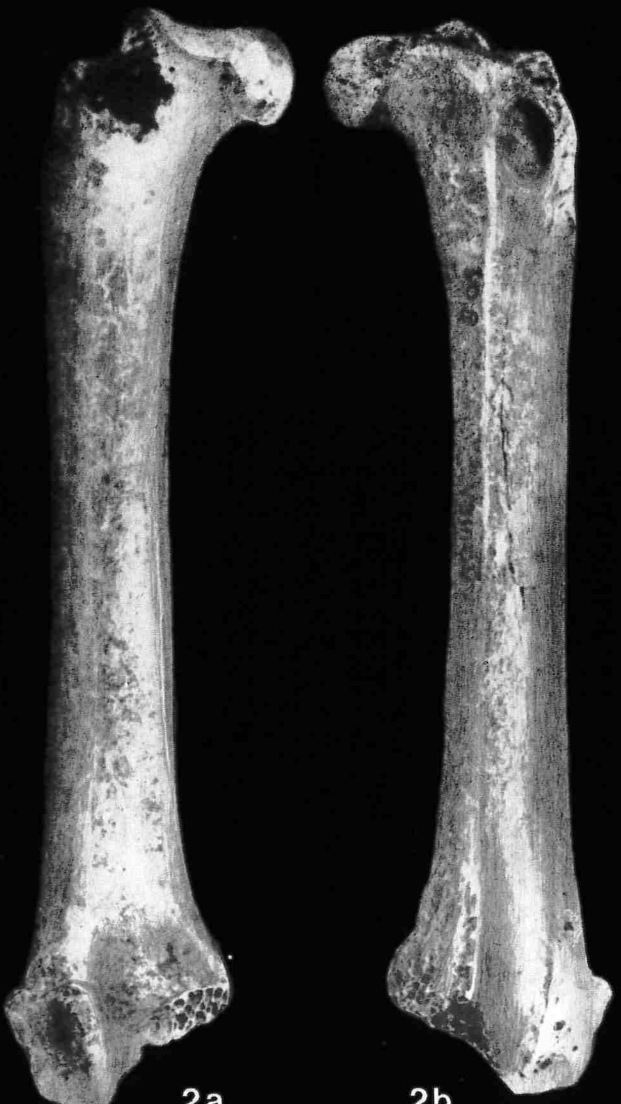


PLATE 6


1


2

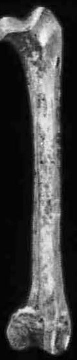

3

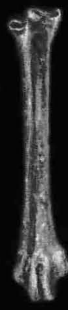

4


5


6


7


8


9


10


11


12


13


14


15


16


17


18


19


20


21


22


23


24


25


26


27


28

PLATE 7


1


2


3


5


6


7


10


11


4


8


9


12


13

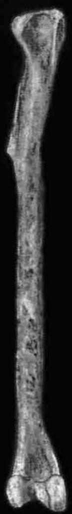

14


15


16


17


19


18


20


21


22


23


24


25


26


27

PLATE 8

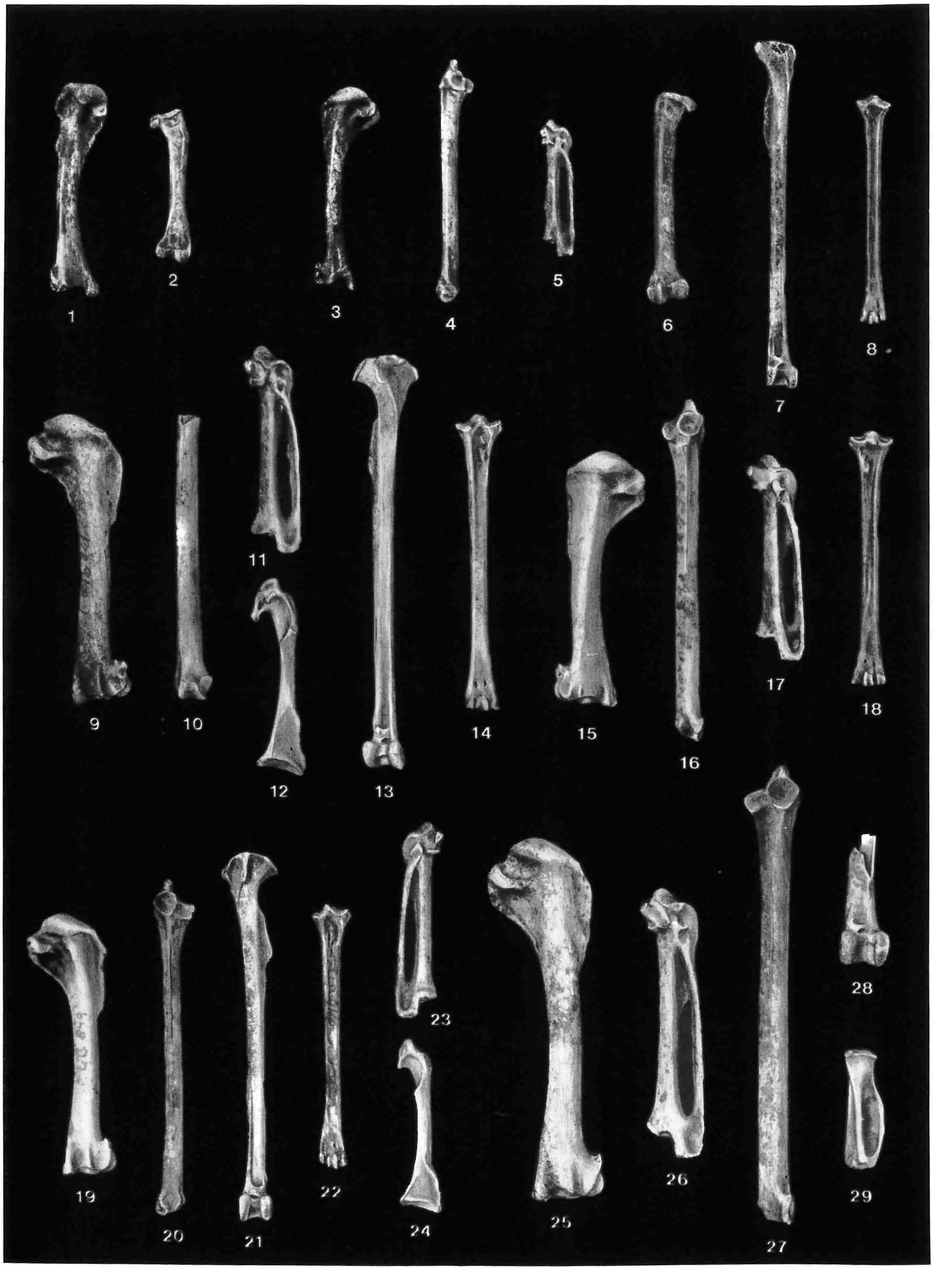
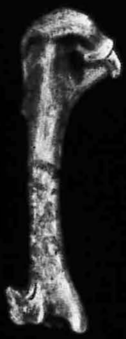


PLATE 9


1


2


3


4


5


6


7

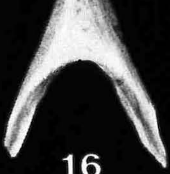

8


9


10


11


12


16


13


14


15


17


18


19


20