# A Pleistocene endemic island form within the genus Athene: Athene cretensis n.sp. (Aves, Strigiformes) from Crete

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#### SUMMARY

A new species of Pleistocene endemic owl, Athene cretensis n.sp. is described from fossil remains from several localities on Crete. The species differs from its probable mainland ancestor A. noctua (Scopoli) by having a slightly larger overall body size, longer wings and disproportionately longer legs, and a morphologically different humerus. One site has provided evidence for a gradual increase in the length of the legs. The long legs reflect an adaptation to a mainly terrestrial life style.

## INTRODUCTION

Since Suriano (in Malatesta, 1980) described 3 bird fossils from Simonelli cave, nothing further has been published on the Pleistocene avifauna of Crete. During the seventies, however, Pleistocene bird remains were collected from several sites on Crete's north-west coast by a team from the Institute for Earth Sciences, Utrecht, in collaboration with the Dept. of Geology and Paleontology of Athens University. Studying this material, the author recognized the presence of well over 50 species of birds. This paper deals only with the fossil material that refers to the genus *Athene* and has been attributed to the new species described below.

## LOCALITIES, MATERIAL

The map in fig. 1 indicates the positions of the four localities that yielded the material studied here. Most of it comes from Liko cave; from that cave 2293 pieces have been identified. The other sites yielded the following: Gerani II: 7 pieces, Gumbus: 33 pieces, Rethymnon fissure: 2 pieces. Mayhew (1977) gives

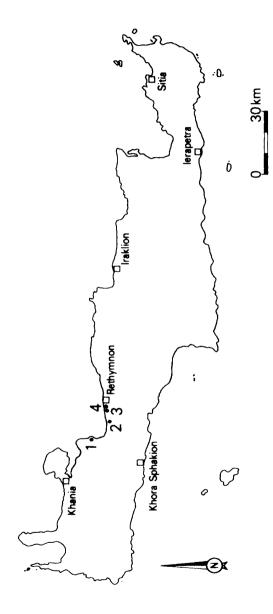


Fig. 1. Map of Crete, indicating the four localities yielding material studied here: 1. Liko cave, 2. Gerani II, 3. Gumbus B,C, 4. Rethymnon fissure.

a short description of these sites; some additional information for Liko cave is given here.

The material is stored in the collections of the Institute for Earth Sciences of the State University Utrecht under the codes Li, Ge, Gu and Re.

## Liko cave

The cave is separated in the middle into a front and a back part by a breccious accumulation. In both parts several layers have been excavated in levels. In the front part the levels were designated by (from above) the codes Li A, Li B, Li C and Li D, in the rear 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. Accidental mixture of material from different levels, e.g. Li a and Li b, resulted in codes such as Li a/b. The code Li 0 is applied to material from unknown levels in the cave, excavated erroneously without any indication of the level of origin.

Just below the upper part of Li a, the general abundance of the fossil species described suddenly disappears; in the upper part of Li a at least one subrecent bone was collected.

Tables 1 and 2 contain a summary of the coded material collected at this site.

#### Gerani II

The upper layer of this cave yielded:

- 1 complete right humerus (Ge III)
- 1 distal right humerus (Ge II2)
- 1 proximal left ulna (Ge II3)
- 1 incomplete left carpometacarpus (Ge II4)
- 2 phalanges: Phal. II, II2, III2

#### Gumbus cave

- 2 proximal right tarsometatarsi (Gu B1,2)
- 2 distal left tarsometatarsi (Gu B3,4)
- 1 distal left humerus (Gu B6)
- 1 distal right humerus (Gu B5)
- 1 incomplete left carpometacarpus (Gu B7)
- 1 proximal left carpometacarpus (Gu B8)
- 2 proximal left scapulae (Gu B9, 10)
- 1 distal left femur (Gu B11)
- 1 proximal right femur (Gu B12)
- 1 proximal left tibiotarsus (Gu B13)
- 1 distal left ulna (Gu B14)
- 1 distal right ulna (Gu B15)
- 1 incomplete left coracoid (Gu B16)
- 7 vertebrae, 1 epistropheus (from Gu B)
- 1 complete left tibiotarsus (Gu C1)
- 1 complete right tibiotarsus (Gu C2)

Table 1. List of the coded skeletal elements per layer in Liko cave. Fragmented bones are included.

Ster	727																	
Cran Ster					902							712						
Syn	716-728		720-724		705	718-728			709-713	712-714		718			712-715			
Qua	714-715 711-713		701-711 715-719 720-724			701-704 712-717 718-728			707-708	704-705		701-702 703-704	708-711		701-705 708-711 712-715			
Max, Mand	714-715		701-711		701	701-704	729	701-702	714-716	701-703	715-718		713-717		701-705			
Scap	701-710	701-702			702-704	705-711		703-706		707-711		705-707			601-610 706-707			
Cor	601-607	109	601-615		601-607	601-632		601-608		601-605		601-618						
Tmt	1-10	1-7	1-83	1-3	9-1	1-77		1–63		1-6		1-14			=		1-3	
Ţţ	101-123	101-105	101 - 170	101-103	101-128	101-174		101-125 1-63		101 - 107		101 - 136		101 - 103	401-412 101-118 1-11		101-102	
Fem	401-411 101-123 1-10	401	401-456	401	401		401-431	401-419		506-510 401-403 101-107 1-6		517-530 504-509 501-503 401-436 101-136 1-14 601-618 705-707					401-402	
Ppdm	501-512 516-525 513-515		521-526			537-540	550-551	522		506-510		501-503	531-532		521-522	533		
Rad	516-525	909	501-518 527-537	501	502504	501-513 514-536	541-546	505-513		501-502 503-505		504-509	511-516		501-509			
Стс		501-501			505-508		548-549	501-504	514-521			517-530			511-520			
Uln	301-332	301 - 304	301-329	301 - 303	301-312	301-352		301-316		301 - 307		201-229 301-330		30 i	301-316			
Hum	201-217	201202	201-271	201-204	201-212	201-262		201-227		201-216		201-229		201	201-222			
	LiV	LiA	LiB	LiD	Lio	Lia		Lia/b		Lib		Lic		Lic/d	Lid		Lie	

Table 2. The number of the various identified skeletal elements per layer in Liko cave.

					ĺ															
	Phal	Tal	Phal	Phal	Tal	Phal	Phal	Phal	Tal	Phal	Phal	Phal	Phal	Tal Ocu	1	Pda	Pda Pddm Vert	l	Atl	Ep
Liv	е.	-	-	6			_	_	4				2					12		
LiA	3	-	4	4	-	-	3	_	3		_		7					!		
LiB	9	15	12	18	7	9	7	6	14	7	7	m	=	Ξ	=			36		
Lio																		2		,
Lia	7	Ξ	9	24	18	9	=	11	4	-		-	6	4	8			26		
Lia/b	3		7	6		_		4	3				4				2	•		
Lib	9	3		7	4	7	3		٤		-	7	_		7		,	7		2
Lic	6	8	'n	20	6	S	4	6	7				7	7	_	-		59	647	. "
Lid	۲	7	4	œ	Π	7	4	9	٤			_	7					61	. –	. –
. I				-				,						-	-			;		•

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1 proximal left tibiotarsus (Gu C3)
5 phalanges: phal I1,2, II1, II2, IV 4
1 talon I
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# Rethymnon fissure

I complete right femur (Re 1) 1 proximal right femur (Re 2)

## METHODOLOGY

# Identification

Morphological comparison between the Cretan material and recent skeletons was carried out in the British Museum, Natural History (Tring), the Rijksmuseum van Natuurlijke Historie (Leiden), the Biologisch - Archeologisch Instituut (Groningen) and in the personal collection of Mme. Mourer-Chauviré (Lvon).

# **Terminology**

The terminology used is after Baumel (1979).

#### Measurements

Measurements were taken with vernier calipers and are given in 0.1 mm units. The maximum lengths and widths in the middle of the major limb bones were measured. For Liko cave, the measurements of the bones from Li a, Li a/b and Li b and from Li c, Li c/d, Li d and Li e were taken together to arrive at a convenient number for statistical treatment. This was possible since both the calculated mean values of the assembled levels and their coefficients of variability diverge very little.

Values determined by extrapolation, which was possible in the case of slightly damaged bones, are included.

For comparison of some measurements the Student's t-test has been used, t is obtained thus:

$$t = (M1 - M2) \sqrt{\frac{(N1 \times N2)/(N1 + N2)}{(N1 - 1) SD_1^2 + (N2 - 1) SD_2^2}}$$

$$N1 + N2 - 2$$

The results are given in the form of a table, in which:

N = number of measured specimens

M = mean

SD = standard deviation

 $V = coefficient of variability: V = \frac{100SD}{M}$ 

The probability values for each value of t and corresponding degree of freedom are derived from statistical tables (Simpson et al., 1960).

Abbrevia	tions	Vert	vertebra(e)
Hum	humerus	Atl	atlas
Uln	ulna	Ep	epistropheus
Rad	radius	Cor	coracoid
Cmc	carpometacarpus	Max	maxilla
Fem	femur	Mand	mandible
Tt	tibiotarsus	Scap	scapula
Tmt	tarsometatarsus	Cran	cranium
Phal	phalange	Ster	sternum
Tal	talon	Qua	quadratum
Ppdm	phalanx proximalis digiti majoris		
Pddm	phalanx distalis digiti majoris		
Pdu	phalanx digiti alulae	Syn	synsacrum
Ocu	os carpi ulnare	Fr	fragment

## **SYSTEMATICS**

Order STRIGIFORMES (Wagler) 1830

Family STRIGIDAE (Vigors) 1825

Genus Athene (Boie) 1822

Athene cretensis n. sp.

Holotype: Complete left humerus (Lic203) (Plate I).

Paratypes: Complete left ulna (Lia319).

Complete left carpometacarpus (Lib501).

Complete right femur (Lia414).

Complete left tibiotarsus (Lia/b101).

Complete right tarsometatarsus (Lia/b2).

Name: After the island of Crete.

Type locality: Liko cave, Crete, Greece.

Age: Middle -Upper Pleistocene?



Plate I, fig. 1 Holotype: left humerus (Li c 203), caudal view ( $\times$ 2). fig. 2 Recent humerus A. noctua, ( $\times$ 2). Arrows indicate morphological difference.

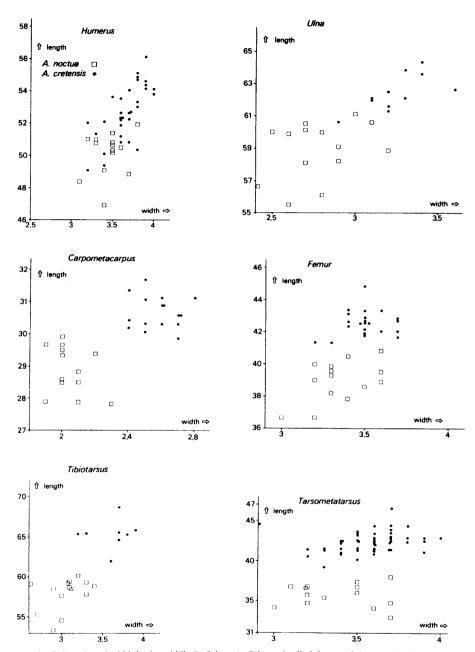


Fig. 2. Length and width in the middle (in 0.1 mm) of the major limb bones of A. cretensis (from Li a, Li b and Li a/b) and A. noctua.

Diagnosis: Species of the genus Athene, with larger body size than A. noctua, and disproportionately longer legs. Legs shorter than in A. cunicularia. Morphologically identical to A. noctua, except in the form of the crista bicipitalis of the proximal humerus.

Dispersion: So far, known only from Crete.

#### THE GENUS Athene AND ITS DISTRIBUTION

The genus Athene comprises 3 recent species (Voous, 1973): A. noctua (Scopoli), A. brama (Temminck) and A. cunicularia (Molina). The long-legged A. cunicularia is restricted to the New World. The small A. brama ranges from Iran eastwards into India and the countries of Indochina. A. noctua, divided into 13 subspecies, inhabits the temperate and Mediterranean zones of the Palearctic.

#### COMPARISONS

## A. Morphological comparisons

The genus Athene can be distinguished from the other genera in the family by various osteological characters. In the skull, the tympanic cavity extends upwards and backwards, and underlies the base of the fossa temporalis. In the coracoid, the processus lateralis is rather small. The vertebral canals open on to the dorsal surface of the synsacrum in long apertures. On the tibiotarsus, the short and feeble fibular ridge is placed rather proximally; it ends distally at a point about  $2/7^{\text{ths}}$  of the total length from the proximal end of the tibiotarsus. The fibula fuses indistinguishably with the tibial shaft at a point about  $2/7^{\text{ths}}$  of the total length from the distal end of the tibiotarsus. In the tarsometatarsus, the posterior edge of the outer rim of the middle trochlea is slightly pointed.

The material is morphologically identical to that of A. noctua, except for the size of the various bones, and for one feature of the proximal humerus; the crista bicipitalis lacks the rather sharp distal processing arch, so the surface of the intumescentia of the facies bicipitalis is smaller (see Plate I).

# B. Biometrical comparisons

# B1. Biometrical comparison of A. noctua and A. cretensis.

The mean lengths of the major limb bones of A. cretensis (from Li a, Li b and Li a/b) and the recent A. noctua are compared. The results are given in

Table 3. Comparison of the mean lengths (in 0.1 mm) of the major limb bones of A. cretensis (from Li a, Li b and Li a/b) and A. noctua.

		A. noci				A. crete	nsis			
	N	Min-Max	М	V	N	Min-Max	M	V	t	Difference
Hum	14	46.9-51.9	50.1	2.7	32	49.1-56.1	52.7	3.3	4.9	4.9%
Uin	14	55.5-61.1	58.9	3.0	11	60.664.3	62.4	1.8	5.7	5.9%
Cmc	13	27.8 - 29.9	28.9	2.6	16	29.8-31.7	30.7	1.7	7.6	6.2%
Fem	14	36.7 - 40.8	39.0	3.2	22	41.3 - 44.8	42.5	1.9	12.2	10.9%
Tt	14	53.460.1	58.0	3.5	8	62.0-68.8	65.4	2.7	8.6	12.8%
Tmt	14	33.0-38.0	35.8	4.0	48	39.2-46.7	42.3	3.1	16.4	18.4%

table 3. All measured bones of A. cretensis are significantly longer than those of A. noctua (cumulative probability significance > 0.99). The differences are given as percentages of the mean lengths of the recent bones. The scatter diagrams in fig. 3 visualize this difference between the two species.

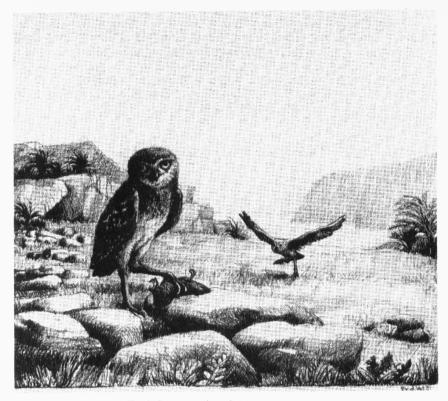


Fig. 3. Reconstruction of A. cretensis.

In table 4, the added mean lengths of the major wing and leg bones of *A. cretensis* (from Li a, Li b and Li a/b) and *A. noctua* are compared. The percentage increase in the length of the legs is more than twice the percentage increase in the length of the wings. The difference is given as a percentage of the total lengths in *A. noctua*.

Table 4. Comparison of the added mean lengths in 0.1 mm of major wing and leg bones of A. cretensis (from Li a, Li b and Li a/b) and A. noctua.

	A. noctua	A. cretensis	Difference	
Wing	137.9	145.7	5.6%	
Leg	132.1	150.2	13.8%	

If the other unmeasured skeletal elements of A. cretensis and A. noctua are compared, one finds that the overall size of A. cretensis is slightly but distinctly larger than that of A. noctua.

B2. Biometrical comparison of A. cretensis from upper (Li a, Li b and Li a/b) and lower (Li c, Li d, Li c/d and Li e) levels in the rear part of Liko cave. Again the mean lengths of the major limb bones are compared. The results are given in table 5. The mean lengths of the humerus, ulna, carpometacarpus and tibiotarsus do not differ significantly between the upper and lower levels. Femur and tarsometatarsus are significantly longer in the upper levels, (cumulative probability significance for fem > 0.95, for tmt > 0.99).

When one compares the other unmeasured skeletal elements from the upper and lower levels one finds no clear size difference.

Table 5. Comparison of the mean lengths (in 0.1 mm) of the major limb bones of A. cretensis in the upper (Lia, Lib, Lia/b) and lower (Lic, Lid, Lic/d) levels in the rear part of Liko cave.

		A. creter	nsis			A. crete	nsis				
		Lia, Lib, I	Lia/b		Lic, Lid, Lic/d, Lie						
	N	Min-Max	M	V	N	Min-Max	М	٧	t		
Hum	32	49.1-56.1	52.7	3.3	18	48.7-55.1	52.7	3.1	0.1		
Uln	11	60.6-64.3	62.4	1.8	2	59.2-62.0	60.6	3.3	0.2		
Cmc	16	29.8-31.7	30.7	1.7	14	29.4-31.9	30.8	2.5	0.7		
Fem	22	41.3-44.8	42.5	1.9	9	40.8-43.0	41.8	1.8	2.4		
Tt	8	62.0-68.6	65.4	2.7	5	63.1-66.3	64.6	2.2	0.8		
Tmt	48	39.2-46.7	42.3	3.1	9	39.9-44.2	41.1	1.9	2.8		

## B3. Comparison of A. noctua, A. cunicularia and A. cretensis.

I did not have any skeletons of A. cunicularia available, but was able to study some skins at the Leiden museum. The length of 6 tarsometatarsi could be estimated within an accuracy of 2 mm. In table 6, the mean lengths of tarsometatarsi of A. noctua, A. cunicularia and A. cretensis (from Lia, Lib and Lia/b) are compared.

Table 6. Comparison of the mean lengths (in 0.1 mm) of the tarsometatarsi of A. noctua, A. cunicularia and A. cretensis (from Lia, Lib and Li a/b. Measurements of A. cunicularia  $\pm$  2 mm.

	N	Min-Max	М	
A. noctua	14	33-38	35.8	
A. cunicularia	6	45-48	45.7	
A. cretensis	48	4047	42.3	

The legs of A. cunicularia are distinctly longer than those of A. cretensis and A. noctua. Comparison of skins of A. cunicularia and A. noctua revealed a larger overall body and wing-size in A. cunicularia, as well as disproportionately longer legs.

## C. Conclusions

- 1. The material shows several diagnostic characteristics of the genus *Athene*. The material is morphologically identical to *A. noctua*, except for the size of the various bones and for one feature in the humerus.
- 2. The major wing and leg bones in the fossil species are significantly longer than in A. noctua. The other skeletal elements are slightly but distinctly larger than in A. noctua. Comparing A. cretensis with A. noctua one notices a progressive increase in the lengths of the distal limb elements relative to the proximal ones (see table 3). One also finds that the increase in the length of the leg is larger than that in the wing, resulting in an allometrical difference in the ratio wing-length/leg-length.
- In Liko cave, a significant increase in length with time is found for femur and tarsometatarsus.
- 4. A. cretensis may have the same overall body-size as A. cunicularia, but its legs are distinctly shorter.

#### DISCUSSION

It is sometimes difficult for a paleontologist to decide whether a new form should be placed in a new species or in a new subspecies. Creating (sub)species on the basis of marginal biometrical or morphological differences can sometimes be dubious. It has proved possible to solve this dilemma by comparing our form with recent subspecies. Athene noctua varies individually, locally and geographically in size and colouring (Vaurie, 1960). In his review Vaurie distinguishes 13 subspecies, on the basis of differences in these features. He illustrates the size differences by giving the wing-lengths; these measurements are not comparable with ours since they involve mainly the length of the manus and the primaries. Allometrical or osteological differences are not reported however, and it is precisely in these features that A. cretensis stands apart from all subspecies.

Ideally, the major limb bones of recent (sub)species should also be defined biometrically so that they can be compared with fossil bones. For this study, we had to take measurements of all available recent skeletons, so that we would have a sufficient number for statistical treatment. These skeletons were indicated mainly as unspecified A. noctua, so the values of the means of our measurements will be intermediate between those of the most extreme subspecies.

Comparison of measurements of A. cretensis with those of A. noctua lunellensis (Mourer-Chauviré) shows that A. cretensis is clearly larger (see Mourer-Chauviré, 1975). A. noctua lunellensis is recovered from the Pleistocene of France and is slightly larger than A. noctua. Other Pleistocene remains of A. noctua are known from sites all over Europe, and from the Middle and Far East (Brodkorb, 1971).

Suriano (in Malatesta, 1980) has described a distal tibiotarsus from Pleistocene deposits in the Simonelli cave (Crete), attributing it tentatively to A. noctua indigena Brehm, although it seemed to be larger. The piece may be a

fragment of A. cretensis. Since this species was found in the nearby sites Gerani, Gumbus and Rethymnon fissure, its presence in Simonelli cave would not be surprising.

From Rodriguez Island, A. murivora (Milne-Edwards), which became extinct in historical times, is known. This species also had long legs (Tt: 71 mm, Tmt: 46 mm, (Lambrecht, 1933)) comparable in length with A. cunicularia.

The genus Athene is generally sedentary and is inclined to a terrestrial way of life. Obviously the sedentary habit contributes to genetic isolation, which favours the formation of (apparently aberrant) local, geographically isolated groups. This may account for the presence of the 13 intergrading subspecies of A. noctua, and for the occurrence of the oriental A. brama, which is sympatric with A. noctua (Vaurie, 1960). Once the genetic isolation is more or less complete, and if local circumstances allow, further separation can occur: A. cretensis on Crete, A. murivora on Rodriguez Island. If we assume the origin of the genus Athene to be located in the Old World, the American A. cunicularia may have arisen from A. noctua in this way. It is notable in this context that the only recent, geographically isolated, subspecies A. noctua somaliensis Reichenow, differs more from its co-subspecies than any of the other subspecies differ from each other.

The inclination towards a terrestrial habitat of the genus is best illustrated by A. cunicularia, which lives mainly on the ground and which, due to its long legs, is an excellent runner. A. noctua also runs regularly in pursuit of its prey. The occurrence of long legs in A. cunicularia, which obviously is capable of superb cursorial locomotion, indicates that the relatively long legs of A. cretensis reflect an adaptation to a more terrestrial life-style. The record from Liko cave shows a gradual trend towards this adaptation. The terrestrial inclination is also indicated by the progressive increase in the lengths of the distal limb elements relative to the proximal ones (see table 3). Such a modification is usually associated with running in quadrupeds (Cade, 1979). Davis (1957) considers the longer tarsus to be probably advantageous for bipedal locomotion, and Grant (1965) regards the larger dimensions of the tarsus of island birds as a primary adaptation to a greater range of perches. The views of these authors seem to agree with ours.

In the Pleistocene on Crete, circumstances probably favoured grounddwelling owls; there were no carnivores, apart from otter, *Isolalutra cretensis* (Symeonidis and Sondaar, 1975). Rodents were abundantly available. Analysis of fossil owl pellets from Liko cave shows that *A. cretensis* probably fed mainly on rodents, especially on *Mus minotaurus* (Bate). There are several plausible explanations for the extinction of *A. cretensis*; extinction of the (main) preyspecies *M. minotaurus*; predation or nichecompetition by subrecently occurring co-carnivores. The arrival of carnivores in subrecent times may have been connected with the arrival of man on the island.

Recently the New Zealand laughing owl Sceloglaux albifacies (G.R. Gray) a ground breeder, has been seriously threatened with extinction, or has already become extinct, due to the carnivores and rats brought in by man.

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